Post-Transplant Root Production, Mortality, and Periodicity of Landscape-Sized Shade Trees

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Abstract

A more thorough knowledge of rooting behavior of transplanted trees is needed to better understand plant establishment. Therefore, the objectives of this research were to: 1) determine if transplant timing affected root system regeneration of northern red oak (*Quercus rubra* L.) and willow oak (*Q. phellos* L.), 2) determine the effect of transplant timing and nursery production system on root, shoot, and trunk growth periodicity of balled-and-burlapped (B&B) and pot-in-pot (PIP) sugar maple (*Acer saccharum* Marsh.), and 3) characterize seasonal patterns of root production and mortality of transplanted sugar maple. No new root growth occurred outside or within the root balls of red or willow oak between November transplanting and January excavation. However, new root growth was observed when November- and March-transplanted oaks were excavated in April, indicating that new root growth occurs primarily in late winter and/or early. Transplanted and non-transplanted sugar maples exhibited a pattern of maximum rates of shoot extension in early May, root length accumulation in late May, and trunk expansion in mid June. Rate of root length accumulation was less in summer and fall. Transplanting did not appear to disrupt the normal growth periodicity of sugar maple, except when transplanted in July. Abundant root length accumulation occurred in the July transplants at a time when root length accumulation had slowed in all other treatments, resulting in the July transplants having similar standing root lengths as the other transplants by fall. Standing root length of non-transplanted PIP sugar maple declined dramatically in spring. While root production in sugar maple was limited to the growing season, root mortality occurred at a steadier rate throughout the year. Most root mortality occurred in winter in transplanted trees and spring and summer in non-transplanted trees. Non-transplanted PIP trees had greater standing root length, production, and mortality than the other treatments. Indices of root activity (analogous to turnover rates) and production:mortality ratios illustrated the dominant role that root production plays relative to mortality in recently transplanted trees. These data indicate that transplanting and the PIP production system disrupt typical patterns of root production and mortality in sugar maple.

Dr. John W. Day

- a good friend

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Chapter 1

Introduction

When field-grown trees are harvested for transplanting, a substantial portion of the root system is lost. This significant loss of roots results in an altered root:shoot ratio that must be restored if establishment is to be successful. During establishment, the proportionally small root system is often unable to supply sufficient water to the crown, despite ample moisture in the surrounding soil. Thus, transplanted trees commonly experience tissue moisture deficits. Until the pre-transplant root:shoot ratio is restored, root growth is usually favored over shoot growth, especially when tissue moisture deficits are encountered. Preferential root growth compared to shoot growth is advantageous, because the risk of tissue moisture deficits is minimized. The commonly observed reduction in shoot growth after transplanting is known as planting check, transplant shock, or transplant stress. The duration of transplant stress depends upon the time needed to restore a functional root:shoot ratio. Rapid regeneration of a new root system decreases the chance of tissue moisture deficits and increases the probability of survival.

Transplant timing affects plant establishment due to seasonal weather conditions (e.g., soil temperature and moisture, relative humidity, wind, etc.) that may affect tissue water relations through moisture availability and transpiration. Seasons also correspond to physiological status of trees (e.g., dormancy, expanding shoots, leaves dropping, etc.) and root regeneration potential. If roots are regenerated soon after transplanting, fall transplanting can potentially help transplants establish faster relative to spring transplanting due to a larger root system that is perhaps better able to support the first post-transplant flush of shoot growth.

Production method affects plant establishment by influencing density, position, and fibrosity of roots and root losses during harvest for transplanting. Root systems of containerized trees typically have greater root densities and more small-diameter roots compared to field-grown trees, but deformed roots, particularly on trees held for long periods in their containers, are thought to interfere with establishment of containerized trees. As much as 100% of the root system of container-grown trees can be transplanted, compared to only 25% or less for a typical field-grown tree grown harvested with a ball of earth wrapped in burlap (B&B).

Early root system regeneration in transplanted trees is poorly understood. A better understanding of post-transplant root system regeneration patterns and relationships between shoot and root growth of newly transplanted trees can enable professionals in the plant sciences to make better plant management decisions and to devise practices that will hasten the establishment of transplanted landscape trees.

The purpose of my research was to quantify early post-transplant root regeneration patterns and to gain insight regarding growth periodicity of transplanted trees. My first objective was to compare post-transplant root and canopy growth of fall- and spring-transplanted northern red oak (*Quercus rubra* L.) and willow oak (*Q. phellos* L.) to determine which season is a better time to transplant these species. The second objective was to determine the periodic patterns of root, shoot, and trunk diameter growth of balled-and-burlapped (B&B) and pot-in-pot (PIP) sugar maples (*Acer saccharum* Marsh.) transplanted at various times of year, and to compare end-of-season root, shoot and trunk diameter growth to determine the effects of transplant timing and production method. Finally, while much research has been conducted on the dynamics of root production and mortality in forest systems and on established trees, little research exists on root mortality in transplanted trees in the landscape. Therefore, the final objective of this research was to characterize seasonal patterns of root production and mortality of sugar maples transplanted from two production systems and at various times of year.

Post-transplant root regeneration was evaluated by excavation of red oak and willow oak root balls, and observation of sugar maples transplanted into rhizotrons. Balled-and-burlapped red and willow oaks were transplanted in November and March. Subsamples were excavated in January and April to determine if root regeneration had occurred. Height and trunk diameter growth of the non-excavated oaks were followed for 3 years following transplant to determine the better season to transplant these species.

B&B and PIP sugar maples were transplanted into rhizotrons in November (leaf drop), December (early winter), March (early spring), April (bud break), and July (bud set). Non-transplanted B&B and PIP trees served as controls. Shoot extension, trunk expansion, and standing root length were followed for 23 months following installation of the first rhizotron to obtain seasonal patterns of post-transplant root, shoot, and trunk growth periodicity. End-of-season shoot extension, trunk expansion, and standing root length were also analyzed to determine influence of treatments. At the end of second-season shoot extension, all transplanted trees were excavated to quantify root regeneration. Finally, first-year patterns of root production and mortality in regenerated root systems were studied. Annual root production and mortality were analyzed to determine effects of treatments. Indices of root activity were calculated to better understand first-year root production and mortality dynamics.

Literature Review

Methods in Root Research

Studies on root growth, mortality, and decomposition are hindered because these processes typically occur belowground where they are not readily visible, and few non-invasive techniques are available to study the activities of root systems. To quote Bloomfield et al. (1996), the “inability to evaluate effectively something that is hidden from view and whose environment must be disturbed as part of our analyses” makes the belowground systems of plants much more difficult to study than the aboveground systems. While some methods of studying roots require less time than others, most of methods used to study roots are extremely time-consuming and tedious. Each method has its own limitations and associated problems that must be considered before selecting the best method to employ in the study. Subsequently, there is not any “best” method for all situations. The “best” or most appropriate method depends on what the researcher desires to accomplish, and often it may be best to employ two methods in the same study (Böhm 1979).

An overview of methods for studying root systems (*Methods of Studying Root Systems*) was written in 1979 by Wolfgang Böhm. To this day, Bohm’s book has remained one of the most widely used texts on this topic. Recently, *Root Methods: A Handbook* (Smit 2000) was published. This book provides a comprehensive update and review of recently developed tools in root studies such as computer-assisted tomography, magnetic resonance imaging, and image analysis using computer software programs.

Methods of studying roots can be broken up into two broad categories: direct and indirect methods. Direct methods allow the researcher to make qualitative observations and quantify root growth based upon actual observations. Indirect methods require the researcher to infer information about the roots based upon factors such as water or nutrient use.

Direct Methods

Many methods of studying roots result in extensive damage to the sample and are consequently categorized as destructive methods. Due to the destructive nature of these methods, in most cases the researcher is not permitted to repeatedly observe changes to the same roots or root system. Destructive methods of measuring root activities include: excavation, monolith, auger, wall profile, glass wall, and modifications of these methods.

The excavation or skeleton method involves removal of the soil surrounding individual roots of entire root systems and is the oldest method used in root research (Böhm 1979). Soil removal from around the roots is accomplished with an assortment of small hand tools (e.g., hand pick, ice pick, forks, screw drivers, forceps, dental picks, or needles) in a similar way that an anthropologist might uncover ancient ruins. In some circumstances, it may be useful to slightly moisten the soil. Following excavation, sections of the root system (or entire root systems as in the case with smaller root systems) may be preserved, mounted, or photographed. Advantages of the excavation method are that it can provide a clear three-dimensional representation of the root system in its entirety and can be useful for studying root grafting and competition between roots (Böhm 1979). Disadvantages are that it is extremely labor intensive and time-consuming. Therefore, it may not be practical to replicate or to use on large specimens. In addition, due the destructive nature of the excavation method, repeated measurements cannot be made. Modifications of the excavation method include the use of water pressure and/or air pressure (blowing or sucking) to remove soil surrounding the root systems (Böhm 1979).

Monolith methods involve removing soil monoliths (pillars or columns consisting of a single mass) from the soil profile and washing the roots from the column (Böhm 1979). The monolith method is frequently used to collect quantitative data. Monolith size and shape varies depending upon the needs, objectives, and resources of the researcher. Single monoliths may be sufficient for small specimens, while numerous monoliths may be necessary for larger specimens. Modifications to the monolith method include the box method, which utilizes a steel box to aide the researcher in obtaining a sample of uniform size and shape. The cage and needleboard methods are two other adjustments to the monolith method. The advantage of the cage and needleboard methods are that they help keep root systems in place as soil is removed and therefore can provide qualitative information (Böhm 1979). As with the excavation method, the monolith methods are usually extremely labor intensive and time-consuming. Thus, only a limited number of samples or replications can be practically prepared (Bloomfield et al. 1996). In addition, monolith methods are destructive, so repeated measurements on the same specimens are not possible.

One of the most widely used methods in ecological root research is the auger or soil-core sampling method (Böhm 1979). The auger method involves the use of cylindrical tubes to obtain soil cores. Several types of hand augers and mechanical augers are available. Once samples are obtained, roots are separated from the soil by washing. Processing of the roots can be extremely time-consuming, often exceeding more than 8 hr per core (Bloomfield et al. 1996). According to Böhm (1979), the auger method is best suited for taking volumetric soil-root samples. Weller [(1964; 1971) cited in (Böhm 1979)] described a technique for studying the spatial distribution of tree roots that involves taking soil samples in concentric rings around the trunk of a tree. Advantages of the auger method are that it is less time-consuming than the excavation or monolith methods, and that compared to other destructive methods, relatively little damage is done to the root systems (Böhm 1979). The relatively small diameter of the corer (often with an inside diameter less than 6 cm) may make it difficult to monitor the activity of coarse roots because only fine roots (<2 mm diameter) occur in sufficient numbers and are distributed randomly enough to be accurately quantified (Vogt and Perrson 1991). Therefore, significant coarse portions of the root system may be missed (Vogt and Perrson 1991). The difficulty sampling coarse roots and misrepresentation of root distribution in samples with low rooting densities are noteworthy disadvantages. However, these problems can be partially overcome by increasing the number of cores or subsampling (Harris et al. 1995). Soil blocks (15 x 15 cm to 1 x 1 m) are recommended to sample coarse roots (>2 mm) (Böhm 1979). Other disadvantages with the auger method are that it provides little information in morphological studies (qualitative data), compaction can occur while obtaining the sample, and sampling subsoil can be difficult. Additional disadvantages are that it may be more difficult to deal with fine root growth and mortality simultaneously (Bloomfield et al. 1996) and that natural growth and mortality may be disturbed (Mäkelä and Vanninen 2000). Finally, the researcher must sacrifice the ability to follow a particular root or root system over time (Vogt and Perrson 1991).

Most of the time and labor associated with the auger method involves washing and cleaning roots (Böhm 1979). In order to reduce time and labor washing and cleaning, the core-break method was developed. With the core-break method, soil cores are broken horizontally in two halves and visible roots on both sides of the break are counted (Böhm 1979). Disadvantages of the core-break method are that it is often not possible to differentiate primary from secondary roots. In addition, counting can be difficult in cores with high root densities. However, problems associated with high root densities can be overcome by comparing the core breaks with specially standardized figures designed for estimating rooting density.

The mesh bag method is particularly well-suited for testing the effects of soil and chemical properties on root growth (Böhm 1979). The mesh bag method works by augering holes, fitting the holes with mesh bags filled with treated or untreated soil, leaving the bags in the soil for a period of time, and then digging the bags up and quantifying the root growth that occurred within the bags.

The profile wall (or trench profile) method involves digging a trench, smoothing one side of the trench (side adjacent to the object of study), removing 3 to 5 mm of soil to expose the roots, and mapping the location and diameter of the roots (Böhm 1979). Roots can be traced onto cross section paper (or millimeter paper), clear plexiglass plastic, or acetate overlays. Alternatively, if there is enough contrast between roots and the soil profile, photos can be taken to document the roots. Böhm (1976) described a method of estimating root length based on the number of root counts on the soil profile. The major advantage of the profile wall method is that it allows the researcher to accurately illustrate the position of roots in a soil profile. In addition, the maps provide a permanent record of the rhizosphere. However, the profile wall method is time-consuming and can be difficult to replicate.

In 1873, Sachs introduced the glass panel root observation window (Böhm 1979). Root observation windows consist of large reinforced glass or plastic windows that are typically installed against a vertical soil profile in a trench. Eventually, the windows and trenches evolved into underground root laboratories (later known as rhizotrons). Using the glass panel method, roots are quantified by mapping the roots on grid paper or tracing the roots onto transparencies or overlays. Colored pens are useful to distinguish observations made at different times. However, the quickest method of quantifying root growth (length) is via the line-intersect method of Marsh (1971), Tennant (1975), and Newman (1966) (discussed later). Photographs can also provide valuable information regarding root turnover (Böhm 1979). When good contrast exists between roots and the soil, photographs can be made and analyzed by computer programs such as WinRHIZO (Régent Instruments, Inc., Québec, Canada).

The major advantages of root observation windows are that they provide a non-destructive means to collect data, and they allow continuous observation of the same root or root system over a period of time. In addition, qualitative data on root color, branching, growth direction, and responses to the environment can be collected (Böhm 1979). Rhizotrons can be expensive to construct and therefore may limit the number of replications for experimental treatments. However, this may be overcome by repeating the study over several years (Böhm 1979). Another disadvantage of root observation windows is that the window-soil interface of rhizotrons does not perfectly replicate natural soil conditions (e.g., temperature, bulk density, moisture, and light conditions), which may influence rooting behavior (Bloomfield et al. 1996). Therefore, special precautions must be taken to reproduce natural soil temperatures (e.g., insulated wraps, protective covers, or mulching), exclude light from the window (e.g., plastic or wooden doors), and prevent air gaps from developing behind the windows. Additionally, it can be difficult to distinguish between live and dead roots, and the windows can get murky in some soils, especially soils with high clay contents. Another consideration is that, when roots contact the window, they may grow along it rather than exploring the soil. However, Böhm (1979) stated, “this does not seem to be as serious as might be thought”. Root growth behind windows was greatest in the first year after installation [(Rogers and Head 1968) cited in (Böhm 1979)]. Subsequently, windows should be installed months prior to the initiation of the experiment. Other considerations regarding root observation windows are that only a small portion of the root system may be observed (Harris et al. 1995) and that the window may not accurately represent the natural heterogeneity of the site.

The installation of minirhizotrons in several locations can partially overcome the problem of spatial heterogeneity within a sampling area (Bloomfield et al. 1996).

Minirhizotrons, whose concept was first proposed by Bates [(1937) cited in (Böhm 1979)], consist of narrow transparent tubes through which small high resolution cameras or video recorders are run. Using computer-aided analysis, large amounts of information (e.g., photographs) can be processed (Smucker 1993). Minirhizotrons can be relatively inexpensive compared to the construction of large trench rhizotrons, permitting the installation of more tubes and increasing statistical soundness of the data compared to the cost of a trench rhizotron (Böhm 1979). Additionally, minirhizotrons result in less damage to the soil and root system. On a cautionary note, Bloomfield et al. (1996) advised that quantification of system-level turnover may only be accurate for relatively homogenous systems, and that in forest systems minirhizotrons may only be more applicable to individual root demographics than ecosystem level quantification. The problem with rhizotrons mentioned previously of the artificial soil-window interface and potential problems with light must still be considered with the minirhizotron. Despite the disadvantages of rhizotrons and minirhizotrons, Böhm (1979) states, "these disadvantages are outweighed by the fact that continuous, exact determinations of major changes in root behavior can be made".

Nuclear magnetic resonance imaging (MRI or NMR depending upon the characterized nuclei) and computer-assisted or computed tomography (CAT or CT) are other nondestructive methods available to characterize soil water extraction by plants, and the internal structure and nature of the soils (e.g., presence of roots and pore size and distribution) (Smit 2000). Both methods can provide high resolution. Disadvantages of these methods are that they require expensive equipment and highly trained operators. In addition, CT requires uniform soil density and non-swelling soils, and MRI does not perform well in high clay soils (Smit 2000).

Many of the affore mentioned field methods (e.g., rhizotron, cage method, needleboard method) can be modified to use with containers or pots. Major advantages of container studies include ease of handling and ability to provide sufficient replications for statistical analysis (Böhm 1979). In addition, the influence of individual factors and/or combinations of factors can be tested more easily than with field-grown specimens. Disadvantages of container studies are limited rooting volume and lack of natural conditions (e.g., soil characteristics, moisture, and competition from other plants, soil flora and fauna) (Böhm 1979). The split-root method is a modification of the container method where a root system is divided between two containers with different treatments (e.g., moisture or fertility) (Böhm 1979). The split-root method is particularly useful to observe root response to two simultaneously applied treatments.

Indirect Methods

Due to the time-consuming nature of many of the direct methods, indirect methods for measuring root growth were developed (Böhm 1979). Many indirect methods rely on changes in water or nutrient use over a period of time to derive information about root systems. A major consideration when employing indirect methods in root studies is that methods maybe based upon inaccurate assumptions. Indirect methods include: methods based on soil moisture content (e.g., gravimetric methods, neutron moisture meter, or time domain reflectometry), use of both radioactive and non-radioactive tracers, and use of mesh bags or porous envelopes.

The gravimetric method is based on the assumption that correlations exist between soil moisture depletion rate and root quantity (Böhm 1979). Therefore, soil samples are weighed at different time intervals to determine moisture loss. Neutron moisture meters work based on the principle that hydrogen atoms of water slow down and scatter the neutrons coming off the probe. An advantage of the neutron moisture meter is that moisture content can be measured over time because of its non-destructive nature. Neutron moisture meters are not as accurate in heterogeneous or organic soils. Time domain reflectometry (TDR) works on the basis that the dielectric constant of water is much higher than soil solids (Smit 2000). Therefore, moisture content can be estimated based upon the transit time of electromagnetic waves along metallic probes. The propagation velocity of the electromagnetic wave decreases as soil moisture increases. With all of the fore mentioned methods, it must be assumed that a correlation exists between the rate of soil water depletion and quantity of roots and that there is limited water loss except via transpiration.

Uptake of both radioactive (^{32}P, ^{86}Rb, or ^{14}C) and non-radioactive tracers (Li, B, or Sr) via soil or plant injection can also be used to infer information about activity of root systems (Böhm 1979). Based upon the assumption that tracer uptake correlates with root activity, spectrophotometric tissue analysis of roots and shoots can be used to infer root activity of non-radioactively labeled specimens. Concentration of radioactive tracers can be determined using counters such as a Geiger-Müller counter. Disadvantages of using tracers are that timing is critical and that these methods are typically destructive and therefore only good for one observation. In addition, working with radioactivity presents health risks.

Line Intersect Method

Root length and root length density (length per unit volume) are common measures in root studies (Böhm 1979). Root length density is commonly used because it has been shown to have a clear association with nutrient and water uptake by plants. According to Newman (1966), the capacity of roots to take up water and nutrients is more closely related to root surface area or total length than to the weight of the root system. However, a problem associated with measuring root length is that great lengths can occur, even in small volumes of soil (Newman 1966). Therefore direct measurement of roots (measured with a ruler) is very time-consuming, even with small soil samples.

In 1966, Newman developed the line intersect method, an indirect method for estimating total root length in a sample. The method was based on the principle that longer roots intercept a line more frequently than shorter roots. The formula used to calculate total root length was: $R=(\pi NA)/(2H)$ where R=root length, N=number of intercepts between the roots and random straight lines, A=area, and H=total length of the straight lines. This method required that a line engraved on an eyepiece be superimposed on an arranged group of roots and ultimately required less time per measurement than direct measurements (Marsh 1971).

In 1971, Marsh modified Newman's formula to: $R=(11/14)(N)$ for a grid of indeterminate dimensions where N=all intercepts of roots with the total length of vertical and horizontal grid lines. Marsh's grid could be used to measure lines such as roots, fibers, roads, streams (on aerial maps), etc. Using this method, a grid was superimposed over the system of lines to be measured. An average of several counts increased accuracy of the measurement. According to Marsh (1971), a count of 100 intersections would be accurate within 3% and a count of 1000 intersections would be accurate within 0.3%. Benefits of this method were that it was quick, inexpensive, and convenient.

In 1975, additional refinements were made to Newman's line intersect method. Using Marsh's grid, Tennant (1975) found that best results were obtained by assigning one count to a root crossing a line, one count to a root end touching a line, one count to a curved portion of a root touching a line, and two counts to the curved portions of a root that lay on or along the line. Tennant (1975) suggested that systematic traversing of vertical and horizontal lines was better than following single roots. Counts were then tallied and converted to length measurements using: R=(11/14)(N)(grid unit). To simplify further, Tennant (1975) established that 11/14 could be multiplied by the grid unit to obtain a conversion factor. For example, 0.7857, 1.5714, and 2.3571 could substitute for 1, 2, and 3 cm grid units. Using thread, Tennant (1975) tested the line intersect method and found that estimates strongly correlated with actual lengths up to 400 cm but that lengths were underestimated with longer lengths of thread. Thus, the size of the grid to be used depends upon the quantity of roots. Tennant (1975) suggested that a 1/2 cm grid be used for samples 1 to 300 cm long, a 1 cm grid be used for samples 75 to 700 cm long, a 2 cm grid be used for samples 275 to 1100 cm long, and a 3 cm grid be used for samples over 600 cm long. However, Böhm (1979) suggested that with samples less than 1 m long a 1 cm grid should be used. A 2 cm grid should be used for samples 1 to 5 m long and a 5 cm grid should be used for samples up to 15 m. Accuracy was greatest when counts are greater than 50 and no more than 400.

Although the direct method of measuring roots may be slightly more accurate, the line intersect method is quicker, more convenient and less expensive, particularly when many samples are to be measured. The direct method of measuring root length (with a ruler) can be particularly time consuming and tedious when the specimen to be measured is branched. Böhm (1979) recommends this procedure only for estimating single roots.

Root and Shoot Growth Periodicity

Many temperate woody species fluctuate between periods of rapid shoot growth during warm seasons and suspension of shoot growth during cold seasons. Not as readily apparent, roots also alternate between periods of abundant growth and periods of little or no growth. The alternation between periods of abundant growth and periods of little growth is thought to serve as a mechanism for coping with environmental stresses (e.g., temperature, drought) in environments with variable conditions (Lyr and Hoffman 1967; Reich et al. 1980). The time at which growth resumes after a period of rest depends on the species as well as on environmental conditions (Lyr and Hoffman 1967).

Morrow (1950) described periodicity as “a set pattern of growth caused by internal (inherent) factors, and the influence of the plant environment acts only to alter this predetermined pattern”. The quantity of root growth in trees depends on species, stage of shoot development, soil moisture content, soil nutrient content, soil temperature, root pruning, top pruning, tree age, soil temperature and moisture, and other factors (Gilman 1990). Competition between roots and shoots for photosynthate can lead to reduced root growth while shoots are expanding (Harris and Fanelli 1999). It has also been suggested that root growth intensity in deciduous fruit trees is limited to specific periods in time and proportional to the amount of shoot growth (Head 1967; 1968). As well, bud break can be delayed due to transplanting. Delayed bud break of evergreen conifers that are lifted in the fall and kept in cold storage may be a result of low carbohydrate/starch levels at outplanting (Jiang et al. 1994; Wang and Zwiazek 1999) and/or slow photosynthetic recovery after transplanting (Jiang et al. 1995; Jiang et al. 1994).

Considerable variation exists in the periodicity of root and shoot growth. Root and shoot growth may occur simultaneously in some species (Cripps 1970; Dickson 1994; Harmer 1990; Harris et al. 1995; Pagès and Serra 1994), while in other species these periods may be coordinated at separate moments in time (Abod and Webster 1989; Bevington and Castle 1985; Deans 1979; Deans and Ford 1986; Harris et al. 1995; Hinesley 1986; Kotze and Geldenhuys 1992; Lathrop and Mecklenburg 1971; Ploetz et al. 1993; Reich et al. 1980; Thaler and Pages 1996). Many authors report that root growth begins prior to shoot growth in spring (Abbott and Gough 1987; Atkinson 1980; Dell and Wallace 1983; Harris and Fanelli 1999; Kaushal et al. 1989; Lyr and Hoffman 1967; Mertens and Wright 1978; Morrow 1950; Wargo 1983), while other authors report that root growth begins after the initial period of shoot elongation (Kaushal et al. 1989) or is simultaneous to the period of shoot growth (Ford and Deans 1977). Harris et al. (1995)

determined that shoot growth began before or simultaneously with the onset of root growth in green ash (*Fraxinus pennsylvanica* Marsh.), scarlet oak (*Q. coccinea* Münchh.), Turkish hazelnut (*Corylus colurna* L.), and tree lilac [*Syringa reticulate* (Bl.) Hara. 'Ivory Silk'] in upstate New York. Theophrastos of Lesbos (372-287 B.C.) observed that roots started growing before shoots in spring (Lyr and Hoffman 1967).

Much of the observed variation in root and shoot growth patterns can be attributed to species differences and climate, which may vary slightly year-to-year. However, the factors listed previously also influence periodicity. Therefore, one must be mindful when relating results of one project to another. In addition, measurement method and root type affected the pattern of root periodicity determined in four species studied by Harris et al. (1995). Lyr and Hoffmann (1967) suggested that much of the existing variability among research projects could be attributed to results that used different species that are indigenous to or at least were grown in different regions and climates and were obtained by different methods.

A review of root and shoot periodicity would not be complete without a brief discussion of the various patterns of shoot growth. Patterns of shoot growth can be divided into three broad categories: determinate, semideterminate, and indeterminate (Dickson 1994). Determinate, fixed, or monopodial species typically produce one flush of growth per year (Kozlowski and Pallardy 1997) and are usually found in regions with distinct seasons where flushing cycles become locked to the seasonal changes. For example, the entire period of growth of American beech (*Fagus grandifolia* Ehrenb.), a common species in much of the eastern United States (Little 1980), lasts approximately 60 days and 90% of annual shoot growth is completed within a 4-week period (Kienholz 1941). Shoots grow rapidly to a late May climax and then cease completely before the end of June. Semideterminate or sympodial species produce multiple, recurrent flushes of shoot growth per growing season and are often characteristic of climates with little seasonal variation (Dickson 1994; Kozlowski and Pallardy 1997). Shoot growth patterns of species that produce individual leaves at regular intervals throughout the growing season are referred to as indeterminate or continuous (Dickson 1994). While growth that occurs in regular intervals is described as cyclic, rhythmic, or periodic (Borchert 1973), growth that occurs in irregular intervals is referred to as episodic, intermittent, or recurrent (Romberger 1963; Zimmerman and Brown 1971).

Borchert (1991) stated that a "true" episodic flush consists of the expansion of the resting bud, the expansion and maturation of new stem and leaves, the formation of a new resting bud, and finally a rest period in which no new leaf or stem elongation takes place. However, in all types of shoot growth patterns, the first flush consists of the expansion of preformed stem units (primordia-node-internode units) contained in the winter bud (Dickson 1994). Late season temperatures were suggested to influence the number of leaf primordia laid down in the winter bud, thereby affecting the following years flush of shoot growth (Kozlowski 1971). As well, late summer droughts are thought to restrict the number of primordia that are laid down in the new bud. Subsequently, stresses endured in a particular year may not show until the following year when shoots expand.

Factors Influencing Shoot Growth

Shoot growth is largely determined by genetic factors and environmental factors such as light, water, temperature, mineral supply, composition of the above and belowground atmosphere, physical and chemical soil properties, insects, other plants, and animals (Kozlowski 1971). The interdependencies of the various environmental factors in combination with genetic factors make it extremely difficult to determine specific contributions of each factor to shoot growth.

Over 50 terms have been used to describe dormant conditions in plants (Martin 1991). Therefore a brief summary of terminology associated with dormancy follows. Dormancy is a general term used to describe all instances when a tissue predisposed to elongate does not do so. Quiescence is a type of dormancy that is triggered by the external environment (a.k.a. aitonomic dormancy). Correlated inhibition is a type of physiological dormancy that is maintained by internal conditions in the plant and not the dormant organ itself (a.k.a. summer dormancy). Rest is another type of physiological dormancy that is maintained by conditions within the dormant organ itself (a.k.a. winter dormancy or autonomic dormancy). Plants in rest won’t come out of dormancy even under favorable environmental conditions. On the other hand, quiescent plants will activate growth once the environmental stress has disappeared. Lang et al. (1987)

simplified the terminology and defined dormancy as "any temporary suspension of growth of any structure containing a meristem". Lang et al. (1987) listed three types of dormancy as: ecodormancy, which is regulated by environmental factors (e.g., temperature extremes, nutrient deficiency, and water stress), paradormancy, which is regulated by physiological factors outside the affected structure (e.g., apical dominance and photoperiodic responses) (a.k.a. correlated inhibition or summer dormancy), and endodormancy, which is regulated by physiological factors inside the affected structure (e.g., chilling responses and photoperiodic responses) (a.k.a. rest or winter dormancy).

Many hypotheses have been suggested to explain the control mechanisms that regulate leaf and internode expansion and primordia initiation. According to Kozlowski (1971), the growth of shoots is a response to climatic and biotic factors that influence internal physiological processes and thus affect the formation and expansion of shoot primordia. Borchert (1991) suggested that water stress was responsible for inducing bud rest and episodic growth. Other authors suggested that abscisic acid and/or cytokinins were responsible. Dickson (1994) suggested, "during a flush, photosynthate movement to roots decreases, water stress and abscisic acid concentrations increase, cytokinin concentrations and/or translocation decrease, primordia development decreases, and leaf growth decreases and buds are set". On the other hand, breaking of bud dormancy was reported to be due to an increase in the ratio of abscisic acid to gibberellin (Goss 1973). Buds are dormant when this ratio is high, and dormancy is broken when the ratio decreases. In some species, dormancy can be broken by application of gibberellic acid to apical buds. Taylor and Dumbroff (1975a) found an increase in cytokinin activity at bud break. Abeles (1973) reported that bud dormancy could be broken by application of ethylene or ethylene-generating chemicals.

According to Reid et al. (1991), resting bud formation is a developmental change that is influenced by photoperiod and is generally promoted by short days. Downs and Borthwick (1956) also proposed that the primary factor for inducing bud dormancy is daylength and that short days induced dormancy, while long days prolonged growth. According to Berrie (1987), as days shorten, buds decrease their metabolic activity and enter a dormant state before low winter temperatures arrive. Buds come out of rest and resume growth once a sum of temperature deficits is achieved and environmental conditions are favorable.

According to Harris et al. (1999), as daylength shortens, buds of many temperate species begin to enter a period of rest and cannot grow despite favorable conditions. By late winter, rest-dormancy is overcome and plants remain quiescent until conditions are favorable, at which time growth will commence. They also state that buds must be exposed to 4 to 8 weeks of low temperatures (-4 to 10 C) in order to come out of rest. For example, depending upon the cultivar, peach [*Prunus persica* (L.) Batsch.] requires 350 to 1200 hr at or below 7 C. Variation among species and provenance also influences the required temperature and time needed to overcome rest. Dormant buds in many species inhibit shoot elongation as well as depress the activities of roots and cambium. Similarly, research of Lathrop and Mecklenburg (1971) suggested that the cold requirement of vegetative bud dormancy in Japanese yew (*Taxus cuspidata* Sieb. & Zucc.) was a function of time and temperature, and that 3 weeks of chilling (-2 to 0 C) were required to break bud dormancy. They also reported that at least 7 weeks of chilling (2 C) was needed to break root dormancy. In sugar maple, approximately 2000 hr of 5 C, which is typically achieved by mid February or March, is necessary to break bud dormancy (Berrie 1987; Taylor and Dumbroff 1975b). Once the 2000 hr is achieved and environmental conditions are favorable, buds come out of rest and shoots resume growth. Dormancy allows plants to better survive adverse conditions.

Perry (1971) suggested that other factors, such as nutrition, water status, temperature, and irradiance, might also play a role in inducing bud dormancy. For example, excess nitrogen can delay dormancy until first frost, which puts plants at risk of being damaged or killed.

Factors Influencing Root Growth

A bimodal pattern of root growth in late spring and autumn (with a period of rest or reduced growth in summer) for trees in seasonal climates (e.g., temperate zone) has been reported by many authors (Cripps 1970; Deans 1979; Deans and Ford 1986; Dell and Wallace 1983; Harris et al. 1995; Harris and Fanelli 1999; Roberts 1976; Wargo 1983). Many woody plants have two distinct periods of active root elongation, one in spring and one in fall (Stone et al. 1962; Stone and Schubert 1959). While an absolute cause for reduced root growth in summer is unknown, unfavorable environmental (e.g., drought or high temperatures) conditions have been suggested to cause reductions in growth (Lyr and Hoffman 1967).

Some authors suggest that summer root growth is related to moisture availability (Lyr and Hoffman 1967) and that moisture stress limits root growth long before the wilting point is reached [(Rogers 1939) cited in (Cripps 1970)]. While root growth may be limited by inadequate soil moisture, roots can quickly resume growth after adequately irrigated (Cripps 1970). However, if soils become exceedingly dry, parts of root systems may die. In addition to suppression of root growth, late summer droughts are also thought to restrict the number of primordia produced in new buds (Kozlowski 1971). Therefore, stress endured one particular year may not affect growth until the following year when shoots expand.

In addition to water deficits, water surpluses can also limit root growth and affect root periodicity (Lyr and Hoffman 1967). When roots are not dormant, excess water can limit root growth by two mechanisms. First, wet soils are typically poorly aerated with low oxygen levels and high carbon dioxide levels. However, while roots are dormant, the oxygen requirements of roots are reduced and roots are less sensitive to low levels of oxygen (Lyr and Hoffman 1967). The second mechanism by which excess water can limit root growth is that wetter soils are often cooler, which results in limited nutrient and water uptake (Kramer and Kozlowski 1960).

Research on young apple (*Malus domestica* Borkh. non Poir.) trees in western Australia suggested that winter dormancy of shoots was the primary seasonal influence on root growth (Cripps 1970). Cripps (1970) suggested that root growth ceased in winter due to dormancy of the shoots and the subsequent lack of photosynthates to support root growth. He also reported that in this research project, minimum soil temperatures reached 8.9 C and should not have been limiting.

While air temperatures influence the breaking of bud dormancy (Berrie 1987; Lyr and Garbe 1995), soil temperatures determine root growth (Bevington and Castle 1985; Harris et al. 1995; Head 1966). Several authors reported that root extension of many temperate species is severely limited when soil temperatures drop below 10 C (Harris et al. 1995; Harris et al. 1996; Headley and Bassuk 1991; Lyr and Hoffman 1967). Bevington and Castle (1985) reported that root growth in citrus (*Citrus* sp.) was limited at temperatures below 22 C. Typically, however, the range of temperatures suitable for root growth is between 2 and 35 C (Lyr and Hoffman 1967). In some species, root growth begins and ceases around 2 or 4 C, while in other species root growth occurs only above 11 C. Each species has a different amplitude or "ideal" range of temperature suitable for root growth, which might be related to the normal climatic amplitude of temperatures in the region to which the plant is indigenous (Lyr and Hoffman 1967). For example, citrus has a favored range with an amplitude of 7 C and strawberries (*Fragaria virginiana* Duchesne.) have a favored range with an amplitude of 16 C. Artificially heating the soil has been used to prolong and induce root growth [(Muromtsew 1962) cited in (Lyr and Hoffman 1967)]. While shoot periodicity remained unaffected by soil heating, a 15% increase in height was noted.

In climates with cold winters, root growth of many species continues after leaves have abscised and shoots have entered a dormant state, eventually ceasing in late autumn (Lyr and Hoffman 1967). Morrow (1950), however, reported that some root growth occurred in sugar maple during winter when soil temperatures were near freezing (0 C). Lyr and Hoffman (1967) suggested that roots lack an internally controlled period of dormancy, which was evident from observations of continuous, prolonged periods of root growth when roots were artificially heated. While root growth ceases during winter in most deciduous plants, root growth can occur in evergreen conifers (or other plants capable of photosynthesis) during winter (Harris et al. 1999; Lyr and Hoffman 1967). Finally, in regions with mild winters and frost-free soils, winter root growth is often observed (Harris and Fanelli 1999; Lyr and Hoffman 1967; Morrow 1950). While low soil temperatures have been emphasized, maximum soil temperatures may be of importance in hot, dry regions or in temperate latitudes during dry periods with high insolation (Lyr and Hoffman 1967). However, the latter case may only affect shallow roots and instead drought may be the primary risk.

Typically, roots will grow at lower temperatures than shoots (Harris et al. 1999). For example, Richardson (1958) observed that roots of silver maple (*A. saccharinum* L.) resumed growth in spring at 5 C, and buds expanded at 10 C. While similar differences likely exist in other trees, differences in temperature optimums vary among species and provenances (Lyr and Hoffman 1967). By mid winter the buds of most trees have overcome endogenous dormancy and remain in a quiescent state until temperatures become favorable (Lyr and Hoffman 1967). While warmer soil temperatures often result in early root growth, bud expansion remains unaffected. Another temperature consideration is that late season temperatures influence the number of leaf primordia formed and therefore, can affect the following year's flush of shoot growth (Kozlowski, 1971).

According to Harris et al. (1999) the "roots of most woody plants do not have a dormant-resting condition independent of the tops". Richardson (1958) observed in silver maple seedlings that initiation of root growth was delayed when the terminal bud was removed at bud break. However, root growth resumed upon development and bud break of another bud. Based upon these findings, Richardson (1958) concluded that buds must be developing and/or active in order for root growth to proceed. In addition, shoots must have leaves in order for root elongation to proceed.

Several authors have suggested the participation of hormones in the regulation of root growth (Harris et al. 1999; Hinesley 1986; Lyr and Hoffman 1967; Richardson 1958; van der Werf and Nagel 1996). The alternating, cyclic nature of root and shoot growth in citrus supports the concept that root growth may be suppressed by shoot elongation due to elevated auxin production in the shoots [(Monselise 1947) cited in (Bevington and Castle 1985)]. Research of Richardson (1958) suggested that a signal from the buds at the time of bud swell in spring was necessary for initiation of root growth and that auxins were transported from shoots to roots.

Recent research indicates that shoot and root growth are strongly influenced by the distribution of carbohydrates and nitrogen. According to Kuehny and Decoteau (1994), nitrogen is the primary element absorbed and utilized during root growth. When nitrogen is scarce, plants respond by reducing shoot growth and increasing root growth. When nitrogen is abundant, shoot growth increased and root growth decreased. While this may not prolong the period of active root growth, it does have an effect on root growth rate. Similarly, Eissenstat and Caldwell (1988) reported that roots have an ability to proliferate in favorable microsites (e.g., zones where water and nutrients had been applied) in early spring.

Mechanisms Influencing Periodicity

The mechanisms that control and affect root and shoot periodicity are still cause for debate. Several theories regarding the mechanisms controlling periodicity exist and are summarized in the following paragraphs.

Some authors (Borchert 1975; 1991; Greathouse et al. 1971; Harmer 1990; Morrow 1950; Reich et al. 1980; Romberger 1963) suggest that the regulation of growth is a consequence of internal physiological or endogenous factors such as changes in levels of growth regulators or genetic variation among species. Others suggest that periodicity is primarily under exogenous or environmental control (Alvim and Alvim 1976) and is strongly influenced by environmental factors such as soil temperature and soil moisture (Atkinson 1980; Lyr and Hoffman 1967; Morrow 1950; Reich et al. 1980). Torreano and Morris (1998) concluded that root elongation rates of loblolly pine (*Pinus taeda* L.) were linearly related to soil water potential and that flushes of root growth were a function of short-term changes in soil water potential. Similarly, Deans (1979) observed the cessation of fine root growth of Sitka spruce [*Picea sitchensis* (Bong.) Carr.] during summer months when soil moisture was low and the resumption of growth upon the rehydration of the soil by precipitation. Hendrick and Pregitzer (1996) also suggested that episodic deep root production was related to periods of high water demand.

The functional balance hypothesis of Brouwer (1962; 1983) suggests that relationship between roots and shoots is continually modified as resource availability changes. Similarly, Borchert (1973) suggested that rhythmic shoot growth in trees is a consequence of feedback mechanisms associated with maintaining a favorable root:shoot ratio. Borchert (1973) proposed a model where rhythmic growth is considered a "manifestation of an internal feedback mechanism in which the individual components are strongly subject to environmental factors". Accordingly, rhythmic growth is a result from water stress caused by an unfavorable root:shoot ratio that results from rapid shoot growth [(Bond 1945) cited in (Harmer 1990)] and the subsequent imbalance between transpiration and absorption (Reich et al, 1980). However, research by Harmer (1990) led the author to conclude that rhythmic shoot growth exhibited by 3-month-old English oak (*Q. robur* L.) seedlings was unrelated to the unfavorable root:shoot ratio resulting from rapid shoot development. However, cotyledons provide a considerable amount of nutrients and energy to seedlings, which may in turn alter normal periodicity patterns. In mature red oak (*Q. borealis* var. *maxima* = *Q. rubra* L.) trees, resumption of root growth in spring occurs at the expense of reserve materials (Lyr and Hoffman 1967). Subsequently, root growth is more likely to continue during periods of shoot growth in mature trees.

Starch reserves declined rapidly during shoot elongation in Sitka spruce (Deans and Ford 1986). The decline in starch reserves during shoot elongation corresponded to a reduction in radial root growth. Deans and Ford (1986) suggested that the “supply of assimilates to roots determines the timing and duration, as well as, the extent of radial growth” and that this may be influenced by the age of the tree and stage of development of the stand. Similarly, Lyr and Hoffmann (1967) also suggested that a reduction in root growth during periods of shoot expansion was due to consumption of assimilates by the growing shoot. Watson and Himelick (1982) stated, “at bud break, the elongating shoots act as a metabolic sink, resulting in a reduced flow of photosynthate to the roots”. The reduced flow of photosynthates to the roots results in a corresponding reduction in root growth.

Asynchronous growth of roots and shoots in ‘Valencia’ orange [*Citrus sinensis* (L.) Osbeck.] trees on rough lemon (*C. jambhiri* Lushington) and Carrizo citrange [*Poncirus trifoliata* (L.) Raf. x *C. sinensis* (L.) Osbeck.] rootstocks support the concept that roots and shoots compete for available assimilates, with the shoot being the stronger sink (Bevington and Castle 1985; Mooney and Chu 1974). Research of Dickson (1989) and Isebrands et al. (1994) determined that little photosynthate produced from mature leaves was translocated to the root system during a flush of shoot growth. However, after a flush of shoot growth (when the leaves had fully expanded) more than 90% of photosynthate was translocated to the roots (Dickson 1991). In support of the concept of periodicity being affected by a limitation of resources, root growth of Atlantic cedar [*Cedrus atlantica* (Endl.) Carr.] decreased during the initial period of stem elongation under ambient conditions but did not decrease when plants were grown in 800 μmol mol^{-}

[1] CO_2 (Kaushal et al. 1989). However, research of Tingey et al. (1996) revealed that temporal patterns of root and shoot growth in ponderosa pine (*P. ponderosa* Douglas ex Lawson) were not effected by additions of carbon dioxide or nitrogen.

Roots are heterotrophic organs whose growth is dependent upon the photosynthetic efficiency of the tree (Lyr and Hoffman 1967). Roots compete with shoots for available carbohydrates. Subsequently, a reduction in light intensity (i.e., shading) will reduce the photosynthetic output of the tree, resulting in a reduction in the supply of available assimilates for shoot growth and ultimately altering the root:shoot ratio.

Mertens and Wright (1978) proposed that the episodic nature of root growth in two cultivars of Japanese holly (*Ilex crenata* Thunb. 'Helleri' and 'Rotundifolia') was a result of "nutrients in excess of what is needed for root growth" being translocated to plant shoots where they are used for protein synthesis and shoot growth. Mertens and Wright (1978) proposed that soil fertility affects root and shoot periodicity in the following way. Growth of shoots results in fewer carbohydrates being available for translocation to the roots. As a result, root growth is reduced. Shoot growth decreases as nutrient levels are depleted within the plant, which results from diminished root growth and insufficient nutrient absorption to sustain shoot growth. However, as carbohydrates become available for translocation to the roots, due to the reduction in shoot growth, root growth and nutrient absorption resume. In support of Mertens and Wrights' (1978) theory, nitrogen concentration in shoot tissue was greatest just prior to initiation of shoot growth and lowest at the cessation of a flush of shoot growth (Gilliam and Wright 1978).

While in many instances, one dominant factor may dictate root and shoot growth periodicity, in most situations root and shoot growth periodicity are a result of an array of factors that together comprise the activities of the plant. In the following sections, examples of asynchronous and synchronous root and shoot growth are provided. Each of the authors came to some conclusion or made a suggestion regarding a cause for the observed results. Studies for the observed patterns of periodicity are grouped according to the cause to which the authors attributed the observed growth patterns. In studies where the authors designated multiple causes, the study was listed only under one subheading.

Examples of Asynchronous/Alternating Root and Shoot Growth

Shoot Growth Thaler and Pages (1996) determined that shoot growth and root development of rubber tree [*Hevea brasiliensis* (A. Juss.) Muell.] exhibited rhythmic/periodic growth patterns and that root development was related to leaf expansion. During leaf expansion, root elongation decreased and root branching increased. This caused morphological differences along the length of the taproot with areas with abundant branching and vigorous secondary root growth alternated with areas of little branching and shorter roots. Similarly, Deans (1979) reported an increase in fine root growth of Sitka spruce as soil temperature increased in spring, followed by a decrease in root growth during the period of shoot extension. Root growth resumed as shoot growth declined.

Root growth of apple has two distinct peaks. The first peak occurs just prior to spring bud break, while the second peak, of greater magnitude, occurs after the cessation of shoot elongation in late summer (Abod and Webster 1989). Root growth was minimal during the period of active shoot growth between mid June and until the end of August. However, after the period of active shoot growth, root growth dramatically increased.

Hormones Using 3-year-old Fraser fir (*Abies fraseri* Pursh Poir.) seedlings that were transplanted at 2-week intervals between 1 August and 15 October and once prior to bud break in spring, Hinesley (1986) determined that seedlings planted in August and early September had significantly greater growth (dry weight, stem diameter, and shoot elongation) than seedlings planted after mid October. He proposed that the reduced growth of spring transplants might be due to drought stress or interference with the balance of root-produced hormones involved with normal shoot extension. Shoot growth was completed in Fraser fir by early July, after which differentiation of the winter bud began. Root growth was greatest in late August and September, after the cessation of shoot extension.

Soil Temperature In rough lemon and Carrizo citrange rootstocks in Florida, Bevington and Castle (1985) found that root growth occurred whenever soil moisture and temperature were favorable, except during periods of shoot growth, when a temporary decline in root growth rate occurred. Shoot growth in lemon and citrange occurred in multiple well-defined flushes, each of which corresponded to low root extension rates. Root growth rate decreased and remained at a low level until shoot elongation ceased.

Thus, the cyclic nature of shoot growth resulted in a cyclic pattern of root growth, with periods of alternating root and shoot growth. Bevington and Castle (1985) established that root extension rate positively correlated with soil temperature, with the greatest root growth occurring in summer when temperatures were above 27 C and limited root growth occurring below 22 C (November until March). Monselise [(Monselise 1947) cited in (Bevington and Castle 1985)], on the other hand, reported that no root growth occurred below 14 C in citrus.

Soil Moisture In addition to studying soil temperature effects on rough lemon and Carrizo citrange, Bevington and Castle (1985) also considered the effects of soil moisture and determined that when soil temperatures were favorable, regardless of shoot activity, soil moisture controlled root growth. Root growth was limited at soil matric potential of -0.05 MPa; however, it resumed 2 days after irrigation. Other research reported limited root growth at -0.75 to -0.80 soil water potential [(Monselise 1947) cited in (Bevington and Castle 1985)]. Therefore, Bevington and Castle (1985) concluded that "the interrelationship between root and shoot growth controls the intensity of root growth at times when soil temperature and water content are not limiting" and that the greatest root growth occurs when shoots are not flushing and soil temperatures and soil water potentials are above 22 C and 0.05 MPa, respectively.

Reductions in root growth during the summer months have been reported by several authors (Deans 1979; Lyr and Hoffman 1967; Roberts 1976). Dell and Wallace (1983) noted that the decline in new root production of jarrah (*Eucalyptus marginata* Donn ex Sm.) in western Australia in early summer corresponded to a decline in precipitation. Root growth occurred during two peaks: one in spring and one following autumn rain (within 2 days). Little root growth was recorded during late winter and summer drought. However, once soils were moistened after a rainfall event, root growth resumed. This finding led Dell and Wallace (1983) to conclude that the reduction in growth was due to a shortage of available water.

Starch Reserves Research of Deans and Ford (1986) examined the bimodal nature of radial root growth in Sitka spruce and the relationship of root growth to shoot extension and the starch dynamics. While a minor peak of radial root growth occurred just prior to shoot extension, a major peak followed shoot elongation. The major period of shoot extension correlated with a reduced rate in stem radial growth and decline in starch reserves. At distances further from the stem, radial root growth was limited only to the period following shoot elongation. The authors concluded that early season radial root growth was sustained by currently-stored assimilates.

Reich et al. (1980) determined that when blackjack oak (*Q. marilandica* Münchh.) and white oak (*Q. alba* L.) seedlings were grown in a growth chamber, they exhibited synchronous flushes of shoot and leaf growth that alternated with periods of root growth. Maximum root growth occurred only when shoots were at rest and resumed after leaf expansion ceased. The duration of one flush of shoot and root growth in white oak seedlings lasted approximately 38 days. Root growth of understory seedlings was not observed in March or April or prior to leaf expansion but occurred for a limited time only after these events. However, in mature white oaks, root growth began approximately 38 days prior to bud break, reached a peak just following cessation of shoot growth, and was largely continuous until winter soil temperatures or soil water potentials became limiting. Only one flush of shoot growth was observed for mature white oaks and understory seedlings. Root growth between leaf drop and bud break was observed in 63.5% of mature trees. The authors concluded that multiple flushes of shoot growth occurred in seedlings when environmental factors were favorable but did not usually occur in mature trees. It was suggested that this was due to the depletion of energy reserves that a tree experiences when a flush of shoot growth occurs (McLaughlin et al. 1980).

In transplanted yew (*T.* x *hunnewelliana* Rehd.), Lathrop and Mecklenburg (1971) reported a decrease in root regeneration potential associated with an increase in shoot growth in spring. The authors proposed that the decrease in root regeneration potential was due to increased competition between shoot and root growth for available carbohydrates or other growth factors. However, the authors also suggested that the decrease in root regeneration potential after shoot growth stopped in summer was not due to competition between roots and shoots since shoots were no longer elongating. Finally, Lathrop and Mecklenburg (1971) concluded that other factors in addition to root dormancy regulate root regeneration potential.

Not Stated Ploetz et al. (1993) established that flushes of root and shoot growth in avocado (*Persea americana* Mill.) alternated on 30- to 60-day cycles. While root growth correlated with soil temperatures, it continued throughout the year. During late fall and winter, growth decreased to one third of the maximum rate. As well, shoot growth was severely diminished during late fall and winter. Black stinkwood [*Ocotea bullata* (Burch.) E. Mey] is another example of a species that exhibits a cyclic alternation in periodicity of root and shoot growth (Kotze and Geldenhuys 1992).

Research on seven red maple (*A. rubrum* L.) and three Freeman maple (*A.* x *freemanii* E. Murray) cultivars grown in containers in Alabama suggested that more than 75% of total height and diameter growth in most cultivars occurred prior to mid-August (Sibley et al. 1999). However, only 25% of root growth occurred by the end of August. Therefore, 75% of the season's total root growth occurred between late August and November.

Examples of Synchronous/Concurrent/Simultaneous Root and Shoot Growth

Winter Dormancy Shoot and root growth occurred concurrently in apple trees (Granny Smith) grown in the Mediterranean climate of western Australia (Cripps 1970). Roots of young trees supplied with adequate moisture and bearing no crop grew continuously and at a constant rate from early spring until late autumn, suggesting that summer soil temperatures (maximum 23.7 C) were not inhibitory. However, when exposed to moisture stress, root growth ceased entirely or was at least severely reduced. Rapid root growth resumed following adequate rainfall. As a result, the period of greatest root extension occurred in late spring/early summer with a peak in early autumn after rain. Little root growth occurred during the winter months, despite the lowest recorded soil temperature being 8.9 C which should hinder but not completely restrict root growth. Subsequently, Cripps (1970) suggested that root growth was not limited by low winter soil temperature but instead was limited by winter dormancy and lack of photosynthesis. Fruiting also reduced root growth. However, Cripps (1970) noted that harvesting the crop resulted in the resumption of root growth. In mature trees there was a tendency for a reduction in root growth to be associated with reduced shoot growth.

Despite Cripps' (1970) findings of concurrent and synchronous root and shoot growth in apple trees, Head (1966) reported that in England root growth of apple occurred prior to shoot growth and that root growth declined during the period of shoot growth. Cripps (1970) suggested that differences in results might be “attributable to differences in prevailing climatic conditions and illustrate the difficulty in applying results of apple root growth studies from one climatic zone to another without considerable qualification”.

Developmental Stage Research on 3-month-old English oak seedlings determined that tap root growth was continuous, while shoot growth underwent a series of rhythmic growth flushes, indicating that root growth and shoot elongation were not coupled (Harmer 1990). Similarly, Pagès and Serra (1994) determined that despite temporary reductions in root growth rate, root and shoot growth of 30 to 45 day old English oak seedlings were not synchronized. However, developmental stage of the plants and attachment of the energy- and nutrient-rich cotyledons may have maintained root growth during the flushes of shoot growth. In fact, Dickson (1994) stated that in northern red oak, root growth rates are constant as long as the cotyledons are attached. Dickson also reported that in older seedlings and seedlings with detached cotyledons, root growth alternated with shoot growth and exhibited an episodic growth pattern. Research on older oaks revealed suppression of root growth during periods of shoot growth (Reich et al. 1980).

In an evaluation of methods for measuring roots (root extension, root length against a grid, and minirhizotron), Harris et al. (1995) determined that root growth periodicity patterns differed depending upon the measurement method and types of roots measured. Using one method to measure roots, alternating patterns of root and shoot were evident. When using another method, growth appeared to occur simultaneously. In central NY, root growth began in middle to late May for scarlet oak, green ash, Turkish hazelnut, and tree lilac (Harris et al. 1995). Scarlet oak and green ash exhibited a bimodal pattern of root length increase with peaks in early summer and early fall, while Turkish hazelnut did not. Tree lilac had a more uniform pattern of root growth. Root growth began in all species when soil temperatures were approximately 12 to 15 C. Root growth ceased as soil temperatures reached 6 to 8 C. Root extension and shoot extension occurred simultaneously. However, greatest root extension occurred after the cessation of shoot extension. Shoot extension began prior to root growth for green ash, hazelnut and lilac.

Periodicity in Sugar Maples

Morrow (1950) reported on root periodicity in a mature sugar maple forest in central New York and determined that in the upper inch of soil root periodicity followed a general pattern of abundant growth in spring, less growth in summer, a slight increase in the fall, and limited growth in winter. Some root growth was reported to occur during winter when soil temperatures were near freezing (0 C). Specifically, he determined that root growth between mid March and late June was approximately 0.6 mm to 1.0 mm per day, while little root growth occurred after late June. He also suggested that annual extension was about three to four inches, of which 80% occurred between mid March and late June. Shoot growth occurred between 1 May and 15 August, with 85% of the annual shoot growth being completed prior to June 15. Approximately half of the annual root growth occurred concurrently with shoot growth. Morrow (1950) observed a decrease in root growth rate at the same time as the cessation of shoot growth. Cambial growth occurred between 1 May and 31 August, with 80% being complete by July 1. Morrow (1950) also reported that cambial activity paralleled shoot growth, except cambial activity lasted about 2 weeks longer. Unfolding of sugar maple leaves occurred 3 weeks after the resumption of spring root growth. However, most root growth occurred at times when the trees were in full leaf.

Morrow (1950) credited root growth in sugar maple to be influenced by several environmental factors, particularly soil temperature and soil moisture. However, he credited the lack of abundant root growth in fall, when soil temperatures and soil moisture were non-limiting, to internal growth mechanisms that dictate an inherent growth pattern, which is influenced by environmental factors such as soil moisture and soil temperature. The reduction and cessation of growth during summer and early fall was attributed to low soil moisture/drought. However, root growth resumed 2 days after precipitation. Late winter and spring root growth were limited by unfavorable soil temperature and resumed when soil temperatures became non-limiting. Morrow (1950) concluded that the growth activities of shoots, cambium, leaves, and roots of sugar maple behaved independently. However, the periods of greatest activity of each of the organs occurred simultaneously. Therefore, it is likely that there was considerable competition between the organs for assimilates. Finally, Morrow (1950) observed that most root growth consisted of the formation of new roots rather than extensions of older roots.

Of note, Morrow (1950) assumed for his research that suberization in hardwoods occurred approximately 1 month after growth began in the spring. This assumption was based upon the findings of Engler [(1903) cited in (Morrow 1950)] who observed that hardwood root tips turned brown in 3 to 6 weeks and turned brown faster (3 weeks) in the summer. Growing root tissues of apple and peach also matured rapidly at soil temperatures above 18 C [(Nightingale 1935) cited in (Morrow 1950)]. Morrow suggested that maturation occurs at a slower rate during winter than other times of year.

Root and shoot growth periodicity of pot-in-pot (PIP) red and sugar maples in southwest Virginia were reported by Harris and Fanelli (1999). Root growth in both red and sugar maple began around 15 March (1995) and 1 April (1996) when substrate temperature neared 10 C. Substantial root growth occurred in both species prior to bud break in early May (1 May both years). However, a temporary interruption in root growth corresponded to bud break. Following the interruption, root growth greatly increased and occurred simultaneously with shoot elongation. In red maple, the greatest root growth occurred in conjunction with the greatest period of shoot growth. However, in sugar maple the greatest root growth occurred just following the single flush of shoot growth. Substantial amounts of root growth occurred in both species after bud set and continued until fall decline**.** A temporary cessation of root growth occurred in sugar maple in August when substrate temperatures were approximately 25 to 30 C. While root growth was greatly reduced as substrate temperatures dropped to 5 to 7 C during autumn, a minimal amount of root growth did occur throughout winter in sugar maple.

Harris and Fanelli (1999) measured 7.5 m of root growth against the 25 cm x 25 cm face of the rhizotron by the end of the project (February 1995 to May 1996). The most rapid root growth in sugar maple occurred around 1 June, which corresponded to the end of the spring shoot growth period. They concluded there to be "no sustained antagonistic pattern of root vs. shoot growth for either species". Instead, the temporary interruption in root growth at the onset of shoot growth represented a transient antagonism. In practical application, the authors concluded that bud break would not be the best time to transplant red or sugar maple due to limited root growth and high potential for water loss through transpiration. Additionally, it was suggested that fall transplanting would better exploit the substantial root growth that occurs prior to bud break and this might aide establishment by increasing the available soil water reservoir that will support the new developing shoots.

Wargo (1979) determined that radial root growth of sugar maple did not commence until substantial deposits of starch were laid down in roots. Additionally, Wargo found starch reserves to be near depletion by spring. Storage reserves were quickly replaced once leaves had fully expanded. Complete replacement of the storage reserves occurred by mid late July. Similar depletion of starch reserves was described following flush periods in northern red oak seedlings (Parker 1979).

Root Death Processes: Senescence, Mortality, Longevity, and Turnover

Root lifespan varies widely. Some small-diameter (fine) lateral roots live only a few weeks (Black et al. 1998), while other roots can live for several years (Lyr and Hoffman 1967). Coarse roots of some woody plants may live as long as the plant (Bloomfield et al. 1996). Differences in longevity are probably a result of combinations of genetics, environmental conditions, and physiological status (Black et al. 1998).

Tree roots can be separated into three structural/functional classes: coarse roots, small roots, and fine roots (Bloomfield et al. 1996). Coarse roots are supportive in nature, typically have low turnover rates, and are long-lived, often as old as the tree. Small roots serve as conduits for water, minerals, and assimilate, and have low turnover rates. Fine roots serve as primary absorptive surfaces for water and nutrients and have the highest turnover rates (Bloomfield et al. 1996; Wargo 1983).

Substantial amounts of carbon are assimilated by plants and transported belowground to produce fine roots (Fogel 1983; Hendrick and Pregitzer 1993a). The flux of carbon from degrading root biomass to the soil is referred to as root ‘turnover’ (Tierney and Fahey 2002) and is a measure of annual production and/or mortality relative to the standing crop (Burton et al. 2000; Gill and Jackson 2000; Hendrick and Pregitzer 1992a; 1993a; Jones et al. 2003). Root turnover refers to the proportion of the root system that dies and is replaced (Burton et al. 2000).

Fine roots comprise significant portions of the belowground biomass of trees. Therefore, root turnover can constitute a major sink for carbon and can be a substantial metabolic cost (Psarras et al. 2000). Srivastava et al. (1986) reported that fine roots comprised 55% of the total root biomass in teak (*Tectona grandis* L.). Estimates of fine root production and replacement (turnover) range between 1.4 to 11.5 $Mg \cdot ha^{-1} \cdot yr^{-1}$ (Fogel 1985; Santantonio and Hermann 1985). Research by Mäkelä and Vanninen (2000) suggested 50 to 100% and 130 to 190% turnover per year of standing fine root biomass of Scots pine (*P. sylvestris*) on a poor site and more fertile site, respectively. Burton et al. (2000) estimated turnover rates of 0.50 to 0.68 per year in a sugar maple-dominated forest. While increased root turnover is another way of saying that a greater proportion of the root system is dying and being replaced, it does not always mean that a greater amount of carbon is being allocated annually to root production (Burton et al. 2000). Carbon allocation to root production instead depends on both the percentage of the root biomass that is replaced annually (turnover) and the total biomass of the standing crop.

Fine root turnover accounts for between 8 to 67% of annual net primary productivity (Grier et al. 1981; Keyes and Grier 1981). Therefore, fine root turnover can be an important source of carbon to soil systems and can contribute more carbon and nutrients to the soil than litter fall (Hendrick and Pregitzer 1992b; Hendrick and Pregitzer 1993b). Vogt et al. (1986) estimated that root mortality added 18 to 58% more nitrogen to soils than litter fall.

Categorization of Processes Effecting Turnover

Processes effecting root turnover can be grouped into three broad categories. The first category results from aboveground demands affecting carbon fixation and allocation (Bloomfield et al. 1996). Total root biomass is controlled, in part, by the source of carbon photosynthate (the leaves) and by competition between different sinks. Therefore, the reduction in biomass of feeder roots may be due to the reallocation of carbon in the roots to different parts of the plant. For example, foliage production, thinning of branches, defoliation, and prolific fruiting can cause significant reductions in biomass of feeder roots.

The second category of processes affecting root mortality and turnover relates to carbohydrate storage capacity (Bloomfield et al. 1996). Differences between young and mature plants illustrate this point. Roots of young seedlings are typically more sensitive to environmental changes than older plants (Bloomfield et al. 1996). The increased sensitivity of seedlings may relate to a lack of carbohydrate reserve. On the other hand, roots of mature trees have a greater store of carbohydrates to buffer against environmental stresses (Kramer and Kozlowski 1979). Longevity of larger roots may relate to the larger amount of carbohydrate reserves. Roots die when there is insufficient carbon to maintain the root (Marshall and Waring 1985).

The third category of processes effecting root turnover relates to soil nutrient, water, and oxygen availability, soil temperature, quantity of toxic elements, and fungal/microbial populations (Bloomfield et al. 1996). Other factors such as hormones, source-sink relations, photosynthesis-respiration balance, mycorrhizal infection, and insects and disease also affect root mortality and turnover (Kramer and Kozlowski 1979). Indeed the microenvironment of the site occupied by the root may also influence the site of root mortality (Bloomfield et al. 1996).

In addition to the categories affecting root turnover, Bloomfield et al. (1996) proposed two models to explain root longevity. In the first model, roots have an indeterminate life span and die when environmental factors are no longer favorable. Death of roots in unfavorable environments lowers maintenance costs for the plant and, thus, can be advantageous for the plant. According to Smucker (1984), respiratory costs of maintaining roots can be quite significant. In the second model, roots have a predetermined life span that is dependent upon a finite supply of starch/carbon. When the supply of starch is exhausted, roots will die (Marshall and Waring 1985). Therefore, root mortality and longevity depends on the plants' capacity to sustain root biomass (Psarras et al. 2000). Kinman [(1932) cited in (Lyr and Hoffman 1967)] suggested that fine roots die when base roots begin to form periderm.

Biotic Effects

In natural systems, fine root dynamics are highly variable and strongly affected by biotic factors (Jones et al. 2003). Early thoughts regarding root longevity were that fine roots lived typically only a few weeks and never longer than one growing season. However, root longevity depends upon many factors, including: species (Black et al. 1998), age/maturity (Black et al. 1998), size, and structural/functional class of the root (Srivastava et al. 1986). Srivastava et al. (1986) reported that turnover rate varies with size and that smaller roots have a quicker turnover than the larger roots. Additionally, root longevity can be influenced by the habit (e.g., evergreen or deciduous) of the plant, longevity being shorter in deciduous species than evergreen species (Black et al. 1998; Bloomfield et al. 1996). For example, after 14 days less than 60% of cherry (*P. avium* L.) roots and 94% of Sitka spruce roots survived (Black et al. 1998). After 63 days less than 8% cherry roots and 47% of Sitka spruce survived. Reid et al. (1993) reported that approximately 8% of kiwi (*Actinidia chinensis* C.S. Liang & A.R. Fergusson) roots survived more than 1 year. Hendrick and Pregitzer (1992a) reported mean age of roots at death in a sugar maple forest ranged between 5.5 and 10 months.

Root longevity is also affected by soil microorganisms (e.g., nematodes, insects, and fungi) (Bloomfield et al. 1996). Fogel (1985) estimated that consumption of fine roots by herbivores in temperate forests was up to 10% of the fine-root standing crop. Ectomycorrhizal infection was also reported to increase root longevity (Harley 1969; Harley and Smith 1983). However, colonization by arbuscular mycorrhizal fungi may also reduce root system longevity (Hooker et al. 1995). Temporal changes in mycorrhizal colonization occur (Sanders and Fitter 1992) and therefore, arbuscular mycorrhizal fungi may affect temporal changes in root longevity.

Abiotic Effects

In addition to the biological factors that influence root longevity, exposure to environmental stresses affect root longevity (Srivastava et al. 1986). Indeed, environmental factors can override genetic control of root turnover in plants (Brown and Scott 1984). However, the environment can only modify root growth and form within the genetic constraints of the species. Abiotic factors influencing root longevity include: soil temperature (Hendrick and Pregitzer 1993b; Jones et al. 2003), soil moisture (Joslin et al. 2000), soil fertility (Gaudinski et al. 2001), and pruning and defoliation in the canopy (Bloomfield et al. 1996; Head 1973; Srivastava et al. 1986). Increased soil moisture resulted in higher rates of production, mortality, and turnover (Jones et al. 2003; Joslin et al. 2000), as well as lower rates of production, mortality, and turnover (Santantonio and Hermann 1985). As well, method used to determine turnover rate may lead to different estimates of turnover rates (Gaudinski et al. 2001). Some authors (Hendrick and Pregitzer 1993a; Hendrick and Pregitzer 1993b; Pregitzer et al. 2000) suggested that high soil temperatures decreased root longevity. Burton et al. (2000) suggested that differences in root lifespan were related to variation in nitrogen availability in the same forests. Evidence exists for both increased (Keyes and Grier 1981; Pregitzer et al. 1993) and decreased (Nadelhoffer et al. 1985; Pregitzer et al. 1993) root longevity in fertile soils.

Roots often proliferate in soil sites where conditions are favorable (e.g., ample soil moisture and nitrogen) and die in sites where growth is unfavorable (Pregitzer et al. 1993). For example, red maple typically has shallow, wide-spreading root systems on wet sites; however, on dry sites red maple can form deep taproots (Bilan 1971). Hendrick and Pregitzer (1996) suggested deep root production was related to periods of high water demand.

Plants must be able to respond to changing environmental conditions in order to better forage for resources in a heterogeneous environment (Hutchings 1988). Therefore, roots have come to exhibit a morphological plasticity, via fine root turnover, that facilitates the proliferation of roots in favorable environments and the shedding of roots after a patch has been depleted (Pregitzer et al. 1993). Hendrick and Pregitzer (1992b; 1993b) reported that addition of nitrogen to a mixed hardwood forest resulted in a rapid increase in fine root production. Similarly, Gross et al. (1993) reported root proliferation in nutrient rich sites. Roots produced in response to increased moisture and nitrogen lived longer than roots of plants that were not given additional water and nitrogen, suggesting that root longevity is also responsive to changes in soil resource availability (Pregitzer et al. 1993). Similarly, research by Mäkelä and Vanninen (2000) suggested 50 to 100% and 130 to 190% turnover per year of standing fine root biomass of Scots pine on a poor site and more fertile site. Finally, Jones et al. (2003) reported that soil moisture and NO_3 mineralization rate were negatively related to pine root mass production and positively related to pine root length production, mortality, and turnover.

Fransen and de Kroon (2001) reported that root proliferation in nutrient rich patches resulted in the depletion of resources in the long-term and that proliferation of roots in nutrient rich patches may serve as a competitive mechanism by which plants whose roots proliferate quickly prevent neighboring plants from obtaining the nutrient resources, thereby reducing the competitiveness of the neighboring plant (Fransen and de Kroon 2001).

Several authors (Burton et al. 2000; Hendrick and Pregitzer 1993a; Kolesnikov 1971; Santantonio and Grace 1987) reported correlations between root production and mortality and seasonal conditions. Many forestry studies have shown modal or bimodal peaks of high live root biomass followed by periods of high dead root biomass (Hendrick and Pregitzer 1992a; 1993a). Peaks of high live biomass were reported to typically occur in the spring and fall. Drops in live root biomass were reported to occur primarily in summer and may result from high temperatures or low moisture levels (Lyr and Hoffman 1967; Teskey and Hinckley 1981). The decrease in summer live root biomass may also be a result of the greater carbon demand of the canopy, which results in the reduction of carbohydrate translocation or carbon allocation to the roots (Vogt et al. 1985). Many authors (Harris and Fanelli 1999; Lyr and Hoffman 1967; Mooney and Chu 1974) have reported root growth decreases during periods of high shoot growth.

Vogt et al. (1986) suggested that tree species growing in cool climates where soils don't typically freeze have greater root biomass than species of warmer climates or cooler climates where soils freeze for part of the year. Vogt et al. (1986) explained that in warm environments, root respiration limits the amount of carbon that can be turned into biomass. In climates where soils freeze, root growth is limited by freezing temperatures, and there is higher root mortality (Lyr and Hoffman 1967; Vogt et al. 1981). However, in cool climates where soils don't freeze, root growth can occur in the cool seasons when root respiration is reduced (Vogt et al. 1989) As a result, plants can accumulate more biomass at less physiological cost to the plant.

Measuring/Quantifying Root Turnover Rates

Studies of root production and mortality are hampered by high spatial and temporal variability, as well as the many fore-mentioned abiotic and biotic factors that affect root growth and mortality (Jones et al. 2003). High spatial variability is especially evident in trees due to the asymmetric, nonrandom distribution of tree root systems (Hendrick and Pregitzer 1992b). Additionally, Jones et al. (2003) cite problems relating to the spatial scale of observation (e.g., submeter scale vs. whole ecosystem scale). For example, on a small scale, root production and nutrient availability may be positively correlated (Jackson and Caldwell 1989; Mou et al. 1995; Pregitzer et al. 1993; Robinson 1994), while at the ecosystem level of scale (e.g., stand level) production and nutrient availability may be negatively correlated (Nadelhoffer 2000). Additional problems associated with measuring root turnover rates are due to the occurrence of simultaneous production and mortality of roots within a sampling interval (Hendrick and Pregitzer 1992a; Kurz and Kimmins 1987). Finally, turnover estimates can vary depending upon the method used to obtain the data (Tierney and Fahey 2002).

Factors such as root elongation, appearance of new roots, and weight accumulation have been used to determine root turnover rates (Bloomfield et al. 1996). Typically, however, fine root production and mortality are estimated from sequential changes in live and dead root mass, which renders the sampling unit unavailable for further study (Hendrick and Pregitzer 1993a). Therefore, new samples must be collected for each subsequent measurement, increasing the sampling variability by adding a spatial variability component (Hendrick and Pregitzer 1993a) that is a result of the asymmetric, nonrandom distribution of tree roots (Hendrick and Pregitzer 1992b).

By their nature, all root turnover studies also have a temporal variability component, which requires that production and mortality of roots between sampling dates be inferred by difference (Santantonio and Grace 1987). Using sequential cores, it was deduced that roots grow and die in “pulses” and that the “pulses” of growth and mortality are relatively independent (e.g., during the growth phase, there is negligible mortality and during the mortality phase there is negligible growth) (Mäkelä and Vanninen 2000). However, in instances of stable biomass levels over a season, sequential coring is not capable of accounting for growth and mortality simultaneously. Therefore, in order not to underestimate production and mortality, the frequency of the sampling interval must be increased in order to capture the pulses (Persson 1978). The large spatial and temporal variation in root biomass and necromass contribute to the problems of analysis and interpretation of data taken through sequential coring (Mäkelä and Vanninen 2000) and may result in the underestimation of mortality rates (Kurz and Kimmins 1987).

Tools such as the rhizotron and minirhizotron can be used to overcome some of the problems associated with techniques that rely solely on physical sampling of root systems. Rhizotrons and minirhizotrons provide a means to study root activity over extended periods of time in a nondestructive manner (Hendrick and Pregitzer 1993a). The small size and portability of minirhizotrons makes them particularly useful for field studies, where they have been used in both natural and agronomic ecosystems (Hendrick and Pregitzer 1993a). Major advantages of rhizotrons and minirhizotrons are that they provide a non-destructive means to collect data, which allows continuous observation of the same root or root system over a period of time. Additionally, qualitative data on root color, branching, growth direction, and responses to the environment can be collected (Böhm 1979). However, while rhizotrons and minirhizotrons may be useful for studying some aspects of root behavior, they cannot be used to measure physical properties of root systems such as biomass and nutrient content (Hendrick and Pregitzer 1993a). Other disadvantages of rhizotron studies include the difficultly in distinguishing between live and dead roots and the difficulty in viewing roots through windows that become occluded (e.g., in soils with high clay contents) (Böhm 1979). Additionally, the rhizotron window-soil interface does not perfectly replicate natural soil conditions (e.g., temperature, bulk density, moisture, and light conditions), which may influence rooting behavior (Bloomfield et al. 1996). Therefore, special precautions must be taken to reproduce natural soil temperatures (e.g., insulated wraps, protective covers, or mulching), to exclude light from the window (e.g., plastic or wooden doors), and to prevent air gaps from developing behind the windows.

Another consideration with rhizotrons is that when roots hit the window, they may grow along it rather than exploring the soil. However, Böhm (1979) stated that it “does not seem to be as serious as might be thought”. Rogers and Head [(1968) cited in (Böhm 1979)] reported that root growth behind windows was greatest in the first year after installation. Subsequently it is recommended that windows be installed months prior to the initiation of the experiment. Other considerations regarding rhizotrons are that only a small portion of the total root system may be observed (Harris et al. 1995) and that the window is spatially fixed. Root activity observed against the window therefore may not accurately represent the natural heterogeneity of the site.

The development of the radiocarbon (^{14}C) method has raised questions concerning accuracy of data obtained using minirhizotrons/rhizotrons (Gaudinski et al. 2001). The radiocarbon method uses of ^{14}C from the atmosphere to estimate fine root turnover (Tierney and Fahey 2002). ^{14}C is a naturally occurring radioactive isotope in the atmosphere that dramatically increased in the 1950's and 60's due to thermonuclear weapons testing (Tierney and Fahey 2002). In a study comparing turnover rates obtained via minirhizotron and radiocarbon methods, Tierney and Fahey (2002) determined that while the radiocarbon method underestimated turnover, the minirhizotron method overestimated turnover. The underestimation of turnover using the radiocarbon method stemmed from the false assumption that all roots had equal probability of dying, irrespective of age (Tierney and Fahey 2002). Instead, there is a decreasing probability of death as roots age. An additional problem related to the exponentially increasing ^{14}C in older roots. Minirhizotrons may overestimate turnover due to inflation of fine root production (Tierney and Fahey 2002). Similarly, Burton et al. (2000) reported that installation of minirhizotron tubes into soil and the resulting disturbance of the rhizosphere likely resulted in increased production against the minirhizotron tubes and subsequently inflated turnover rates.

Root activity has also been documented by mapping roots on grid paper or tracing the roots onto transparencies or overlays (Böhm 1979). More recently, photographs and video have been utilized to document root activity. When good contrast exists between roots and the soil, photographs can be analyzed by computer programs such as WinRHIZO (Régent Instruments, Inc., Québec, Canada).

There are also several indirect methods of measuring fine-root production and mortality, such as the litterfall ratio method (Nadelhoffer and Raich 1992), methods based on balancing nitrogen mineralization budgets (Aber et al. 1985; Nadelhoffer et al. 1985), and methods based upon depletion of starch reserves (Marshall and Waring 1985). The nitrogen budget method assumes that the forest of study takes up all mineralized and atmospheric inputs of available nitrogen, and that the measurement of nitrogen mineralization using the buried bag technique is accurate (Burton et al. 2000). The maximum-minimum live root biomass method uses the difference between the minimum and maximum annual fine root biomass to estimate production (McClaugherty et al. 1982). The min-max method depends upon examination of the physical changes in live and dead root biomass to estimate turnover and assumes that production and mortality do not occur simultaneously during the growing season (Burton et al. 2000). Thus, the min-max method likely underestimates root production and turnover (Burton et al. 2000). To handle the problem of root growth, mortality, and decomposition occurring simultaneously, Santantonio and Grace (1987) proposed the compartment-flow model to estimate fine-root production and turnover rates from biomass and decomposition data.

To conclude, while some sampling methods require less time than others, most are extremely time-consuming and tedious, particularly direct sampling methods (Mäkelä and Vanninen 2000). Each method has its own limitations and associated problems that must be considered before selecting the best method to employ (see previous Methods of Studying Roots section).

Methods of Calculating Turnover

Turnover rates are typically calculated as the annual production (N=total new root length) and mortality (D=total root length that disappeared or died) relative to standing crop (SC=standing root length) (Gill and Jackson 2000), where the sum of the total production and mortality over a sample period is divided by the mean fine root standing crop (Jones et al. 2003). Others have similarly calculated turnover as the average of production and mortality relative to standing crop (Burton et al. 2000; Hendrick and Pregitzer 1993a). Additionally, annual production (Burton et al. 2000; Hendrick and Pregitzer 1993a) or mortality (Burton et al. 2000) relative to standing crop have been used. Finally, Burton et al. (2000) used the ratio of production to mortality as an index of activity in the plants. Production was the sum of all increases in fine root length (e.g., production of new roots and elongation of existing roots) at a single microsite over the duration of the study, while mortality was the sum of all live root length decreases (Jones et al. 2003). Jones et al. (2003) calculated mean standing crop as the average of all weekly measures. Depending on the formula used to calculate turnover, very different rates will be obtained. For example, Hendrick and Pregitzer (1993a) estimated that root turnover in a sugar maple-dominated forest ranged between 0.83 and 0.79 per year using N/SC and 0.76 and 0.66 per year ((N+D)/2)/SC.

The inverse of median fine root longevity has also been used to estimate root turnover (Burton et al. 2000). However, estimates of turnover based on median longevity assume that fine root biomass is at steady state and that fine root age is normally distributed (Fahey et al. 1999; Hendrick and Pregitzer 1992a). Therefore, estimates based on median root lifespan will only be accurate if the rate of mortality remains relatively constant until all roots have died (Burton et al. 2000).

Psarras et al. (2000) calculated turnover as a daily rate by dividing the number of roots that disappeared between consecutive observations in each minirhizotron tube by the elapsed time (in days) between these two observations [turnover = (# dead per interval) / (# days per interval)]. Tierney and Fahey (2002) calculated root turnover by determining the fraction of total fine root length produced annually within four diameter classes, predicting percent annual mortality within each class or cohort, converting root length to biomass for each diameter class, and summing the percent mortality.

Review of the Research Regarding Root Production and Mortality

In a study assessing the patterns of root growth, maturation, turnover, and respiration in 'Mutsu' apple on 'Malling 9' rootstock, Psarras et al. (2000) determined that negligible root growth occurred prior to shoot growth in mid May. New root emergence began in early June. Rate of root emergence peaked late June to early July, declined until late August, and remained low throughout the end of the growing season. Root turnover rates increased as root emergence rate declined and peaked in late August. An additional period of new root emergence occurred in August and September 1997. The cumulative survivorship of new roots was 38 and 64% in 1996 and 1997, respectively. All new white roots turned brown and/or died prior to the end of their first growing season and 50% turned brown and/or dieed within 25 and 19 days of emergence in 1996 and 1997, respectively. While 38% of new 1996 roots were present in late October 1996, 64% of the new 1997 roots were present in late October 1997.

Burton et al. (2000) reported that in a sugar maple-dominated northern hardwood forest, root production and mortality occurred throughout the year and that most production occurred by mid July. Peak root production occurred in June and July. 42% of annual fine root production occurred by late June (1-1.5 months after leaf emergence) and 36% of the annual production occurred in late May and June alone. Less than 5% of annual root production occurred between November and March. Burton et al. (2000) also reported that fine root production in the surface soil (0-10 cm) was 3.5 times greater than at 20 to 30 cm, and 9.2 times greater than at 40 to 50 cm below the surface. Mortality was more evenly distributed throughout the year compared to production and did not occur at the same time of year at all sites. Root mortality was greatest between May and August and occurred at a similar time as maximum root growth. Unlike root production, significant mortality occurred in winter. Median lifespan (i.e., days to 50% mortality) of root cohorts produced in 1994 ranged between 405 and 540 days. Median root lifespan of individual cohorts ranged between 74 and > 500 days, however, most cohorts had a median lifespan of 300 days.

Burton et al. (2000) found that estimates of turnover calculated using annual rate of production were greater than those calculated using annual rate of mortality. This was due to production exceeding mortality. The greater production indicates that the minirhizotron tubes and the surrounding soil had not fully equilibrated. Following rhizosphere disturbances during minirhizotron installation, equilibrium must be established between the tubes and the adjacent soil. As roots recolonize the soil, annual production and mortality should come into an approximate equilibrium, meaning that production must decrease or mortality must increase, or both. Therefore, standing root length against the tube will increase. Burton et al. (2000) reported that the ratio of production to mortality declined from 2.0 in the first year to 1.4 in the second year as the equilibration process proceeded. They concluded that ratios of annual production to standing root length are likely to overestimate turnover, and ratios of mortality to standing root length are likely to underestimate turnover.

Estimates of fine root turnover, based on average annual root production and mortality as a proportion of standing crop in the sugar maple-dominated forest, ranged between 0.50 and 0.68 per year for roots in the upper 30 cm of soil (Burton et al. 2000). They concluded that root longevity and turnover did not correspond to temperature but instead to site differences in nitrogen availability. Longer average root lifespan and lower turnover rates corresponded to increased nitrogen availability, suggesting that roots are maintained as long as the benefit (nutrients) they provide outweighs the carbon cost from respiration of keeping them alive. They also determined that root nitrogen concentrations and respiration rates were higher at sites with increased available nitrogen, suggesting that greater metabolic activity of roots in nitrogen-rich microsites results in greater carbohydrate allocation to roots in the site. They proposed that a reduction in root carbon sink strength occurred when local nutrients are depleted, thereby providing a mechanism through which root longevity is regulated.

Hendrick and Pregitzer (1993a) observed in two sugar maple-dominated forests that over 50% of annual length production occurred prior to midsummer, and that the period of greatest mortality occurred between late summer and winter, with 25 to 40% of total root mortality occurring between October and April. One-third of annual fine root production and mortality in sugar maple occurred simultaneously, resulting in little observable change in total root length (Hendrick and Pregitzer 1993a). Hendrick and Pregitzer (1993a) suggested that the increase and decline in root length were linked to phenological and physiological events occurring in the canopy (i.e., substantial increases in root length occurring as the canopy flushes in late spring). Maximum root length occurred in midsummer when evaporative demands were high and soil moisture was low. A decline in fine root length occurred at the onset of seasonal canopy senescence and leaf fall.

Hendrick and Pregitzer (1993b) reported on root turnover in a sugar maple-dominated forest and suggested that warmer soil temperatures were associated with shorter root lifespans. Similarly, other authors (Amthor 1984; Lawrence and Oechel 1983; Marshall and Waring 1985) reported a correlation between higher soil temperatures and increased root respiration rates. Faster root turnover rates and low winter mortality, relative to growing season mortality, might be due to low maintenance respiration rates in cold soils (Hendrick and Pregitzer 1993b). Higher soil temperatures are not only associated with increased maintenance costs and mortality rates (Hendrick and Pregitzer 1993b), but also with increased activity of soil organisms, which can shorten root longevity (Head 1973).

Research of Jones et al. (2003) on fine root dynamics in overstory and understory gaps in a pine (*P. palustris* Mill.) woodland determined that when understory vegetation was removed, pine root production compensated for reductions in non-pine roots and pine roots. Additionally, understory roots were highly plastic and able to quickly close belowground gaps when the overstory plants were removed. As a result, total growth of pine plus non-pine roots was nearly constant. The 1:1 replacement of pine and non-pine roots across the overstory density gradient and the compensatory growth of pine roots when non-pine roots were artificially removed and suggest a resource-controlled carrying capacity for roots. In other words, the observed compensatory growth reflected an upper limit set by available resources on the belowground density of roots. Jones et al. (2003) suggested that belowground gaps close quickly because root systems of both the overstory and understory plants are highly plastic and capable of rapid response to disturbance.

Jones et al. (2003) concluded that soil moisture and net NO_3 mineralization had the strongest influence on roots in their study, and soil resources and soil temperature had weaker influences. Increased moisture or net NO_3 mineralization resulted in accelerated production, mortality, and turnover (i.e., reduced lifespan) of roots. The authors suggested that plasticity of root response to soil moisture might act to optimize water uptake due to younger, finer roots having greater absorptive capacity and being more efficient than older roots (Eissenstat and Yanai 1997). Similarly, Jones et al. (2003) proposed that root response to NO_3 was a result of young roots having increased potential for nutrient uptake. Therefore, regulation of lifespan could be an adaptive mechanism of pine to maximize uptake in favorable sites. Alternatively, Jones et al. (2003) proposed that reduced root lifespan might be a result of the increased cost associated with uptake and utilization of NO_3 compared to NH_4. Finally, they reported that stand-level results were consistent with previous reports that growth, mortality, and root density increase as soils warm. During cold months productivity and standing crop declined, while during warm months production and standing crop increased.

Kolesnikov (1971) observed that root biomass in gooseberry increased prior to shoot growth. Root mortality increased in older roots (roots produced during the fall of the previous year) at bud break, was greatest during the period of fruit ripening, and decreased after leaf fall. Kolesnikov (1971) identified drought, low oxygen levels, and temperature extremes as factors that increased root mortality. Similarly, Lyr and Hoffmann (1967) suggested that frequent root regeneration occurred as a response to a large fraction of the fine roots being killed periodically by drought or frost, especially in the upper soil layers. Santantonio and Grace (1987) observed in a New Zealand pine plantation that production and mortality peaked in early spring, fell to near zero in summer, and was out of phase with soil temperature at 10 cm. On the other hand, decomposition peaked in early summer, declined to low levels in winter, and was in phase with soil temperature.

Seasonal Effects of Transplanting

Season of transplant is important in two regards. First, season dictates the stage of growth that the plant is undergoing (Harris et al. 1999). Second, seasons correspond to characteristic weather for the specific times of year, which ultimately affect plant growth. While many studies concluded fall planting to be superior to spring planting (Alm 1983; Buckstrup and Bassuk 2000; Harris and Bassuk 1994; Harris et al. 1996; Hinesley 1986; Watson and Himelick 1983; Whitcomb 1984a; Witherspoon and Lumis 1986), other studies concluded fall planting to be inferior (Buckstrup and Bassuk 2000; Harris and Bassuk 1994; Larson 1970; Watson et al. 1986) or have no advantage to spring planting (Harris et al. 2001; Watson and Himelick 1982; Watson et al. 1986). Harris et al. (1999) reported that conifers were commonly transplanted in early fall or late spring and broad-leaved evergreens were commonly planted as growth resumes in spring. Additionally, they reported that transplanting of deciduous trees in temperate climates was easiest in the fall, after leaves have changed color or fallen and before the soil freezes or spring before growth resumes. Lists of species that transplant best in fall and species that transplant best in spring have been complied (Gilman 1997; Schein 1993; Watson and Himelick 1997). Additionally, Dirr (1998) provides recommendations for some species.

While season certainly affects transplant success, many other factors also contribute to the successful establishment of transplanted trees. For example, species variation accounts for some of the responses to transplant during different seasons (Harris and Bassuk 1994; Watson et al. 1986). Other factors influencing transplant success include habit of the plant (e.g., conifer or broad-leafed evergreen) (Harris et al. 1999), pre-planting preparation, soil preparation, planting technique (Acquaah, 1999), post-transplant practices, soil type, site conditions, environmental conditions (e.g., weather, moisture), and production, harvest and handling methods (Buckstrup and Bassuk 2000). The ability of harvested root systems to supply adequate moisture to newly transplanted trees is also a determining factor in transplant success (Harris et al. 1996). Larson (1970) suggested that differences in seasonal effects may be related to root regeneration and bud dormancy, with the greatest root regeneration occurring after chilling requirements for dormancy release have been fulfilled. Despite initial differences between growth of trees transplanted in different seasons, many of the differences in growth between fall- and spring-transplants are overcome after a few years (Buckstrup and Bassuk 2000; Vanstone and Ronald 1981; Watson et al. 1986).

Advantages and Disadvantages of Transplanting Trees During the Different Seasons

Due to favorable conditions, such as increased soil moisture and cooler temperatures and the associated reduced potential for desiccation, fall and spring are often considered to be the best time for transplanting (Harris and Fanelli 1999; Himelick 1981; Watson et al. 1986), particularly if post-transplant care is expected to be minimal. In addition to favorable environmental conditions, many woody plants have two distinct periods of active root elongation that correspond to these favorable conditions, one being in spring and one in fall (Cripps 1970; Deans 1979; Deans and Ford 1986; Dell and Wallace 1983; Harris et al. 1995; Harris and Fanelli 1999; Roberts 1976; Stone et al. 1962; Stone and Schubert 1959; Wargo 1983).

Advantages of fall transplanting include an increased opportunity for trees to regenerate roots prior to shoot growth in spring, more time to develop contact between the roots and soil (Buckstrup and Bassuk 2000), more time to acclimate to the physiological stresses of transplanting before shoots resume growth in spring (Harris and Fanelli 1999), and more time for physiological processes involved with regeneration of roots following the transplant process to get a “head start” (Harris et al. 1996). As a consequence, fall transplanting may result in increased pre-bud break root growth and a larger root system, which can access a greater soil water reservoir to support shoot growth the following spring (Harris and Fanelli 1999; Harris et al. 1996). However, Hinesley (1986) proposed that spring transplanting might interfere with production of root-produced hormones involved in shoot extension. While fall transplanting is recommended in many regions, late-fall transplanting is not advised in climates with severe winters (Harris and Bassuk 1994).

For many species, spring conditions (e.g., ample soil moisture, warm soils) provide optimal conditions for root growth and tree establishment (Acquaah 1999). Cool spring air temperatures also minimize transpirational losses, which help minimize transplant shock. Additional advantages of spring transplanting (prior to bud break) include the avoidance of damaging cold weather and the possibility for root growth prior to bud break. However, spring transplanting at or just prior to bud break is usually ill advised (Dumbroff and Webb 1978; Farmer 1975) and can result in poor root regeneration and growth (Watson and Himelick 1982). For example, Norway maples and green ashes transplanted at bud swell and just prior to bud swell had poor root regeneration and growth (Watson and Himelick 1982).

Many authors cautioned against transplanting in late spring or summer when shoots are rapidly elongating (Dumbroff and Webb 1978; Farmer 1975; Harris et al. 1999; Watson and Himelick 1982; 1983) due to competition between roots and shoots for available carbohydrates and other growth factors (Lathrop and Mecklenburg 1971; Watson and Himelick 1983), and the resulting suppression of root regeneration (Dumbroff and Webb 1978). Watson and Himelick (1982) suggested that the carbohydrate status of root tissue was a limiting factor for root growth when trees are planted during the period of spring shoot growth, a time when total nonstructural root carbohydrates are low. Additionally, they concluded that the period of spring shoot growth was the only time when transplanting “appeared to have a major impact on root regeneration”. Despite the warnings against late spring and summer transplanting, research of Watson et al. (1986) indicated that many species grew more when transplanted in late spring or summer compared to early spring or fall. For example, May-transplanted redbuds (*Cercis canadensis* L.) and July-transplanted Norway maples (*A.platanoides* L.) had greater twig growth than trees transplanted in other months

(Watson et al. 1986). Consequently, Watson et al. (1986) supported “judicious transplanting during summer months”.

Summer transplanting is generally not recommended because of the associated high temperatures, intense insolation, high transpirational losses (Acquaah 1999), potential for drought stress, and risks associated in working with non-dormant plants (i.e., susceptibility to drying and other stresses) (Hinesley 1986). While irrigation is desirable for all transplanted trees, regular irrigation gains a higher level of importance for summer transplants. Despite the negative aspects, advantages of summer transplanting are warm soil and air temperatures, long daylength, and fully developed tree crowns, which produce the carbohydrates necessary for root regeneration (Watson et al. 1986). Some authors recommend the use of antitranspirants or stripping of leaves to reduce the transpirational demand imposed on the tree (Harris et al. 1999).

Benefits of late summer and early fall transplanting include diminished shoot growth, lignification of newly formed tissues, and decreased transpirational demand, which correspond to the short, cool days of fall (Harris et al. 1999). Additionally, late summer and early fall transplanting provide the opportunity for root regeneration to proceed during a time characterized by reduced water stress and allows the establishment of a root system prior to the onset of winter (Hinesley 1986). The regeneration of roots prior to the next shoot growth period (spring) translates to a larger absorbing system capable of better supporting the next flush of spring shoot growth (Watson et al. 1986) and increased vigor (Hinesley 1986).

Research of Watson et al. (1986) provided support for summer transplanting of several species as long as sufficient soil moisture and adequate maintenance were provided, leading the authors to conclude “no general trend emerged to support the commonly held belief that spring and fall are best for transplanting” and “to the contrary, several species performed better when transplanted in late spring and summer”. Hinesley (1986) also concluded late summer and early fall to be the best time to transplant (assuming adequate moisture) and proposed that drought stress and/or an interference with the balance of root-produced hormones involved with normal shoot extension might be responsible for poor growth of spring transplants.

Advantages of winter transplanting are reduced desiccation potential because of cool temperatures, reduced activity in the roots and shoots, and ease of moving frozen root balls (for those species that can withstand being frozen) (Harris et al. 1999). In mild climates plants can be transplanted throughout winter. Disadvantages of winter transplanting include risk of desiccation and cold injury in very cold temperatures (Harris et al. 1999), possibly due to increased hydraulic resistance across roots at temperatures below 45 F (Running and Reid 1980). Harris et al. (1999) caution against moving plants on extremely dry, windy, hot or cold days. As an interesting note, night transplanting was suggested to protect the microorganisms that promote root growth and protect against solar radiation and desiccation.

Research Concerning Season of Transplant

Recently, Buckstrup and Bassuk (2000) compared transplant success of fall- and spring-planted hackberry (*Celtis occidentalis* L.), American hophornbeam [*Ostrya virginiana* (Mill.) K. Koch.], and swamp white oak (*Q. bicolor* Willd.). Half of each species were balled-and-burlapped (B&B) and half were bareroot trees that were dipped in hydrogel, a water-absorbing polymer. After the first year, spring-planted B&B hackberry had slightly greater growth than the corresponding fall-planted B&B trees. However, fall-planted bareroot hackberry had better growth than spring-planted bareroot trees. While little difference was detected between spring- and fall-planted B&B hophornbeam trees after the first year, fall-planted bareroot trees outperformed the spring-planted counterparts, which had a 50% survival rate, after the second year. Fall-transplanted swamp white oaks grew better than the spring-planted oaks, regardless of the production method. However, Buckstrup and Bassuk (2000) found that while the first-year results yielded significant differences among treatments, little difference existed between spring- and fall-transplant treatments after the second growing season.

Lathrop and Mecklenburg (1971) studied the root regeneration potential of yew 6 weeks after transplant in plants that were transplanted at 2-week intervals throughout the year. Few root initials were produced in summer transplants and root regeneration potential increased throughout the fall, peaking in the January. Root regeneration potential decreased throughout the spring and early summer. The decrease in root regeneration potential in spring and early summer corresponded to an increase in shoot growth. The authors proposed that the decrease in root regeneration potential in spring and early summer was due to increased competition between shoot and root growth for available carbohydrates and other growth factors. However, the decrease in root regeneration potential after shoot growth ceased in summer was not due to competition between roots and shoots since shoots were not elongating. They concluded that additional factors other than root dormancy must regulate root regeneration potential.

Larson (1984) studied the effects of seasonal planting on root regeneration and water deficit of Austrian pine (*P. nigra* Arn.) and arborvitae (*Thuja occidentalis* L.) in northern Ohio. Three-year old Austrian pine and arborvitae seedlings were transplanted in mid October (early fall), mid November (late fall), and late April (spring). Survival of Austrian pine 1 year after transplant averaged 15, 60, and 91% for the early fall, late fall, and spring treatments, respectively. Root regeneration 4 weeks after planting was determined for each treatment. Similarly, Stone and Schubert (1959) found fall-planted pine seedlings to be in poor physiological condition to regenerate roots. Percent of Austrian pine seedlings that regenerated roots within 4 weeks of planting was 12, 29, and 60% for the early fall, late fall, and spring treatments, respectively. Larson suggested that poor survival of fall-transplanted Austrian pines was due to poor root regeneration and excessive needle water deficit, which may be an indicator of seedling vigor and likelihood of survival. High needle water deficit was associated with poor root regeneration, which may be a consequence of an inability of the root system to supply adequate moisture to the shoot, resulting in a water deficit.

Difference in survival rate between the spring and fall planted arborvitae was insignificant and averaged 94% for all treatments (Larson 1984). Fewer fall-planted arborvitae regenerated roots compared to spring-planted trees; however, both had at least good root regeneration. While little difference was found between treatments with regard to root regeneration, fall-planted trees averaged 22% less height growth compared to spring transplants. In conclusion, Larson explained the seasonal effects of transplant by proposing that root regeneration was related to bud dormancy, and that the greatest root regeneration potential occurred when the chilling requirements for dormancy release were fulfilled.

Research of the effects of transplanting during March, May, July, or October on tree vigor (determined by annual twig growth) of eight tree species revealed a significant reduction (22 and 38%) in twig growth for the first and second years (and in several species the third year) following transplanting (Watson et al. 1986). However, by the fifth season, annual twig growth of most species exceeded pre-transplanting growth rates and little difference existed between transplant treatments. Watson et al. (1986) concluded that transplant date had no consistent effect on vigor (as indicated by total twig growth) after 5 years and that the minor differences between the different seasons would not be useful in the development of general recommendations for all trees. Subsequently, no general recommendations on best season for transplanting trees in Illinois could be made and instead, only species-specific recommendations could be made.

In the same study, Watson et al. (1986) determined that July-transplanted sugar maples had much greater twig growth after 4 years compared to the May and October-transplanted sugar maples and that mean twig growth equaled twig growth prior to transplant in the fifth year after transplanting. The authors suggested that the July transplant treatment may have faired better due to the ability of the July transplanted trees to regenerate roots for several months before the next shoot growth period, which resulted in a larger root system better able to support spring shoot growth the first year after transplanting.

Assuming sufficient soil moisture was maintained, the July transplant treatment surprisingly resulted in the greatest growth for several species when compared to the other transplant dates (Watson et al. 1986). Concluding, the authors stated, “no general trend emerged to support the commonly held belief that spring and fall are best for transplanting” and “to the contrary, several species performed better when transplanted in late spring and summer” as long as adequate maintenance of the trees is provided. Similarly, other research concluded that season had little influence on root regeneration if adequate soil moisture is maintained (Watson and Himelick 1982).

In a study comparing root growth of Norway maple, green ash, and ginkgo (*Ginkgo biloba* L.) following transplant, Watson and Himelick (1983) reported that season of transplant influenced root growth of only the March-transplanted Norway maples, which were in the early stages of shoot elongation and whose carbohydrate levels were low. In contrast, March-transplanted green ash had not yet begun shoot expansion, which resulted in lessened competition for carbohydrates between the roots and shoots. Subsequently, root regeneration of the March-transplanted green ash during the first year was similar to that of trees transplanted during the other seasons. Because shoot expansion occurs earlier in Norway maple, the March transplant time resulted in increased competition between the roots and shoots. The authors proposed that competition between the roots and shoots for available reserves resulted in a reduction of resources available for root growth. Thus, little competition for resources existed between the roots and shoots of green ash, and substantial competition existed in Norway maple. May-transplanted Norway maples, which were transplanted after shoot elongation was complete and photosynthate production was occurring in the leaves, exhibited no suppression of root regeneration (Watson and Himelick 1983). They concluded that trees should not be transplanted during periods of active shoot growth and elongation.

Watson and Himelick (1982) studied root regeneration of Norway maple, green ash and ginkgo trees that were transplanted in March, May, July and October. Research revealed that regenerated root initials developed primarily from severed root ends and that Norway maple had the greatest capacity for root regeneration compared to ginkgo and green ash. Similarly, other authors [(Bushey 1946; Wilcox 1955) both cited in (Watson and Himelick 1982)] reported root regeneration occurring near the severed ends.

When 3-year-old Fraser fir seedlings were transplanted at 2-week intervals between 1 August and 15 October and once prior to bud break in spring in western North Carolina, Hinesley (1986) found that seedlings planted in August and early September had significantly greater growth (dry weight, stem diameter, and shoot elongation) than seedlings planted after mid-October. He proposed that the reduction in growth of spring transplants was due to drought stress or interference with the balance of root-produced hormones involved with normal shoot extension. Assuming adequate soil moisture, seedlings planted in late summer or early fall grew better than seedlings planted in the spring. Hinesley (1986) cautioned that late summer or fall planting might be more risky because plants are not dormant at the time of transplant and are, thus, more susceptible to drying and other stresses. However, with adequate irrigation and minimal root drying, fall planting allows the establishment of the root system to occur prior to winter, which acts to minimize frost heaving and increase vigor and growth the following season.

Witherspoon and Lumis (1986) determined that in Ontario, root regeneration of littleleaf linden (*Tilia cordata* Mill.) was greatest in fall-dug, fall-planted bareroot trees compared to other digging/planting time combinations. Therefore, the authors concluded that fall was the best season to transplant bareroot littleleaf lindens.

Harris et al. (1996) established that in southwest Virginia, B&B fringetree (*Chionanthus virginicus* L.) transplanted more successfully in fall than spring. Trees transplanted in early fall (11 November) had wider canopies and greater leaf area the following summer than the trees transplanted in late fall (1 December) and spring (14 March). Additionally, early fall-transplanted trees had more root growth after one growing season than the late fall- or spring-transplanted trees. Spring-transplants had the least total leaf area, leaf dry mass, and root extension into the backfill soil. Root growth outside of the original root ball did not occur in any treatment until early July (1 month after bud set). The authors suggested that the lack of root growth prior to bud break in fall-transplanted trees was a result of transplant shock in the fall and low soil temperatures in the spring. Due to the lack of root growth outside of the root ball, the authors cautioned that irrigation needed to be focused on the root balls the first-season after transplant.

In a study comparing the effects of fall and spring harvest and transplant dates on first-season root, shoot, and trunk diameter growth in Turkish hazelnut, Harris et al. (2001) reported that root growth of early fall-transplanted trees began before root growth of spring-transplanted trees. Root growth began 1 to 2 weeks prior to bud break in fall-harvested and planted trees (F-F) and fall-harvested and spring-planted trees (F-S), while in spring-harvested and planted trees (S-S) root growth began 3 weeks after bud break. No new root growth was observed before spring in the fall-harvested treatments. While root growth was delayed for S-S trees, the rate of growth was similar to F-F and F-S trees after root growth began. Finally, height, trunk diameter and root growth were similar for all treatments.

Another study addressing early root system regeneration of sugar maple and northern red oak determined that October-transplanted trees began root regeneration earlier and regenerated more roots in the first-season post-transplant than the November- and March-transplanted treatments (Harris et al. 2002). While the October-, November- and March-transplanted sugar maples began root extension 48, 22, and 0 days before bud break, the October-, November- and March-transplanted red oaks began root extension 4, 21, and 14 days after bud break. Little difference in height and trunk diameter growth between transplant dates was found within each species over the three following years. The authors concluded that in regions with comparable climates, early fall transplanting results in earlier post-transplant root growth which would "likely increase resistance to stress imposed by harsh landscape environments".

Establishment of Transplanted Pot-In-Pot and Field-Grown Trees

Woody landscape plants are typically sold as bareroot, container, or balled-and-burlapped (B&B) plants. Few studies have been conducted that directly compare the establishment of B&B and pot-in-pot (PIP) system (Ruter 1997). Therefore, studies regarding the establishment of trees grown by either B&B and/or PIP production methods were reviewed. While some authors suggested that field-grown, B&B (or tree-spade-harvested) trees grew better than bareroot or container trees (Buckstrup and Bassuk 2000; Gilman 1994; Magley and Struve 1983; Vanstone and Ronald 1981), other authors concluded that bareroot trees grew equally well or better than B&B or container trees (Buckstrup and Bassuk 2000). On the other hand, other authors (Harris and Fanelli 1999; Walker and Johnson 1980) suggested that container trees transplanted better/established quicker than B&B or bareroot trees. Many of the differences in transplant success can be accounted for by species and age differences.

The B&B method of moving trees has been common for centuries, particularly for evergreens (Harris et al. 1999). Typically, B&B trees are field-grown and dug by hand or with a mechanical harvester (tree spade) so that a portion of the root system is contained within a ball of soil (Harris et al. 1999). After the root ball has been dug, it is covered with burlap or other material that is tied in place with rope lacing or wire netting. Usually, tree spades produce soil balls that are narrower and deeper than hand-dug soil balls and often contain fewer feeder roots (Preaus and Whitcomb 1980). However, despite whether trees are dug by hand or tree spade, a considerable amount of root tips and root length is lost (Preaus and Whitcomb 1980). Gilman (1997) determined that transplant success of hand-dug B&B trees was comparable to trees dug and moved using a tree spade.

Transplanting B&B trees has typically been viewed as lower risk than transplanting bareroot trees, which are subject to greater post-transplant stress due to desiccation of roots (Buckstrup and Bassuk 2000). Typically, B&B trees also have a longer planting season than bareroot trees; however, B&B trees should still be planted before late spring (Harris et al. 1999). As a rule, the diameter of the root ball should be 10 to 12 times the trunk diameter at 15 cm above the soil line and since most of the roots are in the upper soil layers, root ball depth need not increase proportionally (Harris et al. 1999). Harris et al. (1999) recommended pruning the roots 1 to 2 years prior to transplanting in order to promote root branching within the root ball. Since roots rarely extend through large air spaces, gaps between the root ball and planting hole are thought to restrict root development (Preaus and Whitcomb 1980). Preaus and Whitcomb (1980) and Gilman (1997) reported little difference between the establishment of hand-dug B&B and tree spade-harvested trees as long as intimate contact is made between the root ball and side of the planting hole. Additionally, glazing of both the exterior layer of soil surrounding the root ball and the soil on the surface inside the planting hole can limit root growth into the adjacent soil and impede normal movement of moisture in the soil (Preaus and Whitcomb 1980).

After World War II, a new method of producing woody plants emerged in southern California, whose unique climate allowed woody plants to be grown in containers outdoors (Whitcomb 1984b). Over the next 20 years, container production of woody plants spread throughout the southern United States. Advantages of producing woody plants in containers include: individual control over seedling growth, mechanization of operations, reduction of planting shock, extended seasons for outplanting, greater control in tree improvement programs, ability to sell plants in full leaf, reduction in weight of the root ball, and minimal mess for the homeowner (Spencer 1981; Whitcomb 1984b). According to Walker and Johnson (1980), plug-type container stock has a better chance of survival than bareroot stock, especially during the hot summer months of July and August. Disadvantages of containerized plants include increased vascular constrictions associated with deformed roots (Gilman and Kane 1990), and the limited time that a plant can be grown in a particular container (Whitcomb 1984b). The length of time that a plant remains in a container will affect eventual root form (Gilman and Kane 1990). The PIP system is a modification to the standard container production system. In the PIP production system, trees are grown in pots that are placed in “socket pots” sunken in the ground. Advantages of the PIP production system include less tipping and greater thermostability.

Harris and Fanelli (1999) reported that one advantage of transplanting container-grown trees vs. B&B or bareroot trees during the growing season is the significant amount of root growth that can occur after bud set while the tree is in full leaf. They cautioned that due to the significant root loss associated with B&B or bareroot plants, trees transplanted during the growing season are likely to experience greater transplant shock unless considerable post-transplant care (e.g., irrigation) is provided to the trees.

Research Pertaining to Establishment of Balled-and-Burlapped and Pot-in-Pot Trees

In a recent study, Buckstrup and Bassuk (2000) compared transplant success of B&B and hydrogel-dipped bareroot hackberry, American hophornbeam, and swamp white oak, half of which were planted in the fall and half of which were planted in the spring. They determined that while first-year results yielded significant differences among treatments, by the second year little difference existed between B&B and bareroot treatments. After the first year, fall-transplanted bareroot hackberry grew better than the corresponding B&B trees. However, spring-planted B&B hackberry had greater shoot growth and less dieback than the spring-planted bareroot trees. While no difference was detected between fall-planted bareroot and B&B hophornbeam after the first year, spring-planted B&B trees grew better than bareroot trees. For swamp white oaks planted in both seasons, B&B trees grew slightly better than bareroot trees. Fall-transplanted swamp white oaks grew better than their spring-planted counterparts, regardless of B&B or bareroot. They also studied the impact of drought on spring-planted B&B and bareroot swamp white oak. Results indicated little difference between treatments (B&B vs. bareroot) in ability to cope with drought stress. Subsequently, the authors concluded that no advantage existed between the production methods.

A comparison of growth between bareroot green ash, black ash (*F. nigra* Marsh.), and hackberry trees and tree spade-harvested trees revealed greater shoot growth of tree spade-harvested plants after one growing season (Vanstone and Ronald 1981). However after two growing seasons, there was no significant difference between growth of bareroot and tree spade-dug trees. Similarly, research of Magley and Struve (1983) revealed greater shoot growth of 7 to 8 cm caliper pin oaks that were harvested with a tree spade compared to similarly sized bareroot (*Q. palustris* Münchh.) pin oaks.

In a 4-year study, Hensley (1986) evaluated growth of B&B, bareroot, and fabric-bag produced green ashes and found little difference in growth (height, caliper, and root dry weight) between the three production methods. However, Heisler et al. (1982) concluded that bareroot 'October Glory' red maples and 'Marshall Seedless' green ashes grew better than B&B trees when planted in parking lot tree pits.

Gilman and Beeson (1996a) determined that while more than 90% of coarse (>10 mm) root weight was within the confines of the root ball of field-grown trees, less than 15% of the fine, absorbing root weight (<2 mm) was within the confines of the root ball. In contrast, all of the roots of container plants are within the confines of the container. Subsequently, little root weight or length is lost during the transplant process of containerized plants and as a result, container-grown trees suffered less moisture stress compared to field- and bag-grown trees. The significant loss of roots experienced by field-grown trees during harvesting translates to less moisture absorbing surfaces and increased risk of moisture stress.

Post-transplant Root Regeneration

Roots systems function to provide anchorage, absorb water and nutrients, store food reserves, and synthesize organic materials, which participate in the regulation of shoot activity (Harris et al. 1999). As well, roots are where most food reserves are stored, where some shoot growth regulators are synthesized, and where inorganic nitrogen is converted into organic amides and amino acid compounds (Wargo 1983). The root system of most trees extends well beyond the edge of the crown (Watson and Himelick 1997). As a result, when trees are harvested for transplanting, only a small portion of the root system is moved with the tree (Watson and Himelick 1983) and most of fine, absorbing roots are lost. Watson and Sydnor (1987) reported that root balls dug according to the American Association of Nurserymen standards contain approximately 5 to 18% of the original fine roots. Gilman (1988) reported less than 10% of total root length of the original root system was contained within the root balls of harvested field-grown trees. Watson and Himelick (1983) reported that in some instances, as little as 2% of the root system was moved with the transplanted trees.

Large-diameter roots contribute disproportionately more weight relative to surface area than small diameter roots. Gilman and Beeson (1996a) determined that while more than 90% of coarse (>10 mm) root weight was within the confines of the root ball of field-grown trees, less than 15% of the fine, absorbing root weight (<2 mm) was within the confines of the root ball. As a consequence, newly transplanted trees must be supported by only a small fraction of the original absorptive surfaces. In contrast to the significant loss of roots that occurs when trees are dug from the field, all of the roots of container plants are within the confines of the container and thus little root weight or length may be lost during transplant. As a result, when field- and bag- and container-grown trees are transplanted, container-grown trees are less likely to suffer moisture stress.

When the root:shoot ratio is altered due to pruning in the canopy or root pruning (e.g., harvesting for transplant), the root:shoot ratio is restored by compensatory growth of the severed organ (Borchert 1973; Wareing 1970). Similarly, Abod and Webster (1989) suggested that after a tree is transplanted, an optimal root length:leaf area ratio is reestablished by coordinating growth to correct the disrupted ratio. Therefore, a major loss of roots due to transplanting can result in stress to the transplanted tree and a corresponding period of reduced vigor in the crown (Watson et al. 1986). Watson et al. (1986) suggested that trees undergo a period of stress and reduced vigor for 4 or more years following transplanting and that reductions in top growth were related to the time required for the replacement of the root system.

“Planting check” has been used to refer to the period of prolonged reduction of top growth that results from transplanting (Mullin 1963). According to Mullin (1963), the duration of planting check depends upon “the time required for trees to rebuild a root system in sufficient proportion to the top to provide the needs of water and nutrients from the soil" and may range from one growing season in favorable conditions (e.g., fertile, well-cultivated soil) to 10 or 20 years. Similarly, Watson et al. (1986) stated that a "balance between the roots and crown must be restored before vigorous top growth can occur" and recommended the implementation of practices that would reduce transplant stress and increase root regeneration.

Factors that affect the duration of planting check include: nutrient status (particularly nitrogen) of the soil, moisture excess (and the resulting oxygen deficiency), moisture deficiency, frost, and competition from other plants (Mullin 1963). To minimize the onset of planting check, plants should be handled during harvest and planting in ways that minimize root loss. Additionally, plants should be planted in soils that are sufficiently drained, planted at proper depths, and supplied with adequate moisture and nutrients. Competition from other species should also be minimized.

Similar to the term "planting check" used by Mullin (1963), Watson et al. (1986) used the term "transplant shock" to refer to the period between transplanting and the resumption of vigorous growth. Transplant shock is a result of the extreme imbalance between the root system and crown and the resulting period of stress and slow growth (Watson et al. 1986) and is characterized by shortened internodal length and small leaves (Struve and Joly 1992). Transplant shock refers to the physiological disorders characteristic of transplanted trees and is often considered a primary cause of poor success rates in planting programs (Watson and Himelick 1983). Leaf scorch and twig dieback are typical symptoms of decline and often are a result of excess or insufficient soil moisture and fine root death (Watson and Himelick 1983). The symptoms of leaf scorch and twig dieback are often seen in transplanted trees where an imbalance between the roots and shoots exists. The primary cause of transplant stress is tissue water deficits resulting from an inability to absorb sufficient soil moisture to support the tree (Carlson et al. 1988; Larson 1984).

It is generally accepted that large trees take longer to establish than small trees (Harris et al. 1999; Struve et al. 2000; Watson 1985). Therefore, the size benefits of planting large trees are often lost following establishment. Watson (Watson 1985) suggested that large trees take longer to establish because more time is required to reestablish the original root:shoot ratio. Additionally, large diameter roots do not regenerate roots as rapidly as small diameter roots (Arnold and Struve 1989; Watson and Himelick 1983).

The significant loss of roots that occurs during transplanting results in a root system that is small proportionally to the aboveground part of the tree (Watson and Himelick 1997; Watson et al. 1986) and until the tree regenerates a new root system, water absorption is limited. The limited size of the transplanted root system relative to the aboveground portion of the tree results in the tree absorbing moisture from the root zone more rapidly than water can move in from the surrounding soil (Watson and Himelick 1997). This results in moisture stress (a common cause of transplant failure) to the tree despite ample moisture in the surrounding soil (Watson and Himelick 1997). As a result of the limited available soil moisture, root growth is reduced, which often limits the rate of shoot growth (Alvim and Alvim 1976). The more rapidly roots are regenerated, the less moisture stress will be imposed upon the tree and the greater the chance of survival (Struve and Moser 1984). Some authors (Harris et al. 1996; Watson and Kupkowski 1991) reported that approximately 4 to 5 months were necessary for roots to grow into the soil surrounding the root ball. Therefore, irrigation should be focused on the root ball for the first several months following transplant.

Physiological changes must occur in a newly transplanted tree if the tree is to survive until a root system is regenerated that can support the tops of the tree (Watson and Himelick 1983). Successful establishment and growth of transplanted trees depends upon the rate of root regeneration and rate of development of a new root system (Harris et al. 2001; Lathrop and Mecklenburg 1971; Stone and Schubert 1959; Watson et al. 1986). According to Lyr and Hoffmann (1967), root regeneration rate “often determines the duration and severity of growth interruptions and losses of increment”. Therefore, practices that minimize injury can be implemented. Watson (1986) reported that unsatisfactory soil conditions at the planting site might reduce root regeneration and prolong the stress of transplanting. However, root pruning prior to harvest can be used to increase the amount of fine root surface area within the root ball (Watson 1986; Watson and Sydnor 1987). Gilman and Kane (1991) reported root regrowth might be promoted by a high proportion of small-diameter roots within the root ball.

If the proper root pruning technique is used, root balls can have several times the amount of fine roots and greater root surface area compared to unpruned plants (Watson 1986). The greater amount of fine roots and surface area should help alleviate post-transplant stress, help hold the root ball together, and aid in the survival and establishment of the newly transplanted tree (Watson 1986). However, Watson cautions that the timing and location of the pruning is critical. Typically, numerous roots are produced from each severed root end (Watson 1986). These replacement roots can average 45 cm (18 in) of growth per year (Watson, 1986). Watson reported that in most cases one (or at most, a few) root will become dominant within a year or two, and the remainder of the small roots will in time die. Eventually, the root system will start to resemble the original root system in both structure and distribution.

Some authors related fibrous root systems and species that are easy to transplant (Fare et al. 1985; Harris et al. 1995). Possible explanations for this phenomenon may be that fibrous root systems have a greater amount of intact lateral roots and a greater absorptive area compared to coarse root systems (Harris and Gilman 1993). Intact lateral roots also initiate elongation sooner than severed roots (Arnold and Struve 1989; Stone and Schubert 1959). Additionally, each severed root will become sites for root regeneration. Along similar lines of thought, Struve and Moser (1984) considered the coarse root system and relatively low root regeneration rate to be the cause of the poor transplantability of scarlet oak. Auxin application increased the number of roots initiated; however, auxin delayed root initiation and elongation (Struve and Moser 1984). Harris et al. (1994) reported that differences in harvested root length might explain some of the variation among species in tolerance of fall transplanting. For example, green ash and tree lilacs transplant successfully in the fall and have much more extensive root lengths within their root balls than scarlet oak or Turkish hazelnut, which are considered more difficult to transplant.

Root regeneration potential has been used to describe the capacity of recently transplanted plants to elongate existing roots and/or initiate new roots (Lathrop and Mecklenburg 1971; Stone et al. 1962). Root regeneration potential has also been correlated with field survival and ease of transplanting (Webb 1976).

Initial root elongation depends heavily on stored reserves (Wargo 1983). However, continued growth appears to depend on new shoot growth for growth substances (Wargo 1983). Root elongation is not only affected by the stresses incurred in the previous growing season (and resulting effect on reserves) but also to the effects of stress during the current season (Wargo 1983). According to Wargo (1983), the consequence of an impaired root system is the reduction in water and mineral absorption and transport to the leaves, resulting in small leaves due to insufficient water absorption during leaf expansion. As well, leaves may be less productive due to transpiration rates exceeding water absorption rates, which causes stomates to close and photosynthetic rates to decline. As a result, mineral absorption and the photosynthetic efficiency of the plant are lowered. Nitrogen metabolism may also be affected by an impaired root system. Injury to the root system can impair amino acid synthesis in the roots, thereby impairing the formation of amino compounds in the shoots and limiting protein synthesis. (Amino acids formed in the roots are transported to the leaves where they are converted to all of the amino compounds necessary for protein formation.) The reduction in protein formation may result in a reduction of shoot and root growth (Wargo 1983). In addition to potential reduction in protein formation, growth regulators formed in the roots and transported to the shoots may also be affected, potentially contributing to the reduction in shoot growth (Wargo 1983).

Transplant success rates can be quite high when proper planting procedures and good maintenance practices are employed. Watson and Himelick (Watson and Himelick 1982) reported 97% survival rate after 1 year and attribute the high success rate to minimizing root ball water deficit and careful post-transplant maintenance. Low success rates of other plantings were attributed to improper handling and planting and lack of regular post-transplant maintenance. A basic knowledge of rooting behavior of transplanted trees is still needed to better understand the establishment of transplanted trees. With an increased understanding of factors relating to a plant’s ability to regenerate roots, better decisions regarding plant management can be made.

Research Regarding Root Regeneration

Watson and Himelick (1982) studied root regeneration of Norway maple, green ash, and ginkgo trees that were transplanted in March, May, July and October 1 year earlier. Research revealed that initiation of root regeneration originated primarily from the callus tissue around the outer margins of the severed roots, particularly smaller roots (less than 4 cm diameter). Thus, past practices such as fertilization, root pruning, irrigation, and production practices (container- versus field-grown), which affect root distribution and density, may also affect root regeneration.

Root density of non-transplanted trees was greater than the corresponding transplants at similar depths and for all seasons (Watson and Himelick 1982). Norway maple had the greatest capacity for root regeneration in absolute numbers and as a percentage of the root regenerated in the control (52%), while ginkgo had the lowest regenerative capacity (25%). May-transplanted Norway maples had the greatest root growth, while March-transplanted trees had the least. Season of transplant had little effect on root growth of green ash and ginkgo. They suggested that only during active shoot growth are carbohydrates available to support regeneration of roots.

Watson and Himelick (1982) compared the amount of nonstructural carbohydrates (food reserves) in twigs and roots of transplanted and non-transplanted trees. As expected, carbohydrate levels of non-transplanted trees varied with season (minimum in spring and maximum in fall) and were consistently greater in the roots. Seasonal fluctuations of carbohydrate levels in transplanted trees differed from the non-transplanted counterparts in that carbohydrate levels decreased from July to October, resulting in slightly higher carbohydrate levels in the fall than the non-transplanted trees. The authors suggested that the higher carbohydrate levels in the transplanted trees were due to the rate of photosynthesis exceeding the rate of carbohydrate use. This imbalance is probably due to the lower energy requirements of the transplanted root system (small system requires less maintenance), and it might stimulate root regeneration as reported in stem cuttings (Stoltz and Hess 1966; Watson and Himelick 1982). Watson and Himelick (1982) attributed the decrease in carbohydrate level in transplanted trees to drought stress.

Total nonstructural carbohydrates in roots were at their lowest levels during the time of spring shoot growth, which happened to be the only time when transplant timing appeared to have a major impact on root regeneration (Watson and Himelick 1982). Subsequently, Watson and Himelick (1982) suggested that root carbohydrate status might be a limiting factor for root growth when trees are transplanted at the time when shoots are elongating in spring. According to Watson and Himelick (1982) root growth is regulated by physiological factors as well as carbohydrate availability. Consequently, factors that affect the photosynthesis (e.g., light, drought, defoliation) also affect root growth and elongation (Watson and Himelick 1982). Levels of carbohydrate reserves fluctuate seasonally. Dumbroff and Webb (1978) reported depletion in total food reserves in May and June, which corresponded to active shoot expansion.

In a Canadian study comparing the effects of early spring photosynthesis on levels of nonstructural carbohydrates in white spruce (*P. glauca* (Moench) Voss.), Wang and Zwiazek (1999) found that uncovered (photosynthesizing) seedlings had higher levels of nonstructural carbohydrates in needles and roots compared to seedlings that were covered. The authors concluded that early spring photosynthesis resulted in starch accumulation in the needles and roots of white spruce bareroot seedlings, and that high carbohydrate levels did not significantly affect root growth potential, time of bud break, and shoot elongation the first-season following transplant. However in the second-season, high carbohydrate levels resulted in more roots and greater shoot growth post-transplant. According to Wang and Zwiazek (1999), delayed bud flush of plants that are lifted and kept in cold storage may be related to low carbohydrate levels (Jiang et al. 1994) and/or slow photosynthetic recovery after transplanting (Jiang et al. 1995; Jiang et al. 1994). Additionally, net photosynthesis is typically low the first several weeks following transplant, which may be due in part to poor root establishment and water stress (Burdett 1990; Grossnickle and Heikurinen 1989; Jiang et al. 1994; Wang and Zwiazek 1999). Low net photosynthesis will result in depletion of energy stores. Wang and Zwiazek (1999) suggest that carbohydrate levels in seedlings may affect seedling establishment by influencing root and shoot growth.

Lathrop and Mecklenburg (1971) reported that few new root beginnings (initials) were produced in transplanted yew during summer months and that root regeneration potential increased throughout fall, with the greatest potential in January. Root regeneration potential decreased throughout the spring and early summer, which also corresponded to an increase in shoot growth in spring. The authors proposed that the decrease in root regeneration potential might be due to increased competition between shoot and root growth for available carbohydrates or other growth factors. However, the authors also suggest that the decrease in root regeneration potential after shoot growth in summer was not due to competition between roots and shoots since shoots were not longer elongating. Finally, Lathrop and Mecklenburg (1971) concluded that other factors in addition to root dormancy must regulate root regeneration potential.

Struve and Joly (1992) determined that transplanted red oak seedlings had significantly reduced leaf surface area and began the second flush of shoot growth later than non-transplanted seedlings. Additionally, the first flush of shoot growth occurred prior to any substantial root regeneration. While CO_2 assimilation rate and stomatal conductance were unaffected by transplanting, predawn xylem water potential was lower in the transplanted seedlings (Struve and Joly 1992). Thus, sufficient water was available to maintain adequate hydration for stomata to remain open. However, the authors noted that transplant-induced reductions in leaf water potential might have occurred in the afternoon. While the number of leaves or stems and stem length of the first flush were unaffected by transplanting, transplanting did result in significantly reduced leaf area. Struve and Joly (1992) concluded that transplant shock in red oak was mediated through the avoidance of internal water deficits via reduced leaf surface area, which reduces whole-plant water use.

Starch content in roots of red oak seedlings averaged 41% during dormancy (Farmer 1975). Metabolism and translocation of root storage compounds is critical to rapid leaf development (Struve and Joly 1992). During the first flush of shoot growth, untransplanted seedlings export carbon from storage reserves in the roots and stems. Struve and Joly (1992) determined that while transplanted seedlings also used stored reserves from roots, less root and more shoot reserves were used to develop the first flush of shoot growth compared to the untransplanted seedlings. Finally, Struve and Joly (1992) found that transplanted seedlings had relatively less shoot dry weight gain and more root dry weight gain compared to non-transplanted seedlings, indicating that transplanting may have increased root sink strength and altered carbon allocation patterns. Auxin applications to transplanted seedlings resulted in increased final seedling dry weight compared to non-auxin-treated transplanted seedlings. Thus, auxin application may have increased root system sink strength and assimilate demand via increased numbers of adventitiously regenerated roots.

Research of Abod and Webster (1989) on apple trees revealed that a large portion of the transplanted root system dies following transplant. Considering that a fraction of the root system is often all that is moved during transplanting, any additional mortality in the root system may result in death of the transplanted tree. Subsequently, they recommend the implementation of practices that would “reduce root mortality and increase speed and magnitude of root regeneration”. Additionally, the authors found root regeneration to be affected by cultivar differences. They proposed that after a tree is transplanted, an optimal ‘functional’ root length:leaf area ratio is reestablished by coordinating growth to correct any disruption to the ratio that results from transplanting practices. This proposal was supported by Abod and Webster’s research on responses of trees with leaves and with leaves removed at planting.

In white ash (*F. Americana* L.), Webb (1976) found a strong positive correlation between root regeneration potential and number of hr of chilling at 5 C. Additionally, a strong negative correlation between time of first bud break and number of hr of chilling was found. He concluded that 2500 hr of 5 C was sufficient to remove physiological dormancy of the buds. Root regeneration potentials were lowest during December and January and highest during April and May. In conclusion, root regeneration potential increased with increased cold storage and peaked in April and May when physiological dormancy of the buds was removed. Bud dormancy was removed after 2500 hr of chilling and this coincided with the beginning of increase root regeneration. Root regeneration in white ash occurs at a time when buds are strongly dormant (e.g., in December and January).

Different species have different root regeneration potentials. For example, Harris and Gilman (1991) determined that 10 weeks after transplanting field-grown Leyland cypress had four times greater dry weight of regenerated roots than laurel oak. Research of Watson and Himelick (1982) also found root regeneration to be species dependent, as well as dependent on the diameter of the severed roots from which new roots will grow. Root regeneration was significant among all root sizes for Norway maple. However, green ash roots with a diameter greater than 4 cm did not regenerate many roots, while roots less than 4 cm had abundant root regeneration. In ginkgo, severed roots frequently died back 10 cm and new roots were regenerated from the living cambium interior of the dieback.

In green ash, Watson and Himelick (1983) observed that roots larger than 2.5 cm diameter were less likely to initiate new roots than smaller roots. Similarly, less root regeneration occurred from larger diameter Norway maple roots than from smaller roots. Watson and Himelick (1982; 1983) reported that new roots primarily regenerate from a callus layer formed near the severed root ends that were cut or damaged during the transplant process, resulting in a significant portion of the regenerated roots being located at the periphery of the root ball. Therefore, particular attention and care should be given to prevent desiccation and further injury to this crucial area of the root system (Watson and Himelick 1982; 1983). Watson and Himelick mention that overwatering can also result in severe injury to the regenerated roots.

In contrast to the shoots of temperate hardwoods, which have a dormant period that can be overcome by chilling, roots do not exhibit a period of innate dormancy (Richardson 1958; Taylor and Dumbroff 1975a) and appear to be dependent on environmental factors such as temperature and moisture (Lyr and Hoffman 1967) as well as endogenous factors in the shoot (Farmer 1975; Larson 1970; Richardson 1958). For example, silver maple seedlings require a physiologically non-dormant bud to produce and export growth factors necessary for root initiation (Richardson 1958). In summary, root initiation depends upon the state of dormancy of the bud, which depends upon chilling requirements and exposure.

In a study comparing root regeneration of pin oak, an easy-to-transplant species, to root regeneration of scarlet oak, a difficult-to-transplant species, Struve and Moser (1984) determined that pin oak regenerated more roots 12 weeks post-transplanting than scarlet oak, and that while bud removal in dormant pin oak seedlings decreased root regeneration (number of regenerated roots and new root length), bud removal had no effect on number of regenerated roots in scarlet oak. However, root length was increased by bud removal in scarlet oak. These findings suggest that buds are a source of a substance involved in promoting root initiation and growth (Struve and Moser 1984). Similarly, Richardson (1958) determined that at least one terminal bud was necessary for root growth in silver maple seedlings. However, the increase in root growth that resulted from the removal of half the buds indicated the production of root-inhibiting substances in the buds of scarlet oak. Along the same lines, Larson (1984) suggested a link between root regeneration and bud dormancy and noted that the highest root regeneration potential occurred after the fulfillment of the chilling requirements necessary for dormancy release. Root regeneration was evident from severed root ends in green ash, considered an easy-to-transplant species, after 17 days (Arnold and Struve 1989).

Struve and Moser (1985) determined that as temperature increased from 10 to 26 C in the root zone of root pruned scarlet oak seedlings, time until initiation of new roots decreased, numbers of initiated new roots increased, and root elongation rate increased. Other authors (Krugman and Stone 1966; Larson 1970) also concluded that soil temperature affected time to root initiation, number of roots initiated, and root elongation rate. Larson (1970) reported that little root regeneration occurred in northern red oak seedlings at temperatures less than 13 C.

Optimum root regeneration temperature varies among species, but typically root elongation decreases and root initiation increases at low temperatures compared to higher temperatures (Struve and Moser 1985). The greatest root regeneration rate in Struve and Moser’s research occurred at 26 C. No roots were regenerated below 10 C. Roots of scarlet oak seedlings initiated growth 6 days following pruning at 26 and 21 C. At 16 C, roots were initiated after 12 days. No elongation or initiation occurred at 10 C. To conclude, root elongation rate and the number of roots initiated per seedling increased with increasing root zone temperature. Maximum elongation occurred at 26 C. While root development and elongation occurred only at temperatures greater than 16 C, root initiation occurred at all root temperatures. Struve and Moser (1985) concluded that the minimum root zone temperature for root elongation was between 10 and 16 C when air and shoot temperatures were relatively low (e.g., 10 C). At temperatures below 16 C root regeneration was significantly retarded. Therefore, the authors recommend transplanting scarlet oak after soil temperatures are warming.

Many woody plants have two distinct periods of active root elongation, one in spring and one in fall (Cripps 1970; Deans 1979; Deans and Ford 1986; Dell and Wallace 1983; Harris et al. 1995; Harris and Fanelli 1999; Roberts 1976; Stone et al. 1962; Stone and Schubert 1959; Wargo 1983). Stone and Schubert (1959) determined that lateral root elongation in ponderosa pine occurred at all times except summer and lateral root initiation was greatest in spring just prior to bud break in spring. In Douglas fir (*Pseudotsuga menziesii* Mirb. Franco.), Stone et al. (1962) found that root regeneration potential increase in fall, was high in winter, and decreased in spring.

Struve et al. (2000) reported that while survival of transplanted small-caliper red oak trees was 100% after 3 years, survival of transplanted large-caliper red oaks was 42% (58% mortality). However, based on trunk caliper and height growth, the large caliper (trunk diameter) trees that did survive established faster than the small-caliper trees (Struve et al. 2000). In addition, Struve et al. (2000) reported that two growing seasons after transplant, shoot extension of non-transplanted trees was 5 times greater than transplanted small caliper trees and 13 times greater than transplanted large-caliper trees.

Transplant Establishment in Urban Environments

Establishment of transplanted trees in urban settings is often unsuccessful. Estimates of mortality vary considerably depending upon numerous environmental factors, amount of post-transplant maintenance, and species tolerances to transplant. One study determined average mortality for transplanted bareroot trees to be 41% 10 years post-transplant (Cool 1976). In the same study, trees that were dug with a tree spade and transplanted with intact root balls averaged 5% mortality over the same period of time.

Urban environments are often characterized by artificial soil horizons with dense, compacted subsoils, and very thin topsoil layers, which result in poor drainage (Watson 1986). Due to poor drainage and infiltration, excess water accumulates in the lowest point, usually the planting hole, where it can remain for weeks resulting in the suffocation of the root system (Watson 1986). The accumulation of excess water results in poor aeration, which result in poor root growth and potentially root death. Temperature, moisture, aeration, soil density, stored energy, disease, fertility, and shipping and storage conditions can also have adverse effects upon establishment of transplanted trees

(Watson and Himelick 1997). In addition, increased rates of vandalism, accumulation of salts, soil compaction, and limited rooting space can have negative consequences. Past practices such as fertilization, irrigation, root pruning, and production methods (e.g., field-grown vs. containerized) employed during production can also effect establishment by influencing root distribution.

Criteria such as the re-establishment of the static branch:root spread ratio (Gilman and Beeson 1996a; Gilman and Kane 1991; Watson 1985), resumption of pre-transplant growth rate (Gilman and Beeson 1996b; Watson et al. 1986), shoot xylem water potential relative to untransplanted controls (Gilman and Beeson 1996b), and unit photosynthetic rate (Struve 1992) have all been used to determine when and if a tree is "established" (Struve et al. 2000). As a general guideline, Watson (1985) proposed an establishment rate of 1-year-per-2.54 cm trunk caliper in climates similar to northern Illinois.

Natural Habitat, Landscape Value, and Growth Characteristics of Sugar Maple, Northern Red Oak, and Willow Oak

Sugar Maple

Sugar maple is a large (21 to 40 m) tree with a rounded, dense crown (Core and Ammons 1958; Little 1980), common to rich woods (Core and Ammons 1958; Wofford 1989) and moist soils of uplands and valleys (Little, 1980). The natural range of sugar maple extends from southeastern Manitoba, east to Nova Scotia, south to North Carolina and northern Georgia, and east to Texas (Core and Ammons 1958; Little 1980) [USDA zones 3 to 8 (Dirr 1998; Gilman 1997)]. Dirr (1998) reported sugar maple to be one of the best of the larger shade and lawn trees, well-suited for lawns, parks, and golf courses where lawns are extensive. Additionally, sugar maple is tolerant of shade and has multicolored (yellow, orange, and red) foliage in autumn that is "unexcelled in fall color" (Dirr 1998; Gilman 1997; Little 1980). However, sugar maple is susceptible to salt damage and is not well-suited for compacted, crowded and polluted conditions (Dirr 1998). Growth rate of sugar maple is slow to medium in youth (Dirr 1998). Dirr (1998) recommended that trees be transplanted balled-and-burlapped into well-drained, moderately moist, fertile soil. Sugar maple is reported to have little pH preference but slight acidity results in slightly greater growth (Dirr 1998). Staley and Dickson (1977) reported 0% loss of 40, 2.5-to-3.2 cm trees, and 0% loss of 41, 3.8-to-5 cm trees. Sugar maple is valued as lumber for furniture and flooring (Little 1980). As well, the sap can be concentrated to produce maple sugar and syrup. Approximately 18 to 227 L of sap per year can be harvested from each tree (121 L of sap are needed to produce 3.8 L) syrup or 2 kg sugar] (Little 1980). Other names for this species include hard maple and rock maple (Little 1980).

Northern Red Oak

Northern red oak is a large (18 to 30 m) tree with a rounded crown of stout spreading branches (Core and Ammons 1958; Little 1980). Northern red oak typically grows in rich woodlands (Wofford 1989) with moist loamy, sandy, rocky, and clay soils (Little 1980). The natural range of northern red oak extends form western Ontario, east to Prince Edward Island, south to Georgia, west to Oklahoma, and north to Minnesota (Core and Ammons 1958; Little 1980) [USDA zones 3b to 7 (8) (Dirr 1998)]. Characteristics that make northern red oak a valuable landscape species are that it grows rapidly, transplants readily, is hardy in city conditions, and endures cold (Little 1980). Similarly, Dirr (1998) reported that northern red oak averaged 60 cm growth per year over a 10-year period in a moist, well-drained soil. In the landscape, northern red oak prefers well-drained, slightly acidic, sandy loam soils (Dirr 1998). Other desirable landscape characteristics of northern red oak are its' ability to withstand polluted air of cities, full sun, and alkaline soils (Dirr 1998; Gilman 1997). Due to its' large size, northern red oak is most appropriate for lawns, parks, golf courses, and commercial areas; however, it is commonly used as a street tree in the midwestern and eastern states (Dirr 1998). Northern red oak is also valued as a lumber species for flooring and furniture (Little 1980). Other names for northern red oak include red oak and gray oak.

Willow Oak

Willow oak is a medium to large (12 to 30 m) tree (Dirr 1998) with a conical or rounded crown of many slender branches (Little 1980). In youth, willow oak has a pyramidal form that develops into a dense oblong-oval to rounded crown at maturity (Dirr 1998). Willow oak typically grows in moist alluvial soils of lowlands, floodplains, or bottomlands of streams (Little 1980; Wofford 1989). The natural range of willow oak extends form New Jersey, south to northwestern Florida, west to eastern Texas, and north to southern Illinois (Little 1980) [USDA zones 5 to 9 (Dirr 1998; Gilman 1997)]. Willow oak has a medium growth rate of 30 to 60 cm per year and should be planted in moist, well-drained soils (Dirr 1998). However, willow oak has been reported to adapt to "virtually impossible habitats" (Dirr 1998), resulting in it becoming a popular and widely planted street and shade tree (Gilman 1997; Little 1980). Willow oak sometimes transplants poorly. Staley and Dickson (1977) reported 40% loss of 30 2.5-to-3.2 cm trees and 26% loss of 76 7.6-to-8.8 cm trees. However, willow oak is generally thought to transplant more readily than some oaks due to its' highly fibrous and shallow root system (Dirr 1998; Little 1980). Willow oak should be transplanted while the tree is dormant, preferably during winter. Considerable pruning in youth is required to train willow oaks to have a central leader (Dirr 1998; Gilman 1997)}. Willow oak is well-suited as a street tree and in large areas such as commercial establishments, golf courses, and parks (Dirr 1998; Gilman 1997).

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Chapter 2

Seasonal Effects of Transplanting on Growth and Pre-Bud Break Root System Regeneration of Northern Red Oak (*Quercus rubra* L.) and Willow Oak (*Q. phellos* L.)

Abstract

Transplant timing potentially affects plant establishment through poorly understood changes in early root system regeneration. Therefore, early post-transplant root regeneration and canopy development of balled-and-burlapped (B&B) November- and March-transplanted northern red oak (*Quercus rubra* L.) and willow oak (*Q. phellos* L.) were studied to determine if season of transplant affected root regeneration and height and trunk growth. Subsamples were excavated in January and April (prior to bud break) to quantify new root growth outside and within the root balls. Height and trunk diameter growth were measured for three growing seasons after transplanting. Survival of red oak in all treatments was 100%. Survival of November- and March-transplanted willow oak was 67% and 83%, respectively. No root regeneration occurred outside or within the root balls of either species during the 71 days between November transplanting and winter excavation. Excavation of transplanted root systems of both species at spring bud break indicated that November-transplanted trees regenerated roots in late winter and/or early spring, not late fall and/or early winter. November-transplanted red oak, but not willow oak, regenerated more roots by spring bud break than March-transplanted trees. Little difference in height and trunk diameter growth was evident between the November- and March-transplanted red oaks throughout the 3 years following transplant. After three growing seasons height growth of willow oak was nearly identical between the November and March transplant treatments. However, November-transplanted willow oaks exhibited greater trunk expansion compared to the March transplants for all 3 years. Overall, season of transplant had little effect on height and trunk diameter growth of red oak, even though November-transplanted trees grew more roots prior to the first bud break following transplant. Among the willow oaks that survived, November transplanting resulted in greater trunk diameter growth. However, considering the

mortality rate of November-transplanted willow oak, March may be a better time to transplant willow oak in climates similar to Blacksburg, VA (USDA plant hardiness zone 6a, AHS plant heat zone 4).

Introduction

The term ‘root growth’ in the following sections refers to elongation of existing roots and/or initiation and elongation of new roots. The term’ root regeneration’ refers to “the restoration or new growth by an organism of organs, tissues, etc., that have been lost, removed, or injured” (Random House 1997).

Root systems of most trees extend well beyond the maximum spread of branches (Watson and Himelick 1997). As a result, when trees are harvested for transplanting, as little as 2% of the root system may be moved with the tree (Watson and Himelick 1983). Watson and Sydnor (1987) reported that root balls dug according to the minimum standards of the American Association of Nurserymen contain approximately 5 to 18% of the original fine roots. Gilman (1988) reported that less than 10% of total root length of the original root system was contained within the root balls of harvested field-grown trees. Large-diameter roots contribute disproportionately more weight relative to surface area than small diameter roots. Therefore, while more than 90% of coarse (>10 mm diameter) root weight was within the confines of the root ball of field-grown trees, less than 15% of the fine, absorbing root weight (<2 mm diameter) was within the confines of the root ball (Gilman and Beeson 1996).

The significant loss of roots that occurs during transplanting results in a root system that is disproportionately small compared to the aboveground portion of the tree (Watson and Himelick 1997; Watson et al. 1986). Until the tree regenerates the lost portion of the root system, water absorption will be limited by the absorptive capability of the much reduced, transplanted root system. The limited size of the transplanted root system relative to the aboveground portion of the tree can result in the tree absorbing moisture from the root zone more rapidly than water can move in from the surrounding soil (Watson and Himelick 1997). Consequently, moisture stress, a common cause of transplant failure, may occur despite the presence of ample moisture in the surrounding soil. Limited available soil moisture may result in reduced root as well as shoot growth

(Alvim and Alvim 1976). Therefore, the more rapidly roots are regenerated, the less moisture stress will be imposed upon the tree and the greater the chance of survival (Struve and Moser 1984).

Season of transplant is important with respect to plant growth because season often correlates to specific stages of growth and maturity (e.g., dormancy, leaf drop, bud set, flowering), as well as specific weather patterns and light characteristics (e.g., temperature, moisture, daylength, and light intensity and quality) that influence plant growth (Harris et al. 1999). While fall transplanting may be superior to spring transplanting for many species (Buckstrup and Bassuk 2000; Harris and Bassuk 1994; Harris et al. 1996; Harris et al. 1999; Hinesley 1986; Watson and Himelick 1983; Witherspoon and Lumis 1986), spring transplanting may be superior (Buckstrup and Bassuk 2000; Harris and Bassuk 1994; Larson 1984) or similar (Harris et al. 2001; Watson and Himelick 1982; 1983; Watson et al. 1986) to fall transplanting for other species. Despite initial differences in growth of trees transplanted in fall vs. spring, many growth differences can disappear after a few years (Buckstrup and Bassuk 2000; Watson et al. 1986). As a result of the diminishing effects over time and inconsistent effects of transplant date, Watson et al. (1986) concluded that no general recommendations for best season to transplant trees (in Illinois) can be made and instead, only species-specific recommendations can be made.

Survival rates differ for fall- and spring-transplanted trees. For example, Buckstrup and Bassuk (2000) reported lower survival rates for spring-transplanted bareroot hophornbeam [*Ostrya virginiana* (Mill.) K. Koch.] trees compared to the fall-transplanted trees. However, Larson (1984) reported higher survival rates for spring-transplanted Austrian pine (*P. nigra* Arn.) seedlings compared to fall-transplanted seedlings and suggested that poor survivability of fall-transplants was due to poor root regeneration and excessive needle water deficit. Many of the reported differences among reports may be due to species-specific responses. While season and species-specific preferences are certainly important (Harris and Bassuk 1994; Watson et al. 1986), other factors, such as habit (conifer vs. broad-leafed evergreen vs. deciduous) (Harris et al. 1999), pre-planting preparation, soil preparation, planting technique (Acquaah 1999), post-transplant practices, soil type, site conditions, environmental conditions (e.g., weather, moisture), and production, harvest and handling methods (Buckstrup and Bassuk 2000) may also influence success rate.

Fall and spring are often considered the best times for transplanting most landscape plants, particularly if post-transplant care is expected to be minimal, due to favorable conditions such as increased soil moisture, cooler air temperatures, the absence of active shoot growth, and the associated reduced potential for desiccation (Harris and Fanelli 1999; Himelick 1981; Watson et al. 1986). Proposed advantages of fall transplanting include an increased opportunity for trees to regenerate roots prior to shoot growth in spring, more time to develop contact between the roots and soil (Buckstrup and Bassuk 2000), more time to acclimate to the physiological stresses of transplanting before shoots resume growth in spring (Harris and Fanelli 1999), and more time for physiological processes involved in root regeneration to occur (Harris et al. 1996). As a consequence, fall-transplanting may result in increased pre-bud break root growth and the development of a larger root system, which can access a greater soil water reservoir to support shoot growth the following spring (Harris and Fanelli 1999; Harris et al. 1996). Additionally, Hinesley (1986) proposed that spring transplanting might interfere with production of root-produced hormones involved in shoot extension. Finally, while fall transplanting is recommended in many regions, late fall transplanting is not advised in climates with severe winters (Harris and Bassuk 1994).

For many species, spring conditions (e.g., ample soil moisture, warming soils) provide optimal conditions for root growth and tree establishment (Acquaah 1999). Additional advantages of spring transplanting (prior to bud break) include the avoidance of damaging cold, cool temperatures that help minimize transpirational loss, and the potential for pre-bud break root growth. However, transplanting at or just prior to bud break in spring is usually ill advised (Dumbroff and Webb 1978; Farmer 1975) and can result in poor root regeneration and growth (Watson and Himelick 1982).

Root regeneration potential and length of time until root regeneration commences varies between seasons. Larson (1984) reported greater root regeneration in spring transplants than fall transplants 4 weeks after transplanting Austrian pine and arborvitae (*Thuja occidentalis* L.). However, Lathrop and Mecklenburg (1971) reported greater root regeneration in fall- and early winter-transplanted yews (*Taxus* x *hunnewelliana* Rehd.

and *T. cuspidata* Sieb. & Zucc.) compared to spring and summer transplants. Similarly, Harris et al. (2002) determined that early fall-transplanted sugar maple (*Acer saccharum* Marsh.) and northern red oak began root growth earlier and grew more roots in the first-season after transplanting than the mid fall- and spring-transplanted treatments. Harris et al. (2001) also reported a greater delay in spring root growth of spring-harvested Turkish hazelnut (*Corylus colurna* L.) trees compared to fall-harvested trees. On the other hand, some plants may not regenerate roots until summer. For example, Harris et al. (1996) observed that regardless of the season of transplant (spring or fall), root growth did not occur outside of the root ball until early July (1 month after bud set) in fringe tree (*Chionanthus virginicus* L.).

Root system regeneration is essential for transplant survival. A basic knowledge of rooting behavior of transplanted trees is still needed to better understand the establishment of transplanted trees. With an increased understanding of factors relating to the dynamics of post-transplant root system regeneration, better decisions regarding plant management can be made, resulting in better transplant establishment of these and other species. The objectives of this project were to compare the growth of November- and March- transplanted red and willow oaks to determine which season is a better time to transplant these species, and to determine when roots resume post-transplant growth.

Materials and Methods

Plant Material Unbranched northern red oak whips (1.5 m) were obtained from J. Frank Schmidt and Sons Co. (Boring, OR) and grown for 2 years in a field bed at the Urban Horticulture Center, Blacksburg, VA [USDA plant hardiness zone map (U.S. Depatent of Agriculture 1990), AHS plant heat zone map 4 (American Horticultural Society 1997)]. Willow oaks were grown from seed at the Urban Horticulture Center. Trees were spaced 1.2 m apart in rows 1 m apart. Soil type was a Groseclose silt loam (clayey, mixed, mesic Typic Hapludults) with pH 6.2. After being grown to landscape size, 30 willow oaks and 30 red oaks of uniform size were selected for use in this project. Mean initial heights (SE mean in parentheses) of the red and willow oaks were 2.66 (0.08) m and 2.38 (0.05) m, respectively. Mean initial trunk diameters of the red and willow oaks, measured 15 cm above the soil line were 40.92 (1.01) mm and 37.17 (0.68) mm, respectively.

Treatments Eighteen trees of each species were randomly assigned to the November transplant treatment (5 November 1999) and 12 trees of each species were randomly assigned to the March transplant treatment (10 March 2000). Trees were planted in a field bed at the Urban Horticulture Center in a completely randomized design, keeping species in separate beds. To assess late fall and early winter root regeneration in the November-transplanted trees, six trees of each species were randomly selected to be excavated in January (N-J). To assess late winter and early spring root regeneration in the November-transplanted trees, six trees of each species were randomly selected to be excavated just prior to spring bud break (N-A). To assess late winter and early spring root regeneration in March-transplanted trees, six trees of each species were randomly selected to be excavated just prior to spring bud break (M-A). Early winter and spring excavation dates were 15 January 2000 and 21 April 2000, respectively. Height and trunk diameter growth of the six remaining trees of each species and planting date were measured for three growing seasons following transplant.

Tree Harvest and Planting All trees were harvested with a mechanical tree digger (tree spade). Root balls were 45 cm diameter. All root balls were wrapped with industry-standard copper sulfate-treated burlap (A.M. Leonard, Piqua, OH), enclosed in wire baskets, and laced with sisal twine (balled-and-burlapped). Trees were planted in a nursery bed in 0.75 m diameter augered holes 2.3 m apart and in staggered rows 1.05 m apart. After positioning the trees in holes, native soil was used to fill the holes around the trees. All twine was loosened from around the tree trunks. Burlap and wire baskets were left in place. However, baskets tops were pulled away from the tops of the root balls. After planting, all trees were flood irrigated and any crevices that opened were filled with soil.

Tree Care: Fertilization, Irrigation, etc. In spring 2000, 200 grams of encapsulated slow release fertilizer (15N-3.9P-10K, Osmocote Plus 15N-9P_2O_5-12K_2O 8-9 Month Northern Formula, The Scotts Company, Marysville, OH) was broadcast over the planting hole of each tree. The same fertilizer and rate was broadcast beneath the canopy of each tree just prior spring bud break in 2001. In spring 2002, 9.8 g N/m^2 of

27N-1.3P-10K fertilizer (27N-1.3P-10K, Statesman Supreme Methex 40 Controlled Release N, 27N-3P_2O_5-12K_2O, Southern States Cooperative, Inc., Richmond VA) were broadcast over both nursery beds. Soil was maintained near field capacity for two growing seasons with a micro-irrigation system (Aquaturret, Stuppy Inc., N. Kansas City, MO). During the growing seasons of 2000 and 2001, trees were irrigated once a week for approximately 1.5 hr. Trees were not irrigated in 2002, except for occasional irrigation due to drought. Weeds were eliminated by hand pulling and applications of RoundUp Pro® (41% glyphosate, Monsanto Company, St. Louis, MO) and pre-emergent herbicides Snapshot 2.5TG (0.5% isoxaben and 2.0% trifluralin, Dow AgroSciences LLC, Indianapolis, IN), Pendulum® WDG (60% pendimethalin, BASF Corp., Research Triangle Park, NC), and Surflan A.S. (40.4% oryzalin, Dow AgroSciences LLC, Indianapolis, IN). Herbicides were diluted and mixed according to manufacturers recommendations.

Measurements and Analysis Height and trunk diameter were measured at the time of transplant and at the end of each growing season. Height of the tallest branch tips was measured with a telescoping meter pole. Trunk diameter 15 cm above the soil line was determined by averaging two measurements, one made parallel to the nursery bed and the other made perpendicular to the nursery bed. Upon excavation, all new root growth outside the original root balls was removed. The surrounding soil was also examined for new root growth into the soil. Root balls were rinsed free of soil and all white roots inside the root ball were removed. White, unsuberized roots were considered to be new roots. Roots length was measured with a ruler. Roots were then dried to a constant weight at 65 C and weighed. Soil and substrate temperatures were monitored with thermocouples (Model HH21 Microprocessor Thermometer, Type J-K-T Thermocouple, Omega Engineering, Inc., Stamford, CT) placed 30 cm deep in a randomly selected AGR, PIPR, FR, and nursery bed. Afternoon temperatures were recorded twice weekly for the duration of the project. All data were subjected to analysis of variance within the GLM procedure of SAS (SAS for Windows Version 8.02, SAS Institute, Cary, NC). Species were analyzed separately. Significance levels were not used. Instead *P* values are reported (Marini 1999).

Results and Discussion

No root regeneration occurred within or outside the root balls of either red or willow oak during the 71 days between transplanting on 5 November 1999 and excavation on 15 January 2000 (Table 2-1). November transplanting occurred during fall leaf abscission, at a time when soil temperatures were generally favorable for root growth. Afternoon soil temperatures dropped below 5 C (considered to be limiting for root growth) by the end of November. Larson (1970) reported that under greenhouse conditions, minimal root regeneration occurred in northern red oak seedlings at temperatures below 13 C. Afternoon soil temperatures dropped below 13 C in mid October. Data from this study indicate that while it may be advantageous to transplant these species in fall, it is not due to late fall and/or early winter root growth. Due to the lack of late fall and early winter root growth, November transplants had to rely on the transplanted root system until root growth commenced in late winter and/or early spring.

Despite the lack of post-transplant root regeneration in late fall and/or early winter, root growth occurred in both red and willow oak prior to bud break in spring. November-transplanted red oaks had greater new root length and dry weight outside the root ball (P = 0.0324 and 0.0689, respectively) and greater total new root length and dry weight at spring bud break than March-transplanted trees (P = 0.0185 and 0.0210, respectively) (Table 2-1). Thus, November-transplanted red oaks in this study began spring shoot growth with more new roots than March-transplanted trees. In contrast, November-transplanted willow oaks had no root growth outside of the root balls at spring bud break. However, while root growth of both the November- and March-transplanted treatments had begun inside the root balls by spring bud break, there was no transplant time effect (P = 0.6482 and 0.6197, respectively). Blacksburg is near the northern extent of the range in which willow oaks can be successfully grown (Dirr 1998; Gilman 1997), and early spring soil temperatures may have limited root growth.

Physiological stresses of transplanting may have prevented late fall and/or early winter root growth. By the time the trees had overcome the physiological stresses of transplanting, low winter soil temperatures likely limited root growth. Therefore, as spring soil temperatures increased and became more favorable for root growth, roots of November transplants may have been in a better state to quickly resume growth compared to the March transplants. March transplants may have still been adjusting to the considerable injury and loss of roots that occurred as a result of transplanting, thereby delaying root the resumption of root growth. Subsequently, November transplants resumed root growth earlier or grew more roots prior bud break than the March transplants. Other authors (Buckstrup and Bassuk 2000; Harris and Fanelli 1999) suggested that fall transplanting provides more time for transplants to acclimate to the physiological stresses of transplanting. Alternatively, late fall and/or early winter root regeneration may have been limited due wound healing responses to the damaging effects of transplanting. As well, roots may have been in a dormant at this time regardless of transplanting.

The increased pre-bud break root growth of the November transplants compared to the March transplants may increase the soil water volume available to support the new developing, non-lignified shoots in spring of the November transplants (Harris and Fanelli 1999; Harris et al. 1996). However, there was little evidence that differences in height or trunk diameter growth were due to season of transplanting for red oak (Table 2-2). Although November-transplanted red oak produced more root length than the March transplants (*P* = 0.1387 and 0.0324 inside and outside of the root ball, respectively), the amount was actually quite small (Table 2-1). Thus, the increased pre-bud break new root length produced by the November-transplanted red oaks compared to the March transplants did not appear to confer any benefit for the November transplants in terms of height and trunk diameter growth in subsequent years (Table 2-2).

Harris et al. (2002) also found that October-transplanted northern red oaks began root growth earlier and produced more roots in the first-season post-transplant than the November- and March-transplanted treatments. Earlier root growth in the Harris et al. (2002) study also did not translate to greater height and trunk diameter growth in the following 3 years. Trees in both projects were kept well irrigated. In circumstances where water is limiting, additional root growth may provide a greater benefit. November-transplanted willow oaks in the current study also produced more root length at bud break compared to the March transplants, but there was little evidence that these differences are due to treatment (*P* = 0.6482). Height growth of the November- and March-transplanted willow oaks was similar all 3 years following transplant (*P* = 0.1918, 0.1178, and 0.7901, respectively). Trunk expansion, however, was greater for the November transplants compared to the March transplants all 3 years ($P = 0.0385$, 0.0287, and 0.0269, respectively).

Survival of November- and March-transplanted willow oak was 67 and 83%, respectively. While November-transplanted willow oaks had greater trunk expansion than the March transplants, these results are based upon the trees that survived. Therefore, November-transplanted willow oaks exhibited greater trunk expansion only if they survived. When taking into account the poorer survival rates of November-transplanted willow oak, March may actually be a better time of year to transplant willow oak in climates similar to southwest Virginia (USDA plant hardiness zone 6a, AHS plant heat zone 4). Due to the lack of late fall and/or early winter root growth in willow oak, November transplants subsisted on the transplanted root system until root growth commenced in late winter and/or early spring. Therefore, November-transplanted willow oak may have been more susceptible to desiccation than March-transplanted willow oak, resulting in poor survival rates. Late fall and/or early winter root growth was also poor among the November-transplanted red oaks. However, survival of both November- and March-transplanted red oaks was 100%. Therefore, November-transplanted red oak may have been less susceptible to desiccation than November-transplanted willow oak.

Of final note, to assess root extension into the surrounding soil, an air spade (Series 2000, Verona, PA) was used to determine root extension after the second growing season (September 2001). Roots were immediately covered and irrigated after inspection. While no roots could be found in two attempts in red oak without greatly disturbing the root zone, roots of one willow oak tree were observed approximately 1.8 m from the tree trunk and were 2.54 cm diameter near the trunk.

Conclusions

The results of this project indicate that under the conditions of this study, November-transplanted red and willow oak do not regenerate roots until late winter and/or early spring. Therefore, while it may be considered advantageous to transplant these species in fall, it is not because of late fall and/or early winter root growth. Instead, fall-transplanted trees may be in a better physiological state to resume root growth in spring. While November-transplanted red oaks began spring shoot growth with more new roots than March-transplanted trees, November- and March-transplanted willow oaks had similar amounts of new roots. No roots were regenerated outside the root balls at spring bud break for any of the willow oak treatments. While root regeneration was greatest outside the root balls of November-transplanted red oaks compared to March-transplanted trees, the earlier planting date did not confer advantages in terms of increased height and trunk diameter growth. In contrast to red oak, November-transplanted willow oaks exhibited greater trunk expansion than the March-transplants, even though each treatment had similar amounts of new roots at bud break. Therefore, under the conditions in this study, root growth prior to the first spring bud break appears not to affect post-transplant height and trunk growth. Therefore, due to the lack of early post-transplant root growth and modest pre-bud break root growth of both November- and March- transplanted red and willow oaks, early first-season irrigation practices should be focused on maintaining adequate soil moisture in the root ball and near adjacent soil.

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Table 2-1. Analysis of variance of regenerated root length and dry weight for northern red oak (*Quercus rubra* L.) and willow oak (*Q. phellos* L.) transplanted on 5 November 1999 or 10 March 2000 and excavated on either 15 January 2000 or 21 April 2000. n=6.

Transplant/Excavation Date	Length (mm)	Dry Wt (g)	Length (mm)	Dry Wt (g)	Length (mm)	Dry Wt (g)
	Inside Root Ball		Outside Root Ball		Total Root Length	
Northern Red Oak						
November-January (N-J)	0.0 (0.0)[z]	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
November-April (N-A)	306.0 (125.8)	0.072 (0.03)	170.8 (88.7)	0.027 (0.02)	476.8 (150.0)	0.098 (0.03)
March-April (M-A)	127.3 (61.3)	0.028 (0.01)	0.0 (0.0)	0.0 (0.0)	127.3 (61.3)	0.028 (0.01)
Willow Oak						
November-January	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
November-April	541.7 (360.7)	0.095 (0.06)	0.0 (0.0)	0.0 (0.0)	541.7 (360.7)	0.095 (0.06)
March-April	390.2 (169.6)	0.065 (0.04)	0.0 (0.0)	0.0 (0.0)	390.2 (169.6)	0.065 (0.04)
			P > F			
Northern Red Oak						
N-J vs. N-A	0.0172	0.0120	0.0324	0.0689	0.0026	0.0025
N-J vs. M-A	0.2826	0.2762	1.0000	1.0000	0.3513	0.3125
N-A vs. M-A	0.1387	0.1051	0.0324	0.0689	0.0185	0.0210
Willow Oak						
N-J vs. N-A	0.1168	0.1294	.	.	0.1168	0.1294
N-J vs. M-A	0.2492	0.2895	.	.	0.2492	0.2895
N-A vs. M-A	0.6482	0.6197	.	.	0.6482	0.6197

[z] SE mean in parentheses

Table 2-2. Analysis of variance of height and trunk diameter growth for northern red oak (*Quercus rubra* L.) and willow oak (*Q. phellos* L.) transplanted on 5 November 1999 or 10 March 2000. n=6.

Transplant Date	Height Growth (m)			Trunk Diameter Growth (mm)		
	2000	2001	2002	2000	2001	2002
Northern Red Oak						
November	0.315 (0.06)[z]	0.657 (0.10)	1.577 (0.04)	4.292 (1.01)	20.425 (2.14)	39.994 (2.75)
March	0.232 (0.04)	0.597 (0.12)	1.342 (0.24)	6.758 (2.05)	23.367 (2.06)	40.881 (5.65)
P > F	0.2747	0.7082	0.3565	0.3056	0.3451	0.8907
Willow Oak						
November	0.578 (0.05)	1.540 (0.17)	2.058 (0.20)	18.925 (1.23)	43.313 (2.74)	79.133 (3.86)
March	0.326 (0.15)	1.064 (0.20)	1.944 (0.32)	12.610 (1.97)	33.250 (2.44)	63.296 (4.02)
P > F	0.1918	0.1178	0.7901	0.0385	0.0287	0.0269

[z] SE mean in parentheses

Chapter 3

Root and Shoot Growth Periodicity of Balled-and-Burlapped and Pot-in-Pot Sugar Maple (*Acer saccharum* Marsh.) Transplanted at Different Times of Year

Abstract

Fundamental information regarding post-transplant root and shoot growth dynamics is needed to better understand tree establishment. The effect of transplanting on root and shoot growth periodicity is unknown. Therefore, periodic root, shoot, and trunk growth of balled-and-burlapped (B&B) and pot-in-pot (PIP) sugar maples (*Acer saccharum* Marsh.) transplanted at either leaf drop (November 2000), early winter (December 2000), early spring (March 2001), bud break (April 2001), or bud set (July 2001) were studied and compared to growth of non-transplanted trees that remained in a field bed and PIP growing system. In addition to studying root and shoot growth periodicity, end-of-season root length accumulation, shoot extension, and trunk expansion were compared among treatments. Transplanted and non-transplanted trees exhibited a pattern of maximum shoot extension in early May, maximum root growth in late May, and maximum trunk expansion in mid June. Maximum root growth was concurrent with early trunk expansion, both of which began at the time when shoot growth rate was decreasing. Root growth was characterized by a pattern of abundant growth in late May and June and less growth in summer and early fall. Based upon the observations in this study, transplanting in November, December, March, and April did not appear to radically disrupt the normal growth periodicity of sugar maple. However, July transplanting resulted in abundant root growth 11 weeks later than the other transplant treatments and non-transplanted treatments. Root mortality was evident for all treatments during winter and early spring but was minimal for the non-transplanted trees in the field. Non-transplanted trees in the PIP system exhibited dramatic declines in standing root length in winter and spring. Transplanting reduced total seasonal shoot extension and trunk expansion. Most transplanted treatments accumulated more standing

root length than the non-transplanted field treatment the first growing season after transplanting. Non-transplanted PIP trees exhibited the greatest standing root lengths.

Introduction

The inherent alternation between periods of abundant growth and little or no growth (periodicity) is thought to serve as a mechanism for coping with environmental stresses (e.g., temperature, drought) (Lyr and Garbe 1995; Reich et al. 1980). Periodic root and shoot growth may occur simultaneously in an apparent coordinated fashion (Cripps 1970; Dickson 1994; Harmer 1990; Harris et al. 1995; Harris and Fanelli 1999; Pagès and Serra 1994) or in an alternating pattern (Abod and Webster 1989; Bevington and Castle 1985; Deans 1979; Deans and Ford 1986; Harris et al. 1995; Harris and Fanelli 1999; Hinesley 1986; Kotze and Geldenhuys 1992; Lathrop and Mecklenburg 1971; Ploetz et al. 1993; Reich et al. 1980; Sibley et al. 1999; Thaler and Pages 1996). Many authors reported the occurrence of root growth prior to spring bud break (Abbott and Gough 1987; Atkinson 1980; Dell and Wallace 1983; Harris and Fanelli 1999; Kaushal et al. 1989; Lyr and Hoffman 1967; Mertens and Wright 1978; Morrow 1950; Wargo 1983). However, others have observed root growth beginning after spring bud break (Harris et al. 1995; Kaushal et al. 1989) or concomitant with shoot growth (Ford and Deans 1977; Harris et al. 1995; Wargo 1983). Differences in prevailing climatic conditions may produce different results in seemingly similar research projects (Cripps 1970).

Many woody plants exhibit a bimodal pattern of root growth, with periods of active root elongation occurring in late spring and autumn interspersed by a period of rest or reduced growth (i.e., summer) (Cripps 1970; Deans 1979; Deans and Ford 1986; Dell and Wallace 1983; Harris et al. 1995; Harris and Fanelli 1999; Roberts 1976; Wargo 1983). While an absolute cause for reduced root growth in summer is unknown, unfavorable environmental conditions (e.g., drought or high temperatures) have been suggested to be the cause (Harris and Fanelli 1999; Lyr and Hoffman 1967).

Root growth periodicity depends on genetic and species responses (Wargo 1983) to multiple interacting and interdependent factors such as root pruning, top pruning (Gilman 1990), soil moisture content (both excesses and shortages) (Bevington and

Castle 1985; Dell and Wallace 1983; Lyr and Hoffman 1967), mineral nutrition (Niemiera and Wright 1982), hormones (Richardson 1958), and transplanting (Harris et al. 2002; Wang and Zwiazek 1999). In addition, stage of shoot development (Bevington and Castle 1985; Cripps 1970) and maturity (age and reproductive) (Cripps 1970; Dickson 1994; Reich et al. 1980) were reported to influence root growth periodicity. Lack of winter root growth might be due to shoot dormancy or the absence of leaves and the subsequent lack of carbohydrate (Cripps 1970). Finally, root type and measurement method may influence perception of root growth periodicity (Harris et al. 1995). In many instances one dominant factor may appear to dictate root and shoot growth periodicity, but in most situations a combination of factors are responsible.

The functional balance hypothesis of Brouwer (1962; 1983) describes the growth relationship between roots and shoots as being continuously modified. Rhythmic shoot growth in trees is a consequence of feedback mechanisms associated with maintaining a favorable root:shoot ratio (Borchert 1973). Accordingly, rhythmic growth may result from water stress caused by an unfavorable root:shoot ratio that results from rapid shoot growth (Harmer 1990) and the resulting imbalance between transpiration and absorption (Reich et al. 1980). Due to the imbalance between transpiration and absorption, newly formed vascular systems may be unable to adequately supply nutrients and water to growing tissues and, as a result, shoot growth may be reduced.

A decline in starch reserves and carbohydrates during shoot elongation and a corresponding reduction in root growth were reported for several species (Deans and Ford 1986; Lathrop and Mecklenburg 1971; Parker 1970; Wargo 1979). Reduced root growth during periods of shoot expansion have been attributed to competition between roots and shoots for photosynthates and the subsequent reduced flow of photosynthates to the roots (Abod and Webster 1989; Bevington and Castle 1985; Deans 1979; Lathrop and Mecklenburg 1971; Lyr and Hoffman 1967; Reich et al. 1980; Thaler and Pages 1996). Dickson (1989) and Isebrands et al. (1994) determined that little photosynthate produced in mature leaves was translocated to the root system during a flush of shoot growth. However, after a flush of shoot growth (when the leaves had fully expanded) more than 90% of photosynthate was translocated to roots (Dickson 1991). Deans and Ford (1986) suggested that tree age affects assimilate supply to roots and consequently the timing and duration of root growth.

Root regeneration potential varies with season (Stone et al. 1962; Stone and Schubert 1959). For example, Larson (1984) reported greater root regeneration potential in spring- vs. fall-transplanted Austrian pine (*Pinus nigra* Arn.) and arborvitae (*Thuja occidentalis* L.), while Lathrop and Mecklenburg (1971) reported greater root regeneration in fall and early winter-transplanted vs. spring- and summer-transplanted *Taxus* spp. Harris et al. (2002) determined that early fall-transplanted sugar maple and northern red oak (*Q. rubra* L.) began root regeneration earlier and regenerated more roots in the first-season post-transplant than the mid fall- and spring-transplanted treatments. Similarly, root growth of spring-harvested Turkish hazelnut (*Corylus colurna* L.) exhibited a greater delay in root growth compared to fall-harvested trees (Harris et al. 2001). Alternatively, fringe tree (*Chionanthus virginicus* L.) did not regenerate roots outside of the transplanted root ball until early July regardless of season of transplant (Harris et al. 1996).

When field-grown trees are transplanted a small fraction (as little as 2%) of the root system is moved with the tree (Watson and Himelick 1983). Transplanted root balls may contain only 5 to 18% of the original fine roots (Watson and Sydnor 1987). Gilman and Beeson (1996) determined that while more than 90% of coarse (>10 mm diameter) root weight was within the confines of the root ball of field-grown trees, less than 15% of the fine, absorbing root weight (<2 mm diameter) was within the confines of the root ball. As a result of the substantial root loss that occurs when a tree is harvested for transplant, transplanted trees must regenerate a new root system, and until the newly transplanted tree does so, water and nutrient absorption will be limited. The quicker a root system is regenerated, the less moisture stress the transplanted tree will undergo and the greater the chance of survival (Struve and Moser 1984). Ultimately, successful establishment and growth of transplanted trees depends upon the rate of the regeneration of a new root system (Harris et al. 2001; Lathrop and Mecklenburg 1971; Watson and Himelick 1982).

Although fall transplanting may be superior to spring transplanting for most species (Alm 1983; Buckstrup and Bassuk 2000; Harris and Bassuk 1994; Harris et al. 1996; Harris et al. 1999; Hinesley 1986; Watson and Himelick 1983; Whitcomb 1984; Witherspoon and Lumis 1986), spring transplanting may be superior (Buckstrup and

Bassuk 2000; Harris and Bassuk 1994; Larson 1970) or have little advantage (Harris et al. 2001; Watson and Himelick 1982; 1983) to fall transplanting for other species. Season of transplant is important with respect to plant growth in two regards. First, seasons correspond to specific weather patterns (e.g., temperature, moisture) and light characteristics (e.g., daylength, and light intensity and quality) that influence plant growth. Second, seasons correlate to specific periods of growth and maturity (e.g., dormancy, leaf drop, bud set, flowering) (Harris et al. 1999). However, other factors such as post-transplant care, site conditions, and production, harvest and handling methods can also influence establishment of transplanted trees (Buckstrup and Bassuk 2000).

A more complete understanding of root system regeneration patterns and relationships between shoot and root growth of newly transplanted trees will enhance fundamental knowledge of root growth ecology. In addition, improved information regarding early root system regeneration can help tree-care professionals make better decisions regarding plant management and transplant timing, as well as devise practices that hasten the establishment of transplanted landscape trees. The objectives of this study were to determine the timing and magnitude of first-season root, shoot, and trunk growth of sugar maples grown in the field and transplanted with root balls wrapped in burlap (B&B) or grown in the pot-in-pot (PIP) system (Ruter 1997) and transplanted at various times of the year.

Materials and Methods

Plant Material Sparsely-branched sugar maples (1.2 m) were obtained from J. Frank Schmidt and Sons Co. (Boring, OR) and grown in a nursery bed or PIP production system for 2 years at the Urban Horticulture Center, Blacksburg, VA [USDA plant hardiness zone map (U.S. Departent of Agriculture 1990), AHS plant heat zone map 4 (American Horticultural Society 1997)]. Trees in the nursery bed were spaced 1.4 m apart in a row. Soil type in the nursery bed was a Groseclose silt loam (clayey, mixed, mesic Typic Hapludults) with pH 6.2. The PIP production system consisted of 51-L containers (B-15, Lerio, Mobile, AL) fitted in 51-L socket containers spaced 1.2 m on center in rows 1.5 m apart. Black landscape fabric covered the area between the sockets, and an underground drainage system ensured that growing containers were never in standing water. Container substrate consisted of unamended pine bark (pH 6.2). In September 2000, 24 uniform-sized field-grown and PIP trees were selected. Mean height for field-grown and PIP trees (SE mean in parentheses) were 2.62 (0.07) m and 2.84 (0.08) m, respectively. Trunk diameters, 15 cm above the soil line, were 69.8 (3.0) mm and 72.0 (1.8) mm for field-grown and PIP trees, respectively.

Treatments Treatments consisted of two production methods (B&B and PIP) and five transplant dates [3 November 2000 (leaf drop), 8 December 2000 (early winter), 16 March 2001 (early spring), 13 April 2001 (bud break), and 13 July 2001 (bud set)]. The July transplant date was selected as the date when twig extension had ceased on at least four of the five shoots being monitored on the non-transplanted control trees. A sixth transplant treatment served as a non-transplanted control. Rhizotrons for the non-transplanted control plants were located in the PIP system and nursery bed and could not be randomized in the same bed as the transplanted trees. Subsequently, the experimental design consisted of a 2 x 5 factorial arranged in a completely randomized design and augmented with two non-transplanted controls (field and PIP trees). There were four replications of each treatment (B&B/November, PIP/November, B&B/December, PIP/December, B&B/March, PIP/March, B&B/April, PIP/April, B&B/July, PIP/July, non-transplanted field, and non-transplanted PIP).

Rhizotron Construction Three types of rhizotrons were constructed. A field rhizotron (FR) was constructed for the non-transplanted field trees. PIP rhizotrons (PIPR) were constructed for the non-transplanted PIP trees. Finally, trees were transplanted into aboveground root observation chambers or rhizotrons (AGR).

On 2 September 2000, one FR with four root observation bays was constructed on the north side of four trees in the nursery bed where the transplanted trees were planted (Figs. A-1 and A-2 in Appendix A). Trees in the FR were spaced 1.4 m apart. The FR was constructed by excavating a 56 cm wide x 6 m long x 56 cm deep trench with a backhoe. To prevent excessive damage to the non-transplanted control trees during the excavation of the rhizotron trench, trees were root pruned with a spade along the length of the trench 2 days prior to excavation. Four bays, each 61 cm wide x 36 cm long, were excavated by hand and extended from the trench to 30 cm from the base of the trees. Plywood retaining walls were installed at the ends of each bay and the backside of the trench. Each plywood panel was held upright by fence stakes. Squares of approximate 40 cm wide x 35 cm high dimensions were cut out of the plywood panels and fitted with clear, polycarbonate plates (GE Worldwide Manufacturing Sites, Mount Vernon, IN). Each clear plate was fastened on the interior of the plywood with screws and sealed with sealant, thereby creating small root observation windows. Burlap was used to minimize erosion of the soil between the bays of the FR. Approximately 8 cm of gravel was spread in the bottom of the trench. Light was excluded from the rhizotron windows by plywood "shutters" and black plastic flaps attached above each shutter. The entire rhizotron (trench plus four bays) was covered with a large sheet of plywood that was removed during measurements. A 25 cm x 25 cm grid with lines in 5 cm increments was drawn on the windows of all rhizotrons.

PIPRs were constructed by cutting 28 cm x 28 cm windows in the sides of 51-L containers and fitting the windows with clear, polycarbonate plates marked with 25 cm x 25 cm grid with lines at 5 cm increments. Sealant was applied around the interior of the windows. Light was excluded from the rhizotron window by the socket-pot (in ground) in which the rhizotrons were inserted (Figs. A-3 and A-4 in Appendix A). Trees transplanted into the PIPR were spaced 1.2 m on center in rows 1.5 m apart. The non-transplanted PIP trees were set into PIPRs on 2 September 2000.

AGRs were constructed from Keeper-Uppers (KU) (Lerio, Mobile, AL). KU are black plastic, flat-topped, pyramidal, bottomless shells with square bases (58 cm x 58 cm wide and 38 cm tall) and circular openings (43 cm diameter) in the top. KU are normally used to protect containerized trees from windthrow and extreme temperature fluctuations in the root zone (Kelting et al. 1998). Windows 30 cm x 30 cm wide were cut out on one side of each KU and fitted with 6.4 mm thick clear, polycarbonate plates. Plates were fastened to the interior of the KUs with screws, thereby creating root observation windows. Sealant (DAP Inc., Baltimore, MD) was applied around the interior perimeter of the window. To exclude light, flaps of black plastic were taped above the windows. Foil-covered plastic bubble insulation (Reflectix Inc., Markleville, IN) was wrapped and glued around each rhizotron (except the area of the window) to stabilize soil and substrate temperatures. Additional foil insulation wraps were made to cover the rhizotron windows and black plastic flaps (Figs. A-5 and A-6 in Appendix A). Insulation flaps were held in place with Velcro tabs (Velcro® Brand Industrial Strength Fasteners, Velcro USA Inc., Manchester, NH). A 25 cm x 25 cm grid with lines in 5 cm increments was drawn on the windows of all rhizotrons. AGRs were spaced 1.2 m apart in beds that were 4.3 m apart and positioned so windows faced north.

Tree Harvest and Planting Field-grown trees were hand dug with 51-cm diameter root balls, wrapped with industry-standard copper sulfate-treated burlap (A.M. Leonard, Piqua, OH), and tightly laced with sisal twine [balled-and-burlapped (B&B)]. Circling roots on PIP trees were pruned to prevent further circling and encourage root exploration into the surrounding soil and substrate. The dense layer (approximately 1) of roots on the bottoms of the root balls of all PIP trees was also removed. Because both B&B and PIP root balls were too wide to pass through the tops of the AGRs, the rhizotrons were carefully lowered over the tops of the trees, making sure not to damage the buds and twigs. Root balls were positioned close to (approximately 2 cm) and centered in front of the windows. After positioning the trees in the rhizotrons, 1:1 (volume:volume) mixture of sphagnum peat and coarse sand was used to fill the space between the root balls and AGR windows. Burlap and twine were loosened from around the tree trunks but left intact around the root ball on field-grown trees. All transplanted trees were flood irrigated after transplanting, and spaces that opened up between the root ball and windows were filled with the peat-sand mixture. All transplanted trees were mulched with approximately 7 cm mixed hardwood mulch after all spaces had been closed. The non-transplanted PIP trees were fitted into PIPRs after pruning circling roots from the outer layer of the root ball and removing the dense root layer at the bottom of the root balls. Unamended pine bark (pH 6.3) was used to fill the spaces between the root balls and PIPR windows. Except for installation of the rhizotron, no modifications were made to the four non-transplanted control trees that were left in the field. The same mixture of sphagnum peat and coarse sand used to fill the space between the root balls and AGR windows was used to fill the space between the soil profile and FR windows.

Tree Care: Fertilization, Irrigation, etc. Trees were fertilized in 2001 and 2002 with 200 grams of encapsulated slow release fertilizer (15N-3.9P-10K, Osmocote Plus 15N-9P_2O_5-12K_2O, 8-9 Month Northern Formula, The Scotts Co., Marysville, OH) just prior spring bud break each year. All trees were irrigated with a micro-irrigation system in such a manner as to maintain soil and substrate moisture near field/container capacity. During the first growing season (2001), trees in the AGR and FR were irrigated twice a week for approximately 2 hr. Trees were irrigated approximately once a week during 2002. Trees in the PIPR were irrigated twice a day for 15 minutes both years. Irrigation occurred less often when sufficient rainfall was received or after leaf drop. Minimal irrigation was applied during the winter months, when trees were dormant. Weeds were eliminated by hand pulling and applications of RoundUp Pro® (41% glyphosate, Monsanto Company, St. Louis, MO) and pre-emergent herbicides Snapshot 2.5TG (0.5% isoxaben and 2.0% trifluralin, Dow AgroSciences LLC, Indianapolis, IN), Pendulum® WDG (60% pendimethalin, BASF Corp., Research Triangle Park, NC), and Surflan A.S. (40.4% oryzalin, Dow AgroSciences LLC, Indianapolis, IN). Herbicides were diluted and mixed according to manufacturers recommendations. Due to strong wind, two trees from the July transplant treatment had to be staked after transplanting. Survival was 100% for all B&B trees. However, three PIP trees died over the course of the project. Two trees (one PIP/March and one PIP/April) died of unknown causes and one tree snapped at the base of the trunk during a windstorm (PIP/March).

Measurements Root length, shoot extension, and trunk diameter were measured from the time of installation of the control rhizotrons (2 September 2000) until after bud set two springs later (9 June 2002 for transplanted trees and 23 July 2002 for the non-transplanted controls). On 10 June 2002 all transplanted trees were excavated to estimate regenerated root mass and length (described below). Growth of the non-transplanted controls was measured until 23 July 2002, at which time shoot extension had ceased and trunk expansion had slowed.

Shoot extension for each tree was determined by obtaining the mean extension of five lateral shoots, which were selected at bud break in spring 2001. Shoots were selected based upon apparent potential for high vigor, assessed by the robustness of the opening bud. When more than 50% of buds on an individual tree were open or had visible leaves, that tree was considered to have achieved bud break. In instances when a shoot developed multiple terminal shoots and buds, the less dominant shoots were pinched back and measurements were taken on the remaining shoot.

Due to excess soil covering the original soil line, all soil above the first major root within root balls of field-grown trees was removed at transplanting. Trunk diameter 15 cm above the soil or substrate line was measured on all trees just after transplanting or installation of the FR and PIPR. Trunk diameter was the mean of two measurements, one made parallel to the nursery bed and the other made perpendicular to the nursery bed. Tree trunks were marked to ensure the same measurement point at each consecutive measurement. Beginning at bud break, shoot extension and trunk expansion were measured weekly and biweekly, respectively, except for the period between fall leaf drop and spring bud break, when measurements were not made.

Root length against rhizotron windows was estimated weekly until root growth apparently ceased in winter. During winter, root length was estimated monthly until early spring, at which time weekly estimations resumed. Root length against the rhizotron windows was calculated using the line-intersect method (Marsh 1971; Newman 1966; Tennant 1975), which uses a grid to approximate length. One count was assigned whenever a root crossed a grid line, a root tip touched a line, or a curved portion of the root touched the line. Two counts were assigned whenever a root segment lay along a line. Root/line intersections were counted by traversing the horizontal lines followed by the vertical lines. Counts were then tallied and converted to length measurements using: $R = (11/14)(N)(\text{grid unit})$ where N = total root/line intersections and grid unit = 5 cm. Due to the development of extraordinarily dense root mats in two of the non-transplanted PIP trees, where it became impossible to accurately count individual roots, the bottom row of the grid was eliminated (Fig. A-7 in Appendix A).

Soil and substrate temperatures were monitored with thermocouples (Model HH21 Microprocessor Thermometer, Type J-K-T Thermocouple, Omega Engineering, Inc., Stamford, CT) placed 30 cm (12 in) deep in a randomly selected AGR, PIPR, FR, and nursery bed. Afternoon temperatures were recorded twice weekly for the duration of the project.

On 10 June 2002, root systems of all transplanted trees were excavated to quantify post-transplant root regeneration. All regenerated roots beyond the original root ball were removed from within the AGR and from 20 cm directly beneath the “footprint” (76 cm x

76 cm) of the rhizotrons. Regenerated roots from each individual tree were stored in a dark 6 C cooler until processing for weight and length measurements.

To determine the relationship between root length and mass, three representative samples of harvested roots from the PIP and three from the B&B treatments were randomly selected. Subsamples of each of the PIP and B&B samples were obtained by visually separating the root systems into four equal sized groups with equal representation of each root diameter class. Root length of ¼ each of the six root systems was quantified using the WinRhizo V5.0A (Régent Instruments Inc., Québec, QC, Canada) root analysis system. Following the estimation of root length, all root systems were dried to a constant mass at 52 C and weighed.

Analysis Two types of graphs were generated to gain a complete picture of post-transplant periodicity (scaled daily growth rate) and growth (accumulated biomass/standing crop). Standing crop refers to the amount of biomass that exists at any moment in time and may also be referred to as accumulated biomass. While the periodicity graphs present data in such a manner that timing and relative magnitude of growth are emphasized, the accumulated biomass/standing crop graphs provide a quantitative depiction of the cumulative changes in length and diameter among treatments.

Scaled daily growth rates were calculated for each individual tree by dividing the change in length (root and shoot) or diameter (trunk) for each measurement period by the maximum recorded measurement for the duration of the study and the number of days between measurements (Harris et al. 1995). The following equation was used: $[((T_x-T_{x-1})/T_{max}) / N] * 100$, where T_x = measurement at time x, T_{x-1} = measurement at the time before x, T_{max} = maximum recorded measurement for the duration of the study (length or diameter), N = number of days between T_x and T_{x-1}. Daily growth rates were scaled to a percentage of the total growth to emphasize the timing and magnitude of shoot, trunk, and root growth and mortality for each individual treatment. Soil temperatures and mean of scaled daily growth rates were plotted over time to produce the seasonal pattern of growth and mortality (i.e., periodicity) of each treatment. Additionally, mean accumulated root length, shoot extension, and trunk expansion were plotted over time to highlight differences in magnitude of growth and accumulated biomass/standing crop among treatments.

End-of-season shoot extension, trunk expansion, root length accumulation (or standing root length), and harvested root data were subjected to analysis of variance to determine significance of treatments. Statistical comparisons were made using linear contrasts within the MIXED procedure of the Statistical Analysis System (SAS) for Windows version 8.02 (SAS Institute, Cary, NC). First-season growth (2001) was equal to the total length or diameter after one growing season. Second-season growth (2002) was equal to the total accumulated length or diameter after two growing seasons (cumulative).

Results and Discussion

Root systems are dynamic organs, where growth (i.e. elongation of existing roots and/or initiation and elongation of new roots) and mortality occur simultaneously. In this study, root growth and mortality were not measured separately. Instead, root lengths reported here incorporate processes of both root growth and mortality and reflect changes in overall length density of live roots (standing crop). The term ‘root growth’ in the following text refers to ‘increases in standing root length’ and is synonymous with ‘accumulations in root length’. A root that disappeared from the viewing area was considered dead (Jones et al. 2003). Therefore, increases in root length signify instances where growth exceeds mortality and decreases in root length indicate that mortality exceeds growth.

Periodicity

Shoot and Trunk Diameter Growth During 2001, maximum rate of shoot extension for all treatments except March-transplanted B&B and PIP trees occurred on 3 May (Figs. 3-1 and 3-2). Maximum shoot extension rate for both B&B and PIP/March transplants peaked 2 weeks prior to the other treatments (16 April). The beginning and seasonal end of shoot extension for non-transplanted trees occurred around 16 April and 17 May, respectively (Figs. 3-2A and 3-2G). Shoot extension in the non-transplanted trees generally ended 3 weeks later (7 June) than transplanted B&B and PIP trees (17

May). In 2002, shoot extension did not exhibit the same well-defined peak as in 2001. Instead, maximum shoot extension rate was on 23 April for the March and July treatments and 9 and 16 May for all other treatments. The beginning and seasonal end of shoot extension during the second year after transplanting (2002) was shifted approximately 1 week later than the first year (2001) (23 April to 31 May). Total duration lasted slightly longer in 2002. Morrow (1950) reported a much longer duration (1 May until 15 August) of shoot growth in a mature stand of sugar maples in central New York (USDA Plant hardiness zone 5a). The longer duration of shoot extension of the trees in Morrows' study was likely due to tree age and climate differences.

Morrow (1950) reported that 85% of annual shoot extension was completed prior to 15 June. In this study, however, 93% and 97% of the total annual shoot extension of transplanted and non-transplanted trees, respectively, was completed by 15 June in 2001. While 87% of annual shoot extension was completed by 10 May in the transplanted trees (averaged across all transplanted treatments except July), the same percentage of extension was completed around 20 May in the non-transplanted trees (average of the B&B and PIP trees). Findings were similar in 2002. Rapid early-season shoot extension has been reported in other temperate species. For example, Kienholz (1941) reported that 90% of annual shoot extension in American beech (*Fagus grandifolia* Ehrenb.) was completed within a 4-week period and the total period of growth lasted approximately 60 days. Since a relatively short period of time was responsible for the majority of shoot growth in sugar maple, landscape managers should reduce additional stresses imposed on the newly transplanted sugar maples (e.g., drought, predator pressure) during this critical period to maximize seasonal growth.

Trunk expansion began as the rate of shoot extension declined, with minimal overlap occurring between the periods of shoot extension and trunk expansion (Fig. 3-2). The rate of trunk expansion was at a maximum between 7 June and 5 July in 2001 and on 10 June in 2002. The beginning and seasonal end of trunk expansion were early June and early September in 2001, respectively. In 2002, the beginning of trunk expansion occurred around mid May, at which time shoot extension had slowed and root growth was well underway. Transplanted trees were harvested on 10 June 2002, which was prior to the seasonal end of trunk expansion in 2002. However, trunk expansion of the non-transplanted trees was followed until 24 July 2002, at which time trunk expansion had slowed. Morrow (1950) reported that trunk expansion of sugar maple paralleled and lasted 2 weeks longer than shoot extension and occurred between May 1 and August 31, with 80% being complete by July 1. In this study, 72% and 48% of total annual (2001) trunk expansion of transplanted and non-transplanted trees, respectively, was completed by 5 July. Eighty percent total annual trunk expansion of transplanted and non-transplanted trees was achieved by 19 July and 2 August 2001, respectively.

Root Growth Approximately 97% of annual (2001) accumulated root length of non-transplanted field trees occurred by late June in this study. Morrow (1950) reported that 80% of annual root growth occurred between mid March and late June. Root growth of non-transplanted PIP trees in this study was much more spread out and only 44% of the total annual accumulated root length had occurred by late June 2001. Averaged across all transplant treatments, 85% and 87% of annual accumulated root length of PIP and B&B trees occurred by late June 2001. Data from this study are similar to that reported by Harris and Fanelli (1999) for root elongation of non-transplanted PIP sugar maples.

The period of maximum root growth in 2001 was variable and occurred between 17 May and 14 June for all treatments except in the July transplants (Fig. 3-1). In 2002, maximum rate of root growth occurred in all treatments between 10 May and 30 May. In 2001, the onset of root growth was between 9 May and 17 May. Similarly, in 2002, the onset of root growth was 10 May, a time when considerable mortality was still occurring in some individuals. Root growth of the non-transplanted PIP trees did not exhibit the dramatic, same well-defined peak of maximum rate of root growth and instead, was more sustained compared to the other treatments (Fig. 3-2). Cessation of root growth in 2001 ranged between mid July and mid September, depending upon the treatment. The time of cessation was determined to be the time when mortality outweighed growth. Transplanted trees were harvested prior to the cessation of root growth in 2002. However, root growth rate in the transplanted trees had begun to decrease just prior to harvest on 10 June.

Similar to the trend shown by Harris and Fanelli (1999) of maximal root growth immediately following shoot growth for non-transplanted PIP sugar maple trees, maximal root growth was observed in this study at a time immediately following the period of maximal shoot extension for transplanted and non-transplanted trees (Fig. 3-2). During a flush of shoot growth, shoots act as a stronger sink than roots (Watson and Himelick 1982). The sink strength of expanding shoots may result in a reduced flow of photosynthates to roots and a corresponding reduction in root growth (Watson and Himelick 1982). As leaves expand and photosynthetic capacity increases (Dickmann 1971), shoots become a source of carbohydrates for the rest of the plant, and root growth resumes.

Regenerated roots were observed in the July-transplanted trees 3 weeks following transplant (2 August 2001), a time when root growth had slowed in the other treatments, and reached a maximum on 16 August (5 weeks post-transplant) for both B&B and PIP July transplants (Fig. 3-1). Root growth in the July-transplanted trees ceased around 15 October. Conditions in this study (e.g., regular irrigation) were favorable for root growth at the July transplanting. Data from this study indicate that summer transplanting of sugar maples can be very successful if root balls are kept well irrigated after transplanting. While root regeneration was apparent in the July-transplanted trees 21 days after transplanting, root regeneration was observed 33 and 26 days after transplanting for the March and April treatments, respectively. Similarly, Kelting (1998) reported root regeneration 38 days post-transplant in March-transplanted red maples. The results of this study indicate that root regeneration was not delayed in fully foliated trees (July) relative to other transplanting dates. Root growth potential may be high during July due to favorable conditions, such as warm soil temperatures, long daylength, and fully developed tree crowns capable of producing carbohydrates that can be used for root regeneration (Watson et al. 1986). April offers warm soils, ample soil moisture, and a reduced potential for desiccation (Acquaah 1999; Harris and Fanelli 1999; Himelick 1981; Watson et al. 1986).

Morrow (1950) concluded that late winter and spring root growth were limited by low soil temperature. While Harris and Fanelli (1999) reported that root elongation in PIP sugar maple began around 1 April (1996) in southwest Virginia when substrate temperature was approximately 10 C, increasing root length in the PIPR in this study began on 5 May in 2001 and 23 May in 2002, when substrate temperatures were approximately 16 C and 13 C (Figs. 3-1B and 3-3). A small amount of root growth occurred around 20 March 2001; however, this increase was only temporary. Harris and

Fanelli (1999) also reported the occurrence of root elongation prior to spring bud break (1 May) and a temporary interruption in root elongation that corresponded to bud break. Their data, however, indicated much more substantial pre-bud break root growth activity than was observed in this study. Similarly, Morrow (1950) reported bud break 3 weeks after the resumption of root growth in spring. Substantial increases in root length were not, however, observed in this study until after shoot growth was well underway. While the differences between the results of the Harris and Fanelli (1999) study and this study may be due to year-to-year variation in weather, differences are more likely due to methods employed in the studies. Harris and Fanelli (1999) followed individual roots to determine when roots were elongating. In this study, the line-intersect method was used to count root/line intersections on a weekly basis, without following individual roots. Therefore, data in this study reflect changes in the standing root crop or changes in total root length. Root growth may have been occurring earlier in this study, but it did not result in increases in root length until growth processes outweighed mortality processes. In other words, root mortality could have been masking root growth processes. However, in a secondary study addressing fine root mortality in the same trees and where the appearance and disappearance of individual roots were tracked (see Chapter 4), substantial pre-bud break root elongation was observed only in the non-transplanted field trees. Therefore, it is likely that increases in net root length in this study were not detected due to root mortality masking root growth.

Harris and Fanelli (1999) reported substantial root elongation after bud set and until leaf drop (1 November) when substrate temperatures dropped below 5 to 7 C. Increases in root length were observed in the non-transplanted PIP trees in this study until late October, when temperatures were approximately 13 C (Figs. 3-1 and 3-2). Afternoon substrate temperatures in the PIPR did not drop below 10 C until after 12 November in 2001. Of note, accumulations of root length in the non-transplanted field trees and transplanted trees slowed between mid July and late October, before soil temperatures dropped to levels unfavorable for root growth. Morrow (1950) credited the lack of abundant root growth in fall, when soil temperatures and moisture were presumably non-limiting, to internal growth mechanisms that dictate an inherent growth pattern that is mediated by environmental factors (e.g., soil moisture and temperature). Observations from this study also suggest an inherent growth pattern.

Harris and Fanelli (1999) also reported a temporary cessation of root elongation in August when substrate temperatures in the PIPR approximated 25 C to 30 C. While little reduction in root growth rate was observed at this time in the non-transplanted PIP trees, a temporary decrease in the rate of root growth was observed in early July (Figs. 3-2G and 3-5). Measured substrate temperatures in the PIPR in this study did not exceed 27 C at any sampling time during the study and, thus, may have remained below the supraoptimal range for sugar maple root growth.

Both Harris and Fanelli (1999) and Morrow (1950) reported minimal root elongation in winter. Similarly, minimal root length accumulation was observed in this study in winter 2000-2001. In winter 2001-2002, however, root mortality dominated the winter root activities of all treatments except the non-transplanted field trees (Fig. 3-4 and 3-5). Surprisingly, substantial mortality occurred in many treatments after 1 May 2002, at a time just prior to the spring flush of shoot growth. While Harris and Fanelli (1999) and Morrow (1950) only reported new growth activity (production), net root growth (production less mortality) was reported in this study. Therefore, root mortality likely occurred in the other studies as well.

Morrow (1950) suggested that, because periods of maximum root and shoot growth occurred at a similar time, considerable competition likely occurs between the organs for assimilates. Stored carbon in roots is essential to growth of roots and leaves early in the growing season (Eissenstat and Yanai 1997). Therefore, root carbon stores may be mobilized to supply carbon to the newly growing shoots. Competition for assimilates between roots and shoots and the expense of maintenance respiration of the roots may be partly responsible for winter and spring root mortality. While substantial root mortality occurred in winter 2001-2002, no mortality was observed over the course of winter 2000-2001 and instead minimal root growth was recorded. This winter root growth did not show up on the graphs because it represented such a minor percentage of the total root length.

In all treatments, 2002 root growth rates were not as great as 2001 growth rates (Fig. 3-2). Root:shoot ratios of transplanted trees eventually reestablish to pre-transplant levels (Kozlowski and Pallardy 1997). A reduction in the rate of root growth in 2002 may reflect this changing growth pattern. Alternatively, root growth activity may have shifted to areas beyond the view of the rhizotron (e.g., surrounding soil). However, upon extraction of the root systems of the transplanted trees, most regenerated roots were found within the AGR (rhizotron surrounding transplanted trees) and only minimal root exploration occurred outside of the footprint of the rhizotron. Trees in the PIPR may not have exhibited as drastic a reduction in root growth during 2002 as the other treatments due to the sizeable mortality that occurred over winter 2001-2002 and the subsequent need to regenerate the lost portion of the root system to support the trees during the summer months. Additionally, non-transplanted trees in the PIPR followed a different pattern of growth, characterized by a longer and steadier rate of root growth that occurred between May 1 and October 1, than the transplanted treatments and non-transplanted, field treatments (Fig. 3-4B). As a result, the spike of root growth that characterized other treatments was not evident in the non-transplanted PIP trees in 2001.

Accumulation of Biomass/Standing Crop

Shoot and Trunk Diameter Growth Among B&B treatments, the non-transplanted trees had more than twice the shoot extension during the first growing season (2001) as the transplanted trees (Fig. 3-4A). However, among PIP treatments, shoot extension of the non-transplanted and transplanted treatments was similar, except for the December and March treatments, which had less extension (Fig. 3-4B).

Compared to the non-transplanted treatments, all transplanted treatments except July (transplanted after shoot extension ceased in 2001) exhibited a reduction in shoot extension the first-season following transplant (Fig. 3-4 and Table 3-2). First-season reductions in shoot extension of the transplanted treatments may be partially attributed to the inadequacies of the newly transplanted root system at supplying sufficient moisture to drive maximum shoot extension (Alvim and Alvim 1976). The terms ‘planting check’ (Mullin 1963) and ‘transplant shock’ (Watson 1986) have been used to refer to the period of prolonged reduction of top growth, which is presumably a consequence of the imbalance between the root system and crown that results from transplanting. The duration of planting check depends upon the time necessary for the reestablishment of a root system that is capable of providing sufficient water and nutrients to the tree (Mullin

1963). Alternatively, reductions in shoot growth may involve wound responses to injuries to the root system incurred during transplanting.

Trunk expansion of PIP trees was not affected by time of transplanting (July excluded) (Fig. 3-4B). However, among the B&B trees, transplanting reduced trunk expansion (Fig. 3-4A). Similar to the reductions in shoot extension and trunk expansion exhibited by B&B transplanted trees in this study, Harris et al. (1998) reported that trunk expansion and twig extension of B&B sugar maples were 29% and 18%, respectively, of non-transplanted trees 2 years after transplanting.

Root Growth Among B&B treatments, April transplants had the greatest accumulation of root length by the end of the growing season and the greatest reduction of root length over winter (Fig. 3-4A). Root growth in the B&B/April transplants lasted approximately 8 weeks longer than the other B&B transplants, resulting in root length increases until late August. Among PIP treatments, accumulations of root length of non-transplanted trees was nearly twice the length of transplanted trees (Fig. 3-4B). [*Note:* Due to the development of a dense root mat (Fig. A-7 in Appendix A) in two trees in the PIPR, the bottom row of the rhizotron grid of each tree was eliminated. Had the root mat not been eliminated, root lengths of the non-transplanted PIP treatment would have been even higher, thus, accentuating any differences between the non-transplanted PIP treatment and the transplanted PIP treatments.] Additionally, root length accumulation of non-transplanted PIP trees continued until much later in the season (early October) compared the transplanted trees (early July). The non-transplanted PIP trees also underwent much greater root mortality during winter and early spring. The more extensive and later growth of non-transplanted PIP trees compared to transplanted PIP trees may have been due to the root systems of the non-transplanted trees in the PIPR being bound by containers. Subsequently, any root growth would probably be detected, resulting in greater root length and possibly extending the time frame of growth. Conversely, roots of the transplanted trees may have reached a density such that growth in the open-bottomed AGR was no longer favorable, and roots may have escaped into the ground below. Research of Jones et al. (2003) determined that when understory vegetation in a pine woodland was removed, pine root production compensated for reductions in non-pine roots. As a result, total growth of pine plus non-pine roots was nearly constant. The authors concluded that there was a 1:1 replacement of pine and non-pine roots and that compensatory growth of pine roots occurred when non-pine roots were artificially removed. Their data supported the notion of a resource-controlled carrying capacity for roots in the rhizosphere. Alternatively, differences in growth of trees in the PIPR and the other PIP treatments might be attributable to substrate and soil temperatures and media factors (native soil vs. pine bark). Summer temperatures in the PIPR were approximately 3 to 6 C warmer than any of the other locations for which temperature was measured (Fig. 3-3) but did not exceed 27 C at any measurement.

Also noteworthy was that standing root length of both the B&B/July and PIP/July treatments was similar to the with the other treatments in less than 8 weeks, including 4 weeks where little root growth actually occurred (Fig. 3-4). Similar to all other treatments except the non-transplanted PIP and B&B/April treatments, growth of the July-transplanted trees exhibited a leveling off of growth after approximately 8 weeks.

While Harris and Fanelli (1999) measured 7.5 m of sugar maple root growth against the 25 cm x 25 cm face of a PIPR over the course of their project (February 1995 to May 1996), over 20 m of root length in the same PIPR system and rhizotron observation area was measured after 1 year in this study (Fig. 3-4B). However, the trees in this project were larger (approximately 0.85 m taller) and therefore had more extensive root systems (Fig. 3-4B).

While 2002 standing root length of non-transplanted field treatment remained relatively unchanged from 2001, standing root length of the non-transplanted PIP treatment in fluctuated more than any of the other treatments (Fig. 3-5). Between late January and mid May 2002, standing root length in the PIPR decreased 31%. Similar to the non-transplanted PIP treatment, all transplanted treatments underwent substantial reductions in standing root length during winter and early spring in 2001-2002, possibly due to microenvironment differences between the types of rhizotrons. Late fall, winter, and early spring temperatures in the AGR and FR were nearly identical (within 1 C). However, cool season temperatures in the PIPR were slightly (1 to 3 C) warmer than the AGR or FR. Differences in substrate and soil characteristics may also have affected root mortality and decomposition. The substrate and soil of the AGRs and FR consisted of native soil with a layer of peat and sand between the root ball (B&B and PIP root balls consisted of native soil and pine bark, respectively) or soil profile and rhizotron windows, while all substrate in the PIPR consisted of unamended pine bark. The combination of pine bark media and warmer temperatures may have contributed to decomposition processes of roots as well as greater activity of soil microorganisms (Head 1973). Alternatively, the first roots regenerated after a tree is transplanted may serve as ‘temporary’ roots and not have as long of an inherent lifespan. Watson and Himelick (1982; 1983) reported that while numerous roots are produced from each severed root end, in most cases one (or at most, a few) root will become dominant with time and the remainder of the small roots will eventually die (Watson 1986). Over time, the root system will begin to resemble the original root system in both structure and distribution (Watson 1986). The observed reductions in standing root length may have been a result of the death of these ‘temporary’ roots. However, these explanations would not explain why the ‘temporary’ roots regenerated by the non-transplanted trees did not exhibit the same pattern during the first winter after the installation of the FR and PIPR.

Interestingly, increases in root length of all treatments during the first spring and summer after transplanting (2001) were markedly greater than increases in root length the following spring (2002) (Fig. 3-4). While root growth of the transplanted treatments was only measured until mid June during 2002, significant root growth had occurred by this time in 2001. The lack of abundant root growth in late May and early June may have been a result of root growth activity mostly occurring outside the bounds of the AGR. Root growth may also have slowed due to a shifting root:shoot ratio. Alternatively, root length density may have reached a steady state where it was no longer favorable for root exploration to occur in this area due to increased competition among roots for resources (as discussed previously).

Analysis of End-of-Season Growth

End-of-season shoot extension, trunk expansion, and root length accumulation were analyzed to determine the effect of production method (PIP vs. field-grown/B&B) and transplant date (November, December, March, April, and July) on cumulative first and second-season post-transplant growth. Plots of the production method and transplant date interaction were created to elucidate the nature of the interactions (Fig. 3-6).

Shoot Growth Due to shoot growth having been completed prior to the July transplant date, the July transplant treatment is excluded in discussion of first-season shoot growth.

Analysis of variance revealed evidence of an interaction between production method and transplant date during the first ($P = 0.0989$) and second seasons ($P = 0.0072$) after transplanting (Fig. 3-6A-B, Tables 3-2 and 3-3). Upon inspection of the interactions, several features become apparent that reinforce earlier conclusions. First, transplanting resulted in dramatic reductions in shoot extension among the B&B treatments during the first growing season after transplant compared to the non-transplanted, field treatment. Among the B&B treatments, transplanted trees had much less shoot extension than non-transplanted trees during the first- and second-seasons after transplant (Fig. 3-6A-B, Tables 3-2 and 3-3). This reduction in shoot growth may be due to an inability of the newly transplanted trees to supply sufficient moisture to drive maximum shoot expansion. Trees in this study were kept well-irrigated. Alternatively, reductions in shoot extension may be a result of competition between the roots and shoots for assimilates, with root regeneration taking precedence over shoot extension. Several authors suggest that after a tree looses a significant portion of its roots (e.g., at transplanting), the root:shoot ratio is restored by coordinating growth to correct the disrupted ratio (Abod and Webster 1989; Borchert 1973; Wareing 1970). As well, roots store carbon and the loss of roots may represent a substantial carbon loss to the transplanted tree. The major root loss due to transplanting results in stress to the transplanted tree and a corresponding period of reduced vigor in the crown (Watson 1986). The interactions also indicate that shoot extension of the non-transplanted, field trees was much greater than the non-transplanted PIP trees for both 2001 and 2002 (Fig. 3-6A-B, Tables 3-2 and 3-3). This difference was probably a result of the confined root systems of PIP trees versus non-confined root systems for field-grown trees. PIP trees had probably reached a “pot-bound” condition by 2001.

Among the transplanted B&B treatments, December transplants exhibited the greatest shoot extension, and after the second-season of growth, shoot extension of the December treatment was greater than November and April treatments ($P = 0.0980$ and 0.0596, respectively) (Fig. 3-6A-B, Tables 3-2 and 3-3). However, among the PIP treatments, the April transplants had the greatest shoot extension for both years. After the first-season, PIP/April shoot extension was greater than shoot extension of the December and March treatments (*P* = 0.0525 and 0.0316, respectively). After the second-season, shoot extension of the PIP/April was greater than the non-transplanted PIP treatment and PIP/December, March, and July treatments (*P* = 0.0110, 0.0064 and 0.0513, respectively).

One final noteworthy feature of the plots of the interactions illustrates the effect of transplanting on shoot extension. The 2001 and 2002 shoot extension data of both the B&B and PIP/July transplants reveal a decline in shoot extension during the first growing season after transplant (Fig. 3-6A-B). (The July treatment was transplanted after shoot flush and subsequent bud set in 2001 and therefore, 2002 shoot extension is really the first-season shoot extension for the July transplants). While the reduction in shoot growth of fall and spring-transplanted PIP trees may be a result of inadequate moisture for maximal shoot extension, July transplants had ample time to regenerate lost roots and regenerated similar root lengths as the other transplanted treatments (Fig. 3-4). Therefore, the July treatments had a similar capability to supply moisture to the transplanted trees as the other transplanted treatments if the initial shock of substantial root loss is overcome. Data from this study indicate that shoot extension in 2002 of the PIP/July transplants did not differ from the shoot extension of the PIP/November, December, and March transplant dates (*P* = 0.2226, 0.4736, and 0.2086, respectively) (Tables 3-2 and 3-3). Similarly, shoot extension in 2002 of the B&B/July transplants did not differ from the shoot extension of any of the other B&B transplant dates. All trees in this project were kept well irrigated throughout the duration of the project. In a study assessing vigor (determined by annual twig growth) of sugar maple following transplanting, Watson et al. (1986) determined that July transplants had much greater twig growth after 4 years compared to the May and October transplant treatments. The authors suggested that the July transplants may have grown more due to the ability of July-transplanted trees to regenerate roots for several months before the next shoot growth period, which resulted in a larger root system that was better able to support spring shoot growth the first year after transplanting. Data from this study regarding shoot extension of the July treatments corroborate the findings of Watson et al. (1986) that sugar maple tolerates summer transplanting.

Trunk Growth July-transplanted trees were excluded from the analysis since most of the trunk expansion in 2001 occurred before transplanting. While there was no evidence ($P = 0.2593$) of a production method and transplant date interaction after the first-season, there was evidence ($P = 0.0993$) of an interaction after the second-season (Fig. 3-6C-D, Tables 3-2 and 3-3). (A similar trend was evident for shoot extension and root length accumulation). Differences among treatments may have become more apparent during the second growing season after transplant due to a delayed response by the trees to the physiological stresses of transplanting. During 2001, trees may have had more stored carbohydrates to 'buffer' some of the adverse treatment effects. However, in 2002 trees may have had fewer stored carbohydrate reserves due to the massive root regeneration that occurred. Therefore, treatment responses may have become more apparent during the second year. However, trunk expansion had just begun when the trees were harvested. Therefore, the change in interaction may not actually reflect differences in treatment responses between 2001 and 2002.

Overall, the PIP treatments had greater trunk expansion compared to the B&B treatments (Fig. 3-6C-D, Tables 3-2 and 3-3), particularly among the spring treatments. The PIP/April treatment had greater trunk expansion than B&B/April treatment in 2001 and 2002 ($P = 0.0121$ and 0.0051, respectively). While the non-transplanted field trees had greater trunk expansion than the B&B/November, March, and April treatments in both 2001 and 2002 (Fig. 3-6C-D, Tables 3-2 and 3-3), trunk expansion among the PIP treatments (both transplanted and not) was similar for all treatments in 2001 and 2002. Among the B&B treatments, trunk expansion of the March and April treatments was less than the December treatment in both 2001 and 2002.

Root Growth No interaction between production method and transplant date was evident in 2001 ($P = 0.1797$) (Fig. 3-6E-F, Tables 3-2 and 3-3). However, in 2002 there was a significant interaction between production method and transplant date ($P = 0.0249$) (see *Analysis of End-of-Season Growth/Trunk Growth*).

Among the B&B treatments, April had much greater accumulated root length than all other B&B treatments (including the non-transplanted field trees) in 2001 and by June

2002 (Fig. 3-6E-F, Tables 3-2 and 3-3). While shoot extension of non-transplanted field trees was greater than shoot extension of transplanted B&B trees in both years, root length increase was among the lowest of all the treatments (only the B&B/November treatment had less root growth). The relatively abundant shoot extension and limited root length increase exhibited by non-transplanted, field-grown trees relative to the transplanted treatments supports the proposal by Wareing (1970) that the pre-transplant root:shoot ratio will be restored following transplanting by a coordination of the growth of roots and shoots.

Among the PIP treatments, non-transplanted trees accumulated more root length than any of the transplanted treatments in 2001 and by June 2002 (Fig. 3-6E-F, Tables 3-2 and 3-3). (See discussion of root mat in *Accumulation of Biomass/Standing Crop/Root Growth*). During 2001, accumulated root length was similar among most of the transplanted PIP treatments. However, by June 2002 the PIP/July treatment accumulated more root length than any of the transplanted treatments. Trees transplanted in-leaf are apparently very capable of quickly regenerating roots, probably due to the photosynthetic machinery being in place and active as long as leaf water stress is avoided.

Root length of the non-transplanted PIP trees and PIP/November treatments was expectedly higher than for the B&B counterparts at the end of 2001 and by June 2002 (Fig. 3-6E-F, Tables 3-2 and 3-3). Root balls of container-grown trees typically are more fibrous than those of field-grown trees (Harris and Gilman 1993). Watson and Himelick (1982; 1983) reported that numerous roots are produced from each severed root end. Therefore, the fibrous root systems of PIP trees would have a greater potential to regenerate a greater number of root tips if root balls are sliced or roots are cut relative to B&B trees. The greater number of regenerated root tips would likely increase the density of roots, thereby increasing the observed root length against the rhizotron windows.

Post-transplant Root Regeneration

While Cripps (1970) reported root growth in the winter immediately following transplanting young apple (*Malus domestica* Borkh. non Poir.) trees in Western Australia, no root growth was observed in any of the transplanted trees in this study until the following spring (Fig. 3-2). Root regeneration was observed on most transplants by mid

May and all transplants by mid June. The number of weeks between the November, December, March, and April transplant dates and the first observed root regeneration were 25, 21, 6, and 4 weeks, respectively. Similarly, root regeneration was observed 38 days post-transplant in March-transplanted red maples (Kelting et al. 1998).

Harris et al. (2002) reported that early fall-transplanted sugar maple began root regeneration earlier and regenerated more roots in the first-season post-transplant than the mid fall- and spring-transplanted treatments. October-, November-, and March-transplanted trees began root regeneration 48, 22, and 0 days, respectively, prior to bud break (Harris et al. 2002). Similarly, Taylor and Dumbroff (1975) reported a rapid burst of growth in late March, approximately 4 weeks prior to bud break, in transplanted sugar maple seedlings. Bud break in this study occurred around 18 April (Table 3-1); however, root regeneration was not observed in any of the transplanted trees until after 2 May or at least 2 weeks after bud break. April transplants regenerated roots 1 week later than any of the other treatments, which may have been a result of physiological stresses or wound responses imposed by the transplanting process. Differences between Harris et al. (2002) and this study may be attributed to year-to-year variation in weather. Additionally, trees in the Harris et al. (2002) study were grown in PIPRs. While no root regeneration was observed in this study prior to bud break in any of the transplanted treatments, modest winter root growth was observed in the non-transplanted PIP trees and just prior bud break in the non-transplanted field trees (see Chapter 4), indicating that early spring temperatures were not limiting. New root growth was observed in all non-transplanted trees in this study 20 to 33 days after the installation of the FR and PIPRs, respectively.

Trees transplanted in July (PIP and B&B) regenerated roots approximately 21 days after transplanting, at a time when root growth was reduced in all other treatments. Cripps (1970) suggested that this type of anomalous root growth was a result of stimulation by root pruning, a result of the transplanting process, when soil temperatures were non-limiting. In four out of the five transplanted treatments, root regeneration began 1 week later in the B&B trees compared to the PIP trees. Due to the highly fibrous nature of container-grown root balls (Harris and Gilman 1993), an increased number of roots would have been cut or broken in the PIP transplants in this study (see description of PIP root ball treatment in *Materials and Methods/Tree Harvest and Planting*). Since numerous roots are produced from each severed root end (Watson and Himelick 1982; 1983), increased root regeneration near the periphery of the root ball is very likely. Therefore, the PIP trees would have a high likelihood of regenerating a greater number of root tips, and as a result they would have an increased chance of a root tip making it to the rhizotron window before a root tip from the less dense root system of a B&B tree. Alternatively, PIP trees may have more root tips initially and thus had more potential for root tip growth.

Analysis of variance suggested that no interaction between production method and transplant date existed in terms of regenerated root dry weight or length ($P = 0.5345$ and 0.5135, respectively) (Fig. 3-7, Tables 3-4 and 3-5). Overall, the PIP treatments regenerated more root length than the B&B treatments ($P = 0.0410$). As well, the B&B and PIP/April treatments regenerated the most root length and dry weight. The PIP/ November and April treatments regenerated more root length and dry weight than December treatment and the B&B/April treatment regenerated slightly more root length and dry weight than July treatment.

Conclusions

While shoot extension and trunk expansion exhibited very uniform and well-defined patterns of growth, much greater variation existed for root growth and mortality with regards to time and duration. Overall, growth periodicity of transplanted and non-transplanted sugar maple followed a pattern of maximum shoot extension in early May, maximum root growth in late May, and maximum trunk expansion in mid June. Similarly, Harris and Fanelli (1999) also reported that maximum root elongation corresponded to the end of the single flush of spring shoot extension (approximately 1 June). The period of maximum root length accumulation in this study was concurrent with trunk expansion, both of which began at the time when the rate of shoot extension was decreasing. Specifically, root growth in this study followed a pattern of abundant growth in late May and June and less growth in summer and early fall. Similarly, Morrow (1950) reported that root growth of mature sugar maple was abundant in spring and less in summer. He attributed the reduction and cessation of growth during the summer and early fall to low soil moisture/drought, primarily because he observed the resumption of root growth 2 days after rainfall. Plants in this study, however, were irrigated regularly, and they still exhibited a reduced rate of root length accumulation during summer and early fall.

While Harris and Fanelli (1999) reported a transient antagonistic pattern of root and shoot growth (i.e., onset of shoot extension coincided with a sharp, temporary decline in root elongation), this pattern was not observed in this study due to the fact that root length accumulation did not occur prior to shoot growth. The slight overlap in periods of shoot, trunk, and root growth activities indicates that considerable competition for assimilates/resources may occur, particularly in May and June when shoot growth is at a maximum and root and trunk growth are beginning activity. Competition for assimilates might potentially be one cause for the observed mortality of roots just prior to maximum root elongation (see Chapter 4).

Based upon the observations in this study, transplanting in November, December, March, and April do not appear to radically disrupt the normal growth periodicity of sugar maple. However, research from a secondary study related to this project (see Chapter 4) indicates that early spring root growth may have been delayed as a result of transplanting. July transplanting did appear to disrupt the normal periodicity of root growth, resulting in a large spike in root growth 4 weeks post-transplant and 11 weeks later than the other transplanted treatments and non-transplanted treatments. This spike in root growth resulted in the accumulated root length of the July treatments being similar to the other treatments by early September (Fig. 3-4A-B).

Morrow (1950) reported that growth periodicity is generally thought of as a set pattern of growth caused by internal (inherent) factors, and that the influence of environment can alter this predetermined pattern. He suggested that root periodicity was primarily correlated with soil temperatures. Data from this study suggest that shoot and trunk growth periodicity is predetermined for the most part, but that root growth can be influenced by transplanting (e.g., delayed root growth in spring and triggered root growth in late July and early August).

Abod and Webster (1989) suggested that after a tree is transplanted, an optimal root length:leaf area ratio is reestablished by coordinating growth to correct the disrupted ratio. Similarly, Kozlowski and Pallardy (1997) asserted that root:shoot ratios of transplanted trees eventually reestablish to pre-transplant levels after time. Therefore, the major loss of roots due to transplanting should result in corresponding period of reduced vigor in the crown (Watson et al. 1986). Reductions in shoot extension and trunk expansion were observed during the first growing season after transplant (Figs. 3-4 and 3-5). As well, the rate of root length accumulation in the transplanted trees was much greater than the non-transplanted trees field trees and was greater during 2001 (first growing season after transplant) than in 2002. The increase in first-season rate of root length accumulation and reduction in shoot extension and trunk expansion of the transplanted treatments relative to the non-transplanted treatments likely reflect the coordination of growth by the tree and compensatory growth of the root system to restore a more favorable root:shoot ratio. Alteration of the root:shoot growth ratio by maximizing root growth and reducing shoot growth favors the moisture balance of the transplant by potentially maximizing absorptive capability and minimizing transpirational losses. Many would argue that abundant root growth and reduced shoot growth is the best scenario for establishment of transplanted trees. Watson et al. (1986) suggested that landscape-sized trees undergo a period of stress and reduced vigor for 4 or more years following transplanting and that reductions in top growth were related to the time required for the replacement of the root system.

The magnitude of wintertime root mortality, particularly in the PIPR, is well illustrated (Fig. 3-4B). While minimal mortality occurred during winter in the FR, significant reductions in root length occurred in most of the transplanted treatments. This finding supports the theory of Watson et al. (1986) regarding the shedding of ‘temporary’ roots. Results of this study also indicate that non-transplanted field-grown trees exhibit different root dynamics than trees in a PIP production system, particularly with regards to root mortality. The cyclic nature of the standing root length in the PIPR may be of interest or relevance to persons studying nutrient and carbon cycling or working with containerized plants (particularly in the PIP system). Finally, these graphs indicate that there is little advantage to fall and spring transplanting compared to summer transplanting regarding post-transplant root regeneration in sugar maple (Fig. 3-4).

Depending upon the response variable (i.e., shoot, trunk, or root growth) one chooses to study, different conclusions on ‘ideal’ time to transplant will be drawn. For example, second-year standing root length (June 2002) indicates that July transplants (both B&B and PIP) are capable of regenerating a root system of similar or greater standing root length as the other transplant dates (Figs. 3-4 and 3-6E-F). However, when results of harvested root length (June 2002) are used, the July transplants (particularly B&B) regenerated little root length and dry weight compared to the other transplant treatments. As a second example, second-year standing root length might suggest that April is a good time to transplant B&B sugar maple (Fig. 3-6F). However, second-year shoot growth would indicate that April is the worst time to transplant B&B sugar maples (Fig. 3-6B). The abundant root growth and poor shoot growth of the B&B/April treatment may be a result of competition between the roots and shoots for assimilates and the limitations of the plant to supply sufficient resources to allow maximum growth of both organs. This also may illustrate the reestablishment of a favorable root:shoot ratio.

While type of tree and season of transplant may influence successful establishment of a transplanted tree, the importance of post-transplant care and the minimization of additional stresses on newly transplanted trees cannot be overstated. Future research projects that could help clarify and explain some of the observation in this project might: 1) explore the possibility of competition among roots limiting root growth (e.g., maximal densities), 2) study the cycling of roots in the PIP system and the implications of cycling relating to nitrogen/nutrient loss in PIP production systems, 3) compare the longevity of roots regenerated after transplanting to the longevity of roots in a stable system, and 4) further explore the consequences of summer transplanting with regards to second and third year shoot growth.

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Table 3-1. Median bud break dates of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4.

Treatment	2001		2002	
	B&B	PIP	B&B	PIP
Control	17 April	19 April	19 April	20 April
November	22 April	17 April	18 April	17 April
December	16 April	24 April	19 April	21 April
March	16 April	20 April	13 April	12 April
April	23 April	23 April	20 April	19 April
July	-	-	15 April	15 April
Overall Median	17 April	20 April	18/19April	18 April

Table 3-2. Mean shoot extension, trunk expansion, and standing root length of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001 n=4.

Treatment	Shoot Extension (cm)		Trunk Expansion (mm)		Root Length (cm)	
	2001	2002	2001	2002	2001	2002
B&B						
Control (non-transplanted)	57.63	88.96	30.38	39.91	443.93	495.99
November (leaf drop)	17.08	40.72	20.99	30.12	335.90	296.61
December (early winter)	24.59	63.33	26.93	35.81	724.83	647.24
March (early spring)	19.66	54.22	16.00	25.58	751.34	684.56
April (bud break)	19.52	37.43	16.83	24.23	1431.97	1284.65
July (bud set)	36.31	48.90	-	-	615.81	666.88
PIP						
Control (non-transplanted) [z]	30.98	53.77	23.71	34.46	1702.07	1411.35
November (leaf drop)	28.40	68.66	28.29	38.79	873.13	843.67
December (early winter)	16.38	42.53	26.48	33.73	680.63	619.74
March (early spring)	10.77	31.30	23.00	32.75	567.68	422.32
April (bud break)	33.19	81.16	29.97	38.57	1145.84	877.39
July (bud set)	27.60	52.16	-	-	1055.81	1091.17

[z] Due to the development of extraordinarily dense root mats in two non-transplanted PIP trees, the bottom row of the rhizotron grid was eliminated. See text for details.

Table 3-3. Analysis of variance of end-of-season shoot extension, trunk expansion, and standing root length of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4.

Effect	Shoot Extension (cm)		Trunk Expansion (mm)		Root Length (cm)	
	2001	2002	2001	2002	2001	2002
	P > F					
Production Method	0.6279	0.3305	0.0102	0.0059	0.4842	0.6063
Transplant Date	0.3374	0.6420	0.2633	0.3275	0.0169	0.0133
Production*Transplant Date	0.0989	0.0072	0.2593	0.0993	0.1797	0.0249
Transplanted vs. Non	<.0001	0.0129	0.1861	0.0661	0.1039	0.0959
B&B vs. PIP						
Control [z]	0.0016	0.0122	0.1516	0.2216	<.0001	0.0002
November	0.1528	0.0430	0.1181	0.0565	0.0593	0.0188
December	0.2967	0.1268	0.9210	0.6371	0.8733	0.9019
March	0.3552	0.1681	0.2170	0.1897	0.5892	0.3407
April	0.0095	0.0045	0.0121	0.0051	0.3424	0.0981
July	-	0.8075	-	-	0.1191	0.0641
B&B						
Control vs. November	<.0001	0.0009	0.0474	0.0329	0.6970	0.3745
Control vs. December	0.0002	0.0621	0.4518	0.3545	0.3145	0.4994
Control vs. March	<.0001	0.0133	0.0037	0.0028	0.2717	0.4006
Control vs. April	<.0001	0.0005	0.0058	0.0013	0.0011	0.0011
Control vs. July	-	0.0049	-	-	0.5363	0.4458
November vs. December	0.3389	0.0980	0.2000	0.2023	0.1667	0.1229
November vs. March	0.7410	0.3167	0.2795	0.3064	0.1404	0.0891
November vs. April	0.7545	0.8058	0.3652	0.1874	0.0004	<.0001
November vs. July	-	0.5422	-	-	0.3162	0.1040
December vs. March	0.5285	0.4973	0.0227	0.0264	0.9238	0.8672
December vs. April	0.5170	0.0596	0.0339	0.0130	0.0148	0.0070
December vs. July	-	0.2848	-	-	0.6944	0.9299
March vs. April	0.9858	0.2149	0.8566	0.7589	0.0186	0.0106
March vs. July	-	0.6911	-	-	0.6254	0.9369
April vs. July	-	0.3940	-	-	0.0055	0.0087
PIP						
Control vs. November	0.7417	0.2702	0.3201	0.3288	0.0049	0.0151
Control vs. December	0.0681	0.4033	0.5456	0.8677	0.0008	0.0011
Control vs. March	0.0406	0.1763	0.8989	0.7509	0.0019	0.0009
Control vs. April	0.7924	0.0648	0.2111	0.3903	0.0700	0.0325
Control vs. July	-	0.9039	-	-	0.0249	0.1577
November vs. December	0.1299	0.0575	0.6917	0.2551	0.4889	0.3193
November vs. March	0.0718	0.0281	0.3480	0.2673	0.3711	0.1299
November vs. April	0.5704	0.3896	0.7340	0.9625	0.3652	0.8888
November vs. July	-	0.2226	-	-	0.5111	0.2718
December vs. March	0.5579	0.4946	0.5353	0.8559	0.7395	0.4719
December vs. April	0.0525	0.0110	0.4811	0.3126	0.1269	0.2893
December vs. July	-	0.4736	-	-	0.1817	0.0408
March vs. April	0.0316	0.0064	0.2431	0.3100	0.1129	0.1210
March vs. July	-	0.2086	-	-	0.1567	0.0190
April vs. July	-	0.0513	-	-	0.7637	0.3780

[z] Due to the development of extraordinarily dense root mats in two non-transplanted PIP trees, the bottom row of the rhizotron grid was eliminated. See text for details.

Table 3-4. Regenerated root dry weight and length of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001, and harvested June 2002. n=4.

Treatment	Dry Weight (g)		Length (m)	
	B&B	PIP	B&B	PIP
November	199.60	257.55	2008.87	2886.34
December	194.05	138.88	1953.01	1556.36
March	134.35	194.30	1352.16	2177.50
April	216.38	280.83	2177.70	3147.28
July	95.85	190.80	964.68	2138.28

Table 3-5. Analysis of variance of regenerated root dry weight and length of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001, and harvested June 2002. n=4.

Effect	Dry Weight	Length
	P > F	
Production Method	0.1564	0.0410
Transplant Date	0.1473	0.1385
Production*Transplant Date	0.5345	0.5135
B&B vs. PIP		
November	0.3733	0.2048
December	0.3963	0.5618
March	0.4511	0.3272
April	0.3594	0.1949
July	0.1495	0.0936
B&B		
November vs. December	0.9315	0.9347
November vs. March	0.3171	0.3394
November vs. April	0.7952	0.8045
November vs. July	0.1167	0.1337
December vs. March	0.3592	0.3814
December vs. April	0.7300	0.7419
December vs. July	0.1366	0.1548
March vs. April	0.2109	0.2321
March vs. July	0.5525	0.5708
April vs. July	0.0705	0.0836
PIP		
November vs. December	0.0747	0.0592
November vs. March	0.4268	0.3989
November vs. April	0.7389	0.7233
November vs. July	0.3063	0.2777
December vs. March	0.4856	0.4591
December vs. April	0.0498	0.0381
December vs. July	0.4243	0.3964
March vs. April	0.3043	0.2758
March vs. July	0.9647	0.9625
April vs. July	0.2038	0.1779

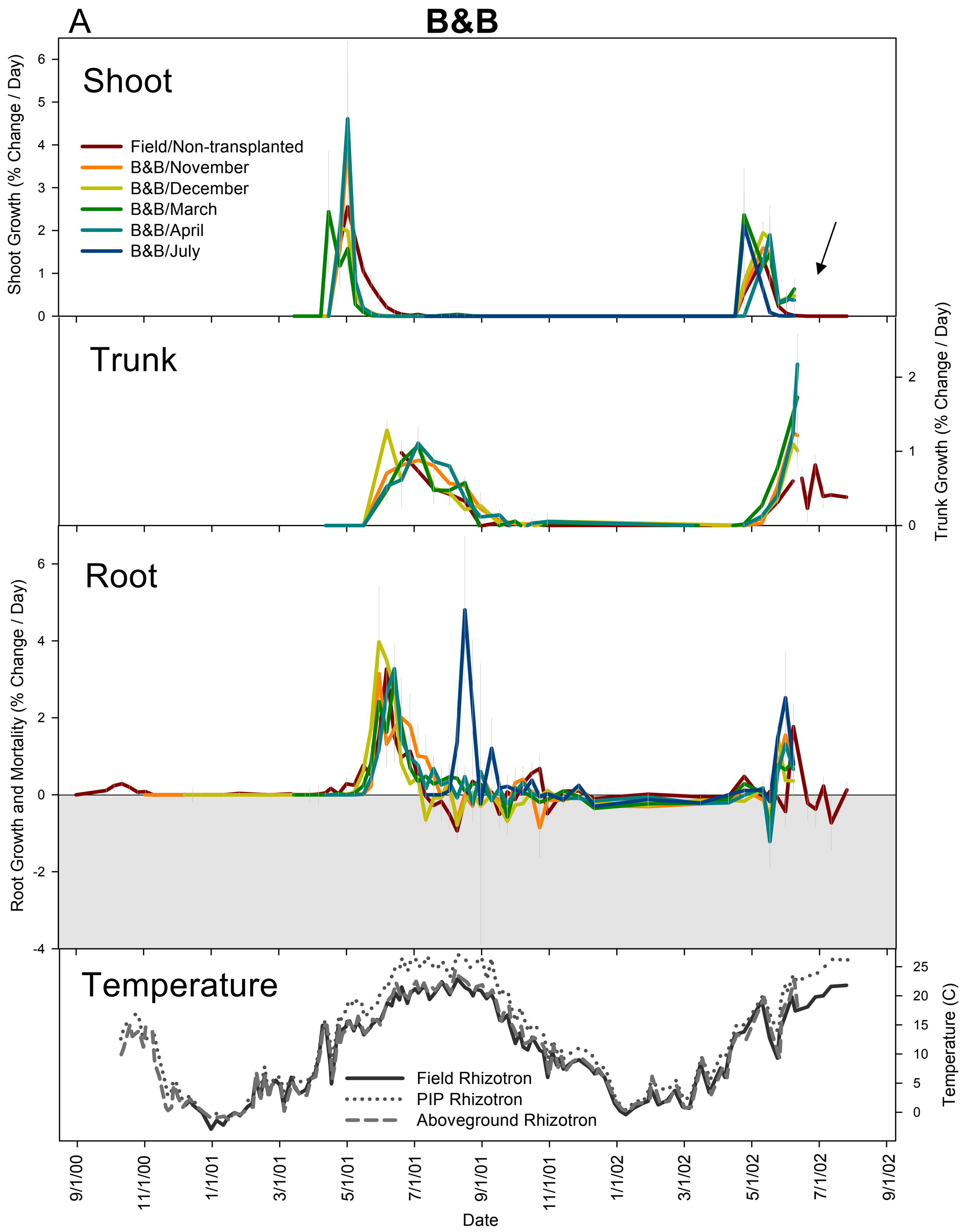
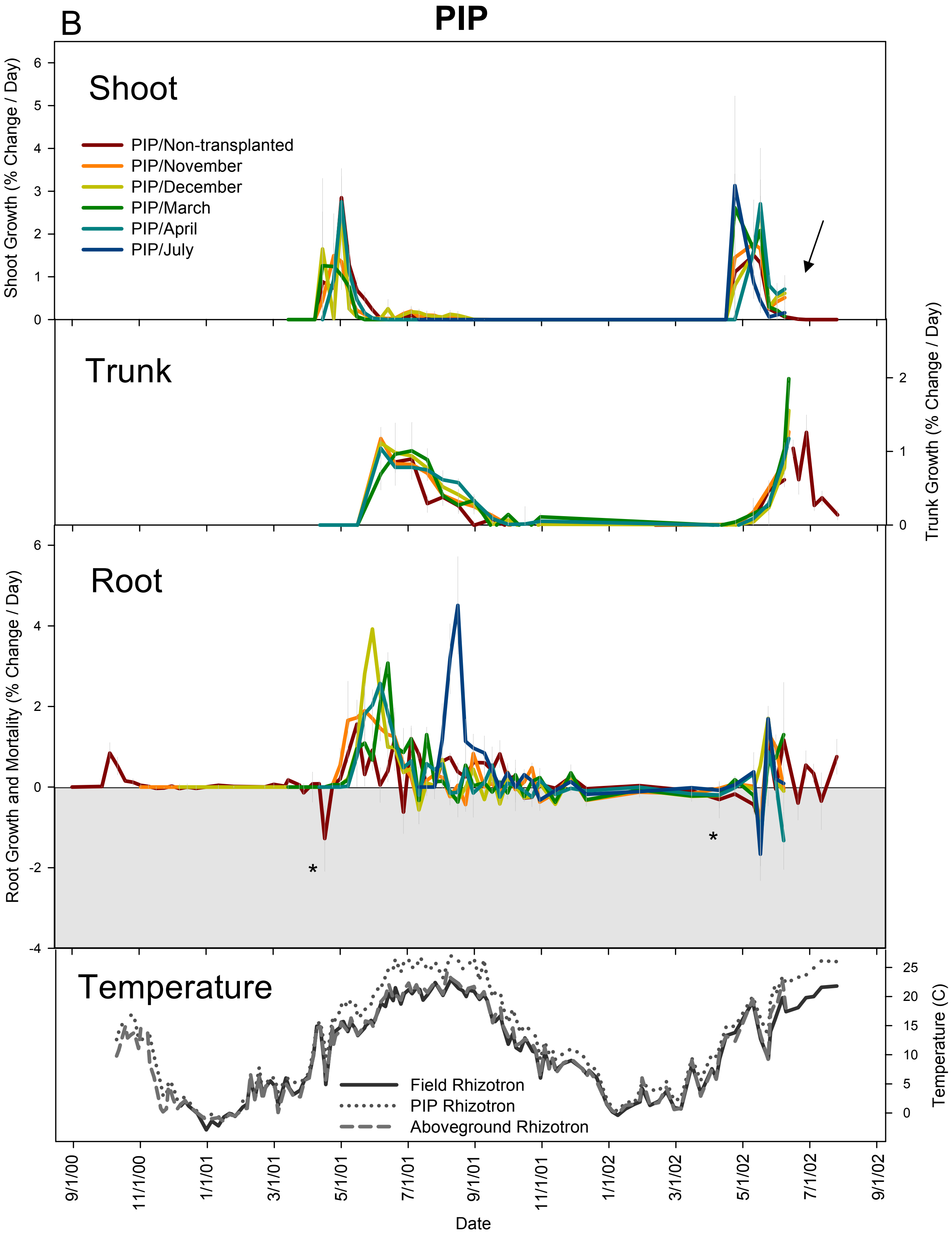


Figure 3-1. Shoot, trunk, and root growth periodicity of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (* denotes the elimination of the bottom row of a rhizotron grid due to the development of extraordinarily dense root mats in two non-transplanted PIP trees. ↑ indicates harvest of the transplanted treatments. See text for details.)


B
PIP
Shoot
Shoot Growth (% Change / Day)
6
5
4
3
2
1
0
PIP/Non-transplanted
PIP/November
PIP/December
PIP/March
PIP/April
PIP/July
Trunk
Trunk Growth (% Change / Day)
2
1
0
Root
Root Growth and Mortality (% Change / Day)
6
4
2
0
-2
-4
*
*
Temperature
Temperature (C)
25
20
15
10
5
0
Field Rhizotron
PIP Rhizotron
Aboveground Rhizotron
9/1/00
11/1/00
1/1/01
3/1/01
5/1/01
7/1/01
9/1/01
11/1/01
1/1/02
3/1/02
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7/1/02
9/1/02
Date

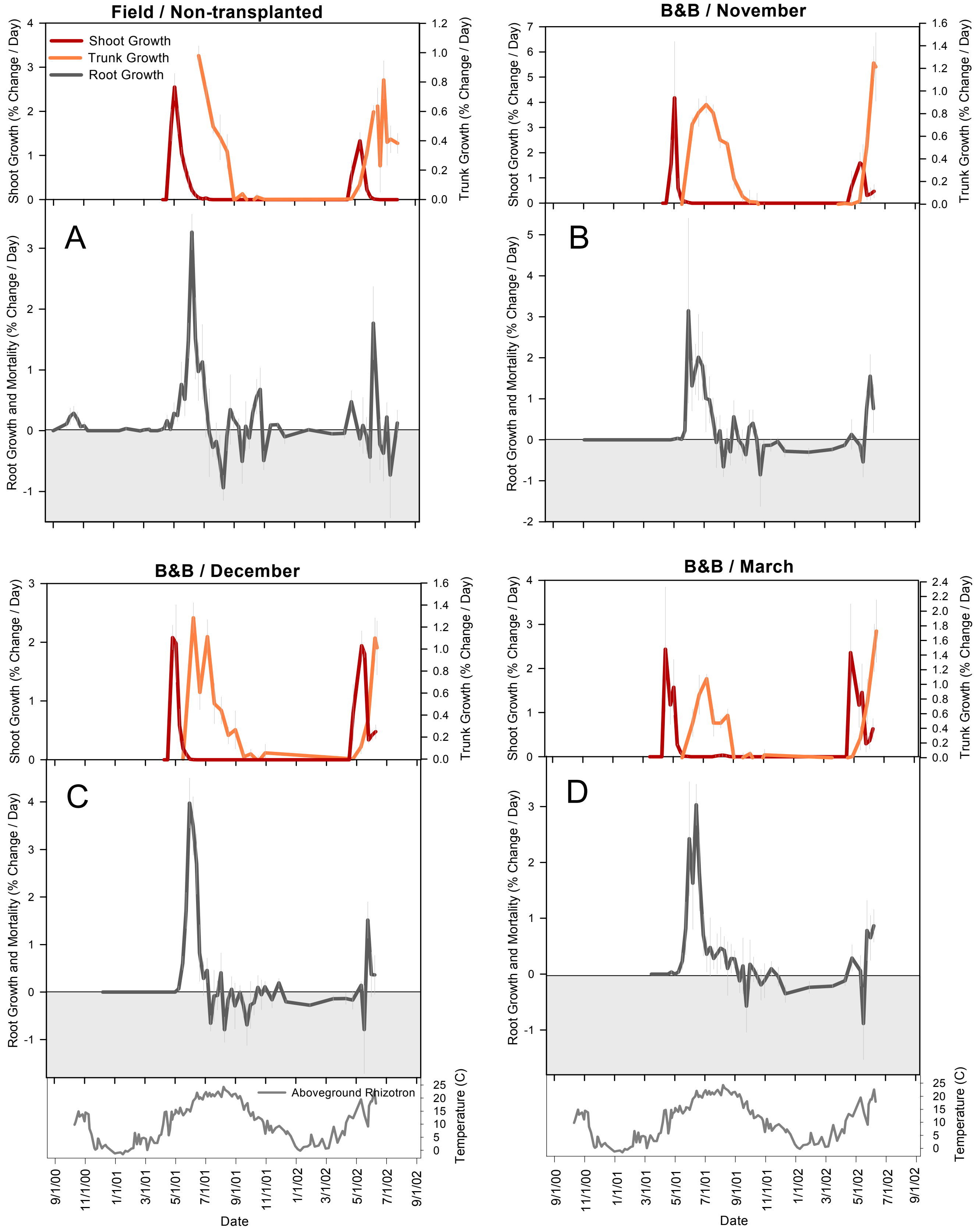
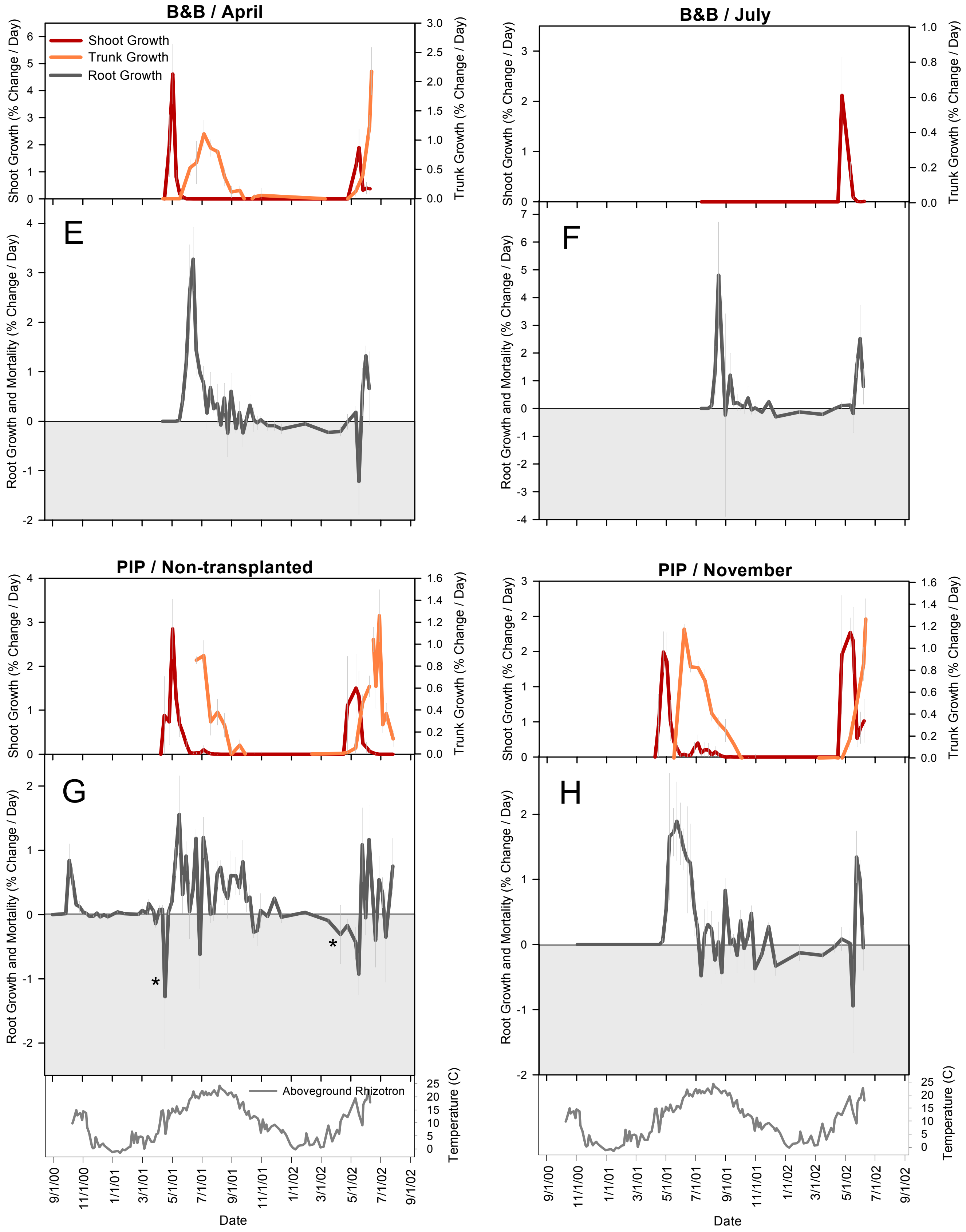
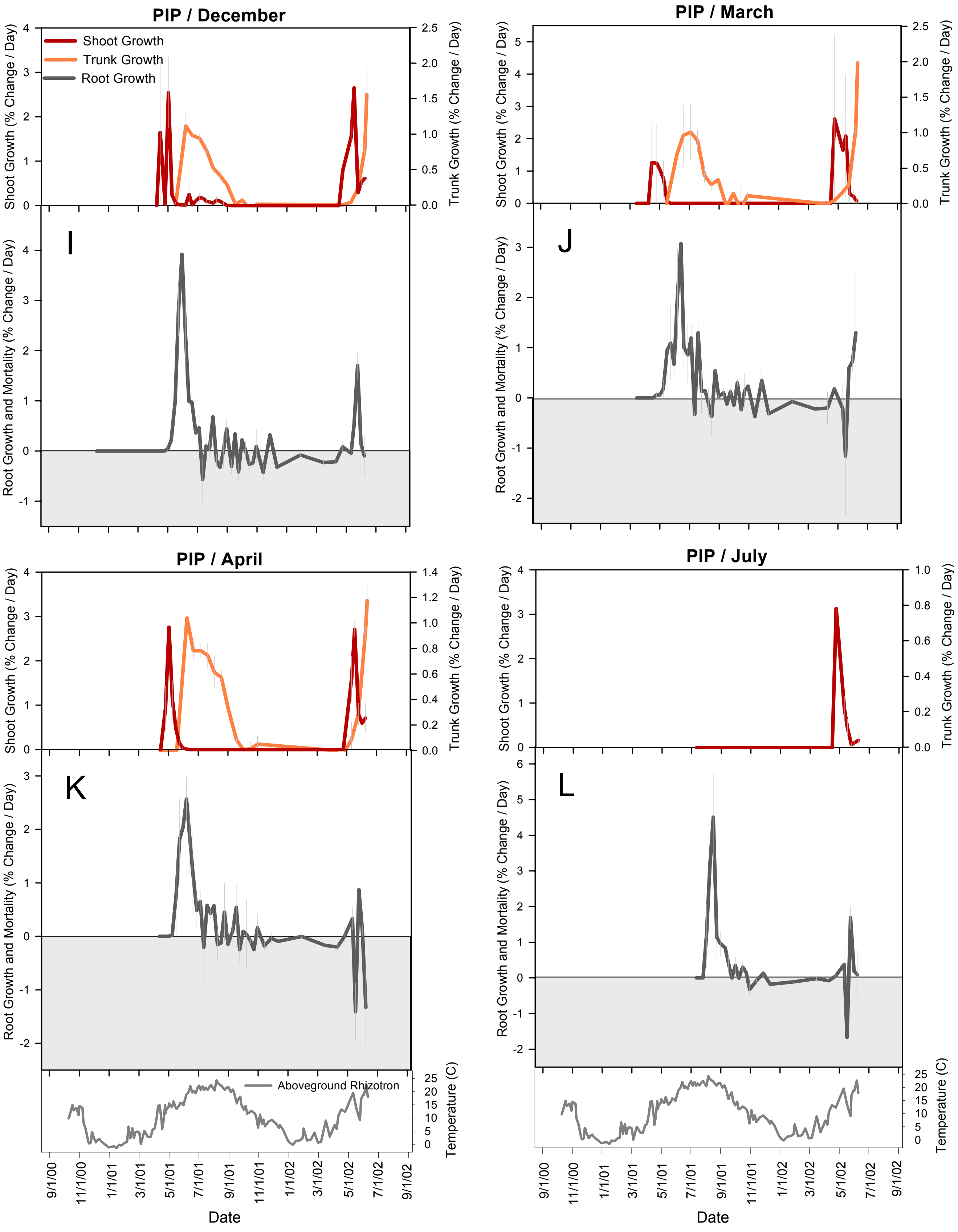


Figure 3-2. Shoot, trunk, and root growth periodicity of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (* denotes the elimination of the bottom row of a rhizotron grid due to the development of extraordinarily dense root mats in two non-transplanted PIP trees. See text for details.)


B&B / April
Shoot Growth
Trunk Growth
Root Growth
E
B&B / July
F
PIP / Non-transplanted
G
PIP / November
H
Shoot Growth (% Change / Day)
Trunk Growth (% Change / Day)
Root Growth and Mortality (% Change / Day)
Aboveground Rhizotron
Temperature (C)
*
*
9/1/00
11/1/00
1/1/01
3/1/01
5/1/01
7/1/01
9/1/01
11/1/01
1/1/02
3/1/02
5/1/02
7/1/02
9/1/02
Date


PIP / December
Shoot Growth
Trunk Growth
Root Growth
I
PIP / March
J
PIP / April
K
PIP / July
L
Shoot Growth (% Change / Day)
Trunk Growth (% Change / Day)
Root Growth and Mortality (% Change / Day)
Aboveground Rhizotron
Temperature (C)
9/1/00
11/1/00
1/1/01
3/1/01
5/1/01
7/1/01
9/1/01
11/1/01
1/1/02
3/1/02
5/1/02
7/1/02
9/1/02
Date

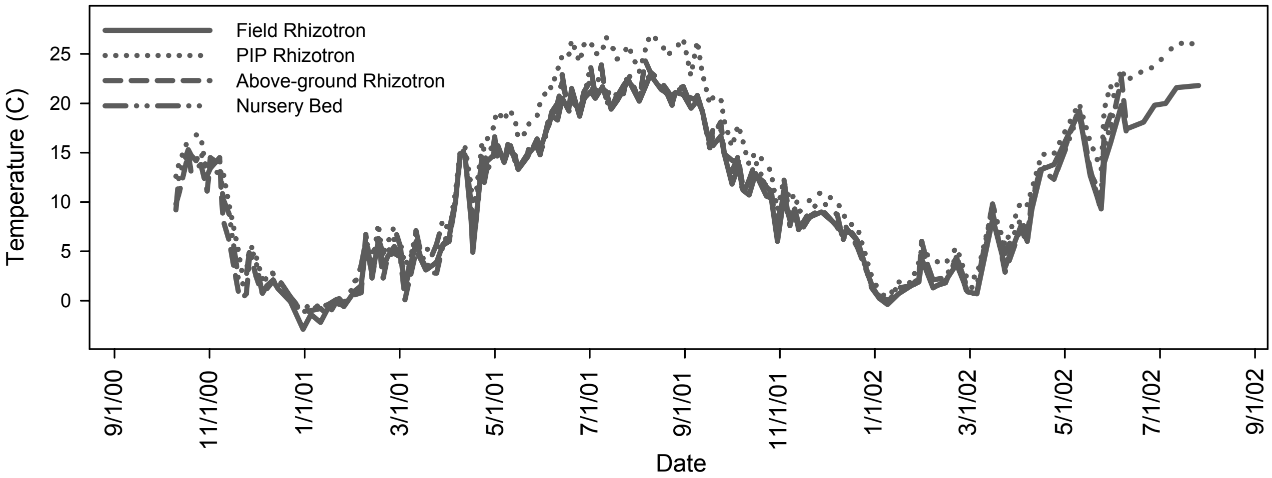


Figure 3-3. Soil temperature at 30 cm depth taken in the field rhizotron, pot-in-pot rhizotron, aboveground rhizotron, and nursery bed.

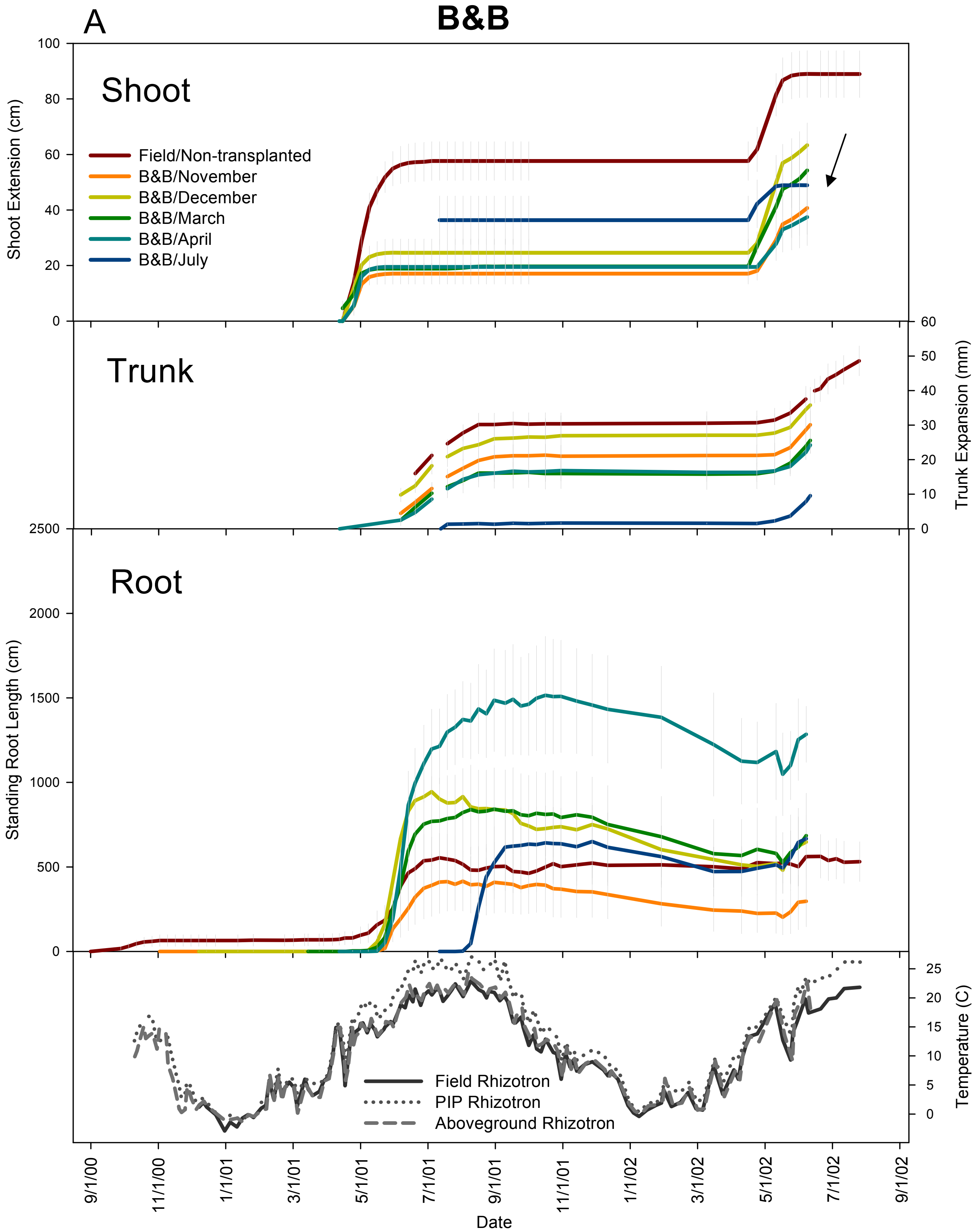
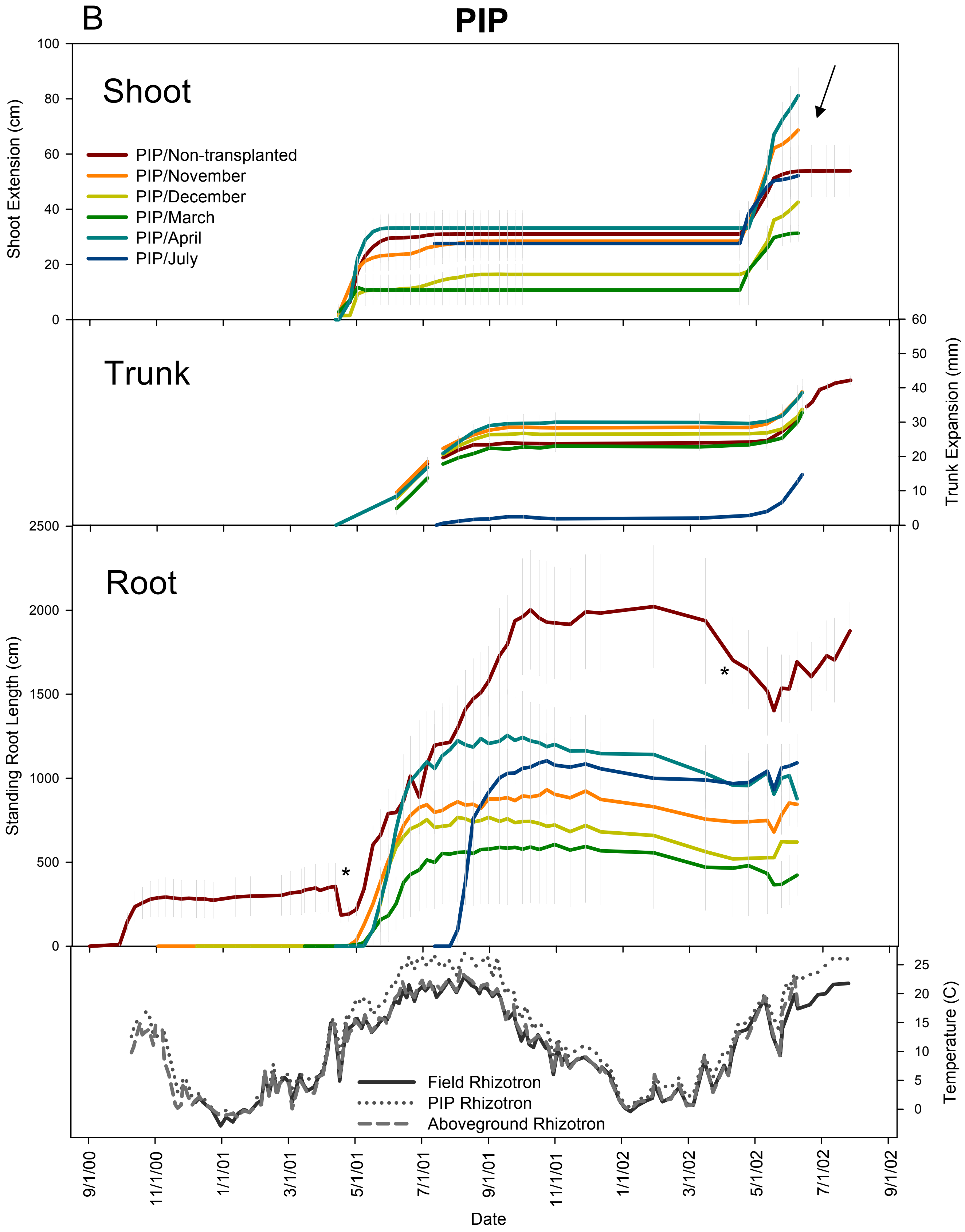


Figure 3-4. Changes in standing shoot length, trunk diameter, and root length of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (* denotes the elimination of the bottom row of a rhizotron grid due to the development of extraordinarily dense root mats in two non-transplanted PIP trees. ↑ indicates harvest of the transplanted treatments. See text for details.)



B
PIP
Shoot
Shoot Extension (cm)
100
80
60
40
20
0
PIP/Non-transplanted
PIP/November
PIP/December
PIP/March
PIP/April
PIP/July
Trunk
Trunk Expansion (mm)
60
50
40
30
20
10
0
Root
Standing Root Length (cm)
2500
2000
1500
1000
500
0
*
*
Temperature (C)
25
20
15
10
5
0
Field Rhizotron
PIP Rhizotron
Aboveground Rhizotron
9/1/00
11/1/00
1/1/01
3/1/01
5/1/01
7/1/01
9/1/01
11/1/01
1/1/02
3/1/02
5/1/02
7/1/02
9/1/02
Date

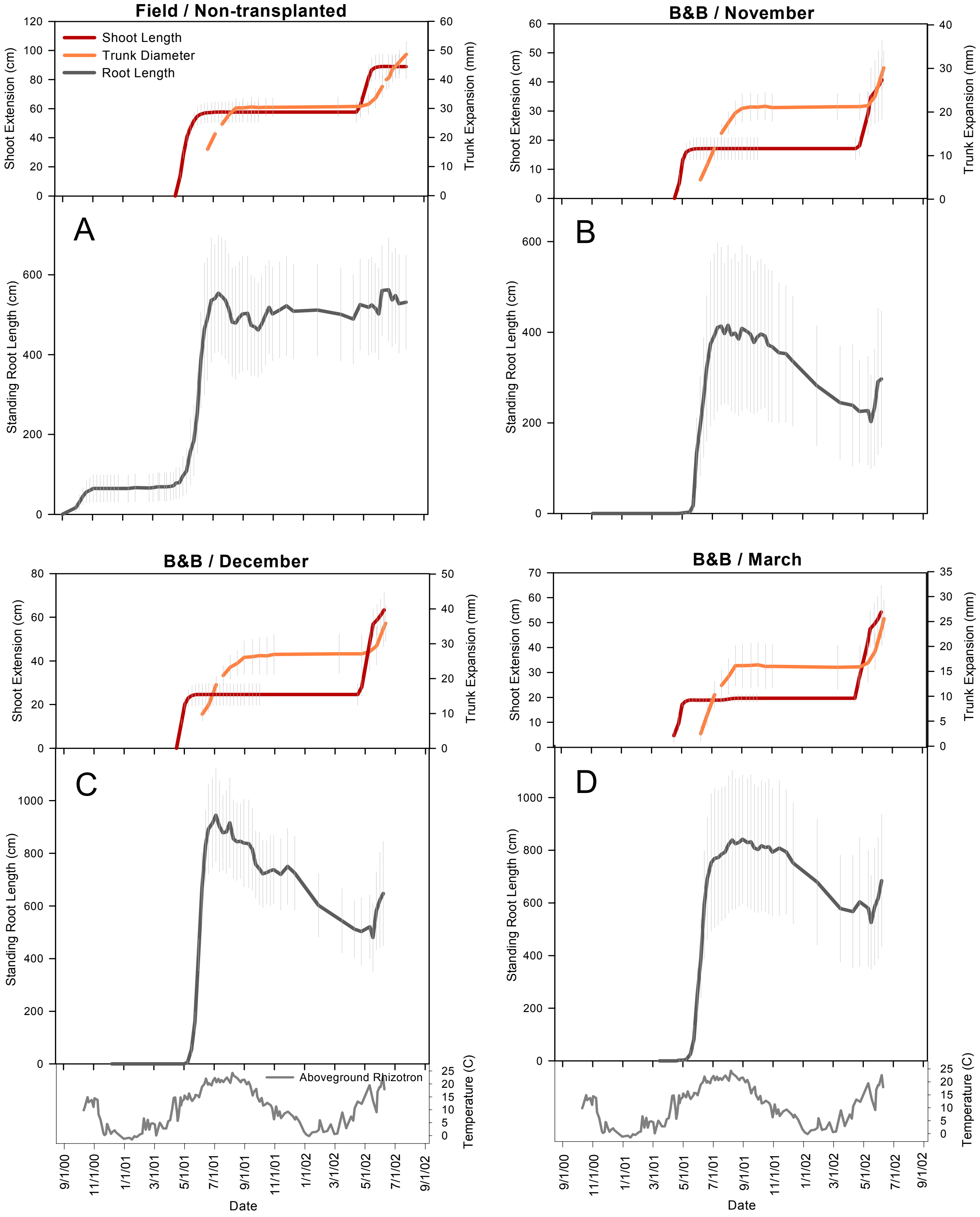
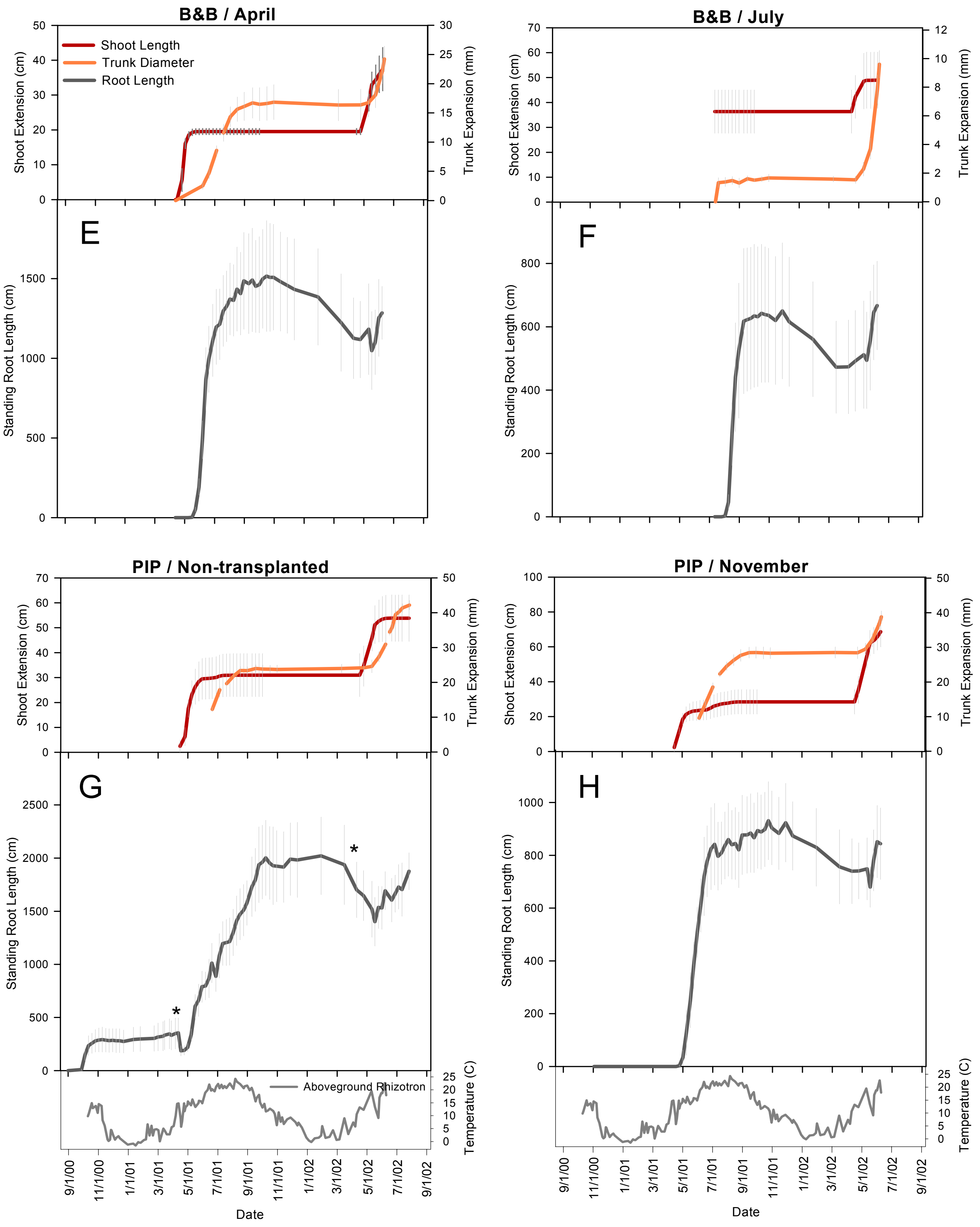
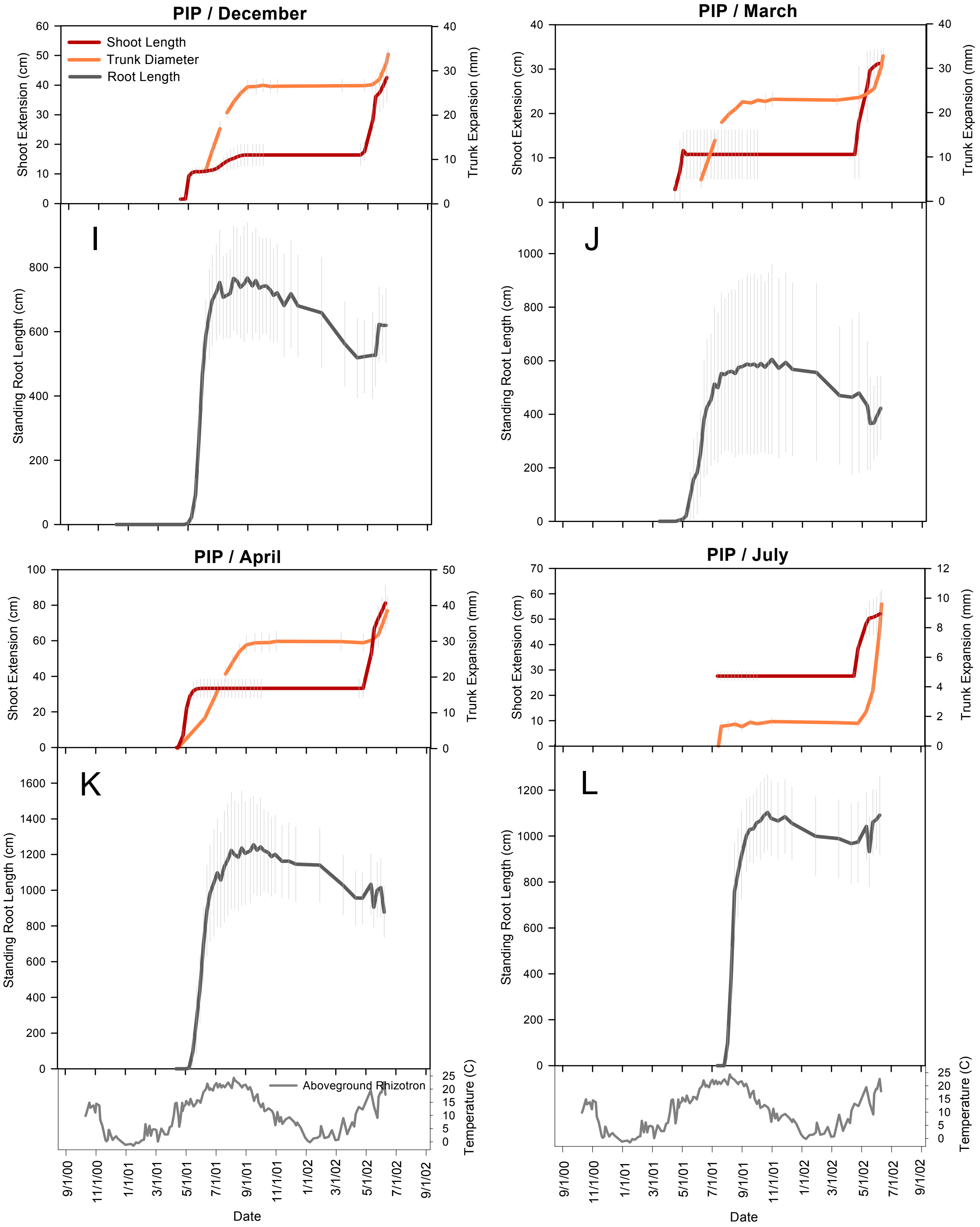


Figure 3-5. Standing shoot length, trunk diameter, and root length of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (* denotes the elimination of the bottom row of a rhizotron grid due to the development of extraordinarily dense root mats in two non-transplanted PIP trees. See text for details.)


B&B / April
Shoot Length
Trunk Diameter
Root Length
Shoot Extension (cm)
Trunk Expansion (mm)
Standing Root Length (cm)
E
B&B / July
F
PIP / Non-transplanted
G
*
*
Aboveground Rhizotron
Temperature (C)
PIP / November
H
9/1/00
11/1/00
1/1/01
3/1/01
5/1/01
7/1/01
9/1/01
11/1/01
1/1/02
3/1/02
5/1/02
7/1/02
9/1/02
Date


PIP / December
Shoot Length
Trunk Diameter
Root Length
Shoot Extension (cm)
Trunk Expansion (mm)
Standing Root Length (cm)
I
PIP / March
J
PIP / April
K
PIP / July
L
Aboveground Rhizotron
Temperature (C)
9/1/00
11/1/00
1/1/01
3/1/01
5/1/01
7/1/01
9/1/01
11/1/01
1/1/02
3/1/02
5/1/02
7/1/02
9/1/02
Date

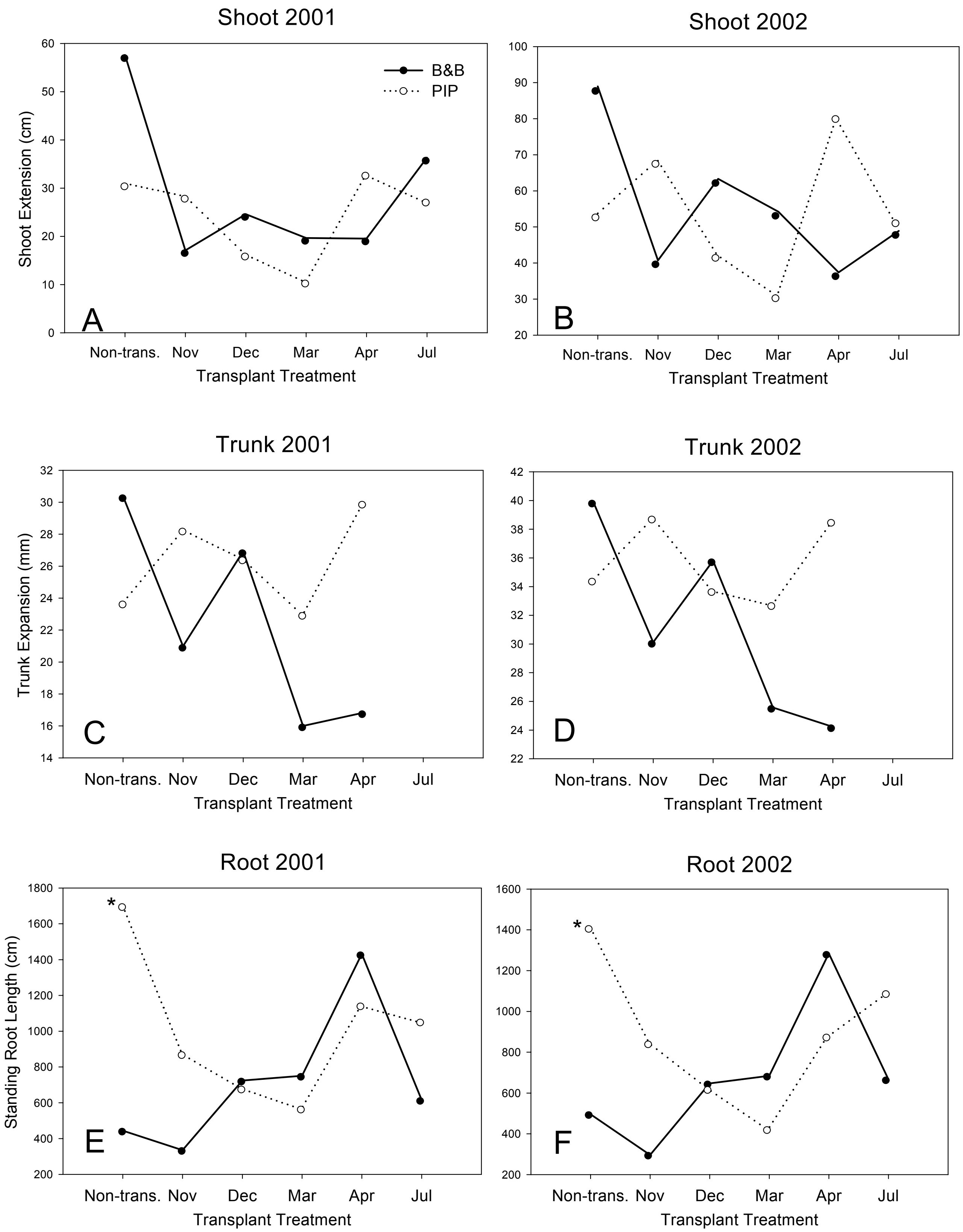


Figure 3-6. Plot of the interaction between production method and transplant date of the end-of-season shoot extension, trunk expansion, and standing root length of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (* denotes the elimination of the bottom row of a rhizotron grid due to the development of extraordinarily dense root mats in two non-transplanted PIP trees. See text for details.)

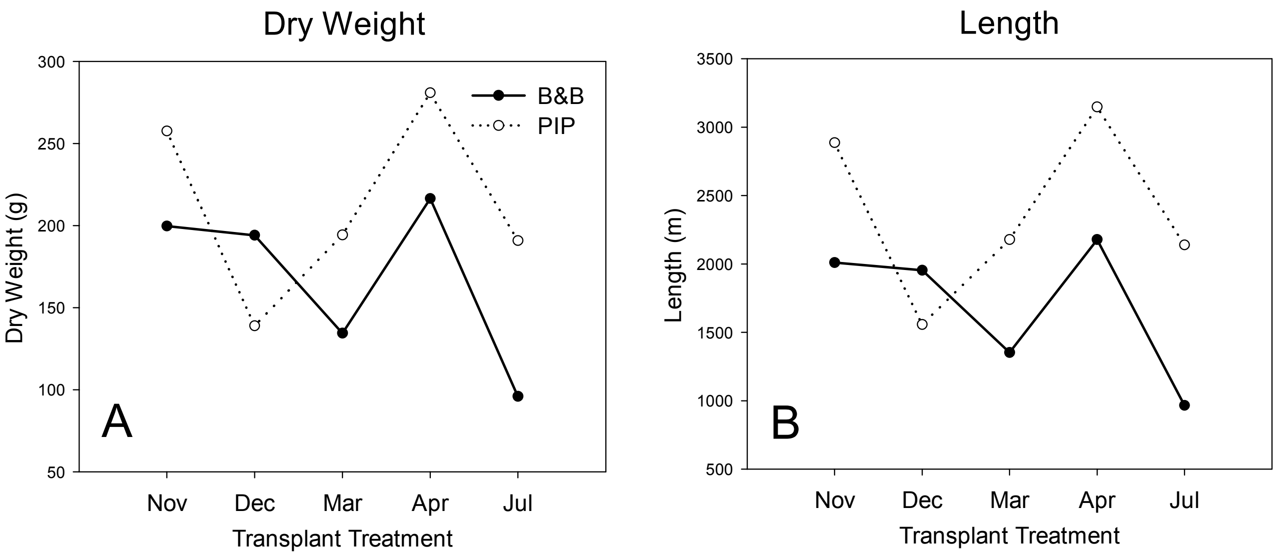


Figure 3-7. Plot of the interaction between production method and transplant date of the regenerated root dry weight and length balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4.

Chapter 4

Dynamics of Root Production and Mortality During Establishment of Balled-and-Burlapped and Pot-in-Pot Sugar Maple (*Acer saccharum* Marsh.) Transplanted at Different Times of Year

Abstract

Basic information regarding redevelopment of root systems following transplanting is needed to better understand tree establishment. Few studies have addressed root mortality in transplanted trees and the effect of nursery growing system on post-transplant root mortality. Therefore, seasonal patterns of root production and mortality were evaluated in transplanted sugar maples (*Acer saccharum* Marsh.). Trees were transplanted into root observation chambers (rhizotrons) from field and pot-in-pot (PIP) growing systems at leaf drop (November 2000), early winter (December 2000), early spring (March 2001), bud break (April 2001), and bud set (July 2001). Patterns of root production and mortality of transplanted trees were compared to non-transplanted trees in a field bed and PIP growing system. Photographs of rhizotron windows were taken over a 1-year period. Appearance and disappearance of individual roots were followed to obtain seasonal trends of root production and mortality. Additionally, annual production and mortality and indices of root activity (analogous to turnover rates) were compared among treatments. While root production ceased in winter in non-transplanted field trees and transplanted trees, wintertime root production was observed in the non-transplanted PIP trees. Root mortality occurred throughout the year in all treatments. However, while highest mortality occurred in winter in the transplanted trees, mortality in the non-transplanted trees mostly occurred in spring and summer. Non-transplanted PIP trees had greater standing root length, production, and mortality than the non-transplanted field and transplanted PIP treatments. Indices of root activity that included production processes relative to standing root length revealed greatest and least activity in the non-transplanted PIP and field trees, respectively. Differences among production:mortality ratios illustrate the degree to which production processes dominate early transplant root dynamics. Results of this study indicate that transplanting and the PIP growing system alter the natural patterns of root production and mortality in sugar maple. Non-transplanted PIP trees exhibited production and mortality dynamics that were atypical of sugar maples in forest settings and different than that of the non-transplanted field trees. The substantial wintertime root mortality and production:mortality ratios in the transplanted trees were greater than previous reports indicated for established sugar maples. The dynamics of the non-transplanted field trees were most similar to reported dynamics of sugar maples in forest settings.

Introduction

When field-grown trees are transplanted, as little as 2% of the root system is moved with the tree (Watson and Himelick 1983). Large-diameter roots contribute disproportionately more weight relative to surface area than small diameter roots. Therefore, while more than 90% of coarse (>10 mm) root weight was within the confines of the root ball of field-grown trees, less than 15% of the fine, absorbing root weight (<2 mm) was within the confines of the root ball (Gilman and Beeson 1996). For transplanted trees to survive, a root system must be regenerated, consisting of the original root ball and new roots that grow into the landscape beyond (Mullin 1963; Richie and Dunlap 1980). The primary cause of transplant stress is thought to be tissue water deficit resulting from an inability to absorb sufficient soil moisture to support the tree (Carlson et al. 1988; Larson 1984; Struve and Joly 1992). Therefore, the rate of recovery from post-transplant water stress is directly proportional to the rate of regeneration of new roots (Nambiar et al. 1979).

Lifespan of individual roots, especially smaller diameter roots, varies widely. While some roots may only live a few weeks (Black et al. 1998), others live for many years (Kolesnikov 1971; Lyr and Hoffman 1967). Differences in longevity may be attributed to genetic factors, environmental conditions, and the physiological status of the tree (Black et al. 1998). Root ‘turnover’ is a measure of annual production and/or mortality relative to the standing crop (Burton et al. 2000; Gill and Jackson 2000; Hendrick and Pregitzer 1992a; 1993a; Jones et al. 2003) and represents a flux of carbon from plant biomass to the soil as roots die (Tierney and Fahey 2002). Annual biomass production and mortality in two sugar maple-dominated forests was estimated at 7300 to 8000 kg·ha^{-1}·year^{-1} (production) and 4800 to 6700 kg·ha^{-1}·year^{-1} (mortality) (Hendrick and Pregitzer 1993a). Hendrick and Pregitzer (1993a) estimated that 40 to 60% of the net primary productivity in the two sugar maple forests was allocated to fine root production. Therefore, root turnover can constitute a major sink for carbon and represent a substantial metabolic cost for trees (Psarras et al. 2000).

Two models have been proposed to explain root longevity and mortality patterns (Bloomfield et al. 1996). In the first model, roots have an indeterminate life span and die when environmental factors are no longer favorable. Mortality of roots in unfavorable environments lowers the maintenance costs for the plant. In the second model, roots have a predetermined life span that is dependent upon a finite supply of starch/carbon that, when exhausted, results in root death (Marshall and Waring 1985). Therefore, root longevity depends on the inherent capacity or fixed pattern of the plant to sustain root biomass (Psarras et al. 2000).

Bloomfield et al. (1996) proposed three broad categories of conditions or processes that might affect root turnover. Processes in the first category are a result of aboveground demands that affect carbon fixation (e.g., foliage production, thinning of branches, and prolific fruiting) and carbon allocation (e.g., competition between sinks). Similarly, Hendrick and Pregitzer (1993a) suggested that the increase and decline in root length were linked to phenological and physiological events occurring in the canopy (e.g., substantial increases in root length occurring after the canopy flushes in late spring). The second category of processes relates to roots' carbohydrate storage capacity (Bloomfield et al. 1996). Relative to seedlings, roots of mature trees have a greater store of carbohydrates to buffer against environmental stresses (Kramer and Kozlowski 1979). Longevity of larger roots may relate to their larger amount of carbohydrate reserves. All roots die when there is insufficient carbon to maintain the root but larger roots may have relatively larger reserves. The third category encompasses factors that affect soil microsite quality (e.g., nutrient, water, and oxygen availability, soil temperature, toxic elements, and fungal/microbial populations) (Bloomfield et al. 1996).

In natural, undisturbed systems, fine root dynamics are highly variable and are strongly affected by biotic and abiotic factors. Biotic factors include: species and habit (e.g., evergreen vs. deciduous) (Black et al. 1998), age/maturity (Bloomfield et al. 1996; Kolesnikov 1971), size, and structural/functional class of the root (Srivastava et al. 1986). Root longevity is also affected by soil microorganisms –both beneficial and pests (e.g., nematodes, insects, mycorrhizae, and fungi) (Bloomfield et al. 1996; Eissenstat and Yanai 1997; Fogel 1985; Harley 1969; Harley and Smith 1983). Exposure to environmental stresses can also affect root longevity (Srivastava et al. 1986). Abiotic factors influencing root longevity could include: soil temperature (Hendrick and Pregitzer 1993b; Kolesnikov 1971), soil fertility (Burton et al. 2000; Jones et al. 2003; Joslin et al. 2000; Pregitzer et al. 1993), soil moisture (Jones et al. 2003; Kolesnikov 1971), other chemical or physical soil conditions (e.g., pH, aeration) (Kolesnikov 1971), and pruning and defoliation in the canopy (Bloomfield et al. 1996; Head 1973; Srivastava et al. 1986). Environmental factors can override genetic control of root turnover in plants (Brown and Scott 1984). However, the environment can only modify root growth and form within the genetic constraints of the species.

Plants must be able to respond to changing environmental conditions to better compete for resources in a heterogeneous environment (Hutchings 1988). Therefore, roots exhibit a morphological plasticity, via fine root turnover, that facilitates the proliferation of roots in favorable environments and the shedding of roots after a soil zone has been depleted (Pregitzer et al. 1993). For example, addition of nitrogen to a mixed hardwood forest resulted in a rapid increase in localized fine root production (Hendrick and Pregitzer 1992b; Hendrick and Pregitzer 1993b), increased longevity, and reduced turnover rates (Burton et al. 2000). Burton et al. (2000) suggested that roots are maintained as long as the benefit (e.g., nutrient supply) they provide outweighs the carbon cost of keeping them alive. Jones et al. (2003) reported that root systems of both the overstory and understory plants in a longleaf pine (*Pinus palustris* Mill.) woodland were highly plastic and capable of rapidly responding to removal of understory and overstory vegetation.

Several authors (Hendrick and Pregitzer 1993a; Kolesnikov 1971; Santantonio and Grace 1987) have reported correlations between root production and mortality and seasonal conditions. Roots may exhibit modal or bimodal peaks of high live root biomass followed by periods of high dead root biomass (Hendrick and Pregitzer 1992a; 1993a).

Jones et al. (2003) reported that, during cold months, root productivity and standing root crop declined, while production and standing crop increased during warm months. Similarly, peaks of high live biomass were reported to occur in summer, and drops in live root biomass were reported to occur primarily in late summer and autumn (Hendrick and Pregitzer 1992a).

Regeneration of a new root system is essential for the survival of a newly transplanted tree. Basic information concerning the redevelopment of a root system following transplant will improve our understanding regarding establishment of landscape trees. While many studies (Gilman and Kane 1990; Harris et al. 1995; Harris et al. 2002; Harris and Gilman 1991; Harris et al. 1996; 1998; Harris et al. 2001; Watson 1986; Watson and Himelick 1982; 1983; Watson et al. 1986) have addressed production processes of regeneration of a root system following transplant, few studies have addressed mortality of regenerated roots in transplanted trees in the landscape. Therefore, the objective of this research was to characterize patterns of first-season root production and mortality of transplanted sugar maples and to determine the effects of transplant timing and production system [grown in a nursery bed and transplanted with root balls wrapped in burlap (B&B) or grown in the pot-in-pot (PIP) system (Ruter 1997)] on these root processes.

Materials and Methods

***Plant Material*, *Rhizotron Construction*, *Tree Harvest and Planting,* and *Tree Care: Fertilization, Irrigation, etc.* sections are identical to those in Chapter 3.**

Treatments Treatments consisted of two production methods (B&B and PIP) and five transplant dates [3 November 2000 (leaf drop), 8 December 2000 (early winter), 16 March 2001 (early spring), 13 April 2001 (bud break), and 13 July 2001 (bud set)]. The July transplant date was selected as the date when twig extension had ceased on at least four of the five shoots being monitored on the non-transplanted control trees. A sixth transplant treatment served as a non-transplanted control. Rhizotrons for the non-transplanted control plants were located in the PIP system and nursery bed and could not be randomized in the same bed as the transplanted trees. Subsequently, the experimental design consisted of a 2 x 5 factorial arranged in a completely randomized design and augmented with two non-transplanted controls (field and PIP trees). There were four replications of each treatment (B&B/November, PIP/November, B&B/December, PIP/December, B&B/March, PIP/March, B&B/April, PIP/April, B&B/July, PIP/July, non-transplanted field, and non-transplanted PIP).

Measurements Due to recorded differences in the vertical and spatial (i.e., north, south, east, and west) distribution of roots (Burton et al. 2000; Gaudinski et al. 2001; Hendrick and Pregitzer 1992b; Psarras et al. 2000; Watson and Himelick 1982; 1983), sites for turnover analysis were selected at the same depth and on the same side (north) of rhizotrons. The far right and left sides of the center row of the grid (12 to 17 cm below the soil surface) on each rhizotron window were traced in red ink and labeled with the tree number. A digital camera (Sony Cybershot, 3.3 mega pixels, Digital Still Camera DSC-P1, Tokyo, Japan) was used to document root production and mortality. Photos were taken at 1600 x 1200 pixels and dated electronically. Rhizotron windows were photographed weekly beginning 28 June 2001 until root production ceased in winter. During winter, rhizotron windows were photographed monthly until early spring, at which time weekly measurements resumed. Photographs were taken until 5 June 2002 for transplanted trees and 24 July 2002 for the non-transplanted controls. Root systems of all transplanted trees were excavated to determine root regeneration. Photographs were taken of the 5 cm x 5 cm labeled left and right center squares on all measurement dates. Color, contrast, and brightness of the images were adjusted and images were viewed for analysis in Adobe Photoshop (version 6.0.1, Adobe Systems Incorporated, San Jose, CA).

Total root length (standing root length), new root length, and dead root length were calculated using the line-intersect method (Marsh 1971; Newman 1966; Tennant 1975). Roots were considered dead on the first date they disappeared entirely and permanently from subsequent images, or appeared to be dead due to change in color (to gray or black) (Jones et al. 2003). Total root/line intersections of the two photographed 5 cm x 5 cm squares were counted to obtain the standing count of roots. Root/line intersections observed for the first time were considered new roots. New root counts were totaled each measurement date to obtain a total new root count for each tree on each measurement date. Individual root/line intersections were tracked over time to determine the date of death of each individual root. Root/line intersections were converted to lengths using: R = (11/14)(N)(grid unit) (Marsh 1971; Newman 1966; Tennant 1975) where N = total root/line intersections and grid unit = 5 cm. The graphs created in this study cover a period extending from 28 June 2001 (approximately 8 weeks after the first roots appeared on the rhizotron windows of the transplanted trees) until 5 June 2002 for transplanted trees and 24 July 2002 for the non-transplanted controls.

Total new root length was the sum of all increases in new root length and was synonymous with annual production (N). Total dead root length (D) was the sum of all root length decreases and was synonymous with annual mortality. Mean standing root length (SC) was calculated as the mean of the four largest measurements from the first growing season. Due to the nature of the treatments (i.e., various transplant times), problems were encountered with the calculation of mean standing root length. The July treatment had 13 weeks of no new root production followed by several weeks of root production. Therefore, when calculating standing root length as mean of all measurements, the July mean was drastically reduced and not representative of the of the standing root length that characterized the other 9 months. Additionally, not all trees exhibited stable standing root lengths at the same time. Therefore, one time period could not be selected to calculate standing root length that would be appropriate for all trees. As a result of these problems, the mean of the first growing seasons' four largest measurements was used to calculate mean standing root length.

The 1-year time interval used to calculate mean standing root length and total new and dead root lengths of the transplanted treatments began on 2 May 2001 and ended on 5 May 2002, and thus represents the first-year production and mortality processes of the regenerated root system. Regardless of the transplant treatment (November, December, March, and April), root growth against the rhizotron windows was observed only after 2 May 2001. Less than half of the trees regenerated roots by 9 May 2001, and slightly over half regenerated roots by 17 May 2001. Minimal root mortality was assumed to occur between 2 May 2001 and 28 June 2001. Photographic documentation of the rhizotron windows began on 28 June 2001. For the non-transplanted treatments, total new and dead root lengths were the sum of all increases and decreases in new and dead root lengths between 28 June 2001 and 3 July 2002. Subsequently, the time period for the analyses of total root lengths, production, mortality, and indices of root activity of the non-transplanted treatments are offset from the transplanted treatments. Due to the period of maximum root production in sugar maple typically occurring between late May and late June (Burton et al. 2000; Harris and Fanelli 1999; Morrow 1950), the offset was used so that a 1-year interval could be used to compare all treatments. Had the May and June root production data not been included, the July transplant treatment would have greatly inflated production values relative to the other treatments due to the July transplanted trees undergoing massive post-transplant root regeneration in August and the period of maximum root production (late May until late June) in the other transplant treatments being missed. The 28 June 2001 to 3 July 2003 time period was used for the non-transplanted treatments, because photographs were taken for this entire period. Due to the existence of roots on the windows of the non-transplanted trees prior to 2 May 2001, no assumptions regarding May and June root production could be made; thus, a complete collection of photos was necessary to determine annual production and mortality. Therefore, while the interval (2 May 2001 until 5 May 2002) for transplanted trees is slightly offset from the interval (28 June 2001 until 3 July 2002) of the non-transplanted tree, all trees underwent a 1 year cycle of production and mortality. I believe the benefits of the 1-year interval (and the resulting offset) outweigh the consequences of not being able to include the May and June production data of the transplanted treatments.

Formulas used to calculate the ‘index of root dynamics or activity’ are analogous to formulas used to calculate root turnover rates. However, due to the nature of this project (i.e., working with transplanted trees), root dynamics in this project are different than steady state dynamics typically found in forest settings and established plants. Trees in this study were regenerating a root system. Transplanted trees in this study were undergoing increased production and did not exhibit steady state root dynamics. As a result, when calculating root turnover, inflated values indicating abundant turnover processes were obtained. These values do not reflect ‘turnover’ as defined by root death and replacement (Burton et al. 2000). Thus, it is more appropriate to refer to values in this study not as turnover but as an index/ratio/indicator of root dynamics or activity that takes into account processes of both production and mortality.

Formulas used to calculate the ‘index of activity’ were: 1) sum of the total new and dead root lengths divided by the mean standing root length [(N+D)/SC where N=total new root length (i.e., annual production), D=total root length that disappeared or died (i.e., annual mortality), and SC=standing root length] (Hendrick and Pregitzer 1992a; Jones et al. 2003), 2) average of the total new and dead root lengths divided by the mean standing root length [(N/SC+D/SC)/2) or ((N+D)/2)/SC] (Burton et al. 2000; Hendrick and Pregitzer 1993a), 3) total new root length divided by the mean standing root length [N/SC] (Burton et al. 2000; Hendrick and Pregitzer 1993a), and 4) total dead root length divided by the mean standing root length [D/SC] (Burton et al. 2000). By using the mean standing root length as the denominator, indices of relative activity are calculated, whereby the activity of each treatment is scaled on an individual basis. The affore-mentioned formulas in descriptive terms are: 1) measure of relative production and mortality, 2) measure of the average relative production and mortality, 3) measure of relative production, and 4) measure of relative mortality. Finally, the ratio of production to mortality (N/D) (Burton et al. 2000) was also calculated as an index of activity.

Soil and substrate temperatures were monitored with thermocouples (Model HH21 Microprocessor Thermometer, Type J-K-T Thermocouple, Omega Engineering, Inc., Stamford, CT) placed 30 cm deep in an AGR, PIPR, FR, and nursery bed. Afternoon temperatures were recorded twice weekly for the duration of the project.

Analysis Two types of graphs were generated to gain a complete picture of post-transplant root dynamics. While Figure 4-1 provides a quantitative depiction of seasonal patterns of standing root length and root production (new root length) and mortality (dead root length) that facilitate comparisons among treatments, Figure 4-2 present data in such a manner that timing and relative magnitude of production and mortality within each treatment are emphasized. All graphs were plotted over time and included soil temperature to produce the seasonal pattern of standing root length and root production and mortality.

Seasonal patterns of standing root length, root production, and mortality were analyzed in the MIXED procedure of the Statistical Analysis System (SAS) for Windows version 8.02 (SAS Institute, Cary, NC) using repeated measures multivariate analysis of variance. Mean standing root length and total root production and mortality data were subjected to analyses of variance to determine significance of treatments. Statistical comparisons were made using single-degree-of-freedom linear contrasts in the MIXED procedure of SAS.

Results and Discussion

Seasonal Patterns of Changes in Standing Root Length and Root Production and Mortality

Analyses of variance revealed evidence of 3-way interactions between transplant date, production method, and day for standing root length, production, and mortality (Table 4-1), indicating that the treatments responded differently over time.

Root Production Periods of abundant root production were restricted to the warmer months of the year (Figs. 4-1 and 4-2). Root production ceased in the transplanted trees at the time of leaf drop in autumn (mid October), when soil temperatures were near 12 to 14 C (Fig. 4-3), and resumed in May, approximately 1 month after bud break (18 May 2002) and when soil temperatures ranged between 10 and 19 C. Root production in the non-transplanted field trees ceased at a similar time as the transplanted trees; however, root production resumed in mid March (approximately 2 months prior to all transplanted treatments) when soil temperatures were near 4 to 8 C and prior to bud break (Fig. 4-2A). Similarly, Burton et al. (2000), Harris and Fanelli (1999), Morrow (1950), and Taylor and Dumbroff (1975) reported substantial root production in sugar maple prior to bud break in spring [Michigan, southwest Virginia, central New York, and Ontario, respectively]. Substrate temperatures in the PIPR in the Harris and Fanelli (1999) study were approximately 10C at the time of early spring root elongation. The difference between the substantial pre-bud break root production in the Harris and Fanelli (1999) study and lack of substantial pre-bud break root production in the non-transplanted PIP trees in this study may relate to the trees in the Harris and Fanelli (1999) study being younger and more established. Alternatively, the delayed root production in the non-transplanted PIP trees in this study relative to the trees in the Harris and Fanelli (1999) may have been due to the trees outgrowing their containers. PIP trees had probably reached a “pot-bound” condition by 2001.

Root production of non-transplanted PIP trees continued throughout the year, with periods of minimal production between late October and early May, and increased production after mid May until the termination of this project. Morrow (1950), Burton et al. (2000), and Harris and Fanelli (1999) also reported slight root production throughout winter. Resumption of significant root production in non-transplanted field trees in mid March and the occurrence of root production in non-transplanted PIP trees throughout winter indicate that early spring soil temperatures were not limiting to early spring root production in the transplanted trees.

The lack of early spring root production prior to bud break in the transplanted trees may relate to the effect of transplanting on tree physiology (i.e., transplant stress) and a lack of readily available assimilates/non-structural carbohydrates to support early spring root production due to root loss at harvest (Watson and Himelick 1982). Alternatively, the lack of early spring root production may represent a wound response. However, November- and December-transplants probably had ample time to overcome any initial response to wounding. Circling roots were removed from the outer perimeter of the PIP transplants, and B&B transplants lost a high percentage of roots at harvest. Watson and Sydnor (1987) reported that root balls dug according to the minimum standards of the American Association of Nurserymen contain approximately 5 to 18% of the original fine roots. Similarly, Gilman (1988) reported less than 10% of total root length of the original root system was contained within the root balls of harvested field-grown trees. Watson and Himelick (1983) reported that, when field-grown trees are transplanted, as little as 2% of the root system is moved with the tree. To meet water requirements and ultimately survive, transplanted trees must quickly regenerate root systems. Subsequently, during the first growing season after transplant a greater proportion of photosynthates may be allocated to root production. As a result, transplanted trees may enter the following spring with a much-reduced store of reserves, which are necessary for early spring root production before leaves have unfolded and resumed photosynthesis. In addition, research of several authors (Bevington and Castle 1985; Deans and Ford 1986; Lyr and Hoffman 1967; Mooney and Chu 1974) suggests that, during shoot expansion, shoots act as a stronger sink than roots. Therefore, early spring root production in the transplanted trees may be restricted due to a limited supply of non-structural carbohydrates in a stressed and physiologically weakened tree. Developing shoots may act as a strong sink for these limited resources, thereby limiting early spring root production. Supporting this theory, a decline in starch reserves and carbohydrates during periods of shoot growth and a corresponding reduction in root growth were reported in several species (Deans and Ford 1986; Lathrop and Mecklenburg 1971; Parker 1979; Vogt et al. 1985; Wargo 1979).

While minimal to no root production was observed in winter in the transplanted and non-transplanted field treatment, some root production was evident in the non-transplanted PIP trees throughout winter (Fig. 4-1). The occurrence of winter root production in the non-transplanted PIP trees and not in non-transplanted field trees may be a production-system effect. Late fall, winter, and early spring temperatures in the PIPR were slightly (1 to 3 C) (Fig. 4-3) warmer than the AGR or FR and thus, may have been more favorable for winter root production. Cool season temperatures in the AGR and FR were nearly identical (within 1 C). In addition, root systems in the PIPR are bound by a container, and root production was therefore restricted to the pot. As a result, production activity in the PIPR would more likely be detected. Conversely, the AGRs are open-bottomed, and the FR is open on all sides but one. Therefore, root production may have been occurring in areas outside the view of the rhizotron windows. Similar circumstances occur in any root observation system where root systems are not confined, as in mini-rhizotron systems. Root systems of trees transplanted in the AGRs and trees in the FR also may have reached a density such that conditions were no longer favorable for production in the localized area near the rhizotron windows. Competition, unfavorable densities, and resource-controlled carrying capacity for roots (Jones et al. 2003; Vogt et al. 1981) may have influenced root exploration into the soil surrounding the FR and AGR. Research of Jones et al. (2003) on fine root dynamics in overstory and understory gaps in a pine woodland determined that, when understory vegetation was removed, pine root production compensated for reductions in non-pine roots by increasing (pine root) production. As a result, total growth of pine plus non-pine roots remained nearly constant. The 1:1 replacement of pine and non-pine roots across the overstory density gradient, and the compensatory growth of pine roots when non-pine roots were artificially removed suggest a resource-controlled carrying capacity for roots. In other words, the observed compensation may reflect an upper limit set by available resources on the belowground density of roots.

Compared to other transplanted treatments, July transplants exhibited a relatively large burst of root production activity late in the summer (Fig. 4-1 and 4-2). Anomalous root growth such as this was most likely a result of stimulation by root pruning (e.g., transplanting) when soil temperatures were non-limiting (Cripps 1970). Trees in the other transplant treatments exhibited similar bursts between mid May and late June (see Chapter 3).

Root Mortality While root production was restricted from early autumn until late spring, root mortality occurred throughout the year, and in all treatments (except the non-transplanted PIP treatment). Root mortality occurred at a much steadier rate compared to root production. Similarly, Burton et al. (2000) reported a more steady distribution of root mortality throughout the year compared to root production.

While all of the transplanted treatments exhibited maximal root mortality in winter, the non-transplanted controls did not (Fig. 4-2). The period of maximum root mortality of the non-transplanted PIP trees occurred in spring just prior to the period of maximum root production in May and June (Fig. 4-2B). The period of maximum root mortality in the non-transplanted field trees occurred at a similar time as the non-transplanted PIP trees. However, due to the pre-bud break root growth that occurred in March and April in the non-transplanted field trees, maximum root mortality followed the period of maximum root production (Fig. 4-1B). In both non-transplanted treatments, maximum root mortality occurred at bud break and while shoots were expanding (see Chapter 3). Similarly, Burton et al. (2000) found that root mortality in sugar maple was highest between May and August and occurred at a similar time as maximum root production (sometimes just prior and other times just following). The physiological "expense" of maintenance respiration [respiration used to maintain existing plant material (Amthor 1984)] of the roots and competition for assimilates between the roots and shoots may be partly responsible for increased rates of root mortality just prior to spring bud break.

Similar to the low rates of root mortality observed in the non-transplanted trees in this study, Hendrick and Pregitzer (1993b) observed low winter mortality relative to growing-season mortality in a sugar maple-dominated forest. Low mortality rates in winter relative to late spring and early summer in the non-transplanted trees in this study may reflect low respiration rates in cold soils (Hendrick and Pregitzer 1993b). Root respiration “costs” can be high, and while maintenance respiration occurs year-round, respiration is greatly influenced by temperature (Kozlowski and Pallardy 1997). Respiration rates typically increase exponentially with increasing temperature (Eissenstat and Yanai 1997; Kozlowski and Pallardy 1997; Lawrence and Oechel 1983), but only over a range of temperatures (usually between 10 and 25 C) (Kozlowski and Pallardy 1997). Previous studies have demonstrated that increased soil temperatures correspond to increased root respiration (Amthor 1984; Lawrence and Oechel 1983; Marshall and Waring 1985). Hendrick and Pregitzer (1993b) suggested that faster root turnover rates and low winter mortality, relative to growing season mortality, might be due to low maintenance respiration rates in cold soils. Higher soil temperatures are not only associated with increased maintenance costs and mortality rates (Hendrick and Pregitzer 1993b) but also correlate with increased activity of soil organisms, which can shorten root longevity (Head 1973).

Alternatively, the observed increase in root mortality in May and June in this study may relate to the greater carbon demand of the canopy and the reduction of carbohydrate translocation or carbon allocation to the roots during shoot growth. Stored carbon in roots is essential to growth of roots and leaves early in the growing season (Eissenstat and Yanai 1997). Therefore, root carbon stores may be mobilized to supply carbon to the newly growing roots and shoots. During the growing season, when trees are actively photosynthesizing, root growth is primarily supported by current season photosynthates (Marshall and Waring 1985). Hobbie et al. (2002) reported that 75% of fine root carbon originated from current-year photosynthate. Dickson (1991) reported that. after a flush of shoot growth, more than 90% of photosynthate was translocated to the roots.

During winter months, when there are no leaves to generate photosynthates, root mortality may be driven by the reallocation of non-structural carbohydrates/resources for winter maintenance respiration of aboveground tissues. As discussed previously (see *Seasonal Patterns of Changes in Standing Root Length and Root Production and Mortality/Root Production*) transplanting imposes a tremendous stress to a tree, and following transplanting, a tree must regenerate a new root system. Root regeneration, particularly at this scale, can represent a tremendous cost for the plant in terms of construction and maintenance. As a result, the transplanted trees in this study may have had insufficient stored reserves to adequately support winter respiration. Alternatively, the abundant wintertime root mortality observed in transplanted trees may represent an inherently shorter lifespan of the first roots regenerated after a tree is transplanted. Watson and Himelick (1982; 1983) reported that, while numerous roots are produced from each severed root end, in most cases one (or at most, a few) root will become dominant within a couple of years and the remainder of the small roots will eventually die (Watson 1986). Therefore, the first roots regenerated after a tree is transplanted may serve as 'temporary' roots that are genetically programmed to grow quickly for maintenance of the newly transplanted tree until a root system is regenerated for long-term purposes. Rapid shoot growth is often associated with shorter-lived, weak-wooded species (Harris et al. 1999). The same principle, that rapidly growing roots will be shorter-lived and less durable, may hold true for root growth.

Substantial root mortality occurred in the non-transplanted PIP trees (Figs. 4-1 and 4-2). Roots of containerized trees (e.g., PIP trees) have a greater proportion of small diameter roots (Harris and Gilman 1993), which may have higher rates of turnover compared to coarser roots (Bloomfield et al. 1996). Root production and mortality in non-transplanted PIP trees followed a similar pattern of moderate activity in late summer/early fall, diminished activity in winter, and abundant activity between late April and July. The first peak of root mortality occurred in late August and early September when substrate temperatures in the PIPR ranged between 22 and 27 C. These temperatures were unlikely lethal. Similar temperatures were recorded in June and July, when mortality was minimal. The period of maximum root mortality occurred in the non-transplanted PIP trees between early May and late June, at times just prior to and concurrent with periods of maximum root production when soil temperatures were warming. The highly dynamic nature (greatest production and mortality of roots) of root systems of trees in PIP production system may be of interest to persons working with containerized trees and interested in carbon and nutrient cycling in the PIP production system.

Standing Root Length Mean standing root length is a combination of root production and mortality processes. As such, the cumulative effects of these processes on standing root length will be revealed in plots of standing root length.

While most of the transplanted treatments underwent a decline in standing root length between late summer and the following spring, standing root length of the non-transplanted field treatment remained relatively stable over winter and underwent a slight decline in spring (Fig. 4-2). Hendrick and Pregitzer (1993a) reported slight declines in standing root length in winter and spring in a sugar maple-dominated forest. Similar to the non-transplanted field trees, non-transplanted PIP trees did not undergo substantial root mortality during winter months. However, substantial root mortality occurred in non-transplanted PIP trees just prior to the periods of rapid root production in early May. As such, the standing root length of the PIP/Control remained relatively stable over winter, declined in late April and May, and then increased in June and July.

Analysis of Mean Standing Root Length and Annual Production and Mortality

As stated previously, data for transplanted treatments were collected between 2 May 2001 and 5 May 2002, whereas data for non-transplanted controls were collected between 28 June 2001 and 3 July 2002. The offset between transplanted and non-transplanted treatments allows the following results to describe 1-year intervals. All trees have therefore undergone a cycle of root regeneration, production, and mortality. Therefore, caution is advised when comparing transplanted vs. non-transplanted trees.

Mean standing root length and annual production and mortality (total new and dead root lengths, respectively) were analyzed to determine the effects of growing system and transplant date. Analyses of variance indicated little evidence of an interaction between production method and transplant date among the response variables (P = 0.6163, 0.7526, 0.5120 for standing root length, root production and root mortality, respectively) (Fig. 4-4, Tables 4-2 and 4-3).

Non-transplanted PIP trees had a higher mean standing root length and annual production and mortality than non-transplanted field trees (P = 0.0011, <0.0001, 0.0002 for standing root length, root production and root mortality, respectively) (Fig. 4-4, Tables 4-2 and 4-3). Due to confinement of root systems of containerized trees, it was expected that non-transplanted PIP trees would have a higher standing root mass than non-transplanted field trees, whose roots can more freely explore the surrounding soil. As a result of the greater standing root length of non-transplanted PIP trees, greater root production and mortality is not surprising. Theories (see *Seasonal Patterns of Changes in Standing Root Length and Root Production and Mortality/Root Production*) on root competition and density may not hold true when a tree is forced to grow in a container and the entire root system is bound by the confines of a pot.

Among the PIP treatments, the non-transplanted treatment exhibited greater root production and mortality than transplanted treatments (Fig. 4-4, Tables 4-2 and 4-3). Similarly, the non-transplanted PIP treatment had greater mean standing root length than most of the PIP transplanted treatments. Only the PIP/April treatment was similar in mean standing root length to the non-transplanted PIP treatment ($P = 0.2668$). However, while root density was similar at a depth of 15 to 20 cm, root density was much greater for the non-transplanted PIP trees than the PIP/April trees at depths below 20 cm (Fig. A-7 in Appendix A). Dense root mats had begun to form in late summer in two of the PIP/Control trees. Harris and Gilman (1993) similarly reported increased root surface area in containerized vs. field-grown trees.

Similar to the high mean standing root length of the PIP/April treatment, the mean standing root length for the B&B/April treatment was higher than other B&B transplanted treatments (Fig. 4-4, Tables 4-2 and 4-3). The B&B/April treatments, however, also exhibited greater annual production and mortality than other transplanted treatments. As with the non-transplanted PIP trees, larger standing root lengths for the April transplants correspond to increased root production and mortality. April transplants may have had greater root production than other treatments due to favorable environmental conditions in April such as ample soil moisture, cool air temperatures, warming soil temperatures, and a reduced potential for desiccation via minimization of transpirational losses (Acquaah 1999; Harris and Fanelli 1999; Himelick 1981). Harris et al. (2002) reported that early fall-transplanted sugar maple began root regeneration earlier and regenerated more roots in the first-season post-transplant than the mid fall- and spring-transplanted treatments. Differences in these results and those of Harris et al. (2002) may be a consequence of the trees in the Harris et al. (2002) study being grown in a PIPR. As well, this study did not have an early fall transplant treatment, nor was there an April transplant date in the Harris et al. (2002) study. The greater root production exhibited by the April transplants did correspond to increased shoot elongation in the PIP treatment (see Chapter 3); however, this did not occur in the B&B treatment. All other comparisons among B&B and PIP treatments were similar.

Analysis of Indices of Root Dynamics/Activity and Ratios of Annual Production to Mortality

Similar trends were evident among three of the formulas used for calculating the indices [(N+D)/SC, (N/SC+D/SC)/2, and N/SC where SC=mean standing root length, N=total new root length or annual production, and D=total dead root length or annual mortality] (Fig. 4-5A-D). Only the index using the D/SC formula exhibited a different pattern and thus, will be discussed separately.

Analyses of variance indicated little evidence of a production method x transplant date interaction for the (N+D)/SC, (N/SC+D/SC)/2, and N/SC indices (Tables 4-4 and 4-5). In all three indices, the non-transplanted treatment in the FR had the lowest values or least activity and the non-transplanted PIP treatment had the greatest values or most activity (Table 4-4).

Burton et al. (2000) reported fine root turnover estimates in a sugar maple-dominated northern hardwood forest as ranging between 0.50 to 0.68 and 0.72 to 1.06 year^{-1} for the (N/SC+D/SC)/2 (average of production and mortality) and N/SC (production) indices. Hendrick and Pregitzer (1993a) reported fine root turnover values using minirhizotrons in a sugar maple-dominated forest ranging from 0.66 to 0.76 year^{-1} and 0.79 to 0.83 year^{-1} for (N+D)/2)/SC and N/SC formulas, respectively. Estimates for the index of activity of the transplanted treatments in this study ranged between 0.67 to 0.89 and 1.02 to 1.25 year^{-1} for the (N/SC+D/SC)/2 and N/SC indices (Table 4-4). The larger index values obtained in this study reflect the root regeneration activities (i.e., increased production) of transplanted trees. Estimates of activity for the non-transplanted field PIP treatments were 0.48 and 0.44 year^{-1} and 1.53 and 1.74 year^{-1} for the (N/SC+D/SC)/2 and N/SC indices, respectively (Table 4-4). Differences among the values of the non-transplanted treatments relative to the transplanted treatments reflect the relatively sparse root production by trees in the non-transplanted field treatment, as well as the high root production and root mortality of trees in non-transplanted PIP treatment. Burton et al. (2000) calculated the standing root length as the mean for the year. Had the yearly mean (vs. the mean of the first growing seasons' four largest measurements) been used to calculate the estimates of activity, the values for the non-transplanted field treatment would have been more similar to estimates reported by Burton et al. (2000) and Hendrick and Pregitzer (1993a). Use of the yearly mean would also have resulted in greater estimates of activity for the transplanted trees, which would not be unexpected.

Analysis of variance of the (N+D)/SC, (N/SC+D/SC)/2, and N/SC indices revealed similar differences among treatments between the three indices. In comparisons of the B&B and PIP production methods, only the non-transplanted treatments exhibited markedly different values (Fig. 4-5A-C, Tables 4-4 and 4-5). As expected, the non-transplanted PIP treatment exhibited much greater activity than the non-transplanted field treatment. The index values of both non-transplanted treatments were also markedly different than those of their transplanted counterparts. While the non-transplanted field treatment had lower values or less activity than the transplanted B&B treatments (P values ranged from < 0.0001 to 0.0813 for all comparisons and all indices), the non-transplanted PIP treatment had greater values or more activity than the transplanted PIP treatments ($P < 0.0001$ for all comparisons and all indices). As previously discussed, root systems of trees in the PIPR were bound by a container and as a result, root densities may have been forced to be higher than optimum to support the shoots. Water and nutrients should not have been limiting in the PIP system. If the root systems of the transplanted trees had been confined, they too may have had a greater density of roots. The greater activity of the transplanted trees relative to the non-transplanted field trees likely represents the stimulation of anomalous root growth as a result of transplanting (Cripps 1970; Watson and Himelick 1982).

Among the B&B transplanted treatments, the B&B/April treatment exhibited greater activity or higher values using the (N+D)/SC, (N/SC+D/SC)/2, and N/SC indices than both the B&B/December and B&B/July treatments due to the B&B/April having particularly large production and mortality (Fig. 4-5A-C, Tables 4-4 and 4-5). As discussed earlier, April may have been a favorable time for root regeneration (see *Analysis of Mean Standing Root Length and Annual Production and Mortality*). All other comparisons among the transplanted treatments (both B&B and PIP) using the (N+D)/SC, (N/SC+D/SC)/2, and N/SC indices revealed no significant differences.

When the index was calculated using the D/SC formula, the interpretation of activity changed slightly. Similar to the other indices, there was little evidence of a production method x transplant date interaction ($P = 0.3693$), and the non-transplanted PIP treatment exhibited greater activity than the non-transplanted treatment field treatment ($P < 0.0001$) (Fig. 4-5, Tables 4-4 and 4-5). The non-transplanted PIP treatment also exhibited greater activity than transplanted PIP treatments using the D/SC formula. While Burton et al. (2000) obtained D/SC (mortality) values ranging between 0.20 to 0.52 year^{-1}, values in this study ranged between 0.26 and 0.56 year^{-1} for the transplanted treatments and were 0.51 and 1.33 year^{-1} for the non-transplanted treatments in the FR and PIIPR, respectively. While relative mortality among the transplanted and non-transplanted field treatments was similar to estimates reported by Burton et al. (2000), the substantial mortality that occurred in the non-transplanted PIP trees resulted in a greater value using the D/SC index.

The ratio of annual production to mortality (total new root length to total dead root length or N/D) was also calculated. Little evidence of a production method x transplant date interaction was apparent ($P = 0.9424$) (Fig. 4-5E, Tables 4-4 and 4-5). While the November treatments had the greatest ratios of production to mortality (5.61 and 6.85 for B&B and PIP, respectively), the non-transplanted treatments had the lowest ratios (0.90 and 1.33 for B&B and PIP, respectively). Among the B&B treatments, November and July treatments had greater production:mortality ratios than the non-transplanted field treatment ($P = 0.0462$ and 0.0720, respectively). Among the PIP treatments, November had a greater production:mortality ratio than the non-transplanted PIP and December treatments ($P = 0.0209$ and 0.0739, respectively). All other comparisons among treatments were not statistically significant.

Production to mortality ratios of the transplanted trees in this study ranged between 2.40 to 6.85 for the first growing season and winter after transplant (Table 4-4). Ratios for the non-transplanted B&B/Control and PIP/Control were 0.90 and 1.33, respectively. Burton et al. (2000) reported ratios of 2.0 and 1.4 for the first and second years following the installation of minirhizotron tubes. The authors suggested that the ratios were high due to the minirhizotron tubes not yet being fully equilibrated with the surrounding soil following installation (Joslin and Wolfe 1999) and that as the soil adjacent to the tubes becomes recolonized by roots, the annual production and mortality ratio would eventually come into an approximated equilibrium. Due to the substantial loss of roots that occurs as a result of transplanting, high ratios of production to mortality should be expected. Trees in this project were in the process of regenerating a root system and subsequently had elevated root production levels. As time passes, the production to mortality ratio would likely decrease.

Different estimates were obtained using the previously discussed indices (Table 4-4). This is a result of each index emphasizing particular root activities. Similar trends in the estimates were evident among the (N+D)/SC, (N/SC+D/SC)/2, and N/SC indices due to their inclusion of production activities, which was a dominant activity in the transplanted trees. Similar to the values that reported in this study, Burton et al. (2000) reported that estimates of fine root turnover were greater when calculated using N/SC compared to D/SC. They suggested that the greater N/SC values were a result of the minirhizotrons having not fully equilibrated following installation (Burton et al. 2000; Joslin and Wolfe 1999). As equilibrium is reached, production and mortality should become nearly equal as production decreases and/or mortality increases. However, while the disturbance of the rhizosphere during the installation of minirhizotrons or rhizotrons is an obstacle for most studies, the disturbance of the rhizosphere was the treatment in this study. Therefore, disturbances associated with rhizotron installation were of little concern for the transplanted treatments. The rhizotrons of the non-transplanted control trees were installed the previous September and thus, were given some time to recover.

Conclusions

Applications from forestry and ecology regarding fine root turnover have been adapted for application to transplanted landscape-sized trees. To my knowledge, root mortality has not been studied in recently transplanted trees of landscape size. Generally, root mortality has been assumed to be a minimal factor in the root dynamics of recently transplanted landscape trees. Indeed, I too assumed that root mortality was minimal for the first several weeks after the initiation of root regeneration. However, in hindsight this assumption may have been false. Data from this study indicate that root mortality is a factor in early dynamics of post-transplant root regeneration.

While root production was limited to the growing season, root mortality occurred year-round and reached a maximum in winter for transplanted trees and late spring for the non-transplanted trees. The observed winter root mortality in transplanted trees may provide support for a theory regarding ‘temporary’ roots in transplanted trees. Early spring root production occurred later in the transplanted treatments relative to the non-transplanted field treatment, suggesting that transplanted trees may lack the carbon resources to support early spring root production. Substantial root mortality prior to periods of root production in all treatments except non-transplanted field trees may indicate competition for resources and a reallocation of carbon within the tree. Finally, non-transplanted trees in the PIPR exhibited production and mortality dynamics that were atypical of sugar maples in forest settings or trees in the FR in this study. The dynamics of the non-transplanted trees in the FR were closer to that of trees in forest. Consequently, the results of this study indicate that transplanting and the PIP production system do disrupt typical patterns of root production and mortality in sugar maple. The highly dynamic nature of the containerized roots in the PIP production system may have consequences that affect nutrition within the PIP system and may be of interest to persons studying carbon and nutrient cycling.

Due to root production processes being such a dominant factor for transplanted trees, indices that include production will likely be similar. Indices such as D/SC that don’t take into account production processes will obtain dissimilar results. The ratio of production to mortality (N/D) probably provides the most useful information. The production:mortality ratio gives us an estimate that, in a healthy forest setting, would be expected to have a value close to 1. In this study, the estimate of the non-transplanted field treatment was closest to 1. Conversely, estimates for the transplanted treatments were much higher, indicating significant production was occurring relative to mortality. The low value of 1.33 value for the non-transplanted PIP treatment is a result of the occurrence of abundant root production and root mortality.

Based upon work of Engler (1903), who reported that hardwood root tips turned brown in three to six weeks, Morrow (1950) assumed that suberization of sugar maple roots occurred 1 month after growth in the spring. Rates of suberization were not calculated in this study; however, suberization was occasionally observed to occur within one week after the first observation of new, white roots. Rapid root elongation [in excess of 5 cm (2 in) week^{-1}] was also observed.

Root longevity was not addressed in this study but since the first regenerated roots appeared on the rhizotron window on 2 May 2001, all of the roots that died in this study prior to the following May are assumed to be less than 1 year in age. Roots in the transplanted trees that died around 22 January 2002 (a period of substantial root mortality) were therefore no more than 9 months old.

Information gained from this research will hopefully contribute to the understanding of root system regeneration and nutrient and carbon cycling in transplanted trees. Future studies that may be of interest might: 1) document root production and root mortality after transplanting other species, 2) study root turnover in established trees in the landscape, 3) document longevity of regenerated roots, 4) follow the pattern of root production and mortality in relation to carbon allocation and translocation within the plant, 5) explore how competition from established trees might limit root production (e.g., maximal densities), 6) study the cycling of roots in the PIP system and the implications of cycling relating to nitrogen/nutrient loss in PIP growing systems, and 7) compare the longevity of roots regenerated after transplanting to the longevity of roots in a stable system.

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Table 4-1. Analysis of variance for comparing patterns of standing root length and root production and mortality of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4.

Effect	Num DF	Den DF	F value	*P* > F
Standing Root Length				
Transplant Date	5	33	4.42	0.0034
Production Method	1	33	3.74	0.0618
Transplant*Production	5	33	2.17	0.0819
Day	26	858	4.97	<.0001
Production*Day	26	858	1.67	0.0198
Transplant*Day	130	858	2.34	<.0001
Transplant*Production*Day	130	858	1.30	0.0188
Root Production				
Transplant Date	5	33	6.32	0.0003
Production Method	1	33	6.83	0.0134
Transplant*Production	5	33	5.25	0.0012
Day	26	858	6.59	<.0001
Production*Day	26	858	1.26	0.1718
Transplant*Day	130	858	2.43	<.0001
Transplant*Production*Day	130	858	1.84	<.0001
Root Mortality				
Transplant Date	5	33	8.70	<.0001
Production Method	1	33	5.87	0.0211
Transplant*Production	5	33	10.06	<.0001
Day	26	858	4.34	<.0001
Production*Day	26	858	2.03	0.0018
Transplant*Day	130	858	1.61	<.0001
Transplant*Production*Day	130	858	1.30	0.0187

Table 4-2. Mean standing root length density and total root production and mortality of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4.

Treatment	Standing Root Length (mm/cm^2)		Root Production (mm/cm^2)		Root Mortality (mm/cm^2)	
	B&B	PIP	B&B	PIP	B&B	PIP
Control	21.80	72.48	8.64	122.77	6.88	44.79
November	16.01	27.16	17.09	30.84	6.68	6.29
December	26.27	21.66	26.71	23.77	9.04	8.45
March	33.44	23.96	35.16	26.32	10.80	6.68
April	62.56	55.26	78.96	63.12	34.18	16.24
July	16.89	34.62	17.68	39.48	4.71	9.63

Table 4-3. Analysis of variance of mean standing root length and total root production and mortality of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4.

Effect	Standing Root Length	Root Production	Root Mortality
		P > F	
Production Method	0.8252	0.8793	0.4001
Transplant Date	0.0074	0.0356	0.0467
Production*Transplant Date	0.6163	0.7526	0.5120
B&B vs. PIP			
Control	0.0011	<.0001	0.0002
November	0.4353	0.5317	0.9652
December	0.7457	0.8931	0.9478
March	0.5872	0.7422	0.7087
April	0.6352	0.5048	0.0721
July	0.2179	0.3235	0.5864
B&B			
Control vs. November	0.6841	0.7003	0.9826
Control vs. December	0.7535	0.4121	0.8105
Control vs. March	0.4155	0.2315	0.6631
Control vs. April	0.0068	0.0028	0.0044
Control vs. July	0.7301	0.6806	0.8105
November vs. December	0.4723	0.6611	0.7936
November vs. March	0.2255	0.4121	0.6475
November vs. April	0.0023	0.0076	0.0042
November vs. July	0.9504	0.9786	0.8274
December vs. March	0.6149	0.7003	0.8444
December vs. April	0.0148	0.0221	0.0082
December vs. July	0.5110	0.6806	0.6319
March vs. April	0.0470	0.0523	0.013
March vs. July	0.2494	0.4274	0.5005
April vs. July	0.0028	0.0081	0.0023
PIP			
Control vs. November	0.0029	0.0002	0.0001
Control vs. December	0.0010	<.0001	0.0003
Control vs. March	0.0083	0.0010	0.0014
Control vs. April	0.2668	0.0160	0.0057
Control vs. July	0.0113	0.0005	0.0004
November vs. December	0.6993	0.7472	0.8105
November vs. March	0.8546	0.8664	0.9716
November vs. April	0.0742	0.1788	0.3101
November vs. July	0.6005	0.6937	0.7111
December vs. March	0.8946	0.9242	0.8727
December vs. April	0.0346	0.1034	0.4254
December vs. July	0.3650	0.4752	0.8959
March vs. April	0.0952	0.1992	0.4134
March vs. July	0.5418	0.6246	0.7895
April vs. July	0.1850	0.3218	0.4981

Table 4-4. Indices of root activity (production and mortality relative to standing root length) of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (SC=standing root length, N=production, D=mortality).

Treatment	Indices of Root Activity				
	(N+D)/SC	(N/SC+D/SC)/2	N/SC	D/SC	N/D
B&B					
Control	0.95	0.48	0.44	0.51	0.90
November	1.65	0.83	1.09	0.56	5.61
December	1.35	0.68	1.02	0.34	3.09
March	1.42	0.71	1.11	0.31	3.37
April	1.77	0.89	1.25	0.53	2.40
July	1.33	0.67	1.03	0.30	5.13
PIP					
Control	3.07	1.53	1.74	1.33	1.33
November	1.42	0.71	1.15	0.27	6.85
December	1.56	0.78	1.11	0.45	2.65
March	1.33	0.67	1.07	0.26	4.22
April	1.46	0.73	1.15	0.31	4.32
July	1.44	0.72	1.15	0.29	4.77

Table 4-5. Analysis of variance of indices of root activity (production and mortality relative to standing root length) of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (SC=standing root length, N=production, D=mortality).

Effect	Index of Root Activity				
	(N+D)/SC	(N/SC+D/SC)/2	N/SC	D/SC	P:M=N:D
			P > F		
Production Method	0.5278	0.5278	0.6305	0.2127	0.5562
Transplant Date	0.5199	0.5199	0.6046	0.6131	0.2639
Prod*Date Interaction	0.4155	0.4155	0.7490	0.3693	0.9424
B&B vs. PIP					
Control	<.0001	<.0001	<.0001	<.0001	0.8487
November	0.2821	0.2821	0.6279	0.0651	0.5886
December	0.3394	0.3394	0.4324	0.4731	0.8495
March	0.7408	0.7408	0.7981	0.7950	0.7631
April	0.1813	0.1813	0.4847	0.1872	0.4410
July	0.6284	0.6284	0.3485	0.9469	0.8784
B&B					
Control vs. November	0.0022	0.0022	<.0001	0.4116	0.0462
Control vs. December	0.0659	0.0659	<.0001	0.2740	0.3423
Control vs. March	0.0347	0.0347	<.0001	0.1992	0.2839
Control vs. April	0.0005	0.0005	<.0001	0.8884	0.5125
Control vs. July	0.0813	0.0813	<.0001	0.1793	0.0720
November vs. December	0.1666	0.1666	0.5412	0.1469	0.2758
November vs. March	0.2736	0.2736	0.8677	0.1018	0.3332
November vs. April	0.5720	0.5720	0.2006	0.8184	0.1680
November vs. July	0.1384	0.1384	0.6403	0.0903	0.8329
December vs. March	0.7651	0.7651	0.4379	0.8445	0.9005
December vs. April	0.0555	0.0555	0.0631	0.2187	0.7650
December vs. July	0.9178	0.9178	0.8850	0.7969	0.3770
March vs. April	0.1016	0.1016	0.2633	0.1561	0.6719
March vs. July	0.6879	0.6879	0.5269	0.9511	0.4471
April vs. July	0.0445	0.0445	0.0847	0.1397	0.2399
PIP					
Control vs. November	<.0001	<.0001	<.0001	<.0001	0.0209
Control vs. December	<.0001	<.0001	<.0001	<.0001	0.5659
Control vs. March	<.0001	<.0001	<.0001	<.0001	0.3075
Control vs. April	<.0001	<.0001	<.0001	<.0001	0.2331
Control vs. July	<.0001	<.0001	<.0001	<.0001	0.1400
November vs. December	0.5211	0.5211	0.7571	0.2589	0.0739
November vs. March	0.7288	0.7288	0.6063	0.9383	0.3520
November vs. April	0.8619	0.8619	0.9610	0.8384	0.3101
November vs. July	0.9497	0.9497	0.9922	0.9238	0.3678
December vs. March	0.3857	0.3857	0.7921	0.3170	0.5773
December vs. April	0.6736	0.6736	0.7374	0.3971	0.5026
December vs. July	0.5626	0.5626	0.7645	0.3003	0.3579
March vs. April	0.6355	0.6355	0.5963	0.8072	0.9738
March vs. July	0.6906	0.6906	0.6119	0.8764	0.8440
April vs. July	0.9080	0.9080	0.9537	0.9081	0.8541

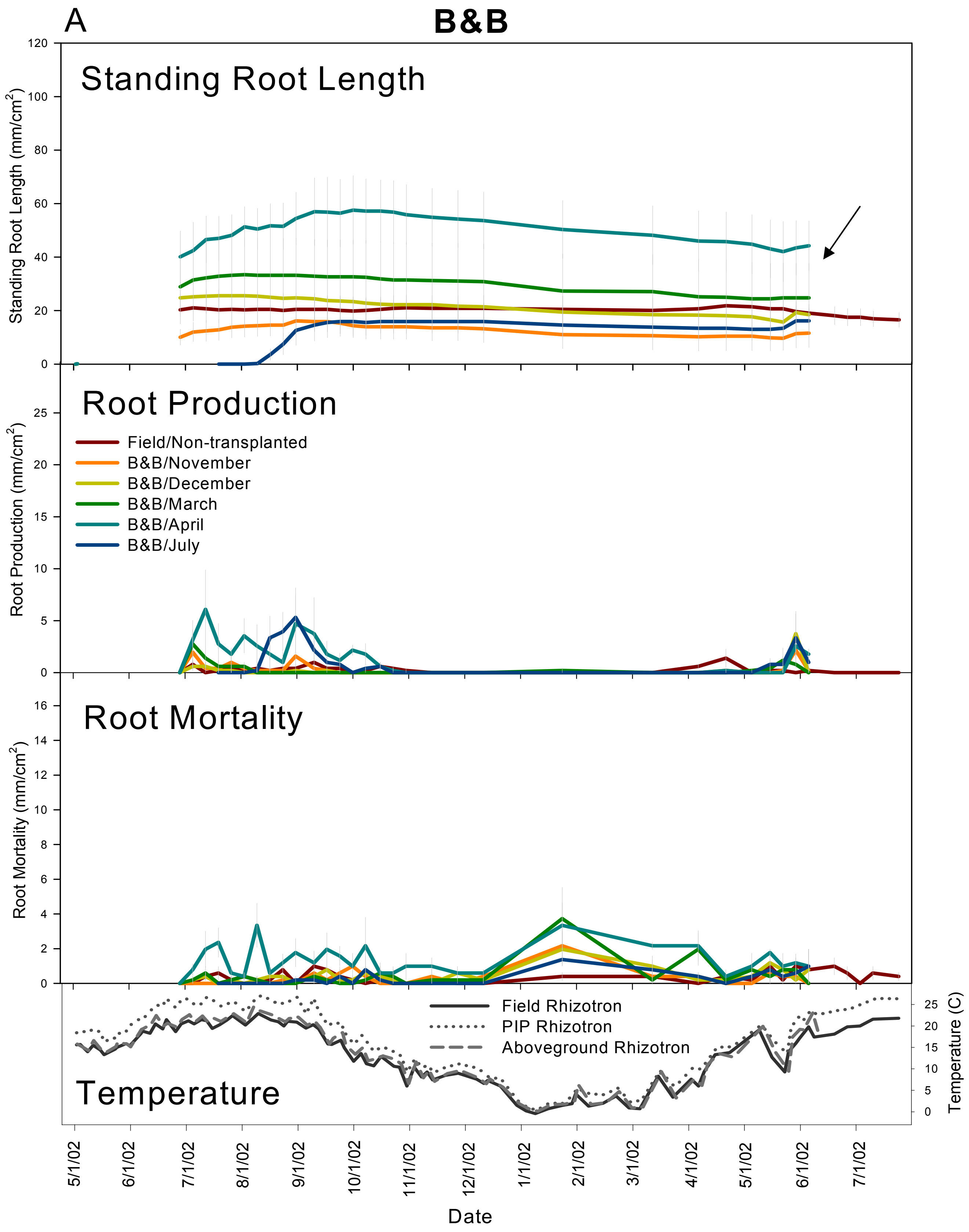
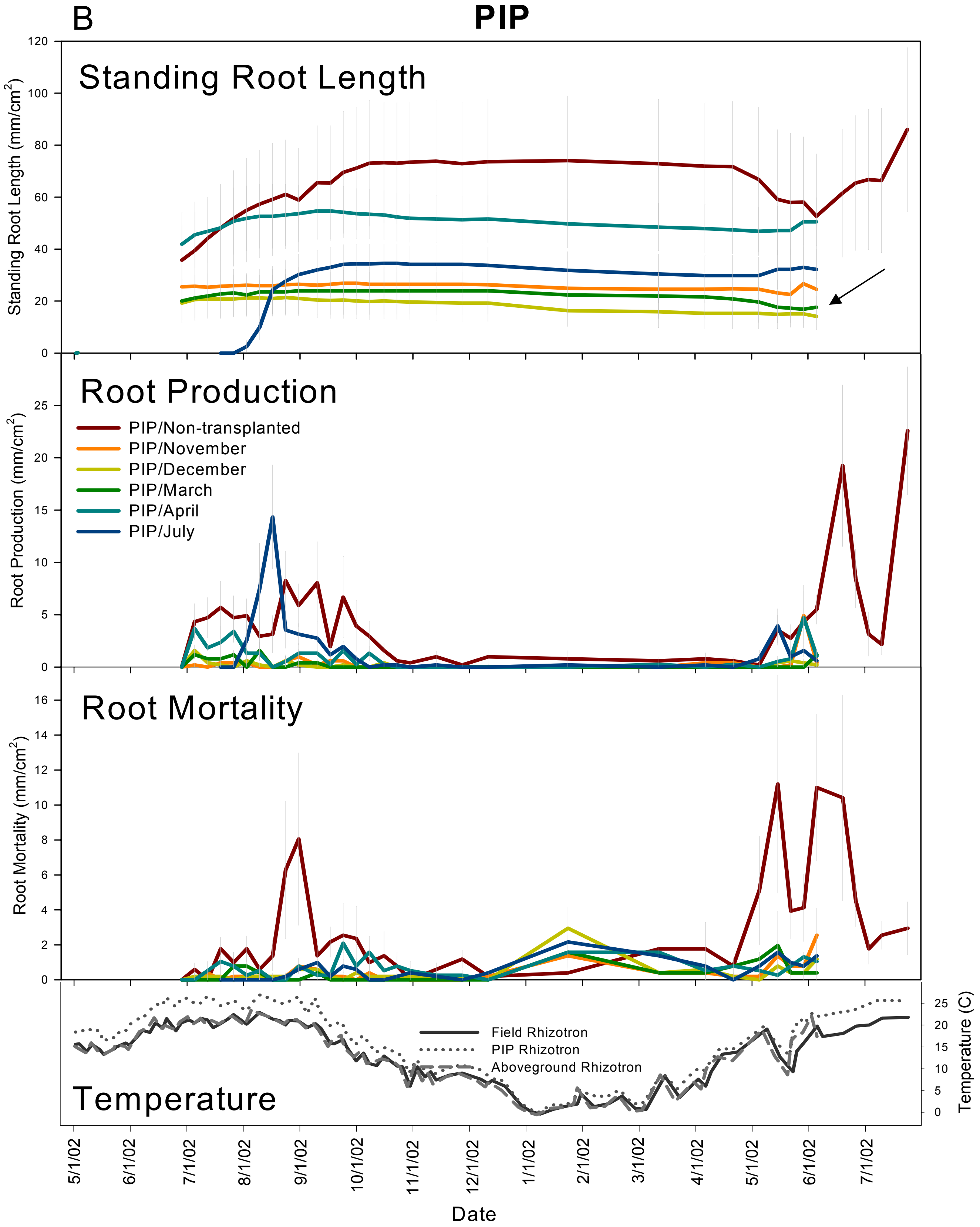


Figure 4-1. Seasonal patterns of standing root length, root production, and root mortality of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (↑ indicates harvest of the transplanted treatments. See text for details.)


B
PIP
Standing Root Length
Standing Root Length (mm/cm^2)
0
20
40
60
80
100
120
Root Production
Root Production (mm/cm^2)
0
5
10
15
20
25
PIP/Non-transplanted
PIP/November
PIP/December
PIP/March
PIP/April
PIP/July
Root Mortality
Root Mortality (mm/cm^2)
0
2
4
6
8
10
12
14
16
Temperature
Field Rhizotron
PIP Rhizotron
Aboveground Rhizotron
Temperature (C)
0
5
10
15
20
25
5/1/02
6/1/02
7/1/02
8/1/02
9/1/02
10/1/02
11/1/02
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6/1/02
7/1/02
Date

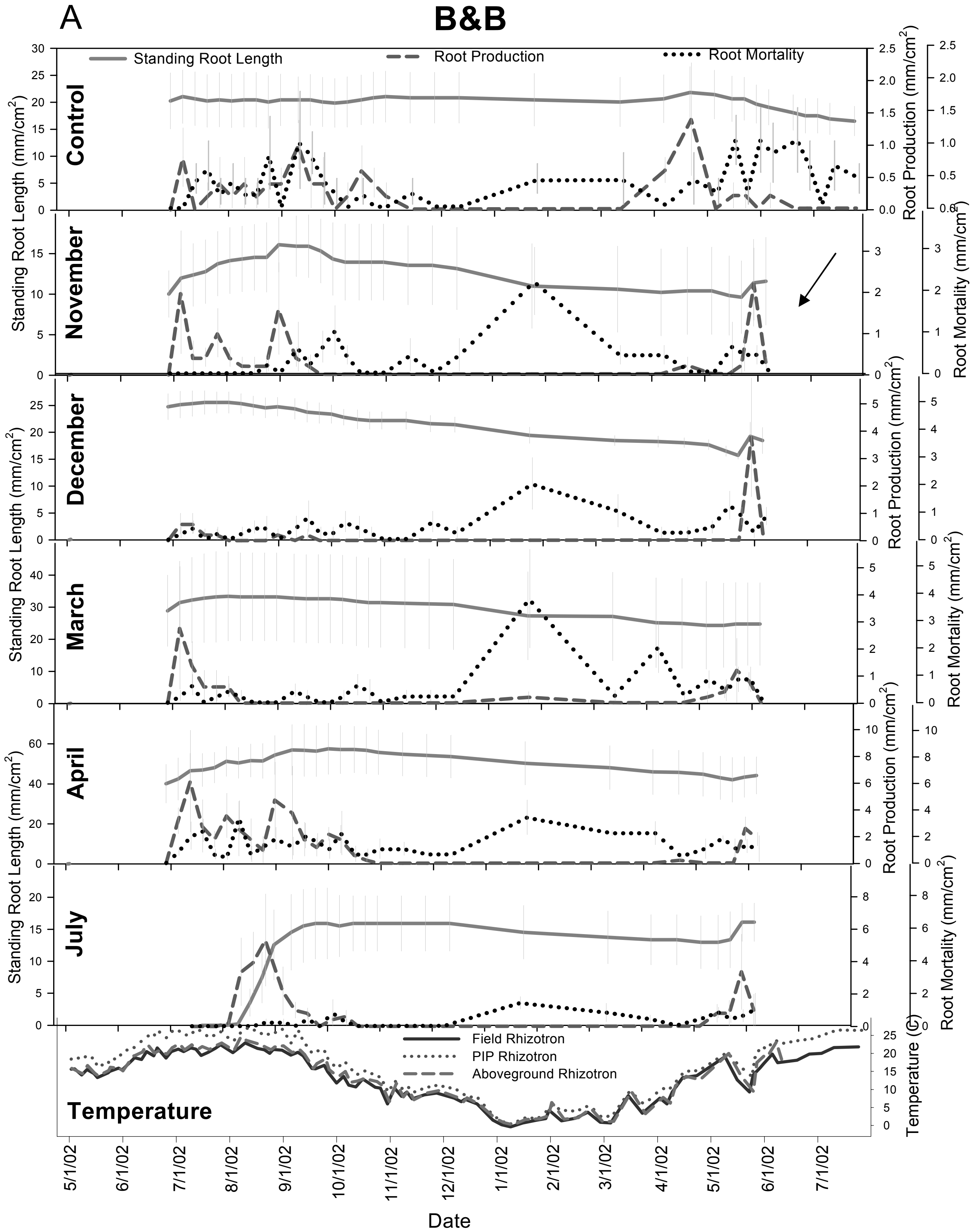
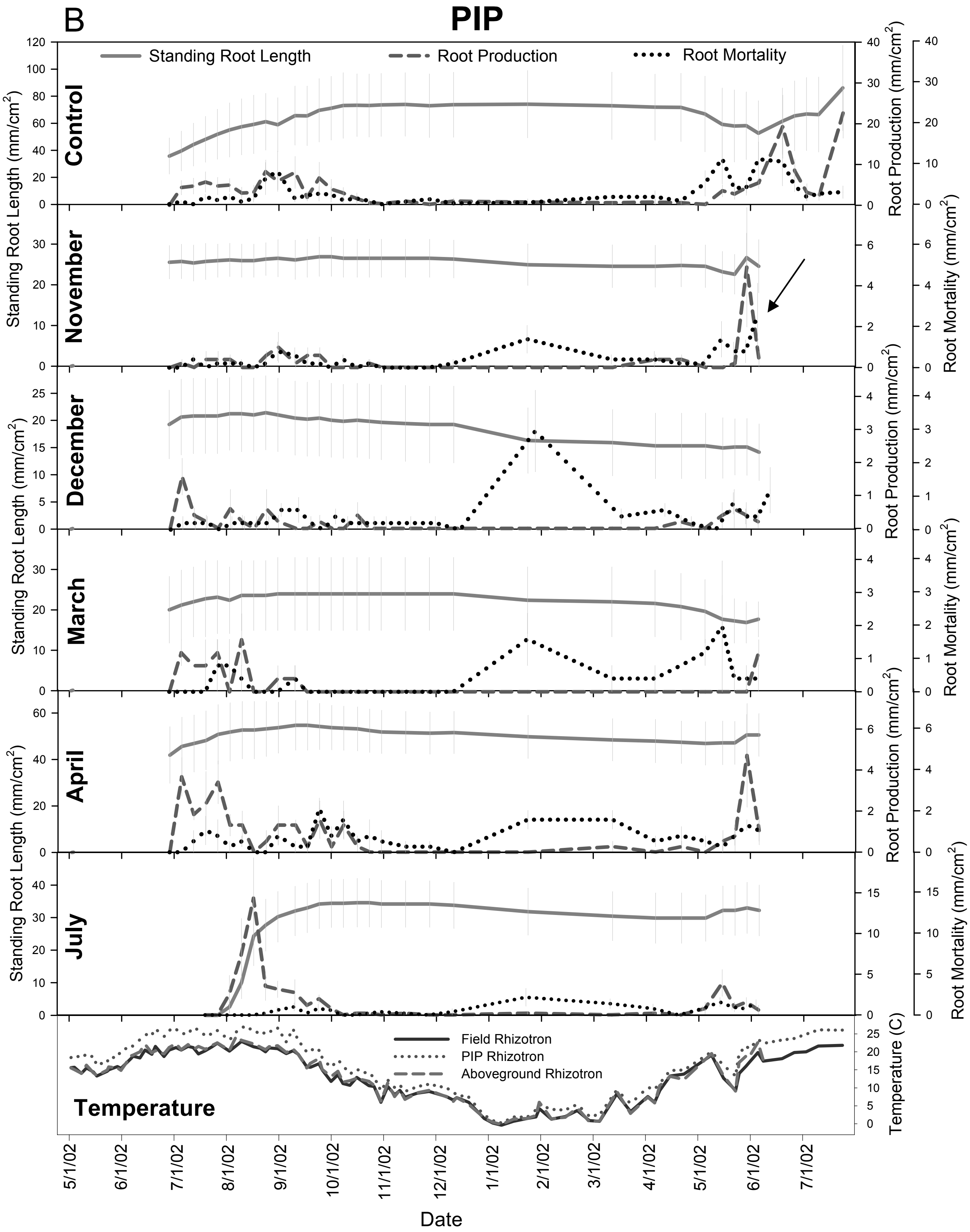


Figure 4-2. Seasonal pattern of standing root length, root production, and root mortality of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4. (↑ indicates harvest of the transplanted treatments. See text for details.)


B
PIP
Standing Root Length
Root Production
Root Mortality
Control
November
December
March
April
July
Temperature
Field Rhizotron
PIP Rhizotron
Aboveground Rhizotron
Standing Root Length (mm/cm^2)
Root Production (mm/cm^2)
Root Mortality (mm/cm^2)
Temperature (C)
5/1/02
6/1/02
7/1/02
8/1/02
9/1/02
10/1/02
11/1/02
12/1/02
1/1/02
2/1/02
3/1/02
4/1/02
5/1/02
6/1/02
7/1/02
Date

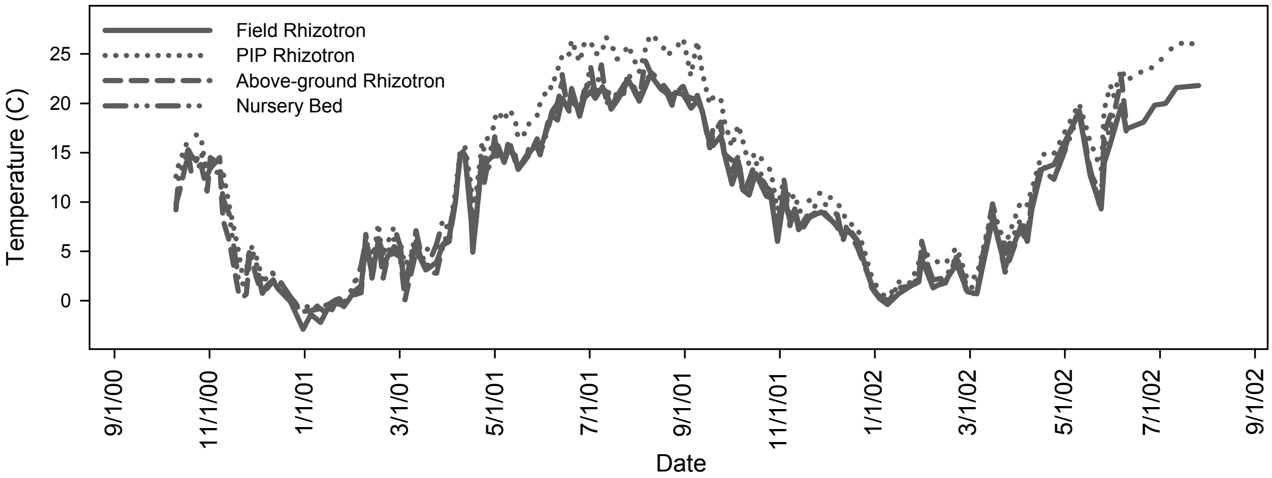


Figure 4-3. Soil temperature at 30 cm depth taken in the field rhizotron, pot-in-pot rhizotron, aboveground rhizotron, and nursery bed.

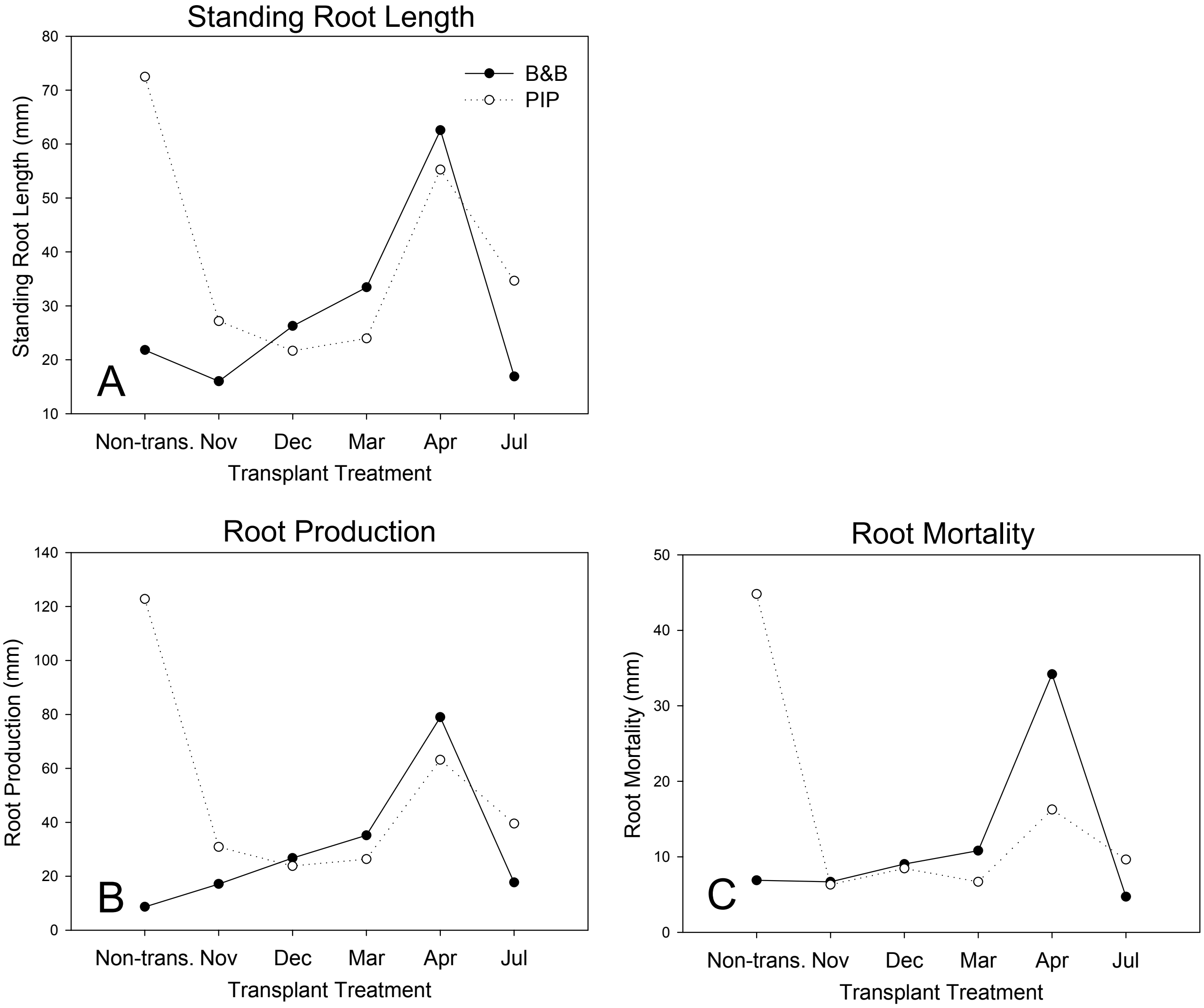


Figure 4-4. Plot of the interaction between production method and transplant date on the mean standing root length and total root production and mortality of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November and December 2000 and March, April, and July 2001. n=4.

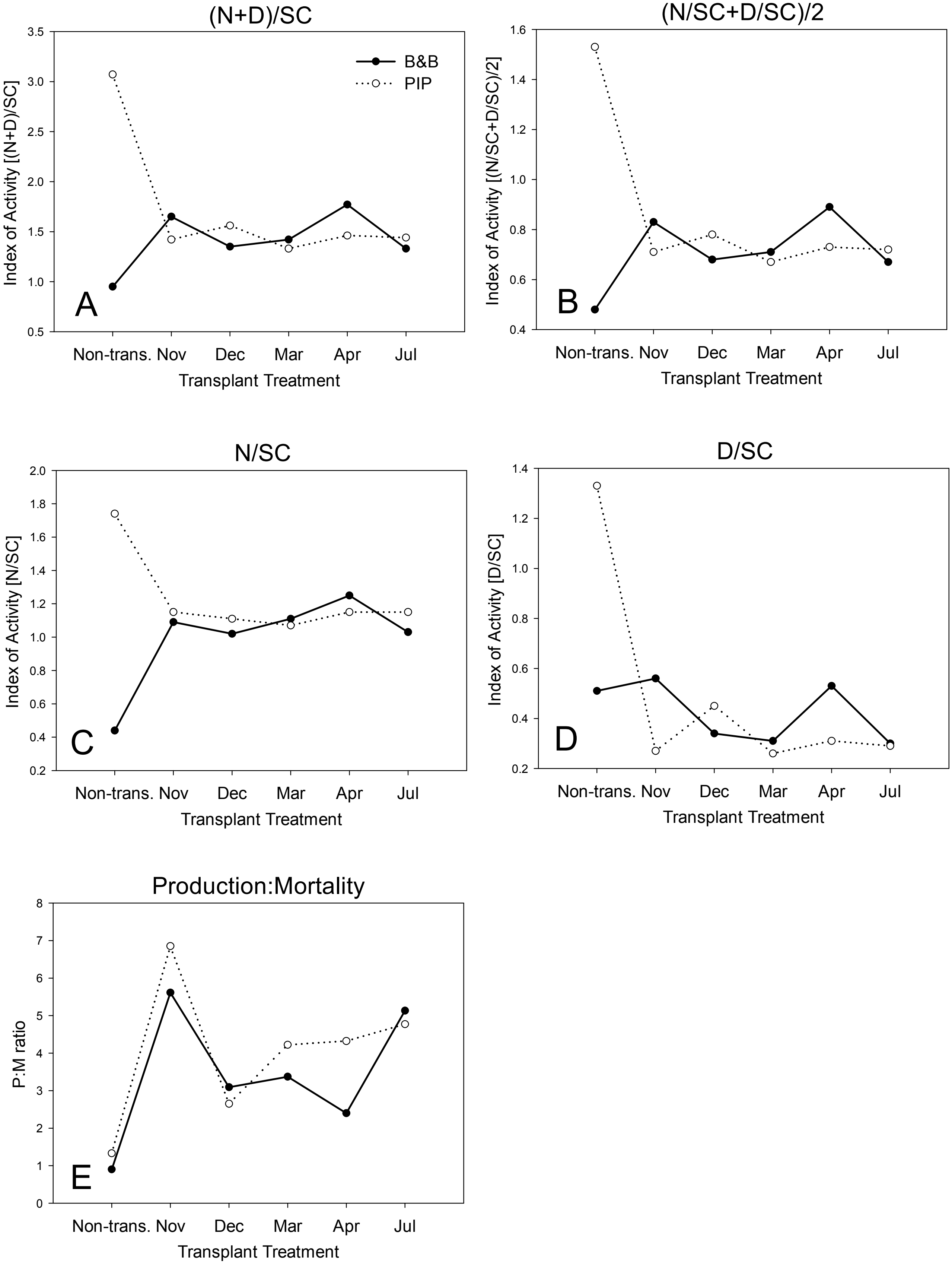


Figure 4-5. Plot of the interaction between production method and transplant date of the indices of root activity (production and mortality relative to standing root length) of balled-and-burlapped and pot-in-pot sugar maple (*Acer saccharum* Marsh.) transplanted in November, December, March, April, and July. n=4. (SC=standing root length, N=production, D=mortality).

Summary

Transplant timing and production method affect the establishment of transplanted trees, potentially through poorly understood changes in early root system regeneration. Root regeneration prior to bud break the first spring after transplanting can help transplants establish faster since they will have a larger root system to support the first post-transplant flush of shoot growth. Therefore, post-transplant root regeneration, root and shoot growth periodicity, and patterns of root production and mortality were studied in balled-and-burlapped (B&B) and pot-in-pot (PIP) landscape-sized shade trees transplanted at various times in the year. Canopy growth was also assessed to determine the influence of transplant time and production method.

Early post-transplant and pre-bud break root regeneration was evaluated by excavation of northern red oak (*Quercus rubra* L.) and willow oak (*Q. phellos* L.) root balls and observation of sugar maples (*Acer saccharum* Marsh.) transplanted into rhizotrons. No root regeneration was observed in any treatment (fall or spring) of any study until spring. While modest root regeneration occurred prior to bud break in both fall- and spring-transplanted red and willow oak, regenerated roots were not observed in any of the sugar maple treatments until approximately 2 weeks after bud break.

Fall-transplanted red oaks had slightly greater pre-bud break root regeneration than the spring-transplanted trees; however, overall regenerated root length was small and did not appear to confer advantages in terms of height and trunk diameter growth. Little difference in height and trunk diameter growth was evident between the fall- and spring-transplanted red oaks throughout the 3 years following transplant. Similarly, little difference was evident between the height growth of fall- and spring-transplanted willow oaks. However, in contrast to red oak, fall-transplanted willow oaks had greater trunk expansion than spring-transplanted trees despite there being similar amounts of regenerated roots at bud break. Similar to the findings in willow oak, increased root regeneration in the April-transplanted B&B sugar maples did not confer increased shoot extension and trunk expansion. As well, increased shoot extension in the April-transplanted PIP sugar maples relative to the other transplanted sugar maples did not correspond to significantly increased root regeneration. Therefore, under the conditions of this study, pre-bud break root growth and abundant root regeneration did not appear to correspond to greater post-transplant shoot growth. While survival for all red oaks was 100%, survival of fall- and spring-transplanted willow oaks was 67 and 83%, respectively. Among the surviving willow oaks, fall transplanting resulted in more height and trunk diameter growth. However, when mortality rates are taken into account, spring may be a better time to transplant willow oak in climates similar to Blacksburg, VA (USDA climate zone 6a).

While shoot and trunk growth of sugar maple exhibited very uniform and well-defined patterns of growth, root growth and mortality exhibited much greater variation with regards to time and duration. All sugar maples in all treatments, except the July transplant, exhibited a pattern of maximum shoot extension in early May, followed by maximum root growth in late May, and maximum trunk expansion in mid June. Maximum root growth and early trunk expansion occurred at the time when shoot extension rate was decreasing. Transplanting did not appear to radically disrupt the normal root and shoot growth periodicity of sugar maple, except when trees were transplanted in July. July transplants underwent substantial root regeneration 4 weeks after transplant and at a time when root growth had slowed in all other treatments. Eight weeks after transplant, the July transplants had ‘caught up’ in regenerated root length to all other treatments except the April-transplanted B&B trees and non-transplanted PIP trees, indicating that there may be little advantage to fall and spring transplanting compared to summer transplanting with regards to post-transplant root regeneration in sugar maple.

Relative to the non-transplanted field trees (the best representative of established trees), first-season shoot extension of the transplanted trees was reduced and root production was increased. The increased root production and reduced shoot extension of the transplanted treatments relative to the non-transplanted field treatment likely reflect a coordination of growth by the tree and compensatory growth of the root system to restore a more favorable root:shoot ratio. Reduced shoot growth and increased root production favors the moisture balance of transplanted trees by potentially minimizing transpirational losses and maximizing absorptive capabilities.

While root production of sugar maple was limited to the growing season, root mortality occurred year-round and reached a maximum in winter for the transplanted trees and late spring and summer for the non-transplanted trees. Relative to production, root mortality occurred at a steadier rate. Compared to the non-transplanted field trees and other reports on root production in sugar maple, the non-transplanted PIP and transplanted treatments exhibited a delay in early spring root production, suggesting that transplanted trees may lack the carbon resources to support early spring root production. Delayed spring root production and substantial winter root mortality indicate that transplanting does disrupt typical patterns of root production and mortality in sugar maple. The altered patterns of root production and mortality (e.g., delayed early spring root production and substantial winter root mortality) may reflect the carbon economy of the transplants.

Indices of root activity (analogous to turnover rates) that included production processes relative to standing root length revealed greatest and least activity in the non-transplanted PIP and field sugar maples, respectively. Differences between production:mortality ratios of the treatments illustrate the degree to which production processes dominate early post-transplant root dynamics in sugar maple. A production:mortality ratio in a healthy forest would be expected to have a value close to 1. In this study, the estimate of the non-transplanted field treatment was 0.9. Conversely, estimates for the transplanted treatments were much higher (2.4 to 6.9), indicating significant production was occurring relative to mortality.

While minimal root mortality occurred over winter in the non-transplanted field trees, significant reductions in root length occurred in winter in most of the transplanted treatments. Similarly, the non-transplanted sugar maples in the PIP system exhibited declines in standing root length in winter and in spring; however, root mortality was much greater in the non-transplanted trees in the PIP system than in any other treatment. As well, the non-transplanted PIP trees had greater standing root length and annual production and mortality than the non-transplanted field trees and transplanted PIP trees. The highly dynamic nature of root systems in the PIP production system may have consequences that affect nutrition within the PIP system and may be of interest to persons studying carbon and nutrient cycling.

Appendix A

Figure A-1. Two photos of the field rhizotron (FR) in nursery bed.

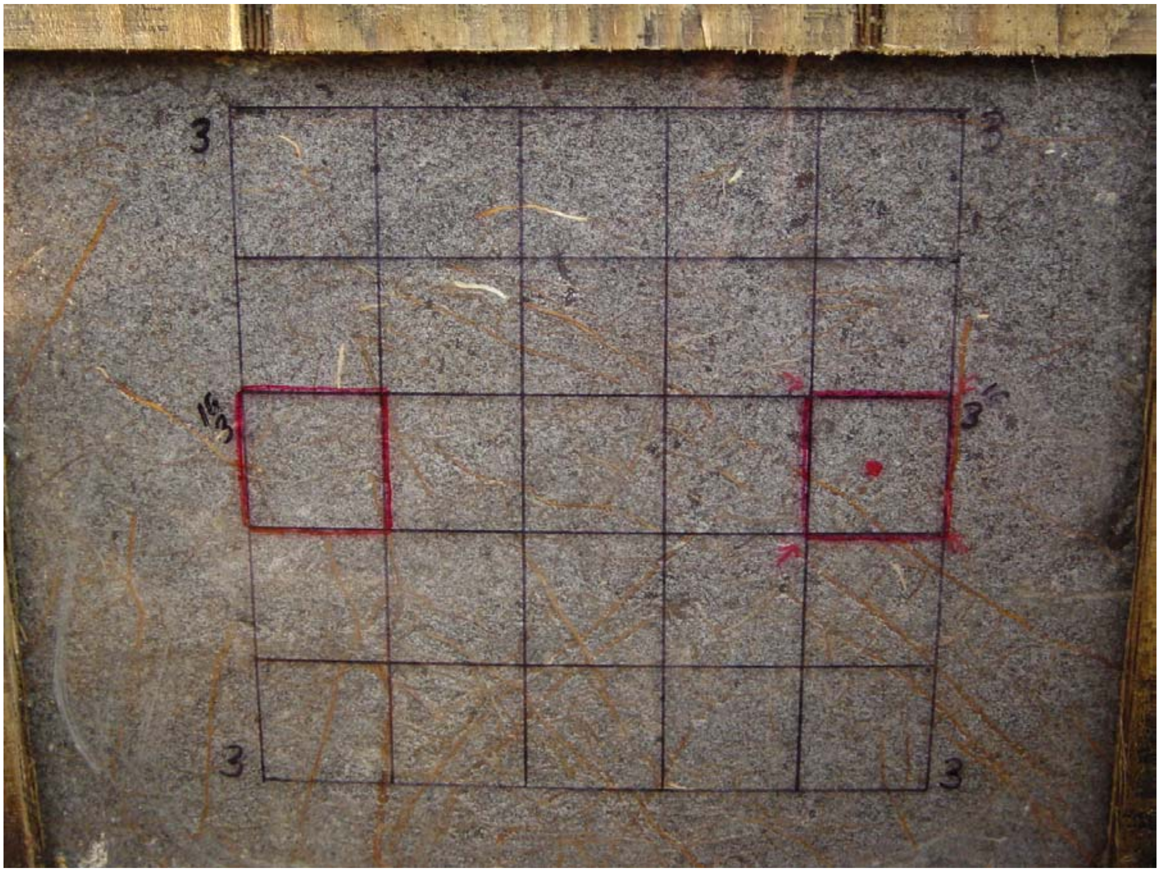


Figure A-2. FR window.

Figure A-3. Pot-in-pot rhizotron (PIPR) in pot-in-pot production system.

Figure A-4. PIPR window.

Figure A-5. Aboveground rhizotron (AGR) in nursery bed.

Figure A-6. AGR window.

Figure A-7. Root mat of a PIP sugar maple.

Vita

Lisa E. Richardson-Calfee received a Bachelor of Science degree in Biology and Zoology from the University of Tennessee, Knoxville in December 1992. In August 1996, Lisa reentered University of Tennessee, Knoxville and in May 1999 received a Master of Science degree in Ornamental Horticulture and Landscape Design. Lisa entered Virginia Polytechnic Institute and State University in August 1999 and received a Doctor of Philosophy degree in Horticulture in August 2003.

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