INFLUENCE OF TRANSPLANTING PRACTICES ON GROWTH AND EMBOLISM LEVELS FOR URBAN TREE SPECIES

by

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Dissertation submitted to the faculty of Virginia Polytechnic Institute and State University in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

in

Horticulture

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March, 1997

Blacksburg, Virginia

Key Words: Cavitation, Embolism, Transplanting
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(ABSTRACT)

Changes in xylem embolism levels due to drought stress or freezing have been documented for a wide variety of plants. High degrees of tissue water stress which lead to increased levels of embolism are also often cited as factors negatively influencing plant establishment. Embolized xylem elements can potentially lead to restriction of stem water flow, thereby reducing growth. Therefore, this dissertation (5 experiments) was undertaken to determine if certain transplanting practices affect embolism dynamics and plant growth of selected urban tree species. Embolism was estimated based on reductions in hydraulic conductance of harvested stem segments. An initial experiment determined the length of time from tissue harvest to embolism measurement that stem samples may be held in cold storage. Results varied between *Fraxinus americana* L. (white ash) and *Acer rubrum* L. × *saccharinum* L. (hybrid red maple), but data suggested white ash stem samples should not be stored more than one day, especially for between-species comparisons. A greenhouse experiment investigated the growth and embolism levels for container-grown *Corylus colurna* L. (Turkish hazelnut) seedlings in response to root pruning. Increasing levels of root pruning from 25 to 50% increased embolism, although plant height also increased. There was no fertilizer level x root pruning interaction for embolism. A field-harvest and greenhouse growth experiment investigated the influence of cold storage duration on plant growth and pre- and post-transplant embolism levels. Embolism levels increased with duration of cold storage for *Acer rubrum* L. (red maple), but not for *Crataegus phaenopyrum* (L.f.) Medic. (Washington hawthorn). After 15 weeks of growth, however, embolism levels were similar for both species. Growth increased with increased cold storage duration for both species. A field experiment investigated the influence of transplant season and root pruning on plant growth and embolism of Turkish hazelnut and *Syringa reticulata* (Blume) Hara (tree lilac). Embolism levels just prior to budbreak and days to budbreak were highest for fall-transplanted Turkish hazelnut. Embolism level was unaffected by treatments. No clear relationship between embolism and growth could be determined for either species the first season after transplanting. Other fall-transplanted Turkish hazelnuts, however, had growth reductions that corresponded to increasing embolism levels two years after transplanting. An additional transplanting experiment examined the influence of root severance at transplanting on water relations of red maple. Stem sap flow (*in vivo*) was reduced within 2 h of harvest, and leaf stomatal conductance was reduced 4 h after harvest. Percent embolism (*in vitro*) was increased within 24 hr of harvest. Results of these experiments indicate that root pruning, and choice of transplant season can reduce plant growth and increase embolism levels. No clear relationship between embolism and growth reduction was evident. Although embolism dynamics are clearly impacted by transplanting, the implications for
transplant success are inconclusive. The role of embolism in transplant success was not clear.
Acknowledgments

I would like to express my thanks and great appreciation to J. Roger Harris, who has provided guidance and editorial advice while serving as my major professor over the past 3 years. I would also like to thank Drs. Alex Niemiera, John Seiler, Greg Welbaum, and Robert Wright, who comprise the remainder of my graduate committee. Their advice and support was crucial as I pursued various research projects. Additionally, Drs. John Barden and Dave Orcutt provided critical research equipment.

I would like to extend special thanks to Jody Fanelli and Matt Kelting who provided much of the physical labor necessary to complete the projects comprising this dissertation. I would also like to thank Marilyn Echols, Donna Long, and Joyce Shelton for their help in making sure everything from slides to paperwork was done properly. Additional special thanks to Suzanne Sparks for help in submitting the document in electronic format and for being a good friend throughout the entire process.

Finally, I would like to thank my husband, Hiram Baldwin, for help with both the physical and mental labor that went into the completion of these projects. His support has contributed significantly to my success. Therefore, this work is dedicated to him.
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INTRODUCTION

Transplanting stress is a term used to describe a complexity of events that occur when a plant is removed from one growing location and replanted at another (Coutts, 1982). Reductions in plant growth due to transplanting have been widely reported for a variety of plant species (Chen et al., 1991; Coutts, 1982; and Watson and Kupkowski, 1991). Transplanting stress is often attributed to alterations in plant water status during the harvesting and transplanting processes and has been considered the most important factor governing plant establishment and growth (Grossnickle, 1988; Kaushal and Aussenac, 1989; and Kramer and Boyer, 1995). These alterations often include more negative water potentials (Coutts, 1982 and Guehl et al., 1993) and decreased transpiration (Coutts, 1982). Since roots are damaged or severed at harvest, immediate root growth or regeneration is important in order for the plant to overcome transplanting stress (Guehl et al., 1993; Lathrop and Mecklenburg, 1971; and Watson and Himelick, 1982). Desiccation of plants during cold storage may also contribute to transplanting stress (Bates and Niemiera, 1996).

Since tree harvest often involves severe root removal (Watson and Himelick, 1982), the influence of root pruning on tree growth must be considered when investigating transplanting stress. Root pruning has been widely reported to reduce vegetative growth of trees (Ferree, 1989; Ferree and Geisler, 1984; and Gilman and Kane, 1990). In some cases, removal of fine roots had a greater impact on growth than removal of coarse and fine roots (Abod and Webster, 1990). Root growth was reported to be stimulated or unaffected by root pruning (Geisler and Ferree, 1984; Gilman and Yeager, 1988; and Laiche et al., 1983). Additionally, root growth was initially inhibited by root pruning, resulting in reduced root:shoot ratios (Geisler and Ferree, 1984). Root:shoot ratio restoration time varied between species (Geisler and Ferree, 1984 and Schnelle and Klett, 1992). Root pruning has been reported to decrease transpiration for some species (Ferree, 1989; Ferree and Geisler, 1984; Geisler and Ferree, 1984) or have no influence (Abod and Webster, 1990).

Temperate zone woody species generally initiate bud dormancy in the late summer and fall and require low temperatures to begin growth in the spring (Haugge and Cummins, 1991). Cold storage of field-harvested bare-root trees is often required to insure the availability of adequate quantities of plant material for spring transplanting (Englert et al., 1993 and Ritchie, 1987). Plant material kept in cold storage may require an excess of 2000 hrs of cold storage to break bud under normal conditions (Ashby et al., 1991). Adequate chilling resulted in increased vegetative growth (Arnold and Young, 1990; Darnell and Davies, 1990; and Donnelly, 1973). Additionally, chilling enhanced root growth and development for Malus (Arnold and Young, 1991) as well as other tree species (Farmer, 1975 and Lathrop and Mecklenburg, 1971). Chilled Picea exhibited increased drought hardiness compared to freshly-lifted seedlings (Blake, 1983). However, Bates and Niemiera (1996) reported that Crataegus phaenopyrum was susceptible to desiccation during cold storage, possibly resulting in increased stem dieback and reduced transplant success.

Fall transplanting offers advantages of convenience to the consumer and an increased sales season to the nurserymen (Hensley et al., 1984). Fall transplanting of ball- and-burlapped Chionanthus offered an advantage for plant establishment.
due to the formation of greater root mass for fall transplants (Harris et al., 1996). However, root regrowth, often cited as an advantage of fall transplanting, follows active shoot growth in several species (Kelly and Moser, 1983). *Fraxinus* and *Syringa* reportedly transplanted well in the fall while *Corylus* and *Quercus* transplanted poorly in the fall (Harris and Bassuk, 1994).

Current theories detailing water transport in trees are based on the cohesion model attributed to Dixon (1914). Dixon’s theory is based on the existence of a tension created by a vapor pressure deficit at the leaf-air interface. The tension is transmitted throughout the plant to the soil utilizing a continuous water column. Anatomical features such as small pit membrane pores and pathway redundancy allow the continuance of water conductance despite pathway interruptions (Tyree and Sperry, 1989). These anatomical features suggest that xylem tissues have developed a predisposition for maintaining continuous water columns (Tyree and Sperry, 1989).

Consensus now exists categorizing xylem tissue as a vulnerable pipeline susceptible to discontinuities resulting from the induction of air into conducting tissue (Zimmermann, 1983). Discontinuities in the xylem due to air are called embolisms and are caused by xylem cavitation (Tyree and Sperry, 1989). Cavitation is the phase change of water from a liquid to a gas inside water-conducting tissue, and an embolism is the air-filled conduit that results (Milburn and Johnson, 1966 and Sperry et al., 1994). Negative xylem water potentials associated with moisture stress or freeze-thaw cycles are the primary causes of embolism, but the mechanism of susceptibility differs depending upon the causal agent of embolism (Sperry et al., 1994).

Susceptibility of xylem to embolism, regardless of season, was initially attributed to vessel diameter, and larger vessels were deemed more susceptible to embolism than smaller vessels (Carlquist, 1982 and Zimmermann, 1983). However, research now indicates that conduit diameter may only be used to predict vessel susceptibility to drought-induced embolism within individual plants (Dixon et al., 1988) or taxa (Sperry and Saliendra, 1994). Pit membrane pore diameter determines a vessel’s susceptibility to drought-induced embolism (Tyree and Sperry, 1989). Generally, large diameter vessels have large pit membrane pore diameters (Sperry and Tyree, 1988). Embolism of non-cavitated vessels adjacent to air-filled vessels is prevented as long as the pressure difference across intervessel walls does not exceed the surface tension of the air-water interface at the pit membrane pore in the wall (Sperry and Tyree, 1988). Therefore, less tension is needed for the spread of embolisms to adjacent vessels when large pit pore openings are present. The above concept provides the basis for the “air-seeding” hypothesis first advanced by Zimmermann (1983). Conversely, severity of freeze-thaw-induced embolism is related to vessel diameter, and large vessels embolize more completely in winter than small vessels (Sperry et al., 1994 and Sperry and Tyree, 1988).

Seasonal changes in xylem embolism levels due to drought stress or freezing have been documented for a wide variety of plant material. Sperry et al. (1988) reported that embolism in *Acer* averaged 30% for the trunk during a growing season with nonlimiting water. Many twigs were 100% embolized over the winter. Later research (Sperry et al., 1994) indicated that embolism levels may approach 90% in mid-winter for some species. Tognetti and Borghetti (1994) reported that embolism levels of *Alnus* were 80% when water potentials declined to -2.0 MPa. *Alnus* xylem embolism levels were between 20 and 30% prior to budbreak and over 80% by midwinter. For *Fagus*, embolism levels were never
less than 28% and were near 80% in winter (Borghetti et al., 1993). Another
experiment involving *Fagus* reported embolism levels between 40 and 65% over the
growing season (Magnani and Borghetti, 1995).

Investigations into the relative susceptibility of tree segments to embolism
indicated that root xylem was more susceptible to embolism than stem xylem (Alder
et al., 1996). Each species exhibits a relationship between water potential and loss
in hydraulic conductance (Tyree and Ewers, 1991), and Zimmermann (1983)
suggested that water potentials during water stress were lowest in minor branches
and leaves as a result of hydraulic constrictions, making these plant parts most
susceptible to embolism. These constrictions functioned to favor one hydraulic
pathway over another, resulting in the preservation of one plant part and the
sacrifice of another (Tyree and Ewers, 1991). Distal branches were more
susceptible to embolism than larger branches and trunk, resulting in the
preservation of larger organs representing higher energy investments (Tyree and
Alexander, 1993). Increased restrictions were measured between leaf and branch
junctions (Tyree et al., 1983), one- and two-year-old stem segments (Joyce and
Steiner, 1995) and major and minor stem junctions (Tyree and Sperry, 1988).

Recovery from high levels of embolism that occur during the winter or in
response to drought generally occurs by positive root pressures that occur in the
spring (Cochard et al., 1994; Sperry et al., 1987; and Sperry et al., 1994), water
potentials that approach 0 MPa for a number of days (Alder et al., 1996; Tyree and
Sperry, 1989), or growth of new conducting tissue (Magnani and Borghetti, 1995
and Sperry et al., 1994). Trees that utilize growth of new xylem to overcome high
levels of embolism must delay leafing out until new xylem growth begins
throughout the tree (Sperry and Tyree, 1988).

Although no direct evidence exists concerning the role of transplanting on
recovery from winter levels of embolism or recovery from drought-induced
embolism, cavitation events in *Tsuga* occurred at water potential values that could
occur in newly planted seedlings in the field (Kavanaugh, 1992). The objective of
this dissertation was to determine if transplanting practices such as root pruning
(chapter two), cold storage (chapter three), season of transplant (chapter four), and
root severance (chapter four and five) effect growth and recovery from dormant
levels of xylary embolism.


Blake, T.J. 1983. Transplanting shock in white spruce; effect of cold-storage and root pruning on water relations and stomatal conditioning. Physiol. Plant. 57:210-216.


CHAPTER ONE

Season of Harvest and Duration of Pre-embolism Measurement Storage Impact Hydraulic Conductance of Stem Samples for *Acer rubrum* L. *x* *saccharinum* L. and *Fraxinus americana* L.

**Additional index words.** Red maple, white ash, embolism, xylem, cavitation

**Abstract**

The influence of length of pre-measurement storage and season of harvest of stem segment samples on hydraulic conductance and % embolism was compared for two tree species since no published guidelines exist concerning storage. Stem sections from a ring-porous species, *Fraxinus americana* L. ‘Autumn Applause’ (white ash), and a diffuse-porous species, *Acer rubrum* L. *x* *saccharinum* L. ‘Autumn Blaze’ (hybrid red maple), were collected from well-established specimens in fall 1995 (October), spring 1996 (April), and summer 1996 (July). Ends of stem sections collected in the fall were either covered with wax or left exposed. Entire sections from all dates were placed in closed plastic bags to prevent desiccation during transport and subsequent storage. Stem sections were either analyzed immediately (0 storage) or held at 20°C for 2 or 4 days. Hydraulic conductance before embolisms were cleared with positive pressure (initial $k_h$), hydraulic conductance after embolisms were cleared (maximum $k_h$), and % embolism were similar for all pre-embolism measurement storage durations within each of the three seasonal sampling periods for hybrid red maple and spring- and summer-collected white ash. Fall-collected white ash samples with 0 storage had higher initial $k_h$, and embolism increased if samples were stored. Embolism was greatest for summer-collected samples and lowest for spring-collected samples for hybrid red maple, but values were similar for white ash. Stem covering did not influence measured parameters. Hybrid red maple stem segments can be stored without significant loss of hydraulic conductivity for up to 4 days, but white ash should not be stored in the fall. Unless maximum levels of native embolism have been reached as determined from laboratory analysis, stem segments of species on which storage data are not available should be processed as soon as possible.
Introduction

Cavitation in vessels results from breaking the continuity of the xylem water column in response to drought or freezing stress and leads to the formation of a water vapor filled discontinuity (Sperry and Tyree, 1988 and Tyree and Sperry, 1988). High levels of embolism, resulting from the replacement of a high water vapor concentration with air containing less water, may impair water conduction, thereby increasing water stress and reducing plant growth and survival (Tyree and Dixon, 1986). Previous research utilizing species native to an arid environment indicated that plants with small vessels were less susceptible to embolism (Carlquist, 1982). However, more recent research suggests that large vessel diameters may predict greater embolism susceptibility within individual plants or species, but vessel diameters are not always indicative of embolism susceptibility between species (Dixon, et al., 1988). Pit membrane diameter, correlated with vessel diameter for individual plants, can predict a vessel’s susceptibility to air-seeded embolism (Tyree and Sperry, 1989).

Sperry and Tyree (1988) quantified embolism by measuring loss of hydraulic conductance of a stem segment. This technique estimates the presence of all nonrepaired cavitations in a stem segment by measuring hydraulic conductance before and after embolisms are removed using positive pressure. Estimations of reductions in hydraulic conductance as an indicator of embolism but is a destructive analysis (Tyree and Sperry, 1989). Additionally, the system described by Sperry et al. (1988) is difficult to transport, requiring the storage of stem samples for transport to the laboratory. Samples may require additional storage prior to embolism measurement due to the limited number that can be analyzed simultaneously.

Research investigating pre-measurement storage durations for stem segments and leaves harvested for measurement of water potential has yielded mixed results. Karllic and Richter (1979) reported that leaves of several species with varying anatomy may be stored for several days without influencing water potential measurements, but only when samples were stored in aluminum bags. Innes and Kelly (1991) indicated that Melicytus Forst. could be stored in airtight plastic bags for 24 h and Alectryon Gaertn. for 47 h without influencing water potentials. Since each species exhibits a relationship between increasing water potentials (more negative) and loss in hydraulic conductance (Tyree and Ewers, 1991), these results suggest that stem samples can be stored under certain conditions without influencing embolism measurements.

Although pre-embolism measurement storage may be required, no published guidelines exist concerning the length of time samples may be stored prior to analysis or influence that season of harvest has on length of storage. Equilibration between the stem segment and the atmosphere inside the plastic bag may result in water loss from the stem. Additionally, storage may have a greater impact on Fraxinus americana L., a ring-porous tree, which has a higher proportion of large vessels compared to Acer rubrum L. x saccharinum L., a diffuse-porous tree. The anatomy of Fraxinus may allow the rapid loss of water from stem segments, resulting in the need for shorter pre-measurement storage durations compared to species with diffuse-porous anatomy. The objective of this experiment was to quantify the influence of season of harvest and duration of storage prior to embolism measurement on hydraulic conductance and % embolism for Acer rubrum L. x saccharinum L. and Fraxinus americana L.
Materials and Methods

Thirty-six, 1 m terminal stem samples were randomly taken from a ring-porous species, *Fraxinus americana* L. ‘Autumn Applause’ (white ash), and a diffuse-porous species, *Acer rubrum* L. × *saccharinum* L. ‘Autumn Blaze’ (hybrid red maple), on 10 and 15 October, 1995, respectively. Stem sections were collected from well-established (3-4 m tall) specimens growing at the Urban Horticulture Center (Blacksburg, Va.) in a Grosclose silty clay loam (clayey, mixed, Typic Hapludult, pH 6.5). Stem ends were either covered with waxed film (Parafilm, American National Can, Greenwich, Conn.) or left exposed. Additionally, stem water potentials were determined using a pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, Calif.) just prior to stem placement in the Sperry apparatus. Both hybrid red maple and white ash stem sections had senescing leaves present. Fifteen 1 m terminal stem sections were selected on 23 April and 22 July, 1996, from the same plants as fall-collected sections, for spring and summer analysis. Hybrid red maple stem sections collected in the spring had fully expanded leaves, but white ash stem sections had not broken bud. All stem samples collected during the summer had leaves. All leaves were left intact. Leaves present on the sampled stem portion were covered with moist towels during analysis to minimize transpirational water loss. Stem sections collected in the spring and summer were not covered with waxed film (no difference in coverage response was measured in the fall), and stem water potentials were not measured (sample error resulted in invalid values for the fall, yielding no basis for seasonal comparisons). All stem sections were placed in plastic bags to prevent desiccation during transport or subsequent pre-measurement storage. Stem sections were either analyzed immediately or refrigerated at 2° C for 2 or 4 days.

One stem section consisting of 1-2 year old wood from each 1 m segment was selected, and stem ends were recut under water to a length of 20 cm to prevent induction of air into cut stem ends (Sperry et al., 1994). Stem segments were then fitted with gaskets, retrimmed with razor blades, and placed in parallel manifolds in the system (Sperry and Tyree, 1988) (Fig. 1). The presence of embolisms was indicated by reduction in hydraulic conductance (Sperry et al., 1988). Hydraulic conductance ($k_h$) is defined as $k_h = \frac{v}{(dP/dl)}$ where $v$ is the flow rate (kg/s) and $dP/dl$ is the pressure gradient (MPa/m). Initial $k_h$ and maximum $k_h$ were measured for each stem section. Fall stem segments were sequentially perfused with tap water using a hydraulic head of 3-5 KPa for measurement of initial $k_h$ (Sperry et al., 1988). After initial $k_h$ was measured, stem segments were flushed with pressurized tap water at 150 KPa for 15 min cycles until maximum $k_h$ was achieved. Spring and summer stem segments were sequentially perfused with a 10 mmol/l oxalic acid solution (Tyree and Sperry, 1988) with a hydraulic head of 3-5 KPa for measurement of initial $k_h$. After initial $k_h$ was measured, stem segments were flushed at 150 KPa with a 10 mmol/l oxalic acid solution for 20 min cycles until maximum $k_h$ was achieved. Reduction in hydraulic conductance (% embolism) was calculated as % embolism = 100(maximum $k_h$ - initial $k_h$)/maximum $k_h$. Oxalic acid was used during the spring sampling period to prevent microbial growth resulting from increased use of the apparatus.

The fall experimental design was a completely random 3 (storage time) x 2 (end coverage) factorial consisting of 6 replications. The spring and summer experimental design was a completely random design consisting of 5 replications. All data were
subjected to analysis of variance and Scheffe’s Multiple Comparison Procedure
(p<0.05, SAS ver. 6.03, SAS Institute, Cary, NC).
Results and Discussion

Hybrid red maple. Initial $k_h$, maximum $k_h$, and % embolism of Acer were not influenced by end coverage during the fall sampling period (data not shown). Failure of end coverage to influence measured parameters can be attributed to the length of stem sections (10 cm) utilized for sampling and laboratory handling of excised stem samples. Each stem section harvested in the field was at least 1 m long. Stem segments utilized for analysis of hydraulic conductance were taken from interior portions of the stem sections. Additionally, stem sections were recut under water to prevent the induction of air into the cut portions of the stem using the method described by Sperry et al. (1988).

Initial $k_h$ was highest for spring-collected stem segments and lowest for summer-collected stem samples (Table 1). Embolism levels reportedly increase as the growing season progresses (Sperry et al., 1994), and by definition, reductions in initial $k_h$ are reported as % embolism. High initial $k_h$ measurements in spring-collected stems indicated refilling of freeze-thaw induced embolisms that typically occur over the winter for diffuse-porous species. Refilling of embolisms for diffuse-porous species has been documented by several researchers using a variety of plant material (Sperry et al., 1994 and Tognetti and Borghetti, 1994). Additionally, new xylem growth may have occurred (Mauseth, 1988).

Maximum levels of $k_h$ were also highest for spring-collected stems (Table 1). There were no differences in maximum $k_h$ for summer- and fall-collected stems. Differences between measurements of maximum $k_h$ can be attributed to physiological and anatomical changes in the plants over the course of the growing season. New growth of xylem would occur in the spring, while any vessels that embolize would be susceptible to infiltration by fungi or growth of tyloses (Mauseth, 1988). Xylem blockage due to fungal growth or tyloses could not be removed using the Sperry apparatus, resulting in diminished maximum $k_h$ measurements in summer- and fall-collected stems.

Percent embolism was highest for summer-collected stems and lowest for spring-collected stems (Table 1). High levels of embolism measured in summer-collected stem samples may be related to xylem tensions occurring in actively growing twigs. Zimmermann (1983) suggested that distal twigs were subject to lower water potentials, making those plant parts more susceptible to embolism. Additionally, Tyree and Sperry (1989) reported that loss of hydraulic conductance for red maple occurred over a relatively small reduction in water potential. This leads to speculation that embolism levels in the trunks could be much lower than embolism levels in the twigs sampled for this study. In our experiment, 1995 fall-collected twigs had lower embolism levels compared to 1996 summer-collected stem samples. Embolism levels may have been lower in 1995 for all sampling dates compared to embolism levels in 1996 or some recovery in embolism levels may have occurred between summer and fall. Embolism recovery between seasons may occur because new stem diameter growth in plants moved down from stem tips to the trunk (Harris, 1993). This new caliper growth may have provided a reservoir of new vessels that rehydrated stem portions sampled in the fall for this experiment. Fall levels of embolism corresponded to embolism levels achieved by other hybrid red maple samples during winter (unpublished data), indicating that fall stem samples had reached their maximum loss of hydraulic conductance before the fall harvest date in October.

Initial $k_h$, maximum $k_h$, and % embolism of hybrid red maple were not influenced by duration of pre-embolism measurement storage, regardless of season.
of harvest (data not shown). Lack of response for initial $k_h$ and embolism to duration of pre-measurement storage can be attributed to the relatively low number of large vessels present in diffuse-porous wood (Mauseth, 1988). Kramer and Boyer (1995) reported that large early-wood vessels were most susceptible to embolism, diffuse-porous vessels were moderately susceptible, and tracheids were least susceptible to cavitation resulting from tensions in xylem. Large vessels typically have larger pit membrane pore diameters which determine a vessel’s susceptibility to embolism (Sperry and Tyree, 1988). Small vessels and subsequently smaller pit membrane diameters increase resistance for water loss to the environment just as they increase resistance to air-seeding when plants are intact in the environment (Sperry and Tyree, 1988 and Zimmermann, 1983). Additionally, Bates and Niemiera (1996) reported that Norway maple has high levels of stem suberization, and this suberization might also be present in red maple and would therefore reduce water loss during storage. Since maximum $k_h$ was not influenced by storage time, reductions in initial $k_h$ can be presumed to be an accurate measure of % embolism and not due to microbial growth which may result when vessels embolize (Mauseth, 1988).

**White ash.** Initial $k_h$, maximum $k_h$, and % embolism of white ash were not influenced by end coverage for the fall sampling period (data not shown). Initial $k_h$ and % embolism among season of harvest was similar among treatments. Maximum $k_h$ was highest for summer-collected samples, and spring-collected stems had the lowest levels of maximum $k_h$ (Table 1). Several possible explanations exist for the increased hydraulic conductance capacities that were measured in the summer. White ash stem samples did not have expanded leaves during the spring sampling date, and ring-porous tree species must delay leafing out until xylem is differentiated throughout the entire tree (Sperry and Tyree, 1988). Therefore functional large vessels were laid down after the spring sampling date. Since older xylem typically exhibits the development of tyloses (Mauseth, 1988), maximum $k_h$ measurements taken in the spring might be expected to be lower than measurements taken in the summer after differentiation of new xylem. Lower $k_h$ levels in the fall might reflect the development of tyloses over the course of the growing season. In addition, Sperry et al. (1991) reported that estimates of xylem vulnerability may be artificially high since flushing may initiate water flow through damaged intervessel pit membranes. Additionally, early-wood vessels from prior years may contribute little water for transpiration, but may influence maximum $k_h$ values since air may be flushed from vessels that were no longer functional or necessary for plant growth (Romberger and Hejnowicz, 1993). Red maple trees slightly more than 1 m in height had sap flow approaching 100 mg•cm$^{-2}$•hr$^{-1}$•MPa$^{-1}$ (unpublished data). When initial $k_h$ values are converted to units having the same magnitude as those reported for sap flow and divided by the approximate leaf area of sampled stem segments, sampled stem segments were found to have flow rates approaching 324 mg•cm$^{-2}$•hr$^{-1}$•MPa$^{-1}$. These estimations suggest that adequate water flow was present to support plant growth in spite of reduced hydraulic conductance. Research suggests that trees will operate just below the water potential resulting in runaway embolism to maximize carbon assimilation (Teskey et al., 1983).

Both initial and maximum $k_h$ were low in the spring, indicating that new large vessels were not present and previous large vessels may have been filled with tyloses. Since white ash grows rapidly in the late spring (Mauseth, 1988), high embolism levels in terminal growing tissue may be an indication of high water demand and growth levels. Distal stems are highly susceptible to water stress-induced embolism, thereby exhibiting higher embolism levels than might be
expected in the central trunk (Zimmermann, 1983). High embolism levels in the summer were measured after leaf and shoot expansion had ceased. Therefore, water demand would be primarily for maintenance and not for shoot extension, allowing the plant to exist at higher embolism levels. Additionally, high embolism levels coupled with slow growth might signal the plant of impending dormancy, although a signal for this event has never been discussed. A significant water reservoir is present in the trunk when trunk embolism levels are low, even when twigs are highly embolized. Trunk embolism may be more indicative of overall stress compared to distal twigs since restrictions in the trunk would limit water available to higher order limbs and twigs. Hydraulic restrictions in a terminal twig would only limit water availability to a small portion of the tree.

There was an interaction between season of harvest and duration of storage for initial $k_h$ and % embolism for white ash (Table 1). Stem segments that were collected in fall and not stored had higher initial $k_h$ values compared to other fall-collected stems (Table 2). All other initial $k_h$ values were similar, indicating that initial $k_h$ levels only changed for samples stored in the fall. This change occurred at day 2. Corresponding % embolism levels also only changed within season of sampling for fall samples. This change occurred at day 4.

Results of this experiment demonstrated that hybrid red maple, a diffuse-porous tree species, can be stored prior to measurement during the fall (October), spring (April), or summer (July) for at least 4 days without affecting hydraulic conductance or % embolism during the particular season of storage. Conversely, white ash, a ring-porous tree species, can be stored prior to embolism measurement in the spring and summer without affecting hydraulic conductance or % embolism, but cannot be stored for 4 days in the fall without affecting embolism. Fall storage results in lowered initial $k_h$ if stored for 2 or 4 days and an increase in % embolism if stored for 4 days. These results are similar to those of Davis and Potter (1982) who examined the stem water potentials of Rhododendron and reported that plants with smaller vessels could be stored for extended periods of time. Our research indicates that great care should be used when storing samples for measurement of hydraulic conductance unless the native levels of embolism in a given species for a given season are known.


Table 1. Influence of season of harvest and duration of pre-embolism measurement storage on reductions in hydraulic conductance \((k_h)\) for *Acer rubrum* L. x *saccharinum* L. (red maple) and *Fraxinus americana* L. (white ash).

<table>
<thead>
<tr>
<th>Season of harvest</th>
<th>Hybrid red maple</th>
<th>White ash</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial (k_h) x 10^{-5} (kg!m!MPa^{-1}!s^{-1})</td>
<td>Maximum (k_h) x 10^{-5} (kg!m!MPa^{-1}!s^{-1})</td>
</tr>
<tr>
<td>Fall(^{2})</td>
<td>2.83b(^{y})</td>
<td>6.96b</td>
</tr>
<tr>
<td>Spring</td>
<td>6.12a</td>
<td>9.95a</td>
</tr>
<tr>
<td>Summer</td>
<td>0.95c</td>
<td>6.53b</td>
</tr>
<tr>
<td></td>
<td><strong>Significance</strong></td>
<td></td>
</tr>
<tr>
<td>Season of harvest (S)</td>
<td>0.0001</td>
<td>p&gt;F</td>
</tr>
<tr>
<td>Duration of storage (ST)(^{x})</td>
<td>0.2883</td>
<td>0.2493</td>
</tr>
<tr>
<td>S * ST</td>
<td>0.1170</td>
<td>0.7237</td>
</tr>
</tbody>
</table>

\(^{2}\)N=36 for fall-collected stem samples, and n=18 for spring- and summer-collected stem samples.

\(^{y}\)Means within columns having the same letter are not different according to Scheffe’s Multiple Comparison Procedure (p<0.05).

\(^{x}\)N=12 for fall-collected stem samples, and n=6 for spring- and summer-collected stem samples.
Table 2. Influence of season of harvest and pre-embolism measurement storage duration on reductions in hydraulic conductance for *Fraxinus americana* L. (white ash)\(^z\).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Initial (k_h) x 10(^{-5}) (kg m (\mu) MPa(^{-1}) s(^{-1}))</th>
<th>% embolism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fall, 0 days storage</td>
<td>2.18(^a)</td>
<td>58.8(^b)</td>
</tr>
<tr>
<td>Fall, 2 days storage</td>
<td>0.79(^b)</td>
<td>63.3(^b)</td>
</tr>
<tr>
<td>Fall, 4 days storage</td>
<td>0.20(^b)</td>
<td>89.5(^a)</td>
</tr>
<tr>
<td>Spring, 0 days storage</td>
<td>0.18(^b)</td>
<td>83.0(^ab)</td>
</tr>
<tr>
<td>Spring, 2 days storage</td>
<td>0.41(^b)</td>
<td>81.7(^ab)</td>
</tr>
<tr>
<td>Spring, 4 days storage</td>
<td>0.26(^b)</td>
<td>87.1(^ab)</td>
</tr>
<tr>
<td>Summer, 0 days storage</td>
<td>0.24(^b)</td>
<td>96.7(^a)</td>
</tr>
<tr>
<td>Summer, 2 days storage</td>
<td>0.23(^b)</td>
<td>93.6(^a)</td>
</tr>
<tr>
<td>Summer, 4 days storage</td>
<td>0.35(^b)</td>
<td>96.6(^a)</td>
</tr>
</tbody>
</table>

\(^z\)N=12 for fall-collected stem samples, and n=6 for spring- and summer-collected stem samples.

\(^y\)Means followed by the same letter within columns are not different according to Scheffe’s Multiple Comparison Procedure (p<0.05).
Fig. 1. Diagram of Sperry apparatus. Water flows from the hydraulic head through an individual stem sample onto the balance which reports weight changes due to water flow to the computer. A computer program calculates hydraulic conductance. After initial measurements are performed on all stem segments, pressurized water is forced through all stem segments until maximum hydraulic conductance is reached.
CHAPTER TWO

Dormant Root-Pruning Influences Embolism Recovery and Early Post-transplant Growth for Corylus colurna L.

Additional index words: Turkish hazelnut, controlled release fertilizer, cavitation, hydraulic conductance, transplanting, root regeneration

Abstract

Root pruning at harvest is a common practice in container and field production systems. Root pruning in conjunction with tree harvest and subsequent transplanting, results in reduced growth, possibly due in part to a restriction in post-transplant water transport caused by a perturbation of normal xylem embolism dynamics. This experiment was initiated to determine the influence of root pruning on growth and embolism levels for container-grown Corylus colurna L. (Turkish hazelnut). Two-year-old bareroot Turkish hazelnut seedlings were glasshouse-grown in 7.5 l pine-bark-filled containers from 15 March to 23 June, 1995. At planting, trees were pruned to remove 0, 25, or 50% of the root system based on root length. Additionally, trees received either no fertilization or controlled release fertilizer 18N-2.6P-9.9K top-dressed at 2.5 or 5.0 g N/container. Percent embolism was higher for trees that underwent root pruning as a group, and embolism levels were highest for plants undergoing 50% root removal. Percent embolism measured at the end of the experiment was not influenced by rate of fertilization. Stem diameter was lowest for root-pruned trees, but tree growth was generally unaffected by root pruning. Root regrowth and root dry mass decreased as rate of fertilization increased from 2.5 to 5.0 g N/container. Although initial growth of Turkish hazelnut was not influenced by 50% root removal, embolism was increased compared to other treatments after 15 weeks growth, indicating a lack of recovery from dormant levels. Although growth was not reduced during the first 15 weeks after transplanting, failure to recover from high dormant embolism levels may have an impact on future tree growth since water conductance may be impaired over an extended period of time.
Introduction

Modifications in plant water status, resulting in early post-transplant stress, are the most important factors governing the establishment of field-grown landscape plants (Grossnickle, 1988 and Kaushal and Aussenac, 1989). A large number of a plant's roots may be lost or damaged during the harvest of field-grown nursery stock (Watson and Kupkowski, 1991), and the ability of the plant to quickly regenerate those roots may influence the plant's capacity to overcome water stress and therefore survive transplanting (Watson and Himelick, 1982 and Lathrop and Mecklenburg, 1971).

Container production has led to greater transplanting success for some difficult-to-transplant trees since the root system is usually placed intact in the planting hole (Harris, 1983). Young trees are generally root-pruned, however, during the lifting process before they are placed in containers (Larson, 1975).

Sperry et al. (1988b) reported that water stress is a primary cause of xylem cavitation leading to embolism. Sperry et al. (1994) indicated that embolism levels increased as the growing season progressed and plants became dormant, and levels approached 90% in mid-winter for some species. Since most field-grown nursery seedlings are harvested when dormant, plants may be severely embolized when transplanted into containers. Failure to quickly regrow roots lost at harvest may prevent rehydration following transplanting. This experiment evaluated the influence of root severance and rate of fertilization on early post-transplant shoot and root growth, and embolism for container-grown Corylus colurna.
Materials and Methods

Two-year-old bareroot *Corylus colurna* L. (Turkish hazelnut) seedlings (Watson's Nursery, West Valley, N.Y.) were grown in 7.5 l containers in a glasshouse using pine bark medium from 15 March to 23 June, 1995. Natural light levels at noon on a sunny day approached 1400 mol m^-2 s^-1. Temperatures were maintained at about 30/20° C (day/night). Plants received either no fertilization or 18N-2.6P-9.9K (controlled release fertilizer, The Scotts Company, Marysville, Ohio) top-dressed at 2.5 or 5.0 g N/container at potting (based on medium and 2x medium recommended rate). Additionally, plants were pruned to remove 0, 25, or 50% of the root system based on root length at planting.

Initial stem embolism levels were determined from 20 cm subsamples (n=6) at planting. Height and stem diameter (10 cm above the soil) were recorded at experiment initiation and termination. Root growth was calculated by subtracting initial water displacement of the entire root systems from final water displacement values. Branch numbers were determined at the end of the experiment, and all expanded leaves were removed and counted. Total leaf areas were measured using a leaf area meter (LI-3000, LI-COR, Lincoln, Neb.). Shoot and root dry mass increases were also determined by subtracting final dry masses from the mean shoot and root dry masses of a sample taken at the initiation of the experiment (n=12), and root:shoot ratio was calculated from these values. Additionally, percentages of xylem embolism were calculated for each treatment (n=2) at the end of the experiment (Sperry et al., 1988a).

The experimental design was a randomized complete block arranged in a factorial consisting of three fertility levels (0, 2.5, or 5.0 g N) and three levels of root removal (0, 25 or 50%) utilizing eight single plant replications. Treatment effects were determined by analysis of variance and single degree of freedom contrasts (SAS ver. 6.03, Cary, NC). Contrasts consisted of comparisons between means of root pruned and not-root pruned treatments, means of plants undergoing 25 or 50% root removal, means of plants receiving fertilizer or no fertilizer, and means of plants receiving 2.5 or 5.0 g of N.
Results and Discussion

**Root pruning.** There were no significant interactions between main effects (data not shown). Root pruning had no influence on plant height when compared to unpruned plants (Table 1). However, for unknown reasons, plant height was higher when plants had 50% of the roots removed compared to plants that underwent 25% root pruning. Stem diameter was highest for plants that were not root pruned. Rate of root pruning did not influence other growth parameters (Table 1 and 2). Many researchers report that root pruning reduced shoot growth in favor of root growth (Ferree, 1989 and Larson, 1975), but reports differ in the severity of the shoot growth reduction (Harris et al., 1973; Insley and Buckley, 1985; and Laiche, et al., 1983). Gilman and Kane (1990) and Warren (1993) reported similar results for stem diameter of a variety of species. Root pruning treatments imposed in the present experiment were severe enough to influence stem diameter, but not other shoot growth parameters, suggesting that more severe root pruning was necessary to induce further growth reductions.

Plants that underwent 50% root pruning were almost 800% more embolized than plants that underwent 25% root removal (Table 2). Since plants were 42% embolized at transplanting (data not shown), removal of 50% of the root system appears to have reduced the recovery of the plant from dormant levels of embolism. Although not tested statistically, plants root pruned 25% were clearly not more embolized than unpruned plants, indicating recovery for plants undergoing 25% root removal. Sufficient water was apparently available to the plants undergoing 50% root removal, so that growth was not reduced in spite of the higher levels of embolism. Different results may have occurred if drought treatments had been imposed on the plants in this experiment.

**Fertilization.** Fertilization increased all growth parameters except plant height compared to plants receiving no fertilizer (Table 1 and 2). However, increasing the rate of fertilization from 2.5 to 5.0 g of N/container did not result in a further increase in growth with the exception of plant height (Table 1). Increased growth in response to the availability of necessary nutrients is well-documented for a wide variety of plant material (Arnott and Brett, 1973; Hensley et al., 1988; Johnson, 1980; Nambiar, 1980; and Philipson and Coutts, 1977) and would be expected unless excessive fertilizer was applied. However, Warren (1993) reported that stem diameter of *Cornus* was not impacted by fertilization, and Hensley et al. (1988) reported that early branching of *Magnolia* was not influenced by fertilization, indicating that fertilizer requirements differ between species and growth stages.

Both root regeneration and root dry mass were reduced when rate of fertilization was increased from 2.5 to 5.0 g of N/container. As a result, root:shoot ratios were reduced for plants that received fertilization, regardless of rate (Table 2). Reductions of root growth at the 5.0 g of N/container rate indicates that root damage may have occurred, suggesting that the optimum level of fertilizer for Turkish hazelnut containers is between 2.5 and 4.9 g of N/container. Marshall (1981) and Nambiar (1980) reported similar reductions in root:shoot ratios for different crops. Rate of fertilization did not have an impact on recovery from dormant levels of embolism (Table 2).

Moderate levels of fertilization (2.5 g of N/container) generally increased growth of *Corylus* while higher rates of fertilization decreased root growth. This root growth increase may increase transplant survival (Watson and Himelick, 1982). Conversely, root pruning had a minimal influence on plant growth.
Embolism levels were increased due to 50% root removal. Gilbertson and Bradshaw (1990) report that trees tend to die at the end of the first growing season or the beginning of the second season due to increased resource demands. Our results suggest that sufficient water for unrestricted shoot extension is available to the plants undergoing 50% root removal in spite of higher levels of embolism. However, the influence of failed embolism recovery on long-term plant growth has not been determined. A growth threshold may exist where this level of embolism fails to provide adequate amounts of water, resulting in growth reductions or gradual plant death.
Literature Cited


Table 1. Height, stem diameter, total leaf area, leaf number, and area per leaf for *Corylus colurna* L. as influenced by rate of fertilization or root pruning.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Height (cm)</th>
<th>Stem diameter (cm)</th>
<th>Branch number</th>
<th>Total leaf area (cm²)</th>
<th>Leaf #</th>
<th>Area per leaf (cm²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Root pruning (%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>52.5</td>
<td>0.80</td>
<td>4.3</td>
<td>616.8</td>
<td>31.8</td>
<td>18.2</td>
</tr>
<tr>
<td>25</td>
<td>49.3</td>
<td>0.71</td>
<td>4.0</td>
<td>639.6</td>
<td>30.2</td>
<td>20.7</td>
</tr>
<tr>
<td>50</td>
<td>53.6</td>
<td>0.72</td>
<td>3.5</td>
<td>678.8</td>
<td>31.0</td>
<td>22.1</td>
</tr>
<tr>
<td>Fertilization (g N/container)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>53.5</td>
<td>0.63</td>
<td>3.0</td>
<td>231.0</td>
<td>19.9</td>
<td>11.8</td>
</tr>
<tr>
<td>2.5</td>
<td>56.0</td>
<td>0.82</td>
<td>4.6</td>
<td>865.2</td>
<td>35.8</td>
<td>25.4</td>
</tr>
<tr>
<td>5.0</td>
<td>55.9</td>
<td>0.79</td>
<td>4.2</td>
<td>839.1</td>
<td>37.2</td>
<td>23.9</td>
</tr>
<tr>
<td>Contrasts</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0% vs. 25 and 50%</td>
<td>0.5312</td>
<td>0.0044</td>
<td>0.1936</td>
<td>0.4808</td>
<td>0.6529</td>
<td>0.1407</td>
</tr>
<tr>
<td>25% vs. 50%</td>
<td>0.0300</td>
<td>0.7651</td>
<td>0.2732</td>
<td>0.5719</td>
<td>0.7857</td>
<td>0.5488</td>
</tr>
<tr>
<td>0 g vs. 2.5 and 5.0 g</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0030</td>
<td>0.0001</td>
<td>0.0001</td>
<td>0.0001</td>
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<tr>
<td>2.5 g vs. 5.0 g</td>
<td>0.9324</td>
<td>0.3713</td>
<td>0.3663</td>
<td>0.7063</td>
<td>0.6507</td>
<td>0.5430</td>
</tr>
</tbody>
</table>

\(^{\dagger}\)N=8.

\(^{\ddagger}\)Percent of root length removed from each plant.
Table 2. Shoot and root dry mass, root regeneration, root:shoot ratio, and % embolism for *Corylus colurna* L. as influenced by rate of fertilization or root pruning.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Shoot dry mass (g)</th>
<th>Root dry mass (g)</th>
<th>Root:shoot ratio</th>
<th>Root regeneration (mg)</th>
<th>Embolism (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Root pruning (%) Y</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>10.5</td>
<td>8.5</td>
<td>0.92</td>
<td>31.4</td>
<td>6.7</td>
</tr>
<tr>
<td>25</td>
<td>9.6</td>
<td>7.3</td>
<td>0.83</td>
<td>24.8</td>
<td>4.4</td>
</tr>
<tr>
<td>50</td>
<td>9.9</td>
<td>7.7</td>
<td>0.87</td>
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<td>34.6</td>
</tr>
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<td>Fertilization (g N/container)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>5.2</td>
<td>5.9</td>
<td>1.20</td>
<td>19.2</td>
<td>13.5</td>
</tr>
<tr>
<td>2.5</td>
<td>12.8</td>
<td>9.9</td>
<td>0.77</td>
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</tr>
<tr>
<td>5.0</td>
<td>12.1</td>
<td>7.9</td>
<td>0.65</td>
<td>25.8</td>
<td>15.9</td>
</tr>
</tbody>
</table>

Contrasts

<table>
<thead>
<tr>
<th>Contrasts</th>
<th>p&gt;F</th>
<th>p&gt;F</th>
<th>p&gt;F</th>
<th>p&gt;F</th>
<th>p&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>0% vs. 25 and 50%</td>
<td>0.3510</td>
<td>0.1892</td>
<td>0.3387</td>
<td>0.2108</td>
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<tr>
<td>25% vs. 50%</td>
<td>0.8045</td>
<td>0.6317</td>
<td>0.6789</td>
<td>0.5261</td>
<td>0.0001</td>
</tr>
<tr>
<td>0g vs. 2.5 and 5.0g</td>
<td>0.0001</td>
<td>0.0003</td>
<td>0.0001</td>
<td>0.0023</td>
<td>0.2782</td>
</tr>
<tr>
<td>2.5g vs. 5.0g</td>
<td>0.4876</td>
<td>0.0470</td>
<td>0.1417</td>
<td>0.0077</td>
<td>0.8851</td>
</tr>
</tbody>
</table>

^N=8 for shoot and root dry mass, root:shoot ratio, and root regeneration. N=2 for embolism.

^Percent of root length removed from each plant.
CHAPTER THREE

Duration of Cold Storage Impacts Water Relations and Early Post-transplant Growth for *Acer rubrum* L. and *Crataegus phaenopyrum* (L.f.) Medic.

**Additional index words:** Red maple, Washington hawthorn, chilling, hydraulic conductance, embolism

**Abstract**

Poor growth of tree seedlings following planting has been attributed to desiccation stress caused by poor handling practices during and after cold storage. Desiccation stress has been shown to increase xylem embolism in stems. Failure to recover from increased embolism may result in reduced post-transplant water conduction and reduced growth. This experiment tests the influence of dark cold storage on embolism recovery and growth of two tree species. Two-year-old *Acer rubrum* L. (red maple) and *Crataegus phaenopyrum* (L.f.) Medic. (Washington hawthorn) trees were harvested on 15 December 1995 and placed in dark cold storage at 4°C for 0, 1, 3, 5, 10, or 15 weeks. Embolism levels and % fresh mass loss were determined after the designated storage durations, and additional replications were grown for 15 weeks in a greenhouse. The % fresh mass reduction for both species increased with storage duration. Embolism increased with storage for red maple, but not Washington hawthorn. Although embolism increased in storage for red maple, no corresponding reduction in growth was observed. No influence on embolism by storage duration could be detected after the 15 weeks of growth for either species. Area per leaf and days to budbreak were not influenced by duration of storage for Washington hawthorn, but area per leaf increased and days to budbreak decreased with increasing storage for red maple. Shoot dry mass and root dry mass increased while root:shoot ratio decreased with increasing lengths of storage for both species. The results of this experiment confirm that increased chilling results in positive early growth, but no evidence for a relationship between increased embolism levels during cold storage and post-transplant growth was found.
Introduction

Survivability and growth of tree species commonly transplanted bare-root are major concerns for both commercial growers and retail consumers. Bare-root seedlings are often placed in cold storage for several months following fall or early-winter digging to insure adequate plant quantities for spring transplanting (Englert et al., 1993 and Ritchie, 1987). Poor growth of seedlings following planting has been attributed to desiccation stress, resulting from poor handling practices both during and after cold storage leading to desiccation stress (Englert et al., 1993 and Webb and von Althen, 1980). Although species vary in sensitivity to desiccation resulting from handling practices, growers often store desiccation-tolerant and desiccation-sensitive species in a similar manner (Englert et al., 1993; Tabbush, 1987).

Murakami et al. (1990) reported that there were no differences in water loss between whole plants of *Crataegus phaenopyrum* and *Acer platanoides*, but *Crataegus* was more sensitive to desiccation. Englert et al. (1993) reported that water loss over a 24 h period was similar for *Quercus*, *Crataegus*, and *Acer* seedlings, but seedlings varied in tolerance to desiccation. Englert et al. (1993) reported that the desiccation sensitivity of *Crataegus* could be partially mediated by the use of antidesiccant compounds. Tabbush (1987) reported that poor growth of desiccated *Pseudotsuga* is not related to its inability to retain water.

Bates (1994) reported that water potentials for both *Acer* and *Crataegus* declined in response to cold storage, and Tyree and Ewers (1991) indicate that each species exhibits a relationship between water potential and loss in hydraulic conductance which is defined as % embolism. Bates (1994) reported water loss for both species was greatest during the first week in storage, but *Crataegus* lost more water than *Acer*. Bates and Niemiera (1996) indicated that desiccation sensitivity of *Crataegus* may be related to cracks in stems. Research (Bates and Niemiera, 1996; Englert et al., 1993, and Murakami et al., 1990) indicates that differences in desiccation tolerance exist between species and the magnitude of water loss may be greatest for desiccation-sensitive species during some portions of cold storage. The objective of this experiment was to determine if water loss during cold storage results in increased embolism levels for a desiccation-sensitive species (*Crataegus phaenopyrum* (L.f.) Medic.) compared to a desiccation-tolerant species (*Acer rubrum* L.). Additionally, post-transplant growth was measured to determine if a growth reduction corresponds with increased levels of embolism.
Materials and Methods

Two-year-old bare-root *Crataegus phaenopyrum* (L.f.) Medic. (Washington hawthorn) and *Acer rubrum* L. (red maple) seedlings (Lawyer Nursery, Plains, Mont.) were planted in the spring of 1995 into a Groseclose silty clay loam (clayey, mixed, Typic Hapludult, pH 6.5) at the Urban Horticulture Center near Blacksburg, Va. Seventy-two plants per species were dug on 15 December 1995, weighed immediately, and placed in dark, cold storage at 4°C for 0, 1, 3, 5, 10, or 15 weeks at 85±5% relative humidity. Plant roots were covered with moist sawdust and were rewetted as needed. Twelve plants per species were allocated to each storage treatment. At this point, plants had received approximately 450 hours of chilling (Richardson et al., 1974). The 12 plants that were not assigned to cold storage were placed in plastic bags and transported directly to a laboratory for determination of embolism prior to storage (Sperry et al., 1988). Stem ends were recut underwater to a length of 20 cm (Sperry et al., 1994), fitted with gaskets, retrimmed with a razor blade, and placed in parallel in the system described by Sperry et al. (1988). Stem segments were then perfused with tap water using a hydraulic head of 3-5 KPa for measurement of initial hydraulic conductance. Stem segments were then flushed with pressurized tap water for 15 min cycles until maximum hydraulic conductance was achieved. Embolism was calculated using the Sperry technique described previously (Sperry et al., 1988).

At the end of each storage period, 12 plants per species were weighed to determine water loss as a percentage of total plant fresh mass. After weighing, 6 plants/species were transported to the laboratory for measurements of hydraulic conductance as described previously.

The remaining six plants per species from each storage duration were potted into 11 l containers filled with pine bark amended with 0.68 kg of micronutrients (Micromax, Grace-Sierra, Milpitas, Calif.) and 3.2 kg of dolomitic limestone per cubic m. Each container was top-dressed with controlled release 18N-2.6P-9.9K (Osmocote, The Scott’s Company, Marysville, Ohio) at the rate of 9 g N/container. Seedlings were grown in a glasshouse for 15 weeks with natural light levels approaching 1400 mol m⁻²s⁻¹ at noon on a sunny day and average temperatures of about 30/20°C (day/night).

Throughout the experiment for each plant, days to budbreak were recorded. Budbreak was defined as having 1 leaf completely unfurled from the bud. At the end of the 15 week growing period, all expanded leaves were removed and counted for leaf area determination using a leaf area meter (LI-3000, Lincoln, Neb.). Shoot and root dry masses were determined and root:shoot ratios were calculated. Additionally, plants were analyzed to determine % embolism.

The post-storage growth experiment was arranged in a randomized complete block design. Seedlings were placed in the storage cooler and the embolism manifold in a completely random manner. All data were subjected to linear regression by the general linear models procedure (SAS ver. 6.03, SAS Institute, Cary, NC). Determination of linear or quadratic significance was based on r² values. Embolism was correlated with % fresh mass reduction using the correlation procedure of SAS. Additionally, treatment means between species at each sampling date were separated using Fisher's Protected Least Significant Difference (p<0.05).
Results and Discussion

Storage. Percent reduction in fresh mass increased linearly for both Washington hawthorn and red maple (Table 1). Increasing the duration of cold storage from 0 to 15 weeks resulted in a linear increase in % embolism for red maple, and the r=0.44. Percent embolism for Washington hawthorn was not influenced by length of cold storage. A correlation (r=0.12) between % fresh mass reduction and % embolism was observed for Washington hawthorn. Bates and Niemiera (1996) reported that stem cracks increased desiccation sensitivity of Washington hawthorn due to increased water loss. Since no increases in embolism levels were observed during storage, maximum levels of embolism may have been reached before plants were harvested. Conversely, water loss from stems may not have been severe enough to influence embolism levels. The stem cracking reported by Bates and Niemiera (1996) could occur in the field prior to harvest. Red maple apparently had not lost enough water prior to harvest and cold storage to reach maximum levels of embolism. Embolism levels attained by red maple during cold storage were similar to levels attained by live trees during winter (unpublished data). A correlation (r=0.44) existed for embolism levels of red maple in response to increasing % fresh mass reduction. This research indicates that embolism during storage was related to increasing water loss.

Differences between species in % fresh mass reduction were evident after 3 weeks of cold storage (Table 1). Red maple lost a higher percentage of its fresh mass on a total weight basis compared to Washington hawthorn from week 3 until week 10 and week 15 (data not shown). After 10 weeks of cold storage, Washington hawthorn lost more of its fresh mass on a total fresh mass basis compared to red maple. For the current experiment, during the first week of storage, Washington hawthorn lost almost 40% of total water lost, and during the first week of storage, red maple lost more than 50% of total water lost. These results concur with Bates (1994) who reported that most water loss occurred during the first week of storage for Washington hawthorn. Regardless of the duration of cold storage, Washington hawthorn consistently had a higher level of embolism compared to red maple, although % embolism of red maple increased more (106%) than Washington hawthorn (18%) over 15 weeks of storage.

Growth. Fifteen weeks after planting, area per leaf were similar for all storage durations for Washington hawthorn (Table 2). Days to budbreak decreased with increasing storage. Area per leaf for red maple increased, and days to budbreak decreased (Table 2). Root and shoot dry masses increased for both species with increasing cold storage, but root:shoot ratios decreased linearly during for both species. Percent embolism after 15 weeks growth was not influenced by duration of cold storage for either species.

Days to budbreak was highest for red maple compared to Washington hawthorn after 0, 1, and 5 weeks of cold storage (Table 2). At experiment termination, there were no differences in days to budbreak between the species, and root:shoot ratios were similar between species regardless of the amount of cold storage. Percent embolism was highest for Washington hawthorn compared to red maple with no storage, but was not different between species for any other duration of cold storage.

Impact of cold storage on red maple and Washington hawthorn growth parameters may be related to differences in chilling requirements for the two species. Murakami et al. (1990) reported that deepest rest for Washington hawthorn occurred in December and Englert et al. (1993) reported that Washington hawthorn...
had a shallow dormancy. These results suggest that little chilling beyond that occurring prior to harvest would be necessary to induce budbreak for Washington hawthorn. Norway maple required 25 days to break bud after experiencing deepest dormancy (Murakami et al., 1990), and Ashby et al. (1991) reported that red maple required more than 2000 h of cold to break dormancy. Those prior results support current results which indicate that Washington hawthorn required fewer days to break bud compared to red maple. Schnelle and Klett (1992) reported that *Malus* leaf size was not influenced by cold storage duration. Inability of cold storage to influence Washington hawthorn leaf size while increasing red maple leaf size could be related to several factors. Leaf size of Washington hawthorn may be weakly related to chilling while a stronger relationship exists between red maple leaf size and chilling. Conversely, Washington hawthorn may have received adequate chilling to prevent any influence of chilling on leaf size. In this experiment, Washington hawthorn received adequate chilling after one week of cold storage to satisfy requirements for budbreak (although three weeks of storage resulted in 5 weeks to budbreak), while red maple required 10 weeks of storage to satisfy their chilling requirement. Haugge and Cummins (1991) consider dormancy to be broken when plants break bud within 2-3 weeks of planting. Ashby et al. (1991) also reported that *Acer* required 10 weeks of chilling for bud break to occur.

Arnold and Young (1990) reported increased fresh weights in response to chilling. Farmer (1979) and Harris et al. (1993) reported that increased chilling increased shoot growth for a variety of trees. Increased root growth had also been related to increased chilling for *Fraxinus* and *Betula* (Harris et al., 1993), *Malus* (Arnold and Young, 1990 and Arnold and Young, 1991), and *Pseudotsuga* (Lavender and Wareing, 1972). Increased shoot and root dry masses for both species due to increased chilling suggest that adequate chilling was required to completely release the trees from dormancy. Differences in leaf area and shoot and root dry mass for Washington hawthorn due to chilling suggest that varying levels of dormancy are responsible for growth processes of different plant parts. Since root:shoot ratios decreased linearly for both species due to increased cold storage, shoot growth rates for both species exceeded root growth rates. Daylength was not held constant during this experiment, and environmental conditions for trees removed from cold storage and planted into the greenhouse later in the growing season were increased. However, Falusi and Calamassi (1990) suggested that chilling completely eliminates dormancy rather than inducing a state where sprouting depends on photoperiod. Additionally, Farmer (1979) indicated that greenhouse light regime had no influence on *Quercus* bud break in December, January, or February. Farmer (1968) reported that influence of daylength on growth of *Liquidambar* seedlings declined after 1200 hrs. Trees in the current experiment acquired 1200 hrs of chilling prior to 5 weeks of cold storage, suggesting that influence of daylength on growth was minimal.

Percent embolism was not influenced by duration of cold storage for either species, and there were no differences in embolism between species for any storage duration except for plants that received no cold storage (Table 2). Storage temperature should have had no influence on embolism response since Sperry et al. (1994) reported that freeze-induced embolism depends on the number of freeze-thaw cycles and not the temperature itself. Red maple had not reached maximum levels of embolism prior to harvest and cold storage. Embolism levels for trees increase as the growing season progresses for several plant species (Sperry et al., 1994 and Sperry et al., 1988), but other research (Tognetti and Borghetti, 1994) indicated a decline in embolism following bud break for *Alnus*.
Results of these experiments confirm that increased chilling results in early growth increases for both a difficult-to-transplant species (Washington hawthorn) and an easy-to-transplant species (red maple). However, water is lost from both species due to cold storage conditions. Although embolism levels do increase for red maple and not for Washington hawthorn during cold storage, no relationship between embolism levels and post-transplant growth was evident.
Literature Cited


Table 1. Influence of duration of storage on % fresh mass reduction, and % embolism for Washington hawthorn and red maple.

<table>
<thead>
<tr>
<th>Duration of storage (weeks)</th>
<th>Regression</th>
<th>L</th>
<th>Q</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>p&gt;F</td>
<td>r²</td>
</tr>
<tr>
<td>Washington hawthorn</td>
<td></td>
<td>p&gt;F</td>
<td>r²</td>
</tr>
<tr>
<td>% fresh mass reduction</td>
<td>0.0</td>
<td>4.0</td>
<td>5.6</td>
</tr>
<tr>
<td>% embolism</td>
<td>60.2</td>
<td>72.8</td>
<td>80.8</td>
</tr>
<tr>
<td>Red maple</td>
<td></td>
<td>p&gt;F</td>
<td>r²</td>
</tr>
<tr>
<td>% fresh mass reduction</td>
<td>0.0</td>
<td>6.4</td>
<td>10.3</td>
</tr>
<tr>
<td>% embolism</td>
<td>22.2</td>
<td>30.8</td>
<td>46.8</td>
</tr>
<tr>
<td>Significance(^{x})</td>
<td></td>
<td>p&gt;F</td>
<td></td>
</tr>
<tr>
<td>% fresh mass reduction</td>
<td>0.1111</td>
<td>0.0043</td>
<td>0.0276</td>
</tr>
<tr>
<td>% embolism</td>
<td>0.0040</td>
<td>0.0010</td>
<td>0.0287</td>
</tr>
</tbody>
</table>

\(^{x}\)N=12 for % fresh mass reduction and n=6 for % embolism.

\(^{x}\)Comparison between species for each sampling date.
Table 2. Duration of storage influences area per leaf, days to budbreak, shoot dry mass, root dry mass, root:shoot ratio, and % embolism for Washington hawthorn and red maple after 15 weeks of growth$^z$.

<table>
<thead>
<tr>
<th>Duration of storage (weeks)</th>
<th>Regression</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L</td>
</tr>
<tr>
<td>Washington hawthorn</td>
<td></td>
</tr>
<tr>
<td>% fresh mass reduction</td>
<td></td>
</tr>
<tr>
<td>0  1  3  5  10  15</td>
<td></td>
</tr>
<tr>
<td>0.0 4.0 5.6 7.7 15.4 10.7</td>
<td></td>
</tr>
<tr>
<td>p&gt;F $^{r^2}$ = 0.49</td>
<td>0.0001</td>
</tr>
<tr>
<td>% embolism</td>
<td></td>
</tr>
<tr>
<td>60.2 72.8 80.8 83.9 74.3 71.2</td>
<td></td>
</tr>
<tr>
<td>p&gt;F $^{r^2}$ = 0.00</td>
<td>0.7381</td>
</tr>
<tr>
<td>Red maple</td>
<td></td>
</tr>
<tr>
<td>% fresh mass reduction</td>
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</tr>
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<td>0.0 6.4 10.3 11.3 7.6 13.3</td>
<td></td>
</tr>
<tr>
<td>p&gt;F $^{r^2}$ = 0.33</td>
<td>0.0001</td>
</tr>
<tr>
<td>% embolism</td>
<td></td>
</tr>
<tr>
<td>22.2 30.8 46.8 30.8 44.0 45.8</td>
<td></td>
</tr>
<tr>
<td>p&gt;F $^{r^2}$ = 0.14</td>
<td>0.0242</td>
</tr>
</tbody>
</table>

Significance$^x$

| % fresh mass reduction     | p>F        |
| 0.1111 0.0043 0.0276 0.0007 0.0413 |            |
| % embolism                 | 0.0040 0.0010 0.0287 0.0095 0.0015 0.0230 |

$^z$N=6.

$^x$Comparison between species for each sampling date.
CHAPTER FOUR

Growth and Embolism Recovery Vary with Transplant Date for Corylus colurna L. and Syringa reticulata (Blume) Hard

Additional index words: cavitation, Turkish hazelnut, Japanese tree lilac, root growth

Abstract

Transplant success for trees results from an interaction between climate and physiological and phenological status of the tree. The impact of transplanting on xylem embolism dynamics and the consequences for transplant success are unknown. The objectives of these experiments were to quantify the influence of transplant time on plant growth and recovery from dormant levels of embolism. Two experiments were conducted. 1) Three transplanting treatments (not-transplanted, late-fall-transplanted, spring-transplanted) were randomly assigned to two-year-old Corylus colurna L. (Turkish hazelnut) and Syringa reticulata (Blume) Hard (tree lilac) in 1994, and 2) Five transplanting treatments [not-transplanted, late-fall-transplanted with 0 or 50% root removal (late-fall-0 or late-fall-50, respectively), and spring-transplanted with 0 or 50% root removal (spring-0 or spring-50, respectively)] were randomly assigned to two-year-old Turkish hazelnut and tree lilac in 1995. Percent embolism, root regrowth, and top growth were measured periodically after transplanting for both experiments. In experiment one, late-fall-transplanted Turkish hazelnut were shorter and had smaller stem diameters than spring- or not-transplanted trees and were more embolized than spring-transplanted trees two growing seasons after transplanting. Late-fall- and spring-transplanted tree lilac had similar heights and stem diameters, but late-fall-transplanted trees were more highly embolized than spring-transplanted trees after two growing seasons. In experiment two, late-fall-transplanted Turkish hazelnut required more days to break bud than not-transplanted trees, but transplanting had no influence on days to budbreak for tree lilac. Transplanting always reduced growth for both species. Pre-budbreak embolism was highest for late-fall-transplanted Turkish hazelnut undergoing 50% root removal, but post-transplant growth was similar to other transplanted treatments. Pre-budbreak embolism levels were least for not-transplanted trees. Recovery from high dormant embolism levels was apparent for not-transplanted tree lilac, and spring-50 trees had not recovered just after budbreak. High levels were measured for all trees during shoot elongation (May). Embolism levels after one growing season were similar for Turkish hazelnut, but higher for spring-50 transplanted tree lilac compared to late fall-0 tree lilac or not-transplanted trees. This experiment indicates that differences in recovery from dormant levels of embolism may exist after 2 growing seasons, and therefore, may be a factor in continued reduced post-transplant growth for some species.
Introduction

Early post-transplant tree water stress plays a major role in transplanting success (Grossnickle, 1988 and Kaushal and Aussenc, 1989). This stress is due in part to the loss of a significant portion of the root system of field-grown plants at harvest (Watson and Kupkowski, 1991). The ability of the plant to quickly regrow roots lost at harvest influences the dynamics of stress relief (Watson and Himelick, 1982 and Lathrop and Mecklenburg, 1971).

Fall transplanting of ball-and-burlapped trees may be preferable to spring transplanting for plant establishment, even if root growth does not precede spring budbreak (Harris et al., 1996). Root growth was reported to be limited in New York state when soil temperatures dropped below 4°C (Good and Corell, 1982 and Harris et al., 1995). Harris and Bassuk (1994) reported good survival for Fraxinus and Syringa, but poor survival for Corylus and Quercus transplanted in the fall in upstate New York. Marion and Alm (1986) reported that Pinus seedlings seemed to transplant poorly in the fall in Minnesota. Hensley et al. (1984) reported good survival of container-grown Cotoneaster transplanted in the fall in Kansas. Harris et al. (1996) reported that post-transplant shoot growth of ball-and-burlapped Chionanthus was greatest for November transplants compared to December or March transplants in western Virginia.

Water stress is a primary cause of xylem embolism (Sperry et al., 1988b). Embolism also increases as trees enter the dormant season and may approach 90% in mid-winter for some tree species (Sperry et al., 1994). Since most field-grown nursery stock is harvested when dormant, plants may be severely embolized at the time of transplanting based on seasonal embolism patterns reported by Sperry et al. (1994). Failure of the plant to quickly regrow lost roots may result in a lack of recovery from dormant levels of embolism and may lead to even higher embolism levels as a result of transplant-induced drought stress. Restrictions in water conductance due to high embolism levels may limit post-transplant shoot extension. Therefore, the objective of this experiment was to quantify the influence of transplant time on plant growth and recovery from embolism.
Materials and Methods

**Experiment one.** Two-year-old bareroot *Corylus colurna* L. (Turkish hazelnut) and *Syringa reticulata* (Blume) Hara (tree lilac) (Watson’s Nursery, West Valley, NY) seedlings were planted in April, 1994. The bare-root seedlings were planted into bottomless 11 l containers placed in 30 cm diameter augured planting holes approximately 30 cm deep in a Groseclose silty clay loam (clayey, mixed, Typic Hapludult) having a pH of 6.5 at the Urban Horticulture Center (Blacksburg, Va.). Bottomless containers were backfilled with native soil. Three bareroot transplanting treatments (late-fall-transplanted, spring-transplanted, or not-transplanted) were randomly imposed on the seedlings. Trees were transplanted to additional bottomless containers at the same location on 7 December 1994 (late fall) so as to insure high native embolism levels, and 14 March 1995 (spring), before budbreak. At both transplanting dates, soil temperatures were below 3°C. At transplanting, 50% of the root system (measured from root tip to primary axis) was removed on all trees. Plants were top-dressed annually with 9.0 g N per container applied as controlled release 18N-2.6P-9.9K (Osmocote, The Scotts Company, Marysville, Ohio). Supplemental irrigation was applied as needed.

Heights and stem diameters (10 cm above the soil surface) were measured on all trees in the spring of 1995, fall 1995 and August, 1996. Shoot dry masses were measured in August, 1996, at experiment termination by drying to a constant mass at 65°C. Root dry masses were not measured due to excessive escape of roots from the bottomless containers. Percent embolism was measured after full leaf-drop (November, 1995), and just prior to budbreak (March, 1996), and experiment termination (August, 1996) according to the method discussed on chapter one (Sperry *et al.*, 1988a). Two plants per species were analyzed at each embolism sampling date.

There were six replications of each treatment per species arranged in a completely randomized design. All data were subject to analysis of variance and Fisher’s Protected Least Significant Difference (p<0.05, SAS ver. 6.03, SAS Institute, Cary, NC). Each species was analyzed separately.

**Experiment two.** Two-year-old Turkish hazelnut and tree lilac (Heritage Seedlings, Boring, Ore.) were transplanted in March, 1995 into the same soil type as described for experiment one. Five transplanting treatments (not-transplanted, late fall- transplanted with 0 or 50% root removal, and spring-transplanted with 0 or 50% root removal) were randomly assigned to two-year-old Turkish hazelnut and tree lilac in 1995. Use of bottomless containers facilitated the complete transfer of the root system for transplanting treatments. Late-fall transplant occurred on 15 December 1995, and the spring transplant occurred on 17 March, 1996. Soil temperatures were below 3°C on both transplanting dates. December 15 was chosen so as to ensure maximum native embolism levels. Plants were fertilized at the same rate for both experiments, but experiment one did not receive supplemental irrigation.

Heights and stem diameters (10 cm above the soil surface) were determined at the initiation of the experiment and monthly from April through late July, 1996. Root dry masses prior to transplanting were determined from a random sample of 12 trees per species. Shoot and root dry masses were recorded at the termination of the experiment in early August, 1996. Root growth was estimated by subtracting the initial root dry mass from the final root dry mass. Root:shoot ratios were calculated based on final root and shoot dry masses. Days to budbreak were measured for each species from the date of the spring transplant. Budbreak was recorded for each plant when one leaf completely emerged from the bud. Area per leaf was determined at the termination of the experiment using a leaf area analyzer (LI-Cor 3000, LI-COR, Lincoln, Neb.). Percent embolism was measured for each
species in November, 1995 (prior to fall transplanting), December, 1995 (two weeks after fall transplanting), March, 1996 (at spring transplanting prior to budbreak), April, 1996 (two weeks after spring transplanting at budbreak), May, 1996 (one month after budbreak), and August, 1996 (experiment termination).

There were 16 replications of late fall transplants and 10 replications of controls (not-transplanted) and spring transplants per species per treatment. This provided 6 replications per treatment per species for measurements at the termination of the experiment. All data were subjected to analysis of variance and Fisher’s Protected Least Significant Difference (p<0.05, SAS ver. 6.03, SAS Institute, Cary, NC). Each species was analyzed separately.
Results and Discussion

**Experiment one** There were no differences in plant heights and stem diameters for either species for the measurements taken in the spring of 1995 (Table 1). After one growing season (fall, 1995), transplanted Turkish hazelnut, regardless of season, were shorter and had smaller stem diameters than the not-transplanted trees. There were no differences in the height of tree lilac seedlings after one growing season (fall, 1995), but the stem diameters were reduced by transplanting. After two growing seasons (late summer, 1996), Turkish hazelnut heights and stem diameters were largest for not-transplanted trees, and the height and stem diameters of spring-transplanted trees were larger than the height and stem diameters of late-fall-transplanted trees. Transplanting, regardless of season, reduced height and stem diameter for tree lilac compared to not-transplanted controls after two growing seasons (Table 1).

At experiment termination (late summer, 1996), not-transplanted Turkish hazelnut had the largest shoot dry masses compared to transplanted trees, and spring-transplanted trees had larger shoot dry masses compared to fall-transplanted trees (Table 2). Not-transplanted tree lilac had the largest shoot dry masses compared to transplanted trees. There were no differences in embolism for either species for measurements taken in Nov., 1995 or March, 1996 (Table 2). However, in Aug., 1996, embolism levels for spring-transplanted Turkish hazelnut were lower than embolism levels for late-fall-transplanted trees. Spring-transplanted tree lilac also had lower embolism levels compared to the not-transplanted and late fall-transplanted trees in Aug., 1996.

Growth reductions due to transplanting can be linked to several factors. Root removal removes a source of stored carbohydrates which may reduce shoot growth (Larson, 1978). Trees in the current experiment underwent 50% root removal, and growth reductions may be due to carbohydrate reserve reduction resulting from root loss. Additionally, water stress is often associated with transplanting, and reduced photosynthetic capacity resulting from water stress may reduce carbon assimilation (Kozlowski and Keller, 1966). Reduced carbon assimilation would also limit plant growth after transplanting. Finally, sufficient water and turgor pressure is required for cell expansion (Mauseth, 1988). There are no data published on possible limitations of cell expansion imposed by high embolism.

Turkish hazelnut growth reductions for fall transplants were expected based on similar reductions in growth reported by Harris and Bassuk (1994) for fall-transplanted Turkish hazelnut in New York. Soil temperatures were less than 3°C for the late-fall 1994 transplant, and temperatures lower than 7°C may limit water uptake by plant roots, thereby increasing the possibility of desiccation (Running and Reid, 1980). Although both late-fall 1994 and spring 1995 transplanting treatments did not influence height growth after one growing season, reductions in height after two growing seasons suggests that spring transplants may have begun to recover from transplant stress while late fall transplants had not. Increased height for spring-transplanted compared to late-fall-transplanted Turkish hazelnut in late summer, 1996 (Table 1) are consistent with the results reported by Harris and Bassuk (1994).

Harris and Bassuk (1994) related response patterns for late-fall-transplanted Turkish hazelnut and tree lilac to differences in root system morphology. Turkish hazelnut has a coarse root system limiting uptake of water that might be available in the winter, and tree lilac has a fine root system, providing more root surface area for water uptake. Although the transplanting environment in southwestern Virginia is not as severe as that of New York, differences in root system morphology may
account for observed differences in plant response to season of transplant in both areas.

Similar embolism values for the November, 1995 sampling (Table 2) was probably due to trees having attained maximum levels of winter embolism and variability between trees as they reached those maximum embolism levels (Sperry et al., 1994). Lowest embolism levels would be expected just prior to spring budbreak since this is the time after refilling of existing vessels or growth of new vessel tissue (Cochard and Tyree, 1990; Sperry et al., 1988b; and Tognetti and Borghetti, 1994). Data in March, 1996 suggest that late-fall-transplanted and not-transplanted Turkish hazelnut (embolism levels decreased from winter levels) had recovered from winter embolism levels while tree lilac had not (embolism levels were still high). Differences in embolism levels after two growing seasons (August, 1996) may be related to differences in transplant stress recovery in response to differing transplant times. Reduced growth of Turkish hazelnut in response to late fall transplanting has been reported by Harris and Bassuk (1994). The coarse root system of Turkish hazelnut might limit water uptake in the winter and might lead to increased levels of embolism. Reduced shoot growth compared to not-transplanted trees and low embolism levels, seen with spring Turkish hazelnut transplants, may indicate that some recovery from dormant levels of embolism had occurred, but growth levels were low, reducing water stress induced embolism which resulted from tensions in quickly growing tissue. Embolism levels seen with not-transplanted trees may be related to xylem tensions that occur naturally in actively growing plant tissue. These data support the contention that Turkish hazelnut transplants poorly in fall since increased embolism coupled with reduced growth would be detrimental for plant survival. However, embolism levels of late-fall-transplanted tree lilac were higher than spring-transplanted trees in August, 1996 (Table 2), but growth was not further reduced for fall transplants compared to spring transplants (Table 1). Embolism levels are similar to those of not-transplanted trees, suggesting that the tree may be functioning to maximize carbon assimilation at the expense of a higher embolism level (Alder et al., 1996 and Tyree and Sperry, 1988). Embolism levels declined for spring-transplanted tree lilac from March, 1996 to August, 1996 (Table 2). Similar reductions in embolism have been measured on not-transplanted trees at the end of the growing season (unpublished data), although a similar response was not measured on other tree lilac in this experiment. Lower levels of embolism in spring-transplanted trees having the same shoot growth as late fall-transplanted trees may be due spring-transplanted trees having a greater root mass than late fall-transplanted trees. Alternately, 48% embolism for Turkish hazelnut may have been severe enough to reduce growth for late fall transplants while 65% embolism for tree lilac may have been insufficient to reduce transplant growth. Similarities of embolism measurements prior to budbreak might indicate recovery from dormant levels of embolism, but insufficient root growth to maintain adequate water reserves for maximum growth throughout the entire growing season. Higher levels of embolism in growing, not-transplanted trees would be expected since increased water demand and carbon assimilation necessary for growth increase the risk of embolism for a plant (Tyree and Sperry, 1988).

Experiment two. Transplanting reduced height of Turkish hazelnut and stem diameter (Table 3) and root growth and shoot and root dry mass for both species (Table 4). Height and stem diameter were similar for all transplanted treatments for Turkish hazelnut and for stem diameter and shoot dry mass of tree lilac by July, but late-fall-transplanted tree lilac, regardless of root pruning treatment, were taller than spring-50 transplants of tree lilac in July (Table 3). Root growth and root dry mass followed the same trend within species for both Turkish hazelnut and tree lilac (Table 4). Late fall-50 or spring transplanting reduced root
growth of tree lilac compared to not-transplanted trees, and late fall-0 root dry masses were similar to all other treatments. Root:shoot ratios for Turkish hazelnut were increased in response to transplanting, indicating compensatory post-transplant root growth (Table 4). However, root:shoot ratios of tree lilac were similar, indicating equal reduction of root and shoot growth. Watson’s (1985) root:shoot reestablishment theory suggests that reestablishment of the tree’s original root:shoot ratio signals the end of transplant stress, and based on that reestablishment theory, tree lilac may be at the end of the process to overcome transplant stress since.

Height of Corylus and stem diameter of Corylus and Syringa transplants in experiment two follow the same pattern as Corylus and Syringa transplants discussed in experiment one, although all experiment one transplants underwent 50% root removal. However, height of Syringa transplants (experiment two) was less than not-transplanted trees after one growing season (Table 3, June) whereas height of Syringa transplants in experiment one was similar to not-transplanted trees (Table 1, fall). Lack of supplemental irrigation may have resulted in growth reductions for Syringa after one year. Since growth of Corylus transplants (experiment one) was reduced with supplemental irrigation and a similar reduction also took place without irrigation, supplemental irrigation may be more important for transplant stress reduction during the first year for Syringa compared to Corylus. Contrary to research by Harris and Bassuk (1994) and experiment one (Table 1), late-fall-transplanted Corylus (experiment two) had similar heights to spring transplants (Table 2). Trees in the Harris and Bassuk (1994) experiment were subjected to 2 days of storage while trees in the present experiment were planted immediately.

Days to budbreak for Turkish hazelnut were higher for late-fall-transplanted trees compared to spring-50 and not-transplanted trees (Table 5). Increased days to budbreak for late-fall-transplanted trees compared to not-transplanted trees may be related to inadequate water resources necessary for shoot extension due to delayed root regrowth (Guehl, et al., 1993) or reduced translocation of growth regulators from roots to shoots (Taiz and Zeiger, 1991). Transplanting had no influence on days to budbreak for tree lilac. Root pruning may not have been severe enough to impact days to budbreak for tree lilac.

Transplanting, regardless of season or root pruning severity, reduced area per leaf for Turkish hazelnut (Table 5) and may be related to reduced water uptake resulting from reduced root regrowth. Reduced water uptake limits cell expansion (Mauseth, 1988) and might be more severe for a coarse-rooted species. Root pruning spring-transplanted tree lilac resulted in a decreased area per leaf but had no effect on late-fall-transplanted trees.

Turkish hazelnut embolism levels were similar for December (two weeks after late fall transplant) (Table 6), suggesting that maximum levels of winter embolism had been reached (Sperry et al., 1994). No effect of transplanting on embolism of Turkish hazelnut was seen until just before spring budbreak (March), at which time late fall-50 trees had the highest embolism levels (Table 6). High levels of embolism in the late fall-50 trees suggest that those trees had not recovered from dormant levels of embolism, perhaps because root growth was insufficient to rehydrate plants or support adequate new xylem growth (Cochard and Tyree, 1990; Sperry et al., 1988b; and Tognetti and Borghetti, 1994). This was probably responsible for the delayed budbreak observed in those trees (Table 5). Wang et al. (1992) reported delayed budbreak for deciduous hardwoods in response to high embolism levels in the late winter. Embolism of late-fall-50 trees was similar to not-transplanted trees at the April sampling date, indicating recovery, but the spring-50 treatments (transplanted one month earlier) now had higher embolism levels than controls. Root pruning Turkish hazelnut by 50% also increased embolism in
Chapter Two. Embolism levels for all treatments were similar by August. Lack of difference between treatments having 32 and 93% embolism levels indicate high variability in embolism measurements and may be indicative of seedling selections used for this research or due to differences between metabolic mechanisms leading to high embolism levels as discussed previously for trees in experiment one. Conversely, embolism may have limited impact on measured growth parameters during most of the growing season.

All tree lilacs (including not-transplanted trees) were highly embolized in March, just prior to budbreak, indicating that recovery from winter embolism levels had not yet occurred (Table 6). High embolism levels in spring-50 transplants in May correlated with low area per leaf and reduced root and shoot growth although similarities exist between spring-50 and other transplanting treatments in all cases. Similar decreases in embolism toward the end of the growing season have been measured for *Acer* (unpublished data).

Gilbertson and Bradshaw (1990) suggest that the beginning of the second growing season may be most important in plant establishment and survival. This experiment indicate that transplanting reduced growth of Turkish hazelnut and tree lilac at least two years after transplanting. Reestablishment of root:shoot ratios of tree lilac after one year for trees in experiment two suggests that transplant stress may be shorter in duration for tree lilac compared to Turkish hazelnut, but differences in embolism for both species after two growing seasons (experiment one) suggest that recovery is not yet complete. Therefore, transplanting stress may last for longer than two years, even in species that transplant easily.

In this study Turkish hazelnut, a difficult-to-transplant species, had reduced growth (Table 1) and higher embolism levels (Table 2) on late-fall- compared to spring- transplanted trees after two growing seasons. However, not-transplanted trees had embolism levels that were similar to both late-fall- and spring-transplanted trees and grew more than transplanted trees. Transplanted tree lilac had similar growth after two growing seasons, whether transplanting occurred in the late fall or spring. Late-fall-transplanted trees were highly embolized at levels similar to not-transplanted trees, but spring-transplanted trees had the lowest levels. Although embolism levels differ, the exact role of embolism in transplanting stress is not known.
Literature Cited


Table 1. Influence of season of transplant on height and stem diameter for transplants of *Corylus colurna* L. (Turkish hazelnut) and *Syringa reticulata* (Blume) Hard (tree lilac) in experiment one

<table>
<thead>
<tr>
<th></th>
<th>Height (cm)</th>
<th>Stem diameter (mm)</th>
<th></th>
<th></th>
<th>Late-summer</th>
<th></th>
<th>Late-summer</th>
<th></th>
<th>Late-summer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Spring 1995</td>
<td>Fall 1995</td>
<td>Late-summer</td>
<td>Spring 1995</td>
<td>Fall 1995</td>
<td>Late-summer</td>
<td></td>
</tr>
<tr>
<td>Turkish hazelnut</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late fall</td>
<td>88.4a</td>
<td>107.4b*</td>
<td>153.4c</td>
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<td>15.7b</td>
<td>24.6c</td>
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</tr>
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<td>180.6b</td>
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<td>30.6b</td>
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<td></td>
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<td>12.3a</td>
<td>27.7a</td>
<td>51.0a</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td></td>
<td></td>
</tr>
<tr>
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<td>15.0b</td>
<td>21.4b</td>
<td></td>
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<td>86.3a</td>
<td>156.0a</td>
<td>11.2a</td>
<td>19.8a</td>
<td>37.5a</td>
<td></td>
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</tbody>
</table>

*Y Means for main effects within columns having the same letter are not different according to Fisher’s Protected Least Significant Difference (p<0.05).

*N=8. Trees first transplanted in late fall 1994 or spring 1995.*
Table 2. Influence of season of transplant on shoot dry mass and seasonal embolism for transplants of *Corylus colurna* L. (Turkish hazelnut) and *Syringa reticulata* (Blume) Hard (tree lilac) in experiment one.

<table>
<thead>
<tr>
<th>Transplant season&lt;sup&gt;z&lt;/sup&gt;</th>
<th>Shoot dry mass&lt;sup&gt;y&lt;/sup&gt; (g)</th>
<th>% embolism&lt;sup&gt;x&lt;/sup&gt; November, 1995</th>
<th>% embolism&lt;sup&gt;x&lt;/sup&gt; March, 1996</th>
<th>% embolism&lt;sup&gt;x&lt;/sup&gt; August, 1996</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turkish hazelnut</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late fall</td>
<td>367.8c&lt;sup&gt;z&lt;/sup&gt;</td>
<td>58.9a</td>
<td>30.8a</td>
<td>48.0a</td>
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<tr>
<td>Spring</td>
<td>718.0b</td>
<td>26.2a</td>
<td>34.3a</td>
<td>17.9b</td>
</tr>
<tr>
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<td>2125.0a</td>
<td>38.4a</td>
<td>15.1a</td>
<td>37.9ab</td>
</tr>
<tr>
<td>Tree lilac</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late fall</td>
<td>280.0b</td>
<td>53.0a</td>
<td>52.9a</td>
<td>65.2a</td>
</tr>
<tr>
<td>Spring</td>
<td>218.6b</td>
<td>48.3a</td>
<td>51.0a</td>
<td>25.6b</td>
</tr>
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<td>718.5a</td>
<td>21.4a</td>
<td>60.0a</td>
<td>73.3a</td>
</tr>
</tbody>
</table>

<sup>z</sup>N=9. Trees first transplanted in the late fall 1994 or spring 1995.

<sup>y</sup>N=2.

<sup>x</sup>Means for main effects within columns having the same letter are not different according to Fisher’s Protected Least Significant Difference (p<0.05).
Table 3. Influence of season of transplant and root pruning on seasonal height and stem diameter for transplants of *Corylus colurna* L (Turkish hazelnut) and *Syringa reticulata* (Blume) Hard (tree lilac) in experiment two.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>1996 Height (cm)</th>
<th>1996 Stem diameter (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>April</td>
<td>May</td>
</tr>
<tr>
<td><strong>Turkish hazelnut</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late fall-0</td>
<td>74.0a</td>
<td>72.0b</td>
</tr>
<tr>
<td>Late fall-50</td>
<td>82.5a</td>
<td>84.4ab</td>
</tr>
<tr>
<td>Spring-0</td>
<td>71.1a</td>
<td>75.1b</td>
</tr>
<tr>
<td>Spring-50</td>
<td>72.8a</td>
<td>76.3b</td>
</tr>
<tr>
<td>Not-transplanted</td>
<td>71.5a</td>
<td>95.5a</td>
</tr>
<tr>
<td><strong>Tree lilac</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late fall-0</td>
<td>76.7a</td>
<td>92.5ab</td>
</tr>
<tr>
<td>Late fall-50</td>
<td>75.3a</td>
<td>86.3ab</td>
</tr>
<tr>
<td>Spring-0</td>
<td>59.0b</td>
<td>9.6bc</td>
</tr>
<tr>
<td>Spring-50</td>
<td>57.4b</td>
<td>70.6c</td>
</tr>
<tr>
<td>Not-transplanted</td>
<td>71.3ab</td>
<td>100.1a</td>
</tr>
</tbody>
</table>

\(^{z}N=10\). Trees first transplanted in late fall 1995 or spring 1996.

\(^{\text{Y}}\)Season of transplant-rate of root pruning. Removal of root system is 0% or 50% of length removed from root tip to axis of primary and secondary roots.

\(^{x}\)Means for main effects within columns having the same letter are not different according to Fisher’s Protected Least Significant Difference (p<0.05).
Table 4. Influence of season of transplant and root pruning on post-transplant root growth, shoot and root dry masses and root:shoot ratio for transplants of *Corylus colurna* L (Turkish hazelnut) and *Syringa reticulata* (Blume) Hard (tree lilac) in experiment two.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Post-transplant root growth (g)</th>
<th>Shoot dry mass (g)</th>
<th>Root dry mass (g)</th>
<th>Root:shoot ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Turkish hazelnut</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late fall-0</td>
<td>56.2b</td>
<td>105.2b</td>
<td>87.4b</td>
<td>0.85a</td>
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<td>47.4b</td>
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<td>78.6b</td>
<td>0.80a</td>
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<tr>
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<td>100.4b</td>
<td>0.89a</td>
</tr>
<tr>
<td>Spring-50</td>
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<td>99.2b</td>
<td>91.3b</td>
<td>0.93a</td>
</tr>
<tr>
<td>Not-transplanted</td>
<td>216.0a</td>
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<td>247.2a</td>
<td>0.60b</td>
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<tr>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late fall-0</td>
<td>93.0ab</td>
<td>113.6b</td>
<td>114.7ab</td>
<td>1.00a</td>
</tr>
<tr>
<td>Late fall-50</td>
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<td>87.9b</td>
<td>60.0b</td>
<td>0.69a</td>
</tr>
<tr>
<td>Spring-0</td>
<td>75.4b</td>
<td>94.8b</td>
<td>97.1b</td>
<td>1.10a</td>
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<td>Spring-50</td>
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<td>54.6b</td>
<td>0.90a</td>
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<tr>
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<td>157.7a</td>
<td>205.7a</td>
<td>179.4a</td>
<td>0.99a</td>
</tr>
</tbody>
</table>

**N=10.** Trees first transplanted in late fall 1995 or spring 1996. Trees were harvested in early August, 1996.

**Y** Season of transplant-rate of root pruning. Removal of root system is 0% or 50% of length removed from root tip to axis of primary and secondary roots.

**X** Means for main effects within columns having the same letter are not different according to Fisher’s Protected Least Significant Difference (p<0.05).
Table 5. Influence of season of transplant and root pruning on days to budbreak and area per leaf for transplants of *Corylus colurna* L. (Turkish hazelnut) and *Syringa reticulata* (Blume) Hard (tree lilac) in experiment two.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Turkish hazelnut</th>
<th>Tree lilac</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Days to budbreak</td>
<td>Area per leaf (cm²)</td>
</tr>
<tr>
<td>Late fall-0</td>
<td>74a</td>
<td>16.9b</td>
</tr>
<tr>
<td>Late fall-50</td>
<td>76a</td>
<td>12.1b</td>
</tr>
<tr>
<td>Spring-0</td>
<td>52ab</td>
<td>13.1b</td>
</tr>
<tr>
<td>Spring-50</td>
<td>37b</td>
<td>11.4b</td>
</tr>
<tr>
<td>Not-transplanted</td>
<td>38b</td>
<td>36.0a</td>
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</table>

*N=10. Trees first transplanted in late fall 1995 or spring 1996.

*N=6.

*Season of transplant-rate of root pruning. Removal of root system is 0% or 50% of length removed from root tip to axis of primary and secondary roots.

*Means for main effects within columns having the same letter are not different according to Fisher’s Protected Least Significant Difference (p<0.05).*
Table 6. Influence of season of transplant and root pruning on seasonal embolism for transplants of *Corylus colurna* L (Turkish hazelnut) and *Syringa reticulata* (Blume) Hard (tree lilac) in experiment two.  

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td><strong>Turkish hazelnut</strong></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Late fall-0</td>
<td>-</td>
<td>15.6a</td>
<td>11.9b</td>
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<td>40.6a</td>
<td>59.5a</td>
<td>34.6ab</td>
<td>22.7b</td>
<td>58.5a</td>
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<td>Spring-0</td>
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<td>-</td>
<td>-</td>
<td>28.7ab</td>
<td>43.0ab</td>
<td>32.9a</td>
</tr>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>69.3a</td>
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</table>

*N=2. Trees first transplanted in late fall 1995 or spring 1996.

November date corresponded with late fall transplant (leaf drop), December date was 2 weeks after fall transplant (deep dormancy), March date corresponded with spring transplant (just prior to budbreak), April date was 2 weeks after spring transplant (just following budbreak), May date was 1 month after budbreak (shoot elongation), and August date corresponded with the termination of the experiment (terminal budset). These dates were chosen because of expected changes in embolism and to determine how transplanting influenced these events.

Removal of root system is 0% or 50% of length removed from root tip to axis of primary and secondary roots.

Means for main effects within columns having the same letter are not different according to Fisher’s Protected Least Significant Difference (p<0.05).
CHAPTER FIVE

Embolism and Sap Flow of *Acer rubrum* L. Influenced by Root Severance during Field-harvest

**Additional index words.** Red maple, field-production, cavitation, hydraulic conductance, stomatal conductance

**Abstract.**

Root severance during field-harvesting may alter the water status of a tree, resulting in water stress. Two experiments were conducted using *Acer rubrum* L. (red maple) to determine the influence of root severance at harvest on sap flow, leaf stomatal conductance, leaf water potential, and xylem embolism. Experiment one utilized 3-year-old trees, and experiment two utilized 2-year-old trees. Trees for experiment one were harvested on 31 May 1996 with a rootball diameter of 30 cm. Rootballs were completely removed from the ground to ensure severance of all roots and then replanted. Sap flow sensors were installed before root severance and remained on trees for one week after harvest. Sap flow was reduced within one day after root severance and remained lower than not-transplanted trees one week after harvest. On 7 June, one week after root severance, transplanted trees had lower leaf stomatal conductance compared to not-transplanted trees, but leaf water potentials were similar. In a second experiment initiated on 20 August 1996, plants were handled in a similar manner as in experiment one. Sap flow was reduced within two h after harvest for transplanted compared to not-transplanted trees. Leaf stomatal conductance was reduced within four h of harvest. Leaf water potentials were not influenced on the day that plants were root severed. Embolism levels increased within 24 h of root severance. These results indicate that transplant stress begins shortly after harvest and not at the actual time of transplant.
Introduction

A well-watered, established tree may lose 60 g of water per square meter of leaf surface area per hour on a sunny, warm day (Vrecenak, 1988). Transplanting can greatly alter the water status of a tree (Grossnickle, 1988; Harris and Gilman, 1993; and Kaushal and Aussenac, 1989). For example, root loss during transplanting may restrict water uptake, resulting in water stress (Grossnickle, 1988; and Watson and Kupkowski, 1991). Blake (1993) reported an increase in stomatal resistance 8 days after unstored seedlings were transplanted, but the difference was not measured after 14 days. Additionally, transpiration of *Malus* was reduced by root pruning (Ferree, 1989; Ferree and Geisler, 1984; and Geisler and Ferree, 1984). In root-damaged *Picea* that survived transplanting, transpiration was reduced, and water potentials remained the same, but water potentials declined in plants that eventually died (Coutts, 1982). Stem sap flow sensors have been used successfully to document mass flow rates of sap in plant stems, estimate transpirational water losses (Steinberg et al., 1989), and provide a tool to evaluate transient changes in stem sap flow for root-severed trees.

Sperry et al. (1994) reported that negative xylem water potentials associated with drought stress are a primary cause of cavitation leading to embolism. Cavitation is the phase change of water from a liquid to a gas, and an embolism is the air-filled vessel that remains (Milburn and Johnson, 1966; and Sperry et al., 1994). Embolism results in reduced hydraulic conductance and inhibits transpiration (Schultze and Matthews, 1988; and Sperry and Pockman, 1993). Sperry and Pockman (1993) reported that leaves exhibited reduced stomatal conductance two days after air injection to induce cavitation, but xylem pressures were not influenced. Additionally, Dixon et al. (1984) examined water potentials, stomatal conductance, and embolism in *Thuja occidentalis* L. in response to laboratory desiccation. In response to dehydration, saplings exhibited a decline in leaf water potentials followed by a rehydration of foliage resulting from release of stem water reserves due to cavitation. Stomatal closure coincided with foliar rehydration.

By understanding all changes that occur in the water status of a plant during the transplanting process, measures can be taken to improve transplant survival in the landscape. However, the influence of root severance on sap flow and embolism levels has not been examined. Therefore, the objective of this experiment was to examine the influence of root severance at harvest on sapflow, leaf stomatal conductance, leaf water potentials, and embolism for field-grown *Acer rubrum* L.
Materials and Methods

**Experiment one.** Two-year-old bareroot *Acer rubrum* L. ‘Red Sunset’ (J. Frank Schmidt and Sons, Inc., Boring, Ore.) were planted at the Urban Horticulture Center near Blacksburg, Va., into a Groseclose silty clay loam (clayey, mixed, Typic Hapludult) with a pH of 6.5 in April, 1994. On May 31, 1996, eight uniform trees were selected, and sensors (SGB 16-WS Dynagauge, Dynamax, Inc., Houston, Texas) were placed at various heights on the main stem, although all foliage was above the sensors. After installation, all sensors were covered with a weather shield, and openings were sealed with silicone. The entire sensor apparatus, and the portion of the stem below the gauge, was covered with aluminum foil to prevent solar radiation from causing external temperature differentials between stem and sensor (Steinberg, et al., 1989). This system uses heat balance technology (Baker and van Bavel, 1987; Ham and Heilman, 1990; and Sakuratani, 1981). Signals (mg/h) were recorded at 60 s intervals, data were averaged every 15 min and data output (recorded by a CR21X data logger, Campbell Scientific, Logan, Utah) every 30 min. Data were reported as 24 h averages (g/h). On 31 May 1996, four trees were randomly selected and harvested with a 30-cm rootball (American Association of Nurserymen, 1980). Trees were completely lifted from the soil to ensure severance of all roots and then replanted into the original hole. All plants were thoroughly watered at transplanting. Sap flow measurements were continued until the evening of 6 June 1996. On 7 June 1996, sap flow sensors were removed. At 1000 h on 7 June 1996, stomatal conductance (*C*<sub>s</sub>) using a porometer (LI-COR LI1600, Lincoln, Neb.) was measured on a fully expanded east-oriented leaf, and leaf water potentials (*v*) using a pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, Calif.) was performed on the same leaf utilized for porometer measurements. Percent embolism (Sperry et al., 1988) was also measured. Stem sections chosen for embolism measurements consisted of the stem area covered by the stem sap flow sensor and the area on either side of the sensor. Light levels averaged approximately 1200 µmol m<sup>-2</sup> s<sup>-1</sup> for the sampling period. Leaf areas were determined using a leaf area analyzer (LI-COR 3000, LI-COR, Lincoln, Neb.). Flow rates were divided by leaf area to determine average flow/cm<sup>2</sup>.

**Experiment two.** On 17 August 1996, a second experiment was conducted utilizing *Acer rubrum* L. (Lawyer Nursery, Plains, Mont.), planted as 1-year-old trees at the Urban Horticulture Center near Blacksburg, Va., in March, 1995, in the same soil type as the first experiment. All parameters for trees and sensors were identical to those utilized in the first experiment. Four trees were dug on 23 August 1996, and four additional trees served as non-transplanted controls. Approximately 0.5 h was required to dig all replications. Rate of sap flow was measured every 60 s and stored as output by the data logger every 15 min. Leaf stomatal conductances and leaf water potentials were recorded every hour after trees were dug (1100 h). Light levels averaged 1250 µmol m<sup>-2</sup> s<sup>-1</sup> for the sampling period. Percent embolism for each tree was determined on 24 August 1996. Additionally, pre-dawn water potential measurements were taken for all treatments (n=4).

All data were subjected to analysis of variance and Fisher’s Protected Least Significant Difference, p<0.05 (SAS ver 6.03, SAS Institute, Cary, NC). Treatments were assigned to trees in a completely random fashion utilizing four replications per treatment.
Results and Discussion

Experiment one. Trees exhibited a reduced sapflow rate the day after transplanting (1 June 1996) compared to not-transplanted trees (Fig. 1). Leaf stomatal conductance ($C_s$), measured at 1000 h on 7 June 1996, was also reduced in response to root severance (Table 1). Leaf water potentials ($\Psi_2$), also measured at 1000 h on 7 June 1996, were similar for transplanted and and not-transplanted trees (Table 1). Percent embolism, also measured on 7 June 1996, increased for transplanted compared to not-transplanted trees (Table 1).

Experiment two. Trees were transplanted at 1100 h on 23 August 1996. Sapflow was reduced for harvested trees within 2 h after root severance (Fig. 2). Leaf $C_s$ was reduced by harvest at 1530 h, within 4 h of harvest (Fig. 3). Leaf 2 did not respond to harvest (Fig. 4), and there were no differences in pre-dawn 2 (data not shown). Percent embolism was higher for harvested trees compared to not-harvested trees within 24 hours of root severance (Table 1).

Not-transplanted trees in experiment one averaged about 40 mg of water loss per hour per cm$^2$ on 1 June 1996 (Fig. 1), and about 60 mg of water loss per hour per cm$^2$ for experiment two, on 23 August 1996 (Fig. 2). Transplanted trees averaged about 15 and 10 mg of water loss per hour per cm$^2$ on 1 June 1996 for experiment one (Fig. 1) and 23 August 1996 for experiment two (Fig. 2), respectively. Values for not-transplanted trees for both experiments were higher than the 60 g/h/m$^2$ reported by Vrecenak (1988) for deciduous trees, but sap flow values of transplanted trees are closer to reported values. Deviations from Vrecenak’s model may result from differences in tree species or the estimated leaf area index he utilized for his calculations. Additionally, Vrecenak’s (1988) numbers were based on a model for deciduous trees, not actual data. Several researchers indicate that water uptake is restricted in transplanted plants due to root loss (Grossnickle, 1988 and Kaushal and Aussenac, 1989), and this reduction in water uptake is evidenced by the reduction in stem sapflow of our trees soon after digging.

In experiment one, one-week after harvest, leaf $C_s$ was approximately 750% less for transplanted trees compared to not-transplanted trees (Table 1). Leaf $C_s$ was reduced by almost 90% for transplanted trees compared to not-transplanted trees within 4 h after root severance (Fig. 3); however, leaf $C_s$ had somewhat recovered by 1630 hr. These results suggest that stomatal closure of transplanted trees has occurred to minimize water loss and embolism resulting from water stress. Tyree and Sperry (1988) demonstrated that many trees operate near the point of catastrophic embolism and use stomatal regulation to control embolism levels. Plants maintained high levels of stomatal conductance until species-dependent low water potentials were reached, and then stomatal conductance was reduced (Dixon et al., 1984). Data from the current experiment agree with Blake (1993), who reported that $C_s$ was reduced 8 days after bare-root seedlings were transplanted. Harris and Gilman (1993) also reported reductions in $C_s$ 3 and 5 days after transplant of field-grown holly. Ferree (1989) and Ferree and Geisler (1984) reported that transpiration was reduced for apple between 10 and 28 days after transplanting. Coutts (1982) also reported reduced transpiration for root-damaged plants. Lack of $C_s$ response for the 1630 sampling time of 23 August 1996 may be related to a decline in leaf $C_s$ of not-harvested trees resulting from stomatal closure rather than a recovery of the $C_s$ for harvested trees. Reduced sapflow rates for not-harvested trees compared to values for the same trees earlier in the afternoon supports this conclusion.

Lack of leaf water potentials response to root severance on 7 June 1996 (experiment one)(Table 1) or 23 August 1996 (experiment two) may be related to
trees reaching critical water potentials triggering massive levels of embolism at
different times during the day due to differences in tree capacitance or root volume
within the root ball. Individual trees did follow the pattern outlined by Dixon et al.
(1984) in which water potentials declined initially, increased temporarily and then
decreased again. Coutts (1982) reported that Picea seedlings that survived
transplanting did not show reductions in 2, whereas seedlings that did not survive
required a long time to exhibit declines in 2. Even though our experiment was
conducted in the summer when trees were fully leafed-out, all trees survived into
the fall.

Transplanting resulted in increases in embolism of trees on 7 June 1996
(experiment one) and 23 June 1996 (experiment two) compared to not-transplanted
trees (Table 1). Percent embolism was increased for Corylus in response to root
pruning in Chapter Two and for early-spring measurements for Turkish hazelnut
and Syringa in Chapter Four. Since all red maple survived into the fall, high
embolism levels observed in transplanted trees may not be detrimental for tree
survival, but short-term growth may be inhibited by a reduction in water
conductance.

Coutts (1982) suggested that the delay in the development of substantial
water stress, as indicated by reduced water potentials, was due to a slow,
progressive increase in resistance to water uptake in the roots. However, reductions
in sapflow that occurred quickly (within 2 hours) after digging in experiment two
suggest that lack of response of red maple leaf 2 may be related to differences in
transpiration lags between plants. Most plants exhibit a lag between transpiration
and adsorption, and the lag may vary for different plants depending on root volume
within the rootball (Kramer and Boyer, 1995).

Post-harvest reductions in leaf C4 in these experiments agree with the
research of Sperry et al. (1994) who reported that embolism inhibits transpiration,
and Sperry and Pockman (1993) who reported that the reductions continued for 2
days. Xylem pressures of those plants were not influenced by increasing embolism.
Dixon et al. (1984) reported that seedlings dehydrated in a laboratory showed an
initial decline in 2 followed by an increase. This resulted from a rehydration event
caused by embolism in the stem. Although not statistically significant, our
harvested trees showed a decrease in leaf 2 at 1330 h (Fig. 4). The rehydration
event, also recorded by Dixon et al. (1984) coincided with massive stomatal
closure, but the slight decrease in leaf 2 followed stomatal closure (Figs. 3 and 4).
In agreement with Dixon et al. (1984), leaf C4 of our trees was low at the end of
experiment one (Table 1).

Reductions in water uptake for red maple occur relatively quickly after field-
harvest. Reductions in sapflow precede reductions in leaf C4. Exactly when
embolism occurs during the 24 h preceding measurement is still unknown, but
based on the research of Dixon et al. (1984), embolism probably would have
occurred between 1400 and 1600 h on 23 August 1996. Transplanting stress
therefore begins at the time of harvest and not at transplanting as is suggested by the
term.


Blake, T.J. 1983. Transplanting shock in white spruce; effect of cold-storage and root pruning on water relations and stomatal conditioning. Physiol. Plant. 57:210-216.


Table 1. Influence of root severance at harvest on leaf stomatal conductance, leaf water potential, and % embolism for field-grown *Acer rubrum* L. 

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Leaf stomatal conductance(^a) (mmol·m(^{-2})·s(^{-1}))</th>
<th>Leaf water potential(^b) (-MPa)</th>
<th>% embolism (experiment 1)</th>
<th>% embolism (experiment 2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not-transplanted</td>
<td>199.8(^a)</td>
<td>-0.18(^a)</td>
<td>10.0(^b)</td>
<td>43.8(^b)</td>
</tr>
<tr>
<td>Transplanted</td>
<td>23.35(^b)</td>
<td>-0.13(^a)</td>
<td>49.5(^a)</td>
<td>85.4(^a)</td>
</tr>
</tbody>
</table>

Significance

<table>
<thead>
<tr>
<th>Treatment</th>
<th>p&gt;F</th>
<th>0.0030</th>
<th>0.1589</th>
<th>0.0003</th>
<th>0.0040</th>
</tr>
</thead>
</table>

\(^a\)N=4.

\(^b\)Leaf stomatal conductance measured for experiment one, 7 June 1996, at 1000 hr.

\(^c\)Leaf water potential measured for experiment one, 7 June 1996, at 1000 h.

\(^w\)Means within the same column having the same letter are not different according to t-test (p<0.05)
Figure 1. Influence of root severance on sapflow for field-grown *Acer rubrum* L. Trees were dug on May 31, 1996. Vertical bars represent ±S.D. of means, n=4.
Figure 2. Influence of digging on sapflow for field-grown *Acer rubrum* L. Trees were dug on August 23, 1996. Vertical vbars represent ±S.D. of means, n=4.
Figure 3. Influence of digging on leaf stomatal conductance for field-grown Acer rubrum L. Trees were dug on August 23, 1996. Vertical vbars represent ±S.D. of means, n=4.
Figure 4. Influence of digging on leaf water potentials for field-grown *Acer rubrum* L. Trees were dug on August 23, 1996. Vertical bars represent ±S.D. of means, n=4.
CONCLUSIONS

The purpose of this dissertation was to quantify the influence of transplanting practices such as root pruning, cold storage, and transplant season on tree growth and embolism levels. In addition, I looked for evidence of a causal relationship between high levels of embolism (more specifically the failure of recovery from embolism) and transplanting resulting in reduced post-transplant growth. Although transplanting clearly affects embolism dynamics, evidence for a causal relationship with reduced growth was slight. In Chapter Two, Turkish hazelnut trees that were root-pruned 50% showed a significant increase in embolism fifteen weeks after planting. Root pruning at harvest for larger field-grown trees ranges from near 50% (Harris and Gilman, 1993) to over 90% (Gilman, 1988) of total root volume, depending on size and species. Root pruning levels approaching 90% might result in increased levels of embolism and increased growth reductions. Although the highest-embolized trees in Chapter Two did not grow less than lower-embolized trees, soil moisture was non-limiting throughout the experiment.

Different results may have been obtained if trees had been subjected to post-transplant drought conditions. In Chapter Three, growth increased with increased duration of cold storage for both species, even though embolism levels increased for red maple. Again, trees were grown in non-limiting soil water conditions. The positive effects of chilling may have also influenced embolism recovery. Roots were not pruned in this experiment. In Chapter Four late-fall-transplanted Turkish hazelnut trees with 50% root removal had the highest levels of embolism, and recovery to lower levels was delayed until well after budbreak. Although budbreak was delayed in these trees, growth that first season after transplant was not reduced compared to transplanted trees with lower levels of embolism. However, growth of another group of Turkish hazelnuts two seasons after transplanting corresponded to differences in embolism levels. Gilbertson and Bradshaw (1990) indicate that the second growing season may be the most important for plant establishment and survival, suggesting that transplanting stress is evident after the first growing season. A cause and effect relationship cannot be assumed, but there is probably enough evidence to warrant additional research. Finally, Chapter Five indicates that red maple showed reduced sap flow and increased embolism levels after summer transplanting. Leaf conductance was also reduced. Since high xylem embolism is associated with reduced water conductance, a causal relationship may exist between high levels of embolism and reduced water flow, although other factors may be responsible in whole or part (e.g. stomatal control, increased root resistance).

Influence of transplanting practices on plant growth have been examined in a number of experiments and are well-documented for a variety of species with varying results (Abod and Webster, 1990; Arnold and Young, 1991; Ashby et al., 1991; Bates and Niemiera, 1996; Coutts, 1982; and Ferree and Geisler, 1984). However, the influence of transplanting practices on embolism levels had not been examined until now. Dixon et al. (1984) reported that cavitation events may free water by releasing tension in the xylem water column and therefore rehydrating the foliage above the embolism on a short term basis, suggesting that recovery from stress-induced embolism is imperative for plant survival.

This dissertation demonstrates that in addition to previously reported growth responses to transplanting practices, embolism dynamics are also affected. However, the exact role of embolism in transplanting stress has not been determined. Since reduced growth in the nursery and the landscape represents a
cost to both nurserymen and homeowners, the role of recovery from dormant embolism in transplant establishment warrants continued investigation.
Literature Cited


Vita

Patricia Rene Knight was born on April 24, 1970, in Roanoke, Alabama. She is the daughter of Jerry and Rudene Knight, who operate a nursery in Roanoke, AL. She graduated from Woodland High School in 1988. She received a Bachelor of Science degree in Landscape Design from Auburn University (summa cum laude) in 1991, and her Master of Science degree in Horticulture from Auburn University in 1994. She enrolled in the doctoral program in horticulture at Virginia Polytechnic Institute and State University in the fall of 1994. She was awarded a Doctor of Philosophy degree in May, 1997. The author married Hiram Dewey Baldwin on June 14, 1991.