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Freeze injury to roots of southern pine seedlings in the USA

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Roots of pine seedlings can be injured by freezing temperatures and the degree of injury is affected by genotype and stage of acclimation. Local sources of *Pinus echinata* and *P. virginiana* that were acclimated by cold temperatures were relatively freeze tolerant when grown in nurseries located where average minimum temperatures ranged from –18 to –23°C. However, seedlings of *P. taeda*, *P. elliottii* and *P. palustris* that were grown in warmer climates were injured by less severe freezes (i.e. –4 to –18°C). Some fast-growing half-sib families from moderate Coastal Plain regions were more susceptible to freezing than Piedmont genotypes located in cooler climates. When seedlings are acclimated to cold weather, the temperature required to cause injury is lower than when seedlings have been deacclimated due to warm weather. For example, in 2004, unusually high temperatures in the month following the winter solstice deacclimated pine seedlings and this resulted in root injury from a –8°C freeze. Shoots did not show symptoms of injury (since they were not actively flushing) and therefore root injury was often overlooked. Many freeze-injured seedlings died within two months of the freeze event. Since freeze injury symptoms to roots were overlooked, foresters offered various reasons (other than the freeze) for the poor seedling performance.

Keywords: acclimation, frost, nursery, *Pinus elliottii*, *P. palustris*, *P. taeda*

Introduction

There are more than 100 *Pinus* species and the southern yellow pines consist of 11 species in the subsection *Australes* (Little and Critchfield, 1969). Pines in this subsection include *P. caribaea, P. cubensis, P. echinata, P. elliottii, P. glabra, P. occidentalis, P. palustris, P. pungens, P. rigida, P. serotina* and *P. taeda*. Although southern yellow pine plantations have been established in several countries including Argentina, Australia, Brazil, Chile, South Africa and Uruguay, published reports of freeze injury to newly planted seedlings in these countries are rare. For example, Poynton (1977) indicated that *P. elliottii* in South Africa is 'perfectly hardy to frost', *P. taeda* is 'very hardy to frost', *P. palustris* is 'very frost resistant' and *P. radiata* is 'exceedingly hardy to frost'. However, he did not indicate if these ratings were for recently planted seedlings or for older stands. Southern yellow pine seedlings have been killed when transplanted just prior to freezes that are –8°C or lower.

Pinus radiata, *P. patula* and *P. oocarpa* (subsection *Oocarpae*) are more sensitive to freeze events than *P. taeda* or *P. echinata* (Saylor, 1969; Bannister and Neuner, 2001). Research on freeze injury to *P. radiata* is primarily from Australia and New Zealand (Menzies and Holden, 1981; Warrington and Jackson, 1981; Greer and Warrington, 1982; Menzies *et al.*, 1987; Neuner and Bannister, 1995). In Argentina, *P. patula* can be injured by temperatures of –5°C (Golfari, 1963) and in South Africa 'young trees' of this species are occasionally killed when freezing temperatures are combined with wind (Poynton, 1977). Therefore, some establishment models indicate that *P. patula* should not be planted during months when temperatures are likely to fall below 0°C (Crous and Mitchell, 2006).

Although freeze injury can occur to recently transplanted *P. taeda, P. elliottii* and *P. patula*, some foresters and landowners might attribute the reduction in survival to some other event. This is because seedlings with freeze-damaged roots are not examined when they show no obvious signs of shoot injury (Krasowski *et al.*, 1993). Therefore, it may be difficult to pinpoint the exact cause of death once the roots have dried and have turned brown. Symptoms of freeze injury to roots typically occur within a week of the freeze, but proper diagnosis may require roots to be removed from the soil and the bark pealed back to reveal the cambium tissue. Orange and brown cambium in the taproot are symptoms of freeze injury.

There are four classes of injury that result from low temperatures: root injury, shoot injury, frost heaving and winter desiccation. Frost heaving and winter desiccation will not be discussed in this review. Since roots are generally less cold hardy than shoots (Ryyppö *et al.*, 1998; Larcher, 2005), the focus of this paper will be on root injury. Freeze injury to roots can be classified into three groups: preacclimation; acclimation; and deacclimation. Preacclimation injury (PAI) typically occurs during the autumn before seedlings have been exposed to a sufficient amount of chilling temperatures (<8°C). Acclimation injury (AI) affects seedlings after they have been acclimatised by long nights and low temperatures. Deacclimation injury (DI) occurs after acclimation (or partial acclimation) has occurred and after a sufficient amount of warm weather has stimulated a resumption of cell division. DI can occur in the winter or early spring (during or just before shoot growth) (Table 1).

Freeze events can be classified as being light, moderate or severe (Michaels, 1991). A moderate freeze occurs when the air temperature is between –2 and –4°C and severe freezes occur when the temperature is below –4°C. In general, plants in the Southern Hemisphere are less tolerant of severe freezes than plants in the Northern Hemisphere but this is likely due to the milder climate of the Southern Hemisphere due to the influence of the oceanic environment (Bannister, 2007).

The United States Department of Agriculture (USDA) divides the USA into 11 'hardiness zones', which are based on an average (n = 13) of the annual coldest temperatures for the period 1974 to 1986. Each zone represents approximately a 5.5°C temperature class. For example, Zone 7 ranges from –12.2 to –17.7°C while Zone 8 ranges from –6.6 to –12.2°C. Each climatic zone is further divided into two subzones (A and B) of approximately 2.75 degree ranges (DeGaetano and Shulman, 1990). Plants that naturally occur in Zone 5 are generally more hardy than plants from Zone 8 (Bannister, 2003). Instead of the US number-letter system, this paper will refer to climatic zones in terms of the zone's more polar boundary (e.g. Bannister and Neuner, 2001). Therefore, USDA Zone 7b will be expressed as Zone –15.0 while Zone 7 will be expressed as –17.7.

Freeze events

Severe freeze events have injured roots of seedlings in both the Northern and Southern Hemispheres. In some cases, temperature data collected prior to the freeze indicates a DI freeze occurred while in other cases an AI freeze occurred. DI freeze events have been reported in 1932, 1938, 1957, 1983 and 2004 (Table 1). Some details of three severe freeze events are described below.

1983 DI freeze

Warm weather occurred during early December and this was followed by record low temperatures throughout the southern USA on 25 December 1983. This freeze killed many orange trees (*Citrus sinensis* [L.] Osbeck) and damage was estimated at US$1 billion. The arctic high pressure system spread quickly over the US (along with associated high winds) and the ground froze at a number of forest tree nurseries. Although air temperatures were often below –10°C, root damage was confined mainly to nurseries located in Climatic Zone –12.2 at latitudes below 34° N (Table 2). Freeze injury to pine roots was not reported in Climatic Zone –23.3 (i.e. Kentucky, Tennessee, Arkansas, Oklahoma). Temperatures at Auburn, Alabama were above 10°C for several weeks prior to the freeze (Figure 1). This PAI freeze resulted in injury to roots of several southern pines (Carlson, 1985; Lantz, 1985; Rowan, 1985).

1985 AI freeze

During early January, temperatures from midnight to 07:00 were below freezing at many nurseries, maintaining pines in an acclimated condition. An AI freeze on 21–22 January 1985 set state records in Virginia (–34°C), North Carolina (–37°C) and South Carolina (–28°C). Temperatures were generally lower than those recorded on 25 December 1983 but an unusually warm period did not precede the freeze (Figure 2). As a result, root injury was not observed on pine seedlings in nurseries. However, needle injury did occur if *P. taeda* families were planted too far north. Genotypes originating from Climatic Zone –9.4 were injured more than families from Zone –12.2 (Hodge and Weir, 1993). In general, fast-growing genotypes were more injured by the freeze than slower-growing genotypes.

2004 DI freeze

Unseasonably warm weather occurred during the first week of January 2004. At some locations, temperatures were above 24°C 48h before the freeze. In some locations, temperatures (1.5m above the ground) dropped from 23°C

Table 1: Year, season and Julian date (JD) of the freeze event, minimum temperature (°C), type of freeze and type of freeze injury reported for southern pines in North America

Year	Season	JD	°C	Type of freeze	Type of injury	Citation
1991	Autumn	309	–7	Preacclimation	Needle burn	South *et al.* (1993)
1950	Autumn	329	–22	Preacclimation	Root cambium and needle burn	Minckler (1951)
1962	Autumn	346	–27	Acclimation	Needle burn	Thor (1967)
1995	Autumn	351	–9	Preacclimation	Needle burn	South (2006)
		355–6		Winter Solstice		
1989	Winter	357	–18	Acclimation	Needle burn	South and Loewenstein (1994)
1983	Winter	359	–15	Deacclimation	Root cambium	Carlson (1985)
2004	Winter	7	–8	Deacclimation	Root cambium	Cameron and Lowerts (2007)
1977	Winter	11	–26	Acclimation	Needle burn	Kolb *et al.* (1985)
1994	Winter	19	–14	Acclimation	Root cambium	South (2006)
1957	Winter	19	–7	Deacclimation	Needle burn	Weber (1957)
1996	Winter	19	–9	Acclimation	Root cambium	South *et al.* (2002)
1985	Winter	21	–18	Acclimation	Needle burn	Hodge and Weir (1993)
1932	Winter	69	–7	Deacclimation	Shoot cambium	Stone (1940)
		79–80		Equinox		
1938	Spring	97	–4	Deacclimation	Branch cambium	Glock (1951)

on 5 January to –8°C on 7 January. Temperatures of –8°C were recorded at Florence, South Carolina, and were –6°C at Shreveport, Louisiana, Meridian, Mississippi, and Fort Valley, Georgia. Although it did not get as cold, the absolute drop in temperature was greater than the 25 December 1983 freeze. Winds associated with the 2004 freeze were about 16–24km h^{-1}. Seedling roots were injured while shoots initially appeared uninjured. As a result, millions of pine seedlings with injured roots were outplanted. Areas with poor seedling survival ranged from Smith County, Texas, through Louisiana, Mississippi, Alabama, Georgia, and into south-eastern South Carolina (Jasper County). Temperatures in Florida were not as cold but at least one *P. palustris* planting chance in the panhandle may have been affected by temperatures below -3°C. Data from weather stations are useful but may not accurately reflect the temperatures in the plantation. For example, frost pockets may be 5°C colder than temperatures recorded at nearby weather stations (Hough, 1945; Fleagle, 1950). It has been estimated that financial losses from the 2004 freeze exceeded US$1 million. Many foresters did not check for root injury and therefore some wondered why so many seedlings were dead by May.

Areas with injured pine seedlings were located in Climatic Zone –15.0 and injured seedlings were mostly from Coastal Plain sources. Although temperatures on January 7 were actually lower in Climatic Zone –17.7, Piedmont sources in this zone escaped injury. For example, Jackson, Tennessee recorded a temperature of –13°C but injury to pine seedlings was not reported. Likewise, no reports of injury were forthcoming from central Arkansas where temperatures dropped to –11°C.

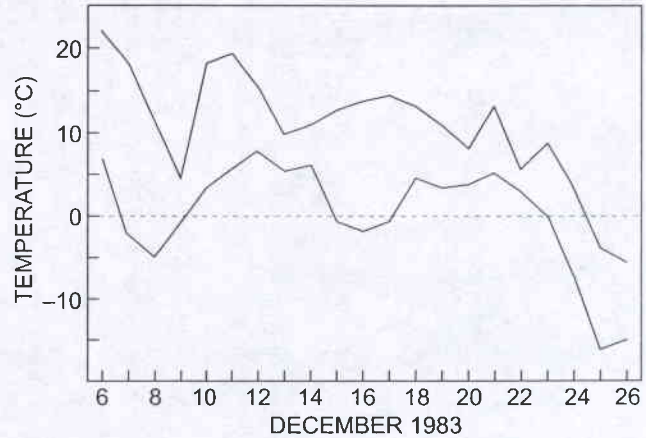

Figure 1: Maximum and minimum temperatures recorded at Auburn, Alabama for three weeks during December 1983. The deacclimation-injury freeze-injured pine seedling roots throughout Zone –12.2

Table 2: Nursery location (latitude-longitude), minimum temperature (°C), USDA climatic zonal limit, and associated root injury to *Pinus* seedlings from an early winter freeze (25 December 1983)

N latitude	W longitude	°C	Zonal limit (°C)	*P. taeda* injury (%)	Nursery manager's comments
37°25'	76°59'	–16	–17.7	0	
37°00'	88°17'	–26	–23.3	0	Severe needle burn on North Alabama source
35°45'	81°42'	–17	–17.7	0	
35°29'	88°43'	–23	–23.3	0	
35°29'	76°56'	–12	–12.2	0	
35°25'	78°01'	–17	–17.7	0	4–8% injury to *P. palustris*
34°45'	92°07'	–18	–17.7	0	No injury to *P. echinata* and *P. virginiana*
34°37'	84°42'	–19	–17.7	0	
33°43'	81°03'	–14	–12.2	0	
33°25'	89°45'	–16	–17.7	0	
33°10'	88°10'	–15	–17.7	3–7	Injury varied with family
32°50'	80°16'	–12	–12.2	0	
32°39'	86°33'	–19	–17.7	3–37	
32°33'	85°22'	–16	–12.2	5–65	10–15% injury to *P. elliottii* and 40–45% to *P. palustris*
32°31'	81°44'	–13	–12.2	0	No injury to *P. elliottii*
32°24'	86°52'	–14	–12.2	<2	<1% injury to *P. elliottii*
32°24'	86°41'	–14	–12.2	10–65	49% injury to *P. elliottii* and 61–88% to *P. palustris*
32°17'	84°27'	–14	–12.2	12–18	18% injury to *P. elliottii* and 1% to *P. clausa*
32°12'	92°48'	–14	–12.2	0	Some frozen bags of seedlings were discarded
32°04'	87°20'	–17	–17.7	0	50% injury to *P. palustris*
31°54'	81°56'	–13	–12.2	0	No injury to *P. elliottii* and *P. palustris*
31°10'	87°26'	–14	–12.2	28–88	53–70% injury to *P. elliottii* and 49–72% to *P. palustris*
31°09'	85°02'	–14	–12.2	1–2	2% injury to *P. elliottii* and < 10% to *P. palustris*
31°01'	89°10'	–14	–12.2	5	9–15% injury to *P. palustris*
31°00'	86°51'	–12	–12.2	10	21% injury to *P. elliottii* and 50% to *P. palustris*
30°55'	94°00'	–13	–12.2	0	Minor needle burn
30°51'	93°45'	–14	–12.2	0	
30°47'	86°57'	–13	–12.2	<4	2–17% injury to *P. elliottii* and 6–63% to *P. palustris*
30°24'	83°13'	–12	–12.2	<5	50% injury to *P. palustris*
29°28'	28°50'	–11	–12.2	0	>50% injury to *P. elliottii* var. *densa*

Discussion

Root injury symptoms

Injured cambial and parenchyma cells were detected from just above the groundline to several centimetres below the root collar (Figure 3). In some cases, the pith of the stem turned brown to black. Many seedlings outplanted after the 2004 freeze exhibited a lack of new root growth. For the southern pines, new root growth is dependent upon current photosynthesis (not stored carbohydrates). As a result, when transport of carbohydrates to the roots is inhibited, new root growth is reduced. Therefore, reduced root growth is a symptom of freeze injury.

Genotype

Freeze injury to pines is under genetic control (Minckler, 1951; Allen, 1961; Thor, 1967; Kolb *et al.*, 1985; Hodge and Weir, 1993; Duncan *et al.*, 1996; Kegley, 1999). In general, *P. echinata* and *P. virginiana* are more freeze tolerant than *P. taeda,* while *P. elliottii* and *P. palustris* are generally less tolerant than *P. taeda* (Bannister and Neuner, 2001). *Pinus palustris* is less tolerant of freeze than the other species (Hodges, 1961) probably because acclimation is not greatly increased by exposure to cold temperatures (Parker, 1961, 1965). As one might expect, cold tolerance of *P. strobus* (subsection *Strobi*) is greater than that for *P. palustris* and this difference might be due to a lack of sugar buildup in *P. palustris* pine needles (Parker, 1959). In some pines, freeze tolerance of needles is related to the sugar content of needles (Orgen, 1997).

Within a species, provenance and mother tree may also affect freeze tolerance. Coastal Plain sources are more susceptible to a freeze than are most Piedmont sources. Certain fast-growing Coastal Plain genotypes are less tolerant of freezes than other genetic sources (Hodge and Weir, 1993; South *et al.*, 2002).

Climatic zone and freeze injury

It seems counter intuitive, but less freeze injury has been reported from more polar nurseries (Zone –23.3) than from nurseries located in warmer climates (Zone –12.2). If a bare-root nursery is located in Zone –23.3, there appears to be little chance of a freeze injuring roots of pines grown from local seed sources. Injury can occur if southern less-hardy seed sources (originating from Zone –12.2) are sown in nurseries located in Zone –23.3. Nurseries located in Zone –12.2 have experienced root injury even when the genetic source is local. For example, in 1983, temperatures dropped below –15°C at both Pinson, Tennessee (35°29'N, 88°43'W) and Opelika, Alabama (32°33'N, 85°22'W) but freeze injury did not occur at Tennessee where the climate is colder (Table 2). Nurseries in Zone –23.3 do experience frost heaving and winter desiccation (Dierauf and Olinger, 1977) but these injuries are different from the injury that results in broken cell membranes (Krasowski *et al.*, 1993). Freeze injury to pines is relatively rare in Zone –6.6 but freeze injury does occasionally occur in this region (Weber, 1957; Olmsted *et al.*, 1993).

Acclimated seedlings vs deacclimated seedlings

Acclimation plays an important role in freeze tolerance of pine seedlings. In general, non-acclimated seedlings are injured at higher temperatures than acclimated seedlings.

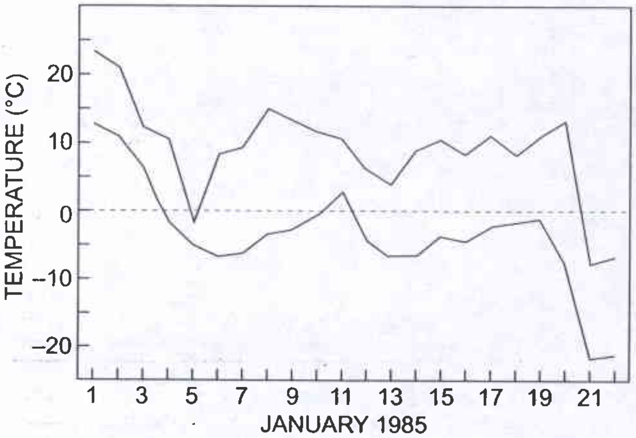

Figure 2: Maximum and minimum temperatures recorded at Auburn, Alabama for three weeks during January 1985. This freeze injured few local pines since preceding the freeze, temperatures from midnight to 07:00 were generally below freezing

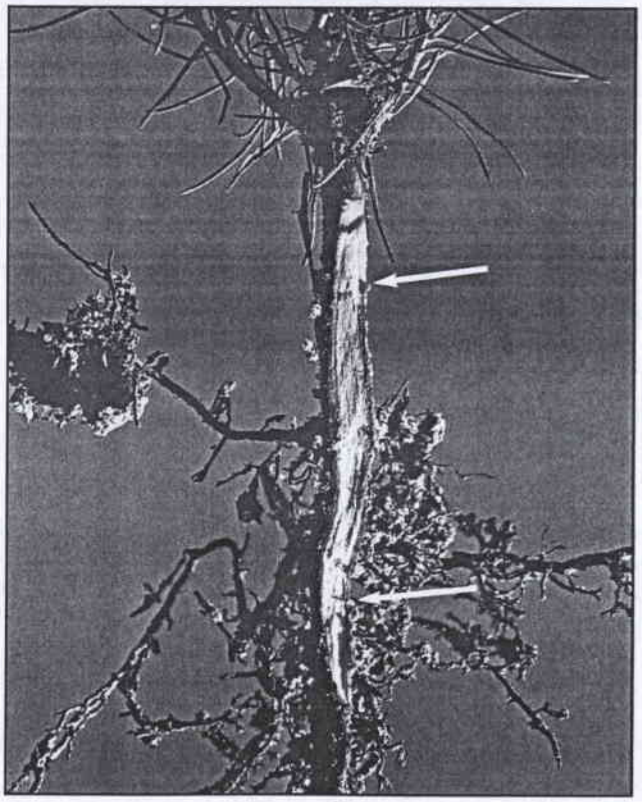

Figure 3: Root injury to a *Pinus taeda* seedling from a –9°C freeze on 7 January 2004. Air temperatures were above 21°C just a few days prior to the freeze. Seedlings that were frozen and then stored at 2°C had red-brown bark that slips with ease and the cambium is spongy and grey-brown in colour. Seedling mortality occurred soon after planting. The brown, freeze-injured cambium in this photo extends from the top arrow to the bottom arrow and is primarily on one side of the seedling

For example, non-acclimated greenhouse-grown *P. taeda* seedlings were killed by a –5°C freezing test while acclimated seedlings survived the freeze (Mexal *et al.*, 1979). Likewise, acclimated seedlings are more freeze tolerant than deacclimated seedlings (Figure 4). For example, acclimated *P. taeda* in New Jersey apparently tolerated a –32°C February 1934 freeze, but two years earlier, new growth of deacclimated seedlings was killed by a light freeze (–1°C) in late spring (Wood, 1936). Therefore, if the temperatures between midnight and 07:00 prior to a hard freeze have been low (e.g. Figure 2), seedlings are less likely to be injured than if temperatures before a freeze were high enough to promote a resumption of cell division (e.g. Figure 1).

Freeze injury is not related to the presence of a terminal bud

The hypothesis stated above has not been rejected by scientific studies. Freeze injury to *P. taeda* was not related to the presence or absence of a terminal bud (South *et al.*, 1993; Duncan *et al.*, 1996). *Pinus taeda* seedlings injured in the 1983 freeze had terminal buds and *P. elliottii* seedlings with terminal buds were injured by a –7°C freeze (Weber, 1957). Although a large seedling is more likely to have a terminal bud than a small seedling (Williams *et al.*, 1988), it has not been demonstrated that a seedling with a terminal bud is more resistant to a freeze than a similar-sized seedling without a terminal bud. The myth that a terminal bud must be present before the shoot can acclimate to cold temperatures may have started with observations in the spring. Injury from a late spring frost is likely to occur when seedlings have broken bud and are growing. The mere presence of a terminal bud does not mean the seedling is acclimated to cold temperatures.

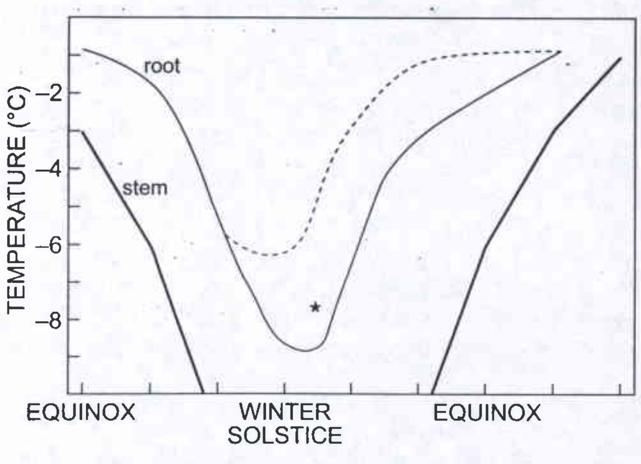

Figure 4: Hypothetical course of hardening patterns for an eight-month-old *Pinus taeda* seedling that was outplanted two weeks prior to the winter solstice. Lines represent a series of temperatures that would injure the cambium at the root collar (thin line) and upper stem (thick line). A –8°C freeze event (star) that occurred three weeks after the winter solstice would be classified as a DI freeze since roots of deacclimated seedlings (dashed line) would be injured. In this example, the temperature would not be low enough to injure roots of an acclimated seedling

Conclusions

Freeze damage to the roots of pine seedlings can occur at temperatures that produce little or no adverse effect on needles or stems of mature pine trees. Since roots are underground, injury may go undetected until months after the freeze when the seedling dies. The injured seedlings typically show no sign of needle injury until conditions favourable for shoot growth trigger resource demands on the root system. At that point, foliage turns brown and seedling death might be mistakenly attributed to some other event (such as a drought, herbicide, or a disease). Some may incorrectly assume that temperatures of –8°C during the winter are not low enough to cause mortality of newly planted pine seedlings. In some cases, freeze injury is not even proposed as a possible reason for unexplained seedling mortality. Perhaps the belief that –8°C temperatures will not injure roots of recently planted seedlings originates from reports that southern pine plantations are very hardy to frost.

Although standing trees may show no outward signs of injury, one-year-old southern pine seedlings exposed to continuous warm periods can be injured by temperatures of –8°C (in winter) or –7°C (in the autumn or spring). Therefore, if a –8°C or lower freeze event occurs in the Southern Hemisphere, foresters might consider checking newly planted pine seedlings to see if injury symptoms are present in the taproot.

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