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Effects of Fall Fertilizer Applications of Mitotic Index and Bud Dormancy of Loblolly Pine Seedlings

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ABSTRACT. A series of studies examined the effects of fall fertilization with diammonium phosphate (DAP) on mitotic index and bud dormancy [as measured by mean days to budbreak (DBB)] of two half-sib seed sources of loblolly pine. The first study tested different rates of DAP (0, 67, and 202 kg N/ha), the second study compared DAP with ammonium nitrate, and the third study examined the effect of different application dates (September 28, October 19, and November 9). An increase in mitotic index of unfertilized seedlings was observed during October and was due to developmental activity which follows initial budset. Differences in mitotic index were observed between families in all three studies. Overall, the Georgia family has a higher mitotic index, but in one study, the Virginia family had higher values in the spring. Both families tended to reach a minimum level of mitotic index at the same time (mid- to late December). However, the Virginia family reached maximum rest (as measured by days to budbreak) about 1 to 2 weeks prior to the Georgia family. Fertilization with DAP in the fall (after budset in September) did not delay the progression of the bud dormancy cycle as measured by days to budbreak in a greenhouse. The overall effect of fall fertilization on increasing the mitotic index was temporary and only lasted for about three weeks after fertilization. These findings indicated that a direct relationship may not exist between the bud dormancy cycle and mitotic index. FOR. SCI. 38(2):336–349.

ADDITIONAL KEY WORDS. *Pinus taeda*, apical meristem, chilling hours, seed source, nursery management.

FOR LOBLOLLY PINE (*Pinus taeda* L.) seedlings, the cessation of shoot growth in nurseries often occurs around the autumnal equinox, and this marks the beginning of the bud dormancy cycle (this beginning is designated as °GS 180 by the "Degree Growth Stage" model proposed by Fuchigami et al. 1982). The duration of the cycle (from °GS 180 to °GS 360) varies with environment (Ritchie and Tanaka 1990) but can last for 6 months. The cycle is characterized by a continuous physiological transition, beginning with a prerest phase and followed by the rest and postrest phases. Decreases in photoperiod mediate the transition from prerest to rest. For bareroot loblolly pine, the time of maximum rest (°GS 270) usually occurs in December (Williams et al. 1988, Gagon and Johnson 1988, Boyer and South 1989). Exposure to chilling temperatures (i.e., 0°C–8°C) promotes the transition from rest to postrest (Romberger 1963, Vegis 1964, Perry 1971, Nooden and Weber 1978, Lavender 1981). Buds remain in postrest (°GS 315 to °GS 360) until environmental conditions are favorable for budbreak.

Loblolly pine seedlings are usually lifted from bareroot nurseries and outplanted between mid-December and mid-February, coinciding with the rest to postrest

transition period (Garber and Mexal 1980). Consequently, studies have evaluated bud dormancy and seedling response to lifting, storing, and outplanting (Garber 1983, Boyer and South 1986, Carlson 1985, Larsen et al. 1986). Seedlings which have experienced sufficient chilling appear more tolerant to handling stresses. However, despite the importance of nursery cultural practices in growing seedlings, a surprising lack of studies investigate the effects cultural practices can have on the bud dormancy cycle.

A nursery cultural practice which has received increased attention is the fall application of nitrogen fertilizers. Fall nitrogen fertilization has been reported to increase survival and height growth of outplanted Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) (Anderson and Gessel 1966, Benzian et al. 1974, Thompson 1983, van den Driessche 1985, 1988, Margolis and Waring 1986). Studies with the southern pines showed varying results. Fall fertilization increased longleaf pine (*Pinus palustris* Mill.) height growth and accelerated emergence from the grass stage (Hinesley and Maki 1980). Experiments with loblolly and slash pine (*Pinus elliottii* Engelm.) have shown varying results. Some have reported no effects or a detrimental effect on survival (Ursic 1956, Gilmore et al. 1959, Duryea 1990). Shoulders (1959) found either a beneficial or detrimental response to fall fertilization depending on the nursery conducting the experiment. None of these investigations with fall nitrogen fertilization monitored the possible physiological changes which regulate the bud dormancy cycle.

Although changes in bud dormancy are evaluated by measuring mean days to budbreak, this test does not provide a rapid evaluation of seedling physiological status (Hawkins and Binder 1990). Procedures for measuring apical meristem mitotic index (MI = number of dividing cells/total number of cells) reported by Carlson et al. (1980) can determine the relative amount of cell divisions present within hours after sampling buds. Although several researchers have reported seasonal changes in MI (Owens and Molder 1973, Carlson et al. 1980, Carlson 1986), only a few have compared MI with changes in mean days to budbreak (Cannell et al. 1990).

Family effects were investigated to observe whether dormancy cycle differences (measured by days to budbreak) were related to changes in MI. Consequently, the studies also examined the relationship between a chilling requirement for rest release and MI in order to evaluate the efficacy of the latter in predicting bud dormancy status.

MATERIALS AND METHODS

Three studies were conducted in consecutive years beginning in 1984. Family effects were studied by comparing two half-sibling seedlots of loblolly pine obtained from geographically different locations. A northern family was from Virginia (approx. 36.90°N lat. 76.95°W long.), while a southern family was from Georgia (approx. lat. 32.07°N long. 81.54°W). Seedlings were grown under natural conditions at Auburn, Alabama, in 144 cm^3 Ray Leach Cell Containers (Ray Leach "Cone-tainer" Nursery, Canby, OR). Each study was a randomized complete block split-plot design with four replications. The whole plot was the fertilizer treatment with families representing subplots.

1984–85 Study

Loblolly pine seed were sown between May 5 and 8, 1984, in containers filled with coarse sand and spaced at a density of 516 per m^2. A fungicide (Captan) was applied prior to germination for damping-off control. The seedlings were fertilized every 2 weeks beginning on May 21. Applications were alternated using Peters' water soluble general purpose 20-20-20 ($N\text{-}P_2O_5\text{-}K_2O$) fertilizer (W.R. Grace & Co., Fogelsville, PA 18051) and a 15-30-15 fertilizer (Miracle-Gro Products Inc., Port Washington, NY 11050). Six applications were made which totaled 17 g/m^2/yr of nitrogen. The seedlings were watered every other day until the end of August when supplemental watering and fertilizer were withheld to promote budset and hardening.

Treatments consisted of three levels of a fall application of diammonium phosphate (DAP). The DAP fertilizer used was a certified A.C.S. grade of ammonium phosphate (dibasic). DAP was applied with a watering can at levels equivalent to 0 (control), 67, and 202 kg N/ha over two application dates of September 28 and October 5. Foliar nitrogen concentration of control seedlings in January was 0.7%.

Chilling hours, defined as the number of hours seedlings experienced temperatures between 0°C and 8°C, were monitored using a TA-51 Omnidata Biophenometer (Omnidata International Inc.). The biophenometer was placed in a weather box located at seedling height. When chilling levels reached approximately 100, 250, 400, and 550 hr, 20 seedlings were randomly sampled from each subplot and moved to a heated glass greenhouse for determination of mean DBB. Photoperiod was extended to 16 hr using 300 W incandescent bulbs. The seedlings were watered on a regular basis. Greenhouse evaluations were conducted every other day until all sampled seedlings had broken bud. The terminal bud was recorded as broken when green tissue was clearly visible between the bud scales.

From each subplot, apical meristem MI was measured on six randomly selected seedlings. Samples for MI were taken every 2 weeks from August 25, 1984, to February 23, 1985. Methods used were those of Carlson et al. (1980) as modified for loblolly pine by Carlson (1986). The difference is that the apical dome rather than the whole bud was used for analysis.

1985–86 Study

Seed were sown between April 19 and 21, 1985, in containers filled with a commercial peat-perlite-vermiculite-pine bark mixture (Fafard Mix #3—Conrad Fafard Inc., Springfield, MA 01101) and spaced at 516 per m^2. For control of fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*), seeds and seedlings were treated with triadimefon (Kelley 1985). Seedlings were also sprayed periodically with malathion to control aphids. During the growing season, the seedlings were fertilized once a week beginning on May 11 with fertilizer types similar to those used in the 1984–85 study. By August 31, approximately 155 mg N had been applied to each seedling. Seedlings were watered every other day until August. Fertilization was stopped and watering reduced in August to promote budset and hardening. Treatments were applied on November 3, 1985, and consisted of DAP (202 kg N/ha), ammonium nitrate (202 kg N/ha), and a control. Ten seedlings per subplot were sampled at each chilling hour level for DBB evaluations. In January, the foliar nitrogen concentration of control seedlings was 0.9%.

1986–87 Study

Cultural practices during the growing season were similar to those used in the 1985–86 study; however, containers were spaced at a density of 258 containers per m^2. Mineral fertilization resulted in application of about 169 mg of nitrogen to each seedling. Fertilization ceased and watering was reduced in August to promote budset and hardening. In January, the foliar nitrogen concentration of control seedlings was 1.6%.

Fertilizer treatments consisted of one application of DAP at a rate equivalent to 202 kg N/ha on September 28, October 19, and November 9. Seedlings receiving no fertilizer served as the control. Two weeks after each fertilizer application date, seedlings were randomly sampled for MI determinations. For DBB evaluations, eight seedlings per subplot were sampled at 100, 250, 400, 550, and 730 chilling hours.

Data Analysis

For each study, analysis of variance for a randomized complete block split-plot design was conducted using Statistical Analysis System procedures (Statistical Analysis System 1987). The main effects of fertilizer treatment and family were considered fixed. Analysis including the main effects of chilling level, or MI sample date was handled as a split plot in space and time (Steel and Torrie 1980). Plot means were used as the observations for all studies. Differences within main effects and their interactions will be discussed as significant at the $\leq 5\%$ level of probability.

RESULTS

Bud Dormancy

Height growth cessation occurred by the last week of August for the Virginia seedlings and by mid-September for the Georgia seedlings. Tightly packed brown bud scales were present on both families by the first week of October. When averaged over sampling times, fertilization had a small but statistically significant influence on DBB (Table 1). Seedlings fertilized with 202 kg/ha (16.0 DBB) broke bud about 1 day quicker than the controls (17.0 DBB). Family appeared to have the greatest influence on DBB. When averaged over the sampling times, Virginia seedlings (18.8 DBB) required an additional 5 days to break bud than the Georgia family (13.7 DBB). An unusually warm fall in 1984 (temperatures in December averaged 4.3°C above normal) prevented sampling at 400 and 550 chilling levels in December. After December, all seedlings growing under natural conditions exhibited some degree of bud swelling and elongation. Consequently, determining time of budbreak after December was not necessary.

The DBB response to fertilizer, family, and chilling effects was similar for the second and third studies (Figure 1). There was no significant interaction between fall fertilization and chilling (Table 1). DBB decreased for the loblolly pine seedlings as the number of chilling hours increased. Averaged over all chilling levels, the Georgia seedlings required fewer DBB than the Virginia seedlings. A family by chilling interaction indicated a difference in the date at which maximum rest

TABLE 1.

Analysis of variance of mean days to budbreak.

Source	1984–85			1985–86			1986–87		
	df	F[1]	P > F	df	F	P > F	df	F	P > F
Rep.	3	15.35	0.0032	3	0.79	0.5442	3	0.23	0.8717
Treat.	2	8.36	0.0184	2	3.07	0.1206	3	2.50	0.1254
Error A MS	6	(0.93)		6	(8.99)		9	(14.69)	
Family	1	33.00	0.0003	1	39.48	0.0001	1	116.98	0.0001
Treat. × Family	2	0.71	0.5181	2	1.94	0.1998	3	1.11	0.3823
Error B MS	9	(9.20)		9	(16.58)		12	(28.56)	
Chill.	1	6.44	0.0849	3	216.93	0.0001	4	463.41	0.0001
Error C MS	3	(5.47)		9	(6.07)		12	(6.63)	
Treat. × Chill.	2	2.58	0.1556	6	1.69	0.1798	12	0.86	0.5954
Error D MS	6	(4.69)		18	(2.37)		36	(7.54)	
Family × Chill.	1	0.00	0.9572	3	26.36	0.0001	4	218.75	0.0001
Error E MS	3	(4.97)		9	(5.35)		12	(1.53)	
Treat. × Family × Chill.	2	0.77	0.5027	6	4.01	0.0100	12	2.16	0.0373
Error F MS	6	(5.73)		18	(2.43)		36	(4.20)	

[1] Error MS within the F column are enclosed in parentheses.

(°GS 270) was obtained. In 1985, the Georgia family achieved maximum rest near December 29 (at least 19 days later than the Virginia family). In 1986, maximum rest for the Georgia family occurred around December 22, at least 8 days after that for the Virginia family.

Apical Mitotic Activity

In the first study, MI declined from a maximum on August 25 to an average minimum of 0.6% on January 12, 1985 (Figure 2A,B). The decline in MI was interrupted by an increase on October 6. This was the first sampling date following the fertilizer applications. A separate analysis of variance using only the October 6 data showed that fertilizer effects on MI were significant ($P > F = 0.0008$). However, when pooled with all sample dates, the fertilizer by date interaction was not significant (Table 3).

In the 1984–85 study, the Georgia family had a slightly higher mean MI value than the Virginia family. A fertilizer by family interaction was due to the Georgia seedlings with 0 or 67 kg N/ha fertilization having a higher MI than the Virginia seedlings. Data trends leading to a family by date interaction showed that, prior to October 6, the Virginia seedlings had the higher MI. Afterwards, with the exception of the October 20 sample, the Georgia seedlings had a higher MI.

A record breaking freeze (−21°C) on January 21 and 22, 1985, caused a majority of the seedlings to exhibit root and shoot damage indicated by a brown discoloration of the root cortex and shoot cambial regions. Consequently, values determined after January 21 were probably influenced by the environmental stress imposed upon the seedlings.

In the 1985–86 study, MI (Figure 2C,D) increased from an average of 5.7% on August 31, 1985, to 9.0% on October 12. A steady decline then followed until December 21 when MI averaged only 0.3%. MI increased by 0.7 percentage

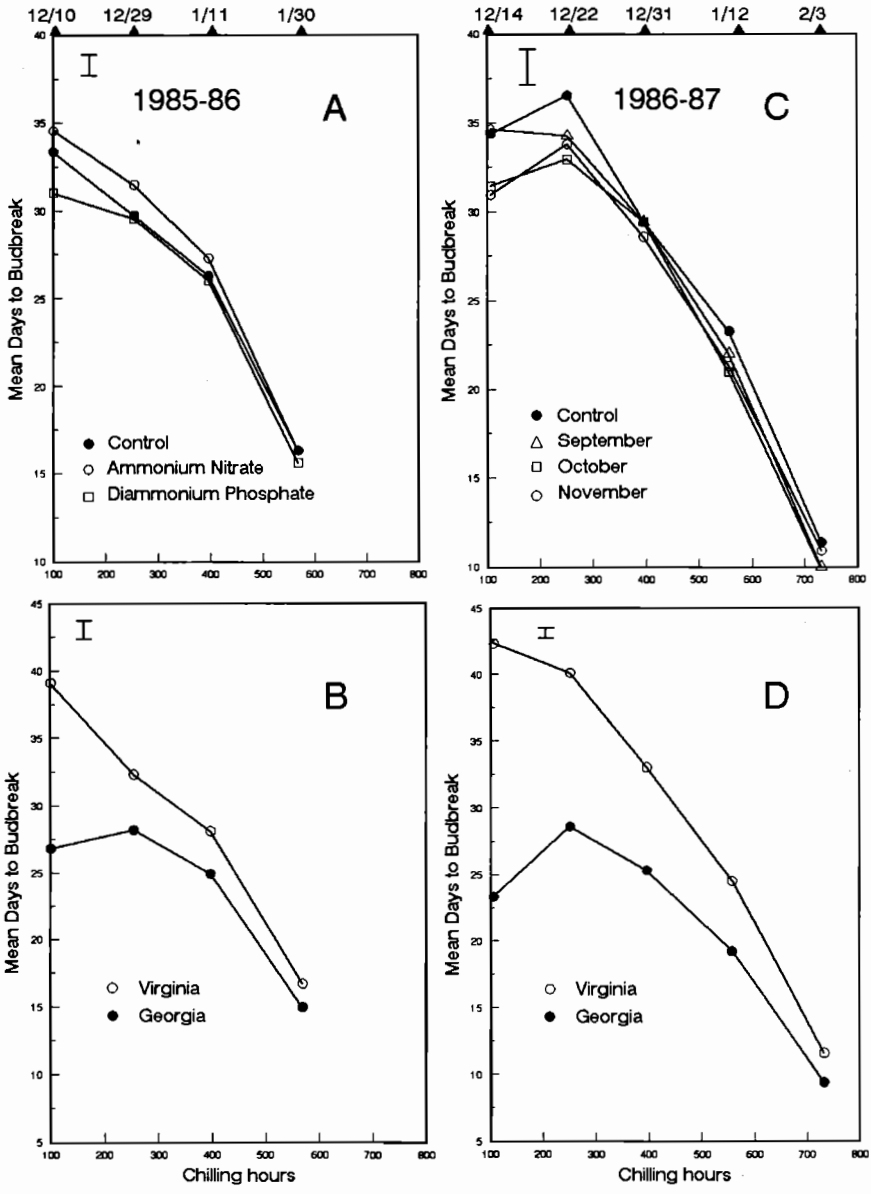

FIGURE 1. Mean days to budbreak for loblolly pine at four chilling levels in relation to fertilizer treatment (A) and family (B) for the 1985–86 study; and fertilizer treatment (C) and family (D) for the 1986–87 study. The vertical bars indicate 1 SE.

points on January 4 and declined to its lowest point of 0.03% on February 1, 1986. Thereafter, MI increased steadily until the last sample date on April 26, 1986, when the values averaged 7.8%.

Overall, seedlings fertilized in 1985 with DAP had slightly higher MI values (Figure 2C). The increase was due primarily to an increase in mitotic activity after February. However, when analyzed separately by sample date, there was no significant fertilizer effect at any sample date. Overall, MI for Georgia seedlings was higher than Virginia seedlings.

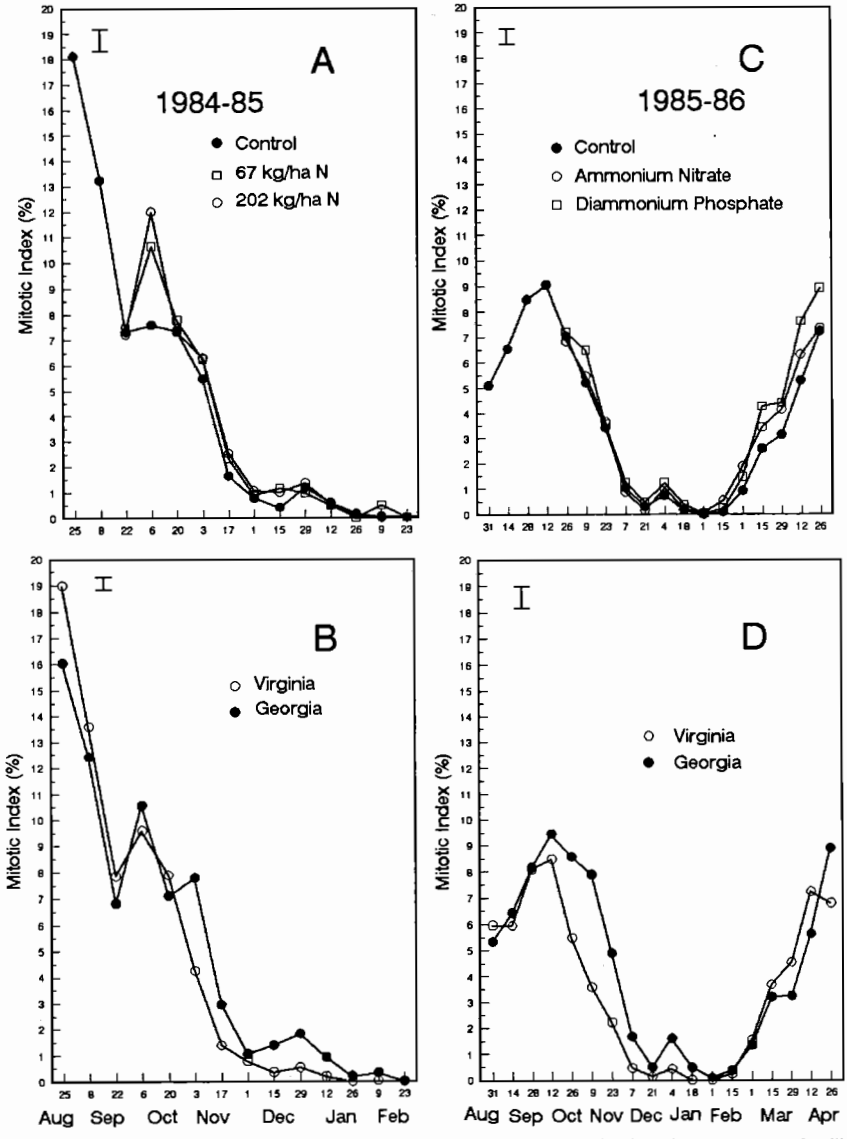

FIGURE 2. Apical meristem mitotic index for loblolly pine by sample date in relation to fertilizer treatment (A) and family (B) for the 1984–85 study; and fertilizer treatment (C) and family (D) for the 1985–86 study. The vertical bars indicate 1 SE.

Data trends leading to the significant family by date interaction showed that, for the majority of the sample dates, the Georgia seedlings had the higher MI (Figure 2B,D). However, for the August 31 sample and the series of sample dates from March 1 to April 12, the Virginia seedlings had the higher MI.

As with the earlier studies, MI in the third study was affected by family and sample date (Table 2). MI for the Georgia seedlings was higher and the values decreased as the fall progressed. However, a simple interpretation of the main effect of fertilizer application date was complicated as a result of confounding with sample date.

TABLE 2.

Analysis of variance of apical meristem mitotic index.

Source	1984–85			1985–86			1986–87		
	df	F[1]	P > F	df	F	P > F	df	F	P > F
Rep.	3	7.31	0.0190	3	1.61	0.2832	3	1.24	0.3511
Treat.	2	2.34	0.1770	2	9.43	0.0140	3	10.36	0.0028
Error A MS	6	(2.91)		6	(1.41)		9	(0.94)	
Family	1	17.39	0.0024	1	18.73	0.0019	1	10.13	0.0079
Treat. × Family	2	9.33	0.0064	2	0.15	0.8637	3	3.46	0.0510
Error B MS	9	(0.80)		9	(2.81)		12	(1.07)	
Date	13	23.63	0.0001	17	183.33	0.0001	2	81.43	0.0001
Error C MS	32	(23.40)		51	(1.26)		6	(2.29)	
Treat. × Date	26	1.00	0.4869	34	1.45	0.0778	3	0.00	1.0000
Error D MS	64	(3.78)		102	(1.12)		9	(0.33)	
Family × Date	13	5.74	0.0001	17	11.06	0.0001	2	2.42	0.1445
Error E MS	32	(1.96)		51	(1.27)		9	(2.44)	
Treat. × Family × Date	26	0.75	0.7943	34	0.33	0.9998	3	0.00	1.0000
Error F MS	64	(2.56)		101	(1.88)		6	(2.29)	

[1] Error MS within the F column are enclosed in parentheses.

A better understanding of how date of fertilizer application influences MI was achieved by conducting a separate analysis for each sampling date (Table 3). The September 28 application caused an increase in MI by October 11 and the November 9 application caused an increase in MI on November 22. However, the increase in MI caused by fertilization on October 19 was not enough to be statistically significant when buds were sampled on November 1.

DISCUSSION

October Increase in Mitotic Activity

The apical meristem MI response to fall fertilization for the first study dictated the timing of fertilizer treatments for the later studies. For the 1984–85 study, a decline in MI was observed until the sample date (October 6) immediately after the fertilizer application (Figure 2A). The increase in MI on October 6 reflected the level of fertilizer applied. Following the increase, MI progressively declined for all treatments with no significant fertilizer influence. Consequently, the timing of the fertilization in the 1985–86 study was changed to see if the increase in October was a true fertilizer effect. As it turned out, the MI showed an increase in October of 1985 even though fertilizer treatments were not applied until November 3 (Figure 2C). MI values determined soon after the application were not significantly different. Thus, the third study examined the possible importance of application date.

An October increase in MI appears to be a normal phenomenon of loblolly pine seedlings. This increase may be the result of greater bud activity occurring after budset (bud scales have formed and seedlings stop growing in height). Apical meristem activity of terminal buds from first-year Sitka spruce seedlings increases after budset in September, allowing for maximum primordia production prior to

TABLE 3.

Apical meristem mitotic index for the 1986–87 study.

Treatment		Mitotic index (%)
Application date		
Control		7.9
9/28/86		8.1
10/19/86		7.0
11/09/86		6.2
		**[1]
Family		
Virginia		7.2
Georgia		8.0
		**
Sample date		
Oct. 11		10.3
Nov. 01		9.1
Nov. 22		5.1
		***
	---------- *Sample date analysis* ----------	
Sample date	*Application date*	
Oct. 11	Control	9.9
	9/28/90	10.7
		**
Nov. 01	Control	8.9
	9/28/86	8.9
	10/19/86	9.4
		ns
Nov. 22	Control	4.8
	9/28/86	4.7
	10/19/86	4.6
	11/09/86	6.2
		**

[1] ns, *, **, *** = not significant at the 5% probability level, significant at the 5%, 1%, and 0.1% probability level, respectively.

the fall frosts (Cannell and Cahalan 1979). The fertilizer-enhanced increase the first year was probably exacerbated by the low nutritional status of the control seedlings. An increase in MI in October of 1981 (Carlson 1986) and the increase in October of 1985 (Figure 2C) indicates the increase can occur naturally without fall fertilization.

Application Time

Unexpectedly, the third study showed that timing of the fertilizer application was not critical in influencing MI (Table 3). Both the September and November applications increased the relative number of cell divisions shortly after fertilization. Carlson et al. (1980) also found increases in MI due to fertilization at planting in both August and October, although the date of cessation of cell division in early December was not altered by such treatments. For our study, the increase in MI was ephemeral since values for the fertilized seedlings were similar to controls within 3 weeks after increases were observed (Figure 2A,C; Table 3).

Timing of Minimal Mitotic Activity

The Virginia seedlings achieved a zero MI by December and/or January (Figure 2B,D). Although the Georgia family reached a MI value below 1%, the level was always greater than zero. Similarly, a minimum of only 3% occurred in late December for a Louisiana source of loblolly pine (Carlson 1986). Regardless of seed source, a minimum MI was reached in mid- to late December. For the Georgia source, this is approximately the same time as maximum rest (°GS 270).

For bareroot Sitka spruce and Douglas-fir, the number of days from °GS 270 until MI reaches zero in mid-December is at least 45 days (Cannell et al. 1990). For the Virginia source, this time was at least 32 days in 1984 and at least 11 days in 1985. Apparently, °GS 270 does not always coincide with the time when MI reaches a minimum value. The timing of the two events may coincide for southern sources (i.e., loblolly from southeast Georgia) but, apparently the further north the seed source, the greater the difference in timing. For many conifers species, °GS 270 should occur several weeks before MI is near zero and not just after as some have proposed (Cannell et al. 1990).

Regardless of stock type, species, or location, the MI of these seedlings appears to reach a minimum at about the same time (Figure 3). For example, container-grown Douglas-fir in Oregon, bareroot Sitka spruce and Douglas-fir in Scotland, and container-grown loblolly pine in Alabama all reach a minimum value in mid- to late December. Although northern species and sources may reach lower values than southern genotypes, the date when they reach the minimum is usually within a 4-week period.

Temperature and the Cell Cycle

It was thought that, as fall progressed, the reductions in mean daily temperatures would influence the fertilizer response. As temperatures decrease, cell division

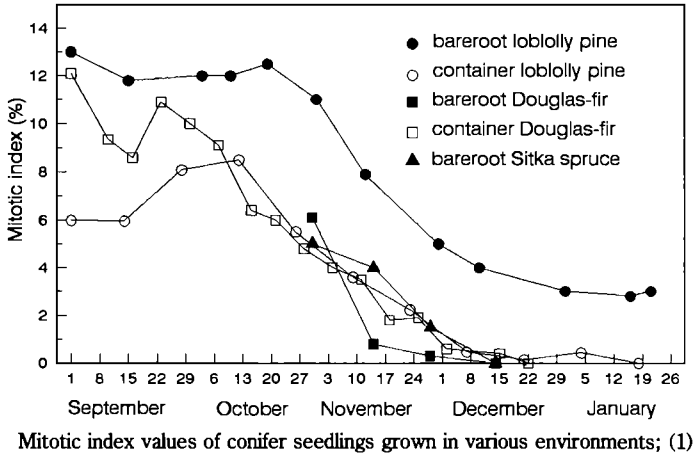

Figure 3. Mitotic index values of conifer seedlings grown in various environments; (1) a Louisiana source of loblolly pine grown in a bareroot nursery in Oklahoma (Carlson 1986); (2) a Virginia source of loblolly pine grown outside in containers in Alabama; (3) a Washington source of Douglas-fir seedlings grown in a bareroot nursery in Scotland (Cannell et al. 1989); (4) Washington and Oregon sources of Douglas-fir seedlings grown in containers in a greenhouse in Oregon (Carlson et al. 1980); (5) a Queen Charlotte Islands source of Sitka spruce seedlings grown in a bareroot nursery in Scotland (Cannell et al. 1989).

rates also decrease (Evans and Savage 1959, Wimber 1966, Verma 1980). The annual MI trend for loblolly pine appears to follow the mean monthly temperature cycle (Carlson 1986). This pattern was also observed for the 1985–86 study (Figure 4). Because temperatures are warmer in the fall, the early fall applications would be expected to increase MI more than later applications.

The reductions in MI as the fall season progressed are difficult to explain. Theoretically, MI should not have decreased if reductions in temperature decrease all phases of the cell cycle proportionally (Rost and Gifford 1977). However, Evans and Savage (1959) demonstrated a differential response between mitotic rate and cell cycle rate. The result was a reduction in MI with decreasing temperatures. Both Douglas-fir and ash (*Fraxinus* spp.) are blocked at the G1 phase of the cell cycle when MI is zero (Owens and Molder 1973, Cottignies 1979). The arrest is probably due to a lack of proteins needed to initiate the transition from G1 to S (Van't Hof 1974). This hypothesis supports Tuan and Bonner's (1964) contention that rest is associated with the repression of DNA-dependent RNA synthesis. Apparently, loblolly pine, as postulated by Carlson (1986), has a subpopulation of stem apex cells which differ in cell cycle properties. Alternatively, a temperature- or photoperiod-mediated increase in cell cycle length is not accompanied by a block in the G1 phase.

The higher MI of the Virginia family in the spring may be an adaptive ability to function better than the Georgia family under cooler growing conditions (Worrall and Mergen 1967). Although the MI was lower, the Georgia family broke bud earlier in the spring. These data agree with those of others (Cannell et al. 1990; Donna E. Macey, Canadian Forest Service, Victoria British Columbia, personal communication) who also conclude that there is no direct relationship between MI and bud dormancy during the spring. Apparently, the temperature requirements for budbreak and cell division in the apex may not be the same (and differ by genotype). Fielder and Owens (1989) suggest that during early shoot elongation,

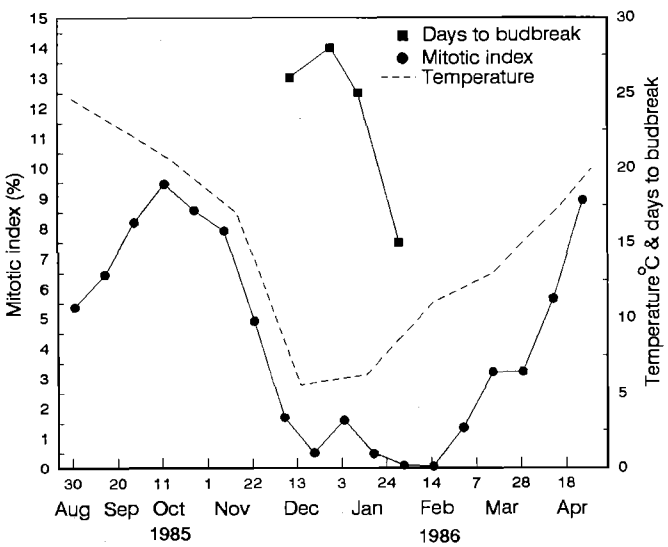

Figure 4. Relationship between mitotic index, mean monthly temperature, and mean days to budbreak for the Georgia loblolly pine family for the 1985-1986 study.

cell division and cell elongation are two independent processes. Since shoot apical meristem activity is not responsible for budburst (Romberger 1963), it is not surprising that there is a lack of direct relationship between MI and budburst.

CONCLUSION

The practical application of MI information appears limited. For the loblolly pine families studied, there is no direct relationship between DBB and apical meristem cell divisions. Any apparent correlations are likely coincidental and not the result of a cause and effect relationship. This is in contrast to the suggestion by some that maximum rest (°GS 270) always coincides with the cessation of apical meristem cell division (Carlson 1986, O'Reilly et al. 1989, Cannell et al. 1990). Both families of loblolly pine reached a minimum MI value at about the same time, while their timing for °GS 270 differed.

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