Arboriculture & Urban Forestry 2026. 52(5):471–483
https://doi.org/10.48044/jauf.2026.019

# Experimental Evidence of the Impacts of Different Root-Pruning Intensities on Post-Transplant Water Potential and Xylem Hydraulic Conductivity in Two Tree Species

**By Toshihiro Umebayashi, Yasuhiro Utsumi, and Yuzou Sano**

**Abstract.** To improve transplanting techniques, it is necessary to understand root-pruning induced declines in xylem water transport and post-transplant environmental effects. In this study, we evaluated the relationship between water potential and hydraulic conductivity ($K_s$) in saplings of *Larix kaempferi* and *Betula maximowicziana*, whose roots were pruned in order to improve our understanding of the transplanting technique. Root-pruning treatments were applied to saplings of both species based on their basal root diameters. After transplanting, the water potential and $K_s$ were measured. In addition, the vulnerability curve was obtained using a centrifuge method by quantifying the relationship between decreasing xylem pressure and the percentage loss of $K_s$, allowing a comparison of water stress tolerance between the two species. *Betula maximowicziana* had higher $K_s$ and was more vulnerable to water stress induced embolism than *L. kaempferi*. In *L. kaempferi*, no decrease in $K_s$ was observed regardless of the level of root pruning, and all saplings survived after transplanting. In *B. maximowicziana*, saplings subjected to root pruning exhibited a decline in the water potential during midsummer, along with a reduction in $K_s$. Moreover, the number of dead saplings increased with increasing levels of root pruning. For the two species, a relationship was found between increasing level of root pruning and post-transplant mortality in the more water stress vulnerable species, *B. maximowicziana*. The relationships among post-transplant changes in water potential, reductions in $K_s$ associated with root pruning, and sapling survival provide a useful framework for selecting transplanting methods and improving transplant success rates.

**Keywords.** *Betula maximowicziana*; *Larix kaempferi*; Root Pruning; Transplant; Vulnerability Curve.

## INTRODUCTION

Plant transplantation is a technique used to artificially position plants for purposes such as stable crop production, rapid forest regeneration, and urban greening. However, there remains a pressing need to develop labor-efficient and economically viable transplantation methods (Korbik et al. 2025). In the case of trees, saplings for transplantation may be cultivated over several years in containers or in field nurseries before being relocated to different regions (Struve 2009), making them especially susceptible to transplant shock.

Transplant shock is generally induced by the loss of a large portion of the root system during transplanting (i.e., root pruning)(Watson 1985). In particular, during the transplantation of balled and burlapped stock, up to 95% of the total root system may be lost (Harris and Bassuk 1993), which has been reported to result in a substantial reduction in water uptake after transplantation (Poni et al. 1992; Wang et al. 2014; Dong et al. 2016; Benson et al. 2019). Currently, a variety of transplantation methods are used, including bare-root stock, balled and burlapped stock, container-grown stock, and fabric container stock. Among these methods, container-grown stock is relatively expensive but has the advantage of allowing transplantation without root pruning (Harris and Bassuk 1993). On the other hand, the other methods involve varying levels of root loss depending on the technique, but all require root pruning and therefore may impose substantial stress on saplings. Consequently, no single transplantation method is optimal for all situations. Survival rates after transplantation and recovery from

©2026 International Society of Arboriculture

transplant shock are thought to be influenced by multiple factors, including tree species, environmental conditions, physiological status of the saplings, timing of transplantation, cultivation management, and root system type (Bevington and Castle 1985; Fare et al. 1985; Gilman 1990; Watson 2005). Therefore, it is necessary to quantitatively evaluate the effects of changes to the water-conducting pathway caused by root loss and the susceptibility to water stress arising from damage to the xylem water transport system. Accordingly, this study aimed to establish a method for quantitatively evaluating the effects of different intensities of root loss/removal on the water transport system.

Woody plants draw water up from the soil through their xylem conduits (tracheids and vessels). Since this water uptake is a consequence of a negative pressure that pulls the water upwards (Tyree and Zimmermann 2002; Umebayashi et al. 2016), the water column in the conduits is vulnerable to embolism. Therefore, at the time of root pruning, it is considered that embolism occurs at the cut sites and that the embolized area expands due to an increase in xylem negative pressure resulting from reduced water uptake caused by the root loss.

The vulnerability of xylem water transport pathways can be quantitatively assessed using a vulnerability curve, which illustrates the decline in hydraulic conductance with decreasing xylem water potential (Sperry and Tyree 1988; Bush et al. 2010; Schreiber et al. 2013). By examining the reduction in hydraulic conductance in transplanted individuals with root pruning, it is expected that tree species with high transplant tolerance can be identified.

In this study, we conducted a transplant experiment on two species growing in the Northern regions of Japan. As shown in Figure 1, 3 levels of root-pruning intensity were established based on basal root diameter, and the effects on water transport after transplantation were examined. One species was *Betula maximowicziana*, a broadleaf tree commonly found in riparian forests, and the other was *Larix kaempferi*, a deciduous conifer. These two species were selected in order to determine the effects of root pruning and water transport on transplant shock that comes from sapling production and planting for a coniferous species used in afforestation in Japan and a broadleaf species vulnerable to water stress. To establish a method for evaluating water transport function in trees transplanted after root pruning, we focused on (1) investigating the influence of root pruning on hydraulic conductivity ($K_s$) and mortality rate, and (2) examining relationships between species vulnerability to embolism, midday water potential, and the survival of saplings with different levels of root pruning.

To evaluate species-specific vulnerability to embolism, we calculated the slopes of vulnerability curves and the water potential at which $K_s$ decreased by 50% ($P_{50}$) in saplings of both species using the centrifuge method. Using these parameters, we tested the hypothesis that the slopes of vulnerability curves measured for each species and the magnitude of

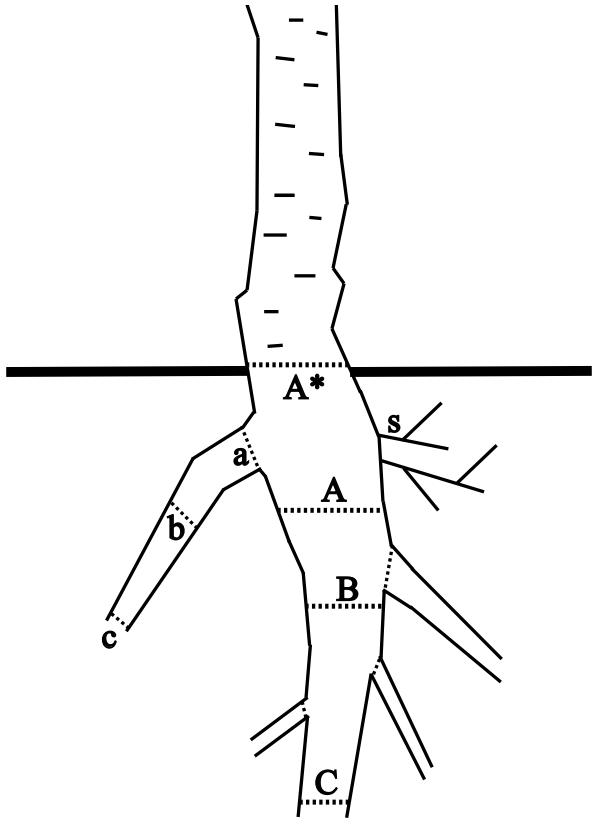


**Figure 1. A methodological diagram of root pruning before the transplant (see also Figures S1A–C for representative photographs). (A*) The maximal diameter of the stem at ground level. (A) The dotted line shows the cut position for a 100% root loss on the main root (the same diameter as A*). (B) The dotted line shows the cut position for a 75% root loss (three-quarters of the diameter of A). (C) The dotted line shows the cut position for a 50% root loss (one-half diameter of A). (a) The dotted line shows the position for a 100% root loss on a lateral root (the base diameter of that lateral root). (b) The dotted line shows the cut position for a 75% root loss on a lateral root (three-quarters of the diameter of that lateral root). (c) The dotted line shows the position for a 50% root loss on a lateral root (one-half diameter of that lateral root). (s) Finer roots with diameters below 1 mm.**

©2026 International Society of Arboriculture

declines in $K_s$ observed in transplanted saplings subjected to different root-pruning intensities could serve as useful indicators for selecting tree species suitable for transplantation. We predicted that *B. maximowicziana*, a riparian species that forms vessels, would exhibit increased declines in $K_s$ and higher mortality with increasing root-pruning intensity. In contrast, *L. kaempferi*, which forms tracheids and has greater tolerance to water stress, was expected to show little decline in $K_s$ even at higher levels of root pruning and consequently no mortality. In addition, we examined whether periodic measurements of water potential in both species could be used to quantitatively assess water stress conditions.

## MATERIALS AND METHODS

### Preparation of Samples

The transplanting experiment of two species was conducted at the Sapporo Experimental Nursery of Hokkaido University, Sapporo, Japan (43.068948, 141.337325). According to the temperature and precipitation data obtained from Sapporo Regional Headquarters, Japan Meteorological Agency (at 15 m above sea level), the yearly mean air temperature and total precipitation in 2016 were 9.3 °C and 1,360 mm, respectively. In the Appendix (Table S1), the air temperature and precipitation data for each month from April to October 2016 are listed. We collected 2-year-old *L. kaempferi* saplings ($n$ = 25) from the nursery of Forestry Research Institute (Bibai, Japan), Hokkaido Research Organization, and 2- to 3-year-old *B. maximowicziana* saplings ($n$ = 25) from the nursery of Teshio Experimental Forest, Hokkaido University, respectively. All saplings were carefully dug out with a shovel after leaf fall in the previous year and were cultivated at the Sapporo Experimental Nursery of Hokkaido University until the start of this experiment. This was done in order to grow and compare the two species under the same environmental conditions. To assess the effects of winter freezing stress and excavation on branch dieback or mortality, all the harvested saplings were cultivated in the same plot at the Sapporo Experimental Nursery of Hokkaido University for approximately 6 months prior to the start of the experiment. The mean height values of *L. kaempferi* and *B. maximowicziana* saplings were 86.5 cm ± 16.1 cm (mean ± SD) and 75.2 cm ± 20.6 cm, respectively, and their stem basal diameters were 13.2 mm ± 2.0 mm and 7.9 mm ± 1.9 mm, respectively.

### Experiments

The transplant experiment was conducted between 12:00 and 14:00 on 2016 May 16. This time period was chosen because the negative pressure in xylem was high, and embolism formation due to root pruning was expected to become pronounced in the saplings. Ten saplings of each species designated as the control samples were transplanted without root pruning (five of which were used to calculate stem vulnerability curves), and the roots of the remaining fifteen saplings of each species were pruned and the trees transplanted. The roots of all saplings including controls were soaked in water (approximately 5 min), cleaned from mud (Figure S1A), and left under water to prevent dehydration (approximately 1 min). Afterwards, the roots were cut outside of the water. The root-pruning treatment was classified into 3 classes ($n$ = 5 in each class) based on the basal root diameter of the pruned saplings. The root-pruning procedures are shown in Figure 1. For a 100% root loss treatment, the main root was cut at the point where the diameter matches the widest stem diameter at ground level, because the size and structure of the main roots varied widely among the samples (Figures S1B, S1C). Subsequently, all of the remaining lateral roots with diameters over 1 mm were cut at the base. For 75% and 50% root loss, the main root was cut at 75% or 50% of the diameter of the widest stem, respectively, and then all of the remaining lateral roots with diameters over 1 mm were cut at positions with 75% or 50% of the diameter of their bases, respectively. All saplings, including controls, were planted immediately after the root-pruning treatment. The saplings were thoroughly watered on the day of transplantation and planted after soil moisture was saturated (Figures S1D, S1E). After planting, irrigation was continued once every 2 weeks.

Xylem water potential was measured using a pressure bomb (Model 3000; Soilmoisture Equipment Corp., Goleta, CA, USA) between 13:00 and 14:00 the day after the transplant and 1, 3, and 5 months after the transplant. Leaves were bagged for at least 30 min to equilibrate with branches before their removal from the plant (Umebayashi et al. 2019). From each individual, three leaves were collected for *B. maximowicziana* and three shoot tips for *L. kaempferi*, and the mean midday xylem pressure was calculated for each sapling. Until October, the mortality of the transplanted individuals was assessed based on

©2026 International Society of Arboriculture

external appearance, and the cumulative mortality rate was recorded in Table 1. A sapling was considered dead when all the leaves had fallen and the shoot apex had necrosed. Those that died in October were also collected, and it was reconfirmed that their stem cross sections were desiccated. Approximately 5 months after the transplant (2016 October 3), all saplings were tightly wrapped in plastic bags humidified with damp towels before they were dug out of the ground at predawn. Collected saplings were soaked in water, and we were able to confirm the formation of new roots in the surviving saplings. We brought these samples back to our laboratory, where the segments of approximately 160 mm of length were excised from a stem approximately 10 cm above the ground level under water to measure the hydraulic conductivity divided by the stem cross-sectional area ($K_s$). Heartwood had not formed in the cross sections of any segments. Five saplings were excluded from this procedure and used to acquire data to make vulnerability curves. The sample edges were trimmed with a sterile razor blade, and basal diameters in *L. kaempferi* and *B. maximowicziana* were 8.2 mm ± 1.1 mm and 7.2 mm ± 0.9 mm, respectively. Each stem segment was attached to a Tygon® tubing apparatus (Saint-Gobain S.A., La Défense, Courbevoie, France) filled with 20 mM KCl solution to measure $K_s$. The $K_s$ value was calculated by dividing the pressure-driven flow (corrected for background flow) (Hacke et al. 2000; Torres-Ruiz et al. 2012) by pressure gradient (induced by a 4-kPa to 6-kPa hydraulic head). After measuring the $K_s$ in *B. maximowicziana*, all stem segments were flushed with 20 mM KCl solution filtered through a 0.2-μm filter for 30 min at approximately 75 kPa to remove air emboli, and we measured $K_{s\ max}$. In contrast, *L. kaempferi* segments were not flushed because decreases in $K_s$ after flushing have been reported in conifers (Pittermann and Sperry 2006), and a similar phenomenon was also confirmed in our preliminary test.

The vulnerability curves for each species were plotted from 5 stem segments of each species using the static centrifuge method. All saplings were shipped to the Kasuya Research Forest Laboratory (Kyushu University, Sasaguri, Japan) in low temperature conditions (below 10 °C) on the day of collection using an express home delivery service (Chilled Type, Cool TA-Q-BIN; Yamato Holdings Co., Ltd., Tokyo, Japan). The stem segments of approximately 150-mm length were excised under water. Before the $K_s$ measurement, sample edges were trimmed with a sterile razor blade until the branch length was approximately 145 mm. Basal diameters in *L. kaempferi* and *B. maximowicziana* were 8.3 mm ± 0.6 mm and 6.8 mm ± 1.5 mm, respectively. All segments of *B. maximowicziana* were flushed with 20 mM KCl solution for 30 min at approximately 75 kPa to remove pre-existing air emboli.

All segments were secured with a custom-built rotor and centrifuged for 5 min at a pressure of –0.5 MPa (Kubota Corp., Tokyo, Japan) with their ends submerged in water-filled plastic reservoirs (Alder et al. 1997). After centrifugation, the segments were attached to a Tygon® tubing apparatus filled with 20 mM KCl solution in order to obtain their initial hydraulic conductivity divided by the stem cross-sectional area ($K_{s\ initial}$) values. The $K_{s\ initial}$ was calculated using the same method as described above, by dividing the pressure-driven flow (corrected for background flow)(Hacke et al. 2000; Torres-Ruiz et al. 2012) by pressure gradient (induced by a 4-kPa to 6-kPa hydraulic head).

**Table 1. Tree heights, stem basal diameters, and mortality rates of the transplanted saplings of both species ($n$ = 5) with pruned roots, recorded on 2016 October 3. Data are presented as "mean ± standard deviation". Control-VC means saplings making the vulnerability curve. VC (vulnerability curve).**

| | *Betula maximowicziana* | | | *Larix kaempferi* | | |
|---|---|---|---|---|---|---|
| **The level of root pruning** | **Tree height (cm)** | **Stem basal diameter (mm)** | **Mortality rate (%)** | **Tree height (cm)** | **Stem basal diameter (mm)** | **Mortality rate (%)** |
| Control-VC | 107.0 ± 15.9 | 10.1 ± 2.4 | 0 | 71.4 ± 11.0 | 13.7 ± 2.0 | 0 |
| Control | 80.8 ± 11.0 | 8.0 ± 1.4 | 0 | 95.2 ± 11.4 | 14.4 ± 2.5 | 0 |
| 50% loss | 60.4 ± 10.3 | 7.3 ± 1.2 | 20 | 77.0 ± 17.1 | 12.3 ± 1.9 | 0 |
| 75% loss | 68.5 ± 5.5 | 7.9 ± 1.5 | 40 | 88.6 ± 10.1 | 12.7 ± 1.6 | 0 |
| 100% loss | 59.2 ± 9.6 | 6.3 ± 0.9 | 100 | 100.2 ± 13.1 | 13.1 ± 2.0 | 0 |

©2026 International Society of Arboriculture

After the measurement of $K_{s\ initial}$, the centrifuging process was repeated under progressively more negative pressure values until –2.5 MPa or –5.0 MPa ($K_s$ approached zero) at –0.5 MPa intervals. The relationship between water potential and the percentage loss of conductivity (PLC, $n = 5$)(PLC = $100 \times [1 - K_s / K_{s\ initial}]$) was plotted, and the vulnerability curve was fitted using a Weibull function (Neufeld et al. 1992). All data were collected within 3 days of harvesting the plants.

### Statistics

To examine interspecific differences in $K_{s\ initial}$ under control treatments, a *t*-test was performed. In addition, to evaluate differences among root-pruning levels within each species, analysis of variance (ANOVA) was conducted using R statistical software (version 4.1.2; R Core Team 2021), followed by Tukey's honestly significant difference (HSD) test as a post hoc analysis.

## RESULTS

The vulnerability curves for stem segments of *B. maximowicziana* had significantly higher $K_{s\ initial}$ (by a factor of 3.0)(Figure 2A) and were more vulnerable to embolism than the stem segments of *L. kaempferi* (Figure 2B). The percent loss of hydraulic conductivity (PLC) at a pressure of –1.5 MPa showed 23.7% ± 10.1% (mean ± SD) in the stem segments of *B. maximowicziana* and 3.0% ± 0.5% in *L. kaempferi* segments. The PLC of *B. maximowicziana* increased drastically at pressures lower than –1.5 MPa (85.1% ± 13.0% at a pressure of –2.0 MPa), while the PLC of *L. kaempferi* showed almost no increase up to –2.0 MPa (2.8% ± 8.0% at a pressure of –2.0 MPa). The $P_{50}$ values of *B. maximowicziana* and *L. kaempferi* were –1.72 MPa and –2.90 MPa, respectively (Table 2).

Dead saplings of either species were not detected in June (Figure S2). However, many fallen leaves were observed in July in saplings of *B. maximowicziana* with 100% root loss (Figure S2C). On 2016 August 2, midday xylem water potential reached –1.6 MPa ± 0.3 MPa in saplings of *B. maximowicziana* with 75% root loss (Table 3)(Figure S2D). All saplings with 100% root loss had died by that time. The mortality rate recorded on October 3 differed widely among treatments in both species. In *B. maximowicziana*, 3 saplings of 75% root loss and 4 saplings of 50% root loss survived. Thus, for *B. maximowicziana*, mortality rate increased with the increased level of root pruning. The water potential in the surviving *B. maximowicziana* saplings with 75% root loss recovered at the pressure of –1.3 MPa ± 0.1 MPa. On the other hand, the decrease in water potential of *L. kaempferi* saplings during the experimental period was not large. All saplings of *L. kaempferi* survived irrespective of the level of root pruning (Table 1).

New roots were observed in all surviving saplings. The loss in $K_s$ was detected in surviving *B. maximowicziana* saplings with pruned roots, but the decrease

**Table 2. Water potential values (MPa) corresponding to $P_{50}$ (50% loss of hydraulic conductivity) and $P_{88}$ for the two species, estimated using the centrifuge method.**

| | Percentage loss of conductivity | |
|---|---|---|
| | $P_{50}$ (MPa) | $P_{88}$ (MPa) |
| *Betula maximowicziana* | −1.72 | −2.04 |
| *Larix kaempferi* | −2.90 | −3.85 |

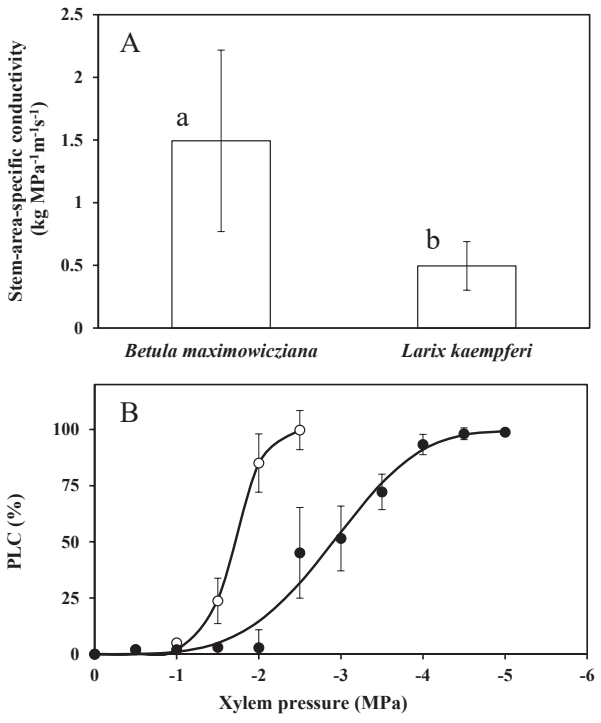


**Figure 2. Hydraulic conductivity characteristics of the stems of the two species used in the centrifuge method. (A) Initial hydraulic conductivity divided by the stem cross-sectional area ($K_{s\ initial}$) in two species (*t*-test, $P = 0.05$). (B) Vulnerability curves of the two species. (●) indicates *Larix kaempferi* and (○) indicates *Betula maximowicziana*. Conductive capacity in the vulnerability curves is expressed as percentage loss of conductivity (PLC) relative to the initial conductivity shown in (A). Error bars represent ±1 SD for $n = 5$ samples. Data were fitted with a Weibull function.**

©2026 International Society of Arboriculture

did not occur in *L. kaempferi*, regardless of the level of root pruning (Figure 3). In *B. maximowicziana* saplings, no significant difference in $K_s$ was observed between 50% and 75% root loss (Figure 3).

## DISCUSSION

In this study, at one month after transplantation, the midday water potential values of saplings of neither species showed a decline sufficient to be associated with a reduction in $K_s$ (Table 3). However, the decrease in midday water potential was induced in many saplings of *B. maximowicziana*, and saplings subjected to higher levels of root pruning tended to exhibit lower water potential values in August (Table 3). In addition, many saplings could not survive the later stages of this experiment, and the mortality rate

**Table 3. Midday water potential of both species (*n* = 5; control, *n* = 10) by months, listed by treatments. Data are presented as mean ± standard deviation.**

| | Water potential (MPa) | | | |
|---|---|---|---|---|
| **The level of root pruning** | **May (one day later)** | **June (one month later)** | **August** | **October** |
| *Betula maximowicziana* | | | | |
| Control | −0.7 ± 0.1 | −0.9 ± 0.1 | −1.1 ± 0.2 | −1.0 ± 0.1 |
| 50% loss | −0.8 ± 0.1 | −1.0 ± 0.2 | −1.3 ± 0.2 | −1.4 ± 0.3[a] |
| 75% loss | −0.8 ± 0.1 | −1.0 ± 0.1 | −1.6 ± 0.3 | −1.3 ± 0.1[b] |
| 100% loss | −0.7 ± 0.1 | −1.0 ± 0.2 | – | – |
| *Larix kaempferi* | | | | |
| Control | −0.6 ± 0.2 | −0.9 ± 0.1 | −1.1 ± 0.2 | −1.1 ± 0.1 |
| 50% loss | −0.6 ± 0.1 | −0.9 ± 0.1 | −1.0 ± 0.1 | −1.1 ± 0.1 |
| 75% loss | −0.6 ± 0.2 | −0.8 ± 0.2 | −1.0 ± 0.2 | −1.1 ± 0.1 |
| 100% loss | −0.7 ± 0.1 | −0.9 ± 0.1 | −1.2 ± 0.2 | −1.1 ± 0.1 |

[a] *n* = 4
[b] *n* = 3
– all saplings were dead

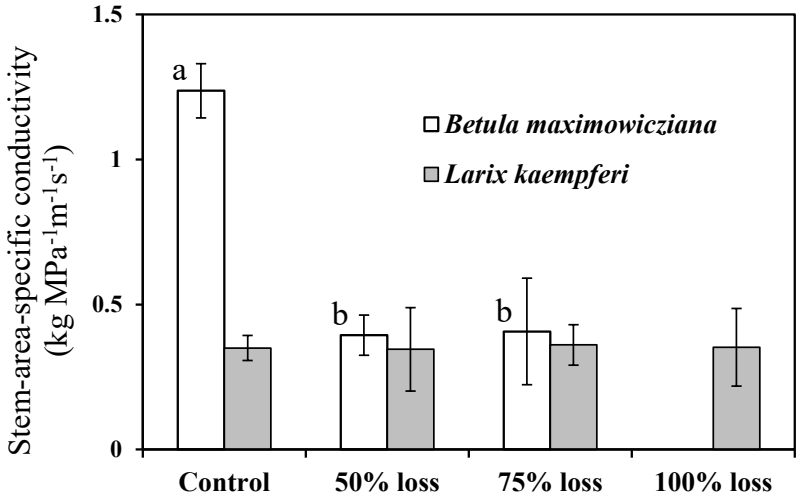


**Figure 3. Hydraulic conductivity of surviving saplings of the two species after transplanting under each root-pruning treatment. Error bars are ±1 SD for *n* = 3 to 5 samples. Dieback of all saplings was induced in 100% root loss *B. maximowicziana* saplings. To evaluate differences among root-pruning levels within each species, analysis of variance (ANOVA) was conducted using R statistical software (R Foundation, Vienna, Austria), followed by Tukey's honestly significant difference (HSD) test as a post hoc analysis. For *B. maximowicziana*, different letters above each column indicate significant differences according to Tukey's HSD test (*P* = 0.05). No significant differences were observed in *L. kaempferi*.**

©2026 International Society of Arboriculture

increased with the increased level of root pruning in *B. maximowicziana*. In contrast, no reduction in $K_s$ was observed in any of the transplanted *L. kaempferi* saplings. In healthy plants, water moves from roots to leaves as a consequence of pressure gradients, and water transport in saplings is mainly controlled by leaves. In transplanted saplings whose roots were subjected to pruning, a sufficient water supply cannot be achieved until the water transport pathway from soil to roots has recovered, and serious decreases in stomatal conductance and water potential are induced by increasing the level of root pruning (Benson et al. 2019). This concurs with the results of our research in which the transplanted saplings whose roots were pruned in mid-May were more vulnerable to water stress during midsummer. In addition, the number of embolized xylem conduits may have increased on the side that the plant was cut while root pruning (Torres-Ruiz et al. 2015).

Post-transplantation measurements of water potential in *B. maximowicziana* indicated that xylem negative pressure reached its maximum in August. Moreover, the decline in water potential became more pronounced with increasing levels of root pruning, potentially leading to a further reduction in $K_s$. Furthermore, once xylem dysfunction occurred in the stem, little recovery of $K_s$ was observed even when water stress was alleviated in October (Table 2). In contrast, in *L. kaempferi*, even saplings subjected to the 100% root-pruning treatment in August maintained water potentials of −1.2 MPa ± 0.2 MPa, and no reduction in $K_s$ was observed (Table 3).

Results from the vulnerability curves revealed that, in *B. maximowicziana*, a loss in $K_s$ occurred under pressure conditions below −1.5 MPa (Table 2)(Figure 2). In saplings subjected to the 75% root-pruning treatment, the mean water potential in August reached −1.6 MPa, which is consistent with the vulnerability curve indicating the occurrence of stem embolism formation (i.e., an increase in PLC). In contrast, in the vulnerability curve of *L. kaempferi*, a decrease in $K_s$ was detected only below −2.5 MPa (Figure 2B). These results suggest that species-specific vulnerability curves are useful indicators for selecting tree species with high tolerance to transplantation. In species vulnerable to water stress, increasing levels of root pruning enhance sensitivity to summer water stress, resulting in higher mortality rates (Tables 1 and 3). Therefore, for such species, it is desirable to select transplanting techniques that minimize root loss during transplantation.

Urli et al. (2013) reported that the lethal threshold of drought stress in broadleaved species occurs around $P_{88}$. Among the surviving *B. maximowicziana* saplings subjected to root pruning, the lowest $K_s$ was observed in a sapling from the 75% root-pruning treatment, with a value of 0.20 kg $MPa^{-1}$ $m^{-1}$ $s^{-1}$ (Figure 3). This corresponds to an 88% reduction relative to the control $K_{s\,max}$ (i.e., the value after refilling following $K_s$ measurement; 1.60 ± 0.29 kg $MPa^{-1}$ $m^{-1}$ $s^{-1}$). In addition, our data clearly showed that the $K_{s\,max}$ of *B. maximowicziana* tended to be lower in saplings subjected to the 50% and 75% root-pruning treatments (0.64 ± 0.15 and 0.76 ± 0.55 kg $MPa^{-1}$ $m^{-1}$ $s^{-1}$, respectively) than in the control. It is well known that tyloses and/or gums can form within embolized vessels (De Micco et al. 2016), and the observed reduction in $K_{s\,max}$ suggests that embolisms may have already formed in the stem at the time of root pruning. Therefore, in species vulnerable to water stress, a reduction in $K_{s\,max}$ may occur in individuals planted after root pruning, and evaluating hydraulic function solely based on PLC may lead to an underestimation of the decline in water transport capacity. In this context, assessment based on $K_s$ is useful for understanding the hydraulic properties of saplings after transplantation. Future studies incorporating spatial analyses of embolized areas in saplings after root pruning would further improve our understanding of the relationship between reductions in $K_s$ and survival.

In conclusion, our methods, including root pruning, were shown to be effective for evaluating species-specific tolerance to water stress that arises after transplantation. In *L. kaempferi*, which forms tracheids and is relatively tolerant to water stress, no reduction in $K_s$ or mortality was observed in saplings subjected to root pruning. In contrast, in *B. maximowicziana*, which forms vessels and is more vulnerable to water stress, declines in water potential during midsummer and increases in mortality were observed with increasing levels of root pruning. In *B. maximowicziana*, the reduction in $K_s$ was suggested to be induced not only by hydraulic disruption at the time of root pruning but also by summer water stress. Therefore, as hypothesized, the slope of the vulnerability curve, the magnitude of $K_s$ reduction after transplantation, and the monitoring of post-transplantation water potential are useful indicators for evaluating

©2026 International Society of Arboriculture

post-transplant survival potential and provide important information for species selection in planting practices. Species with higher tolerance to water stress tend to exhibit higher survival rates after transplantation. Although this study focused solely on the effects of root pruning, it is well known that multiple factors, including seasonal conditions, weather, soil properties, and post-transplant management interact in complex ways during actual transplantation practices (Harris and Bassuk 1993). Therefore, further studies adopting more comprehensive perspectives are required (Brancalion and Holl 2020).

## LITERATURE CITED


Alder NN, Pockman WT, Sperry JS, Nuismer S. 1997. Use of centrifugal force in the study of xylem cavitation. *Journal of Experimental Botany*. 48(3):665-674. https://doi.org/10.1093/jxb/48.3.665

Benson AR, Morgenroth J, Koeser AK. 2019. The effects of root pruning on growth and physiology of two Acer species in New Zealand. *Urban Forestry & Urban Greening*. 38:64-73. https://doi.org/10.1016/j.ufug.2018.11.006

Bevington KB, Castle WS. 1985. Annual root growth pattern of young citrus trees in relation to shoot growth, soil temperature, and soil water content. *Journal of the American Society for Horticultural Science*. 110(6):840-845. https://doi.org/10.21273/JASHS.110.6.840

Brancalion PHS, Holl KD. 2020. Guidance for successful tree planting initiatives. *Journal of Applied Ecology*. 57(12):2349-2361. https://doi.org/10.1111/1365-2664.13725

Bush SE, Hultine KR, Sperry JS, Eheleringer JR. 2010. Calibration of thermal dissipation sap flow probes for ring- and diffuse-porous trees. *Tree Physiology*. 30(12):1545-1554. https://doi.org/10.1093/treephys/tpq096

De Micco V, Balzano A, Wheeler EA, Baas P. 2016. Tyloses and gums: A review of structure, function and occurrence of vessel occlusions. *International Association of Wood Anatomists Journal*. 37(2):186-205. https://doi.org/10.1163/22941932-20160130

Dong T, Duan B, Zhang S, Korpelainen H, Niinemets Ü, Li C. 2016. Growth, biomass allocation and photosynthetic responses are related to intensity of root severance and soil moisture conditions in the plantation tree *Cunninghamia lanceolata*. *Tree Physiology*. 36(7):807-817. https://doi.org/10.1093/treephys/tpw025

Fare DC, Gilliam CH, Ponder HG. 1985. Root distribution of two field-grown *Ilex*. *HortScience*. 20(6):1129-1130. https://doi.org/10.21273/HORTSCI.20.6.1129

Gilman EF. 1990. Tree root growth and development. II. Response to culture, management and planting. *Journal of Environmental Horticulture*. 8(4):220-227. https://doi.org/10.24266/0738-2898-8.4.220

Hacke UG, Sperry JS, Pittermann J. 2000. Drought experience and cavitation resistance in six shrubs from the Great Basin, Utah. *Basic and Applied Ecology*. 1(1):31-41. https://doi.org/10.1078/1439-1791-00006

Harris JR, Bassuk NL. 1993. Tree planting fundamentals. *Journal of Arboriculture*. 19(2):64-70. https://doi.org/10.48044/jauf.1993.012

Korbik M, Swoczyna T, Latocha P. 2025. Pre-planting and planting factors and practices affecting urban tree growth: With a special focus on the root system and its condition—A review. *Plants*. 14(3):387. https://doi.org/10.3390/plants14030387

Neufeld HS, Grantz DA, Meinzer FC, Goldstein G, Crisosto GM, Crisosto C. 1992. Genotypic variability in vulnerability of leaf xylem to cavitation in water-stressed and well-irrigated sugarcane. *Plant Physiology*. 100(2):1020-1028. https://doi.org/10.1104/pp.100.2.1020

Pittermann J, Sperry JS. 2006. Analysis of freeze-thaw embolism in conifers. The interaction between cavitation pressure and tracheid size. *Plant Physiology*. 140(1):374-382. https://doi.org/10.1104/pp.105.067900

Poni S, Tagliavini M, Neri D, Scudellari D, Toselli M. 1992. Influence of root pruning and water stress on growth and physiological factors of potted apple, grape, peach and pear trees. *Scientia Horticulturae*. 52(3):223-226. https://doi.org/10.1016/0304-4238(92)90023-6

R Core Team. 2021. R version 4.1.2. Vienna (Austria): R Foundation for Statistical Computing. https://cran.r-project.org/bin/windows/base/old/4.1.2

Schreiber SG, Hamann A, Hacke UG, Thomas BR. 2013. Sixteen years of winter stress: An assessment of cold hardiness, growth performance and survival of hybrid poplar clones at a boreal planting site. *Plant, Cell & Environment*. 36(2):419-428. https://doi.org/10.1111/j.1365-3040.2012.02583.x

Sperry JS, Tyree MT. 1988. Mechanism of water stress-induced xylem embolism. *Plant Physiology*. 88(3):581-587. https://doi.org/10.1104/pp.88.3.581

Struve DK. 2009. Tree establishment: A review of some of the factors affecting transplant survival and establishment. *Arboriculture & Urban Forestry*. 35(1):10-13. https://doi.org/10.48044/jauf.2009.003

Torres-Ruiz JM, Jansen S, Choat B, McElrone AJ, Cochard H, Brodribb TJ, Badel E, Burlett R, Bouche PS, Brodersen CR, Li S, Morris H, Delzon S. 2015. Direct x-ray microtomography observation confirms the induction of embolism upon xylem cutting under tension. *Plant Physiology*. 167(1):40-43. https://doi.org/10.1104/pp.114.249706

Torres-Ruiz JM, Sperry JS, Fernandez JE. 2012. Improving xylem hydraulic conductivity measurements by correcting the error caused by passive water uptake. *Physiologia Plantarum*. 146(2):129-135. https://doi.org/10.1111/j.1399-3054.2012.01619.x

Tyree MT, Zimmermann MH. 2002. *Xylem structure and the ascent of sap*. 2nd Ed. Berlin (Germany): Springer-Verlag Berlin Heidelberg. 284 p. https://doi.org/10.1007/978-3-662-04931-0

Umebayashi T, Morita T, Utsumi Y, Kusumoto D, Yasuda Y, Haishi T, Fukuda K. 2016. Spatial distribution of xylem embolisms in the stems of *Pinus thunbergii* at the threshold of fatal drought stress. *Tree Physiology*. 36(10):1210-1218. https://doi.org/10.1093/treephys/tpw050

Umebayashi T, Sperry JS, Smith DD, Love DM. 2019. 'Pressure fatigue': The influence of sap pressure cycles on cavitation


©2026 International Society of Arboriculture

vulnerability in *Acer negundo*. *Tree Physiology*. 39(5):740-746. https://doi.org/10.1093/treephys/tpy148

Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S. 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiology*. 33(7):672-683. https://doi.org/10.1093/treephys/tpt030

Wang Y, Bertelsen MG, Petersen KK, Andersen MN, Liu F. 2014. Effect of root pruning and irrigation regimes on xylem water relations and xylem ABA and ionic concentrations in pear trees. *Agricultural Water Management*. 135:84-89. https://doi.org/10.1016/j.agwat.2013.12.017

Watson G. 1985. Tree size affects root regeneration and top growth after transplanting. *Journal of Arboriculture*. 11(2):37-40. https://doi.org/10.48044/jauf.1985.009

Watson WT. 2005. Influence of tree size on transplant establishment and growth. *HortTechnology*. 15(1):118-122. https://doi.org/10.21273/HORTTECH.15.1.0118

## ACKNOWLEDGEMENTS

We thank Dr. Yoko Watanabe and Dr. Yasuyuki Ohno from Japan for support. This work was supported by a KAKENHI Grant-in-Aid for Young Scientists (B)(no. 16K18713).

*Toshihiro Umebayashi (corresponding author)*
*Tohoku University*
*Graduate School of Life Sciences*
*Laboratory of Functional Ecology*
*Aramaki-Aoba, Aoba-ku*
*Sendai, Japan*
*Hokkaido University*
*Research Faculty of Agriculture*
*Sapporo, Japan*
*+81-22-795-7732*
*toshiumebayashi@gmail.com*

*Yasuhiro Utsumi*
*Kyushu University*
*Ashoro Research Forest*
*Ashoro, Japan*

*Yuzou Sano*
*Hokkaido University*
*Research Faculty of Agriculture*
*Sapporo, Japan*

**Conflicts of Interest:** The authors reported no conflicts of interest.

**Résumé.** Afin d'améliorer les techniques de repiquage, il est nécessaire de comprendre la réduction de la circulation hydrique dans le xylème, induite par la taille des racines, ainsi que les effets environnementaux suite au repiquage. Dans cette étude, nous avons évalué la relation entre le potentiel hydrique et la conductivité hydraulique ($K_s$) chez des jeunes plants de *Larix kaempferi* et de *Betula maximowicziana*, dont les racines avaient été taillées avec l'intention d'améliorer notre compréhension de la technique de repiquage. Diverses techniques de taille des racines ont été appliquées à des jeunes arbres des deux espèces en fonction du diamètre de leurs racines au collet. Après la repiquage, le potentiel hydrique et les valeurs $K_s$ ont été mesurés. De plus, la courbe de vulnérabilité a été obtenue à l'aide d'une méthode de centrifugation, en quantifiant la relation entre la diminution de la pression du xylème et le pourcentage de perte de $K_s$, ce qui a permis de comparer la tolérance au stress hydrique entre les deux espèces. *Betula maximowicziana* présentait des valeurs de $K_s$ plus élevées et était plus sensible à l'embolie induite par le stress hydrique que *L. kaempferi*. Chez *L. kaempferi*, aucune diminution de $K_s$ n'a été observée, sans égard à la technique d'élagage racinaire utilisée, et tous les jeunes plants ont survécu après leur repiquage. Chez *B. maximowicziana*, les plants ayant subi une taille des racines ont présenté une baisse du potentiel hydrique au milieu de l'été, ainsi qu'une diminution de $K_s$. En outre, le nombre de plants morts s'est accru à mesure que l'intensité de la taille des racines augmentait. Pour ces deux espèces, il a été constaté une corrélation entre l'augmentation de l'intensité d'élagage des racines et la mortalité post-repiquage chez l'espèce la plus vulnérable au stress hydrique, soit *B. maximowicziana*. Les relations entre les variations du potentiel hydrique après le repiquage, les réductions de $K_s$ liées à la taille des racines et la survie des jeunes plants procurent un cadre utile pour le choix des techniques de repiquage en vue d'améliorer le taux de réussite de celles-ci.

**Zusammenfassung.** Um die Verpflanztechniken zu verbessern, ist es notwendig, die durch den Wurzelschnitt verursachten Einbußen beim Xylem-Wassertransport sowie die Umwelteinflüsse nach der Verpflanzung zu verstehen. In dieser Studie untersuchten wir den Zusammenhang zwischen Wasserpotenzial und hydraulischer Leitfähigkeit ($K_s$) bei Jungbäumen von *Larix kaempferi* und *Betula maximowicziana*, deren Wurzeln beschnitten wurden, um unser Verständnis der Verpflanztechnik zu vertiefen. Die Wurzelbeschneidungsbehandlungen wurden bei Jungbäumen beider Arten entsprechend ihres basalen Wurzeldurchmessers durchgeführt. Nach der Umpflanzung wurden das Wasserpotenzial und $K_s$ gemessen. Darüber hinaus wurde die Anfälligkeitskurve mithilfe einer Zentrifugenmethode ermittelt, indem der Zusammenhang zwischen abnehmendem Xylemdruck und dem prozentualen Verlust von $K_s$ quantifiziert wurde, was einen Vergleich der Wasserstresstoleranz zwischen den beiden Arten ermöglichte. *Betula maximowicziana* wies höhere $K_s$-Werte auf und war anfälliger für durch Wasserstress verursachte Embolien als *L. kaempferi*. Bei *L. kaempferi* wurde unabhängig vom Ausmaß des Wurzelschnitts kein Rückgang des $K_s$-Werts beobachtet, und alle Jungbäume überlebten die Verpflanzung. Bei *B. maximowicziana* zeigten die dem Wurzelschnitt unterzogenen Jungbäume im Hochsommer einen Rückgang des Wasserpotenzials, begleitet von einer Verringerung des $K_s$-Werts. Zudem stieg die Anzahl der abgestorbenen Jungbäume mit zunehmendem Ausmaß des Wurzelschnitts. Bei beiden Arten wurde ein Zusammenhang zwischen zunehmendem Ausmaß des Wurzelschnitts und der Sterblichkeit nach der Umpflanzung bei der gegenüber Wasserstress anfälligeren Art, *B. maximowicziana*, festgestellt. Die Zusammenhänge zwischen den Veränderungen des Wasserpotenzials nach der Umpflanzung, den mit dem Wurzelschnitt verbundenen Verringerungen von $K_s$ und dem Überleben der Jungbäume bieten einen nützlichen Rahmen für die Auswahl von Umpflanzmethoden und die Verbesserung der Umpflanzungserfolgsraten.

©2026 International Society of Arboriculture

**Resumen.** Para mejorar las técnicas de trasplante, es necesario comprender la disminución del transporte de agua en el xilema inducida por la poda de raíces y los efectos ambientales posteriores al trasplante. En este estudio, evaluamos la relación entre el potencial hídrico y la conductividad hidráulica ($K_s$) en plántulas de *Larix kaempferi* y *Betula maximowicziana*, cuyas raíces fueron podadas a fin de mejorar nuestra comprensión de la técnica de trasplante. Los tratamientos de poda de raíces se aplicaron a plántulas de ambas especies según sus diámetros de raíz basal. Después del trasplante, se midieron el potencial hídrico y la $K_s$. Además, se obtuvo la curva de vulnerabilidad mediante un método de centrifugación, cuantificando la relación entre la disminución de la presión del xilema y la pérdida porcentual de $K_s$, lo que permitió comparar la tolerancia al estrés hídrico entre las dos especies. *Betula maximowicziana* presentó una $K_s$ más alta y fue más vulnerable al embolismo inducido por estrés hídrico que *L. kaempferi*. En *L. kaempferi*, no se observó disminución de $K_s$ independientemente del nivel de poda de raíces, y todas las plántulas sobrevivieron tras el trasplante. En *B. maximowicziana*, las plántulas sometidas a poda de raíces mostraron una disminución del potencial hídrico a mediados del verano, junto con una reducción de $K_s$. Además, el número de plántulas muertas aumentó con el incremento de los niveles de poda de raíces. Para ambas especies, se encontró una relación entre el aumento del nivel de poda de raíces y la mortalidad postrasplante en la especie más vulnerable al estrés hídrico, *B. maximowicziana*. Las relaciones entre los cambios postrasplante en el potencial hídrico, las reducciones de $K_s$ asociadas a la poda de raíces y la supervivencia de las plántulas proporcionan un marco útil para seleccionar métodos de trasplante y mejorar las tasas de éxito del trasplante.

©2026 International Society of Arboriculture

## Appendix

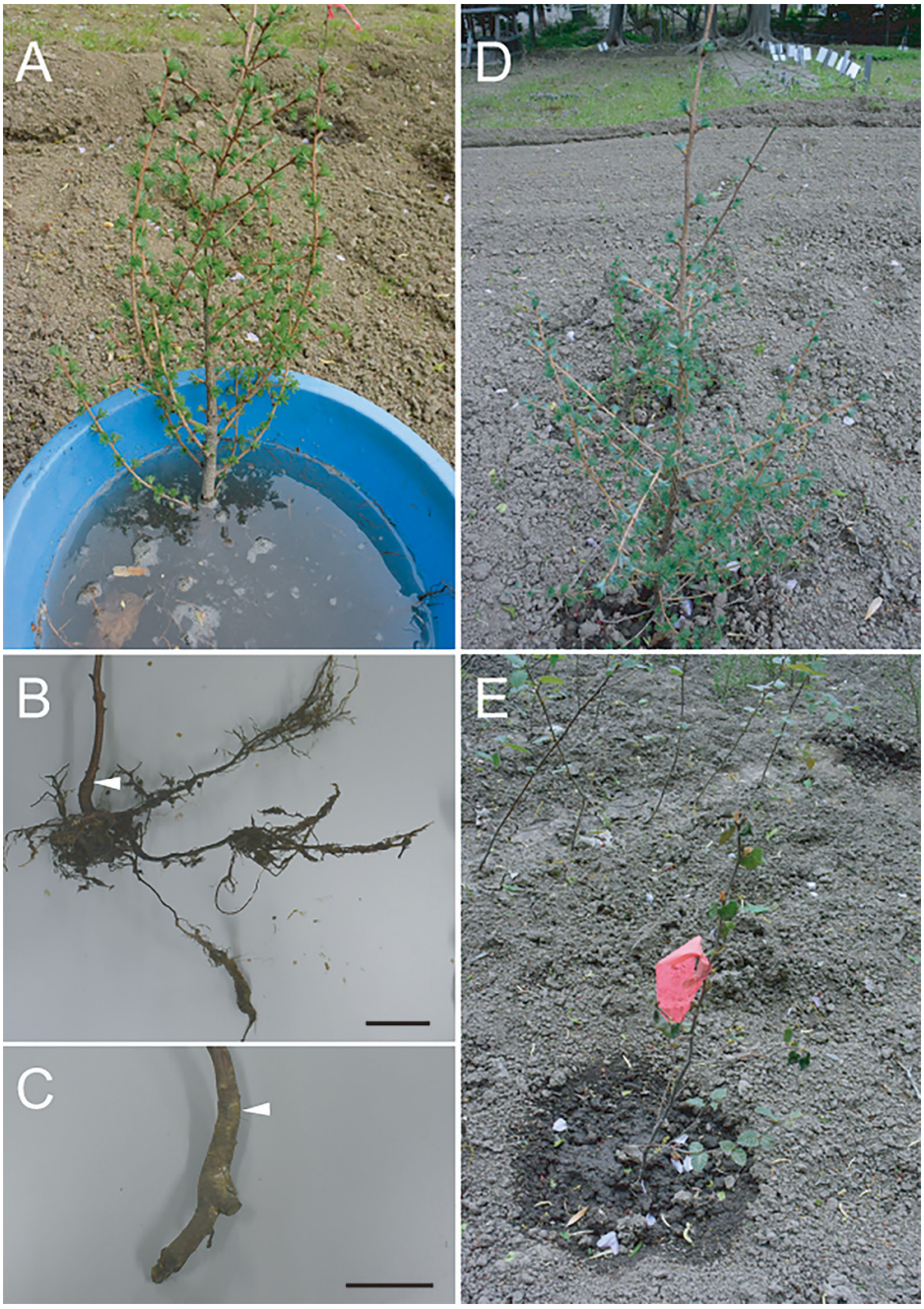


**Figure S1. Photographs of saplings before and after the root-pruning treatment. (A) A *Larix kaempferi* sapling soaked in water before the root-pruning treatment. (B) Roots of control saplings of *Betula maximowicziana*. (C) Roots of *B. maximowicziana* saplings subjected to the 100% root-loss treatment. (D) *L. kaempferi* saplings after transplanting. (E) *B. maximowicziana* saplings after transplanting in the nursery. Arrowheads in (B) and (C) indicate the positions corresponding to the maximal stem diameter at ground level. Scale bars in (B) and (C) represent 5 cm.**

*Appendix continued on next page*

©2026 International Society of Arboriculture

**Appendix. Continued.**

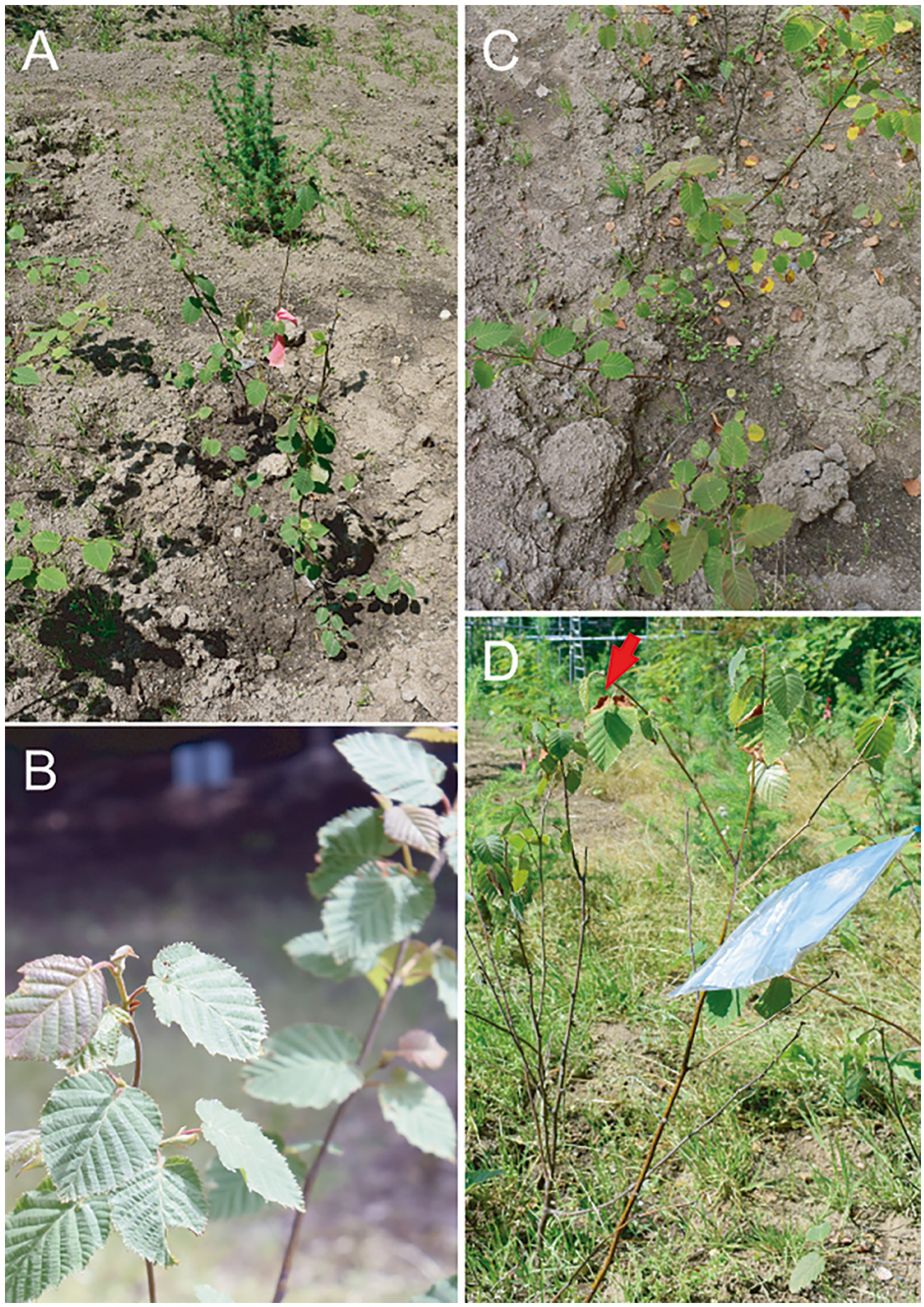


**Figure S2.** ***Betula maximowicziana*** **saplings after the transplant. (A–C) Saplings with 100% root loss on June 6 (A, B) and July 1 (C). (D) A sapling with 75% root loss on August 2. An arrow shows the observed dried part of the leaf.**

©2026 International Society of Arboriculture

**Table S1. Monthly air temperature (maximum and minimum) and precipitation data for Sapporo, Japan, from April to October 2016.**

| | Air temperature (°C) | | Precipitation (mm) | Humidity (%) |
|---|---|---|---|---|
| | Maximum | Minimum | | |
| April | 21.0 | 0.1 | 58.5 | 58 |
| May | 29.7 | 1.7 | 40.5 | 58 |
| June | 28.4 | 8.4 | 112.5 | 73 |
| July | 30.5 | 13.4 | 118.5 | 75 |
| August | 31.9 | 15.1 | 279.0 | 73 |
| September | 31.1 | 9.5 | 107.0 | 72 |
| October | 24.7 | 0.5 | 78.0 | 58 |

©2026 International Society of Arboriculture