PHYSIOLOGICAL ASPECTS OF POPULATION VARIATION IN GROWTH AND POSSIBLE IMPLICATIONS TO ACCELERATED TESTING [1/]

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ABSTRACT. --The reliability of accelerated tests for assessing genetic variation in shoot growth is discussed based on analysis of some physiological aspects of growth variation and potential physiological responses of progeny to artificially altered environmental conditions. Population and family variation in shoot growth is considered a function of the number and length of stem units, which are ultimately influenced by apical and subapical meristem activity and the availability of assimilate. Considering various physiological expressions of growth variation, discussion of the physiological bases of and potential for significant genotype x environment interaction between accelerated and non-accelerated assessments of growth variation is presented.

INTRODUCTION

The subject that I have been asked to address is whether or not tests of genetically diverse plant material conducted in controlled (i.e., accelerated) environments are likely to yield accurate and reliable information on the relative growth of progeny. Several approaches can be taken to address this issue. A quantitative approach would invariably include analysis and partitioning of the genotype X environment (G x E) interaction component of variance derived from genetic tests in accelerated and non-accelerated environments and comparison of the age-age correlations from studies in such contrasting environments. Recently, such retrospective analyses have been completed (Bongarten and Hanover 1985; Bridgewater and Williams, this volume) for a few species and indicate that accelerating tree growth for progeny evaluation may be problematical.

An alternative to the quantitative approach is to examine some of the physiological aspects of growth variation among tree populations and families and then to speculate on the physiological impact of growing trees under accelerated as opposed to non-accelerated conditions.

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Clearly, this approach is more prospective and speculative than the quantitative perspective and is limited by an incomplete understanding of the physiological factors underlying genetic variation in growth. Nevertheless, a physiological approach can provide insight into the potential for a differential response of progeny to artificially altered environmental conditions. This paper will examine some physiological aspects of growth variation among tree populations and, based on this information, discuss the possibilities for G x E in accelerated environment assessments of growth variation. Although this discussion will be general with respect to species, most of the information is derived from research with north temperate conifers, including my own studies of genetic variation in bud morphogenesis and shoot development in Abies balsamea.

PHYSIOLOGICAL ASPECTS OF GROWTH VARIATION

Annual shoot growth of woody plants can be considered as a product of the number of stem units produced on a shoot and the length of those stem units (Cannell 1978; Figure 1), where a stem unit is defined as a needle node and its subtending internode (Doak 1935). Following this model, it is possible to examine the relative contributions of these two shoot growth components to genetic variation in growth among populations or families. Such an approach may be particularly useful because the production and elongation of stem units are influenced largely by meristematic tissues which are functionally and spatially distinct. The number of stem units comprising a shoot is a function of activity of the apical meristem, while stem unit elongation is a function of activity of the subapical or rib meristem (Zimmerman and Brown 1971, Cannell et al. 1976). Although these meristems are activated at different times and by independent mechanisms (Cannell 1978), they do not appear to be totally independent because they draw from a common pool of assimilate.

The relative contribution of number and length of stem units to genetic variation in shoot length has been examined for several species and appears to depend more on the level of genetic comparison than on species under study (Kremer and Larson 1983, Bongarten 1986). At the provenance level, most of the variation in shoot length is the result of differences in number rather than length of stem units (Table 1). That is, fast-growing provenances achieve growth superiority simply by producing a greater number of needle internodes than slow-growing provenances; mean length of stem units is relatively consistent among provenances. In contrast, when examining phenotypic variation among trees within provenances or genetic variation among half-sib families within provenances, mean stem unit length is at least as important as number of stem units in determining variation in annual shoot extension (Table 1). In fact, thorough analyses of genetic and environmental variation in shoot growth components in Pinus banksiana and Picea pungens revealed that mean stem unit length was the primary determinant of shoot growth at the family within provenance level (Kremer and Larson 1983, Bongarten 1986).

Number of Stem Units

Most of the variation in shoot growth among provenances is attributed to differences in number of stem units and, at least for Abies balsamea provenances (DeHayes and Hawley 1985), stem unit production is consistent over time ($r=0.76$, $P>0.01$, $n=10$) and space ($r=0.98$, $P>0.01$, $n=5$). The number of stem units produced on a shoot is determined by the number of needle primordia initiated on the embryonic shoot. The number of needle primordia is a function of the rate and duration of needle primordia initiation the season prior to elongation ("fixed" or preformed growth) and the amount of "free" growth (Figure 1). "Free" growth refers to the initiation of needles and elongation of their internodes the same season (Jablanczy 1971). Free growth is the only growth evident on germinants, occurs to a limited extent on young seedlings, and is rare on mature trees of most north temperate conifers. The cessation of free growth in germinants is triggered by increasingly long nights in late summer and differential provenance response to nightlength may result in variation in the duration and amount of growth of first-year seedlings. Beyond the initial growing season, the contribution of free growth to stem unit production becomes progressively smaller, while the contribution of preformed growth becomes progressively larger.

The relative importance of variation in rate and duration of apical dome activity to variability in preformed needle primordia production and number of stem units seems to vary among species. For instance, provenance variation in needle primordia production in Pinus contorta is largely a function of provenance differences in the rate of needle primordia initiation around the apical dome (Table 2). In contrast, provenance variation in needle primordia production in Picea sitchensis and Picea glauca is primarily a result of provenance differences in the duration of initiation (Table 2). The relatively low correlations between primordia production and rate and duration of apical dome activity among Abies balsamea provenances (Table 2) are a result of different primordia production strategies for different provenances, rather than a lack of variation in the various bud development characteristics. That is, some Abies balsamea provenances produce a large number of needle primordia because they maintain a long period of functional primordia initiation, while others initiate primordia at a rapid rate for a relatively short period of time (Table 3). In fact, the three Abies balsamea provenances that initiate the most primordia (stem units) and are fastest-growing utilize different mechanisms toward the production of numerous primordia (Table 3). Trees from provenance 90 (NY) produced the most primordia and longest shoots because they maintained functional primordia initiation 35% longer than the average of all provenances. In contrast, the high primordia production of trees from provenance 87 (QUE) is a function of an extremely rapid rate of primordia initiation and was accomplished despite an extremely short period of functional primordia initiation. Finally, trees from provenance 07 (VT) accomplish high primordia production by combining a relatively rapid rate of production with an above-average period of initiation.

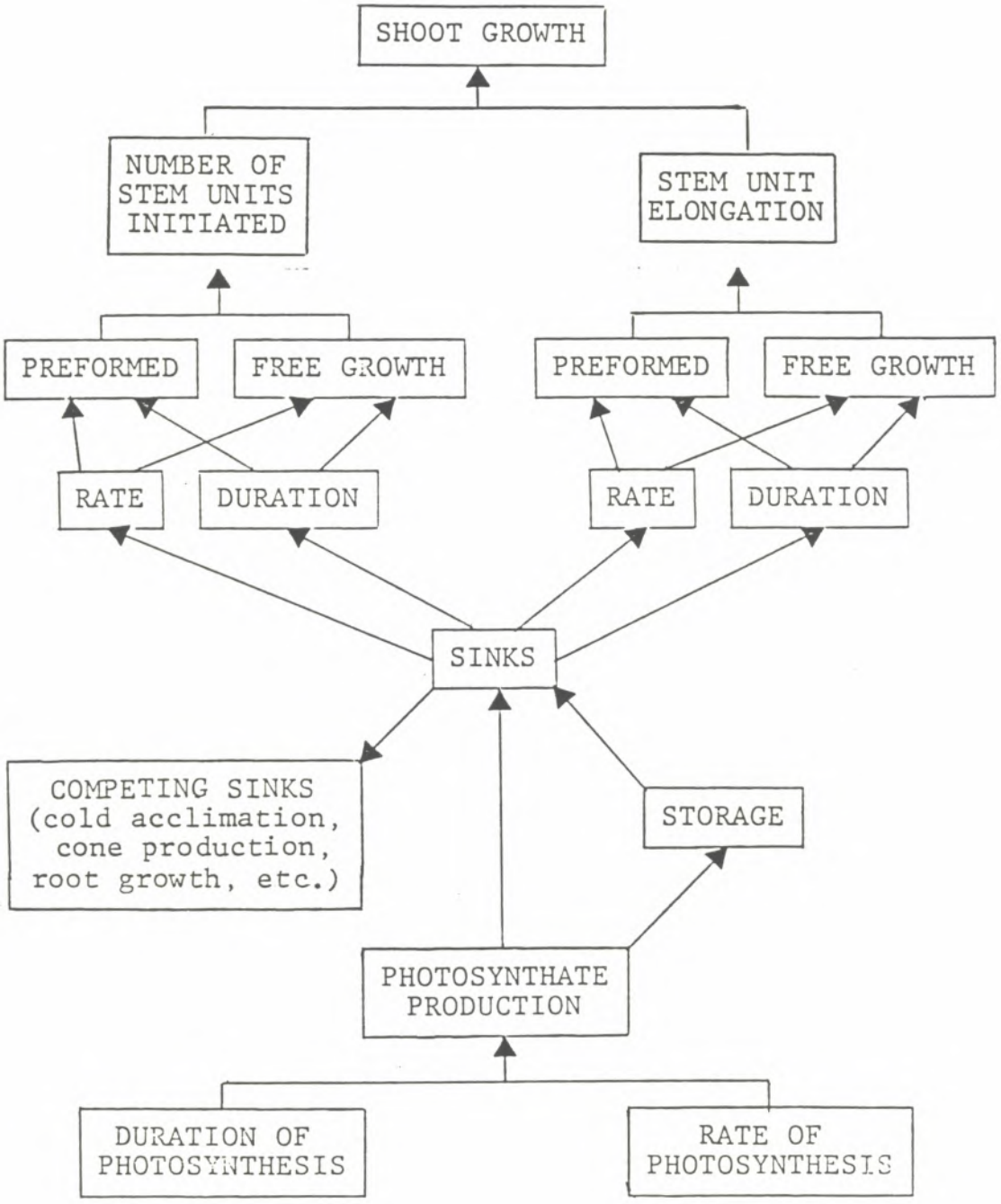

Figure 1. Hypothetical representation of variation in shoot growth as a function of apical (number of stem units initiated) and subapical (stem unit elongation) meristem activity and the production and distribution of photosynthate.

Table 1. Correlations among shoot growth traits at the provenance, family, or individual tree levels for various species of conifers.

Species	Level of comparison	Correlation(r) of shoot length and: No. of stem units	Length of stem units	Ref.[1/]
Lodgepole pine	prov.	0.84	-0.11	A
Lodgepole pine	prov.	0.91	0.44	A
Int. Douglas-fir	no. prov.	0.90	0.12	B
Int. Douglas-fir	so. prov.	0.76	-0.48	B
Blue Spruce	prov.	0.74	0.41	B
Balsam fir	prov.	0.66	0.14	C
Balsam fir	prov.	0.74	0.44	C
Sitka spruce	full sibs	0.70	0.63	A
Int. Douglas-fir	tree/no. prov.	0.42	0.61	B
Int. Douglas-fir	tree/so. prov.	0.80	0.64	B
Blue spruce	1/2 sib/prov.	0.35	0.69	B
Jack pine	1/2 sibs	0.45	0.51	D
Balsam fir	tree/prov.	0.44	0.72	E

[1/] A-Cannell et al. 1976; B-Bongarten 1986; C-DeHayes and Hawley 1985; D-Kremer and Larsen 1983; E-DeHayes et al. 1983.

Table 2. Correlations between needle primordia production and duration vs. maximum rate of apical dome activity for several coniferous species.

Species	Duration	Rate	Ref.[1/]
	- - r - - - -		
Lodgepole pine	-0.57	0.72	A
Sitka spruce	0.75	-0.10	A
White spruce	0.89	-0.48	A
Balsam fir	0.57	0.30	B

[1/] A-Cannell and Willett 1975; B-DeHayes and Hawley 1985.

Rate of initiation. Variation in rate of primordia initiation closely parallels variation in the volume of meristematic tissue in the apical domes of conifer shoot apices (Cannell et al. 1976). This relationship appears to exist whether variation is considered seasonally, developmentally (Gregory and Romberger 1972), at the provenance level, or among branches within individual trees (DeHayes et al. 1983). As the size of the apical dome increases, the rate of primordia initiation increases proportionately. Thus, rate of primordia initiation increases in spring and decreases in late summer and fall in approximate proportion to changes in size of apical domes (Sucoff 1971, Cannell and Willett 1975, Figure 2).

Variation among provenances in maximum rates of primordia initiation is also closely associated with variation in dome size. In fact, most of the variation in primordia production among provenances of Pinus contorta was explained by differences in the seasonal pattern of dome development (Cannell et al. 1976) and provenance mean number of primordia was strongly correlated with apical dome diameter in Abies balsamea (DeHayes et al. 1983). Furthermore, correlations between apical dome diameters throughout a growing season and subsequent plastochron were positive and highly significant for trees representing 11 provenances of Abies balsamea. Provenance variation in seasonal development of the apical dome and rate of primordia initiation is illustrated for two Abies balsamea provenances in Figure 2.

Reasons for genetic variation in apical dome size and hence plastochron have not been clearly established and, in fact, provenance variation in maximum rate of primordia initiation in Abies balsamea appears unrelated to geographic or climatic conditions of the parental populations. As a result, the implication of an adaptive mechanism as an underlying cause for population differences in dome size seems unlikely. From a physiological standpoint, however, it is likely that variation in dome size is related to differences in the rates in which photosynthate is supplied to apical meristems (Cannell et al. 1976), since primordia initiation is energy consumptive. As a result, it would seem that provenances with large apical domes and a rapid rate of initiation may exhibit enhanced photosynthate production or preferential allocation of photosynthate to shoot apices during initiation periods.

Duration of initiation. Provenance variation in the duration of apical meristem activity in late summer and autumn generally accounts for a considerable proportion of the variation in number of primordia (and stem units) initiated within terminal buds. Although there is little question that the cessation of apical activity is under strong genetic control (at least for geographically distant provenances), the mechanism(s) responsible for differential cessation has not been clearly elucidated. Considerable circumstantial evidence suggests the involvement of a photoperiodic or a temperature x photoperiod stimulus as a trigger for the cessation of apical activity (Roberts and Wareing 1975, Cannell et al. 1976), but conclusive empirical evidence has not been provided. Much of the evidence for photoperiodic involvement is

RELATIONSHIP BETWEEN RATE OF PRIMORDIA INITIATION AND DOME DIAMETER

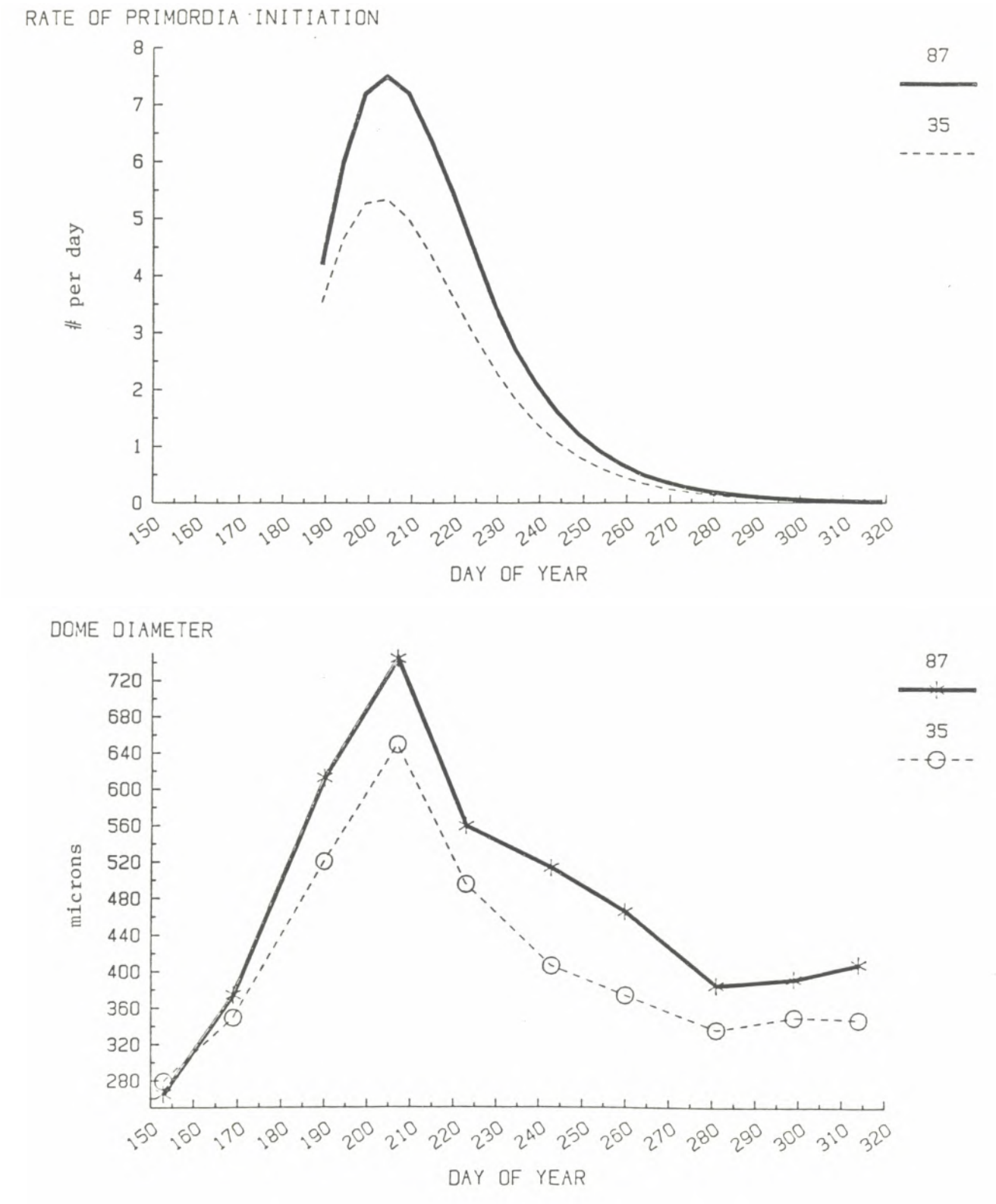

Figure 2. Variation between two Abies balsamea provenances (No. 87 from QUE and No. 35 from ONT) in rate of primordia initiation and apical dome diameter.

Table 3. Variation among Abies balsamea provenances in aspects of bud morphogenesis.

Provenance	Primordia Initiation: Maximum Rate	Primordia Initiation: Duration	Number Initiated
	– – – % of mean – – –		
90 NY	89.9	135.1	371
07 VT	118.3	101.4	348
87 QUE	136.6	83.8	329
70 MI	79.5	120.3	283
21 ONT	106.2	91.9	281
72 MAN	101.1	91.9	265
64 MI	94.2	91.9	248
57 WI	84.4	101.4	246
35 ONT	97.3	85.1	239
46 ONT	96.2	86.5	238

Table 4. Provenance and/or family mean height correlations in accelerated and non-accelerated tests.

Species	Basis of Comparison	Correlations Among: Families	Correlations Among: Provenances	Ref. [1/]
Blue Spruce	Age 2	0.23	0.28	A
	Age 5	0.29	0.40	A
	Age 7	0.35	0.43	A
Lodgepole Pine	Age 2	0.24	--	B
Blue Spruce	Size (x 28.5cm)	0.09	0.53	A
	Size (x 62.5cm)	0.30	0.48	A

[1/] A-Bongarten and Hanover 1985; B-Wheeler, 1979.

based on correlations between the cessation of apical meristem activity and either date of "bud-set" (photoperiodically induced) in free-growing seedlings or latitude and climatic conditions of provenances. Indeed, provenance mean duration of primordia initiation and date of cessation of apical meristem activity are strongly correlated with latitude and precipitation characteristics of the parental stands of Abies balsamea. In general, southerly populations initiate primordia later into the season than northerly populations, in keeping with what would be expected in response to a photoperiodic trigger for cessation of primordia initiation. Similar patterns of variation have been reported for other *species as* well (Pollard et al. 1975, Pollard 1974, Cannell and Willett 1975, Burley 1966). Despite such evidence, controlled environment studies with Picea glauca and Picea mariana seedlings have shown that varying light intensity and photoperiod at constant temperatures (22° C) had little effect on bud morphogenesis, but relatively low temperatures (10° to 20° C) at an eight-hour photoperiod promoted the cessation of activity compared to high temperatures (25 °C) (Pollard and Logan 1977). Interestingly, however, there was no evidence of temperature x provenance effects of bud morphogenesis in either species even though widely divergent provenances were compared (Pollard and Logan 1979). Furthermore, provenance variation in the cessation of initiation was observed in seedlings grown at constant temperatures (22.5°C) under short days (8-hour photoperiod) (Pollard 1974). Since most empirical data would suggest that variation in the cessation of meristematic activity is the result of a provenance x environmental trigger interaction, it is probable that low temperature alone is not the trigger for cessation of initiation. A photoperiod/temperature stimulus or an internal trigger that is phenologically dictated are more likely explanations.

Variation among populations in the duration of initiation is also paralleled by variation in apical dome size. Populations with an extended duration of apical meristem activity maintain large apical domes later into autumn than populations with early cessation of meristematic activity. Such a seasonal pattern in dome size was clearly evident among provenances of Abies balsamea (Figure 2). To the extent that differences in apical dome size are a function of photosynthate production or allocation, variation among provenances in duration of initiation can also be expected to be associated with seasonal activity of the photosynthetic apparatus (Figure 1).

Stem Unit Length

The elongation of stem units, which collectively represents shoot elongation, is a function of activity of the subapical meristem. This meristem influences both the division and elongation of cells at the shoot apex (Zimmerman and Brown 1971). Unlike the case with provenance variation in the number of stem units, provenance variation in stem unit length is generally small (hut significant) and at best only weakly correlated with shoot length. Furthermore, variation among Abies balsamea provenances in stem unit length is not consistent over time

(r=0.337, P>0.05, n=10) or over space (r=0.238, P>0.05, n=5), further suggesting a relatively small component of genetic variation at the provenance level in this growth characteristic. As noted in Table 1 and some recent analyses of shoot growth components (Kremer and Larson 1983, Bongarten 1986), stem unit length is often strongly associated with shoot growth variation at the half-sib family and tree within provenance levels and heritabilities are often higher for stem unit length than number of stem units.

As with number of stem units, it is not uncommon for variation in shoot growth to be considered as a function of the rate and duration of shoot elongation (Figure 1). However, since growth variation among provenances of most species is primarily a function of number rather than length of stem units, such consideration is not appropriate at the provenance level for most species. In fact, in Abies balsamea provenances, variation in rate and duration of shoot elongation is primarily a function of the number of stem units preformed in the bud the previous summer and fall (DeHayes and Hawley 1985) rather than of elongation phenomena. That is, provenances that had initiated numerous stem units within buds either required a greater period of time for subsequent elongation or elongated more rapidly than provenances with relatively few stem units. As a result, when growth variation is shown to be primarily a function of number of stem units and all stem units are preformed, variation in timing, rate, and/or duration of stem unit (shoot) elongation has little meaning with respect to shoot growth variation.

Although it is well-known that stem unit elongation is influenced by current season environmental conditions, it is also clear that genetic variation in stem unit length exists at all levels in most species and can be a particularly important component of growth at the genotypic level. Although the mechanism(s) by which stem unit length may vary is by no means thoroughly understood, there is considerable circumstantial evidence to suggest that variation in stem unit length is influenced by the availability of assimilate during the period of cell division and enlargement associated with shoot elongation. For instance, the reduction in stem unit and shoot length of Abies balsamea provenances from one season to the next was shown to be strongly correlated with average cone production per provenance during an unusually heavy cone crop the second year (DeHayes and Hawley 1985). In contrast, the number of stem units initiated during and prior to the season of cone production was not correlated with average cone production. Presumably, photosynthetic reserves were allocated to embryo, megagametophyte, and cone development during spring and early summer at the expense of shoot elongation. Similarly, Bongarten (1978) found longer stem units on Pseudotsuga menziesii trees which suffered frost damage the spring prior to shoot elongation than on undamaged trees. Once again, it is assumed that available photosynthate was funneled into the relatively few surviving shoots. Furthermore, number of stem units and mean stem unit length have been shown to be negatively correlated for Abies balsamea provenances (DeHayes and Hawley 1985) and

half-sib families of Pinus banksiana (Kremer and Larson 1983) and Picea pungens (Bongarten 1986). It is probable that the extent to which any stem unit elongates is influenced by the total number of stem units that are simultaneously elongating in much the same way that cone development in Abies balsamea represented an alternative carbohydrate sink.

Variation among populations or progenies in mean stem unit length may reflect either the differential strength of a transient competing sink (e.g., a heavy cone crop) or, in the absence of such transient sinks, inherent variation in photosynthate production, storage, and/or allocation phenomena. Because population variation in stem unit length is usually small, it is unlikely that variation in any or all of the photosynthetic phenomena is a result of adaptation to macroenvironmental conditions or a simple phonological response. In fact, population variation in mean stem unit length might be expected to be an indirect result of a transient competing sink and, therefore, not consistent from year to year. Variation among half- or full-sib progenies probably reflects inherited variability in photosynthetic characteristics and would be expected to be consistent over time as has been shown for some species (Bongarten 1986). Photosynthate storage in year-old needles is probably important for cell division and enlargement very early in the season, whereas photosynthate production and the preferential allocation of photosynthate to elongating shoots (perhaps at the expense of root or radial growth) may contribute more to shoot growth later in the spring.

POSSIBLE IMPLICATIONS TO ACCELERATED TESTING

The merits of greenhouse and indoor culture (including optimal irrigation, fertility, and temperature and photoperiod extension) in accelerating the growth of woody plants are well known (Downs and Borthwick 1956, Downs and Piringer 1958, Read and Bagley 1967, Hanover et al. 1976, Hanover 1977, Hanover and Bongarten 1977) and will not be discussed here. The primary concern is whether genetic tests conducted in accelerated environments provide an accurate assessment of the relative growth of genetically diverse plant material. As noted by Hanover and Bongarten (1977), key elements in the utility of accelerated testing are the extent of genotype x test (accelerated vs. nonaccelerated) environment interaction and the strength of age-age growth correlations from accelerated as opposed to traditional tests.

Potential Sources of G x E

The greenhouse and nursery environments typically differ in several respects, including spacing, soil texture and structure, fertility, moisture regime, wind exposure, and other factors. However, most of these factors also differ from one nursery to the next, are not unique to the accelerated environment, and are less critical to the present analysis. Of perhaps greater importance as potential sources of G x E are those aspects of the accelerated environment which almost always differ from all outdoor nursery environments. The most conspicuous of these include photoperiod and temperature regimes and these factors may

potentially influence growth during the active elongation phase and the late- or post-growth phase involving bud set and hardening before field planting.

Relatively few studies have been conducted that are designed to examine the differential response of tree populations or families to accelerated growth conditions, but circumstantial and some direct evidence suggests that a significant G x E component may be present in some cases. For instance, although most species exhibit a positive growth response to extended photoperiod and/or greenhouse culture, data of Downs and Borthwick (1956) and Hanover et al. (1976) show that species respond very differently to such accelerated conditions. That is, some species which exhibit relatively fast growth under long photoperiods are relatively slow growing under short photoperiods or natural daylengths. Generally, an inherited differential response among species can be indicative of a potential differential response among populations or individuals within species. In fact, Downs and Piringer (1958) noted a differential growth response among seedlings from Pinus ponderosa and Pinus taeda provenances exposed to a range of photoperiods under greenhouse conditions. Furthermore, height correlations for half-sib families or provenances of Picea pungens and Pinus contorta in accelerated and non-accelerated tests were generally low Table 4); this was the case whether correlations were examined for trees of the same age or approximately the same size. These data indicate that, at least for some species, accelerated and non-accelerated tests of genetically diverse plant material provide somewhat different assessments of relative growth rate.

Possible Physiological Explanations For G X E

Clearly, the relatively low correlations between accelerated and non-accelerated tests and the significant G X E that has been noted in some cases are indicative of modified physiological expression of trees growing in different environments. Although the only way to be certain of the presence or absence of G X E in such assessments is to make retrospective comparisons between accelerated and non-accelerated tests, information on physiological aspects of growth variation provides an opportunity to speculate as to the likelihood of and the reason(s) for significant G X E between accelerated and non-accelerated tests. The likelihood and magnitude of G X E between accelerated and non-accelerated tests depends on the physiological nature of growth variation for a given species, the environmental or internal physiological trigger(s) responsible for the cessation of primordia initiation, and whether the G X E is caused during the active growth phase or the post-growth hardening phase of the accelerated environment. Although the mechanism responsible for the cessation of primordia initiation has not been empirically established, the ensuing discussion is based on the assumption that a photoperiod or photoperiod/temperature trigger is involved. Also, the physiological explanations for G X E during the active and post-growth phases will be discussed separately.

Active growth phase. If we disregard the potential for interaction associated with soil, fertility, and moisture regimes in the accelerated environment, then the probability and nature of G X E will depend primarily on the physiological nature of genetic variation in shoot growth in ambient environments. For instance, genetic variation in shoot growth may simply be a function of the duration of "free growth" in indeterminant species or germinants of determinant species, or may be a result of differences in number or length of stem units. The expectations of the significance of G X E between accelerated and non-accelerated tests for several physiological aspects of growth variation is briefly described in Figure 3.

If genetic variation in shoot growth in non-accelerated tests is solely a result of differences in the duration of free growth, then one would expect little or no variation in growth among populations or families grown under accelerated conditions. This lack of expression of growth variation would be expected because variation in the duration of free growth is primarily a result of population response to different critical night lengths. Under artificially induced long days, critical night lengths are not likely to occur and seedlings will either grow continuously or set bud in response to some other environmental or stress factor in the accelerated environment. Data from an assessment

	If Genetic Variation in Non-accelerated Tests is Due Primarily t Differences in:		
	Duration of Free Growth	Duration of Stem Unit Init.	Rate of Stem Unit Init.
	Then in Accelerated Tests One Would Expect:		
1. Response --	1. Slight growth variation	1. Subtle differences in rate will predom.	1. Accentuation (growth diff.
2. Reason --	2. No differential response to SD	2. No differential response to SD or low temperatures	2. Extended peri for expressio of rate diff.
3. Exp. GxE --	3. High	3. High	3. Low

Figure 3. Expectations of G x E between accelerated and non-accelerated tests based on physiological aspects of variation during the active growth phase.

of localized population variation in Betula alleghaniensis in Vermont (Murdock 1981) shows that growth variation attributed to differences in the duration of free growth are not expressed in accelerated environments (Table 5). When grown under a 24-hour photoperiod in an indoor accelerated environment, no growth differences were evident among populations representing physiographic and climatically distinct regions. However, following outdoor planting seedlings from the mild climate Champlain Valley population ceased growth in response to relatively long critical nights (short days) and therefore grew later in the season and more than seedlings from other regions.

If population variation in shoot growth is primarily a result of variation in the number of stem units initiated during and subsequent to the free growth phase, then the relative performance of populations under accelerated conditions will depend on the extent to which duration versus rate of primordia initiation influences the number of stem units initiated (Figure 3). If variation in duration of primordia initiation is most important in non-accelerated tests and there are at least small differences in rate of initiation, then the differences in rate of initiation would he expected to predominate in the accelerated environment. This is because the accelerated environment is lacking the combination of short days and cool temperatures which may serve as triggers for the cessation of apical meristem activity. As a result, duration of initiation is artificially eliminated as a component of current or subsequent growth and populations which exhibit a relatively rapid rate of initiation would he expected to initiate more stem units in a given period of time. If seedlings grow continuously in the accelerated environment, the growth advantage of the rapid initiating populations would become compounded over time and perhaps persist for many years after field planting. Such a growth response to accelerated conditions may be at least a partial explanation for the differential growth of P. pungens provenances in accelerated and non-accelerated environments (Bongarten and Hanover 1985). Under non-accelerated test conditions southern provenances were fastest-growing, whereas in the accelerated environment northern provenances were generally fastest growing, but gradually lost their growth superiority after field planting (Table 6). Since it has been shown that P. pungens provenances differ primarily in duration of primordia initiation, it seems possible that the contradictory pattern of growth exhibited in the accelerated environment may result from the predominant expression of subtle provenance differences in rate of primordia initiation in the accelerated environment. However, this explanation is only speculative at this time.

If rate of primordia initiation is primarily responsible for shoot growth differences among populations, then one would expect similar relative performance of populations in accelerated and non-accelerated tests and, therefore, low G X E (Figure 3). In fact, it is possible that population differences would be accentuated under accelerated conditions because of an extended period of time for differences in rate of initiation to be expressed. Interestingly, in P. contorta rate of

Table 5. Height of Betula alleghaniensis seedlings from diverse populations after accelerated and subsequent nursery growth (after Murdock 1981).

VT Population	Families per population	Height when grown in: Accel. (11 wks)	Nursery (27 wks)	Growth cessation in nursery
	no.	cm		days past 6/30
Champlain Valley	24	15.4a	42.7a	52a
Green Mountains	24	15.4a	33.3b	43b
Eastern Piedmont	32	14.7a	34.5b	42b

Table 6. Correlations between height and latitude of blue spruce provenances grown under accelerated and non-accelerated conditions (from Bongarten and Hanover, 1985).

Test conditions	Height-latitude correlations at ages:		
	1 or 2	5	7
Accelerated	+0.39**	0.00	-0.32**
Non-accelerated	-0.59**	-0.52**	-0.48**

primordia initiation has been indicated as the primary explanation for provenance differences in shoot growth (Cannell and Willett 1975) and the provenance mean correlation between greenhouse and subsequent field height is very high (r=0.96**) (Perry and Lotan 1978). This high correlation is consistent with expectations for low G X E between accelerated and non-accelerated tests in cases where rate rather than duration of primordia initiation is a major growth influencing factor.

In situations where genetic variation in growth is primarily a result of variation in stem unit length (as is the case with variation among half-sib families of most species), the growth response to varying conditions is complicated and it is difficult to speculate on the influence of accelerated conditions and progeny performance. Nevertheless, in such situations it is very likely that the relative performance of progeny is highly dependent on photosynthate availability during the periods of cell division and enlargement associated with shoot growth. As a result, the relative performance of progeny under accelerated and non-accelerated conditions would be expected to be influenced by the importance of and impact of the accelerated environment on photosynthate storage, production, and allocation. In ambient environments it is likely that stored photosynthate (mostly in the previous years' needles) plays an important role in shoot elongation, especially during cell division in early spring prior to budbreak. In contrast, in accelerated environments where growth is continuous, seedlings are probably dependent primarily on current photosynthate production for elongation and there is probably little storage occurring. For species which exhibit cyclic growth under accelerated conditions, the significance of storage to subsequent growth depends on whether the recently extended needles become photosynthetic sources rather than sinks before the next flush.

Current photosynthate production is probably the primary source of photosynthate for plants growing under accelerated conditions. As a result, progeny capable of producing the most photosynthate under the relatively uniform accelerated conditions would be expected to grow

Fastest in that environment. Whether or not the same progeny would be capable of high photosynthate production in the temporally and spatially variable outdoor environment is not known. If variation in photosynthate production is simply a function of differences in leaf area, then progeny performance may be similar across environments if the same families produced more or larger leaves in all environments. However, given the importance of variation in the seasonal pattern of photosynthate production and net assimilation to growth in ambient environments (Ledig and Perry 1969, Ledig 1969), it would seem unlikely that progeny photosynthetic characteristics would be similar in accelerated and non-accelerated environments. Relatively low family mean correlations between accelerated and non-accelerated environments (Table 4, Perry and Lotan 1978) would support such a contention.

Finally, the allocation of photosynthate to seasonally competing sinks such as root and radial growth is certainly influential in dictating photosynthate availability for shoot growth in outdoor environments. Furthermore, the strength and timing of such competing sinks is very likely to vary among half-sib families and therefore have an influence on family variation in shoot growth. Because temporal patterns of photosynthate allocation are probably quite different for seedlings growing continuously in accelerated environments, it is unlikely that the availability of photosynthate would he similar for families across such contrasting environments.

Post-growth phase. Generally, the environmental conditions which are to prevail during active growth in accelerated tests are precisely determined after lengthy analysis and often considerable expense. In contrast, very often relatively little attention is given to the details of the post-growth environment during which time the subsequent year's bud is formed and plants are hardened prior to field planting. In fact, in many greenhouse tests, supplemental light and temperature are abruptly terminated in late autumn to encourage the cessation of shoot growth and hardening. In our indoor growth facility, we have noted that the nature of the post-growth hardening environment can result in two- to three-fold differences in shoot growth during the subsequent outdoor growing season for Abies balsamea seedlings. Yet, because embryonic shoot development and bud formation are influenced by photoperiod and temperature and are under relatively strong genetic control, we also recognize that the post-growth environment is a potential source of G X E with respect to shoot growth the season following field planting. This potential component of G X E is often ignored during assessment of the reliability of accelerated testing.

Although it is somewhat difficult to speculate on the bud morphogenetic response of diverse plant material to the environment associated with the post-growth phase, it is clear that the rate and duration components of stem unit initiation can be differentially altered by the nature of the environmental change from the active to the post-growth phase. For instance, an abrupt reduction in temperature and photoperiod from the active to the post-growth phase might he expected

to result in the cessation of both shoot elongation and apical meristem activity. As a result, relatively few stem units would he initiated and shoot elongation would he expected to be similar for all populations during the subsequent growing season. In cases where growth differences result primarily from variation in number of stem units, one would expect a considerable G X E component between accelerated and non-accelerated tests as a result of such an abrupt change in environmental conditions during the post-growth phase. Similarly, a change to short days with continued warm temperatures would be expected to promote the cessation of elongation and the active initiation of stem units on the embryonic shoot. However, if a photoperiod-temperature interaction is responsible for triggering the cessation of meristematic activity, then this trigger would be removed and differences in duration of initiation would not be expressed. As a result, variation in the number of stem units in the accelerated tests would reflect differences in the rate of initiation regardless of the mechanism responsible in tests conducted in ambient environments. It is feasible to speculate on other potential morphogenetic modifications associated with the post-growth environment, but I will leave such speculation to the discretion of the reader. Suffice it to say, that a gradual reduction in photoperiod and temperature during the post-growth phase will probably most closely approximate the ambient environment and promote a reasonably natural expression of apical meristem activity.

CONCLUSION

When one considers possible physiological explanations for shoot growth variation among tree populations and families, it appears that the potential for significant G X E between accelerated and non-accelerated assessments of growth variation is considerable. Although this conclusion is derived from an analysis based largely on circumstantial evidence and speculation, the relatively few empirical comparisons of genetic variation in growth in accelerated and non-accelerated environments tend to support this perspective.

Because G X E reflects a differential physiological response of plant material in varying environments, the potential for G X E is influenced by the physiological nature of growth variation for the species, populations, and/or families under study. As a result, it is not safe to assume that patterns or expressions of genetic variation in shoot growth in accelerated environments accurately reflect variation in non-accelerated environments. Clearly, additional direct comparisons of shoot growth variation in accelerated and non-accelerated environments are necessary to quantify the level of G X E and ultimately determine the utility of accelerated environment tests of growth variation of genetically diverse plant material.

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