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Effects of desiccation on post-planting stress in bareroot Corsican pine seedlings

SABINE GIRARD,[1–3] ANDRE CLEMENT,[2] HERVE COCHARD,[1] BRUNO BOULET-GERCOURT[3] and JEAN-MARC GUEHL[1]

[1] *Equipe Bioclimatologie et Ecophysiologie Forestières, INRA Centre de Nancy, F-54280 Champenoux, France*

[2] *Equipe Sol et Nutrition, INRA Centre de Nancy, F-54280 Champenoux, France*

[3] *Institut pour le Développement Forestier, 23 avenue Bosquet, F-75007 Paris, France*

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Summary We examined the post-planting consequences of pre-planting exposure stress on two-year-old, bare-root Corsican pine (*Pinus nigra* Arnold. ssp. *laricio* var. *Corsicana*) seedlings. Seedlings were lifted from a nursery and exposed to ambient conditions for periods of up to 192 h before being planted in minirhizotrons. Exposure decreased seedling water potential, CO_2 assimilation rate, leaf conductance and new root elongation, and increased mortality after planting. During exposure, needle total nonstructural carbohydrates (TNC) concentration (expressed on a dry mass basis) decreased by 0.31 mg g_{dm}^{-1} h^{-1}; however, needle and root TNC concentrations remained high (> 100 mg g_{dm}^{-1}) at planting, even in those treatments leading to severe seedling mortality. More than 90% of the seedlings with predawn water potentials lower than –1.3 MPa at planting did not elongate new roots and did not survive, whereas a similar percentage of seedlings with a predawn water potential above this value at planting elongated new roots and survived, suggesting that this value corresponds to a turgor threshold below which new root formation is inhibited. At planting, embolization of xylem conduits in roots and shoots was low for seedlings in all of the exposure treatments.

Keywords: CO_2 assimilation, embolism, leaf conductance, new root elongation, plant carbohydrate status, plant water status, xylem.

Introduction

Mechanical damage and perturbation of the functional continuity between soil and roots as a result of transplanting seedlings induce a stress that affects crucial processes including water and nutrient uptake, stomatal function and photosynthesis and may induce plant mortality. Water stress (Sands 1984, Aussenac and El Nour 1986, Grossnickle 1988, Kaushal and Aussenac 1989, Burdett 1990, Omi et al. 1991, Haase and Rose 1993, Jiang et al. 1995) and an insufficient supply of carbohydrates for metabolic and growth processes (Stupendick and Shepherd 1980, Puttonen 1986, Guehl et al. 1993) have been identified as the main components of transplanting stress. The physiological constraints induced by these stresses may hinder or delay root regeneration after transplanting, a process that is essential for the establishment of bare-root nursery plants (Stone 1955). However the precise mechanisms underlying the interrelationships between plant water status, photosynthetic activity, carbohydrate reserves and root regrowth are not fully understood.

Exposure of seedlings to drying ambient conditions, as may occur during the period between lifting in the nursery and planting in the field, exacerbates the effects of transplanting stress. Only a few hours of exposure may cause a significant decrease in survival (Hermann 1967, Coutts 1981, Tabbush 1987). The sensitivity of seedlings to desiccation depends on dormancy status (Hermann 1964, 1967, Mullin 1967, Coutts 1981, Ritchie 1986) and on the part of the plant that is exposed (Coutts 1981, Sucoff et al. 1985).

The present study was designed to assess the effects of short-term exposure to ambient conditions on transplanting stress in Corsican pine (*Pinus nigra* Arnold. ssp. *laricio* var. *Corsicana*), a species that is widely used for reforestation in southern Europe and for which substantial mortality occurs after transplanting (Kaushal and Aussenac 1989). The hypotheses tested were: that reduced root regrowth as a result of exposure is associated with (1) reduced carbon availability and (2) altered water status as a result of decreases in plant hydraulic conductance caused by embolism in the xylem conduits (Tyree and Sperry 1989, Cochard 1992).

Materials and methods

Plant material and experimental set-up

On January 7, 1992, 80 two-year-old (2 + 0) bare-root seedlings (source 'Bassin Parisien;' average height = 12.8 cm; root collar diameter = 4.2 cm; projected leaf area = 55 cm^2) were randomly lifted from a nursery near Auxerre, northeastern France. Intact seedlings were exposed to ambient conditions

(8 °C, at a vapor pressure deficit (VPD) of 0.43 kPa, and a 12-h photoperiod at a photon flux density of 40 μmol m^{-2} s^{-1} (400–700 nm)) for 0, 48, 120 or 192 h. At the end of each exposure period, 20 seedlings were randomly chosen for analysis. A subsample of ten seedlings was used to measure predawn needle water potential (Ψ_{wp}) and embolism-induced losses of hydraulic conductivity in root and shoot segments. The remaining ten seedlings were planted in minirhizotrons ($3 \times 30 \times 70$ cm containers with a transparent side to facilitate root observations) filled with sphagnum peat. The minirhizotrons were placed in a phytotron for 50 days providing a day/night air temperature of 22 ± 0.2/10 ± 0.2 °C; a day/night VPD of 1.06/0.12 kPa, a 12-h photoperiod at a photosynthetic photon flux density of 275 ± 15 μmol m^{-2} s^{-1} provided by fluorescence tubes and an ambient CO_2 concentration of 440 ± 30 μmol mol^{-1}. The growing substrate was maintained at field capacity throughout the experiment by irrigating the seedlings every second day. Needle predawn water potential, leaf gas exchange, new root elongation and bud development were followed periodically until Day 50 after transplanting.

On March 4, 1993, 100 two-year-old, bare-root seedlings from the same source and nursery as in 1992 (average height = 11.1 cm; root collar diameter = 3.6 mm; projected leaf area = 47 cm^2), were randomly taken from the nursery. After lifting, the intact seedlings were exposed to ambient conditions (8 °C at a VPD of 0.43 kPa in darkness) for 0, 8, 32, 56 or 104 h. At the end of each exposure period, 20 seedlings were randomly choosen. A subsample of ten seedlings was used to measure predawn needle Ψ_{wp}, needle relative water content (RWC), needle water potential components, root and needle carbohydrate concentrations and root and shoot hydraulic conductivity. The remaining ten seedlings were planted in minirhizotrons and grown in the phytotron under the same conditions as described for the 1992 experiment, except that the photoperiod was extended to 14 h. Predawn needle Ψ_{wp}, leaf gas exchange, new root elongation and bud development were followed periodically until Day 50 after transplanting.

Hydraulic conductivity and conductivity losses

The extent of embolism in the xylem conducting vessels was assessed in 20-mm lengths of basal stem and taproot of the treated seedlings by measuring the losses of hydraulic conductivity as described by Sperry et al. (1988) and Cochard and Tyree (1990). Hydraulic conductivities were measured by perfusing a degassed distilled water solution containing 0.1% HCl (pH = 2) through samples under 0.065 MPa of hydraulic pressure. The percentage loss of hydraulic conductivity (L) was calculated as:

$$L = \left(\frac{k_m - k_i}{k_m}\right)100, \quad (1)$$

where k_i and k_m (kg m s^{-1} MPa^{-1}) denote the hydraulic conductivities of the sample in its actual initial state after storage and after refilling the xylem conduits (perfusion with a solution under a 0.1 MPa pressure), respectively.

Curves of vulnerability to embolism characterizing the Corsican pine seedlings were assessed in ten unexposed control plants that were dehydrated by enclosing them in a pressure chamber and raising the pressure to between 2.75 and 6.5 MPa until the pressure equilibria were obtained. At that point the pressure was slowly lowered to atmospheric pressure. The percentage loss of hydraulic conductivity was then measured by the procedure described above. Curves of vulnerability to embolism were determined by relating the percentage of loss of hydraulic conductivity to xylem water potential.

Water status and gas exchange measurements

Predawn needle water potential (Ψ_{wp}) was determined on one needle per seedling with a Scholander pressure chamber. Immediately after measurement of Ψ_{wp}, four other needles from the same seedling were introduced into a syringe, immediately frozen in liquid nitrogen, and kept frozen at –18 °C. Before the water contents were expressed from the syringe, needles were thawed for 15 min at room temperature. The osmotic potential (π, MPa) of a 10-μl sample was measured with a vapor pressure osmometer (Wescor 5500, Logan, UT). Needle pressure potential (Ψ_p, MPa) was calculated as the difference between Ψ and π. Needle relative water content (RWC) was estimated as:

$$RWC = \left(\frac{FW - DW}{FW_{ft} - DW}\right), \quad (2)$$

where FW is the needle fresh weight, DW the dry weight and FW_{ft} the fresh weight at full turgor, i.e., after saturation in distilled water for one day. We assumed that the non-osmotic water fraction did not vary during the exposure periods (Wyn Jones and Gorham 1982), and estimated the osmotic potential at full turgor (π_0) as:

$$\pi_0 = \pi RWC.$$

Gas exchange measurements were made in the phytotron, 5 h after the beginning of the photoperiod, with a portable gas exchange measurement system (LI-6200, Li-Cor, Inc., Lincoln, NE). Carbon dioxide assimilation rate (A, mol m^{-2} s^{-1}) and needle conductance to water vapor (g, mmol m^{-2} s^{-1}) were calculated by means of the classical equations of von Caemmerer and Farquhar (1981). At the end of the experiments, seedlings were harvested and their projected needle surface area was measured with a leaf area meter (Delta-T Devices, Cambridge, U.K.).

Growth parameters

Before planting in the minirhizotrons, the seedlings were root pruned to remove all of the white root tips. Thus, only the suberized and suberizing parts of the root system were present at planting. The number and length of newly elongating white roots were assessed weekly after transplanting by taking a print of the growing roots visible through the transparent side of the minirhizotrons. Bud break index at the moment of planting was assessed as the number of days necessary to reach the

stage of swollen buds with opened scales. Mortality was recorded at the end of the experiments.

Carbohydrate measurements

Analyses were performed on lyophilized needle and root tissues. The lyophilized tissues from ten seedlings per treatment were pooled and finely ground. Soluble carbohydrates were extracted from 0.4 g dry matter in 12 ml of ethanol (80%) at 60 °C. The supernatant was collected by centrifugation for 15 min and a second extraction of the pellet was carried out with 8 ml ethanol. The pellet was saved and analyzed for starch. The two supernatants were combined, purified on cation and anion exchange columns (Amberlite IRN-77 (H^+), Pro Pabo, France; A-G 1,8 × (HCO_3^-), Biorad, Richmond, CA), and evaporated to dryness under vacuum at 60 °C. The residue was redissolved before high pressure liquid chromatography determination of the carbohydrates (Clement et al. 1992). The sugars were quantified against external standards. The most abundant soluble carbohydrates were glucose, fructose and pinitol. Sucrose, melezitose and inositol were also detected but in low concentrations (< 5 mg g_{dm}^{-1}).

Starch was extracted from 0.1 g (needle samples) or 0.05 g (root samples) of the ethanol-insoluble pellet by shaking with KOH at room temperature. Aliquots of this solution were analyzed spectrophotometrically (340 nm) after addition of amyloglucosidase (EC 3.2.1.3) and hexokinase (Boehringer-Mannheim, Mannheim, Germany). Carbohydrate concentrations were expressed on a tissue dry weight basis.

Statistics

One-way ANOVA was used to determine the effects of exposure duration on the different variables (Ψ_{wp}, π_0, Ψ_p, RWC, bud break index and new root elongation 50 days after planting) within each year. Significance levels quoted are at $P < 0.05$.

Results

Effects of exposure on plant water relations

In both 1992 and 1993, exposure of bare-root seedlings to the air caused a significant decrease in needle Ψ_{wp} (Table 1), but the effect was faster and more pronounced in January 1992 than in March 1993. In 1993, needle RWC was about 7% lower in plants exposed for 8 h than in unexposed control plants (Table 1). However, the 8-h exposure treatment had no effect on Ψ_p or Ψ_{wp}, but it decreased π_0 by about 0.17 MPa. Needle RWC further decreased from 0.90 to 0.81 between 56 and 104 h exposure, and turgor loss almost occurred ($\Psi_p = 0$) after 104 h of exposure (Table 1). Osmotic potential at full turgor increased from −2.1 MPa in seedlings in the 8-h exposure treatment to −1.7 MPa in seedlings in the 104-h exposure treatment.

In both shoots and roots, curves of vulnerability to embolism (Figure 1) were characterized by the onset of embolism at about −4.0 MPa and complete loss of hydraulic conductivity at about −6.0 MPa. The actual values of loss of conductivity in seedlings in the various exposure treatments were consistent with the vulnerability curves. The highest conductivity losses were observed in roots of seedlings in the 192-h exposure treatment. Although Ψ_{wp} of seedlings in the 192-h exposure treatment reached −4.5 MPa, the loss of conductivity did not exceed 30% for roots and was only 10% for shoots.

Effects of exposure on carbohydrate concentrations

After 104 h of exposure, needle soluble carbohydrates were depleted by 25% compared with those of unexposed control seedlings (Figure 2), as a result of reductions in glucose and fructose concentrations. Pinitol concentration was not affected by the exposure treatments. Needle starch concentration (about 10 mg g^{-1}) was low compared with soluble carbohydrate concentration. Root starch concentration was higher than

Table 1. Plant water status (Ψ_{wp}, needle predawn water potential; RWC, needle relative water content; π, needle osmotic potential; π_0, needle osmotic potential at full turgor; Ψ_p, pressure potential) and bud break index at the moment of planting, mortality and new root elongation after planting, in the seedlings from the different exposure treatments in January 1992 and March 1993. For a given date and variable, mean values not sharing a common letter are statistically different ($P \leq 0.01$, ANOVA followed by Fisher's PLSD separation test).

	At planting						After planting	
	Exposure duration (h)	Ψ_{wp} (MPa)	RWC	π_0 (MPa)	Ψ_p (MPa)	Bud break index (days)[1]	Mortality (n = 10)	New root elongation (cm per 50 days)[1]
January 1992	0	−0.33 a	nd[2]	nd	nd	> 50	1	22.9
	48	−2.84 b	nd	nd	nd	> 50	10	0
	120	−3.86 c	nd	nd	nd	> 50	10	0
	192	−3.83 c	nd	nd	nd	> 50	10	0
March 1993	0	−0.15 a	0.94 a	−1.91 b	1.75 a	23.7 a	0	126.3 a
	8	−0.31 a	0.86 b	−2.08 a	1.77 a	24.5 a	1	104.4 a
	32	−0.20 a	0.89 b	−2.01 ab	1.81 a	24.0 a	0	99.2 a
	56	−0.27 a	0.90 ab	−1.75 c	1.48 b	29.4 a	0	103.3 a
	104	−1.94 b	0.81 c	−1.68 c	0.11 c	67.3 b	6	7.7 b

[1] Mean value for surviving plants only.
[2] nd = Not determined.

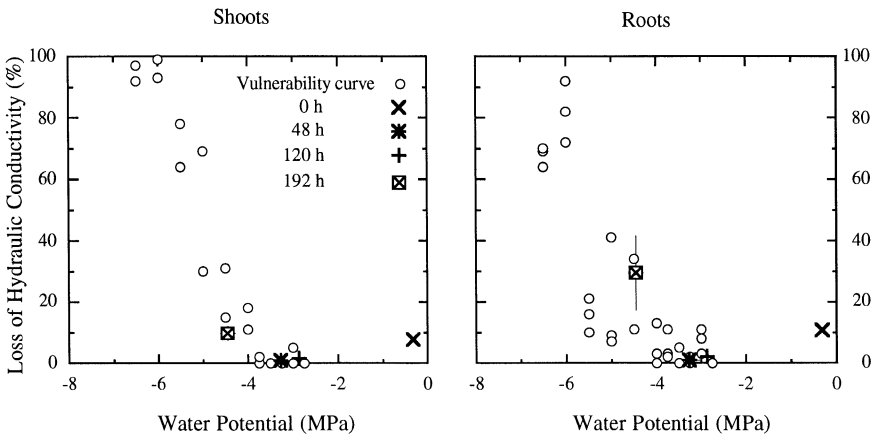

Figure 1. Curves of vulnerability to embolism (circles) and actual losses of hydraulic conductance in stems and roots during exposure (January 1992 experiment). Bars denote ± 0.5 SEM. There are small differences between the Ψ_{wp} values presented here and those given in Table 1 because two different subsamples of seedlings were used.

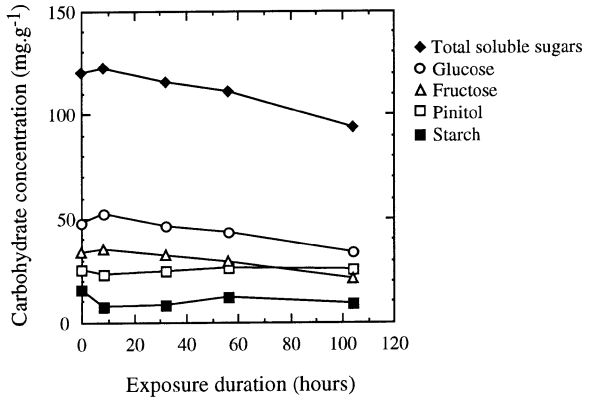

Figure 2. Time course of needle carbohydrate concentrations during exposure (March 1993 experiment). Data points are the means of three replicates from the ground pooled material of ten plants within each treatment.

that of needles (91 mg g^{-1}). Neither starch nor soluble carbohydrate concentrations of roots were affected by the exposure treatments (data not shown).

Seedling survival, new root elongation and bud break

None of the exposure treatments caused visible damage to the seedlings in either 1992 or 1993. In January 1992, all of the exposed seedlings died without having regenerated new roots (Table 1), whereas the unexposed control seedlings regenerated new roots from Day 18 after transplanting, but no bud break was observed within 50 days after transplanting. In March 1993, almost no seedlings died in the 8-, 32- and 56-h exposure treatments (Table 1) and bud break as well as root growth started about ten days after transplanting. There were no significant differences in root regeneration and bud break index between seedlings exposed for 0, 8, 32 and 56 h (Table 1). Only four out of the ten seedlings in the 104-h exposure treatment survived after transplanting (Table 1), and root regeneration and bud break in the surviving seedlings were delayed compared with plants in the shorter exposure treatments (Table 1, Figure 3).

Time course of water potential, and gas exchange after planting

In 1992, the unexposed control plants exhibited a progressive decrease in Ψ_{wp} from −0.33 MPa, just before planting, to about

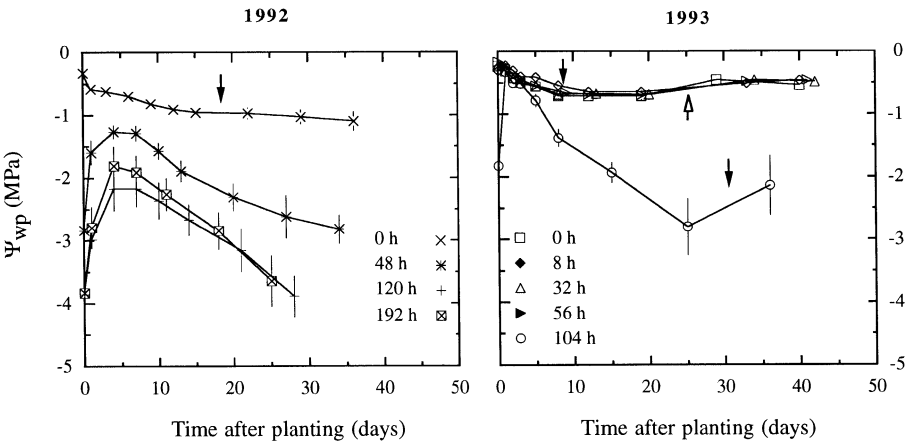

Figure 3. Time course of predawn needle water potential (Ψ_{wp}) after planting of seedlings subjected to different exposure durations. Data for both experimental years are presented. Vertical bars denote ± 0.5 SEM. Black arrows indicate the onset of root regeneration and the white arrow indicates the onset of new shoot growth.

−1.1 MPa at 37 days after planting (Figure 3). The decrease in Ψ_{wp} was most pronounced during the first 18 days following planting, before new roots appeared. No clear alterations in *A* and *g* occurred in the unexposed control seedlings after planting, whereas in the exposed seedlings, there was a distinct increase in Ψ_{wp} followed by a decline (Figure 3), with maximum values occurring four days after planting. Among the treated seedlings, those subjected to the longest exposure periods (120 and 192 h) exhibited the lowest Ψ_{wp} values. Exposure caused significant reductions in both *A* and *g* after planting (Figure 4).

In 1993, all seedlings exposed for less than 104 h exhibited a decrease in Ψ_{wp} until Day 8 after planting (Figure 3). Afterward, Ψ_{wp} increased slightly, concomitantly with root regeneration. Both *A* and *g* (Figure 4) of these seedlings increased steadily after planting, and the increase was more pronounced following Day 30 after transplanting when new, but still nonphotosynthesizing, shoot axes developed. Seedlings in the 104-h exposure treatment displayed lower Ψ_{wp}, *g* and *A* values than seedlings in the shorter exposure treatments, and recovery of these parameters only occurred after new roots appeared.

Relationship between plant water potential and new root elongation

At the individual seedling level, new root elongation was closely related with Ψ_{wp} measured just before and 10 days after transplanting (Figure 5). More than 90% of the seedlings with a Ψ_{wp} lower than −1.0 MPa at planting died after transplanting, whereas about 90% of the seedlings that displayed Ψ_{wp} values above this threshold survived (Figure 5). None of the seedlings with a Ψ_{wp} lower than −1.3 MPa 10 days after planting produced new roots.

Discussion

Exposure of lifted seedlings to ambient conditions exacerbated the effects of transplanting stress on root regeneration and

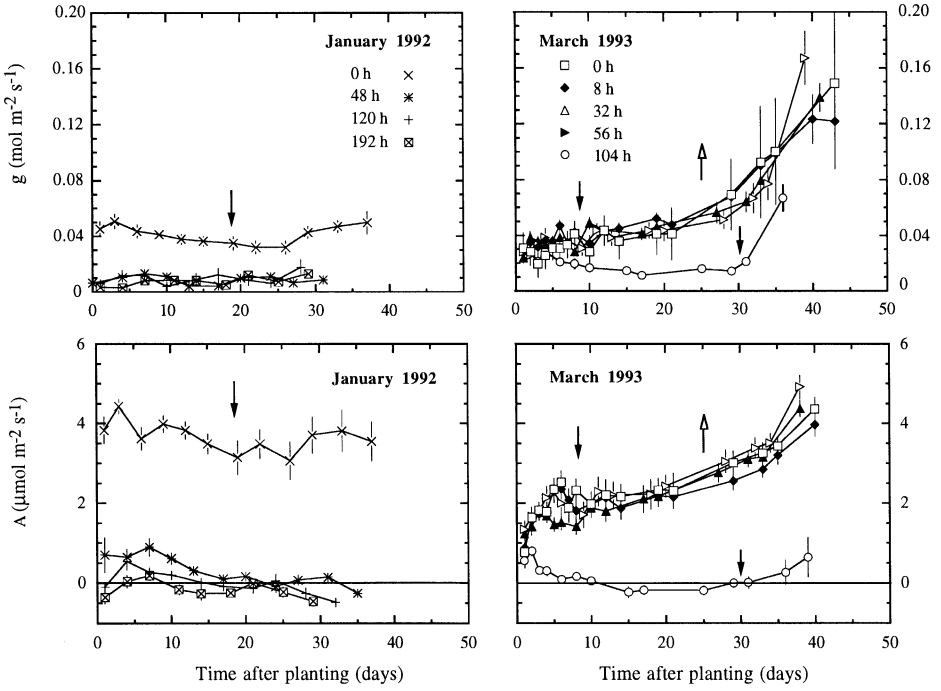

Figure 4. Time course of needle conductance for water vapor (*g*) and CO_2 assimilation rate (*A*) after planting of seedlings subjected to different exposure durations. Data for both experimental years are presented. Vertical bars denote ± 0.5 SEM. Black arrows indicate the onset of root regeneration and white arrows indicate the onset of new shoot growth.

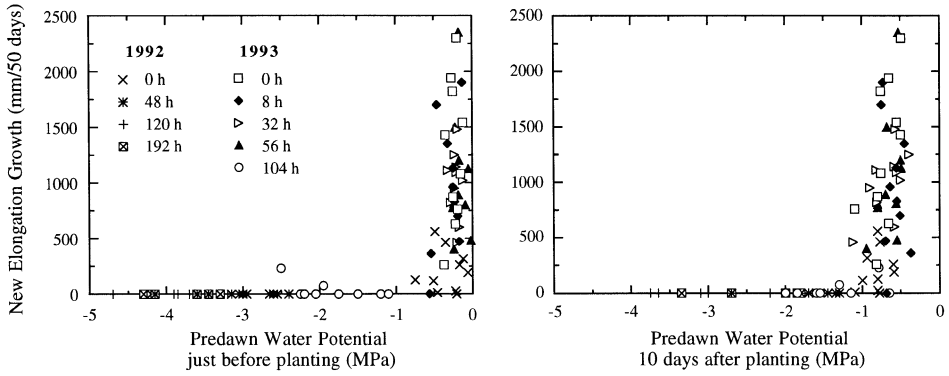

Figure 5. Relationship between needle predawn water potential (Ψ_{wp}) measured either just before planting or 10 days after planting and cumulative new root elongation 50 days after planting. Data are for individual seedlings subjected to different exposure durations for both experimental years.

plant mortality. The effects of exposure were more pronounced in January 1992 than in March 1993 even though the unexposed control seedlings lifted in March 1993 displayed greater new root elongation after planting than those lifted in January 1992. Our results differ from those observed for *Pseudotsuga menziesii* (Mirb.) Franco by Hermann (1967) and Ritchie (1986), and for *Picea sitchensis* (Bong.) Carrière. by Coutts (1981) and Deans et al. (1990), all of whom reported a lower resistance to root exposure in post-dormant seedlings than in dormant seedlings. Our findings also conflict with those of (Riedacker and Arbez 1983) who reported maximum root regeneration in December and January for Corsican pine. The reasons for the differences in timing of maximum root regrowth and seedling sensitivity to exposure remain unclear, although we suspect that differences in climate and nursery conditions are contributing factors.

Although CO_2 assimilation was lower in seedlings that exhibited little new root elongation than in seedlings undergoing active root elongation, *A* and *g* of seedlings exposed for 104 h only started to recover after new roots appeared, suggesting a control of *g* and *A* by the roots rather than the reverse (cf. Grossnickle and Blake 1985, Brisette and Chambers 1992).

The decrease in needle total nonstructural carbohydrate (TNC) concentration corresponded to a needle respiration rate of about 0.12 mg CO_2 g_{dm}^{-1} h^{-1}. In 1993, mortality occurred in seedlings that had a needle TNC concentration of 100 mg g_{dm}^{-1}, which is fivefold higher than the survival threshold found for *Pinus sylvestris* L. needles by Puttonen (1986), suggesting that depletion of needle carbohydrates was not the primary reason for lack of early root regeneration and mortality in the exposed plants. However, carbohydrate depletion might have partly contributed to the inhibition of root regeneration in the treated plants that exhibited low *A* for several weeks after transplanting. It has been suggested that reduced availability of carbohydrates, or their sequestration for osmoregulation, limits root regeneration in bare-root transplanted conifer seedlings (e.g., Puttonen 1986, Guehl et al. 1993, Jiang et al. 1995).

Water stress, both at and after transplanting, was most pronounced in seedlings from the longest exposure treatments (Figure 3). Seedlings from the exposure treatments that caused reductions in Ψ_{wp} at the time of planting, displayed a distinct transitory rehydration phase during the first days after planting that may have been associated with the high soil–plant water potential gradient (soil was maintained at field capacity). The decrease in Ψ_{wp} of the treated seedlings after transplanting coupled with the finding that xylem embolism in roots and shoots was not involved in this decrease (Figure 1), indicate that the exposure treatments increased the resistance to water transfer in the external root tissues.

Plant water status played a crucial role in determining the extent of new root elongation as shown by the close relationship between Ψ_{wp} measured 10 days after planting, i.e., at the time of potential root regeneration, and root growth potential. The threshold value of about −1.3 MPa, below which no root regeneration occurred, is close to the value of −1.5 MPa found in the same species by Aussenac and El Nour (1986) and Kaushal and Aussenac (1989) in root pruning studies. Although we did not make any direct measurements of root turgor, the value of −1.3 MPa probably corresponds to turgor loss, or to the turgor threshold below which new root growth is inhibited. In needles, turgor loss occurred at about −2.0 MPa (Table 1), which supports earlier studies showing that turgor loss occurs at higher water potential values in roots than in shoots in coniferous species (Kandiko et al. 1980, Ritchie and Schula 1984).

In conclusion, root regrowth capacity of Corsican pine seedlings was sensitive to exposure as a result of exposure-induced water stress. Poor root regrowth capacity and the development of water stress were not associated with inhibition of CO_2 assimilation or depletion of carbohydrate reserves. Furthermore, xylem embolism was not involved in the development of water stress during exposure. We conclude that predawn water potential at the time of transplanting was a reliable predictor of the ability to regenerate new roots and of seedling mortality after planting, with a threshold value of −1.3 MPa below which new root growth was inhibited and mortality was close to 100%. The identification of this threshold could be of importance from a practical point of view for the evaluation of seedling quality (Cleary and Zaerr 1980, Lopushinsky 1990).

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