A note on root development, bud activity, and survival of Douglas-fir, and survival of western hemlock and noble-fir seedlings, following exposure to ethylene during cold storage[1]

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Three cold storage experiments were conducted with bare-root Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings from coastal Oregon and eastern Washington Cascade sources. The objectives were to determine the effects of ambient, below-ambient ($KMnO_4$ pellets), and 0.5 and 5 ppm ethylene during short-term storage on subsequent root development (expt. 1) and bud activity (expt. 2), and to relate these results to survival in the field after prolonged cold storage (expt. 3). Root numbers and lengths were measured 28 days following a 7-day storage period after lifting seedlings on September 27 and December 1. In the coastal source, root numbers and lengths in the 5 ppm ethylene treatment were, respectively, 46 and 49% greater in September, and 22 and 13% greater in December, than the controls. No comparable treatment effects were found for the Cascade source. Neither the $KMnO_4$ nor the 0.5 ppm ethylene treatments affected root development in either seed source. For terminal buds in the controls, the number of days to 50% bud break was increased 2–8 days by a 30-day cold storage period compared with a 7-day period. For the coastal source, no increase in the time to 50% bud break was observed in the 5 ppm ethylene treatment. Seedling survival was evaluated in the field for the same treatments following 4 months cold storage for the Douglas-fir sources, coastal western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and noble fir (*Abies procera* Rehd.). Survival for the 5 ppm ethylene treatment compared with the control was increased by 55% in the coastal Douglas-fir source and by 13% in western hemlock. These results suggest that stimulated root development and bud activity may be partially responsible for the observed survival increase following cold storage at elevated ethylene levels.

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Trois expériences d'entreposage au froid furent conduites avec des semis à racines nues de Douglas taxifolié (*Pseudotsuga menziesii* (Mirb.) Franco) issus de provenances de la région côtière de l'Orégon et des Cascades dans l'est de l'État de Washington. Ces expériences avaient comme objectifs de déterminer les effets de la concentration ambiante d'éthylène, d'une concentration d'éthylène inférieure à la concentration ambiante (pastilles de $KMnO_4$) et de 0,5 et 5 ppm d'éthylène pendant un entreposage de courte durée sur le développement racinaire subséquent (expt. 1) et l'activité au niveau des bourgeons (expt. 2) et de relier ces résultats à la survie au champ après une période prolongée d'entreposage (expt. 3). La longueur et le nombre de racines furent mesurés 28 jours après une période d'entreposage de 7 jours qui suivait l'arrachage des semis le 27 septembre et le 1 décembre. Chez la provenance d'origine côtière, la longueur et le nombre de racines étaient 49 et 46% plus élevés en septembre 13 et 22% plus élevés en décembre que les témoins pour le traitement avec 5 ppm d'éthylène. Les traitements n'avaient pas d'effets comparables chez la provenance des Cascades. Les traitements avec $KMnO_4$ et avec 0,5 ppm d'éthylène n'ont pas influencé le développement des racines chez ni l'une ni l'autre des provenances. Dans le cas du bourgeon terminal chez les semis témoins, le nombre de jours requis pour atteindre 50% de débourrement a été augmenté de 2 à 8 jours par une période d'entreposage au froid de 30 jours comparativement à une période de 7 jours. Dans le cas de la provenance côtière, aucune augmentation du temps requis pour atteindre 50% de débourrement n'a été observée pour le traitement avec 5 ppm d'éthylène. La survie des semis a été évaluée au champ pour les mêmes traitements après 4 mois d'entreposage au froid avec les provenances de Douglas taxifolié et des provenances côtières de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et de sapin noble (*Abies procera* Rehd.). Comparé au témoin, le traitement avec 5 ppm d'éthylène a augmenté le taux de survie de 55% chez la provenance côtière de Douglas taxifolié et de 13% chez la provenance de pruche de l'Ouest. Ces résultats suggèrent que la stimulation du développement racinaire et de l'activité au niveau des bourgeons serait en partie responsable de l'augmentation observée du taux de survie suite à un entreposage au froid en présence de niveaux élevés d'éthylène.

[Traduit par la rédaction]

Introduction

Ethylene as a natural plant hormone has been intensively investigated (Beyer 1985), and many studies have shown that elevated ethylene levels during storage can cause defoliation and loss of vigor in herbaceous plants; however, knowledge of its role in regulating conifer seedling physiology is limited (Zaerr and Lavender 1980). Ethylene has been reported to reduce the vigor of fall-lifted Fraser fir (*Abies fraseri* (Pursh) Poir.) (Hinesley and Saltveit 1980), and Barnett (1980) observed that an ethylene absorbent enhanced survival of planted loblolly pine (*Pinus taeda* L.) seedlings.

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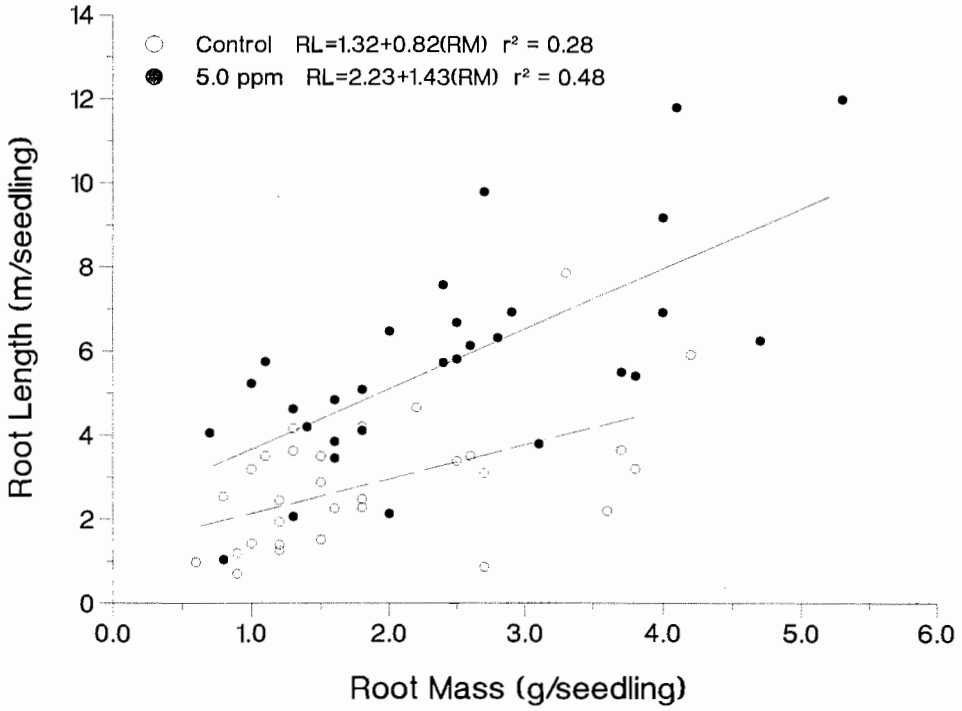

FIG. 1. Relation between individual seedling dry root mass (RM) and total new root length (RL) after 28 days following 7 days cold storage for the control and 5 ppm ethylene treatments. Measurements are from the coastal Douglas-fir source lifted on September 27.

However, Johnson and Stumpff (1984) found that an ethylene concentration of 4 ppm improved survival and growth of spring-lifted loblolly pine seedlings. Blake *et al.* (1989) showed that exposing coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) seedlings to 0.5 ppm ethylene during cold storage apparently reduced vigor, whereas 5 ppm increased vigor, relative to controls. Ethylene at 5 ppm was also reported to increase survival, apical bud activity, and new root formation of February-lifted Douglas-fir, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), and white fir (*Abies concolor* (Gord. & Glend.) Lindl.) seedlings that did not receive fungicide root dips before storage (Alvarez and Linderman 1983). Neither mycorrhizae nor selected rhizoplane microorganisms were affected by the ethylene treatments in the latter study. This suggests that the ethylene effects could be a purely physiological response rather than a consequence of increased fungistasis (Smith 1973) or from increased plant resistance to infection (Schier and Campbell 1978; Darvill and Albersheim 1984).

We hypothesized, if enhanced survival results largely from a physiological stimulation, then (*i*) significant increases in survival-related physiological traits, such as root development and bud activity, should be evident; (*ii*) physiological responses should be more pronounced during the fall months (van den Driessche 1977; Lavender 1964; Roberts *et al.* 1974); and (*iii*) differences in the ethylene response among seed sources should exist that correspond to patterns of growth cessation and cold tolerance (Campbell and Sorensen 1973; Lavender and Overton 1972). The objectives of the current study were to test these hypotheses by: (*i*) evaluating the effects of four storage – ethylene exposure treatments, in two contrasting seed sources of Douglas-fir, on root development and bud activity following lifting in late September and early December; (*ii*) relating these responses to field survival for the same treatments following prolonged cold storage; and (*iii*) evaluating the effects of these treatments on field survival of two other species, western hemlock and noble fir.

Methods

Two contrasting seed sources of 2 + 0 Douglas-fir from the Industrial Forestry Association bare-root nursery near Toledo, Washington (U.S.A.), and four storage treatments were used in each of three experiments. Separate storage and treatment replications were used to maintain each experiment as independent as possible in order to strengthen interpretations about the relationship between physiological effects and survival in the two seed sources. The sources were a coastal Oregon Douglas-fir from 150 to 300 m in elevation and an eastern Washington Cascade Douglas-fir from 750 to 900 m. Coastal Washington western hemlock from 0 to 150 m and Washington Cascade noble fir from 900 to 1150 m were used in the field survival experiment only. Each source was grown separately within the nursery. The four basic storage treatments were a control (representing ambient ethylene levels), an ethylene absorbent ($KMnO_4$ pellets) to establish below-ambient ethylene levels, 0.5 ppm ethylene, and 5 ppm ethylene. Seedlings were stored at 1°C in 8-L plastic Maraflex shrink bags (American Can Corp., San Francisco, Calif.), which have a low permeability to ethylene (personal communication, Dr. David Tingey, U.S. Environmental Protection Agency, Corvallis, Oreg.). Each replication was stored in a separate bag. Nominal concentrations of either 0.5 or 5 ppm ethylene were established by injecting a specific quantity of ethylene in air from a standard tank into each bag. Actual concentrations, based on gas chromatographic analysis (Alvarez and Linderman 1983), varied from 0.4 to 0.7 ppm for the 0.5 ppm treatment, and from 3.5 to 6.6 ppm for the 5 ppm treatment.

Expt. 1: The effects of short-term ethylene exposure during cold storage on root development

A short-term storage period was used to evaluate root responses in order to avoid excessive or variable seedling mortality and molding,

TABLE 1. Root development after 28 days for each Douglas-fir seed source following four 7-day ethylene storage treatments on two lifting dates

Treatment	Coastal source		Cascade source	
	Length (m/seedling)	No. of seedlings	Length (m/seedling)	No. of seedlings
September 27 lifting				
Control	3.45	153	4.09	169
$KMnO_4$	3.29	164	4.82	189
0.5 ppm ethylene	3.60	163	4.71	202
5.0 ppm ethylene	5.15	224	4.61	191
Contrast, control vs. 5.0 ppm *p*-level	0.06	0.05	0.33	0.34
December 1 lifting				
Control	4.76	170	3.63	143
$KMnO_4$	4.41	169	3.16	121
0.5 ppm ethylene	4.36	167	3.78	140
5.0 ppm ethylene	5.40	208	3.38	133
Contrast, control vs. 5.0 ppm *p*-level	0.36	0.14	0.60	0.64

NOTE: Data are adjusted means following covariance analysis using root mass. The $KMnO_4$ and 0.5 ppm treatments were not significantly different from the control using Dunnett's test ($p = 0.05$). $N = 30$ observations per mean.

which can occur when storing seedlings in the fall (Blake *et al.* 1979, 1989). These factors can confound average growth effects and make physiological interpretations difficult. Previous research indicated that ethylene-related root responses were detectable after a 7-day storage period (Blake *et al.* 1989). The design consisted of three replications of 10 seedlings each per treatment in a completely randomized design. Seedlings were lifted on September 27 and December 1 and stored for 7 days. Following storage, seedlings were planted in pots containing a mixture of peat–vermiculite, watered regularly, and maintained in a greenhouse at 20–27°C under natural day length. After 28 days the total number of new roots was recorded by 1 cm length classes for each seedling. Statistical analysis of the total number and length of new roots was conducted using root mass as a covariate because of the small size and limited replication (Fig. 1). Adjusting means for average root mass reduced variation between replicates and increased treatment *F*-values. Dead seedlings were excluded from the analysis. Four seedlings from the September lifting of the coastal source and two from the eastern Cascade source died. In the December lifting, two seedlings from the coastal source and none from the eastern Cascade source died. Comparisons between the control and the absorbent or 0.5 ppm treatments were made with Dunnett's test (Steel and Torrie 1960). The control and 5 ppm treatment were compared using a preplanned orthogonal contrast.

Expt. 2: The effects of ethylene levels and length of cold storage on time to bud break

Additional seedlings of each source were lifted on September 27 and December 1 to examine the effect of ethylene levels and storage period on time to bud break in a common environment. An extended 30-day storage period was included to enhance the detection of potential storage effects and treatment interactions. The experimental design was a completely randomized split plot, with the basic storage treatments as main effects and storage periods, 7- or 30-days, as subplots within each lifting date. Three replicates of 30 seedlings each were used to evaluate each storage period and treatment. At the end of the 30-day storage period, gas samples were withdrawn from the storage bags, using evacuated test tubes sealed with a serum stopper, to determine the final ethylene status. The samples were analyzed using the procedures of Alvarez and Linderman (1983). Seedlings were planted immediately after the designated storage period in a common transplant bed at the nursery site. The plots were kept weed free, but not irrigated or fertilized. The number of active terminal and lateral buds was recorded at 2- or 3-day intervals in the spring. Buds considered active had open scales and some new green tissue visible. The earliest bud activity occurred around April 1, and the number of days to 50% (median) bud break for the terminal and lateral buds was determined relative to this date. For lateral buds, the day that half of the seedlings had half or more of their buds (of those that eventually developed) active was used as the number of days to 50% bud break. The total number of lateral buds per seedling, including those that did not develop, was not recorded. Main effect comparisons between the control and other treatments were made as in the previous experiment. Within each lifting date – storage treatment, a preplanned orthogonal contrast was used to compare the effect of storage period on time to 50% bud break for terminal and lateral buds.

Expt. 3: The effects of ethylene levels during cold storage on initial survival

On December 3, seedlings from each source were lifted and sorted into 16 groups of 25 seedlings. The basic storage treatments were randomly assigned to provide four replications within each seed source. The bags were stored for approximately 4 months. A prolonged storage period was selected to increase possible treatment-related mortality effects. At monthly intervals the treatments were renewed by transferring seedlings to new bags and adding ethylene to maintain concentrations at desired levels. After the 4-month treatment period, seedlings were planted near the geographic location where the seed was collected. None of the planting locations received site preparation to control competing vegetation. The coastal Douglas-fir was planted just north of Corvallis, Oregon, on March 27. The eastern Cascade Douglas-fir was planted on March 28 near White Salmon, Washington. The western hemlock was planted on March 16 just north of Hoquim, Washington, and the noble fir near Mineral, Washington, on May 31. Each replication was planted as a single row in a randomized block design.

Survival was first evaluated between 6 and 8 weeks after planting at about the time of bud break, and a second time during late summer. The second evaluation was not completed for the eastern Cascade Douglas-fir because of a midsummer frost that killed many seedlings or for the noble fir because of road access problems. Analysis of variance for survival was made following arc-sine transformation of percentages. Comparisons between the control and the other storage treatments were made as in the previous experiments.

TABLE 2. Number of days to 50% bud break in April–May for coastal Douglas-fir seedlings following exposure to four ethylene treatments for either a 7- or a 30-day cold storage period on two lifting dates

	Terminal buds			Lateral buds		
	Days to 50% bud break			Days to 50% bud break		
Treatment	7-day period	30-day period	Contrast level (p)*	7-day period	30-day period	Contrast level (p)*
September 27 lifting						
Control	30	37	0.01	28	28	1.00
$KMnO_4$	30	32	0.55	26	27	0.84
0.5 ppm ethylene	30	29	0.81	27	26	0.84
5.0 ppm ethylene	32	30	0.55	29	27	0.42
December 1 lifting						
Control	31	39	0.00	25	31	0.00
$KMnO_4$	29	34	0.01	25	29	0.01
0.5 ppm ethylene	29	33	0.18	21	28	0.00
5.0 ppm ethylene	30	32	0.40	24	28	0.01

NOTE: $N = 3$ observations of 30 seedlings per mean. Main effects of storage treatments were not significant for any lifting date, bud type, or period. Probability levels (p) ranged from 0.22 to 0.69.
*Probability level for preplanned contrast between the 7- and the 30-day storage periods within each treatment.

TABLE 3. Number of days to 50% bud break in April–May for eastern Cascade Douglas-fir seedlings following exposure to four ethylene treatments for either a 7- or a 30-day cold storage period on two lifting dates

	Terminal buds			Lateral buds		
	Days to 50% bud break			Days to 50% bud break		
Treatment	7-day period	30-day period	Contrast level (p)*	7-day period	30-day period	Contrast level (p)*
September 27 lifting						
Control	28	30	0.85	27	27	1.00
$KMnO_4$	27	30	0.63	26	28	0.25
0.5 ppm ethylene	29	35	0.08	27	31	0.04
5.0 ppm ethylene	30	33	0.63	28	28	1.00
December 1 lifting						
Control	27	32	0.04	23	30	0.00
$KMnO_4$	27	31	0.12	25	29	0.01
0.5 ppm ethylene	26	33	0.01	21	28	0.00
5.0 ppm ethylene	28	34	0.02	27	30	0.03

NOTE: $N = 3$ observations of 30 seedlings per mean. Main effects of storage treatments were not significant for any lifting date, bud type, or period. Probability levels (p) ranged from 0.09 to 0.99.
*Probability level for preplanned contrast between the 7- and the 30-day storage periods within each treatment.

Results

For the coastal Douglas-fir source lifted on September 27, total length and number of new roots per seedling were increased by 49 and 46%, respectively, in the 5 ppm ethylene treatment compared with the control (Table 1). For the December 1 lifting date, root length and root numbers in the 5 ppm ethylene treatment were greater than for the control, but the differences were not significant. Neither the ethylene absorbent nor the 0.5 ppm ethylene treatment affected root development. None of the ethylene treatments significantly affected root numbers or lengths of the eastern Cascade Douglas-fir source on either lifting date.

The main storage treatments had no effect on average number of days to bud break for either the terminal or lateral buds of the coastal Douglas-fir seedlings, regardless of lifting date (Table 2). For the 30-day storage period, the mean days to bud break for the terminal bud was greatest for controls, and the contrast between the 7- and 30-day storage period was highly significant for both lifting dates. Time to 50% bud break for the terminal bud was not increased significantly by the 30-day storage period in either the 0.5 or 5 ppm ethylene treatment. Lateral bud activity in seedlings lifted on September 27 was not affected by the extended storage period, regardless of treatment. However, for seedlings lifted on December 1, lateral bud activity in all treatments was delayed to a similar degree by longer storage.

No main effects on bud activity were significant for the eastern Cascade source (Table 3). For the September 27 lifting, all 30-day storage treatments had slightly slower terminal bud break, but only the 0.5 ppm ethylene treatment

TABLE 4. Average ethylene concentrations (ppm) at the end of the 30-day storage period for the two Douglas-fir seed sources, the two lifting dates, and the four ethylene treatments in the timing of bud break experiment (expt. 2)

Treatment	Coastal source		Cascade source	
	September 27	December 1	September 27	December 1
Control	0.228	0.111	0.243	0.065
$KMnO_4$	0.072	0.051	0.076	0.031
0.5 ppm ethylene	0.398	0.556	0.431	0.468
5.0 ppm ethylene	3.45	2.97	3.61	3.29

TABLE 5. Percent survival for coastal and eastern Cascade Douglas-fir, western hemlock, and noble fir sources lifted December 3 and exposed to four ethylene storage treatments

Seed source	% survival by storage treatment				Contrast, control vs. 5.0 ppm (p-level)
	Control	$KMnO_4$	0.5 ppm	5.0 ppm	
Spring (6–8 weeks postplanting)					
Coastal Douglas-fir	62	87	92	97	0.01
Cascade Douglas-fir	92	91	94	92	1.00
Western hemlock	77	69	69	88	0.03
Noble fir	92	95	92	96	0.34
Summer (16 weeks postplanting)					
Coastal Douglas-fir	38	74	76	93	0.02
Western hemlock	56	51	53	69	0.17

NOTE: N = 100 observations per mean. The $KMnO_4$ and 0.5 ppm treatments were not significantly different from the control using Dunnett's test (p = 0.05).

appeared to have significantly slower terminal and lateral bud activity. For the December 1 lifting, 30-day storage delayed lateral bud break about equally in all treatments, whereas terminal bud break was somewhat slower in the two ethylene treatments. Analysis of air samples taken at the end of the 30-day storage period showed that actual concentrations were less than nominal amounts (Table 4). Ethylene concentrations in the control bags of the coastal and eastern Cascade Douglas-fir sources were similar, and bag concentrations measured at the end of the 30-day storage decreased between the September 27 and December 1 lifting dates.

Increasing the concentration of ethylene to 5 ppm during cold storage significantly improved initial field survival of coastal Douglas-fir and western hemlock seedlings (Table 5). The ethylene absorbent and the 0.5 ppm ethylene treatment did not significantly affect survival compared with the control level. Late summer survival, 16 weeks after planting, was substantially lower across all treatments, and differences between the control and 5 ppm ethylene treatments increased. Storage treatments had no effect on initial survival rates of the Cascade Douglas-fir or noble fir seedlings. Initial survival was above 90% in these sources, despite the long period of cold storage.

Discussion

Prolonged storage coupled with late season planting and a lack of competition control probably enhanced seedling mortality above normal levels for the coastal sites. No animal damage was observed, nor was mold apparent on the stored seedlings. For the coastal Douglas-fir source, the very poor survival in the control was strongly related to high mortality in two of the four replications. The remaining two replications averaged close to the $KMnO_4$ and 0.5 ppm ethylene treatment means. In agreement with previous reports with conifer seedlings (Alvarez and Linderman 1983; Johnson and Stumpff 1984; Blake *et al.* 1989), this study showed that maintaining high concentrations of ethylene (3–5 ppm) in a cold storage environment can improve seedling vigor and survival. However, the effect is clearly seed-source dependent either as a result of the sensitivity of individual sources per se, or because of their varying sensitivity to ethylene (Roberts *et al.* 1987). Seed sources of Douglas-fir can display large differences in survival following cold storage (Jenkinson and Nelson 1978; van den Driessche 1977). The apparent lack of treatment effects in eastern Cascade Douglas-fir and noble fir may also result from the overall high survival, which would mask treatment differences. However, the pattern of survival among treatments and between contrasting seed sources is closely linked with the observed short-term effects on root development and terminal bud activity. Empirical studies have correlated both the speed of terminal bud break and initial root growth with survival (Larsen *et al.* 1986). While bud activity for the Cascade source in September was decreased by the 0.5 ppm ethylene treatment, previous observations (Blake *et al.* 1989) that this treatment might be detrimental during cold storage were not confirmed. It is unclear whether the original observations, which were based upon subjective scores of vigor, were spurious or the detrimental responses to 0.5 ppm ethylene may vary with cultural practices or seedling sources, which changed between studies. The addition of an ethylene absorbent to storage bags did not consistently improve root development, bud activity, or survival, as observed by Barnett (1980) and Johnson and Stumpff (1984).

The levels of ethylene observed in the control bags (Table 4) are generally higher than those measured during monitoring of operationally stored seedling in polyethylene-lined kraft bags (personal observations of senior author), but less than the levels observed in a previous experiment (Blake *et al.* 1989). The only common trend among these observations is for concentrations to decrease with later fall lifting dates and to increase with length of storage. This suggests that the bag concentration levels may be controlled by a seasonally variable rate of synthesis and metabolism within the seedlings (Savidge 1988). While the mechanisms for ethylene metabolism and biochemical regulation have been partially elucidated (Beyer 1985), it is difficult to link these directly to the stimulation of root development and terminal bud activity by the 5 ppm treatment. Normally ethylene, at much lower concentrations, behaves as an antiauxin and inhibits root growth. The only similar root physiological responses to high concentrations of ethylene were observed by Crossett and Campbell (1975). They found a fivefold increase in lateral root elongation following transfer of barley roots that had been exposed to 10 ppm ethylene into an ethylene free environment. These concentration levels are near maximum saturation levels for known ethylene-mediated reactions.

If these root and bud physiological responses are mediated by known ethylene hormonal reactions, then it should be possible to readily reduce the effects using traditional inhibitors, such as silver nitrate and aminoethoxyvinylglycine (Beyer 1985). The extremely high concentrations needed to cause a measurable response may be related to the cold storage temperature, which could affect the conformation of the membrane reaction site, and also to a seasonal decrease in ethylene metabolism itself. There is circumstantial evidence, primarily the response of the coastal Douglas-fir, to support Beyer's (1979) hypothesis that endogenous rates of ethylene synthesis are positively associated with tissue sensitivity to exogenous ethylene. Although growth responses were observed following relatively short duration exposure periods, it is possible that an ethylene-mediate increase in disease resistance is partly responsible for the enhanced survival. Ethylene has been observed to reduce stem decay (Schier and Campbell 1978), stimulate phytoalexin production (Darvill and Albersheim 1984), and induce decay-resistant extractive synthesis in tree stems (Shain and Hillis 1973; Savidge 1988; Wolter 1977).

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