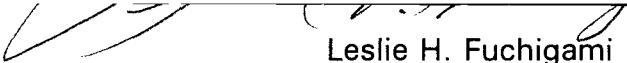


AN ABSTRACT OF THE THESIS OF

Michael D. Remmick for the degree of Master of Science in Horticulture  
presented on July 5, 1995, Title: The Effects of Desiccation Stress and  
Antidesiccant Application on The Water Relations and Transplant  
Establishment of Dormant Bare Root Deciduous Nursery Stock.

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Abstract approved



Leslie H. Fuchigami

Flowering dogwood (*Cornus florida* L.), river birch (*Betula nigra* L.), Washington hawthorn (*Crataegus phaenopyrum* Medic.), and European beech (*Fagus sylvatica* L.) are difficult to transplant in the dormant bare root condition. Previous research and observations by nurserymen have indicated that a low capacity for root regeneration or sensitivity to water stress are factors which reduce the performance of these species. Apple rootstock (*Malus domestica* Borkh.) layers M.9 and M.26 EMLA are relatively easily transplanted; however, exposure to desiccating conditions can decrease establishment and regrowth.

Applications of auxins or antidesiccants improve survival and establishment of bare root transplants. The first objective was to study the combined effect of pre-planting applications of each material in a factorial experiment with seedlings of birch and dogwood. Seedling roots were treated with auxin (0 or 500 ppm IBA, indole-3 butyric acid) and antidesiccant (0 or 50 % Moisturin-4, Burke's Protective Coatings, Washougal WA). Budbreak and establishment responses such as stem

dieback, visual rating, or regeneration of shoots or roots were quantified.

IBA treatments did not affect budbreak, but tended to reduce root regeneration in birch and increase shoot regeneration in dogwood.

Antidesiccant treatments to roots had no effect.

The second research objective was to determine the response of the above six taxa to the site of antidesiccant application. In a factorial experiment, antidesiccant was applied to roots (R), stems (S), roots + stems (RS), or neither organ (control). Root treatments (R or RS) had no effect on budbreak or establishment in M.9, M.26, or beech; but delayed budbreak in dogwood, reduced final budbreak in hawthorn, and increased stem dieback in hawthorn and birch. Root treatments did not improve budbreak or establishment in any taxon.

Treating stems with antidesiccant (S or RS) was either beneficial or had no effect, except that it reduced budbreak (final and initial) in beech. Final budbreak was, however, highest in the other five taxa when stems were treated. Of all antidesiccant treatments, applications to stems only (S) resulted in the highest rates of initial (within the first four weeks of planting) budbreak in dogwood, M.26, and birch. In M.9, budbreak was highest in both the RS and S treatments. Despite treatment effects in budbreak, establishment of beech or birch seedlings was not affected by stem treatments. In the other taxa, establishment was improved with both stem treatments (S and RS), except in M.9 where root regeneration was highest in RS, lowest in the R and control treatments, and intermediate in S.

With the apple rootstocks only, a third objective was to quantify an additional establishment variable: the specific sap conductivity ( $k_s$ ) of stems after 175 days of growth. In M.26, plants receiving either stem treatment

had the highest  $k_s$ ; however, in M.9 the  $k_s$  of the RS treatment was highest, S was intermediate, and R or control, the lowest.

The final objective was to further investigate the effects of the S and RS antidesiccant treatments with attention to the relationship of antidesiccant treatment to  $k_s$  of field-harvested (mid-winter) Washington hawthorn, both at, and 14 to 20 days after, planting: Control, S, or RS treatments were applied either before, after, or without desiccation stress (13.5 h pre-planting exposure of roots and stems to 19 °C and ≈25% R.H.). In desiccated seedlings, the S treatment favored recovery from stress, resulting in rates of budbreak equal to those of non-stressed plants. In contrast, the RS treatment impaired water uptake and recovery from desiccation stress with a resulting decrease in budbreak rate similar to desiccated controls. Mortality was highest in desiccated seedlings in the RS treatment. The effects of the antidesiccant treatments were similar whether applied before or after exposure to desiccation. With antidesiccant application (S or RS), non-stressed seedlings maintained high water potential (pre-planting levels), but did not show improved budbreak compared to non-stressed controls.

Change in seedling fresh weight (from that of the pre-planting or pre-desiccation fresh weight) was closely related to xylem water potential (XWP) 14 to 20 days after planting. XWP at that time tended also to be highest in those treatments which also improved budbreak rate (except in non-stressed controls which had high rates of budbreak in spite of low water potential after planting).  $k_s$  was highest in non-desiccated hawthorn before planting; however, 14 to 20 days after planting, there were no treatment differences in  $k_s$ . Initial and final  $k_s$  was low across treatments and did not appear to influence budbreak or survival. Low values for  $k_s$ , and the resulting lack of

treatment differences, were attributed to exposure of stems to freezing conditions in the field prior to harvest.

In conclusion, little or no benefit was gained from either auxin or antidesiccant treatments to roots; in fact, either treatment may be detrimental. In M.26, birch, and dogwood the S treatment had the highest initial budbreak rate; however, final budbreak and establishment were equal with that of the RS treatment. In hawthorn, higher rates of budbreak in S treatments were associated with recovery from water stress. In M.9, establishment was improved most by the RS treatment despite similarly high rates of budbreak in either the S or RS treatments.

The Effects of Site of Desiccation Stress and Antidesiccant Application on  
the Water Relations and Transplant Establishment of Dormant Bare Root  
Deciduous Nursery Stock

by

Michael D. Remmick

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Michael D. Remmick, Author

To my grandmother **Becca** who died before the completion of this work.

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**THE EFFECTS OF DESICCATION STRESS AND ANTIDESICCANT  
APPLICATION ON THE WATER RELATIONS AND TRANSPLANT  
ESTABLISHMENT OF DORMANT BARE ROOT DECIDUOUS NURSERY  
STOCK**

**CHAPTER ONE**

**Introduction**

Compared to balled and burlapped or container-grown materials, bare root transplants represent perhaps the most difficult class of nursery stock to establish successfully (Kozlowski & Davies, 1975b and Struve, 1990). The difficulty arises largely from reduced water uptake in the roots caused by the harvesting and handling methods of bare-root production (Grossnickle, 1988 and Sands, 1984). Bare root harvesting invariably removes all of the primary (feeder) roots (Gilman, 1988; Rowan, 1983; and Watson & Himelick, 1982) which are most capable of water uptake (Baxter & West, 1977 and Johnson et al., 1988). In addition, during post harvest handling and storage, the entire transplant is exposed to air of varying humidity and temperature for periods ranging from a few days to six or more months before being replanted (Englert, 1992; Insley & Buckley, 1985; Lefevre et al., 1981; Simpson, 1984; and Webb & Von Althen, 1980). Even after replanting, bare-root plants remain particularly vulnerable to vagaries in climate or cultural practices during the establishment period (Bates & Niemiera, 1994; Becker et al., 1987; Guehl et al., 1993; Kaushal & Aussénac, 1989; Larson & Whitmore, 1970; and Odlum & Colombo, 1987). The large-diameter, well-suberized roots which remain after a typical harvesting operation are too resistant to water uptake to overcome the large water deficits which often occur in the stems of transplants (Baxter & West, 1977). Therefore, substantive regeneration of new white

roots must occur before resumption of vigorous shoot growth can take place (Kozlowski & Davies, 1975a and Struve, 1990). Root regeneration can be enhanced in certain species with applications of auxins (Struve et al., 1983), thereby improving survival percentages and establishment (Kelly & Moser, 1983; Lee & Hackett, 1976; and Prager & Lumis, 1983).

Water loss prior to seedling establishment, and its associated stress development, has been determined to be one of the most serious impediments to successful transplanting (Guehl et al., 1993; Kaushal & Aussénac, 1989; Kozlowski & Davies, 1975a and b). The mechanism of water stress-induced damage to transplants is, however, not known (Guehl et al., 1993). Water stress is manifested as low water potential (tension) in the xylem (Scholander et al., 1965). High levels of tension develop in the xylem of branches or entire plants exposed to desiccation or drought stress (Chen et al., 1991; Englert et al., 1993; Murakami et al., 1990; and Scholander et al., 1965). Sap tension at high levels has been demonstrated to cause cavitation events which rapidly lead to embolisms in the xylem (Borghetti et al., 1989; Sperry & Tyree, 1988 and 1990; Tyree & Dixon, 1986; and Tyree et al., 1992). The efficiency of xylem water transport is reduced as the percentage of embolized elements increases (Tyree & Ewers, 1991; Tyree & Sperry, 1989; and Tyree et al., 1992). Such embolism-induced reductions in water transport have been shown to lead to reduced vigor and stem dieback in deciduous trees (Sperry & Pockman 1993 and Sperry et al., 1993). Inherent differences in vulnerability to drought-induced embolism has even been implicated as a factor which determines the distribution of woody species (Tyree & Sperry, 1988). Recent work has further demonstrated that transplanting-induced water

stress induces cavitation events which are linked to reduced vigor or seedling mortality (Kavanagh, 1994).

Emboli are considered to be irreversible during critical drought or desiccation stress periods (Tyree & Sperry, 1988). This is because their repair (accomplished by refilling of air-blocked elements, or by the growth of new wood) necessitates the return to a non-water-stressed condition (Cochard & Tyree, 1990 and Tyree & Yang, 1992). Avoidance of desiccation-induced embolism may therefore be one of the primary factors determining the success of transplanting (Guehl et al., 1993). Perhaps tolerance to transplanting-induced desiccation stress, which varies between species (Bates & Niemiera, 1994; Briggs, 1939; Englert et al., 1993; and Murakami et al., 1990) or even between cultivars (Chen et al., 1991), depends on the level of resistance to stress-induced embolism.

Inasmuch as the most obvious impact of desiccation is manifest in stems, the impact of transplanting and desiccation exposure on the root system has received much attention (Coutts, 1981; Grossnickle, 1988; Insley & Buckley, 1985; Johnson et al., 1988; Magnussen, 1986; Mullin, 1971; Mullin & Bunting, 1979; Murakami et al., 1990; Rowan, 1983; Sands, 1984; and Slocum & Maki, 1956). This is because transplanting disrupts the hydraulic contact between the soil water and that of the transplant (Grossnickle, 1988; Rowan, 1983; and Sands, 1984). Roots of dormant deciduous trees are known to lose water at faster rates than stems (Murakami et al., 1990) and roots are more susceptible to desiccation damage than stems (Insley & Buckley, 1985 and Sperry & Saliendra, 1994).

Reduction of water loss during post-harvest handling or after transplanting has been shown to improve survival and regrowth of

transplanted trees (Bates & Niemiera, 1994; Becker et al., 1987; Englert et al., 1993; Kozlowski & Davies, 1975b; Larson & Whitmore, 1970; Lefevre et al., 1991; Ranney et al., 1989; Sands, 1984; Simpson, 1984; Slocum & Maki, 1956; and Williams et al., 1990). Applications of film-forming antidesiccants to either stems only (Englert et al., 1993 and Tukey & Brase, 1931), roots only (Slocum & Maki, 1956) or both roots and stems (Englert et al., 1993 and Tukey & Brase, 1931) improve establishment of bare-root transplants, chiefly by reducing water loss. Little is known about the relative effectiveness of targeting only roots or stems. Some evidence suggests; however, that applications of certain materials such as clay slurries or molten paraffin to roots may be detrimental in certain species (Mullin and Bunting, 1979 and Tukey & Brase, 1931).

- The objectives of the current study were therefore to determine:
- 1: the effectiveness of preplanting root treatments of auxin, alone or in combination with antidesiccant, in improving budbreak and establishment of transplant-sensitive species.
  - 2: the effects of imposed desiccation stress (exposure) on the conductivity of the xylem to water, both before and after planting, and its relationship to budbreak and growth of transplants.
  - 3: the site of antidesiccant application (roots, stems, both roots and stems, or neither organ) which best ensures budbreak and regrowth in a range of dormant deciduous nursery stock.

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## CHAPTER TWO

### Literature Review

#### **Water stress and poor transplant establishment**

##### *Stress development before planting (after harvest)*

In temperate-zone nursery practice, the mass-production of dormant, defoliated, bare-root transplants involves the sowing of seeds, the rooting of cuttings, or layerage (also called stooling or marcottage). These propagation practices may be performed in the greenhouse, cold frame, or directly in the field (Hartmann & Kester, 1983). After growing plants in the field for at least one season, bare root harvesting is commenced in the dormant season. The harvesting operation may begin as early as mid-autumn and continue until early in the spring. After harvesting, transplants are graded, washed, and often stored for some period of time before shipping and/or replanting. Storage regimes for transplants vary between 'heeling-in' outdoors in sawdust to placement in cold storage (Englert, 1992). Cold storage is typically maintained at temperatures between -2 to +5° C and relative humidity ranging between 90 and 99% (Englert et al., 1993a). High relative humidity can be maintained by some combination of fogging, misting, or the periodic application of water to the bundled seedlings and to the floor of the facility. Small-sized material may receive additional packaging before entering cold storage such as wrapping in kraft paper or polyethylene with the addition of a packing material such as moistened wood shavings or moss (Lefevre et al., 1991; and Webb & Von Althen, 1980).

After a period of a few days to several months in storage, the transplants are shipped. Shipping may vary in duration from one to several

days and provide the potential for significant exposure to desiccation stress (Englert, 1992 and Insley & Buckley, 1985). Upon arrival at their final destination, transplants would be ideally transplanted immediately. Often, however, planting is delayed and further cold storage or heeling-in may occur before final outplanting. In some cases stock may be left exposed for several hours or even days before it is properly re-stored or planted (Insley & Buckley, 1985 and Slocum & Maki, 1956).

Desiccation stress, arising during pre-planting exposure of bare root transplants, and its consequent reduction in survival, has been documented for practically each step in the production process described above: at harvest (Briggs, 1939 and Mullin, 1971); during storage (Englert et al., 1993a, Lefevre et al., 1991; and Webb & Von Althen, 1980); or immediately prior to planting (Briggs, 1939; Coutts, 1981; Englert et al., 1993b; Insley & Buckley, 1985; Murakami et al., 1990 Slocum & Maki, 1956). Water loss during exposure is recognized as a serious problem for transplant regrowth and survival.

During exposure, water is lost faster from exposed roots than from exposed shoots (Murakami et al., 1990). Lateral or small diameter roots lose water faster than taproots which have a lower surface to volume ratio (Insley & Buckley, 1985). Development of water stress, evidenced by low xylem water potentials, is rapid during desiccation exposure. Water potential has been shown to decrease at rates of up to *ca.* 2 MPa (megapascals) · h<sup>-1</sup> (Coutts, 1981). As a consequence, the effects of even a short exposure can have detrimental effects on subsequent establishment and regrowth. For example, reductions in growth or survival were seen after only 30 and 60 min exposure in *Pinus taeda* and *Pseudotsuga menziesii*, respectively (Slocum & Maki, 1956 and Aussencac et al., 1988) or within 12 h in *Betula*,

*Crataegus*, or *Fraxinus* (Englert et al., 1993b and Insley & Buckley, 1985). *Acer platanoides*, *Malus domestica*, or *Quercus rubra* are more resistant to desiccation stress during the dormant period, requiring 48 h of desiccation for injury or death to occur (Chen et al., 1991 and Englert et al., 1993b).

The influence of a suite of physiological criteria have been evaluated and/or implicated in the negative response of transplants to desiccation-induced stress prior to transplanting: Reduced carbohydrate or protein reserves, lack of dormancy/quiescence, reduced water content and/or water potential, reduced hydraulic conductivity, and death or damage of roots have been associated with decreases in growth or survival following desiccation exposure. Levels of carbohydrate reserves at transplanting show a good relationship to regrowth and survival in conifers (Guehl et al., 1993) but not in deciduous tree species (Struve, 1990). Tolerance to desiccation or transplanting in general has almost always been shown to be highest in midwinter when plants are fully dormant (Englert, 1993b, Mc Creary & Tecklin, 1994; Mullin, 1971, and Murakami et al., 1990, Omi et al., 1991). This is of obvious importance; however, transplanting failure occurs in certain sensitive species despite a dormant condition (Englert, 1992). Water content and water potential always decrease during desiccation stress. Many workers have identified threshold minima for preplanting water potential (typically between -2.0 to -2.5 MPa) below which mortality occurs (Aussenac, 1988 and Bates & Niemiera, 1994). The threshold values for water potential or water content vary with the time of year (dormancy) and the species, and direct correlation of regrowth to preplanting water potential has most often been poor (Lefevre et al., 1991).

Desiccation exposure before planting reduces water uptake capacity of the roots, limiting seedling establishment (Insley & Buckley, 1985 and

Johnson et al., 1988). This will be further reviewed in the next section. Decreases in hydraulic conductivity during desiccation stress of whole plants have been demonstrated following desiccation exposure, but consequences on regrowth were not studied (Tyree et al., 1992). The effects of changes in hydraulic conductivity have recently been studied, but only after transplantation (Kavanagh, 1994). The possible influence of stress-induced changes in hydraulic conductivity on seedling establishment will be reviewed in the next sections.

#### *Stress development after planting*

The inability of roots to take up sufficient water to relieve internal water deficits/stresses has been cited as the major reason for the reduced water potentials and growth rates of transplants relative to untransplanted individuals. This reduction in water uptake and its influence on transplant water stress has been attributed to several factors, including: decrease in root to shoot ratio (Kozlowski & Davies, 1975a), poor root/soil contact (Grossnickle, 1988 and Sands, 1984), low soil temperature or osmotic potential (Grossnickle, 1988 and Larson & Whitmore, 1970), lack of root system ramification (coarseness) (Struve, 1990), and drought/desiccation induced damage to the water transport system (Kavanagh, 1994).

In a typical transplanting operation, the root to shoot ratio is reduced drastically. Watson & Himelick (1982) found that up to 98 % of the root system was left in the ground when specimen-sized ( $\geq 1.5$  m) trees of seven species were harvested with a tree spade. Gilman (1988) found that a similar quantity of roots (91 to 95 %) were left in the ground following digging of three-year old transplants of three other species. Insley & Buckley (1985) showed that in addition to roots lost at harvest, all fine-diameter

lateral roots, the kind best suited to water uptake, are also the most likely to suffer damage from post-harvest desiccation. Rowan (1983) found that loss of 50% or more of these fine lateral roots resulted in 30 to 95 % mortality of seedlings of *Pinus taeda*.

Another problem which arises at the level of the root is the poor root to soil contact of transplanted versus non-transplanted trees (Burdett, 1990). Formation of air pockets over a significant portion of the root surface is a common occurrence when transplanting bare-root trees (Grossnickle, 1988 and Sands, 1984). Transfer of soil water to roots through these pockets is relegated to only the vapor phase which is obviously much less efficient than water transfer via direct hydraulic contact (Sands, 1984). It has been concluded, then, that the only means by which transplants can effectively restore water uptake is to re-establish intimate contact with the soil, by new root regeneration (Burdett, 1990 and Grossnickle, 1988).

Most bare root material is planted in the early spring, when soil temperatures are low relative to air temperatures (Struve, 1990). Root permeability is reduced with decreasing temperature, probably through a combination of membrane phase transition, decreased metabolic activity and/or turgor of root cells as well as the associated increase in the viscosity of water itself (Grossnickle, 1988 and Kramer, 1940). A combination of low soil temperatures and poor hydraulic contact with the soil was attributed to water stress in transplanted seedlings of *Pinus* and *Picea* (Grossnickle, 1988) or low soil temperature and osmotic potential (Larson & Whitmore, 1970). In addition, new root regeneration decreases with decreasing soil temperature (Struve, 1990).

Ease of transplanting increases with decreasing diameter of roots or increasing ramification (Struve, 1990), provided that these roots are not

killed by preplanting desiccation (Insley & Buckley, 1985). The coarseness of root systems is a relative concept, qualified by comparing numbers of first- and second-order lateral branches present. Survival and root regeneration capacity in coarse-rooted genera such as oaks (*Quercus*) may be improved by cultural practices such as root-wrenching (pruning) that encourage development of lateral roots (Struve, 1990). Increased survival of well-ramified seedlings is attributed to better hydraulic contact with the soil imparted by their higher surface to volume ratio (Kozlowski & Davies, 1975a). New root regeneration also increases with increasing numbers of lateral roots because each individual branch serves as a site for regeneration or elongation to occur (Aussenac et al., 1988; Kozlowski & Davies, 1975a; and Struve, 1990).

Return to pre-transplant shoot:root ratios concomitant with new root regeneration is a necessary prerequisite for the survival of transplanted trees (Struve, 1990). In addition to replacing lost or damaged roots, new root growth also vastly improves hydraulic contact with the soil which is lost due to air-pocket formation at transplanting and by lack of ramification. Furthermore, it is known that mass flow of water from moister to dryer parts of the soil profile is too slow to keep up with the transpirational demands of plants (Struve, 1990). Therefore, actively growing roots are necessary to access moister regions of the soil (Grossnickle, 1988).

The overall uptake of water into the transplant increases with new root regeneration. Baxter and West (1977) found that actively growing roots of apple trees had a rate of conductance (termed relative conductivity in original citation) three times higher than that of dormant roots. Johnson et al. (1988) similarly found that hydraulic conductivity of roots of *Pinus strobus* increased 2.25 times with 25% new root regeneration, compared

with dormant roots. The differences found between new (actively growing) and old roots (dormant) in either study were attributed to differences in suberization. New root regeneration is necessary in order to restore the original root volume and increase the absorptive portion of the root system (Kozlowski & Davies, 1975a and Struve, 1990) and improve hydraulic contact with the soil of the outplanting site (Sands, 1984). This is especially true where permeability of roots present at transplanting has been further lowered by desiccation stress (Insley and Buckley, 1985) or by low soil temperature (Grossnickle, 1988).

The mechanism by which water stress causes decreased growth and survival of transplant-sensitive species is not known (Guehl et al., 1993). Loss of carbohydrate reserves has been demonstrated following drought or desiccation stress, but in the case of deciduous plants, it is not clear if it is of primary importance (Watson, 1985 and Struve, 1990). Chen et al. (1991) suggested that differences in the desiccation tolerance of various apple clones may reside in either the wood or bark tissue. This difference, if it resides in the wood, may be the differences in vulnerability to water-stress induced damage to water transport in various taxa (Guehl et al., 1993). Differences in susceptibility to such damage have been demonstrated between species (Tyree & Ewers, 1991). Decreases in stem water transport capacity have been related to leaf or stem dieback and mortality in *Betula occidentalis* (Sperry & Pockman, 1993 and Sperry et al., 1993). Kavanagh (1994) reported that damage to xylem occurs following transplanting because of reduced water uptake by the disturbed roots of seedlings of *Tsuga heterophylla*. The effect of desiccation stress in dormant bare-root seedlings of deciduous species prior to planting awaits further study.

## Water stress and water transport

### *Water transport and cavitation in woody plants*

It is widely accepted that water transport in the xylem of plants is almost always accomplished under tension. Dixon (1914) first proposed that the cohesive properties of water allow the propagation of negative pressure (physically equivalent to a tension or a pulling force) generated in the leaves to the soil water via the xylem sap. These tensions are created by the retreat of water into the minute-sized pores within the matrix of cellulose fibers at the surface of cells in the leaves during evapotranspiration. The capillary forces there maintain a negative matric potential, which is balanced by tension in the water within xylem elements. It is this tension which forms a water potential gradient that is propagated down the stem to the roots. In the roots, it is the pressure gradient present in the xylem that allows the uptake of soil water.

Of course, the successful movement of water in the xylem depends on the continuity of the water column. This is to say that if any breaks in its continuity between the roots and leaves occurred, then the propagation of tension (hence the flow) would necessarily be arrested (Tyree & Sperry, 1988). It is known that the measure of the cohesive strength of a liquid in the laboratory is limited by our inability to remove all, including even the minutest ( $\mu$ ) bubbles from the measurement device. This is because bubbles in liquid expand or contract in a manner proportional to the pressure of the liquid. Of course, the expansion of the bubble breaks any cohesion in the liquid, lowering the estimate of the liquid's strength. Water has high cohesiveness because of hydrogen bonding. Pure water has been documented to remain liquid at tensions exceeding 25 MPa before cavitation

(Briggs, 1950). Theoretic calculations of the tensile strength of water are actually much higher than measured values, but bubbles always limit experimental measurement of it.

In contrast to glass capillaries, xylem elements are differentiated in the water-filled state and without hydrophobic cracks that would contain nucleating bubbles (Tyree & Sperry, 1989). In plants, water transport is normally within the range of - 1 to - 2 MPa; although much lower hydrostatic pressures occur commonly in desert plants and mangroves (Tyree & Sperry, 1988). Evolution of higher tensions than these is normally prevented by stomatal regulation (Sperry et al., 1993 and Tyree & Sperry, 1988). However, when stomatal control is no longer sufficient at checking stress development (such as during drought or desiccation exposure), then breaks in the xylem continuity called cavitation events can occur (Tyree & Sperry, 1989; Zimmermann, 1983). A similar situation occurs in leafless stems which have no stomates to control water loss. Cavitations in plants always occur at much higher pressures than those which Briggs (1950) had found for pure water. This observation suggests that the minimum pressure sustainable by xylem is, like the glass capillary, limited by the enlargement of bubbles (air seeding). These bubbles come from the pores in the xylem, and the logarithm of the cavitation pressure for any individual element is believed to be directly proportional to the pore size of the element (Zimmermann, 1983). In fact, the 'air-seeding' hypothesis has received much experimental support (Crombie et al., 1985; Sperry & Tyree, 1988 and 1990; and Tyree & Dixon, 1986) as well as some criticism (Zimmermann et al., 1993).

### *Embolism*

Unless a cavitated element is quickly refilled, the eventual result of a cavitation event is embolism. An embolized xylem element is defined as having become filled with air which diffused-in from the surrounding tissue (Sperry & Tyree, 1988 and Tyree and Dixon, 1986). Cavitated xylem elements are estimated to become fully embolized (at equilibrium with surrounding tissues) within 15 m (Tyree & Sperry, 1989). Repair of emboli is possible (discussion of this point will be reserved for the end of this section); however, during a critical drought or desiccation stress event, emboli are essentially irreversible (Tyree & Sperry, 1988). With embolism, the hydraulic efficiency or permeability of the stem is reduced, *i.e.* there is greater resistance to water flux. To maintain a given level of water flux (to supply evaporational or transpirational demand) in an embolized stem, even greater tensions are necessary. With each successive xylem element that is lost, the tension on the remainder of the elements must be increased to maintain the same level of sap flux, thus resulting in even more cavitations (Tyree & Ewers, 1991). This is how an 'embolism cycle' begins (Tyree & Sperry, 1988). When embolism cycles continue until all conductivity has been lost, 'runaway cavitation' is said to have occurred (Tyree & Sperry, 1988). If this situation is extrapolated to seedling establishment, where a certain level of cavitation at planting is expected and where water loss is expected to continue after planting (due to reduced water uptake discussed in the previous section) then runaway cavitation can result.

Embolism can be induced by desiccating (or droughting) excised twigs (Sperry & Tyree, 1988 and 1990; and Tyree & Dixon, 1986) or entire seedlings (Borghetti et al., 1989; Lo Gullo & Salleo, 1991; and Tyree et al., 1992). But it may also be induced during the winter by cycles of freezing

and thawing. Exposure to alternate freeze-thaw conditions during the winter have been shown to result in 84 to 95 % embolism in the stems or twigs of *Acer*, *Betula*, *Populus*, and *Quercus* (Cochard & Tyree, 1990; Sperry et al., 1988b and Sperry & Sullivan, 1992). The mechanisms by which stems and twigs become embolized during the winter are believed to be though precipitation of dissolved air during freezing of xylem sap or by direct loss of water from sublimation or evaporation (Sperry et al., 1988b and Sperry & Sullivan, 1992). Although xylem elements do not contain bubbles, the sap does have appreciable quantities of dissolved gases (Zimmermann, 1983). Ice is a poor solvent for gases compared to water, therefore bubble formation occurs in xylem lumina with the phase transition. When xylem tension is generated in the plant after thawing, larger bubbles expand and form embolisms (Sperry & Sullivan, 1992).

The second means of embolism formation in the winter involves the direct loss of water from xylem cells, either by sublimation or evaporation, without immediate replenishment (due to frozen soil). This type of damage is usually isolated to the south and west sides of the trunk where local heating may occur on cold but sunny days (Sperry et al., 1988b and Tyree & Sperry, 1989). This has relevance to transplants in that the plants may be exposed many times to sufficient cold to induce embolisms in the field before harvest. In addition, evaporative loss in bare-root plants continues after harvesting without replenishment of water from the roots (Englert et al., 1993 and Lefevre et al., 1991). Together, these mechanisms likely contribute to embolism at the time of their eventual outplanting.

### *Effects of embolism*

The principal biological consequence of embolism is the measurable negative impact it has on the efficiency of water transport in the xylem (Sperry et al., 1988a; Lo Gullo & Salleo, 1991 and Tyree et al., 1992). Borghetti et al. (1989) showed that water transport in droughted seedlings of *Picea* showed greatly reduced rates of stomatal and stem conductance following rewetting than did non-stressed controls. This indicates that drought-induced cavitation events sustained during the stress period had reduced water conducting efficiency in the stems. It has been shown in maple (*Acer saccharum*) or Eastern white cedar (*Thuja occidentalis*) that woody plants can tolerate a small level of embolism (5 to 15 %, respectively) and still affect normal growth and water transport (Tyree & Sperry, 1989). The tolerance of some level of embolism in plants is imparted by the redundancy of the hydraulic architecture of stems (Tyree & Ewers, 1991). However, when embolism increases beyond the tolerable maximum of a given species, however, the embolism cycle begins (Tyree & Sperry, 1988, 1989).

The effects of xylem failure are becoming increasingly recognized as one the major limiting factors to plant distribution and adaptation to habitats (Tyree & Ewers, 1991 and Tyree & Sperry, 1989). Species differ in their vulnerability to cavitation. Vulnerability to cavitation can be quantified by determining the range of xylem tensions over which complete loss of conductivity occurs (Cochard et al., 1992; Sperry & Saliendra, 1994; Tyree & Ewers, 1991; and Tyree & Sperry, 1989). For those species for which these 'vulnerability curves' have been constructed, it has in fact been demonstrated that their relative resistance to cavitation corresponds to the

lowest level of soil water potential normally experienced in their native habitat (Tyree & Ewers, 1991).

In an individual plant, xylem failure has been shown to limit growth and productivity and even result in dieback or death. The effect of experimentally reducing hydraulic conductance of stems of intact plants, either by notching stems (Sperry et al., 1993) or by direct air-seeding (via air-injection) (Sperry & Pockman, 1993) have recently been studied in *Betula*. In either case, if stomatal regulation was unable to control transpirational water loss to meet the reduced sap flux, an embolism cycle was begun which terminated with nearly complete embolism, resulting in the death of tissues distal to the notched or injected stems. Conversely, where stomata responded sufficiently to reduce evaporative flux (and hence stem xylem tensions in the notched or injected zones) no dieback occurred.

It has been suggested that xylem cavitation and embolism formation may limit establishment of transplanted seedlings (Guehl et al., 1993). Kavanagh (1994) showed that cavitation occurred in seedlings of *Tsuga* as a response to low water uptake in the roots following planting in adequately watered soils. Dieback, leaf loss, and mortality in seedlings were attributed to water stress-induced cavitation and their resulting decrease in stem water conductance.

#### *Repair of damaged xylem*

Repair of desiccation-induced damage to the xylem is possible. The two major mechanisms are by refilling or by new wood growth. The first mechanism, refilling, has been documented in certain temperate zone genera which exhibit root and/or stem pressure, such as *Vitis* or *Acer* in the spring (Sperry et al., 1987; Sperry et al., 1988b; and Tyree & Sperry, 1989). It has

been proposed (Tyree & Sperry, 1989) that such reversal in the spring may be a more general phenomenon, and personal observation of bleeding sap in *Betula*, *Malus*, or *Juglans* would support this. Embolized vessels of *Vitis* were shown to recover maximum conductivity as a consequence of dissolution and expulsion of bubbles by root pressure immediately prior to leaf expansion in May (Sperry et al., 1987). Yang & Tyree (1992) developed a model which predicted that time required for recovery of hydraulic conductivity of completely embolized stems of *Acer* depends on stem anatomical characteristics and water relations: The recovery time was estimated to increase with: 1: increasing fraction of the stem cross section occupied by vessels, 2: increasing conduit diameter, 3: increasing stem diameter, and 4: decreasing xylem water potential. Sobrado et al. (1992) further concluded that for a given xylem water potential, the rate of recovery increased with decreasing initial levels of embolism. The results of Yang & Tyree's model were in agreement with actual measurements, and further showed that eventual recovery (by means of bubble dissolution) in stems of *Acer* was possible even at slightly negative pressures ( $\geq -0.06$  MPa). Additionally, rate of bubble dissolution was found to be essentially independent of temperature (Tyree & Yang, 1992).

Recovery of embolism at lower water potentials (-0.101 MPa) in *Vitis* have been reported (Salleo & Lo Gullo, 1989). However the minimum pressure required for collapse of bubbles, consisting entirely of water vapor, is estimated to be -0.098 MPa. In contrast, embolisms contain mostly air with a low proportion of water vapor (compared to newly-cavitated elements), therefore recovery at such low pressures is considered unlikely (Tyree & Yang, 1992).

The high pressures required for embolism repair by refilling led Tyree & Sperry (1988) to conclude that emboli sustained during critical drought stress are essentially irreversible. Extrapolating this to transplants which may endure water stress (< -1.5 MPa) for periods of 150 to 190 d following transplanting (Kaushal & Aussenac, 1989 and Sands, 1984) it is unlikely that embolisms incurred during transplanting stress dissolve in any short time after transplanting. Therefore, if seedling water relations are not improved, such embolism may lead to death of the transplant (Kavanagh, 1994).

The growth of new conductive tissue (wood), is a response generally associated with certain ring porous genera such as *Quercus* which lose nearly 100 % of their most efficient earlywood vessels to embolism during summer drought or freeze-induced embolism in winter (Cochard & Tyree, 1990). In these species, recovery of hydraulic conductance sufficient to support the new leaves occurs by regeneration of earlywood vessels. These wide-diameter conduits are more efficient than the narrow-diameter latewood vessels which normally survive without embolism over the winter (Zimmermann, 1983). Sperry et al. (1993) induced an *in situ* reduction in hydraulic conductance in *Betula* to monitor the effects of said reduction on stomatal control of transpiration. They found that if trees were notched in June while the cambium was still active, recovery of normal rates of stomatal and hydraulic conductance were attained by new wood growth. Similarly, Kavanagh (1994) found that significant levels of cavitation occurred in seedlings of *Tsuga* following transplanting. However, despite reduction in hydraulic conductance, and a corresponding quantity of foliage, some 80 % of the seedlings resumed growth within two months.

Considering the near-total loss of hydraulic conductivity before and after planting, the severe reductions in the ability of transplanted roots to

take up water at planting, as well as several months of low xylem water potential (which would preclude refilling mechanisms documented in untransplanted trees) endured by transplants: It is proposed that those individuals which recover from transplanting do so by means of new wood regeneration before, or concomitant with, budbreak and shoot elongation.

### **Methods of improving transplant establishment**

#### *Applications of auxin*

Because new root regeneration is a chief means to overcome transplant shock, effort has been devoted to the use of plant growth regulators (particularly auxins and their synergists) to enhance root regeneration and improve transplant establishment. The most commonly used auxin is indole-3-butyric acid (IBA) applied in an organic solvent for fast (5-15 sec.) dips or its potassium salt in aqueous solution for longer (5 - 60 min.) soaks. Toothpicks impregnated with auxin solutions have also been inserted into roots of large-caliper transplants (Struve et al., 1983). For most species, the optimal auxin concentrations range from 1000 to 3000 ppm. In *Quercus* and other species, however, lower concentrations (between 100 and 500 ppm) show better results (Moser, 1978 and Struve et al., 1983)

The means by which auxins promote root regrowth are not known (Struve, 1990). The principle benefit of auxin applications is to encourage initiation of greater numbers of new roots. It is an effective treatment in many genera, including *Quercus*, *Acer*, *Pistacia*, *Juglans*, *Cercis*, and *Nyssa* (Lee & Hackett, 1976; Moser, 1978; and Prager & Lumis, 1983). Auxin application is, however, not always beneficial: Struve & Joly (1992) found no effect of IBA applications on seedlings of *Quercus rubra*. Similarly, auxin

alone had no effect on seedlings of *Betula*, *Tilia*, or *Fraxinus*, however the effectiveness of IBA was enhanced by combining it with synergists  $\beta$ -naphthol or nicotinic acid in *Prunus americana* (Prager & Lumis, 1983). In general, the induction of greater quantities of roots with auxin treatment comes at the cost of reduced root elongation or increased time to regeneration (Kelly & Moser, 1983; Struve & Moser, 1984; and Struve & Rhodus, 1988). In most of the above cases, though, the long term effects on shoot growth outweighed short term reductions in root growth.

#### *Applications of antidesiccant*

Film-forming compounds have been shown to be effective at reducing transpiration of deciduous trees in leaf (Davies & Kozlowski, 1974; Gale & Hagan, 1966; Hummell, 1990; Kozlowski & Davies, 1975a and b; and Ranney et al., 1989) and in conifers (Odlum & Colombo, 1987; Simpson, 1984; and Williams et al., 1990). Coatings of various materials applied to roots of bare root seedlings have also been studied, including: mud slurries (Slocum & Maki, 1956), hydrogels (Magnussen, 1985), or water soaks before planting (Mullin, 1971). Such treatments have either improved establishment slightly, had no benefit or were even detrimental (Mullin & Bunting, 1979). Relatively few papers have addressed the potential use of film-forming antidesiccants as a post-harvest or pre-planting treatment for bare root deciduous plants (Englert, 1992).

Water loss from bare-root seedlings of *Quercus rubra*, *Acer platanoides*, and *Crataegus phaeopyrum* was reduced up to 80 % over untreated controls, when treated with antidesiccant (Englert, 1992 and Englert et al., 1993b). For *Crataegus* (considered most transplant-sensitive species of the three), the water loss reduction by antidesiccant applications

significantly improved survival and establishment. In a field experiment with *Crataegus phaeopyrum*, Englert (1993b) found that antidesiccant applications to stems only prior to field transplanting produced the same results as applications to both roots and stems prior to transplanting in the greenhouse. Similarly, Tukey & Brase (1931) reported that application of paraffin to stems only was found to be beneficial to survival of sweet cherries and roses compared to treating the entire transplant. For some rose varieties, however, treatment of entire plants was equally beneficial.

Although most manufacturers of polymer film coatings imply or specify that bare-root seedlings be treated with applications of antidesiccant to both stems and roots, there appears to be little evidence in the literature that this is necessary. Furthermore, because antidesiccant compounds are formulated to provide a barrier to water movement (Gale & Hagen, 1966), treatment of roots may provide a further decrease in their permeability to water following transplanting. For reasons outlined in the above sections, treatments which decrease the permeability of roots of transplanted trees may best be avoided. However, because it is known that significant water loss occurs through stems after transplanting (Bates & Niemiera, 1994 and Schönherr & Ziegler, 1980) applications of antidesiccant only to stems only may provide the best protection to newly transplanted seedlings without leaves.

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## CHAPTER THREE

### Effect of preplanting antidesiccant or auxin treatments on budbreak and regrowth of dormant deciduous transplants

#### **Abstract**

The effects of root applications of 500 ppm indole-3 butyric acid (IBA) or 50 % Moisturin-4 antidesiccant (Burke's Protective Coatings, INC., Washougal, WA, USA) on budbreak and establishment of seedlings of the transplanting-sensitive species flowering dogwood (*Cornus florida* L.) and river birch (*Betula nigra* L.) were evaluated. Applications of antidesiccant to roots at any level of IBA treatment were found to be of no benefit for budbreak or establishment of either species. IBA applications to roots of flowering dogwood seedlings tended to increase new shoot regeneration; however, budbreak or visual rating (0 to 5, dead to excellent regrowth) were not affected. In contrast, IBA applications to river birch reduced root regeneration, but had no effect on budbreak or shoot growth.

Establishment and budbreak response to applications of 50 % Moisturin-4 antidesiccant to stems and roots were evaluated for the above two species as well as for European beech (*Fagus sylvatica* L.), Washington hawthorn (*Crataegus phaeopyrum* Medic.) and layers of apple (*Malus domestica* L.) rootstock clones M.9 and M.26 EMLA which had been desiccated for 38 hr.

Applications of antidesiccant to roots reduced final budbreak percentage in Washington hawthorn and delayed budbreak in flowering dogwood. Similarly, stem dieback in Washington hawthorn and river birch were higher in response to root treatment with antidesiccant. There was no

response to level of root treatment seen in apple rootstocks or European beech.

Applications of antidesiccant to stems of European beech seedlings induced a slight reduction in budbreak; however, in all other taxa, treatment of stems, at both levels of root treatment resulted in higher percentages of final budbreak. Moreover, applications of antidesiccant to stems only was found to increase initial rates of budbreak more than the other three treatments in all taxa except European beech or M.9.

Despite differences in budbreak response, establishment of European beech or river birch was not effected by stem or root antidesiccant treatment. In all other taxa, however, stem treatment reduced dieback and increased new shoot growth. In addition, stem treatments increased visual rating in flowering dogwood and new root regeneration and  $k_s$  of M.26 EMLA. In contrast, M.9 showed the greatest increase in new root regeneration and  $k_s$  when applications of antidesiccant were made to both roots and stems.

It is concluded that antidesiccant applications to stems, either alone or in combination with treatment of roots, may improve budbreak and establishment of bare root nursery stock. Application to stems only may advance budbreak in certain taxa, but treatment of both roots and stems may be required for best establishment in others

## Introduction

The duration of reduced growth and elevated levels of internal water stress in transplants is determined by the rate at which new roots are regenerated (Guehl et al. 1993; Kaushal & Aussenaac, 1989; Kozlowski & Davies, 1975b; Struve, 1990). This is because it is typically only the

coarsest part of the root system that remains after harvesting (Gilman, 1988; Kozlowski & Davies, 1975a; Struve et al., 1983). New white roots have a much higher rate of water uptake than coarse roots (Baxter & West, 1977; Grossnickle, 1988; and Watson & Himelick, 1982). In addition to reduced water uptake ability, coarse root systems have a reduced capacity to regenerate new roots, relative to fine root systems (Struve, 1990).

The capacity for new root formation is influenced by genotype (Kozlowski & Davies, 1975a; Struve, 1990) internal water relations of the transplant (Aussenac et al., 1988; Guehl et al., 1993), water relations of the soil (Larson & Whitmore, 1970), intimacy of hydraulic contact with the soil (Sands, 1984), lifting date and storage regime (Omi et al., 1991). Reduced root regeneration capacity, whatever its cause, has been linked with delay or failure in transplant establishment of conifers (Burdett, 1987; Ritchie & Dunlap, 1980; Sands, 1984; Stone et al., 1962) or deciduous trees (Kozlowski & Davies, 1975a and b; Struve, 1990; Watson, 1986; Watson & Himelick, 1982).

Application of auxins to roots has been studied in many dicotyledonous species and is a technique used by arboriculturists to increase the root regeneration in large caliper transplants of various difficult-to-transplant species (Hartwig & Larson, 1980; Lee & Hackett, 1976; Lumis, 1982; Prager & Lumis, 1983; Struve, 1990). Because IBA applications can increase the eventual quantity of new roots produced (Lee & Hackett, 1976, Prager & Lumis, 1983 and Struve, 1990) water uptake is improved, resulting in reduced transplant shock and improved establishment.

Species differ in drought resistance and tolerance to transplanting (Bates & Niemiera, 1994; Briggs, 1939; Insley & Buckley, 1985; and Ranney et al., 1991). Chen et al. (1991) demonstrated that desiccation resistance of

grafted apple trees (*Malus domestica*) varied with the rootstock clone. Antidesiccants have been shown to reduce water loss and improve establishment and survival percentages of bare root deciduous trees (Tukey & Brase, 1931 and Englert et al., 1993). Roots of dormant deciduous plants lose water at higher rates than exposed stem tissue (Murakami et al., 1990); therefore, the effects of targeting roots with applications of mud slurries or water soaks as well as the choice of root-packing materials for storage on the seedling's subsequent establishment have been studied: Mullin & Bunting (1979) found that coating roots of coniferous species with kaolinite slurries was rarely beneficial and sometimes detrimental. However, soaking roots of both deciduous and coniferous species reverses some negative effects of desiccation during root exposure of bare-root transplants between harvest and planting (Insley & Buckley, 1985 and Mullin, 1971). Tukey & Brase (1931) and Webb & Von Althen (1980) also concluded that protecting roots from exposure during storage with various moistened packing materials improved survival of coniferous and deciduous bare-root transplants.

Given that antidesiccants reduce water loss (and the concomitant development of water stress), their use in combination with auxin applications could further improve establishment. River birch (*Betula nigra* L.) and flowering dogwood (*Cornus florida* L.) are difficult species to transplant (Warren, 1992 personal communication). Observations by nursery producers indicate that the transplant difficulty for these two species may be related either to a low capacity to regenerate roots, susceptibility to water loss or both.

Washington hawthorn (*Crataegus phaeopyrum* Medic.) (Englert et al., 1993, Murakami et al., 1990) and European beech (*Fagus sylvatica* L.) are also difficult to transplant (Warren, 1992 personal communication).

Susceptibility to water loss has been determined to be the primary impediment to successful transplanting of hawthorn (Englert et al., 1993 and Murakami et al., 1990). Application of the antidesiccant Moisturin-4 (Burke's Protective Coatings, Washougal, WA) to roots and stems at rates of 50% or higher reduced water loss during exposure as well as increase survival of transplanted Washington hawthorn (Englert et al., 1993). Tukey & Brase (1931) compared the benefits of treating stems only or roots and stems of bare-root transplants with film barriers (paraffin) to reduce post-harvest water loss. In that study no roots only treatment was employed. Application of paraffin to stems only was found to be beneficial to survival of sweet cherries or roses compared to treating the entire transplant. For some rose varieties, however, treatment of roots and stems was equally beneficial.

Whereas the importance of maintaining favorable internal water relations of liner stock during the period between harvest and establishment is well-established (Aussenac et al., 1988; Englert et al., 1993; Guehl et al., 1993; Kaushal & Aussenac, 1989; Kozlowski & Davies, 1975a and b; Larson & Whitmore, 1970; Ranney et al., 1989; Sands, 1984; Simpson, 1984; Slocum & Maki, 1956), the mechanism by which excessive desiccation stress impedes establishment is not understood (Guehl et al., 1993). It is known that woody species differ with respect to their vulnerability to xylem cavitation under drought or desiccation stress, but the studies where this was determined did not address transplant establishment (Cochard et al., 1992; Sperry & Saliendra, 1994; and Tyree & Ewers, 1991).

Guehl et al. (1993) first advanced the idea that cavitation events leading to lethal levels of xylem embolism may be among the possible mechanisms limiting forest tree establishment. The possible link between transplanting difficulty and cavitation vulnerability has only recently been

studied (Kavanagh, 1994). In that work, seedlings of the transplant-sensitive species Western hemlock (*Tsuga heterophylla*) showed reduced growth and mortality following field planting which was attributed to cavitation events recorded in seedlings. Severe xylem cavitation was induced by decreasing xylem water potential during field establishment.

The objectives of this study involving six taxa of dormant (defoliated) deciduous, dicotyledonous nursery stock were:

- 1) to determine whether applications of auxin and/or antidesiccant to roots improves budbreak and establishment of river birch and flowering dogwood seedlings.
- 2) to determine whether antidesiccant applications to roots and/or stems improves establishment of river birch, flowering dogwood, Washington hawthorn, European beech seedlings, or desiccation-stressed M.9 or M.26 EMLA apple rootstock layers .
- 3) and to determine the effect of antidesiccant treatments applied to stems or root zones of apple rootstock layers on stem sap conductance after 175 days of establishment.

## **Materials and Methods**

### *Seedling plant material*

One hundred (each) one-year seedlings of European beech (*Fagus sylvatica*), Washington hawthorn (*Crataegus phaenopyrum*), or flowering dogwood (*Cornus florida*) or two-year branched seedlings of river birch (*Betula nigra*) were harvested bare-root between 25 January and 4 February 1993 from field seedbeds at J. Frank Schmidt, Co., Gresham, OR, USA. On 4 February all seedlings were transported to Oregon State University (OSU)

campus, wrapped in two layers of 0.95 mil polyethylene bags, and placed in 2° C cold storage. Within three days of arrival, plants were washed to remove excess soil or debris from the roots and stems and replaced in cold storage as above. Between 17 and 24 May 1993, after sorting for uniformity, lateral roots (< 3.0 mm diameter) were pruned to within 2.5 cm of the main root axes (> 5.0 mm diameter) and the plants were replaced in storage. Between 25 and 26 June, plants were removed from storage, sorted into uniform groups of three (based on stem length, caliper, and root number). Each group of three represented one replication, of which there were three (see experimental design below). Treatments were assigned to three replicates (three seedlings per replicate) by a random mechanism. Treatments (see below) and outplanting were then executed within 24 h.

#### *Apple rootstock layers*

100 (each variety) one-year layers of M.26 EMLA or M.9 apple rootstocks harvested in November 1992 were obtained from Willow Drive Nursery, Ephrata, WA. Apple rootstocks were stored in moist shingletoe and 0.95 mil polyethylene to maintain humidity and stored at 2 ° C. On 1 June 1993 the layers were removed and graded for uniformity in size. After grading for uniformity in size, roots (if present) were pruned to within ca. 2.0 cm of the stem axis, as per grower instructions. Rootstocks were then rinsed to remove excess shingletoe and the stems recut to a length of 50.0 cm. The basal and terminal cut ends of the layers were then dipped to ca. 2.0 mm depth in 45° C paraffin to limit water loss from the cut ends. As above, treatments were replicated three times, with replicates representing groups of three layers having with uniform caliper and root-stub number. Treatments (see below) were applied after five more days of cold storage.

*Antidesiccant/IBA factorial treatments*

Roots of river birch or flowering dogwood were treated with 1. IBA (500 ppm indole-3 butyric acid dissolved in 25% methanol and diluted with distilled water plus 0.5% Sur-Ten surfactant [Cyanamid Corp.]), 2. antidesiccant (Moisturin-4 [Burke's Protective Coatings, Washougal, WA], distilled water, and methanol 2:1:1 [v/v/v] plus 0.5% Sur-Ten surfactant), 3. IBA and antidesiccant, or 4. distilled water/methanol/surfactant only. Abbreviations for treatments 1 to 4 are IBA, AD, IBA + AD, control, respectively (Table A.2). Roots of plants receiving IBA and antidesiccant treatment were allowed to surface-dry after IBA treatment and before application of antidesiccant solution.

*Stem/root antidesiccant factorial treatments*

Antidesiccant was applied to 1. stems only (S), 2. roots only (R), 3. stems + roots (RS), 4. or neither organ (control) (Table A.1) with a nylon-bristle paintbrush. Antidesiccant solutions for European beech and Washington hawthorn seedlings or apple rootstock layers consisted of 1:1 (v/v) Moisturin-4 and distilled water or distilled water (100%) to organs not receiving antidesiccant application. Antidesiccant solutions for river birch and flowering dogwood seedlings consisted of 2:1:1 (v/v/v) Moisturin-4, distilled water, and methanol plus 0.5% Sur-Ten surfactant or 3:1 (v/v) distilled water/methanol plus 0.5% Sur-Ten surfactant. For antidesiccant treatments of apple rootstock layers, the 'root zone' for apple layers was the lower third of the layer where root initiation in the stool bed had occurred. The remaining 2/3 of the layer was treated as the 'stem'. Apple rootstock layers (only) were subjected to an additional 38 h of desiccation exposure in

the laboratory. Laboratory conditions during desiccation constituted 19 - 20° C and 30 - 35 % RH.

#### *Planting*

Following antidesiccant treatment, plants were allowed to air-dry (15 to 45 m) on racks elevated 5 cm from the floor. European beech, flowering dogwood, or Washington hawthorn were returned to cold storage and planted within 24 h in "gallon" containers of (13 x 15 cm capacity) containing a 1:1:1:2 (v/v/v/v) sandy loam field soil, river sand (1/4" minus), fine sphagnum peat, and #8 slow-screen white pumice mix. River birch seedlings and apple rootstocks were potted in fiber containers (Western Pulp and Manufacturing, Corvallis, OR) of 15 x 35 cm capacity.

Plants were arranged randomly (by replicate) in a greenhouse regulated for venting at 22° and 15° C day/night temperatures. Plants were watered to container capacity and maintained in a well-watered state throughout the experiment. Non-experimental "guard" plants were placed on the borders of the experiment to minimize "edge-effects".

#### *Budbreak quantification*

Budbreak scores were made on weekly to tri-weekly intervals starting 8 July (11 days after planting for river birch and flowering dogwood or 14 days after planting for European beech and Washington hawthorn) or 20 July 1993 for apple rootstocks (28 days after planting). Buds were counted as broken if they had emerged from bud scales. Budbreak counts were expressed as a percentage derived from the following formula:

$$\text{Budbreak (\%)} = (\text{broken buds} \cdot \text{total number of buds}^{-1}) \cdot 100$$

For river birch only simple counts of broken buds were measured. Budbreak scores continued until 31 August for European beech, 2 September for river birch, 12 September for flowering dogwood, 11 October for Washington hawthorn, or 14 December for apple rootstocks.

#### *Evaluation of establishment*

Treatment effects on establishment were evaluated after the final budbreak score for each species. Dry weights (>36 hr at 65°C) of regenerated roots, leaves, and stems were expressed as a percentage of the dry weight of the original portion of the seedling (measured at harvest), derived from the following formula:

$$\text{Dry weight new organ (\%)} = \frac{\text{(dry weight regenerated [new] organ} \cdot \text{dry weight original portion of plant})}{100}$$

Stem dieback was also expressed as a percentage of the dry weight of the total original stem portion, derived by the following formula:

$$\text{Stem dieback (\%)} = \frac{\text{(dry weight dead stem} \cdot \text{(dry weight dead stem + dry weight live stem)}^{-1})}{100}$$

In addition to the above, the appearance of flowering dogwood plants at harvest was visually rated on a scale of zero to five (Fig. A.1):

0 = dead

1 = stem dieback > 50%, no new shoot growth observed

2 = stem dieback > 50%, limited new shoot growth present

3 = stem dieback 10 - 50%, moderate shoot growth present

4 = stem dieback < 10%, moderate to good shoot growth

5 = no stem dieback, good shoot regrowth

The hydraulic technique of Sperry et al. (1988) was used to measure the sap-conducting capacity of apple rootstock stems: Stem sections of ca.

10.0 cm length were cut at approximately 5.0 cm above the root zone and under tapwater to avoid artifactual air-seeding of severed vessels. Cut ends were then recut under tapwater with sharp razor blades in order to remove ends of xylem elements crushed by the shears. A tapwater-filled section of Tygon tubing was then attached to the proximal end of stem segments, forming a tight seal. The tapwater was then replaced with perfusion solution (100 mM KCl, repeatedly filtered to 0.2  $\mu$ ). The stem + Tygon segment was then affixed to a length of tubing containing perfusion solution elevated one m above the segment to obtain a pressure head of 0.01 MPa. The flux ( $F$ ) of perfusion solution ( $\text{kg s}^{-1}$ ) through the stem segment was measured by affixing a cuvette containing a piece of dry tissue paper against the distal end of the stem segment and reweighing the tared cuvette + paper every 30 to 60 s to the nearest 0.001 g. From the average of four such  $F$  measurements, the specific conductivity ( $k_s$ ) (expressed in units of  $\text{kg MPa}^{-1} \text{m}^{-1} \text{s}^{-1}$ ) was determined from the following equation (Tyree & Ewers, 1991):

$$k_s = (F(dP \cdot dx^{-1})^{-1}) \cdot A_w^{-1}$$

Where  $dP$  = pressure gradient of the perfusing solution (1.0 m above the sample = 0.01 MPa),  $dx$  = the length of the stem segment in m, and  $A_w$  = transverse-sectional area of the wood in  $\text{m}^2$  (average of the de-barked transverse-sectional area for each end of the segment).

#### *Experimental design and statistical analysis*

To accomplish the first objective, four root treatments (IBA + AD, AD, IBA, or control) were applied in a two by two factorial design to river birch or flowering dogwood seedlings (Table A.1). For the second objective, four antidesiccant treatments (R, S, RS, or control) were applied to all six

taxa, also in a two by two factorial design (Table A.2). In either experiment, treatments were replicated three times, with three plants per replicate.

Both experiments were analyzed using the general linear models procedure of version 6.11 of SAS (SAS Institute, 1991). Where significant interactions in means of main-effects occurred, contrasts between treatment effects were performed to quantify differences in means. Fresh weights of individual transplants, weighed before antidesiccant application (or desiccation treatment), was recorded and analyzed as a covariate for all response parameters measured. No significant effect of the fresh weight covariate were found for any response. Budbreak percentages for each scoring date were analyzed individually and weighted for original bud number.

## Results and Discussion

### *IBA/antidesiccant root treatment (objective one)*

There were no significant differences in mean budbreak percentages or final establishment parameters in either river birch or flowering dogwood receiving any combination of root antidesiccant or IBA treatment prior to outplanting (Tables A.3 and A.4). In flowering dogwood, however, root treatments including IBA (IBA +) tended to increase new shoot regeneration compared to those which did not have IBA (IBA -) with 86.7 and 33.2 % regeneration, respectively. In contrast to flowering dogwood, river birch tended to show a negative response to the IBA + treatments, with a 54 % reduction in new root regeneration, relative to IBA - seedlings.

The lack of antidesiccant effect in either species may have been due to the lack of exposure of seedlings to stressful conditions. Positive effects of

antidesiccant applications to roots have been demonstrated in a few cases, however the benefit was seen only when seedlings had been exposed to desiccation (Magnussen, 1986 and Mullin, 1971). The lack of large effects of root applications of auxin parallel the findings of Prager & Lumis (1983), where 3000 ppm IBA sprayed on roots did not significantly increase new root regeneration in spring-dug European birch (*B. pendula*), littleleaf linden (*Tilia cordata*), or green ash (*Fraxinus pennsylvanica*). In that study, IBA combined with β-naphthol or nicotinic acid significantly increased new root regeneration in European birch and wild plum (*Prunus americana*). Perhaps the addition of such synergists and/or higher concentrations of IBA may have induced a more pronounced response in the current study. That IBA treatments tended to increase rooting in flowering dogwood, but not in river birch, may also be explained by the inherent differences in the root regeneration capacity of each species (Struve, 1990). Flowering dogwood has a coarser root system than does river birch: Roots are classified for fineness or coarseness relative to some standard by comparing the number of first- and second-order lateral roots present on the main root axes (Struve, 1990). Because plants with fibrous root systems are generally easier to transplant (Struve et al., 1983), the effect of a root-promoting treatment may not be as great on plants of a naturally fibrous-rooted species than on those of an inherently coarse-rooted species.

#### *Antidesiccant root/stem applications (objective 2)*

##### Response to root treatment

There were few instances where budbreak or final establishment were affected by root treatment without a significant interaction being present.

European beech and both apple rootstock clones fit in this category (Tables A.5, A.6, and A.7). For two variables; however, means of the root main effect were significantly different (without a significant RxS interaction), these were: budbreak percentage of flowering dogwood (three to four weeks after planting) and Washington hawthorn (final budbreak %) (Tables A.8 and A.9) and stem dieback percentage of river birch and Washington hawthorn (Tables A.9 and A.10). Significant RxS interactions will be treated separately in the next section.

Mean budbreak percentages of flowering dogwood seedlings that did not receive root antidesiccant treatment (Root -) were significantly higher than those in the root treatment groups (Root +) on the first and third sampling dates (day 11 and 23, respectively) (Table 3.1). Although budbreak of the Root + treated flowering dogwoods was significantly lower only during the first four weeks after planting, the delay is clearly a negative response. In contrast, Washington hawthorn showed no response initially, but final (day 100) budbreak percentages of Root + plants tended to be lower than those in the Root - treatment. Similarly, mean stem dieback in Washington hawthorn and river birch was significantly higher in the Root + treatment (Table 3.1).

The lack of response of European beech to root treatment with antidesiccant may be due to its coarse root system: Thick, unbranched roots have relatively limited value in water uptake (Struve, 1990), therefore beech seedlings may have relied on internal moisture reserves to initiate new roots and shoots. Beech seedlings did not show evidence of water stress, therefore the presence of a film barrier on the root surface of this coarse-rooted species (which requires new root regeneration for any significant water uptake) should not have imparted any additional benefit or detriment.

Table 3.1 Effects of root applications of antidesiccant on percent budbreak or percent dieback in flowering dogwood, Washington hawthorn, or river birch.

| Taxon       | Variable            | Sig. | Root Antidesiccant Treatment |              |
|-------------|---------------------|------|------------------------------|--------------|
|             |                     |      | +                            | -            |
| Dogwood     | Day 11 <sup>y</sup> | .05  | 6.0 % (3.0)                  | 23.3 % (1.8) |
|             | Day 23              | .05  | 10.2 % (2.9)                 | 22.8 % (7.3) |
| Hawthorn    | Day 100             | .06  | 9.1% (3.8) <sup>x</sup>      | 23.0 % (3.8) |
|             | Dieback             | .05  | 33.4 % (9.8)                 | 16.1 % (7.9) |
| River birch | Dieback             | .08  | 77.1 % (4.9)                 | 61.9 % (7.9) |

<sup>z</sup> + / - denotes stems treated or not treated with antidesiccant, respectively.

<sup>y</sup> Day indicates days after planting.

<sup>x</sup> (Standard error in parentheses)  $n = 6$ .

The same explanation may be applied to the lack of response in apple rootstock layers to root applications of antidesiccant. Here, the "root system" consisted of well-suberized root stubs pruned to *ca.* 2.0 cm before planting. Again, a coarse root system relative to the other seedling trees. In apple rootstocks, these root stubs were most likely insufficient for significant water uptake. Production of new roots would have therefore been the principal mechanism by which internal water deficits could have been relieved (Baxter & West, 1977 and Kozlowski & Davies, 1975a). New root initiation is believed to be largely reliant on reserves of growth factors such as carbohydrates and moisture present at the time of planting (Aussenac et al., 1988). Water loss during desiccation was reduced most when roots and stems were protected with antidesiccant, slightly less when only stems ( $\approx$  67% coverage of the layer) were coated and much less when root zones only ( $\approx$ 33% coverage of the layer) or neither organ were protected (data not shown). Thus the lack of response to root treatment in apple rootstocks

may be a reflection of the fact that neither the controls nor the root treatments sufficiently protected the layers against water loss during desiccation. In contrast, the stems only treatment reduced water loss enough to show a beneficial response comparable to treating the entire layer with antidesiccant.

Negative responses to Root + treatments in Washington hawthorn, river birch and flowering dogwood parallel findings of Mullin & Bunting (1979) who showed that mud slurry applications to roots were sometimes detrimental. The general detriment of treating root systems of seedlings with antidesiccant will be further discussed in the next section.

#### Budbreak Response to stem treatment

Budbreak percentages of Stem + European beech were lower (Table A.5) than in the Stem - treatment starting from the fourth week after planting (Figure 3.1). This was the only negative response to the Stem + treatments in this study.

Budbreak in Washington hawthorn ranged between 9 and 23 % by the final scoring date (day 100), but variability was high, obscuring treatment effects (Table A.9). In flowering dogwood, the mean budbreak percentages of the stem + and - treatments were different (Table A.8) during the entire course of the study except during the third and fourth weeks (Figure 3.2). In addition, a significant R x S treatment interaction was found on the fourth sampling date (day 31) in flowering dogwood (Table A.8). The interaction was induced by the high budbreak percentage of the S + treatment (Table 3.2). Finally, the budbreak response to stem antidesiccant treatment in M.9

Figure 3.1 Percent budbreak of European beech (*Fagus sylvatica*) following treatment of stems with water (■) or antidesiccant (□).

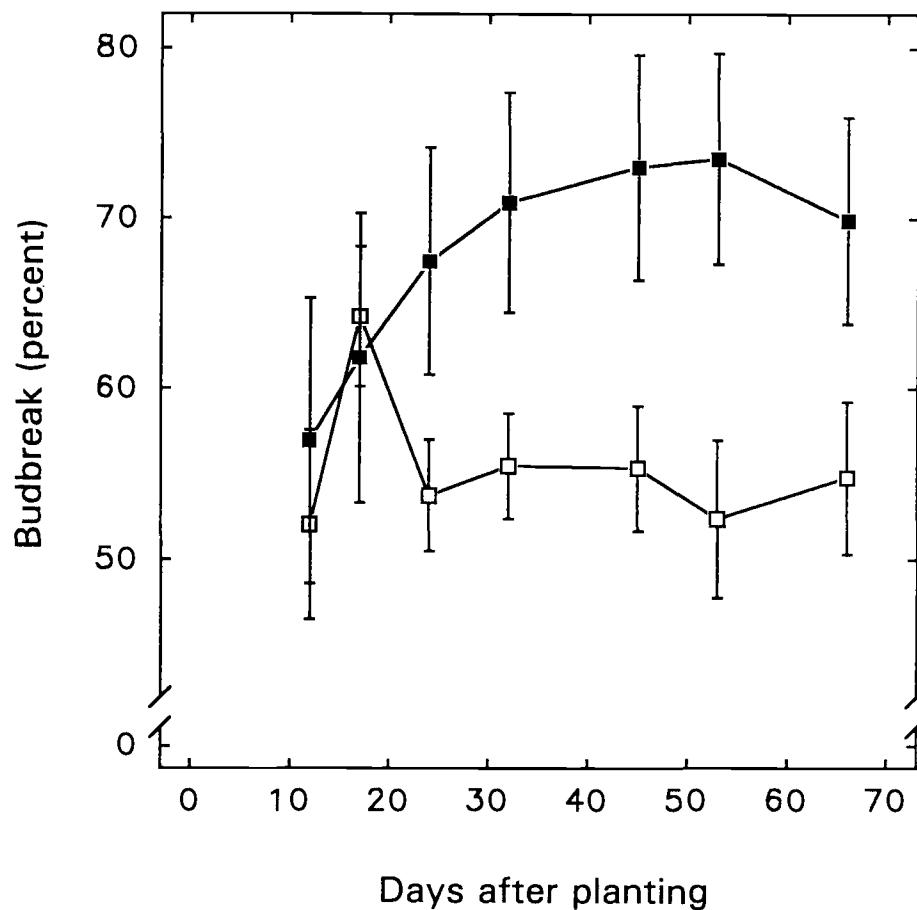


Figure 3.2 Percent budbreak of flowering dogwood (*Cornus florida*) following treatment of stems with water (■) or antidesiccant (□).

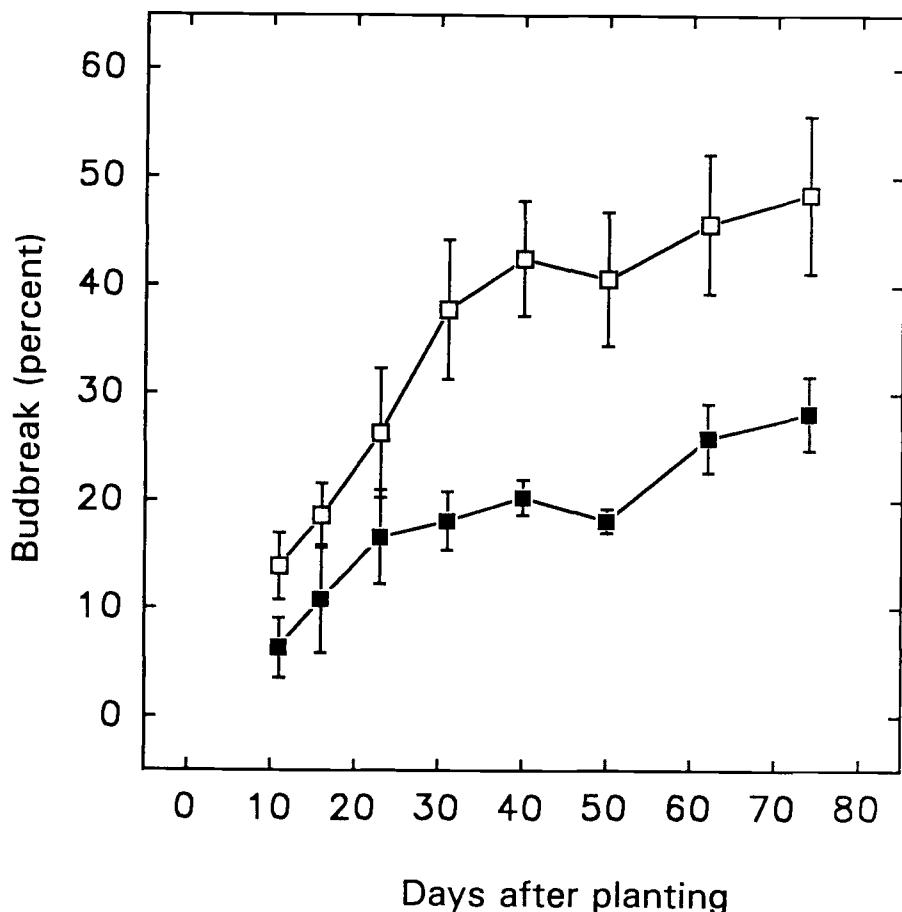


Table 3.2 Effects of stem applications of antidesiccant on stem dieback, visual rating, new root or shoot regeneration, or specific conductivity ( $k_s$ ) in Washington hawthorn, flowering dogwood, M.9 or M.26 EMLA apple rootstocks.

| Taxon     | Variable            | Sig.  | Stem Antidesiccant Application |                          |                      |                          |
|-----------|---------------------|-------|--------------------------------|--------------------------|----------------------|--------------------------|
|           |                     |       | + z                            |                          | -                    |                          |
| Hawthorn  | Dieback             | .002  | 8.0 %                          | (4.8)y                   | 41.5 %               | (7.4)                    |
| Dogwood   | Rating <sup>x</sup> | .003  | 3.67                           | (0.42)                   | 1.89                 | (0.19)                   |
|           | New shoot           | .008  | 112.3 %                        | (22.7)                   | 33.2 %               | (6.4)                    |
| M.9       | Dieback             | .004  | 0.9 %                          | (0.2)                    | 18.8 %               | (5.7)                    |
|           | New shoot           | .0001 | 9.7 %                          | (1.3)                    | 1.7 %                | (0.5)                    |
| M.26 EMLA | Dieback             | .004  | 1.5 %                          | (0.1)                    | 59.4 %               | (14.0)                   |
|           | New shoot           | .0006 | 13.9 %                         | (1.4)                    | 2.6 %                | (1.2)                    |
|           | New root            | .0003 | 15.0 %                         | (2.6)                    | 1.8 %                | (0.9)                    |
| $k_s^w$   |                     | .0001 | $24.0 \times 10^{-6}$          | ( $2.0 \times 10^{-6}$ ) | $4.6 \times 10^{-6}$ | ( $2.0 \times 10^{-6}$ ) |

z + /- denotes stems treated or not treated with antidesiccant, respectively.

y (Standard error in parentheses) n = 6.

x Visual rating (0 = dead, 5 = excellent quality) (figure A.1).

w Specific conductivity ( $k_s$ ) kg · MPa<sup>-1</sup> m<sup>-1</sup> s<sup>-1</sup>.

apple rootstock was similar to the overall budbreak patterns of flowering dogwood (Figure 3.3 A). Differences in the mean budbreak percentages of the Stem + and Stem - groups of this taxon were significant starting from the second budbreak scoring date, (Table A.7).

The response of M.26 EMLA to stem treatment of antidesiccant differed from M.9. The difference in response was manifest as a significant RxS interaction over the first 50 days from planting (Table A.6) which was induced by higher initial rates of budbreak in the S treatment, as compared to the other three antidesiccant treatments: RS, R, or control (Figure 3.3 B). By the 57th day; however, both stem + treatments (S and RS) broke bud in equally high rates (Table A.6). As stated above, the same RxS interaction occurred in flowering dogwood on day 31 (Table A.8). Finally, in river birch the R x S treatments also tended to interact (Table A.10) from the second through fifth budbreak scoring dates (Figure 3.4). As seen in EMLA.26 or flowering dogwood, this interaction was induced by significantly higher budbreak in the S treatment compared to the other three treatments.

A possible explanation for the difference in budbreak response of M.9 compared to flowering dogwood on day 31, river birch, or M.26 EMLA may lie in root morphology: The root systems of the latter three taxa are better ramified or/and of finer diameter than those of M.9. The root surface area of M.9 was therefore much smaller than that of the other three varieties. Antidesiccant films form a significant barrier to water movement (Englert et al., 1993; Gale & Hagen, 1966). This barrier would be effective not only for water movement out, but for movement into the transplants as well. Untreated roots would therefore be more efficient at water uptake than treated roots, resulting in better internal water relations in transplants not

receiving root treatment. Furthermore, the presence of a film antidesiccant on stems would reduce water loss, adding to the benefit no root treatment.

Because establishment (resumption of shoot growth) depends on the relief of internal water stress (Guehl et al., 1993, Kaushal & Aussenac, 1989; Kozlowski & Davies, 1975a; Struve, 1990), transplants in the S treatment would be expected to have the best internal water relations where sufficient root surface for water uptake existed (*viz.* river birch, flowering dogwood, or M.26 EMLA). Conversely, for M.9 (which lacked significant root surface for absorption) either the S or RS treatments should have the best water relations.

These results could have important implications for transplant establishment because the period after transplanting is characterized by high levels of internal water stress which limits shoot growth (Kozlowski & Davies, 1975b). Water influx in transplants is greatly reduced prior to new white root regeneration (Johnson et al., 1988 and Baxter & West, 1977) but water loss continues even after planting (Bates & Niemiera, 1994) thus increasing internal water deficits (Kaushal & Aussenac, 1989). Regrowth of stems, however, appears to be essential for root regeneration (and the concomitant reduction of internal water stress) as well as the subsequent survival of spring-planted trees (Kelly & Moser, 1983). Increasing initial budbreak and shoot growth with antidesiccants could therefore work towards reducing the duration of the period of high water stress, resulting in better establishment.

Figure 3.3 A: Percent budbreak of M.9 apple rootstock (*Malus domestica*) following treatment of stems with water (●) or antidesiccant (○). B: Percent budbreak of apple rootstock M.26 EMLA following antidesiccant treatments to stems only (□), roots only (■), roots and stems (▽), or neither organ (▼).

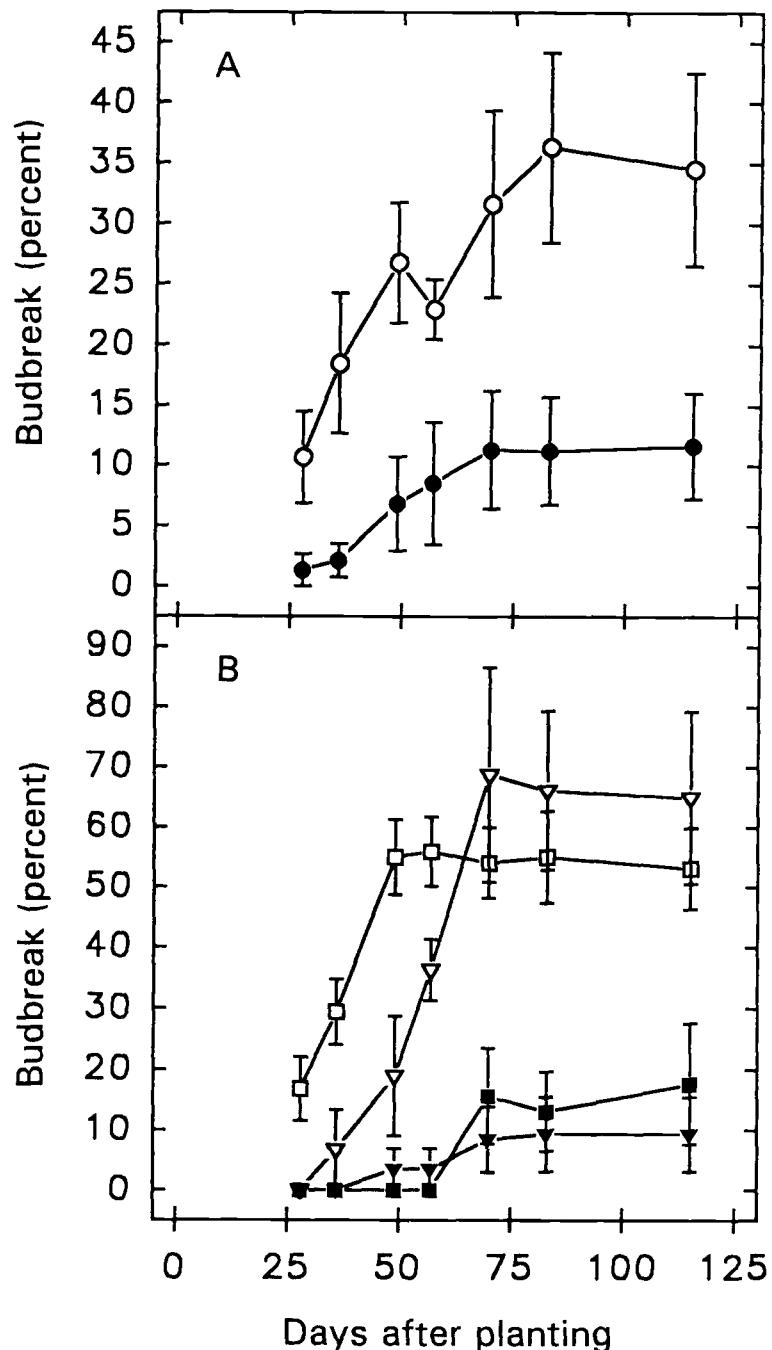
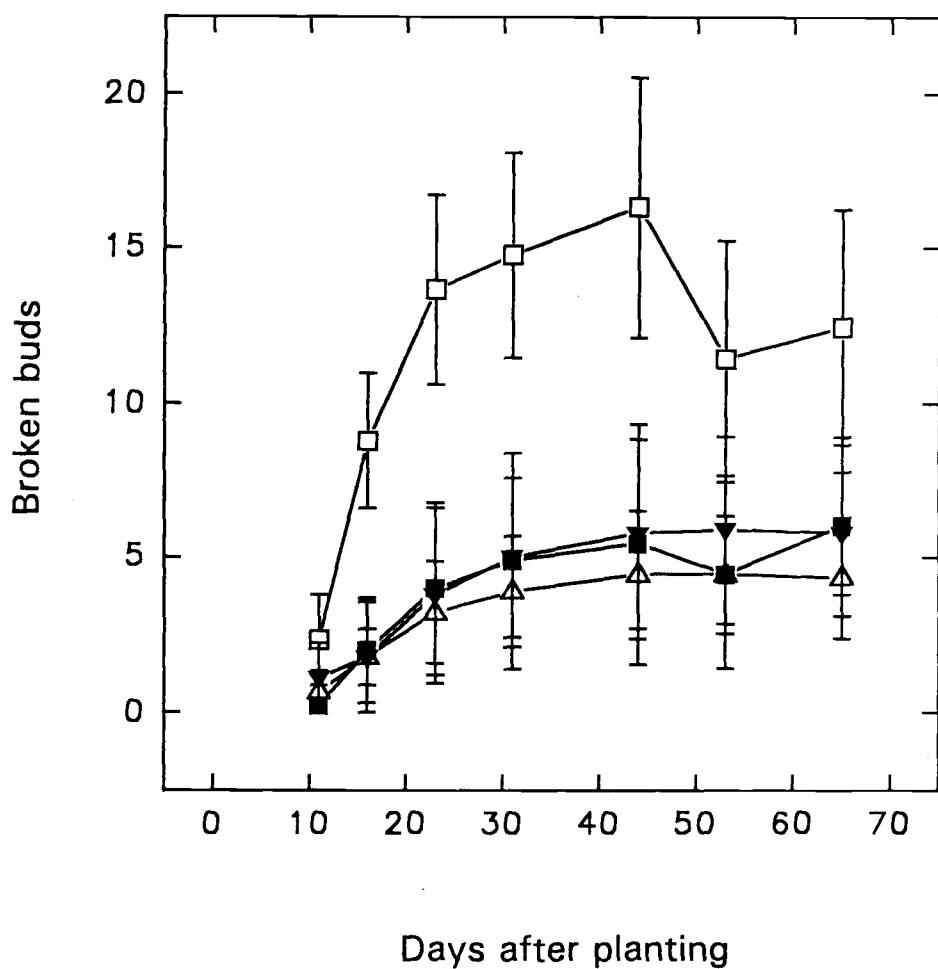


Figure 3.4 Number of growing buds of river birch (*Betula nigra*) following antidesiccant treatments to stems only (□), roots only (■), roots and stems (Δ), or neither organ (▽).



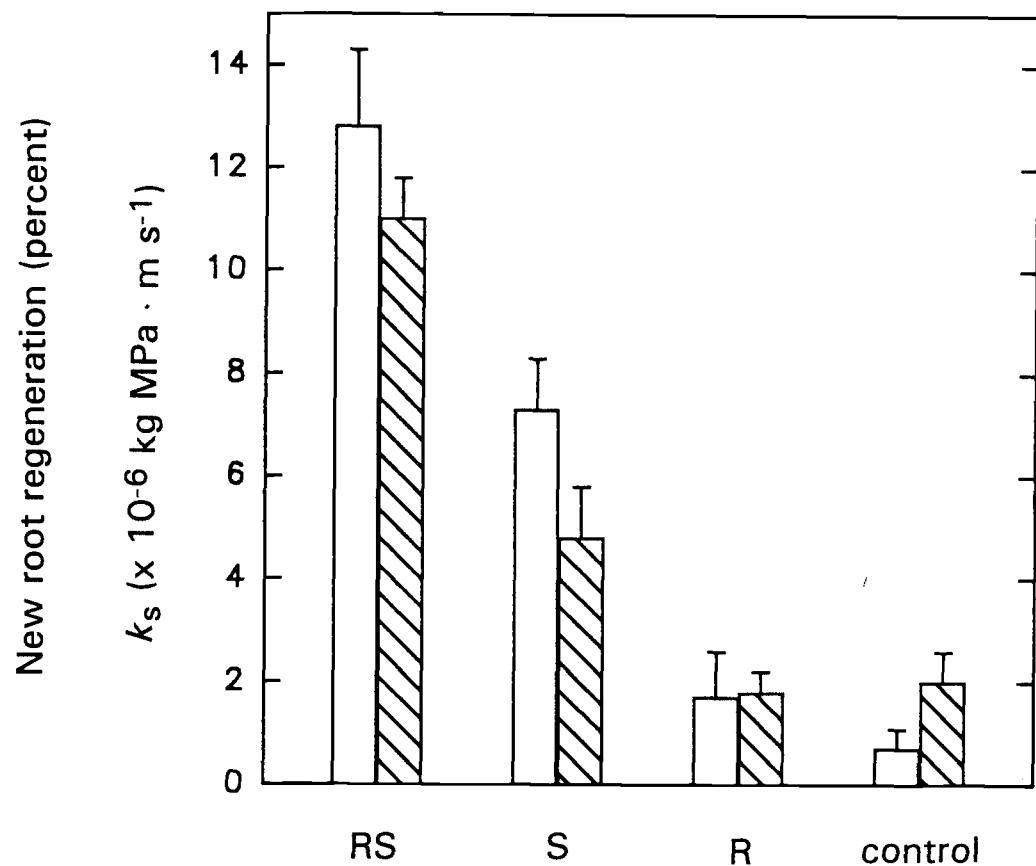
### Establishment responses stem treatment

Despite differences in mean budbreak response to stem antidesiccant treatment found in European beech and river birch, there were no significant differences in establishment for either species (Tables A.5 and A.10). Final budbreak ranged from 50 to 72 % in beech, and between 4 to 12 growing buds in river birch. This suggests that although treatments may have influenced budbreak, there was no long-term effect on final establishment. Indeed, budbreak percentages of the treatments tended equalize with time in both species (Figures 3.1 and 3.4). Again, the overall lack of treatment response in European beech may have been due to uniformly good water relations before planting. In absence of desiccation stress, antidesiccant treatments often have no, or sometimes detrimental, effect (Mullin & Bunting, 1979; Ranney et al., 1989; and Tukey & Brase, 1931). Ambiguous establishment response in river birch seedlings, however, was likely due to higher levels of variability within treatments (Table A.10). In all other taxa (Washington hawthorn, flowering dogwood, or M.9 and M.26 EMLA apple rootstocks), stem treatments resulted in significant differences in at least one of the establishment responses measured (Table 3.2 and Figure 3.5):

Stem dieback was highest in the Stem - treatments of Washington hawthorn and both apple rootstock varieties (Table 3.2). Stem dieback was not quantified in flowering dogwood; however, visual rating (defined in materials and methods and Figure A.1) which incorporates a measure of dieback was significantly higher in the Stem + treatments (Table 3.2).

Post-planting desiccation stress most likely induced higher levels of stem dieback or lower visual rating in Stem - hawthorns and dogwoods.

Figure 3.5 Effects of antidesiccant applications to roots and stems (RS), stems only (S), roots only (R), or control treatment (neither organ treated) on final establishment parameters in M.9 apple rootstock (*Malus* hybrid): Panel A: New root regeneration percentage. Panel B: Specific conductivity ( $k_s$ ).



Schönherr & Ziegler (1980) found that periderm of lenticels of European birch (*Betula pendula*) is quite permeable:  $7.4 \cdot 10^{-8}$  cm s<sup>-1</sup> for periderm 250  $\mu$  thick. This work established that significant water loss can occur in defoliated stems, even though it is at a reduced rate relative to roots (Insley & Buckley, 1985 and Murakami et al., 1990). The addition of a film barrier to any plant organ reduces water loss as a function of its thickness, porosity, and permeability to water vapor (Gale & Hagen, 1966). Film-forming antidesiccants such as Moisturin-4, which was used in this study, have been shown to reduce water loss from stems of plants such as Washington hawthorn (Englert et al., 1993).

In apple rootstocks not receiving antidesiccant application to stems (Stem -), higher levels of stem dieback can be attributed to excessive water loss during the pre-planting desiccation stress event. Greater levels of water loss in the Stem - treatments resulted because  $\approx$ 67 to 100 % of each layer was not protected during the 38 h desiccation period by the antidesiccant film barrier (see application procedure in materials and methods). Water loss most likely continued at a higher rate in the Stem - apple rootstocks after planting, resulting in additional stress.

Although stem dieback in Washington hawthorn was highly influenced by stem treatment, no significant differences in new root or shoot regeneration percentage were found (Table A.9). Values for root or shoot regeneration in this taxon ranged from 1 to 10 % and 8 to 16 %, respectively. Root regeneration was not measured in flowering dogwood. However, shoot regeneration in this taxon was greater in the Stem + treatments (Table 3.2), indicating that increases in budbreak rate had long term effects on establishment in this species. In both apple rootstock varieties, mean new shoot growth was also significantly higher in the Stem

+ treatments (Table 3.2). The same trend occurred for new root regeneration and specific conductivity ( $k_s$ ) in Stem + M.26 layers (Table 3.2).

Conversely, new root regeneration and  $k_s$  of M.9 showed a different response in that a significant RxS treatment interaction was found (Table A.7). Unlike previously cited RxS interactions, this effect was found to be due to higher mean values for the root regeneration and  $k_s$  variables in the RS treatment (Figure 3.5). Higher means in the RS treatment in M.9 are most likely a reflection of the initial levels of desiccation stress endured by the layers during the pre-planting stress exposure: Plants receiving the RS treatment were better protected from water loss than those receiving the other treatments because the film barrier covered the entire plant (see materials and methods). Conversely, M.9 layers receiving the S treatment were better-protected than the Stem - treatments, (R or control). Therefore, despite lack of a clear effect on budbreak (Figure 3.3 A), long term effects on the establishment of M.9 were influenced by internal water relations at planting, which were in turn influenced by antidesiccant treatment. In other unpublished studies with M.9, there was no difference in establishment response between these four treatments when no desiccation exposure was applied (data not shown).

$k_s$  of M.9 did not recover from the effects of the pre-planting desiccation exposure. Desiccation stress results in the buildup of internal xylem tensions which may lead to cavitation and eventual embolism in the stem xylem (Kavanagh, 1994; Tyree & Dixon, 1986; Tyree et al., 1992; and Sperry & Saliendra, 1994). Emboli reduce permeability of the xylem to water transport (Tyree & Dixon, 1986 and Tyree & Ewers, 1991). The reduction in

permeability is irreversible unless new wood growth or refilling occur. Either repair mechanism requires favorable water relations.

Because new wood growth occurred in both apple rootstock clones, varietal differences in treatment response in terms of  $k_s$  may be due to some internal characteristic of M.26 which renders it more resistant to cavitation than the other. In fact, a genetic difference in desiccation tolerance on the cellular level was suggested as an explanation for differential response of apple rootstock clones to desiccation stress by Murakami et al. (1990).

Kavanagh (1994) showed that stress-induced cavitation events are linked to reduced vigor and increased mortality of transplanted Western hemlock seedlings. The current study supports these findings in that new root growth was highest in M.9 layers which had the best water relations and  $k_s$  at planting. What is perhaps most surprising is that budbreak or new shoot regeneration did not also show a similar reduction.

### Conclusion

Applications of 50 % Moisturin-4 antidesiccant to roots either alone or in combination with 500 ppm indole-3 butyric acid (IBA), did not result in significant increases in budbreak or establishment of one-year seedlings of flowering dogwood or two-year seedlings of river birch. Budbreak percentage of flowering dogwood tended to be higher in plants receiving IBA treatment, but IBA applications tended to decrease root regeneration in river birch. Applications of either antidesiccant or IBA to roots of these species are concluded to be of no value in the establishment of non-desiccated seedlings in these two species.

Treating roots of seedlings or root zones of apple rootstock layers with 50% Moisturin-4 antidesiccant, either alone or in combination with stem

applications, imparted no significant benefit. In fact, the overall effect of root applications of antidesiccant was negative in Washington hawthorn or flowering dogwood seedlings, as it also tended to be in river birch. Stem applications of antidesiccant were found to be slightly detrimental to budbreak in European beech at both levels of root treatment. Applications of antidesiccant compounds to stems of European beech or to roots of seedling Washington hawthorn, flowering dogwood seedlings are therefore not recommended.

Applications of antidesiccant to stems (Stem +), alone or in combination with root treatment, increased budbreak percentages in flowering dogwood and M.9 and M.26 EMLA apple rootstocks; visual rating in flowering dogwood; and stem regeneration in both apple rootstock varieties. Stem + treatments also tended to increase initial rates of budbreak in Washington hawthorn. Similarly, Stem + treatments reduced stem dieback in Washington hawthorn and both apple rootstock varieties (M.9 and M.26 EMLA) as well as increase root regeneration and specific conductivity ( $k_s$ ) in M.26 EMLA.

Application of antidesiccant to stems only (S) was found to singularly increase initial levels of budbreak in M.26 EMLA, flowering dogwood, and river birch. However, the effect of the S treatment in these taxa disappeared within 30 to 50 days of planting, at which time budbreak levels of the roots + stems (RS) antidesiccant treatments became statistically equal to those of the S treatment. In contrast, the RS treatment (applied after exposure to desiccation stress) resulted in the highest levels of new root regeneration and  $k_s$  in M.9.

Because antidesiccants are designed to prevent water movement into and out of plants, applications of antidesiccant to transplants are concluded

to be most effective when made to stems, because this is the site of loss of water vapor after planting. Similarly, protection against water loss from aerial portions during imposed desiccation stress (apple rootstocks) or after planting and prior to new shoot regeneration (all taxa) by antidesiccant applications to the appropriate organs contributed significantly towards improved establishment. Budbreak percentages may be advanced in some taxa when applications are made to stems only, however applications of antidesiccant to both roots and stems may result in the best establishment of certain taxa, such as M.9 apple rootstock if treatments are applied prior to exposure to desiccation.

The evidence provided here for a generally beneficial response to stem treatment with antidesiccants across species warrants further comparisons of the stems only versus root + stem antidesiccant treatments in seedling transplants.

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## CHAPTER FOUR

### Effect of desiccation stress and application site or time of antidesiccant on water relations and budbreak of Washington hawthorn (*Crataegus phaenopyrum* Medic.) seedlings

#### **Abstract**

The effect of treating dormant bare-root Washington hawthorn (*Crataegus phaenopyrum* Medic.) seedlings with Moisturin antidesiccant (Burke's Protective Coatings, Washougal, WA, USA) at rates of 50% (in water): without, before, or after exposure to 13.5 hr. desiccation stress was compared to untreated control seedlings receiving or not receiving desiccation stress. Survival, budbreak, changes in fresh weight, xylem water potential (XWP), and specific conductivity of the xylem ( $k_s$ ) were quantified before and 14 to 20 days after planting.

Applications of antidesiccant to stems only of seedlings which had been desiccated prior to planting resulted in recovery from stress (increased XWP) and rates of budbreak comparable to non-stressed seedlings. Antidesiccant applications to stems only were equally effective whether applied before or after the desiccation exposure. Applications of antidesiccant to both stems and roots decreased water loss and stress development during desiccation exposure compared with application to stems only applications or untreated controls, but had a detrimental effect on water uptake and budbreak after planting. Stressed controls responded similarly to seedlings treated with antidesiccant to roots and stems.

XWP 14 to 20 d after planting were significantly correlated ( $R^2 = 0.85$ ) to changes in seedling fresh weight relative to the original seedling fresh weight (prior to planting and/or desiccation stress). XWP measured

two to three weeks after planting was generally a good indicator of rate of budbreak. In contrast,  $k_s$  (either before or 14 to 20 days after planting) appeared to have little relationship with seedling budbreak rate.

## Introduction

Washington hawthorn is a desiccation-sensitive species which is difficult to transplant bare-root (Englert, 1992; Englert et al., 1993; and Murakami et al., 1991). Antidesiccants or other coatings such as mud slurries have been beneficial for improving transplant establishment (Ranney et al., 1989; Simpson, 1984; Slocum & Maki, 1956; Kozlowski & Davies, 1975b). The antidesiccant Moisturin-4 (Burke's Protective Coatings, INC., Washougal, WA), applied at rates of 33 % or higher, has alleviated post-harvest water loss and improving establishment of bare root seedlings of various species including Washington hawthorn (Englert et al., 1993).

Tukey & Brase (1931) compared the benefits of treating stems only or roots + stems of dormant bare root nursery stock with paraffin. Application of paraffin to stems only was found to be beneficial to survival of cherry and rose transplants compared to treating the entire transplant. For some rose varieties, however, treatment of entire plants was equally beneficial. Applications of antidesiccant to stems only increased initial rates of budbreak in seedling river birch and flowering dogwood compared to no treatment or treatment of entire plants. Similarly, M.26 EMLA apple rootstock layers showed increased initial rates of budbreak following applications of antidesiccant to stems only prior to desiccation (Chapter 3). When only stems of Washington hawthorn seedlings were treated with Moisturin at rates of 25 % or higher prior to May transplanting in the field (without

supplemental irrigation) stem dieback was reduced compared to control seedlings (Englert et al., 1993)

The beneficial response to treating stems-only with antidesiccant, compared with treating both roots and stems, are perhaps explained by the resistance to water uptake by roots of dormant bare-root transplants (Baxter & West, 1977; Coutts, 1981; Grossnickle, 1988; and Sands, 1984). Addition of a further barrier to water uptake, such as a film-forming antidesiccant, increases this resistance. Defoliated stems of transplants continue to lose significant quantities of water, even after transplanting (Bates & Niemiera, 1994; Coutts, 1981; Insley & Buckley, 1985; and Murakami et al., 1990). After transplanting, then, the presence of a barrier on the stems only, such as an antidesiccant film, would reduce water loss compared to plants with untreated stems. Such protection from water loss improves internal water relations relative to untreated plants (Englert et al., 1993, Ranney et al., 1989). Transplants exhibit increased survival and regrowth as water potential increases (Aussenac et al., 1988; Guehl et al., 1993; Kaushal & Aussenac, 1989; and Kozlowski & Davies, 1975 a and b). Some practical reasons for avoiding treating all organs of the crop are: 1. it requires greater amounts of product and 2. applications to roots require that transplants be harvested, washed, and dried before application (Tukey & Brase, 1931). For transplants which will endure desiccation stress after planting, it is hypothesized that applications of antidesiccant to stems only should improve establishment compared to applications of antidesiccant to roots and stems or not at all.

Desiccation of bare-root seedlings prior to planting can increase resistance of roots to water uptake. In Sitka spruce (*Picea sitchensis*), desiccation periods of 1.9 h greatly increased resistance to root water uptake

(Coutts, 1981). Slocum & Maki (1956) found that exposure of roots to air for as little as 0.5 hr. induced a measurable reduction in regrowth and survival in bare-root loblolly pine (*Pinus taeda*). Englert et al. (1993) showed that when antidesiccants, such as Moisturin, are applied to both roots and shoots of Washington hawthorn prior to desiccation stress, water loss and stem dieback decreased and survival increased after transplanting. Protecting roots of bare-root trees from water loss after harvesting can positively influence survival and performance (Tukey & Brase, 1931 and Webb & Von Althen, 1980). Therefore, when bare root plants are exposed to water stress before planting, it is hypothesized that treatment of roots and shoots should promote better establishment than treating stems only.

The link between water stress and transplant establishment has been well-established experimentally (Aussenac et al., 1988; Englert et al., 1993; Guehl et al., 1993; Kaushal & Aussenac, 1989; Kozlowski & Davies, 1975a and b; Larson & Whitmore, 1970; Ranney et al., 1989; Sands, 1984; Simpson, 1984; Slocum & Maki, 1956). The mechanism by which desiccation stress limits establishment, however, is not well-known (Aussenac et al., 1988 and Guehl et al., 1993). Xylem transport results from tension (*i.e.* negative hydrostatic pressure) propagated basipetally to the roots (Tyree & Sperry, 1989). Although xylem tensions between -1 to -2 MPa are necessary for water transport in plants (Tyree & Sperry, 1989; Tyree & Ewers, 1991; and Zimmermann, 1983), lower water potentials can lead to breakage (cavitation) in the continuity of the water column in individual xylem elements. Water stress can reduce xylem water potentials to almost -10 MPa in some cases (Tyree & Sperry, 1989). Cavitation events occur when internal tensions cause bubble radii in xylem pores to be reduced to levels below that of the pore itself. Bubbles then enter the lumen of the

xylem element and expand instantaneously to re-establish equilibrium with ambient pressure (Zimmermann, 1983). Air replaces the water vapor in the cavitated void within about 15 min (Tyree & Sperry, 1989) though diffusion or precipitation from xylem sap, resulting in an embolism (Lo Gullo & Salleo, 1991; Tyree & Dixon, 1986; and Tyree & Sperry, 1988 and 1989). That such events occur during dehydration stress has been supported by numerous studies (Crombie et al., 1985; Borghetti et al., 1989; Kavanagh, 1994; Tyree & Dixon, 1986). Alternatively, use of positive pressure (achieved by air-injection) to induce gradients of the same magnitude between the outside and inside of xylem elements also induces cavitation (Cochard et al., 1992; Sperry & Pockman, 1993; Sperry & Tyree, 1988; and Tyree et al., 1984). Thus, it is largely agreed that the pore diameter of the individual elements limits the degree of tension that plants can sustain before their xylem sap cavitates.

The impact of cavitation on water transport can be quantified by determining the change in the specific conductivity of the stem (Sperry et al., 1988a). Specific conductivity ( $k_s$ ) is the flux of water through a stem segment of known length and diameter driven by a known pressure gradient. Higher levels of  $k_s$  indicate greater permeability or efficiency of water transport.

When embolism in excess of 5 to 30 % occurs in woody stems, water transport necessary for optimum growth is reduced (Tyree & Sperry, 1989). However, the effect of embolism in stems has more serious consequences on water transport than the simple restriction of water supply to leaves. Because of the reduction in conductivity, the water potential gradients necessary to maintain water transport at levels present prior to embolism are increased. Increasing pressure gradients lead to further cavitation events

which, in turn, increase reduction in conductivity and further increases the pressure gradients necessary to maintain pre-embolized levels of water transport (Tyree and Sperry, 1988 and 1989). This phenomenon is termed "runaway cavitation" which, if left unchecked by either reduction in transpiration or relief of water stress by irrigation results in leaf loss, stem dieback, and/or loss of vigor (Kavanagh, 1994; Sperry et al., 1988b; Tyree & Sperry, 1989; and Tyree & Ewers, 1991).

Guehl et al., 1993 suggested that xylem cavitation may a possible mechanism by which water stress limits transplant establishment. Kavanagh (1994) demonstrated that cavitation events induced by post-transplant water stress are linked to loss of vigor or mortality of Western hemlock (*Tsuga heterophylla*) seedlings. Transplanted bare root apple rootstock layers which showed signs of reduced vigor (such as low budbreak percentage and poor regrowth) and stem dieback also had lower  $k_s$  (Chapter 3). The  $k_s$  of apple rootstocks appeared to be related to the performance of transplants during establishment, however measurement of  $k_s$  *a posteriori* did not explain whether or not there was a relationship between the  $k_s$  at planting, and the eventual establishment of the layers.

The objectives of this experiment were to determine:

1. if antidesiccant applications to stems only or roots and stems results in reduced water stress and increased budbreak in non-stressed or stressed (before planting) Washington hawthorn seedlings,
2. if the effects of antidesiccant treatments are the same when the product is applied either before or after preplanting desiccation stress, and
3. if specific conductivity ( $k_s$ ) and pre- and post-planting water relations affect the budbreak response of Washington hawthorn seedlings.

## Materials and methods

### *Plant material*

Approximately 200 one-year, single-stemmed Washington hawthorn (*Crataegus phaenopyrum* Medic.) seedlings were harvested bare root from seedbeds at J. Frank Schmidt Nursery, Boring, OR, USA on either 12 or 14 January, 1994. Both harvest dates were rainy with air temperatures not exceeding 5° C. Upon digging, seedlings were immediately wrapped in two layers of 0.95 mil polyethylene, transported to Oregon State University campus (Corvallis, Oregon) and placed in cold storage (2 °C). Soil and debris were washed from roots and stems within 24 h of digging. Fifteen days later, seedlings were removed from storage, graded for uniformity in stem diameter ( $\approx$  1.0 cm base caliper) and stem length ( $\approx$  1 m). After grading, lateral or main-axis roots were pruned-back to 3.0 mm diameter. Seedlings were then rewrapped in clean polyethylene and returned to cold storage until treatment 10 to 14 days later. Following applications of treatments, seedlings were potted in 15 x 35 cm fiber containers (Western Pulp and Manufacturing, Corvallis, OR, USA) containing a 1:1:1:2 (v/v/v/v) sandy loam field soil, 1/4" (8.0 mm) minus river sand, fine sphagnum peat, and #8 slow-screen white pumice mix and placed in a 21/15 °C (minimum day/night temperatures) greenhouse. Greenhouse conditions were monitored during the first three weeks of the study: daily humidity fluctuated between 85% at night to 30% at midday. 24 °C was the highest temperature recorded during the the first three weeks.

### *Change in fresh weight*

For seedlings receiving pre-planting stress, the 'before planting' fresh weight was that which was measured after desiccation stress. For non-stressed seedlings the original seedling fresh weight is also the 'before planting' fresh weight.

Percent fresh weight change ( $\Delta FW$ ) during pre-planting desiccation stress was derived from:

$$\Delta FW \text{ (desiccation)} = ([FW \text{ before} - FW \text{ original}] / FW \text{ original}) \times 100$$

Percent fresh weight change after planting, relative to the 'before planting' fresh weight was derived from:

$$\Delta FW \text{ (after planting)} = ([FW \text{ after} - FW \text{ before}] / FW \text{ before}) \times 100$$

Percent fresh weight change after planting, relative to the original fresh weight was derived from:

$$\Delta FW \text{ (from original)} = ([FW \text{ after} - FW \text{ original}] / FW \text{ original}) \times 100$$

Changes in fresh weight 'from original' or 'after planting' were measured 14 to 20 days after planting.

### *Xylem water potential*

Xylem water potential (XWP) was measured on stem apices of approximately 5-7 cm length in a pressure chamber (PMS Instrument Co., Corvallis, OR). Samples were measured immediately prior to stem conductivity measurements.

### *Conductivity measurement*

The hydraulic technique of Sperry et al. (1988a) was used to measure the specific conductivity of stems. Zimmermann & Jehe (1981) showed that between 85 and 90 % of the vessels of *Prunus serotina*, a semi-ring porous

species, are 10 cm long or less. Therefore, to ensure that a high proportion of vessels had at least one intact end (not cut open on both ends) in the excised stem section, sections of 10.0 ( $\pm$  0.5) cm length were cut between  $\approx$  9 and 19 cm from the base of seedlings (visualized as being the junction of root/stem at the former soil-line) under tapwater to avoid artifactual air-seeding during cutting. Cut ends of segments were recut under tapwater with sharp razor blades in order to remove ends of xylem elements crushed by the shears. A tapwater-filled section of Tygon tubing was attached to the proximal end of stem segments, forming a tight seal. The tapwater was replaced with perfusion solution (100 mM KCl, repeatedly filtered to 0.2  $\mu$ ). The stem + Tygon segment was affixed to a length of tubing containing perfusion solution elevated to a height of one m above the segment to obtain a pressure head of 0.01 MPa). The flux ( $F$ ) of perfusion solution ( $\text{kg} \cdot \text{s}^{-1}$ ) through the stem segment was measured by affixing a cuvette of known weight containing a piece of dry tissue paper against the distal end of the stem segment and reweighing the tared cuvette and paper every 30 to 60 s to the nearest 0.001 g. From the average of four such  $F$  measurements, the specific conductivity ( $k_s$ ) (expressed in units of  $\text{kg MPa}^{-1} \text{m}^{-1} \text{s}^{-1}$ ) was determined from the following equation (Tyree & Ewers, 1991):

$$k_s = (F \cdot dP^{-1} \cdot dx^{-2}) \cdot A_w^{-1}$$

Where  $dP$  = pressure gradient of the perfusing solution (1.0 m above the sample = 0.01 MPa),  $dx$  = the length of the stem segment in m, and  $A_w$  = transverse-sectional area of the wood in  $\text{m}^2$  (average of the de-barked transverse-sectional area of each end of the segment).

### Budbreak

Budbreak (buds broken · total buds on stem<sup>-1</sup>) scores were begun 13 days after planting, and continued at one- to three-week intervals until the 82nd day following planting.

Initial rates of budbreak were derived by fitting a linear regression to the budbreak scores for each replicate: Budbreak scores were linearized by the logit-transformation [log (budbreak (1 - budbreak)<sup>-1</sup>)]. Regressions were fit through at least the first three dates, with later dates being added incrementally with new regressions fit until a total of nine separate regressions (for each successively added date) had been fit for each replicate. The slope coefficient of the individual regression with the highest correlation coefficient ( $R^2$ ) for each replicate was used to represent the initial rate of the budbreak curve (i.e. the portion before the plateau). Additionally, the  $R^2$  (rarely below 0.90) for each regression was used as a weight in the separation of means for the budbreak slope coefficients.

### Treatments

A solution of 1:1 distilled water / Moisturin-4 antidesiccant (Burke's Protective Coatings, Washougal WA) with 0.5 % Sur-Ten surfactant (American Cyanamid Co., Princeton, NJ) was prepared 24 h before treatment. Treatments consisted of applications of antidesiccant solution with a nylon-bristle paintbrush to stems-only either before, after, or without desiccation stress (abbreviated S-B, S-A, or S-No, respectively) or to roots and stems before, after or without desiccation stress (abbreviated RS-B, RS-A, or RS-No, respectively). There were two antidesiccant controls, one with non-stressed and another with stressed seedlings.

Desiccation stress consisted of exposure of seedlings to 13.5 h air-drying at 19 °C and 25 % R.H. Non-stressed seedlings were exposed to only enough air-drying as was necessary to achieve a surface-dry state of the applied antidesiccant ( $\approx$  15 to 45 min).

#### *Experimental design*

The eight treatments were randomly assigned to individual trees. Budbreak response was measured over the course of 82 days. Survival percentage was determined after 156 days, plants were scored as dead if no budbreak had occurred. Budbreak rate and survival percentage was scored on 9 to 10 seedlings per treatment.

Treatment effects on seedling water relations variables ( $\Delta$  FW, XWP, and  $k_s$ ) were measured on subsamples of each treatment at two different sampling periods: 7 to 0 days before planting (10 February), or 14 to 20 days after planting (between 26 February and 4 March). Dates for the 'after planting' period coincided with the first signs of budbreak. Plants harvested for water relations measurements after planting were removed in one randomly selected block (one individual per treatment, total 8 plants) for each set of measurements. Sample sizes for XWP or  $k_s$  'before planting' and 'after planting' ranged between 10 and 14 and 4 and 5, respectively.

Statistical analysis was performed using the general linear models procedure of version 6.11 of SAS (SAS Institute, 1991). Fresh weights of each individual transplant (weighed before treatment) were analyzed as a covariate for all response parameters measured. No significant effect of the fresh weight covariate were found for any response. Analysis of residuals of the raw  $k_s$  data indicated the need for a log transformation which preceded the performance of contrasts or means separation procedures.

Treatment means for variables quantified for any given sampling period were separated using the Waller ratio ( $K = 100$ ). Differences between mean XWP or log-transformed  $k_s$  before and after planting were contrasted by individual t-tests. Data presented in tables or figures are actual data.

## Results

### *Seedling water relations before planting*

Plants receiving antidesiccant treatment before desiccation stress to roots + stems (RS-B), stems only (S-B) and no treatment lost 2.6, 5.4, and 9.7 % of their pre-desiccation fresh weight, respectively. Non-stressed plants had the highest mean XWP, followed by RS-B, S-B, and stressed untreated plants which had the lowest XWP (Table 4.1). All treatment differences in mean fresh weight loss and XWP were significant at  $p = 0.05$  (Appendices 4.1 and 4.2)

Mean specific conductivity ( $k_s$ ) of non-stressed plants before planting was higher than the mean  $k_s$  of desiccated controls, RS-B, or S-B seedlings or (Table 4.1). However, in contrast to the above trends for fresh weight loss and XWP, there was no significant difference between treatments within the desiccated group for mean  $k_s$ , indicating that  $k_s$  was similarly reduced by 13.5 hr. desiccation stress.

### *Changes in seedling water relations after planting*

Change from the fresh weight before planting was strongly influenced by treatment combination (Appendix 4.2). Non-stressed control plants showed the largest of their original (before planting) fresh weight (Table A.11 and Figure 4.1). RS-No and RS-B treatments also showed a mean decrease

in fresh weight following planting, however the loss in these treatments was not as severe as it was for the non-stressed controls (Table A.11). Among stressed seedlings, only the RS-B treatment showed a net loss of fresh weight from the before planting (post-desiccation) fresh weight, indicating a continuation of fresh weight loss sustained during imposed desiccation stress. In all other desiccated treatments, mean fresh weight change, relative to fresh weight before planting was positive (Figure 4.1).

In contrast to the change in fresh weight from before planting fresh weight, comparisons of fresh weights after planting to their original fresh weights showed that all treatments sustained a net loss in fresh weight over the course of the study. Mean change from original fresh weight of S-B and S-No seedlings, though near zero, was not different from treatments which showed larger losses (Table 4.1).

There were significant treatment differences in mean XWP after planting (Appendix 4.14). Effects of relatively large levels of water loss seen in non-stressed controls compared to RS-No, S-No, and S-A were reflected in the lower mean XWP of this treatment (Table 4.1). Mean XWP of the latter three treatments was higher than that of the RS-B or RS-A treatments, with XWP of stressed controls intermediate between all treatments (Table 4.1).

Across treatments, XWP tended to be higher when net change in fresh weight loss (relative to the 'original' fresh weight) approached 0 % (Table 4.1). The change from the original fresh weight was in fact found to be correlated to the XWP after planting (Figure 4.2). XWP at planting was not, however, correlated with fresh weight change during desiccation stress or fresh weight change relative to the 'at planting' weight. In addition, no correlation was found with levels of  $k_s$  to either the XWP after planting or with changes in fresh weight.

Table 4.1 Mean xylem water potential (XWP) and specific conductivity ( $k_s$ ) before and after planting and percent change from original fresh weight ( $\Delta FW$ ) after planting in Washington hawthorn seedlings, by treatment.  
(abbreviations defined in Materials and Methods)

| Variable         | time of sampling   | Treatments            |          |          |          |          |         |           |           | Control<br>Stressed |
|------------------|--------------------|-----------------------|----------|----------|----------|----------|---------|-----------|-----------|---------------------|
|                  |                    | Control               |          |          |          |          |         |           |           |                     |
|                  |                    | non-stressed          | RS-No    | S-No     | RS-B     | S-B      | RS-A    | S-A       |           |                     |
| XWP <sup>z</sup> | before             | -0.70                 | -0.70    | -0.70    | -2.46    | -3.20    | -4.25   | -4.25     | -4.25     |                     |
|                  | after              | -2.84 bc <sup>y</sup> | -1.01 a  | -1.04 a  | -2.77 bc | -1.43 ab | -3.32 c | -1.17 a   | -2.25 abc |                     |
|                  | Sign. <sup>x</sup> | 0.0001                | 0.46     | 0.46     | 0.48     | 0.0003   | 0.03    | 0.0001    | 0.0001    |                     |
| $k_s^w$          | before             | 9.72                  | 9.72     | 9.72     | 3.67     | 2.92     | 3.91    | 3.91      | 3.91      |                     |
|                  | after              | 6.40 a                | 5.86 a   | 12.94 a  | 4.44 a   | 8.97 a   | 4.18 a  | 3.69 a    | 3.49 a    |                     |
|                  | Sign. <sup>x</sup> | 0.11                  | 0.20     | 0.84     | 0.58     | 0.007    | 0.45    | 0.74      | 0.83      |                     |
| $\Delta FW$      |                    | -5.06 cd              | -1.43 ab | -0.50 ab | -6.93 d  | +0.12 a  | -6.84 d | -2.70 abc | -3.45 bc  |                     |

<sup>z</sup> XWP in MPa.

<sup>y</sup> Means within row followed by the same letter are not different at the 0.5 level (Waller K-ratio).

<sup>x</sup> Significance level of t-test, before and after means.

<sup>w</sup>  $k_s$  ( $\times 10^{-8}$  kg MPa $^{-1}$  m $^{-1}$  s $^{-1}$ ).

Figure 4.1 Percent change from fresh weight at planting ( $\{[FW \text{ at harvest} - FW \text{ at planting}] / FW \text{ at planting}\} \times 100$ ) of Washington hawthorn seedlings harvested 14 to 20 days after planting. Desiccation constituted 13.5 hours exposure; stem + root or stems only indicate sites of antidesiccant (AD) treatment; vertical bars indicate SE ( $n = 4 - 5$ ).

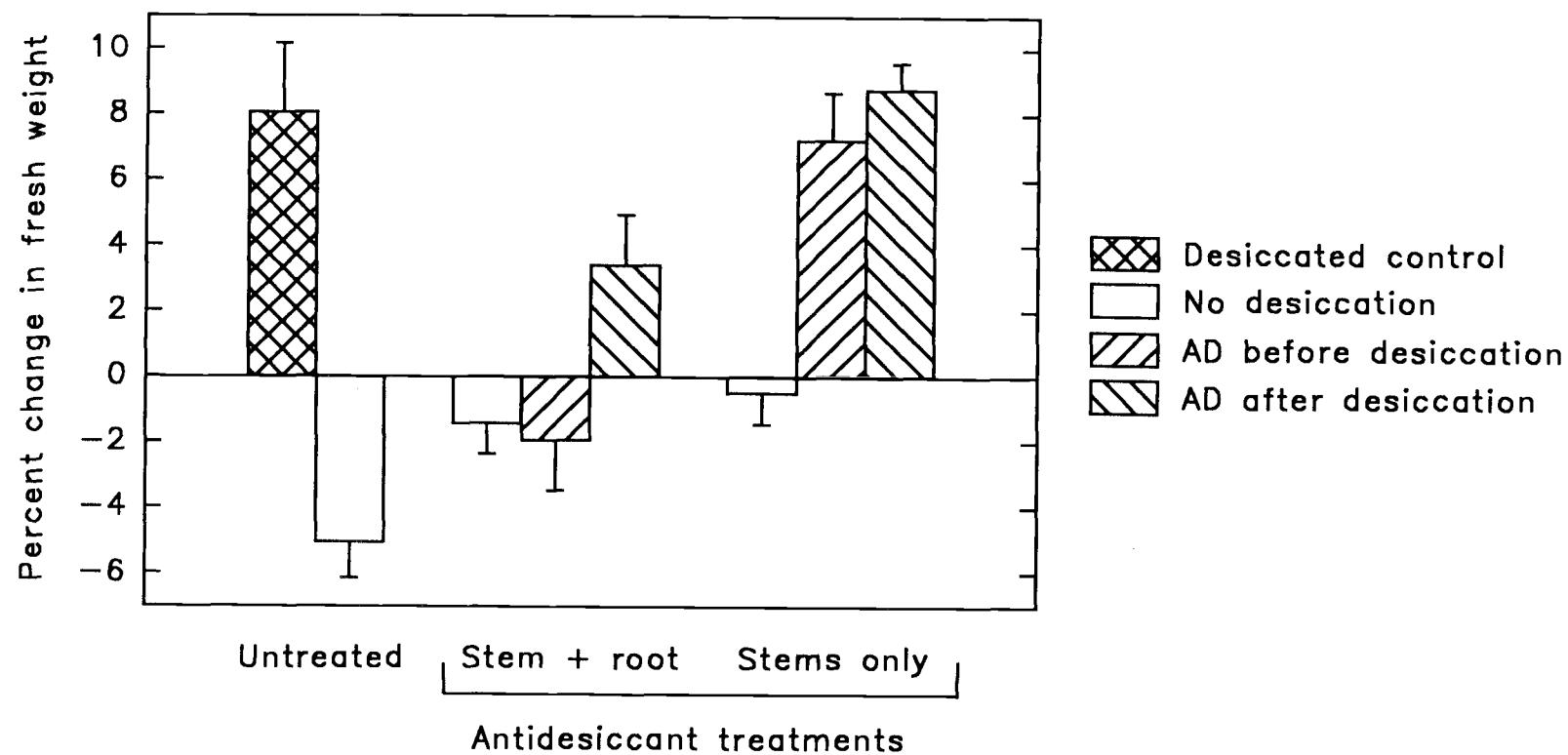
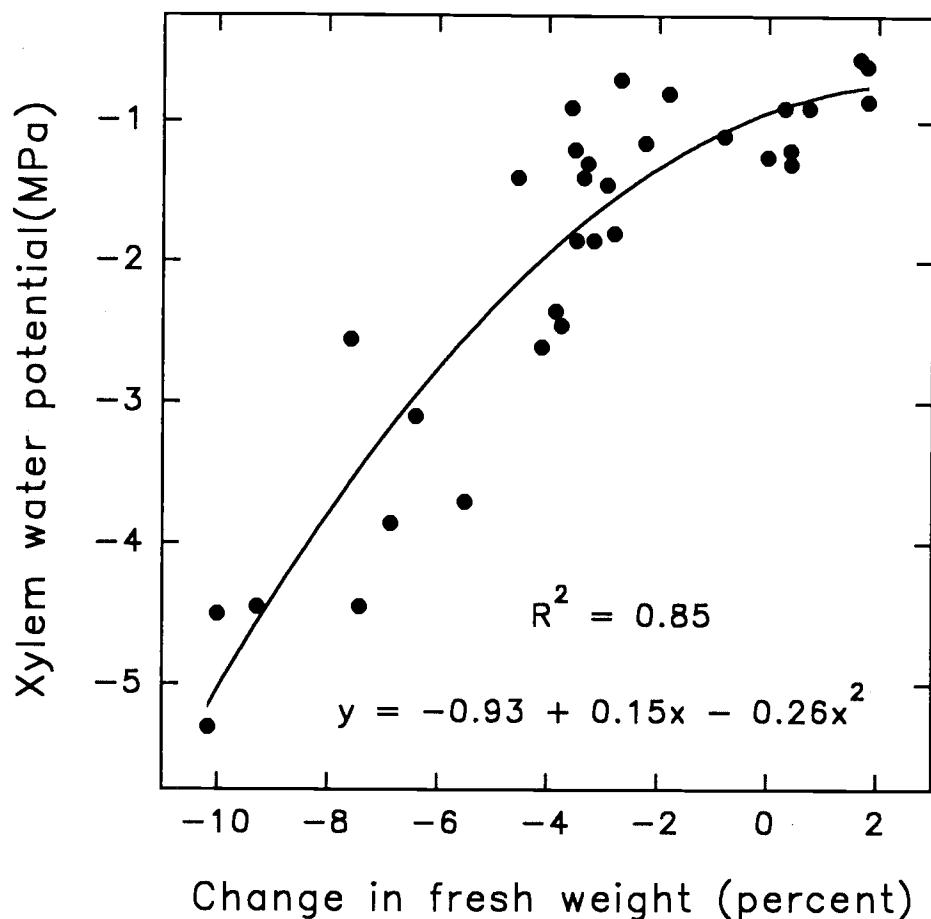


Figure 4.2 Correlation of percent change in original seedling fresh weight with xylem water potential after planting (14 to 20 days) in Washington hawthorn (*Crataegus phaeopyrum*).



XWP for each treatment after planting was contrasted to the mean XWP before planting (Table 4.1). No change in mean XWP for the RS-No, S-No, or RS-B treatments was found, indicating that XWP remained high in the former two treatments and low in the latter treatment after planting. In contrast, the non-stressed control was the only treatment which showed a mean decrease, whereas all other treatments showed an increase in mean XWP after planting (Table 4.1).

Despite large differences in treatment means for  $k_s$ , no differences were found between treatments after planting (Appendix 4.1). Similarly, there was little change in  $k_s$  between before or after planting (Table 4.1). Mean  $k_s$  for the S-B treatment did show a significant increase after planting, however, this was an exception to the general trend of no change or slightly decreasing values for  $k_s$  (Table 4.1).

#### *Effect of antidesiccant and stress treatments on budbreak and survival*

The first budbreak was seen 13 days after planting (Figure 4.3). Initial budbreak rates were strongly influenced by treatment (Appendix 4.2), with all non-stressed treatments breaking bud at similar high rates (Figure 4.4). Of the desiccated treatments, only those in the stems only group (whether treated before or after desiccation) had rates of budbreak as high as those of non-stressed seedlings. Survival percentages were high overall, and roughly followed budbreak trends (Figure 4.5).

Figure 4.3 Budbreak of Washington hawthorn seedlings. Panel A: desiccated (13.5 h) control (no Antidesiccant treatment). Panel B: non-stressed plants. Panel C: desiccated plants treated with antidesiccant before desiccation stress. Panel D: desiccated plants treated with antidesiccant after desiccation stress. AD indicates antidesiccant treatment; vertical bars indicate SE ( $n = 9 - 10$ );  $\circ$  indicates AD applications to roots + stems,  $\bullet$  to stems only, and  $\nabla$  indicates no AD treatment was applied.

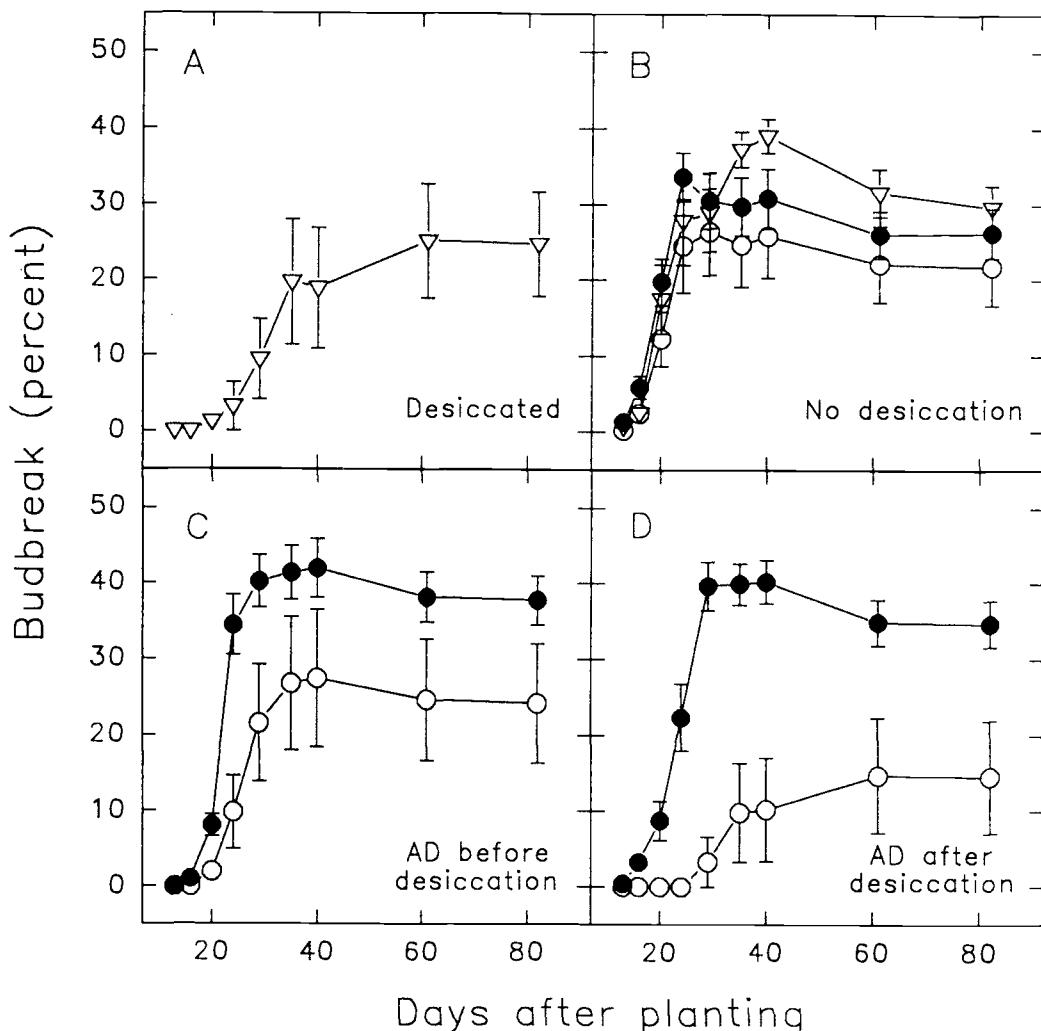


Figure 4.4 Budbreak rate (slope coefficient of regression, see text for definition) of Washington hawthorn seedlings. Desiccation constituted 13.5 hours exposure; stem + root or stems only indicate sites of antidesiccant (AD) treatment. Bars topped with the same letter are not significantly different at Waller ratio ( $K = 100$ ).

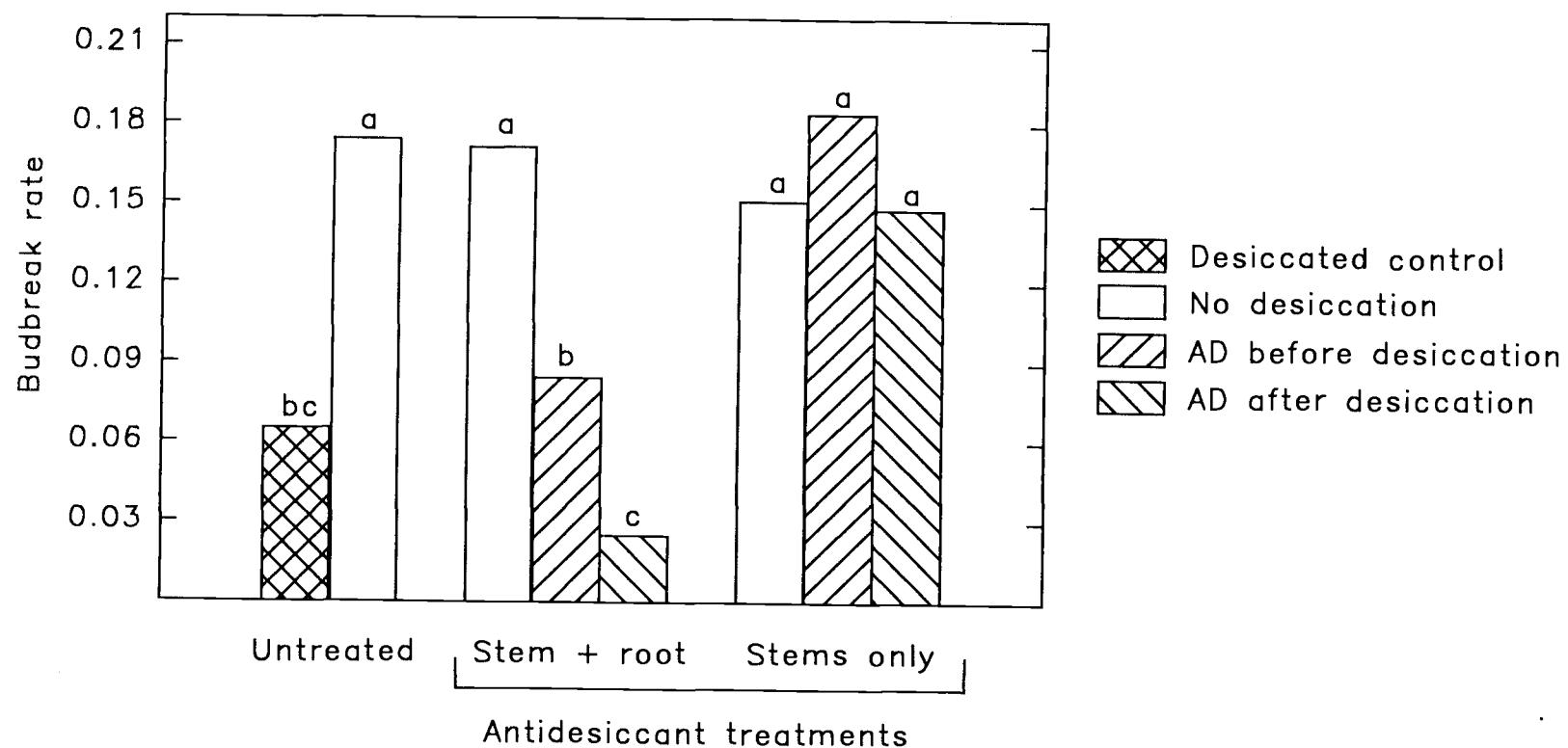
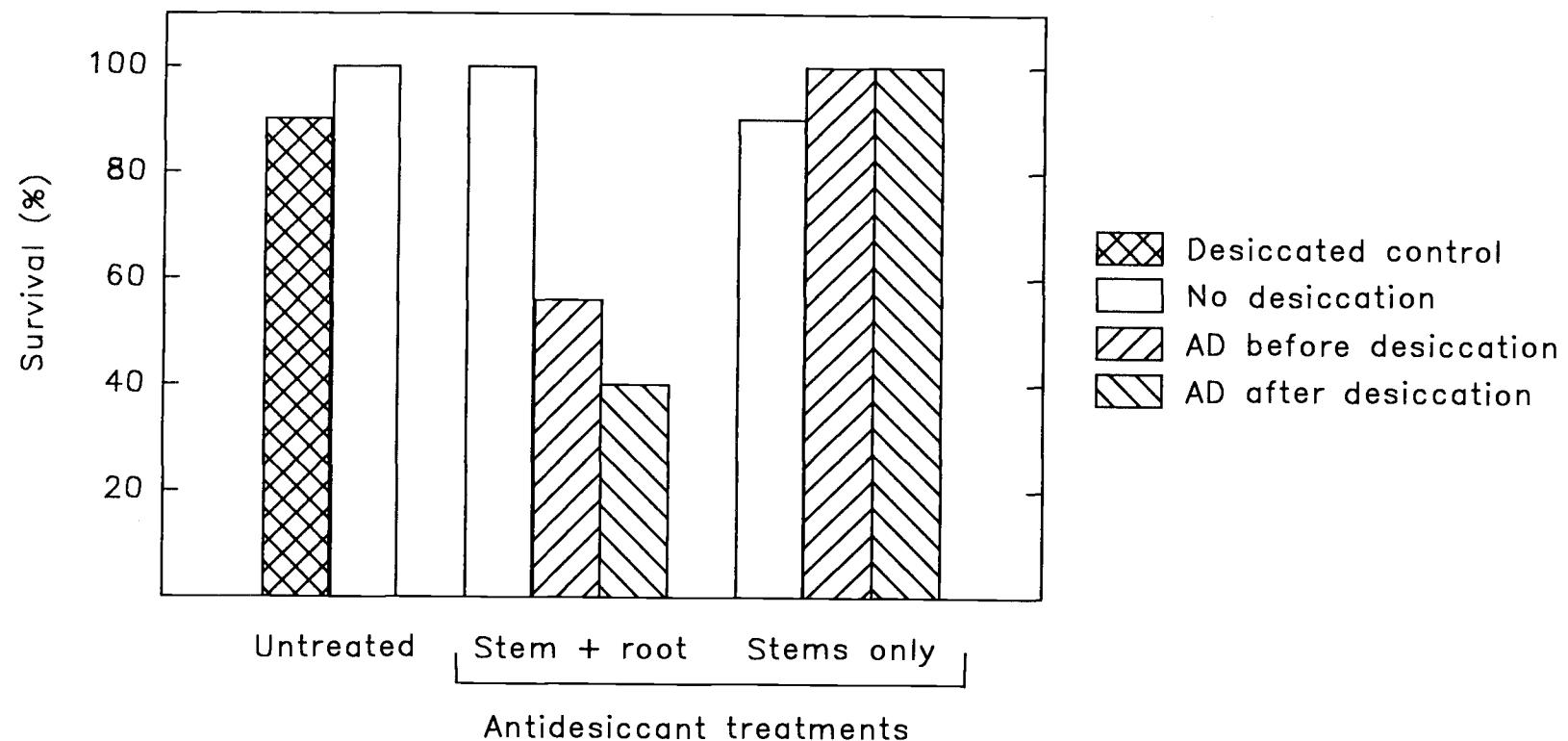


Figure 4.5 Survival percentages of Washington hawthorn seedlings. Desiccation constituted 13.5 hours exposure; stem + root or stems only indicate sites of antidesiccant (AD) treatment.



## Discussion

### *Seedling water relations before planting*

The effect of antidesiccant and desiccation treatments on fresh weight loss or XWP support the work of Englert et al. (1993) who showed that the antidesiccant Moisturin reduces rates of water loss and maintains higher XWP during exposure of bare root Washington hawthorn. Mean specific conductivity ( $k_s$ ), however, differed only between desiccation treatments, with no significant differences in  $k_s$  found between antidesiccant treatments. These results suggest that although significant reductions in water loss or stress development can be attained with antidesiccants, the effect of 13.5 hr. pre-planting desiccation exposure was equally detrimental to stem conductivity in all antidesiccant treatments.

$k_s$  in dormant hawthorn seedlings were low, compared to  $k_s$  values found for actively-growing apple rootstocks: ca. 1.1 and  $2.4 \times 10^{-5}$  kg MPa $^{-1}$  m $^{-1}$  s $^{-1}$  for M.9 and M.26 EMLA, respectively (Chapter 3). This observation suggests that (although not measured) the percentage embolism of field-grown Washington hawthorn in mid-winter may be relatively high. The large percentage embolism present in hawthorn seedlings at harvest does not necessarily indicate that severe pre-harvest water stress had occurred. Rather, exposure to freezing conditions (minima between -10 and -13 °C) prior to their harvest in late January may have accounted for the generally low values for  $k_s$  which were obtained. Freeze/thaw cycles during the winter have been shown to result in 84 to 95 % embolism in the stems or twigs of *Acer*, *Betula*, and *Populus* (Sperry et al., 1988b and Sperry & Sullivan, 1992). Although there are no air pockets within the lumen of conductive xylem (Sperry & Tyree, 1988 and Tyree & Sperry, 1989), xylem

sap does contain dissolved air (Zimmermann, 1983). Phase transition induces embolisms through the precipitation of this dissolved air in the xylem sap upon thawing (Tyree & Sperry, 1989).

Non-stressed Washington hawthorn seedlings had an average xylem tension of -0.7 MPa before planting (Table 4.1). This tension most likely arose during the bare-root harvesting and handling process (Englert, 1992 and Simpson, 1984) and is low enough to have precluded the dissolution of any freeze-induced embolisms present in the xylem of the seedlings (Tyree & Sperry, 1989). If hawthorns were as heavily embolized ( $\approx 90\%$ ) as the other species listed above, then  $k_s$  may have already been too low to find large differences induced by 13.5 hr. desiccation stress.

#### *Changes in seedling water relations after planting*

In stressed or non-stressed controls and seedlings in the S-B or S-A treatments, XWP after planting was influenced by the antidesiccant treatment, but not by the desiccation treatment. The data suggest that any treatment which either maintains or allows recovery of the 'original' fresh weight of a seedling tended to improve its water relations (Figure 4.2). In non-stressed seedlings, both antidesiccant treatments maintained a higher level of XWP by retaining a higher percentage of the original fresh weight, relative to non-stressed controls (Table 4.1). Similarly, desiccated plants treated with antidesiccant to stems only (either before or after desiccation stress) showed a recovery of fresh weight much higher than either the RS-B or RS-A treatments. The recovery (or retention) of fresh weight was reflected in the high XWP found in all plants receiving the stems only treatment. Stressed controls showed an intermediate recovery of fresh weight and mean XWP after planting (Table 4.1).

Differences in fresh weight change (relative to 'original' weights) of seedlings were likely due to uptake of water by the roots and/or its retention in the stems after planting. Water uptake by roots in the RS-A or RS-B seedlings was reduced compared to the controls or S-B and S-A seedlings. The reduced water uptake of the RS treatments may be due to 1. the lack of regeneration of highly-absorptive new white roots (Baxter & West, 1977; Grossnickle, 1988; and Sands, 1984) and 2. the presence of the film barrier itself on the root system (Chapter 3). The different levels of recovery of XWP or fresh weight seen in the RS-A, S-A, and control plants (which all had the same level of stress before planting) reflect the influence of the site of application of the film barrier discussed above: RS-A seedlings showed the lowest XWP or fresh weight gain resulting from the film barrier on the roots, whereas S-A plants had no coating on the roots and were able to take up more water, resulting in higher XWP. Controls, which were intermediate, had the advantage of uncoated roots, but without protection against stem water loss (Table 4.1).

The relationship of XWP to net change in 'original' fresh weight (Figure 4.2) parallels findings of Bates & Niemiera (1994) who showed significant increases in XWP of dormant Norway maple (*Acer platanoides*) and 'Yoshino' cherry (*Prunus yedoensis*) occurred within 3 to 6 days from planting in well-watered soil. In the current study, no correlation was found between XWP measured after planting and the loss of fresh weight during desiccation exposure before planting. This finding parallels the lack of relationship of XWP before planting to eventual seedling survival found elsewhere (Coutts, 1981). Thus, although decreasing the level of desiccation stress at planting has a positive influence on seedling survival (Chen et al., 1991; Englert et al., 1993; Insley & Buckley, 1985; Mullin, 1971; Murakami et al., 1990; and

Slocum & Maki, 1956), it is the ability of plants to take up water and relieve internal water stress during establishment which is of the greatest importance (Bates & Niemiera, 1994; Becker et al., 1987, Coutts, 1981; Grossnickle, 1988; Guehl et al., 1993; Kaushal & Aussenaac, 1989; Larson & Whitmore, 1970; and Sands, 1984). Therefore, XWP may be a more accurate predictor of transplant performance, if measured at some point after planting (Becker et al., 1987 and Guehl et al., 1993).

The tendency for decrease in  $k_s$  seen in the non-stressed control treatment was likely induced by the significant drop in XWP observed after planting, relative to the other non-stressed treatments, RS-No or S-No (Table 4.1 and Figure 4.1). In contrast, the mean  $k_s$  of S-B plants significantly increased after planting (Table 4.1). This increase may reflect a possible repair mechanism in this treatment. Repair of air-blocked xylem occurs in woody plants when water potential of intact (conductive) xylem elements adjacent to damaged ones approaches or exceeds atmospheric pressure for sufficient lengths of time. The duration of time required for refilling decreases with increasing XWP (Tyree & Sperry, 1989). In this treatment, the mean XWP increased from -2.5 to -1.4 MPa after planting. Although this change represents relief of xylem sap tension, -1.4 MPa is still considered to be too low for such repair to have taken place (Tyree & Sperry, 1989). Perhaps chance variability within the five subsamples (as evidenced by a highly conductive outlier) may have artificially raised mean  $k_s$  values after planting for this treatment.

Considering results for both  $k_s$  and XWP, it appears that although seedlings in some treatments were successful at taking-up soil water sufficient to induce significant relief of xylem tensions, there was no convincing evidence that this relief in turn resulted in any significant change

in  $k_s$  after planting. Overall increases in  $k_s$  (indicating refilling or repair) were likely prevented by low XWP (< - 0.5 MPa) across treatments. Conversely, decreases in  $k_s$  after planting (which would have indicated further cavitation had occurred) were prevented either by lack of further decrease in XWP (as for RS-No, S-No, or RS-B) or by increases in XWP (as in stressed controls, RS-A, S-B, and S-A) (Table 4.1). The unstressed control treatment was an exception to this conclusion, in that its XWP and fresh weight both decreased significantly after planting (Table 4.1 and Figure 4.1). There was, additionally, weak evidence that mean  $k_s$  for the treatment also dropped correspondingly (Table 4.1).

#### *Effect of antidesiccant and stress treatments on rate of budbreak*

As stated above, return to original (pre-stressed) fresh weight by water uptake was found to be directly related to increasing XWP (Figure 4.2). Mean budbreak rate tended to be higher in treatments with higher mean XWP (Figure 4.3 and Table 4.1). It is therefore suggested that budbreak rate (and presumably the eventual establishment of the seedling) may be positively related to water uptake after planting. Water loss after planting, due to interference of water uptake and transport, is a major factor in the failure of transplanted seedlings (Bates & Niemiera, 1994; Coutts, 1981; Insley & Buckley, 1985; and Sands 1984). Higher levels of water uptake (which increases XWP) are promoted by reducing water loss from stems (Bates & Niemiera, 1994). In addition, the presence of film coatings on roots of transplants has been shown to be detrimental to seedling survival (Tukey & Brase, 1931 and Chapter 3), most likely due to reduced water uptake.

In the current study, desiccated plants treated with antidesiccant to stems only (either before or after stress) attained significantly higher levels of net water uptake, XWP, and budbreak compared to desiccated seedlings treated with root + stem applications of antidesiccant (Table 4.1 and Figure 4.3). These levels of budbreak were equal to rates attained by unstressed seedlings, indicating that applications of antidesiccant to stems only induced recovery from pre-planting water stress whether applied before or after exposure to stress. Conversely, budbreak rates of stressed controls, RS-A, and RS-B were all significantly lower, indicating that no treatment or applications of antidesiccant to both roots and stems did not adequately aid in recovery from pre-planting desiccation stress (Figure 4.3).

The reduction in budbreak found in stressed controls or RS-A and RS-B seedlings are attributed to reduced water potential and losses of original fresh weight occurring before and after planting. These support the findings of others where relief of internal water stress is shown to be a prerequisite to regrowth and survival of transplanted conifer (Becker et al., 1987; Coutts, 1981; Kaushal & Aussenac, 1989 and Guehl et al., 1993) or dicotyledonous seedlings (Bates & Niemiera, 1994; Ranney et al., 1989). Similarly, it was found that higher rates of budbreak of M.26 EMLA layers, river birch and flowering dogwood seedlings were associated with antidesiccant applications to stems only, compared to root + stem treatments (Chapter 3).

Unstressed control seedlings sustained water loss and stress development similar to stressed controls or RS-A and RS-B seedlings (Table 4.1), yet rates of budbreak were not reduced as in the former three treatments (Figure 4.1). This treatment, then appears to be an exception to the above-stated findings, but it supports the findings of Becker et al. (1987) who showed that although biomass accretion in stressed seedlings of *Pinus*

*resinosa* was reduced by moisture deficits incurred after transplanting, but that shoot elongation was not. A possible explanation for the lack of effect of water stress after transplanting on budbreak or shoot elongation may be that water stress in the unstressed controls developed gradually (over 14 to 20 days). Gradual water stress development has been shown to induce osmoregulation in cereals which allows for continued growth at lower water potentials (Morgan, 1984).

Overall, there appeared to be little relationship of  $k_s$  to seedling budbreak performance or survival. This should not, however, necessarily imply that water transport in seedlings is unrelated to their establishment. It may be, rather, that the measurement technique employed was not precise enough to detect important differences. Sperry & Saliendra (1994) state that  $k_s$  values of unflushed stems have limited value in making interpretations of water stress effects on trees. Alternatively, any refilling which might have occurred throughout the 156 day study may have taken place after the final sampling date for the 'after planting' measurements (day 20). Perhaps measurement of percent embolism (obtained from comparing flushed versus unflushed stem conductances) or a later set of 'after planting' sampling dates would have yielded more useful information on treatment effects in the current study.

## Conclusion

Survival percentage was 90 to 100 % in all non-stressed treatments, desiccated controls or desiccated plants receiving applications of antidesiccant to stems only. Seedlings receiving antidesiccant to roots and stems before and after stress had 56 % and 40 % survival, respectively. Similarly, budbreak rate was highest in non-stressed seedlings or in

desiccated seedlings receiving antidesiccant applications to stems only.

Budbreak rates of desiccated controls or desiccated root + stem treatments were lower.

Non-desiccated seedlings and seedlings treated with antidesiccant to roots and stems before desiccation stress lost water after planting, whereas all other treatments increased in fresh weight after planting. Net change in seedling fresh weight in all treatments was negative, relative to their original (pre-stress) fresh weight. The loss in original fresh weight was most severe in untreated controls (stressed and unstressed) and in seedlings receiving antidesiccant treatment to roots and stems (applied either before or after desiccation stress).

XWP and  $k_s$  were highest in non-stressed plants before planting, but there were no treatment differences in  $k_s$  after planting. XWP after planting decreased in non-stressed controls and increased in pre-stressed controls or stressed plants receiving applications of antidesiccant to stems only and roots and stems (applied after desiccation stress). XWP of non-stressed plants receiving antidesiccant treatments or stressed plants receiving antidesiccant to both stems and roots (before stress exposure) did not change after planting.

A significant relationship ( $R^2 = 0.85$ ) between change in fresh weight (relative to original fresh weight) and XWP after planting was found.

Budbreak was also found generally to be higher in those treatments which showed higher XWP after planting.

In conclusion, applications of antidesiccant to stems only of Washington hawthorn seedlings, either before or after stress, contributed to increased budbreak rate and recovery from water stress. In contrast, applications of antidesiccant to roots and stems, either before or after stress,

were detrimental to budbreak and seedling water relations after planting. Antidesiccant applications to non-stressed Washington hawthorn seedlings had no additional benefit to budbreak rate but maintained better water relations after planting. XWP measured 14 to 20 days after planting appeared to be a good indicator of eventual budbreak rate of Washington hawthorn seedlings.

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**APPENDIX**

**Appendix 4.1 Analysis of variance for xylem water potential (XWP) and log-transformed specific conductivity ( $k_s$ ) of Washington hawthorn seedlings after desiccation exposure before and after planting (after).**

Dependent Variable: XWP before

| Source          | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|----|----------------|-------------|---------|--------|
| Model           | 3  | 89.49495295    | 29.83165098 | 125.96  | 0.0001 |
| Error           | 43 | 10.18355769    | 0.23682692  |         |        |
| Corrected Total | 46 | 99.67851064    |             |         |        |

| R-Square | C.V.      | Root MSE  | XWP before Mean |
|----------|-----------|-----------|-----------------|
| 0.897836 | -18.81735 | 0.4866487 | -2.5861702      |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------|----|-------------|-------------|---------|--------|
| TREAT  | 3  | 89.49495295 | 29.83165098 | 125.96  | 0.0001 |

Dependent Variable:  $k_s$  before

| Source          | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|----|----------------|-------------|---------|--------|
| Model           | 3  | 11.24712258    | 3.74904086  | 12.00   | 0.0001 |
| Error           | 46 | 14.37634297    | 0.31252920  |         |        |
| Corrected Total | 49 | 25.62346555    |             |         |        |

| R-Square | C.V.      | Root MSE  | $k_s$ before Mean |
|----------|-----------|-----------|-------------------|
| 0.438938 | -3.282702 | 0.5590431 | -17.029967        |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------|----|-------------|-------------|---------|--------|
| TREAT  | 3  | 11.24712258 | 3.74904086  | 12.00   | 0.0001 |

Dependent Variable: XWP after

| Source          | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|----|----------------|-------------|---------|--------|
| Model           | 7  | 28.16666892    | 4.02380985  | 3.89    | 0.0042 |
| Error           | 29 | 30.02225000    | 1.03525000  |         |        |
| Corrected Total | 36 | 58.18891892    |             |         |        |

| R-Square | C.V.      | Root MSE  | XWP after Mean |
|----------|-----------|-----------|----------------|
| 0.484056 | -51.01149 | 1.0174724 | -1.9945946     |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------|----|-------------|-------------|---------|--------|
| TREAT  | 7  | 28.16666892 | 4.02380985  | 3.89    | 0.0042 |

Dependent Variable:  $k_s$  after

| Source          | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|-----------------|----|----------------|-------------|---------|--------|
| Model           | 7  | 3.58872724     | 0.51267532  | 1.37    | 0.2515 |
| Error           | 32 | 11.97171107    | 0.37411597  |         |        |
| Corrected Total | 39 | 15.56043831    |             |         |        |

| R-Square | C.V.      | Root MSE  | $k_s$ after Mean |
|----------|-----------|-----------|------------------|
| 0.230632 | -3.631140 | 0.6116502 | -16.844578       |

| Source | DF | Type III SS | Mean Square | F Value | Pr > F |
|--------|----|-------------|-------------|---------|--------|
| TREAT  | 7  | 3.58872724  | 0.51267532  | 1.37    | 0.2515 |

**Appendix 4.2 Analysis of variance for percent change in fresh weight from original fresh weight (FW change 1) and change in fresh weight from fresh weight at planting (FW change 2) and budbreak rate (rate) in Washington hawthorn seedlings.**

Dependent Variable: FW change 1

| Source          | DF | Sum of Squares | Mean Square | F Value          | Pr > F |
|-----------------|----|----------------|-------------|------------------|--------|
| Model           | 7  | 217.07860259   | 31.01122894 | 6.07             | 0.0003 |
| Error           | 26 | 132.81888456   | 5.10841864  |                  |        |
| Corrected Total | 33 | 349.89748715   |             |                  |        |
| R-Square        |    | C.V.           | Root MSE    | FW change 1 Mean |        |
| 0.620406        |    | -69.60725      | 2.2601811   | -3.2470484       |        |
| Source          | DF | Type III SS    | Mean Square | F Value          | Pr > F |
| TREAT           | 7  | 217.07860259   | 31.01122894 | 6.07             | 0.0003 |

Dependent Variable: FW change 2

| Source          | DF | Sum of Squares | Mean Square  | F Value          | Pr > F |
|-----------------|----|----------------|--------------|------------------|--------|
| Model           | 7  | 825.20370334   | 117.88624333 | 16.00            | 0.0001 |
| Error           | 26 | 191.57769876   | 7.36837303   |                  |        |
| Corrected Total | 33 | 1016.78140210  |              |                  |        |
| R-Square        |    | C.V.           | Root MSE     | FW change 2 Mean |        |
| 0.811584        |    | 112.3967       | 2.7144747    | 2.4150842        |        |
| Source          | DF | Type III SS    | Mean Square  | F Value          | Pr > F |
| TREAT           | 7  | 825.20370334   | 117.88624333 | 16.00            | 0.0001 |

Dependent Variable: rate

| Source          | DF | Sum of Squares | Mean Square | F Value   | Pr > F |
|-----------------|----|----------------|-------------|-----------|--------|
| Model           | 7  | 0.24419295     | 0.03488471  | 7.71      | 0.0001 |
| Error           | 71 | 0.32131729     | 0.00452560  |           |        |
| Corrected Total | 78 | 0.56551024     |             |           |        |
| R-Square        |    | C.V.           | Root MSE    | rate Mean |        |
| 0.431810        |    | 53.58255       | 0.0672725   | 0.1255494 |        |
| Source          | DF | Type III SS    | Mean Square | F Value   | Pr > F |
| TREAT           | 7  | 0.24419295     | 0.03488471  | 7.71      | 0.0001 |

Table A.1 Treatment combinations applied in auxin (IBA) versus antidesiccant (AD) treatment of roots factorial.

|               |   | IBA treatment         |         |
|---------------|---|-----------------------|---------|
|               |   | +                     | -       |
| Antidesiccant | + | AD + IBA <sup>y</sup> | AD      |
|               | - | IBA                   | control |

<sup>z</sup> + / - denotes treated and not treated, respectively

<sup>y</sup> ADIBA, AD, IBA, or control denote: IBA + antidesiccant, antidesiccant only, IBA only or neither factor, respectively

Table A.2 Treatment combinations applied in stem versus root antidesiccant treatment factorial.

|                |   | Stem treatment  |         |
|----------------|---|-----------------|---------|
|                |   | +               | -       |
| Root treatment | + | RS <sup>y</sup> | R       |
|                | - | S               | control |

<sup>z</sup> + / - denotes treated and not treated, respectively

<sup>y</sup> RS, R, S, or control denote: roots + stems, roots only, stems only, or neither organ, respectively, received antidesiccant treatment.

Table A.3 Summary statistics of budbreak and new root and shoot growth of river birch seedlings treated with indole-3 butyric acid (IBA) or antidesiccant (AD) applications to roots.

| ANOVA <sup>z</sup>      | Variables Quantified |             |            |                     |           |           |           |           |           |           |
|-------------------------|----------------------|-------------|------------|---------------------|-----------|-----------|-----------|-----------|-----------|-----------|
|                         | Establishment        |             |            | Buds broken, by day |           |           |           |           |           |           |
|                         | New root             | New shoot   | Dieback    | Day 11              | Day 16    | Day 23    | Day 31    | Day 41    | Day 53    | Day 65    |
| Error mean <sup>2</sup> | 8.31                 | 449         | 188        | 0.34                | 3.63      | 15.27     | 15.15     | 19.58     | 11.73     | 13.07     |
| Source (AD)             |                      |             |            |                     |           |           |           |           |           |           |
| Mean <sup>2</sup>       | 2.38                 | 355         | 155        | 0.15                | 0.08      | 0.23      | 0.23      | 0.23      | 0.45      | 0.08      |
| P - value               | 0.61                 | 0.40        | 0.39       | 0.53                | 0.88      | 0.91      | 0.91      | 0.92      | 0.85      | 0.94      |
| 'AD -' (SE)             | 4.19 (0.99)          | 35.4 (7.4)  | 72.3 (4.5) | 0.3 (0.3)           | 1.4 (1.4) | 3.1 (1.5) | 3.6 (1.3) | 4.2 (1.4) | 3.8 (1.0) | 4.3 (1.2) |
| 'AD +' (SE)             | 3.30 (1.43)          | 24.6 (9.0)  | 79.5 (5.7) | 0.1 (0.1)           | 1.2 (0.9) | 3.4 (1.4) | 3.8 (1.6) | 3.9 (2.0) | 3.4 (1.5) | 4.1 (1.6) |
| Source (IBA)            |                      |             |            |                     |           |           |           |           |           |           |
| Mean <sup>2</sup>       | 22.74                | 524         | 3          | 0.59                | 4.10      | 1.57      | 5.79      | 8.89      | 7.79      | 11.34     |
| P - value               | 0.14                 | 0.31        | 0.91       | 0.23                | 0.32      | 0.76      | 0.55      | 0.52      | 0.44      | 0.38      |
| 'IBA -' (SE)            | 5.13 (1.33)          | 36.6 (9.0)  | 75.4 (4.5) | 0.4 (0.3)           | 1.9 (0.9) | 3.6 (1.5) | 4.4 (1.8) | 4.9 (2.0) | 4.4 (1.6) | 5.2 (1.6) |
| 'IBA +' (SE)            | 2.37 (0.76)          | 23.4 (7.1)  | 76.4 (6.1) | 0.0 (0.0)           | 0.7 (0.5) | 2.9 (1.4) | 3.0 (1.0) | 3.2 (1.2) | 2.8 (0.8) | 3.2 (1.1) |
| Source<br>(ADxIBA)      |                      |             |            |                     |           |           |           |           |           |           |
| Mean <sup>2</sup>       | 1.15                 | 0           | 49         | 0.15                | 0.45      | 0.75      | 1.56      | 4.90      | 0.45      | 10.08     |
| P - value               | 0.72                 | 0.98        | 0.63       | 0.53                | 0.73      | 0.83      | 0.76      | 0.63      | 0.85      | 0.41      |
| 'IBA + AD' (SE)         | 1.62 (0.85)          | 17.8 (9.0)  | 82.0 (9.2) | 0.0 (0.0)           | 0.4 (0.4) | 2.8 (1.0) | 2.8 (0.3) | 2.4 (1.2) | 2.4 (1.2) | 2.2 (1.1) |
| 'AD' (SE)               | 4.99 (2.57)          | 31.3 (16.8) | 77.0 (8.3) | 0.2 (0.1)           | 2.0 (1.7) | 4.0 (2.8) | 4.9 (3.5) | 5.4 (3.9) | 4.4 (3.0) | 6.0 (2.9) |
| 'IBA" (SE)              | 3.13 (1.27)          | 29.0 (11.8) | 70.7 (8.4) | 0.0 (0.0)           | 1.0 (1.0) | 3.0 (3.0) | 3.2 (2.2) | 4.0 (2.3) | 3.2 (1.2) | 4.2 (2.0) |
| Control (SE)            | 5.26 (1.47)          | 41.9 (9.8)  | 73.8 (5.2) | 0.7 (0.7)           | 1.8 (0.9) | 3.2 (1.6) | 3.9 (1.8) | 4.4 (2.1) | 4.4 (1.9) | 4.3 (2.0) |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

Table A.4 Summary statistics of budbreak, visual rating, and new shoot growth of flowering dogwood seedlings treated with indole-3 butyric acid (IBA) or antidesiccant (AD) applications to roots.

| ANOVA <sup>z</sup>      | Variables Quantified |             |                  |            |            |            |             |             |             |             |
|-------------------------|----------------------|-------------|------------------|------------|------------|------------|-------------|-------------|-------------|-------------|
|                         | Establishment        |             | Budbreak, by day |            |            |            |             |             |             |             |
|                         | Rating               | New shoot   | Day 11           | Day 16     | Day 23     | Day 31     | Day 40      | Day 50      | Day 62      | Day 74      |
| Error mean <sup>2</sup> | 0.99                 | 2245        | 478              | 1831       | 2087       | 1571       | 2591        | 2445        | 2355        | 2588        |
| Source (AD)             |                      |             |                  |            |            |            |             |             |             |             |
| Mean <sup>2</sup>       | 0.34                 | 2041        | 434              | 2620       | 6578       | 1397       | 2741        | 2447        | 7680        | 4877        |
| P - value               | 0.57                 | 0.37        | 0.37             | 0.27       | 0.11       | 0.37       | 0.33        | 0.35        | 0.11        | 0.21        |
| 'AD -' (SE)             | 2.50 (0.53)          | 73.0 (26.8) | 8.7 (2.7)        | 16.1 (4.9) | 23.7 (5.2) | 23.9 (4.8) | 24.8 (6.0)  | 21.7 (5.9)  | 29.1 (5.3)  | 31.4 (5.0)  |
| 'AD +' (SE)             | 2.16 (0.31)          | 46.9 (15.8) | 4.8 (1.1)        | 7.9 (2.8)  | 11.3 (2.8) | 18.5 (2.4) | 17.9 (3.4)  | 15.6 (2.5)  | 18.0 (3.4)  | 22.9 (4.0)  |
| Source (IBA)            |                      |             |                  |            |            |            |             |             |             |             |
| Mean <sup>2</sup>       | 2.38                 | 8595        | 118              | 479        | 154        | 1735       | 65          | 2           | 1902        | 560         |
| P - value               | 0.16                 | 0.09        | 0.63             | 0.62       | 0.79       | 0.32       | 0.88        | 0.98        | 0.40        | 0.65        |
| 'IBA -' (SE)            | 1.89 (0.19)          | 33.2 (6.4)  | 6.4 (2.8)        | 10.9 (5.0) | 16.6 (4.4) | 18.1 (2.7) | 20.3 (1.7)  | 18.1 (1.1)  | 25.9 (3.2)  | 28.2 (3.4)  |
| 'IBA +' (SE)            | 2.78 (0.52)          | 86.7 (26.7) | 7.1 (1.4)        | 13.1 (3.6) | 18.4 (5.6) | 24.3 (4.5) | 22.4 (7.0)  | 19.2 (6.6)  | 21.2 (6.3)  | 26.1 (6.0)  |
| Source (ADxIBA)         |                      |             |                  |            |            |            |             |             |             |             |
| Mean <sup>2</sup>       | 0.93                 | 2547        | 0                | 614        | 1383       | 825        | 5208        | 2200        | 759         | 8           |
| P - value               | 0.36                 | 0.32        | 0.98             | 0.58       | 0.44       | 0.49       | 0.19        | 0.37        | 0.59        | 0.96        |
| 'AD + IBA' (SE)         | 2.33 (0.58)          | 59.1 (30.9) | 5.4 (0.6)        | 7.9 (1.9)  | 10.2 (2.0) | 19.9 (3.9) | 14.3 (6.1)  | 12.9 (4.5)  | 13.6 (5.0)  | 21.8 (7.9)  |
| 'AD' (SE)               | 2.00 (0.33)          | 34.7 (12.2) | 4.2 (2.4)        | 7.8 (6.0)  | 12.4 (5.9) | 17.2 (3.4) | 21.6 (2.4)  | 18.3 (1.6)  | 22.5 (3.7)  | 23.9 (4.2)  |
| 'IBA' (SE)              | 3.22 (0.91)          | 114.3 (43)  | 8.8 (2.6)        | 18.3 (6.0) | 26.5 (9.1) | 28.7 (8.1) | 30.5 (12.0) | 25.5 (12.5) | 28.9 (10.7) | 30.4 (10.0) |
| Control (SE)            | 1.78 (0.22)          | 31.7 (7.3)  | 8.5 (5.4)        | 13.9 (9.0) | 20.8 (6.6) | 19.1 (5.0) | 19.1 (2.6)  | 18.0 (1.9)  | 29.3 (5.2)  | 32.4 (4.8)  |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

Table A.5 Summary statistics of budbreak and new root and shoot growth of European beech seedlings treated with antidesiccant applications to roots (R) and stems (S).

| ANOVA <sup>z</sup>      | Variables Quantified |             |                  |             |             |             |             |             |             |
|-------------------------|----------------------|-------------|------------------|-------------|-------------|-------------|-------------|-------------|-------------|
|                         | Establishment        |             | Budbreak, by day |             |             |             |             |             |             |
|                         | New root             | New leaf    | Day 12           | Day 17      | Day 24      | Day 32      | Day 45      | Day 53      | Day 66      |
| Error mean <sup>2</sup> | 60.41                | 91.03       | 3029             | 3271        | 1839        | 1694        | 1620        | 1820        | 1710        |
| Source (R)              |                      |             |                  |             |             |             |             |             |             |
| Mean <sup>2</sup>       | 17.11                | 1.70        | 5963             | 560         | 333         | 305         | 248         | 833         | 795         |
| P - value               | 0.61                 | 0.90        | 0.20             | 0.69        | 0.68        | 0.68        | 0.71        | 0.52        | 0.51        |
| 'R -' (SE)              | 8.75 (3.06)          | 18.0 (2.3)  | 61.9 (5.8)       | 64.7 (7.4)  | 61.8 (6.7)  | 64.4 (6.6)  | 64.6 (6.7)  | 64.7 (7.2)  | 64.0 (6.5)  |
| 'R +' (SE)              | 6.37 (2.81)          | 17.2 (4.4)  | 47.1 (6.8)       | 61.4 (5.8)  | 59.5 (5.3)  | 62.0 (5.6)  | 63.8 (6.5)  | 61.2 (7.2)  | 60.7 (6.0)  |
| Source (S)              |                      |             |                  |             |             |             |             |             |             |
| Mean <sup>2</sup>       | 34.10                | 6.53        | 1361             | 12          | 7475        | 8943        | 11597       | 16220       | 8480        |
| P - value               | 0.47                 | 0.80        | 0.52             | 0.95        | 0.08        | 0.05        | 0.03        | 0.02        | 0.06        |
| 'S -' (SE)              | 9.25 (3.36)          | 18.3 (4.4)  | 57.0 (8.3)       | 61.8 (8.5)  | 67.5 (6.7)  | 71.0 (6.5)  | 73.0 (6.6)  | 73.5 (6.2)  | 69.9 (6.1)  |
| 'S +' (SE)              | 5.87 (2.33)          | 16.8 (2.23) | 52.1 (5.5)       | 64.2 (4.1)  | 53.7 (3.3)  | 55.5 (3.1)  | 55.3 (3.7)  | 52.4 (4.6)  | 54.8 (4.4)  |
| Source (RxS)            |                      |             |                  |             |             |             |             |             |             |
| Mean <sup>2</sup>       | 0.15                 | 0.06        | 241              | 24          | 551         | 800         | 2288        | 1059        | 917         |
| P - value               | 0.96                 | 0.98        | 0.79             | 0.93        | 0.60        | 0.51        | 0.27        | 0.47        | 0.54        |
| 'RS' (SE)               | 4.79 (3.57)          | 8.4 (5.1)   | 43.0 (5.3)       | 63.0 (4.2)  | 50.0 (2.5)  | 51.2 (1.3)  | 50.1 (2.8)  | 47.3 (6.3)  | 49.8 (7.0)  |
| 'R' (SE)                | 7.94 (4.91)          | 10.3 (5.2)  | 51.3 (13.7)      | 59.8 (12.1) | 68.9 (6.8)  | 72.8 (6.4)  | 77.5 (4.4)  | 75.0 (4.9)  | 71.6 (3.7)  |
| 'S' (SE)                | 6.96 (3.63)          | 14.4 (13.0) | 61.2 (6.4)       | 65.5 (8.1)  | 57.5 (5.8)  | 59.7 (5.3)  | 60.6 (5.7)  | 57.4 (6.2)  | 59.8 (5.1)  |
| Control (SE)            | 10.55 (5.5)          | 16.2 (5.9)  | 62.7 (11.4)      | 63.9 (14.5) | 66.1 (13.2) | 69.1 (12.8) | 68.6 (13.4) | 72.0 (12.9) | 68.1 (13.0) |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

**Table A.6 Summary statistics of budbreak, specific conductivity ( $k_s$ ), stem dieback, and new root and shoot growth of M.26 EMLA apple rootstock layers treated with antidesiccant applications to roots (R) or stems (S).**

| ANOVA <sup>z</sup>      | Variables Quantified |             |             |            |                  |            |             |             |             |             |             |
|-------------------------|----------------------|-------------|-------------|------------|------------------|------------|-------------|-------------|-------------|-------------|-------------|
|                         | Establishment        |             |             |            | Budbreak, by day |            |             |             |             |             |             |
|                         | New root             | New shoot   | Dieback     | $k_s$      | Day 28           | Day 36     | Day 49      | Day 57      | Day 70      | Day 83      | Day 115     |
| Error mean <sup>2</sup> | 17.6                 | 10.3        | 635         | N/A        | 0.024            | 0.059      | 0.126       | 0.060       | 0.364       | 0.263       | 0.330       |
| Source (R)              |                      |             |             |            |                  |            |             |             |             |             |             |
| Mean <sup>2</sup>       | 19.7                 | 11.9        | 436         | F = 1.25   | 0.242            | 0.242      | 1.365       | 0.467       | 0.414       | 0.181       | 0.347       |
| P - value               | 0.32                 | 0.31        | 0.43        | 0.30       | 0.01             | 0.01       | 0.01        | 0.02        | 0.32        | 0.43        | 0.34        |
| 'R -' (SE)              | 9.68 (4.46)          | 7.24 (2.71) | 36.5 (15.9) | 13.0 (4.4) | 8.4 (4.4)        | 14.7 (7.0) | 29.2 (12.0) | 29.7 (12.1) | 31.3 (10.8) | 32.2 (11.1) | 31.2 (10.6) |
| 'R +' (SE)              | 7.12 (2.13)          | 9.23 (2.84) | 24.4 (16.3) | 15.9 (5.0) | 0.0 (0.0)        | 3.3 (3.3)  | 9.4 (6.1)   | 18.1 (8.4)  | 42.2 (14.7) | 39.6 (13.6) | 41.3 (13.2) |
| Source (S)              |                      |             |             |            |                  |            |             |             |             |             |             |
| Mean <sup>2</sup>       | 522.7                | 378.1       | 10065       | F = 58.53  | 0.242            | 1.100      | 4.264       | 6.836       | 8.688       | 8.653       | 7.355       |
| P - value               | 0.0006               | 0.0003      | 0.004       | 0.0001     | 0.01             | 0.003      | 0.0004      | 0.0001      | 0.001       | 0.0004      | 0.002       |
| 'S -' (SE)              | 1.80 (0.89)          | 2.62 (1.15) | 59.4 (14.0) | 4.6 (1.5)  | 0.0 (0.0)        | 0.0 (0.0)  | 1.7 (1.7)   | 1.7 (1.7)   | 12.0 (4.6)  | 11.2 (4.1)  | 13.4 (5.6)  |
| 'S +' (SE)              | 15.00 (2.6)          | 13.85 (1.4) | 1.5 (0.1)   | 24.4 (2.0) | 8.4 (4.4)        | 18.1 (6.4) | 37.0 (9.6)  | 46.1 (5.6)  | 61.4 (9.0)  | 60.6 (7.3)  | 59.0 (7.6)  |
| Source (RxS)            |                      |             |             |            |                  |            |             |             |             |             |             |
| Mean <sup>2</sup>       | 69.5                 | 1.2         | 445         | F = 0.02   | 0.242            | 0.462      | 0.931       | 0.218       | 0.069       | 0.063       | 0.0190      |
| P - value               | 0.08                 | 0.74        | 0.42        | 0.89       | 0.01             | 0.02       | 0.02        | 0.09        | 0.68        | 0.64        | 0.82        |
| 'RS' (SE)               | 11.31 (1.7)          | 14.53 (2.9) | 1.5 (0.3)   | 26.0 (3.8) | 0.0 (0.0)        | 6.7 (11.5) | 18.9 (17.1) | 36.3 (8.6)  | 68.7 (30.9) | 66.1 (22.9) | 64.9 (24.8) |
| 'R' (SE)                | 2.92 (1.55)          | 3.94 (1.98) | 47.3 (28.3) | 5.8 (3.1)  | 0.0 (0.0)        | 0.0 (0.0)  | 0.0 (0.0)   | 0.0 (0.0)   | 15.6 (13.7) | 13.1 (11.4) | 17.6 (17.3) |
| 'S' (SE)                | 18.69 (4.2)          | 13.17 (0.8) | 1.4 (0.0)   | 22.7 (1.7) | 16.8 (9.1)       | 29.4 (9.3) | 55.0 (10.9) | 56.0 (10.0) | 54.1 (10.3) | 55.0 (13.2) | 53.1 (11.8) |
| Control (SE)            | 0.67 (0.58)          | 1.31 (0.98) | 71.5 (5.6)  | 3.3 (0.6)  | 0.0 (0.0)        | 0.0 (0.0)  | 3.4 (5.9)   | 3.4 (5.9)   | 8.4 (9.4)   | 9.3 (10.8)  | 9.3 (10.8)  |
| Contrast <sup>x</sup>   |                      |             |             |            |                  |            |             |             |             |             |             |
| Mean <sup>2</sup>       | --                   | --          | --          | --         | 4723             | 9015       | 22469       | 6461        | --          | --          | --          |
| P - value               | --                   | --          | --          | --         | 0.002            | 0.005      | 0.0003      | 0.01        | --          | --          | --          |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

<sup>x</sup> Contrast denotes t-test summary for budbreak of stems only treatment (S) versus roots + stems (RS).

Table A.7 Summary statistics of budbreak, specific conductivity ( $k_s$ ), stem dieback, and new root and shoot growth of M.9 apple rootstock layers treated with antidesiccant applications to roots (R) or stems (S).

| ANOVA <sup>z</sup>      | Variables Quantified |             |             |            |                  |             |            |             |             |             |             |
|-------------------------|----------------------|-------------|-------------|------------|------------------|-------------|------------|-------------|-------------|-------------|-------------|
|                         | Establishment        |             |             |            | Budbreak, by day |             |            |             |             |             |             |
|                         | New root             | New shoot   | Dieback     | $k_s$      | Day 28           | Day 36      | Day 49     | Day 57      | Day 70      | Day 83      | Day 115     |
| Error mean <sup>2</sup> | 3                    | 3.7         | 61          | N/A        | 0.088            | 0.173       | 0.115      | 0.135       | 0.339       | 0.382       | 0.370       |
| Source (R)              |                      |             |             |            |                  |             |            |             |             |             |             |
| Mean <sup>2</sup>       | 31                   | 14.3        | 239         | F = 13.77  | 0.002            | 0.001       | 0.490      | 0.164       | 0.030       | 0.000       | 0.022       |
| P - value               | 0.01                 | 0.09        | 0.08        | 0.006      | 0.88             | 0.95        | 0.07       | 0.30        | 0.78        | 0.99        | 0.82        |
| 'R -' (SE)              | 4.03 (1.55)          | 4.59 (1.42) | 14.3 (6.9)  | 3.4 (0.8)  | 6.5 (3.3)        | 10.2 (3.7)  | 10.6 (3.1) | 12.3 (3.0)  | 20.4 (7.5)  | 23.3 (10.0) | 24.4 (10.5) |
| 'R +' (SE)              | 7.25 (2.61)          | 6.77 (2.37) | 5.4 (2.9)   | 6.2 (2.0)  | 5.5 (3.8)        | 10.4 (7.0)  | 22.3 (7.4) | 19.2 (6.3)  | 20.5 (5.1)  | 24.0 (5.7)  | 21.7 (4.9)  |
| Source (S)              |                      |             |             |            |                  |             |            |             |             |             |             |
| Mean <sup>2</sup>       | 237                  | 189.0       | 961         | F = 57.24  | 0.364            | 0.364       | 1.693      | 0.934       | 1.669       | 2.567       | 2.118       |
| P - value               | 0.0001               | 0.0001      | 0.004       | 0.0001     | 0.08             | 0.08        | 0.005      | 0.03        | 0.06        | 0.03        | 0.05        |
| 'S -' (SE)              | 1.19 (0.48)          | 1.71 (0.47) | 18.77 (5.7) | 1.9 (0.3)  | 1.3 (1.3)        | 2.1 (1.4)   | 6.8 (3.9)  | 8.6 (5.1)   | 11.8 (5.3)  | 11.7 (4.9)  | 11.6 (4.4)  |
| 'S +' (SE)              | 10.08 (1.5)          | 9.65 (1.26) | 0.88 (0.24) | 7.6 (1.4)  | 10.7 (3.8)       | 18.5 (5.8)  | 26.1 (5.1) | 23.0 (2.5)  | 29.2 (4.8)  | 35.6 (7.1)  | 34.5 (8.0)  |
| Source (RxS)            |                      |             |             |            |                  |             |            |             |             |             |             |
| Mean <sup>2</sup>       | 15                   | 10.0        | 240         | F = 15.22  | 0.016            | 0.089       | 0.275      | 0.017       | 0.677       | 0.310       | 0.424       |
| P - value               | 0.05                 | 0.14        | 0.08        | 0.005      | 0.68             | 0.49        | 0.16       | 0.73        | 0.20        | 0.39        | 0.32        |
| 'RS' (SE)               | 12.82 (1.5)          | 11.65 (1.8) | 0.89 (0.42) | 10.5 (0.8) | 11.0 (11.1)      | 20.8 (20.2) | 36.1 (6.5) | 27.3 (5.0)  | 23.4 (6.1)  | 31.3 (7.6)  | 27.6 (4.9)  |
| 'R' (SE)                | 1.67 (0.90)          | 1.89 (0.96) | 9.84 (4.67) | 1.8 (0.4)  | 0.0 (0.0)        | 0.0 (0.0)   | 8.5 (14.8) | 11.1 (19.2) | 17.5 (18.0) | 16.7 (16.7) | 15.8 (15.4) |
| 'S' (SE)                | 7.34 (0.97)          | 7.65 (0.79) | 0.86 (0.34) | 4.8 (1.1)  | 10.4 (9.7)       | 16.1 (9.2)  | 16.1 (7.3) | 18.7 (3.3)  | 34.9 (14.5) | 39.9 (25.5) | 41.4 (28.1) |
| Control (SE)            | 0.72 (0.36)          | 1.53 (0.41) | 27.71 (7.7) | 2.0 (0.6)  | 2.6 (4.5)        | 4.2 (3.9)   | 5.1 (0.6)  | 6.0 (1.3)   | 6.0 (1.3)   | 6.6 (1.7)   | 7.4 (0.4)   |
| Contrast <sup>x</sup>   |                      |             |             |            |                  |             |            |             |             |             |             |
| Mean <sup>2</sup>       | 45                   | --          | --          | F = 28.98  | --               | --          | --         | --          | --          | --          | --          |
| P - value               | 0.005                | --          | --          | 0.0007     | --               | --          | --         | --          | --          | --          | --          |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

<sup>x</sup> Contrast denotes t-test summary for budbreak of roots + stems (RS) versus stems only (S).

Table A.8 Summary statistics of percent budbreak, visual rating, and new shoot growth of flowering dogwood seedlings treated with antidesiccant applications to roots (R) or stems (S).

| ANOVA <sup>z</sup>      | Variables Quantified |             |                  |            |            |            |            |             |             |             |
|-------------------------|----------------------|-------------|------------------|------------|------------|------------|------------|-------------|-------------|-------------|
|                         | Establishment        |             | Budbreak, by day |            |            |            |            |             |             |             |
|                         | Rating               | New shoot   | Day 11           | Day 16     | Day 23     | Day 31     | Day 40     | Day 50      | Day 62      | Day 74      |
| Error mean <sup>2</sup> | 0.56                 | 1513        | 540              | 1664       | 1739       | 1023       | 1396       | 2249        | 2656        | 3447        |
| Source (R)              |                      |             |                  |            |            |            |            |             |             |             |
| Mean <sup>2</sup>       | 0.59                 | 2063        | 2896             | 1773       | 9482       | 9183       | 1298       | 1198        | 5020        | 5533        |
| P - value               | 0.33                 | 0.28        | 0.05             | 0.33       | 0.05       | 0.02       | 0.36       | 0.49        | 0.21        | 0.24        |
| 'R -'Y (SE)             | 3.00 (0.57)          | 85.8 (25.4) | 14.2 (3.8)       | 18.2 (4.6) | 29.0 (5.4) | 34.9 (7.6) | 34.2 (6.9) | 31.7 (6.5)  | 40.4 (5.7)  | 43.1 (5.5)  |
| 'R +' (SE)              | 2.56 (0.44)          | 59.6 (21.7) | 6.1 (1.5)        | 11.3 (3.8) | 14.0 (3.7) | 21.0 (3.4) | 28.7 (5.4) | 27.1 (6.8)  | 31.2 (7.1)  | 33.5 (8.1)  |
| Source (S)              |                      |             |                  |            |            |            |            |             |             |             |
| Mean <sup>2</sup>       | 9.52                 | 18748       | 3548             | 4095       | 4720       | 19907      | 25665      | 25381       | 18439       | 19406       |
| P - value               | 0.003                | 0.008       | 0.03             | 0.16       | 0.14       | 0.002      | 0.003      | 0.01        | 0.03        | 0.05        |
| 'S -' (SE)              | 3.67 (0.42)          | 33.2 (6.4)  | 6.4 (2.8)        | 10.9 (5.0) | 16.6 (4.4) | 18.1 (2.7) | 20.3 (1.7) | 18.1 (1.1)  | 25.9 (3.2)  | 28.2 (3.4)  |
| 'S +' (SE)              | 1.89 (0.19)          | 112 (22.7)  | 13.9 (3.1)       | 18.6 (3.0) | 26.3 (6.1) | 37.8 (6.5) | 42.6 (5.3) | 40.6 (6.2)  | 45.7 (6.4)  | 48.4 (7.3)  |
| Source (RxS)            |                      |             |                  |            |            |            |            |             |             |             |
| Mean <sup>2</sup>       | 1.33                 | 2571        | 1108             | 235        | 2793       | 7582       | 3149       | 1025        | 99          | 1           |
| P - value               | 0.16                 | 0.23        | 0.19             | 0.72       | 0.24       | 0.03       | 0.17       | 0.52        | 0.85        | 0.99        |
| 'RS' (SE)               | 3.11 (0.73)          | 84.5 (39.8) | 7.9 (1.6)        | 14.7 (5.0) | 15.5 (5.8) | 24.9 (5.7) | 35.9 (9.5) | 35.8 (12.3) | 39.9 (12.8) | 43.0 (14.9) |
| 'R' (SE)                | 2.00 (0.33)          | 34.7 (12.2) | 4.2 (2.4)        | 7.8 (6.0)  | 12.4 (5.9) | 17.2 (3.4) | 21.6 (2.4) | 18.3 (1.6)  | 22.5 (3.7)  | 23.9 (4.2)  |
| 'S' (SE)                | 4.22 (0.22)          | 140 (15.3)  | 20.0 (3)         | 22.5 (2.3) | 37.1 (5.9) | 50.7 (3.2) | 49.2 (2.7) | 45.5 (4.2)  | 51.6 (3.0)  | 53.9 (3.5)  |
| Control (SE)            | 1.78 (0.22)          | 31.7 (7.3)  | 8.5 (5.4)        | 13.9 (9.0) | 20.8 (6.6) | 19.1 (5.0) | 19.1 (2.6) | 18.0 (1.9)  | 29.3 (5.2)  | 32.4 (4.8)  |
| Contrast <sup>x</sup>   |                      |             |                  |            |            |            |            |             |             |             |
| Mean <sup>2</sup>       | --                   | --          | --               | --         | --         | 17118      | --         | --          | --          | --          |
| P - value               | --                   | --          | --               | --         | --         | 0.004      | --         | --          | --          | --          |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

<sup>x</sup> Contrast denotes t-test summary for budbreak of stems only treatment (S) versus roots + stems (RS).

Table A.9 Summary statistics of budbreak and new root and shoot growth of Washington hawthorn seedlings treated with antidesiccant applications to roots (R) or stems (S).

| ANOVA <sup>z</sup>      | Variables Quantified |             |             |                  |             |             |             |             |             |             |            |            |
|-------------------------|----------------------|-------------|-------------|------------------|-------------|-------------|-------------|-------------|-------------|-------------|------------|------------|
|                         | Establishment        |             |             | Budbreak, by day |             |             |             |             |             |             |            |            |
|                         | New root             | New shoot   | Dieback     | Day 14           | Day 19      | Day 26      | Day 34      | Day 47      | Day 55      | Day 68      | Day 81     | Day 100    |
| Error mean <sup>2</sup> | 121                  | 192         | 175         | 3342             | 5636        | 8941        | 11814       | 10617       | 4886        | 4673        | 4340       | 3484       |
| Source (R)              |                      |             |             |                  |             |             |             |             |             |             |            |            |
| Mean <sup>2</sup>       | 99                   | 109         | 896         | 9858             | 18426       | 21779       | 27247       | 13183       | 7529        | 3618        | 12922      | 17046      |
| P - value               | 0.39                 | 0.47        | 0.05        | 0.12             | 0.11        | 0.15        | 0.17        | 0.30        | 0.25        | 0.41        | 0.13       | 0.06       |
| 'R -' (SE)              | 8.7 (5.4)            | 15.3 (6.4)  | 16.1 (7.9)  | 13.1 (6.2)       | 17.3 (7.2)  | 21.1 (7.9)  | 24.2 (8.3)  | 20.2 (6.6)  | 13.1 (6.2)  | 15.5 (5.2)  | 21.1 (4.8) | 23.0 (3.8) |
| 'R +' (SE)              | 2.9 (2.1)            | 9.3 (3.3)   | 33.4 (9.8)  | 2.6 (2.6)        | 2.9 (2.7)   | 5.5 (5.2)   | 7.0 (6.7)   | 8.3 (7.7)   | 3.8 (3.6)   | 8.8 (4.2)   | 8.8 (3.8)  | 9.1 (3.8)  |
| Source (S)              |                      |             |             |                  |             |             |             |             |             |             |            |            |
| Mean <sup>2</sup>       | 33                   | 10          | 3356        | 12283            | 8011        | 12166       | 12803       | 11529       | 10037       | 6204        | 1523       | 706        |
| P - value               | 0.61                 | 0.82        | 0.002       | 0.09             | 0.27        | 0.28        | 0.33        | 0.33        | 0.19        | 0.28        | 0.57       | 0.67       |
| 'S -' (SE)              | 4.1 (3.2)            | 13.2 (3.8)  | 41.5 (7.4)  | 2.0 (1.3)        | 5.4 (4.5)   | 7.4 (5.1)   | 9.5 (6.1)   | 8.5 (5.4)   | 3.3 (3.1)   | 8.1 (2.6)   | 12.9 (3.5) | 14.7 (3.8) |
| 'S +' (SE)              | 7.5 (5.1)            | 11.4 (6.4)  | 8.0 (4.7)   | 13.6 (6.4)       | 14.8 (7.1)  | 19.2 (8.6)  | 21.7 (9.6)  | 20.0 (8.7)  | 13.6 (6.3)  | 16.1 (5.9)  | 17.0 (6.2) | 17.4 (5.7) |
| Source (RxS)            |                      |             |             |                  |             |             |             |             |             |             |            |            |
| Mean <sup>2</sup>       | 0                    | 0           | 19          | 3435             | 993         | 0           | 723         | 3479        | 553         | 11          | 105        | 13         |
| P - value               | 0.98                 | 0.99        | 0.75        | 0.34             | 0.69        | 0.99        | 0.81        | 0.58        | 0.75        | 0.96        | 0.88       | 0.95       |
| 'RS' (SE)               | 4.7 (4.3)            | 8.4 (5.1)   | 15.4 (7.6)  | 5.2 (5.2)        | 5.8 (5.3)   | 10.9 (10.4) | 13.9 (13.4) | 16.6 (15.0) | 7.6 (7.1)   | 12.7 (7.9)  | 10.4 (7.4) | 10.4 (7.4) |
| 'R' (SE)                | 1.2 (0.7)            | 10.3 (5.2)  | 51.4 (10.1) | 0.0 (0.0)        | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)   | 0.0 (0.0)   | 4.9 (2.9)   | 7.1 (3.7)   | 7.8 (3.9)  |            |
| 'S' (SE)                | 10.2 (10.1)          | 14.4 (13.0) | 0.6 (0.3)   | 22.1 (10.3)      | 23.8 (11.9) | 27.4 (13.9) | 29.5 (15.0) | 23.4 (11.8) | 19.5 (10.7) | 19.6 (10.0) | 23.6 (9.6) | 24.4 (7.8) |
| Control (SE)            | 7.1 (6.3)            | 16.2 (5.9)  | 31.5 (8.6)  | 4.0 (2.1)        | 10.8 (8.5)  | 14.8 (8.8)  | 18.9 (9.7)  | 17.0 (8.5)  | 6.7 (6.1)   | 11.3 (3.9)  | 18.7 (3.8) | 21.6 (3.1) |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

Table A.10 Summary statistics of budbreak and new root and shoot growth of river birch seedlings treated with antidesiccant applications to roots (R) or stems (S).

| ANOVA <sup>z</sup>      | Variables Quantified |             |            |                  |           |            |            |            |            |            |
|-------------------------|----------------------|-------------|------------|------------------|-----------|------------|------------|------------|------------|------------|
|                         | Establishment        |             |            | Budbreak, by day |           |            |            |            |            |            |
|                         | New root             | New shoot   | Dieback    | Day 11           | Day 16    | Day 23     | Day 31     | Day 44     | Day 53     | Day 65     |
| Error mean <sup>2</sup> | 11.02                | 504         | 176        | 2.85             | 8.69      | 21         | 25         | 35         | 27         | 23         |
| Source (R)              |                      |             |            |                  |           |            |            |            |            |            |
| Mean <sup>2</sup>       | 3.74                 | 494         | 688        | 2.08             | 34.5      | 62         | 58         | 69         | 23         | 19         |
| P - value               | 0.58                 | 0.35        | 0.08       | 0.42             | 0.08      | 0.12       | 0.17       | 0.20       | 0.38       | 0.39       |
| 'R - 'Y (SE)            | 6.09 (1.03)          | 46.5 (7.8)  | 61.9 (7.1) | 1.5 (0.8)        | 5.3 (1.9) | 8.4 (2.8)  | 9.3 (3.0)  | 10.4 (3.4) | 7.9 (2.5)  | 8.4 (2.6)  |
| 'R +' (SE)              | 4.98 (1.42)          | 33.7 (8.9)  | 77.1 (4.9) | 0.7 (0.5)        | 1.9 (1.1) | 3.9 (1.8)  | 4.9 (2.0)  | 5.6 (2.2)  | 5.2 (2.0)  | 5.9 (1.6)  |
| Source (S)              |                      |             |            |                  |           |            |            |            |            |            |
| Mean <sup>2</sup>       | 2.02                 | 144         | 414        | 4.90             | 34.45     | 78         | 91         | 112        | 54         | 47         |
| P - value               | 0.68                 | 0.61        | 0.16       | 0.23             | .08       | 0.09       | 0.09       | 0.11       | 0.20       | 0.19       |
| 'S - ' (SE)             | 5.13 (1.33)          | 36.6 (9.0)  | 75.4 (4.5) | 0.4 (0.3)        | 1.9 (0.9) | 3.6 (1.5)  | 4.4 (1.8)  | 4.9 (2.0)  | 4.4 (1.6)  | 5.2 (1.6)  |
| 'S +' (SE)              | 5.95 (1.18)          | 43.5 (8.4)  | 63.6 (8.0) | 1.7 (0.9)        | 5.3 (2.0) | 8.7 (2.9)  | 9.9 (2.9)  | 11.1 (3.3) | 8.7 (2.5)  | 9.1 (2.4)  |
| Source (RxS)            |                      |             |            |                  |           |            |            |            |            |            |
| Mean <sup>2</sup>       | 16                   | 2.15        | 430        | 0.45             | 39.12     | 85         | 87         | 100        | 23         | 52         |
| P - value               | 0.87                 | 0.67        | 0.16       | 0.70             | 0.07      | 0.08       | 0.10       | 0.13       | 0.38       | 0.17       |
| 'RS' (SE)               | 4.96 (1.87)          | 36.0 (10.4) | 77.2 (7.2) | 1.1 (1.1)        | 1.8 (1.8) | 3.8 (2.8)  | 5.0 (2.6)  | 5.8 (3.1)  | 5.9 (3.0)  | 5.8 (2.0)  |
| 'R' (SE)                | 4.99 (2.57)          | 31.3 (16.8) | 77.0 (8.3) | 0.2 (0.1)        | 2.0 (1.7) | 4.0 (2.8)  | 4.9 (3.5)  | 5.4 (3.9)  | 4.4 (3.0)  | 6.0 (2.9)  |
| 'S' (SE)                | 6.93 (1.57)          | 51.1 (13.6) | 50.1 (9.3) | 2.3 (1.5)        | 8.8 (2.2) | 13.7 (3.1) | 14.8 (3.3) | 16.3 (4.2) | 11.4 (3.8) | 12.4 (3.8) |
| Control (SE)            | 5.26 (1.47)          | 41.9 (9.8)  | 73.8 (5.2) | 0.7 (0.7)        | 1.8 (0.9) | 3.2 (1.6)  | 3.9 (1.8)  | 4.4 (2.1)  | 4.4 (1.9)  | 4.3 (2.0)  |
| Contrast <sup>x</sup>   |                      |             |            |                  |           |            |            |            |            |            |
| Mean <sup>2</sup>       | --                   | --          | --         | --               | 107.93    | 225        | 233        | 278        | --         | --         |
| P - value               | --                   | --          | --         | --               | 0.008     | 0.01       | 0.02       | 0.02       | --         | --         |

<sup>z</sup> model d.f. = 3, error d.f. = 8, treatment sample size = 3.

<sup>y</sup> -/+ denote not treated and treated, respectively

<sup>x</sup> Contrast denotes t-test summary for budbreak of stems only treatment (S) versus the mean for all other treatments (RS, R, and control) combined.

Table A.11 Mean, standard error (SE), and Waller ratio ( $K = 100$ ) grouping for percent change in fresh weight relative to fresh weight before planting for each treatment in Washington hawthorn. Treatment abbreviations defined in materials and methods.

| Treatment               | Mean  | SE   | Waller |
|-------------------------|-------|------|--------|
| NS <sup>z</sup> control | -5.06 | 0.96 | d      |
| RS-No                   | -1.43 | 1.08 | c      |
| S-No                    | -0.50 | 0.94 | c      |
| RS-B                    | -1.96 | 1.52 | cd     |
| S-B                     | 7.22  | 1.44 | a      |
| RS-A                    | 3.40  | 1.53 | b      |
| S-A                     | 8.76  | 0.83 | a      |
| Stressed control        | 8.04  | 2.12 | a      |

<sup>z</sup> NS denotes non-stressed.

Figure A.1 Range of flowering dogwood (*Cornus florida*) seedlings to which visual ratings were assigned at harvest (12 September, 1993). Scale 0 = dead, 5 = excellent quality.

