INJURIES TO TERMINAL SHOOTS CAUSE MULTIPLE-LEADERED NURSERY SEEDLINGS

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ABSTRACT

Multiple-leadered conifer seedlings are discarded by Ontario provincial tree nurseries as being unacceptable for planting. Extensive losses of millions of seedlings have occurred in some years. Diagnostic studies conducted at several nurseries showed that the multiple-leadered condition followed injuries to shoot terminals, after which seedlings had reduced apical dominance. Most of the injuries observed were associated with herbicide applications or were related to the lack of cold hardiness. These injuries were prevalent late in the first (1-0) year of growth or during the winter of the first year, respectively. Seedlings became multiple leadered as new terminals grew from axillary buds below the injuries. The suggestion is made that first year (1-0) seedlings are more vulnerable than older seedlings because shoot growth continues as long as growing conditions are favorable. In the first year, shoots stayed vegetatively active longer than older seedlings, and in some situations normal resting buds were not formed.

Other causes of terminal injuries such as insect defoliation and late spring frosts were noted as well. In these instances the injuries and causes thereof were obvious.

RÉSUMÉ

Les pépinières provinciales de l'Ontario rejettent les semis de conifères à pousse apicale multiple parce qu'ils sont impropres à la plantation. Certaines années, les pertes se sont chiffrées à des millions de semis. Dans plusieurs pépinières, on a diagnostiqué que cet état était consécutif à des blessures aux pousses terminales qui ont réduit la dominance apicale des semis. La plupart des blessures observées étaient reliées à des applications d'herbicide ou à un manque de résistance au froid. Elles sont survenues en majorité vers la fin de la première (1-0) année de croissance ou durant l'hiver de la première année. La pousse apicale est devenue multiple parce que des bourgeons axillaires situés sous les blessures se sont développés. On pense que les semis de la première année (1-0) sont plus vulnérables que les autres parce que la croissance de leurs pousses se poursuit aussi longtemps que les conditions sont favorables. La première année, les pousses sont demeurées végétativement actives plus longtemps que les semis plus âgés, et dans certains cas, les bourgeons de repos ne se sont pas formés.

On a également noté d'autres causes de blessures des pousses terminales comme la défoliation due aux insectes et les gels tardifs printaniers. Dans ces cas-là, les blessures et leurs causes étaient évidentes.

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TABLE OF CONTENTS

Cover photo: Multiple-leadered seedling

INTRODUCTION

Millions of seedlings grown in Ontario provincial nurseries are rejected each year because grading rules specify that only single-leadered (SL) seedlings are acceptable for planting. Multiple-leadered (ML) seedlings (cover photo), especially those with four or more terminals, tend to be shorter than SL seedlings and many also do not satisfy size criteria. Nursery managers want to grow SL seedlings of fairly uniform size so that the entire production can be shipped. The large percentage of seedlings rejected because of ML results in a direct loss of seedling production scheduled for regeneration projects. Processing efficiency is also reduced as the presence of cull seedlings prohibits bulk packaging in the field. All species of conifers grown are affected to some extent, but the problem is especially severe for white spruce (**Picea glauca** [Moench] Voss), black spruce (**P. mariana** [Mill.] B.S.P.), and occasionally white pine (**Pinus strobus** L.) or jack pine (**P. banksiana** Lamb.). Cull commonly reaches 40% and has ranged up to 65%.

The ML phenomenon is readily explained. Injury to the tip of the terminal shoot stops growth along that axis, and results in the proliferation of shoots from sites below the injury. This results in reduced apical dominance, and affected seedlings tend to remain in the ML state. Detection of the injuries and identification of the cause, however, are often difficult.

It is not known when ML problems first became acute. An excessive amount of ML, sometimes called cabbage-heading, was recognized among jack pine at the Gogama nursery in 1957. Since then the magnitude of the ML problem has varied annually among the nurseries, with all nurseries experiencing significant losses at least once.

Initially, insects or diseases were suspected causes of ML. Vaartaja, et al. (1964) reported no evidence that disease caused the high incidence of white pine ML in 1962. Springtail insects were postulated as a possible cause of ML by Baggott (1971). Over the years, numerous samples of ML seedlings have been examined by pathologists and entomologists at the Great Lakes Forest Research Centre. Except for a few obvious injuries, such as feeding by the spruce budworm (**Choristoneura fumiferana** [Clem.]), no pest was firmly implicated. A study conducted at the Swastika, Midhurst, and Thunder Bay nurseries in 1978 showed considerable ML in the presence of negligible numbers of springtails (Syme 1978 in Gross 1979). Further, weekly observations made at these nurseries between 1978 and 1980, reported herein, did not implicate any insect or disease except where a small percentage of ML was caused by free-feeding defoliators such as spruce budworm.

It is possible to injure terminals in a number of ways so as to cause ML. Krause (personal communication, 1963) determined that lodged grains of ammonium nitrate fertilizer killed terminal tips and caused ML. Early in the present study, the author used droplets of concentrated 20-20-20 fertilizer, the crushing of terminal tips, and a jet of hot air to cause ML injuries. However, there is no evidence that these types of injury have caused ML.

The magnitude of ML losses and the complex nature of terminal injuries stimulated a series of observational studies designed to diagnose the ML problem. Observations for 1978 (Gross 1979) focused attention on cold-hardiness, and herbicide application and established that the peak period of susceptibility to injury occurred from about the time when terminal buds were initiated to when seedlings became dormant. However, many SL seedlings had terminal injuries at the end of the 1978 season which were difficult and, in some cases, impossible to detect. Hence, the studies were continued in 1979 and 1980.

Preliminary reports (Gross 1979, 1982) have been useful in defining the ML problem and in determining the type of research required to solve the ML dilemma. Some adjustments in fertilizer schedules and weed control programs have been made at the nurseries in response to early information. This report summarizes the results of observational studies undertaken at the Thunder Bay, Swastika and Midhurst forest stations in a total of 16 nursery compartments.

METHODS

Each compartment selected for observation was sampled by 10 randomly located 25-tree plots. Seedlings in the plots were selected in five-tree clusters systematically arranged around the plot centre. Individual trees were identified by color-coded toothpicks.

Seedlings on the plots were examined at weekly intervals through the growing season. Before the plots were rated, normal and abnormal appearing shoots of seedlings selected elsewhere were dissected and examined so that symptoms of injuries could be identified. Then terminal tips were rated for injury symptoms, the presence and size of terminal buds, and the appearance of new terminal shoots. At monthly intervals, seedling height, diameter 1 cm above ground, and the length of terminal and lateral shoots were recorded.

Whenever possible, the same compartments and 25-tree plots were used in consecutive years to follow seedlings through all phases of production. About eight compartments per year were studied in this manner.

A more detailed description of methods can be made available on request.

RESULTS AND DISCUSSION

Injury Response

Seedlings that became ML were the direct result of injuries to the terminals of leading shoots, frequently to the terminal meristem. The injury response seemed to be a function of the amount of shoot tip affected and the vegetative state of the tip when injured. Shoot primordia are present at the base of most needle initials near the terminal meristem. A localized injury reaction at the shoot apex seemed to stimulate a response from a cluster of shoot primordia. Formation of a cluster of small buds lacking a normal dominant terminal bud (see Fig. 1d) typically followed this reaction to localized injury. More extensive injuries caused a growth response from axillary buds lower on the seedling.

Time of Injury and the ML Response

Most injuries occurred prior to the onset of growth in the second (2-0) year. Frequently, susceptibility to injury was related to cold-hardiness, and injuries occurred during the dormant season. Injuries, usually related to herbicide applications, were also abundant just before seedlings achieved dormancy in the first (1-0) year. A critical period of susceptibility to injury seemed to start about the time that shoot extension was almost complete (> 90%). This was slightly earlier than the time when terminal buds were being initiated (reported previously in Gross [1979]). The critical period seemed to end with dormancy. Terminals were considered to be dormant when mature-looking buds covered with normal bud scales were present.

Other obvious causes of injury such as late spring frosts and insect feeding were observed. Diagnosis of the cause and timing of these injuries was relatively straightforward.

The percentage of seedlings that were ML by the end of the first growing season in these observational studies was low, averaging 2-5% ML. Those that were ML seemed to have responded to injuries that occurred before the end of July. Usually this ML response was associated with obvious causes such as herbicide, animal or insect feeding, etc., and the injured terminals were conspicuous. However, throughout the history of ML, instances of substantial ML were reported in the first (1-0) year, with no evidence of injury. The logical assumption is that the ML response was stimulated by a minute injury to the shoot apex, which caused a proliferation of shoots. In view of the obscure character of many of the injuries observed in these tests (Fig. 1), it is possible that associated injuries were overlooked for some of the early occurrences of ML. In these tests, the percentage of ML that occurred in the first (1-0) year without obvious injury was low (<1%).

Most ML resulted from injuries that occurred late in the growing season or during dormancy. Most of the affected seedlings were SL and appeared normal (Fig. 1a, 2a) at the end of the first growing season. The ML condition developed soon after growth started in the second (2-0) year. The presence of new growth flushing early in the growing season concealed the evidence of previous injury. This aspect of the ML problem helps explain early difficulties with diagnosis.

The growth pattern of seedlings in the first year differs from that of subsequent years. In the first year, the terminal meristem continues to grow and initiate needle primordia as long as conditions are favorable. In subsequent years, shoot extension is evident from shoot initials preformed in buds. Shoot extension occurs in a short period of 4 to 6 weeks, after which new buds are formed. Hence, terminal meristems can remain active for a much longer period in the first year of seedling growth than in later years. Seedlings in nurseries are fertilized and irrigated. This provides an extended period of favorable growth conditions. First-year (1-0) seedlings generally set buds at least one month later than older seedlings. With fertilizer applications in late summer it was not unusual for a large portion of the first-year (1-0) seedlings to pass through the dormant season without terminal buds. In these instances, terminal meristems were somewhat succulent and susceptible to cold damage, being protected only by a sheath of needle primordia. This terminal character seems to be normal for jack pine, but spruce seedlings with a mature bud are more cold hardy, especially in the northern nurseries during severe winters with shallow snow cover.

The size and activity of the terminal meristem and the adjacent region of shoot expansion is another aspect of shoot growth influencing susceptibility to injury. This locus is larger and more active early in the season than later. (The latter part of the season seems to be a critical period for injuries.) Certain materials such as growth regulators are translocated to this site, and concentra-

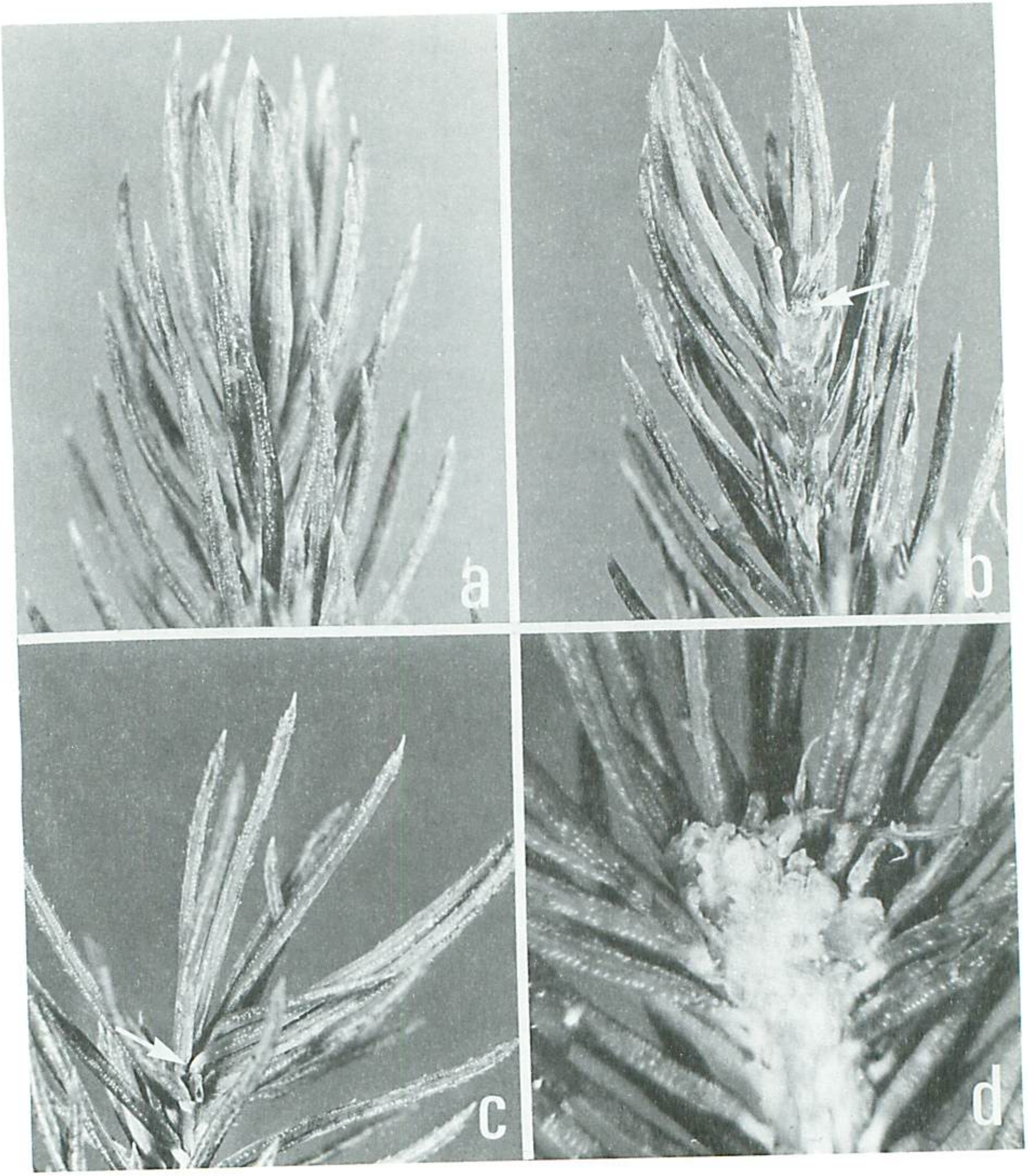

Figure 1. Injured terminal shoots of 1-0 white spruce. (a) Normal appearing terminal, (b) The same terminal shown in 1(a) dissected to show the dead shoot tip, (c) Terminal needles bent at an acute angle usually indicated an injury similar to that of the dead shoot tip in 1(b), (d) A cluster of small abnormal buds typical of the reaction to injuries such as those in 1(b) and 1(c).

tion of materials such as herbicides seems to be related to the occurrence of injuries (Webb 1981).

Dormant buds obviously are resistant to cold injury, and probably to other types of injury, particularly those caused by chemicals. However, most nursery cultural practices are discontinued late in the season and the degree of dormancy is difficult to rate or observe, as most related characters are concealed by the bud cap. Seedlings over one year old had well formed buds at the time first-year seedlings were prone to injury late in the growing season. Bud abnormalities (Fig. 2) were common among the first-year (1-0) seedlings of some tests. The presence of abnormalities seemed to be related to cold hardiness, as was indicated by the size of the shoot initials in buds. Hence, cold hardiness, at least, requires mature buds with well formed shoot initials.

Seedling Character Relative to ML

Desirable characters for nursery seedlings are: 1) good growth potential, including adequate size to withstand competition after planting; 2) a single dominant terminal shoot; 3) good root:shoot ratio; 4) the presence of a large, injury-free terminal bud, as subsequent shoot growth is a function of bud size (Hellum 1967).

No significant difference was found between ML and SL seedlings with respect to stem diameter at 1 cm above ground, total oven-dry weight, or root:shoot ratio. ML seedlings seem to have the same bulk as SL seedlings, but they lack desirable form and are shorter. Total seedling height (Fig. 3) and terminal shoot length (Fig. 4) were reduced by about 20% for ML in comparison with SL seedlings. Most of the reduction occurred on seedlings with

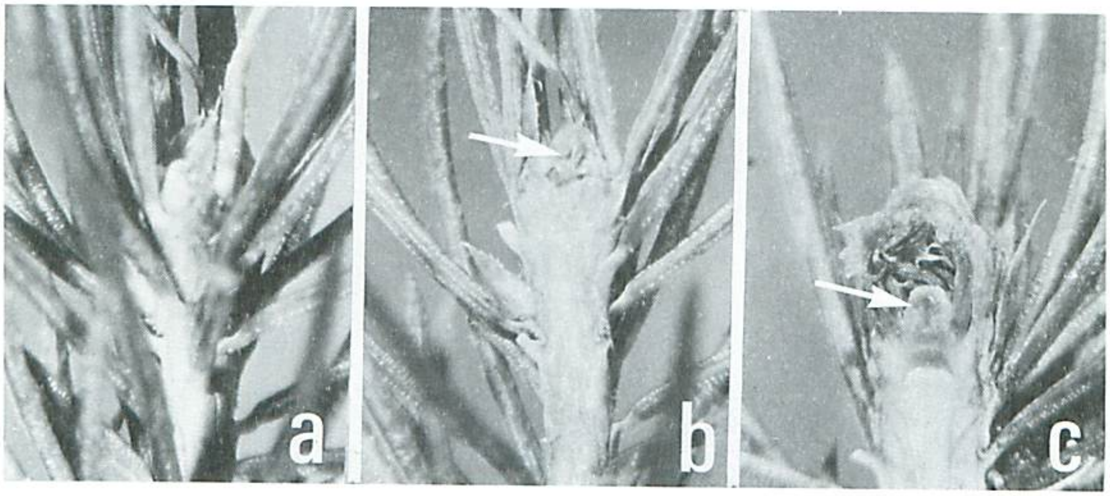

Figure 2. Abnormal terminal buds on 1-0 white spruce. (a) Shoot tip with a normal appearing bud, (b) The same bud as in 2a dissected to show that the shoot initial was missing, c) Growth response of a partially dead shoot initial. Note that the needles forming on the uninjured part of the shoot are distorted from trying to push off the bud cap. Damaged buds such as this usually fail.

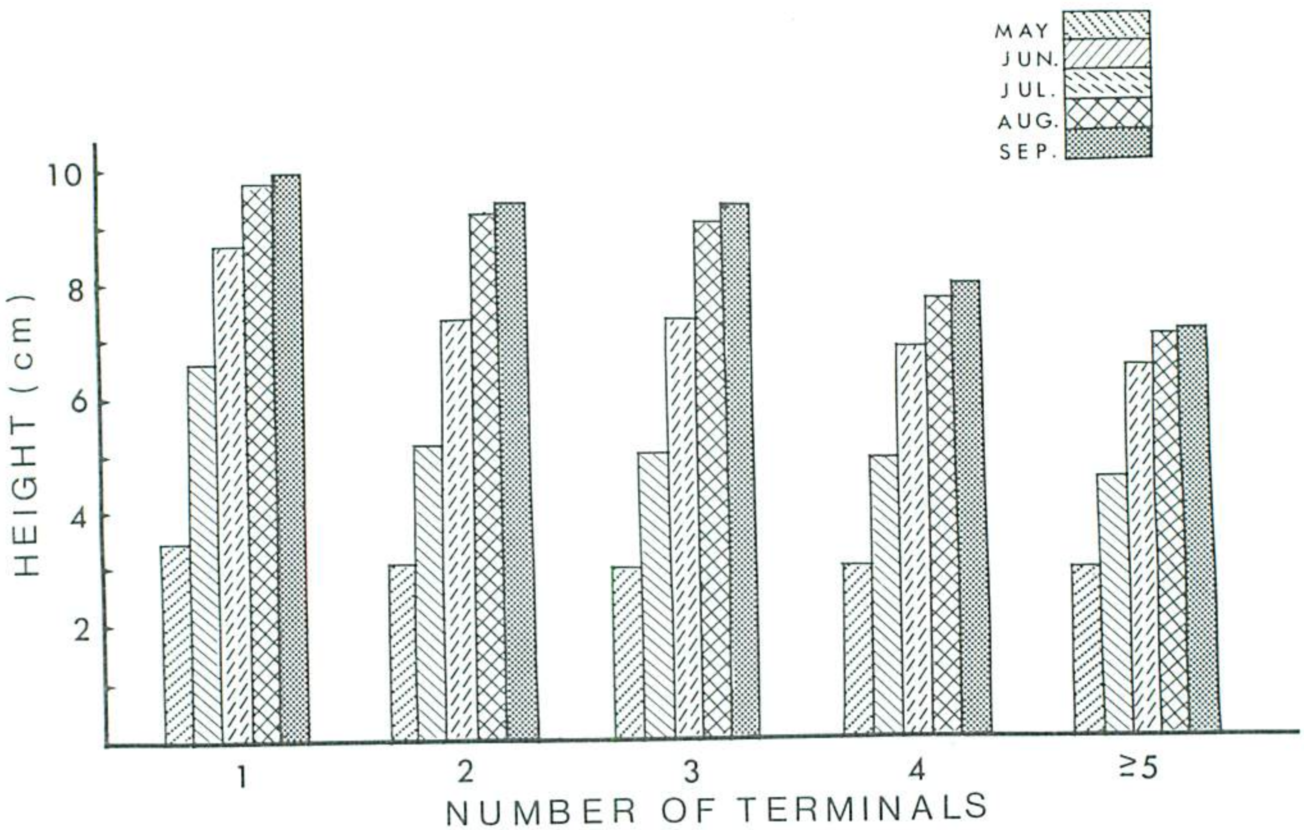

Figure 3. Height growth of 2-0 white spruce relative to the number of terminals present on a seedling.

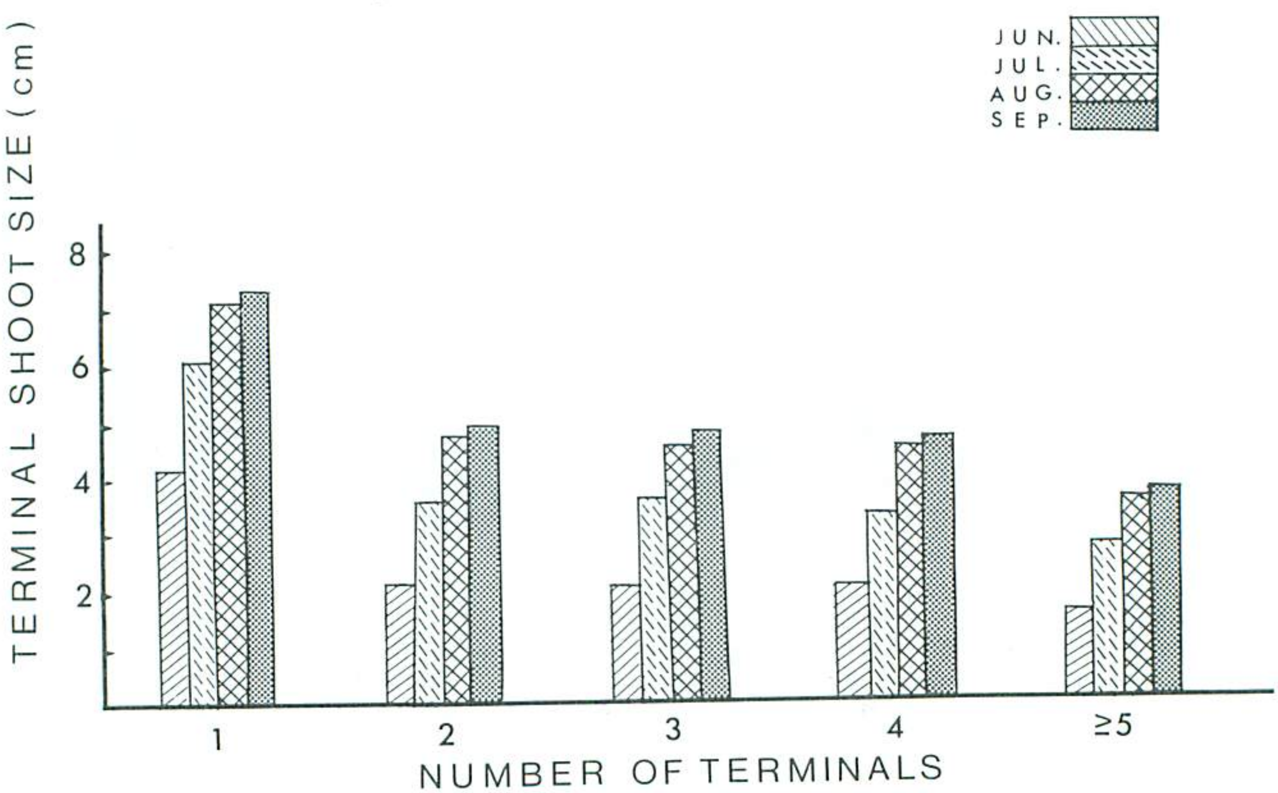

Figure 4. Terminal shoot growth of 2-0 white spruce relative to the number of terminals present on a seedling.

more than three terminals (Fig. 3 and 4). Double-leadered seedlings were about the same size as SL seedlings. The general impression that ML seedlings are shorter than SL seedlings seems to be influenced largely by the appearance of the more severe cases of ML.

The current terminal shoots of seedlings with ML tend to be more slender, have fewer needles, and set smaller terminal buds (Fig. 5). Bud size was inversely related to the number of terminals on a seedling (Fig. 5 and 6, Table 1) and buds were initiated later in the season relative to the number of terminals on a seedling (Fig. 6). This seems to support the general impression that terminals on ML seedlings are prone to injury. There terminals remain active for a longer period, and the smaller buds, set later in the season, probably do not achieve the same level of cold-hardiness as the larger buds on SL seedlings.

Seedlings that complete shoot extension in a short time also tend to set larger buds (Fig. 6). Ultimate shoot size was about the same for 2-0 white spruce that developed buds 8 mm^3 in volume and larger, but the shoots with the larger buds seemed to complete shoot growth

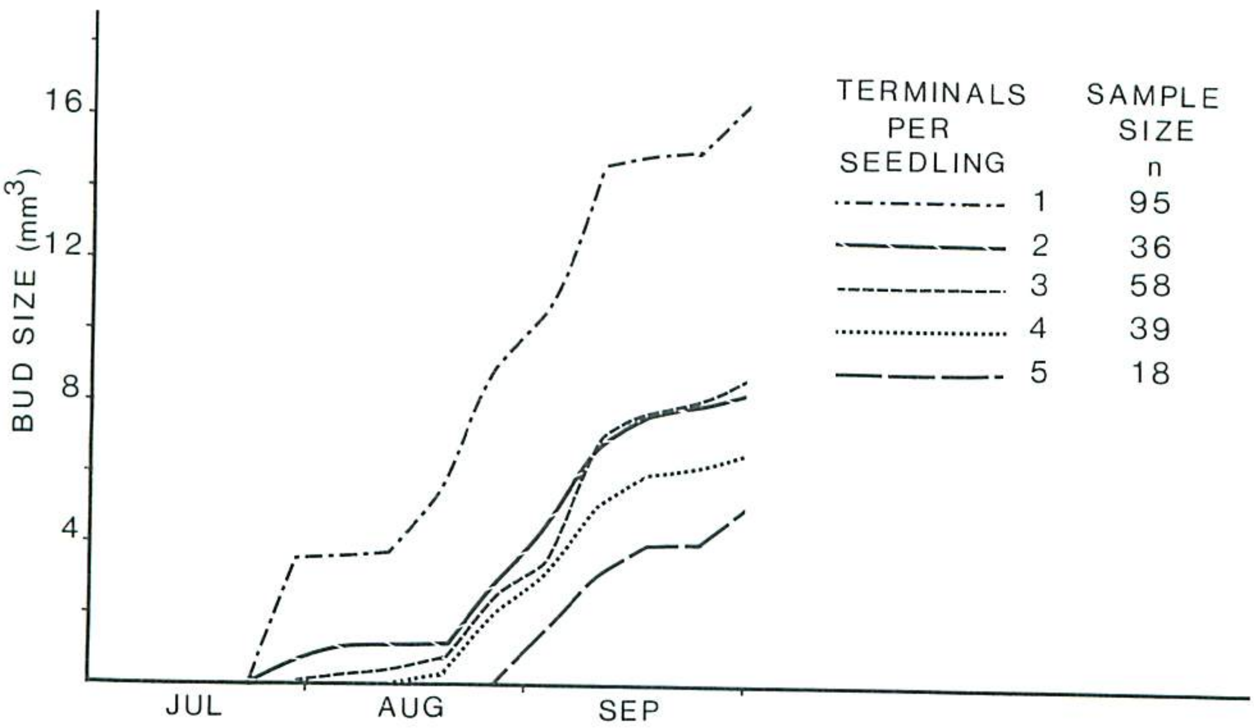

Figure 5. Average bud size relative to the number of terminals on 2-0 white spruce seedlings. Note that the date on which buds were initiated also seems to be a function of the number of terminals on a seedling. Bud size for terminals with dead or missing tips was not included in this analysis.

earlier in the season (Fig. 6). Also, most of the buds 8 mm^3 and smaller were on new terminals produced in the second year after the original terminal was injured (Table 1).

Well formed dormant buds seem to be resistant to the kinds of injuries that result in ML. Data also indicated that there are growth differences which are correlated with bud size (Table 2, Fig. 6). Naturally, large shoots set large buds, but other characters seem to indicate genetic control. Shoots that set large buds also initiated buds earlier and completed shoot extension faster than shoots with smaller buds. Genetic selection could produce seedlings that are better adjusted to nursery culture and are resistant to terminal injuries.

Table 1. Terminal bud size for 2-0 white spruce seedlings.[a]

Bud size (mm^3)	Sample size (n)	Terminals per seedling (X)	% of buds on new terminals
1	16	4.4	94
4	116	3.8	89
8	145	3.1	81
15	85	2.1	48
35	28	1.3	14
	390	3.0	28

[a]Bud size was inversely related to the number of terminals on a seedling. Most of the buds 8 mm^3 or smaller were on new terminals produced when the initial terminal shoot was injured.

Table 2. Damage sustained by 1-0 white spruce injured by severe winter exposure.

Damage	Seedling height (cm)	Shoot initials (mm^3)	Terminal bud (mm^3)	Sample size (n)
Unaffected	4.34	4.27	8.74	25
Terminals with necrotic needles	5.48	1.30	5.91	11
Terminals with dead shoot tips	6.95	0.10	1.52	19

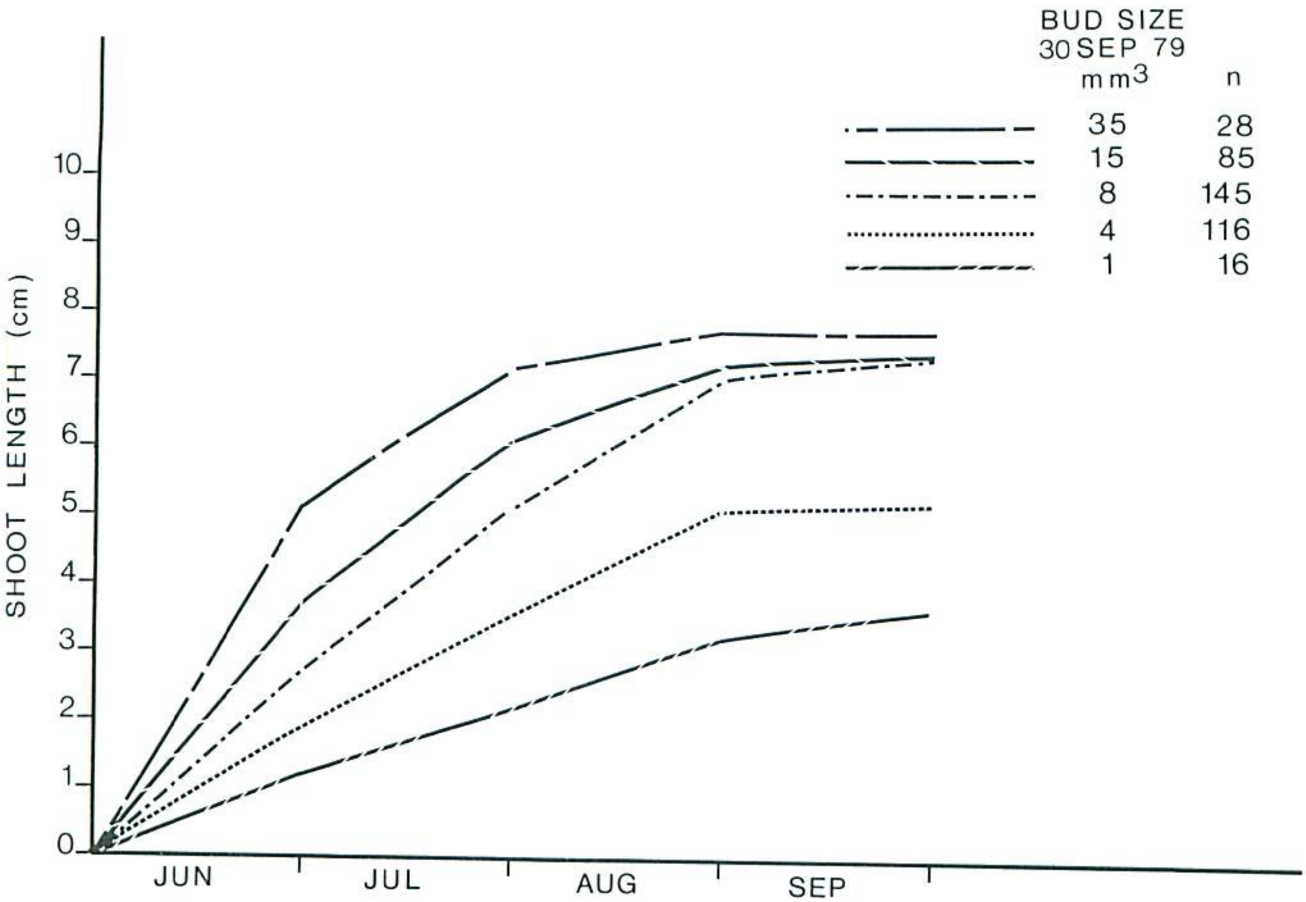

Figure 6. Terminal shoot growth for 2-0 white spruce relative to the size of terminal bud present at the end of the season. Shoots on terminals with buds 8 mm^3 or larger achieved essentially the same length; however, shoot growth was completed earlier for shoots with buds larger than 8 mm^3. The seedlings depicted here are the same as those for Table 1, hence most of the shoots with buds 8 mm^3 or smaller were on new terminals.

Causes of Injury

Diagnosing the causes of ML was difficult. The injured site was often small and obscured by needles (Fig. 1) or by a bud cap (Fig. 2). The ML character frequently became evident long after the causal event. Also, a combination of causal events, differing in kind, frequently contributed to the overall percentage of ML in a compartment.

Anything that destroys the terminal meristem can cause the ML reaction. Terminal damage often followed the application of herbicides or the occurrence of adverse weather. The severity of reaction varied with the vegetative state of seedlings at the time of the causal event, and other factors, such as fall application of fertilizer, seemed to enhance susceptibility to injury.

It is possible that some causal events were overlooked or failed to occur in the observed sample compartments. However, there was considerable ML and several types of injury seemed important.

Cold injury: Severe winter exposure can kill terminals. The amount of damage sustained is correlated with cold-hardiness and is based on the size and presence of terminal buds (Table 2). Damage was inversely proportional to terminal bud size and the size of shoot initials within the buds. Damage was directly proportional to seedling height--an indication that size was accumulated at the expense of cold-hardiness. The tallest seedlings tended to have terminal tips that remained vegetative or had small buds. Black spruce seemed to suffer less damage than white spruce in situations in which both species were exposed to the same conditions. Again, most of the damage was done to trees in the 1-0 size class.

Damage from winter exposure was associated with low snow cover at the Swastika nursery in the winter of 1978-1979. The injury seemed to be the result of exposure to cold rather than to warm temperatures. The latter cause "winter browning", which is due to desiccation of exposed foliage resulting from photosynthetic activity on bright warm days when water supply is inhibited by frozen roots. Foliage below the snow is unaffected and usually buds and stems survive. In this instance there was no evidence of snow depth on the seedlings, and terminal buds and shoot tips were killed.

Late summer frosts as well can apparently cause damage similar to that resulting from severe winter exposure. This did not happen during the present study. However, any freeze that occurs while seedlings are actively growing can cause the tip kill.

Heat Injury: Hot dry winds have been observed to cause tip injuries that lead to ML. This kind of injury is most likely to occur in the fall after normal irrigation has been stopped. Nursery operators seem to have recognized this hazard, and this condition has not been observed in recent years. The damage is similar to that caused by late summer frost or severe winter exposure. Hence, damage is probably also related to degree of dormancy at the time of the hot winds.

Another type of heat injury seems to cause transplant shock that leads to ML. Extremely harsh transplant conditions were experienced at Swastika nursery in June 1978. Hot, sunny days with clear, cold nights (25 to 30°C max to -5° min) seemed to have caused injuries to 2-0 spruce that were being transplanted. Most of the seedlings had flushed new shoots that averaged about 2 cm long, and a large portion of these succulent shoots wilted at the time of transplanting. Transplants that wilted frequently developed ML by the end of the season. Those that did not wilt stopped growing, and set an unusually large cluster of five or six buds of approximately the same size at the terminal. Initial growth from these terminals in 1979 had the ML character until the new shoots were about 5 cm long. Then the central shoot remained upright and dominant. This emphasizes the importance of the central terminal meristem to tree shape.

Herbicide Injury: There is little doubt that herbicide applications cause terminal injuries which result in ML. The phytotoxic effects have been obvious in some instances and specific herbicides or times of application are now avoided. Second applications of Dacthal, for example, have been discontinued. Dacthal, Geseguard, and Amitrole have all been associated with terminal injuries. Granted, ML was present long before the widespread use of herbicides; however, it is apparent that herbicide damage is part of the current problem. Research by Dr. D.P. Webb (1981) of the Great Lakes Forest Research Centre indicates that herbicides are translocated to terminal tips in phytotoxic amounts. Injuries associated with herbicide applications can be difficult to detect (Fig. 1 and 2). Hence, screening tests probably missed some of the injuries and resultant ML. Also, times of application need to be tested. If results are compiled at the end of the first year (1-0) of growth, most ML resulting from injuries late in the 1-0 season is missed, as ML occurs in the second (2-0) year.

Except for herbicide applications late in the growing season during the critical period, most herbicide treatments appear to be harmless to seedling form. Most applications have had little immediate effect on seedling form or caused only minor distortion followed by recovery. However, in other cases similar applications have caused injuries (Fig. 1), and this suggests that additional factors such as background level of herbicides, soil condition, or weather contribute to the occurrence of herbicide injuries.

Herbicide injury takes various forms. Usually some form of needle or terminal tip distortion is followed by dead or missing terminal tips, the production of a cluster of small buds without a dominant terminal bud, or an abnormal bud containing a cluster of small shoot primordia instead of a single, well formed shoot initial. A common form of distortion is the shoot tip perched at an acute angle to the shoot axis (Fig. 1c). Necrotic, chlorotic, or completely missing shoot initials (Fig. 2) within buds that otherwise appeared normal also seemed to be associated with the herbicide reaction. The connection is difficult to establish because the injury can be concealed in a bud which appears normal. It is possible that all these types of injury could be caused by other agents; however, they appeared more abundant in association with herbicide applications.

The typical "albino" chlorosis caused by herbicides was not common. Seedlings with this type of chlorosis subsequently became stunted but not necessarily ML.

Insect Injury: Defoliator insects such as spruce budworm do cause injuries that lead to ML. In June 1979 about 10% of the 2-0 white spruce at Midhurst and Swastika nurseries suffered terminal injuries from budworm feeding. The insect usually feeds along the side of a shoot and often devours the terminal tip. Low numbers of other tortricid larvae were present later in the season and caused similar damage. This type of injury was not important in the first-year (1-0) seedlings which are small when budworm is active. However, considerable damage to older seedlings was evident in 1979 by the time infestations were controlled.

Aphids were observed feeding on a small percentage of 2-0 white spruce at Midhurst and Swastika nurseries. This feeding seemed to cause some distortion, but did not result in a significant amount of terminal damage or ML.

Springtail insects were unimportant, at least over the 1978-1980 study period.

Other Causes of Injury: Terminal injury from mechanical thinners, and bird or rodent feeding were observed. Not much damage from these causes was observed on the study plots; however, in one compartment, terminal injuries of up to 10% of the seedlings resulted from animal feeding.

Unrelated Phenomena: Several other phenomena suspected earlier of having a connection with ML now appear to be blameless. Seed cap retention on very young seedlings caused distortion of the stem as the shoot grew out between cotyledons. This condition proved incidental to ML. Also, shoot tips of spruce had a character wherein needle tips toward the shoot tip curve in a common direction. This condition, described as "tip swirl", was initially rated as a type of distortion. The character tended to disappear as buds developed.

Symptoms of nitrogen and phosphorus deficiency were also observed. While mineral nutrition seems important in achieving adequate cold-hardiness, no direct link to ML was observed.

SUMMARY AND CONCLUSIONS

The ML condition of nursery stock results from various kinds of terminal injuries. Most injuries seemed to be related to cold-hardiness, or occurred late in the growing season when stock was susceptible to injury. This period seemed to start when shoot extension slowed (>90% complete) or as buds were initiated, and ended with dormancy. Several causes of injury were observed. Reaction to herbicide and cold injury seemed to be associated with the major occurrences of ML. The intensity of cold injury varied inversely with bud size and other indicators of dormancy and cold-hardiness. While considerable growth can be achieved in September if high fertility is maintained, adequate cold-hardiness seems to have been sacrificed to obtain this growth.

The reaction to herbicide was more complex. Not all materials and times of application caused the same intensity of damage. Late-season applications during the critical period usually caused at least some injury, but the amount of damage was difficult to rate since many injuries which occurred were within buds that were normal in overall appearance.

Until the roles of fertilizer level and reaction to herbicide in the ML problem are more fully elucidated, these materials should be used with caution and should not be applied during the critical period late in the growing season. This is especially important for seedlings in their first year (1-0) when the critical period of susceptibility to ML injuries appears to be somewhat more prolonged.

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