SEED SOURCE VARIATION AND GROWTH CONTROL OF SUGAR MAPLE (*Acer saccharum* Marsh.) SEEDLINGS

By

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ABSTRACT

SEED SOURCE VARIATION AND GROWTH CONTROL OF SUGAR MAPLE (*Acer saccharum* Marsh.) SEEDLINGS

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Sugar maple (*Acer saccharum* Marsh.) seedlings grow slowly in the natural environment. Height growth occurs for about 8 weeks, then a resting bud is formed that will generally remain dormant until exposed to about 2000 hours of chilling. This slow and determinate growth characteristic presents a formidable barrier to forest geneticists who want to genetically evaluate seed sources and to commercial nurserymen who desire high quality seedlings in a relatively short time. Accelerated-optimal-growth (AOG) is a concept in tree production which combines containerized greenhouse production with control of growth and development by regulating factors which primarily affect tree growth. If the application of these factors to sugar maple could produce greater growth during the normal growing period and/or override the determinate growth characteristic and allow continuous growth, then it would be advantageous to researchers and nurserymen

concerned with growing sugar maple. For these reasons various methods for regulating growth of sugar maple were studied.

Results showed that seedlings grown in a greenhouse under continuous light (AOG) were much taller than seedlings produced in the outdoor nursery, even though they were grown for equal periods of time under identical natural daylight photoperiods. Seed source differences were detectable for AOG seedlings after 4 and 16 months from germination but only after 16 months for those grown in the nursery. Differences in several growth variables between peninsulas and correlation of 16-month AOG results with environmental factors indicate the existence of different races between the Upper and Lower Peninsulas of Michigan. This conclusion was further supported by seed morphology. Based on AOG results, Upper Peninsula trees grow much smaller than those from the Lower Peninsula and Eastern Upper Peninsula trees grow taller than Western Upper Peninsula trees. If these patterns exist after AOG and nursery seedlings have been grown in common environments for several years, then the AOG system would have considerably reduced the time required for genetic evaluation.

Sugar maple growth and development during the normal growth period were accelerated or otherwise controlled by carbon dioxide fertilization, temperature, and exogenous foliar applications of gibberellic acid (GA_3), GA_7, A_{4+7}, and benzyladenine (BA). Applied GAs and BA affect height growth, component dry weights, total dry weight, leaf area, and root:shoot ratio. GA_7 also affected root growth. The determinate growth nature of maple can be overridden and the growth apparently extended indefinitely by growing seedlings under continuous light and treating the resting bud with either GA_7 or GA_3 or by complete defoliation of the seedling. Budbreak response to bud applications of GA_7 or GA_3 is dependent upon time since budset. GAs were only effective when applied during about 2 months after budset. Defoliation treatments were effective up to at least 6 months after budset. Relatively low temperature (20° C vs 30° C) growing conditions partially prevented the cessation of determinate growth.

Triacontanol, a recently discovered growth regulator, had no affect on growth of sugar maple.

The photosynthetic and respiratory mechanisms of seedlings grown in either a constant CO_2 concentration or varying temperature regimes became adapted to those growth conditions. The temperature-adapted mechanisms readapt to different temperatures after 1 month. CO_2-adapted seedlings were not able to readapt to lower CO_2 levels after 2 weeks of exposure at the lower levels. Transfer of seedlings adapted to CO_2 or temperature levels to a lower CO_2 concentration or different temperature environments greatly decreases net photosynthesis.

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Carbon exchange rates of seedlings decreased as the seedlings aged and entered dormancy, with peaks in photosynthesis immediately after budset. At 32 weeks after germination, dark respiration exceeded net photosynthesis. There were no differences in rates among leaf types of similar chronologic age.

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INTRODUCTION

Sugar maple (*Acer saccharum* Marsh.) is a North American tree species native to the United States and Canada. Its natural range extends over most of the Eastern United States and Southeastern Canada. It is one of the largest and most important hardwoods within its range and is most valuable for its beautiful wood, maple syrup and sugar source, shade tree, and aesthetic qualities (Fowells 1965).

The importance of these qualities makes genetic improvement of sugar maple a worthwhile undertaking. However, the relatively slow growth and determinate growth habit of sugar maple seedlings make genetic improvement a very slow process with useful information coming many years into the future. This limitation has hindered the accumulation of information about the amounts and geographic distribution of variation.

Sugar maple is a particularly difficult species to induce to grow continuously. It generally grows for only about 8 weeks and sets a resting bud that will remain dormant until it has experienced about 2000 hours of chilling (Taylor and Dumbroff 1975). Seedlings express this response even when grown in protective greenhouse environments where there is no apparent stress situation. This presents significant problems for the tree geneticist, breeder, and commercial nurseryman attempting to study or grow sugar maple. This problem is not unique for sugar maple but is also encountered with other valuable hardwood species. Thus, information acquired about its growth control can likely be applied to many other species.

One way of obtaining both earlier genetic evaluation and larger seedlings in a shorter period of time is to implement cultural practices that offer the greatest potential for increasing growth and development. Accelerated-optimal-growth (AOG) is a relatively recent growth concept that applies such cultural practices to produce larger and more vigorous seedlings in a shorter period of time. It incorporates various natural and artificial factors of the growth environment into a system that provides for programmed tree growth (Hanover 1972, 1976, 1977; Logan and Pollard 1976).

Before growth and development of sugar maple seedlings can be successfully accelerated and otherwise regulated, it is necessary to determine how they are affected by various cultural practices during different developmental states. The main objective of this study was to investigate the effects of growth-stimulating factors on growth during both the grand period of growth, i.e., the period of growth and development from bud break to terminal bud formation, and the inductive phase, i.e., the period of cessation of growth during which growth and development may resume under suitable conditions (Samish 1954; Vegis 1964). A second objective was to gain a better understanding of the utility of these factors for genetic evaluation and commercial seedling production.

CHAPTER I

ACCELERATED GROWTH FOR EARLY GENETIC EVALUATION OF SUGAR MAPLE

Abstract

A method is described for accelerating juvenile growth and development of sugar maple (*Acer saccharum* Marsh.) seedlings for early progeny and provenance evaluation and plantation establishment. Outdoor nursery treatments revealed few seedlot differences and no provenance differences at 4 and 16 months of age. In contrast, accelerated seedlings exhibited pronounced seedlot and provenance differences at both ages. Accelerated trees had a 29 and 80% height superiority at 4 and 16 months, respectively. This was due to increased number of nodes and internode length, rather than more growth flushes. Provenance differences in height, date of bud-break, number of nodes, and growth flushes revealed by the accelerated treatment and supplemented by seed characteristics indicate existence of Upper and Lower Peninsula races in Michigan. If long-term observations and correlative analyses of both nursery and accelerated

treatments support these provenance and peninsula differences, then accelerated growth can considerably shorten the time required for genotypic evaluation of sugar maple.

Introduction

Forest tree seedlings used for genetic testing are often produced in outdoor nurseries. Such seedlings are often characterized by slow growth rates and may produce trees of poor quality for establishing genetic plantings. This means that the investigator must either wait several years before seedlings can be planted in test plantations or establish plantations with small and poor quality trees that are susceptible to stress and competition. Assuming trees of acceptable quality are produced, several years must generally elapse before reliable genetic variation patterns can be discerned. Consequently, forest geneticists need methods that accelerate the identification of superior genotypes. The accelerated-optimal-growth (AOG) concept is a practical method that may partially overcome the time limitations imposed by traditional methods and thereby better control seedlings' size and quality and perhaps reduce the time required to identify superior genotypes. AOG is based upon the programmed control of growth by the use of light, temperature, mineral nutrients, water, carbon dioxide, growth-regulating chemicals, container dimensions, etc. (Hanover, 1977, 1976; Hanover et al. 1976).

Applying the AOG concept to greenhouse production of containerized seedlings allows the investigator increased control over growth, development, and physiological status of seedlings. Thus, seedlings can be produced in a few months rather than years. A potential problem with the use of the AOG concept or greenhouse culture for accelerating tree improvement is the effect of growth control factors on either short- or long-term changes in seed source ranking (Faulkner 1967). The objectives of this study were: (a) to determine if such rank changes occur in sugar maple (*Acer saccharum* Marsh.), (b) to compare the magnitude of growth of AOG and nursery-produced seedlings, and (c) to investigate the use of AOG for use in making genetic evaluations.

Materials and Methods

Sugar maple seeds from 12 geographic areas were collected in Michigan's Upper and northern Lower Peninsulas (Figure 1). Three to 10 individual trees were collected from each area for a total of 91 seedlots. Seedlots were kept separate by individual parents for establishment of a half sib-progeny test. When possible, seeds were collected from trees which were average or

FIGURE 1. Location of the areas in Michigan from which sugar maple seeds were collected. Numbers refer to climatic data found in Table 5.

better than others in the stand in form and height. Otherwise, selections were from accessible trees with sufficient seed.

Seeds were air-dried at room temperature to 30% moisture. Seed width, wing width, wing length, and wing angle were measured on random samples from each seedlot. Before sowing, the seeds were stratified 4 months in moist perlite at 3° C. Seeds were then sown in plastic cases containing 5 X 5 X 28 cm polycoated paperboard plant bands filled with a 1:1:1 peat-perlite-topsoil potting mix. Those sown directly in the nursery soil were also spaced at 5 X 5 cm. The experimental design consisted of 6 trees of each seedlot in each of 3 blocks in each of 3 growth environments. The 3 growth treatments consisted of seedlings grown in the ground in the outdoor nursery and in plantbands in both the outdoor nursery and greenhouse. Greenhouse-grown seedlings were exposed to continuous light with the normal dark period being replaced by supplemental light from fluorescent tubes producing 50 $\mu Ecm^{-2}s^{-1}$ at plant level. Moisture and nutrient element levels were maintained near optimum.

Trees were grown in their respective environment for 16 months (including a leafless dormancy interruption of 5 months). After the first frost all trees were exposed to natural photoperiod and temperatures. Shortly after budbreak the AOG trees were again exposed to continuous light and warm temperatures in the greenhouse environment. Therefore, length of growing season was essentially identical for the greenhouse and nursery treatments. At the end of the growth periods, measurements were made of height, budbreak, internode length, node number, and number of growth flushes.

Results and Discussion

Production Methods

After all treatments had grown 4 months (first growing season) AOG seedlings were 29% taller than those grown outside (Table 1). There was no difference between the outdoor nursery treatments. By the end of the first growing season, nursery grown trees exhibited few seedlot differences and no provenance differences. However, it was possible to discern pronounced seedlot and provenance differences in AOG trees. After the second season, AOG trees were 80% taller than nursery trees (Table 1, Figure 2). Thus, AOG trees not only maintained their height superiority but increased it at an accelerated rate. Again, after 16 months there was no height difference between nursery treatments. After 16 months AOG seedlings averaged 24 to 40% more nodes and averaged internode lengths 29 to 44% greater than nursery treatments. However, there was no increase in the number of flushes in the AOG trees (Table 1).

TABLE 1. Effect of three production methods on mean growth of half-sib sugar maple progeny.

Production Method	Height		Nodes	Flushes	Internode Length
	4 mo.	16 mo.	16 mo.	16 mo.	16 mo.
	cm	cm	Number	Number	cm
Nursery (ground)	7.4 a[1]	13.7 a	2.2 a	1.1 a	6.2 a
Nursery (plant bands)	7.9 a	14.0 a	2.5 a	1.2 a	5.6 a
AOG[2]	10.0 b	25.0 b	3.1 b	1.2 a	8.1 b

[1]Within columns, values followed by the same letter are not significantly different from one another at the 5% level of probability by Duncan's Multiple Range Test.

[2]Accelerated-optimal-growth.

FIGURE 2. Sixteen-month-old sugar maple seedlings grown for 2 periods of 4½ months each under 2 cultural methods. Seedlings on the left were grown in plant bands in an outdoor nursery, while those on the right were grown in plant bands under accelerated-optimal-growth (AOG) conditions. Seedlings represent the tallest of the 2 treatments.

FIGURE 2

Second season growth characteristics of AOG trees were significantly correlated with first season characteristics only for the following variables (second season characteristics given first): height vs. height, flush number vs. height, node number vs. node number (Table 2). Although statistically significant, all correlations were low. The low correlation between first and second season height for AOG seedlings suggests that subtle environmental interactions are taking place or genotype expression changes with age. Thus, prediction of second season height or any other measured growth characteristic based upon first season height or number of nodes does not appear to be feasible.

Statistical comparison of growth characteristics for nursery-grown trees revealed a few seedlot differences but no provenance or peninsular differences (Table 3). In contrast, AOG trees exhibited seedlot, provenance, and peninsular differences in height, but not in node number or number of flushes. Since there were few seedlot differences in the nursery-grown treatments, it was not possible to determine the influence of the treatments on the change in seedlot ranking.

Variation Patterns

LP seedlings were 10% taller than UP seedlings after one season and 29% taller after two. Second season heights of trees from the eastern UP averaged

TABLE 2. Correlation coefficients between growth characteristics at 4 months of age with those at 16 months for sugar maple seedlings grown by the AOG[1] method.

Characteristics at 4 Months	Characteristics at 16 Months[2]			
	Height	Number Flushes	Number Nodes	Nodes/Flush
	r			
Height	0.36**	0.40**	0.20	0.18
Number nodes	0.12	0.22	0.47**	0.17

[1]Accelerated-optimal-growth.

[2]df = 82.

**Significant at the 1% level.

TABLE 3. Growth characteristics of sugar maple seedlings from various seed sources in Michigan's Upper and Lower Peninsulas.

Seed Source Comparisons[2]	Accelerated-Optimal-Growth					Nursery[1]			
	Budbreak at 16 mo.	Height at 4 mo.	Height at 16 mo.	Node at 16 mo.	Flush at 16 mo.	Height at 4 mo.	Height at 16 mo.	Node at 16 mo.	Flush at 16 mo.
	Days	cm	cm	Number	Number	cm	cm	Number	Number
Between Peninsulas									
Upper Peninsula	19 a[5]	10 a	24 a	3.1[6]	1.2[6]	8[6]	14[6]	2.5[6]	1.2[6]
Lower Peninsula	21 b	11 b	31 b	3.6	1.2	8	14	2.4	1.2
Within Peninsulas									
Western UP[3]	18 a	9 a	22 a	2.9	1.2	8	14	2.5	1.2
Eastern UP	21 b	10 a	25 b	3.2	1.2	8	14	2.5	1.2
Northern LP[4]	19 a	11 a	31 c	3.6	1.2	8	14	2.4	1.2
Western LP	24 c	11 a	30 c	3.5	1.2	8	14	2.4	1.2

[1]Seedlings grown in plant bands.

[2]Statistical analysis using Students t-test for comparisons of unequal size.

[3]Upper Peninsula.

[4]Lower Peninsula.

[5]Within columns and within "between peninsulas" and "within peninsula" comparisons, means followed by the same letter are not significantly different at the 5% level.

[6]Values in these columns are not significantly different at the 5% level.

11% taller than their western counterparts, while those from the northern LP averaged 24% taller than those from the eastern UP. There was no difference between northern LP and western LP sources. Northern UP sources were 41% taller than western UP sources at 16 months. These height differences were due to differences in internode length since the number of flushes or nodes did not differ with provenance (Table 3). Thus there was no provenance-photoperiod interaction with respect to flush or node number. Budbreak of UP trees was earlier than LP trees. Those from the western UP broke bud 3 days earlier than those from the eastern UP. Seedlings from the northern LP broke bud earlier than those of either the eastern UP or western LP. This observation suggests that northern LP trees may be well adapted for growth in the western UP. Since their growth is greater than those from the western UP, it may be advantageous to use northern LP trees in the western UP when establishing sugar maple plantings in the western UP. Differences in progeny height growth between the two peninsulas and between the eastern and western UP are important to anyone handling seed or seedlings from these sources. The differences in height growth and consequently volume could conceivably affect lumber or fiber yields, assuming the trend holds true for the adult trees.

Height at 16 months was positively correlated with growing season, and with mean annual and mean January temperatures, and negatively correlated with latitude (Table 4). The actual climatic conditions at the locations of the seed sources are presented in Table 5. Mean annual temperature and growing season accounted for 82 and 58%, respectively, of the variation in height growth. These correlations suggest that height growth is an adaption to the temperature and length of growing season under which the parent trees have evolved and is of selective advantage in these environments. Obviously, seedlings which are defoliated prematurely by frost and then reflush or which fail to harden properly will have a lesser chance of survival than seedlings which grow rapidly but cease growth before damaging frost. The number of flushes, number of nodes, and nodes per flush were not correlated with any source variable (Table 4).

Source also affected budbreak with UP seedlings breaking bud an average of 4 days earlier than those from the LP. Budbreak in northern LP trees was earlier than in those from the eastern UP. Western LP trees were much later than any other source. Surprisingly, date of budbreak was not correlated with growing season. However, it was correlated with mean annual temperature and negatively correlated with latitude (Tables 4 and 5). Eighty-two percent of the variation in budbreak could be

TABLE 4. Correlation of characteristics of 16-month-old sugar maple seedlings grown under AOG with environmental variables at the seed source.

Source Variables	df	Date[1] of Budbreak	Height at 16 Months	Number of Flushes	Number of Nodes	Nodes per Flush
		----	----	r	----	----
Length of growing season (days)	5	.66	.76*	.17	.21	-.68
Latitude (degrees)	10	-.65*	-.67*	-.11	-.04	-.25
Mean annual temperature (°C)	3	.91*	.90*	.09	.13	.11
Mean July temperature (°C)	3	.46	.67	.10	.10	.14
Mean January temperature (°C)	5	.69	.75*	.04	.05	.09

[1]Base of measurement was the date the first seedling broke bud.

*Significant at the 5% level of probability.

TABLE 5. Climatic variables at seed source locations.

Climatic Variables	Seed Source Locations											
	Western Upper Peninsula				Eastern Upper Peninsula				Northern Lower Peninsula		Western Lower Peninsula	
	1	2	3	4	5	6	7	8	9	10	11	12
Length of growing season (days)	120	140	120	90	140	130	135	130	130	130	150	160
Latitude (minutes)[1]	207	242	206	186	159	188	211	205	160	154	56	48
Mean annual temperature (°C)	40	42	40	41	43	42	41	41	43	43	47	47
Mean July temperature (°C)	66	66	67	66	67	66	63	65	67	66	70	70
Mean January temperature (°C)	17	17	14	14	18	18	18	14	20	19	24	25

[1]Latitude equals 43°00' plus minutes listed in the table.

attributed to mean annual temperature. The correlation coefficient between length of growing season and mean annual temperature was 0.93. The lack of correlation of budbreak with growing season may be partially due to limited numbers of observations. Trees evolving in areas of high mean annual temperature are probably exposed to a relatively long and warm growing season. This suggests that early flushing of buds is characteristic of trees from environments where mean annual temperature is low. Seedlings adapted to regions with short growing seasons tend to flush early and, thus, capitalize on suitable growing conditions. The observation that UP trees broke bud 4 days earlier than those from the LP suggests that this is an important long-term survival mechanism, especially when they are naturally relatively slow growing due to the probable trade-off of growth rate for cold hardiness.

Certain sugar maple seed characteristics also exhibit within and between peninsula differences (Table 6). Seeds collected from the UP had wings closer together, and with greater wing length and width than LP seedlings from the western LP. Those from the western UP had smaller wing angles but shorter wing length and width than those from the eastern UP. Sources from the northern LP had a greater wing angle and smaller wing width than those from the western LP. Seed width did not differ with sources (Table 6).

TABLE 6. Comparisons of characteristics of sugar maple seed collected from parents growing in Michigan's Upper and Lower Peninsulas.

Seed Source Comparisons[1]	Seed Characteristics			
	Wing Angle	Wing Length	Wing Width	Seed Width
	Degrees	mm	mm	mm
Between Peninsulas				
Upper Peninsula	17 b[2]	22 b	9 b	16 a
Lower Peninsula	24 a	19 a	7 a	15 a
Within Peninsulas				
Western UP[3]	13 c	22 b	8 c	16 a
Eastern UP	21 b	30 c	9 d	15 a
Northern LP[4]	19 b	20 ab	7 b	15 a
Western LP	32 a	18 a	6 a	15 a

[1]Statistical analysis using Student's t-test for comparisons of unequal size.

[2]Within columns and within "between peninsula" and "within peninsula" comparisons, means followed by the same letter are not significantly different at the 5% level of probability.

[3]Upper Peninsula

[4]Lower Peninsula

Seed characteristics were correlated with environmental variables (Table 7). Wing angle was not significantly correlated with any parameter, though within and between peninsula differences were evident. Wing length and width were strongly correlated (negatively) with mean July temperature, which accounted for 97 and 81% of the variation in wing length and width, respectively. Thus, high temperatures during seed development may cause a reduction in length and width of the wings. Mean July temperature was not associated with differences in seed width or wing angle, and no seed characteristic was correlated with growing season or mean annual temperature. These patterns of variation show no clear adaptive advantage of the seed characteristics with respect to their source environments.

The contrast between growth and seed characteristics of parents and seedlings from Michigan's two peninsulas suggests the existence of different races of sugar maple. Similar results have been observed by Wright (1972) for several conifer species. He reasoned that the peninsula differences are due primarily to differences in climatic selection pressures and the range gap between peninsulas. The UP has generally lower seasonal temperatures, shorter growing season, and different photoperiods. These factors may act individually or interact in a subtle manner such that they effect the fitness of sugar

TABLE 7. Correlations between characteristics of sugar maple seed collected from parents growing in Michigan's Upper and Lower Peninsulas and several source variables.

Source Variables	df	Seed Characteristics			
		Wing Angle	Wing Length	Wing Width	Seed Width
		Degrees	mm	mm	mm
		----------------r----------------			
Length of growing season (days)	5	-.32	-.47	-.53	-.73
Latitude (degrees)	10	.24	.78**	.46	.69**
Mean annual temperature (°C)	3	-.71	-.81	-.78	-.87
Mean July temperature (°C)	3	-.68	-.98**	-.90*	-.48
Mean January temperature (°C)	5	-.09	.76*	-.73	-.86*

*/** Significant at 5 and 1% levels, respectively.

maple. This difference in selection pressure has been operating since the glaciers retreated from the region. Consequently, trees in the UP should be more cold hardy than those in the LP. Because cold hardiness and growth rate are generally negatively correlated, UP trees might be expected to grow more slowly. This was indeed what was observed. Perhaps this accounts for the observation of less growth and earlier budbreak for western UP vs. eastern UP and UP vs. LP trees.

The range gap between the two peninsulas created by the Straits of Mackinac is about 4 miles from the tree line on each peninsula. Since sugar maple is primarily bee pollinated (Kirbel and Gabriel 1969), the vast majority of sugar maple seed falls within a relatively short distance of the source (Wright 1976). Gene flow is greatly inhibited by this small range gap. The only natural avenues open for gene flow from the LP into the UP are around Lake Michigan via Wisconsin and around Lake Huron via Ontario. Both routes are several hundred miles long. Thus, distance in a continuous range can also act as an isolating mechanism. The combination of distance, range gap, and different selection pressures may have facilitated the development of distinct races between the two peninsulas.

When the observation of peninsula differences in growth characteristics, correlation of these growth characteristics with environmental factors at the source of origin, seed differences between peninsulas, differences in selection pressure, and the barrier to gene flow are evaluated collectively, then there seems to be good evidence that distinct races exist between peninsulas. This will be determined by evaluation of AOG and nursery-produced seedlings upon outplanting. If confirmed, then the use of AOG for early genetic evaluation would have considerably reduced the time required to make meaningful genetic evaluations. This study provides evidence that it is possible to extract meaningful and representative genetic information from certain provenance or progeny test grown for a relatively short time under growth accelerating conditions. Consequently, accelerated growth techniques seem to have potential as tools for early genetic evaluations of forest tree species.

CHAPTER II

GROWTH-REGULATING CHEMICALS FOR ACCELERATING SUGAR MAPLE SEEDLING GROWTH

Abstract

The possibility that growth regulators might be used to accelerate and/or manipulate growth and development of sugar maple (*Acer saccharum* Marsh.) was investigated. Repeated foliar sprays of gibberellins (GA_3, GA_{4+7}, GA_7) greatly increased stem elongation at all concentrations and slightly increased total dry weight at low concentrations. They increased internode length and leaf numbers and reduced root growth, thereby decreasing the root:shoot ratio. GA_7 and GA_{4+7} were more effective than was GA_3. Benzyladenine (BA) increased dry weight of both root and shoot at low concentrations and inhibited stem elongation at all concentrations tested. At high concentrations, BA inhibited both root and shoot growth. The root:shoot ratio increased with increasing BA concentrations. Response to GA varied with seed source. Seedlings grew more under continuous light than under natural photoperiod. The GA growth effect was more pronounced under continuous light.

After 2 months of inactivity, resting buds were easily induced to grow by a single drop of GA_7 or GA_3 solution. BA had no effect on budbreak and indole-3-acetic acid (IAA) was only slightly effective. At 4 and 6 months no hormone treatment could induce budbreak, but complete defoliation was 100% effective at all three times. Leaving a single leaf on the seedling completely inhibited budbreak. The new growth produced after GA-induced budbreak consisted of more and longer internodes than did that after defoliation-induced budbreak.

The results indicate that exogenous applications of BA and certain GAs provide a method for controlling growth and development of sugar maple seedlings.

Introduction

Accelerated-optimal-growth (AOG) is a relatively recent cultural system developed for controlling seedling growth by varying the environmental conditions in which a seedling is grown. These components may include light, temperature, mineral nutrients, carbon dioxide, growth-regulating chemicals, etc. (Hanover 1976, 1977; Hanover et al. 1976). Incorporation of the AOG concept with greenhouse production of containerized seedling systems allows acceleration of growth and development of tree seedlings, resulting in a larger product in a much shorter period of time. Large seedlings can often be produced in months rather than years.

AOG implies use of a growing cycle that produces seedlings of desired size and physiological status for outplanting at a predetermined time. Before such a cycle can be efficiently and/or successfully implemented, it is important to know how to control height growth and especially bud dormancy. Seedlings of several tree species exhibit a relatively strong determinate growth habit under AOG conditions. They typically exhibit one or two flushes of terminal growth followed by formation of a resting bud while environmental conditions are still favorable for continued growth. At this time, height growth will usually not resume until the resting bud has been exposed to a prolonged cold treatment. Sugar maple (*Acer saccharum* Marsh.) exhibits such behavior. Once it has formed a resting bud, approximately 2000 hours of cold chilling are required to induce budbreak. The ability to delay budset and thus produce large seedlings in a short period of time requires a knowledge of the factors regulating this determinate growth habit. One method of regulating meristematic activity is to apply growth regulators (Wareing and Phillips 1970). Our purpose was to determine if growth of sugar maple seedlings could be controlled by application of chemical growth regulators and/or by defoliation.

Materials and Methods

Sugar maple seed for the following experiments were collected from Michigan sources and kept separate by seedlot. Seeds were air-dried at room temperature to about 30% moisture and stratified in moist perlite for 4 months at 3° C. Germinated seedlings were sown in 5 X 5 X 28 cm polycoated paper plant bands contained in plastic cases and filled with a peat-topsoil (1:1) potting mix. Seedlings were grown in a greenhouse under natural daylight plus 100 $\mu Ecm^{-2}s^{-1}$ of continuous fluorescent light during the normal dark period, unless otherwise stated.

Experiment 1. To investigate the potential for controlling growth with plant hormones, seedlings were treated at 12 weekly intervals with foliar sprays of GA_3, a GA_{4+7} mixture (donated by Abbot Labs, Chicago; sample was predominately GA_7), or N-6-benzyladenine (BA). Growth regulators were dissolved in 95% ethanol and applied at 0, 150, 300, 600, and 1200 ppm in a water solution with 0.1% Tween-80. Seedlings were grown under both natural and continuous photoperiods to determine the effects of photoperiod and photoperiod-chemical interaction upon growth and budbreak. Treatments included 2 photoperiods, 3 hormones, and 5 concentrations of each hormone, and in a factorial arrangement of 30 treatments. Six trees of each of 5 seedlots were used per treatment. Hormone treatments began 6 weeks after planting, and growth was recorded weekly for 12 weeks and dry weight was determined at the end of 12 weeks.

Experiment 2. To compare the effectiveness of GA_3 and GA_7 in accelerating growth, seedlings were sown in a randomized complete block design with 3 replicates of GA_3 and GA_7 were applied as 6 weekly foliar sprays at 0, 50, 100, 200, and 400 ppm in a water solution with 95% ethanol and 0.1% Tween-80 6 weeks after planting and at weekly intervals thereafter. Plot means were derived from measurements of 36 trees. At age 14 weeks, height, component dry weight, and leaf area were measured.

Experiment 3. A third experiment was designed to determine if bud dormancy could be broken either by hormone application or defoliation and to determine if effectiveness varied with time of treatment. Experimental design was 4 randomized complete blocks of 11 treatments times 3 stages of development, using 24 trees per treatment per stage. Treatments were GA_7, GA_3, BA, IAA (0, 400, and 800 ppm), complete defoliation, and both ethanol-treated and nontreated controls. Hormones were dissolved in 95% ethanol and applied as a single drop to the terminal bud. One-year-old seedlings were treated 2, 3, or 4 months after budset. Both time of budbreak and growth in height were recorded.

Experiment 4. To determine the degree to which leaves control budbreak, 1-year-old trees with 3 foliated nodes, which had set buds 2 months earlier, were partially or wholly defoliated. Eight (Figure 1) defoliation treatments were applied in a randomized complete block design with 3 blocks. Six trees were used per treatment per block and budbreak was recorded.

Results and Discussion

Experiment 1. Effects of hormone treatment. Treatment of sugar maple with GA_3 and GA_{4+7} greatly accelerated height growth, response increasing with increasing GA concentration for seedlings grown in both natural and continuous photoperiods (Figure 2). GA_{4+7} was generally more effective than GA_3. In contrast, BA inhibited growth slightly, as previously reported (Fox 1964). Seedlings treated with concentrations of GA greater than 300 ppm were very spindly and had small leaves, while those treated with BA were short and stocky. Seedlings grown under continuous light were taller than similarly treated seedlings under natural light in almost all cases.

The distribution and accumulation of total and component dry weights were very different for GA vs. BA treated seedlings. GAs increased total dry weight at slightly low concentrations, but not at high levels (Figure 3). GA_{4+7} was more effective at low levels

FIGURE 1. Defoliation treatments used to determine effects of defoliation on budbreak of sugar maple seedlings. Vertical line represents seedling stem and horizontal lines represent leaves remaining after pruning.

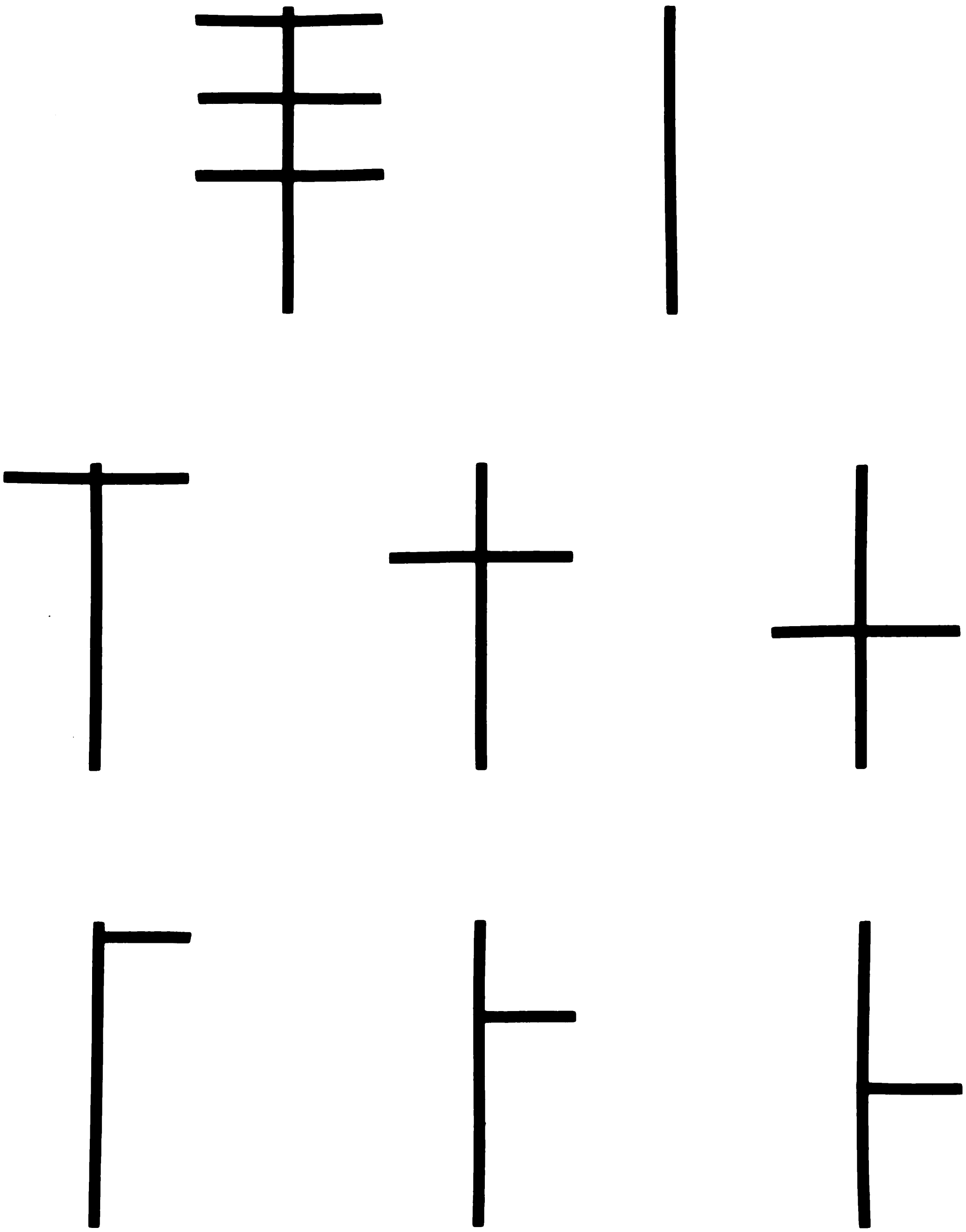


FIGURE 1

FIGURE 2. Growth response of sugar maple seedlings to hormone and photoperiodic treatments. Vertical lines equal the standard error of the mean.

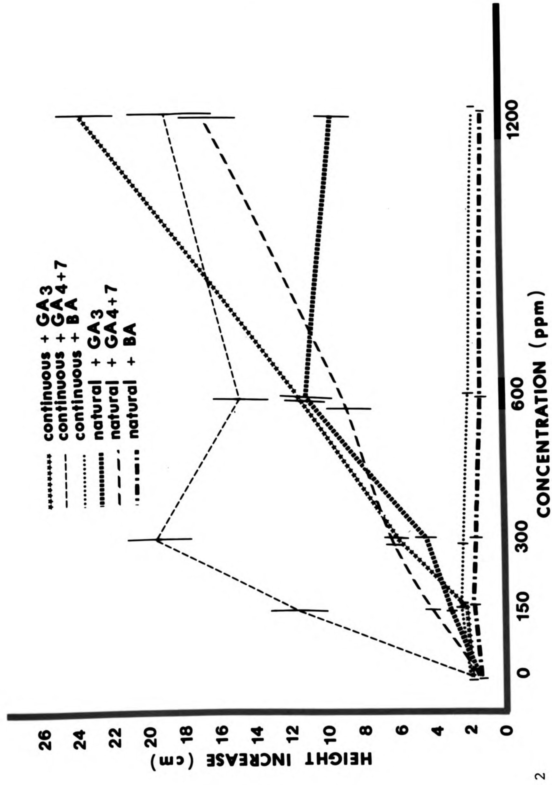
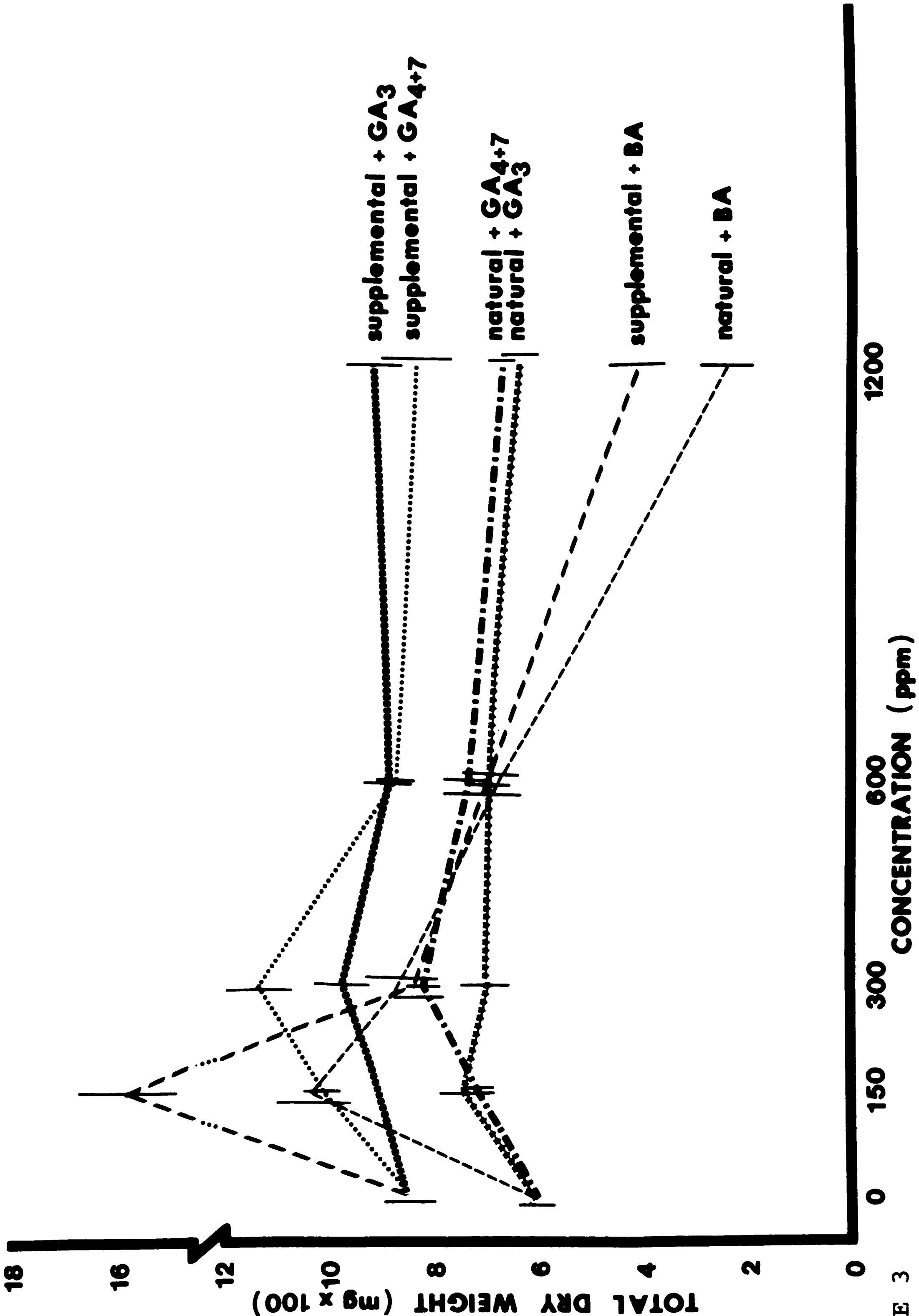

continuous + GA 3
continuous + GA 4+7
continuous + BA
natural + GA 3
natural + GA 4+7
natural + BA
HEIGHT INCREASE (cm)
CONCENTRATION (ppm)
0
150
300
600
1200
0
2
4
6
8
10
12
14
16
18
20
22
24
26

FIGURE 2

FIGURE 3. Effects of hormone and photoperiod treatments on total dry weight accumulation of sugar maple seedlings. Vertical lines equal the standard error of the mean.



TOTAL DRY WEIGHT (mg x 100)
18
16
12
10
8
6
4
2
0
CONCENTRATION (ppm)
0
150
300
600
1200
supplemental + GA_3
supplemental + GA_{4+7}
natural + GA_{4+7}
natural + GA_3
supplemental + BA
natural + BA

FIGURE 3

under both photoperiods than was GA_3, suggesting that GA_7 may be the active GA in sugar maple stem elongation. BA greatly increased dry weight at 150 ppm but strongly decreased it at higher concentrations under both photoperiods. The increase was due to increased root and shoot dry weights (Figure 4). GA_{4+7} and GA_3 increased only shoot dry weight (Figure 4). Root:shoot ratios for the 2 GA treatments generally decreased with increasing concentration, indicating an alteration of the normal distribution of photosynthate (Figure 5). In contrast, the root:shoot ratio of BA-treated seedlings increased with increasing concentrations due to an inhibition of root growth, rather than to a redistribution of photosynthate. This inhibitory effect of cytokinins on root growth has been observed for other species (Gaspar and Xhauffaire 1967).

Significant interactions between seedlot and gibberellin concentration were evident, with certain seedlots being much more responsive to GA than were others. Some seedlings grew very rapidly, then the upper portion of the shoot died. These seedlot interactions could be due to either differences in sensitivity or to differences in the seedlings' ability to absorb and translocate the exogenously applied GAs. No such interactions were observed with BA.

FIGURE 4. Dry weight distribution of sugar maple seedlings treated with various hormones and photoperiods. (A) Gibberellin A_{4+7} (B) Gibberellin A_3 (C) N-6-Benzyladenine. Photoperiods consist of natural and continuous consisting of natural plus fluorescent light during the natural dark period. Vertical lines equal the standard error of the mean.

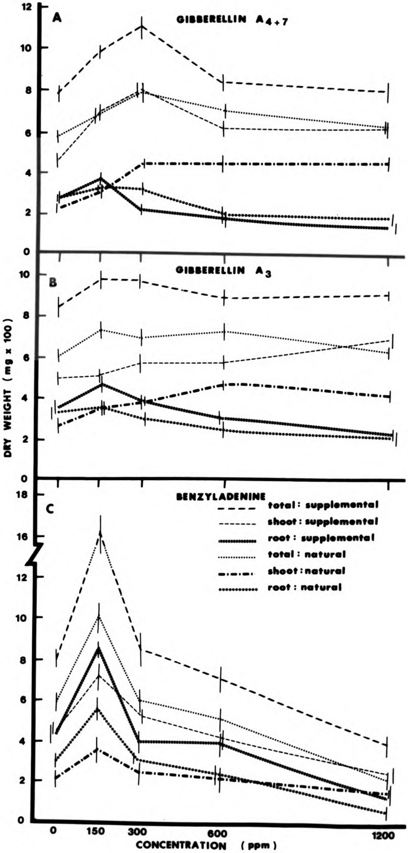

A
GIBBERELLIN A_{4+7}
B
GIBBERELLIN A_3
C
BENZYLADENINE
total : supplemental
shoot : supplemental
root : supplemental
total : natural
shoot : natural
root : natural
DRY WEIGHT (mg x 100)
CONCENTRATION (ppm)
0
150
300
600
1200

FIGURE 4

FIGURE 5. Effects of various hormone and photoperiod treatments on the root:shoot ratio of sugar maple seedlings. Vertical lines equal the standard error of the mean.

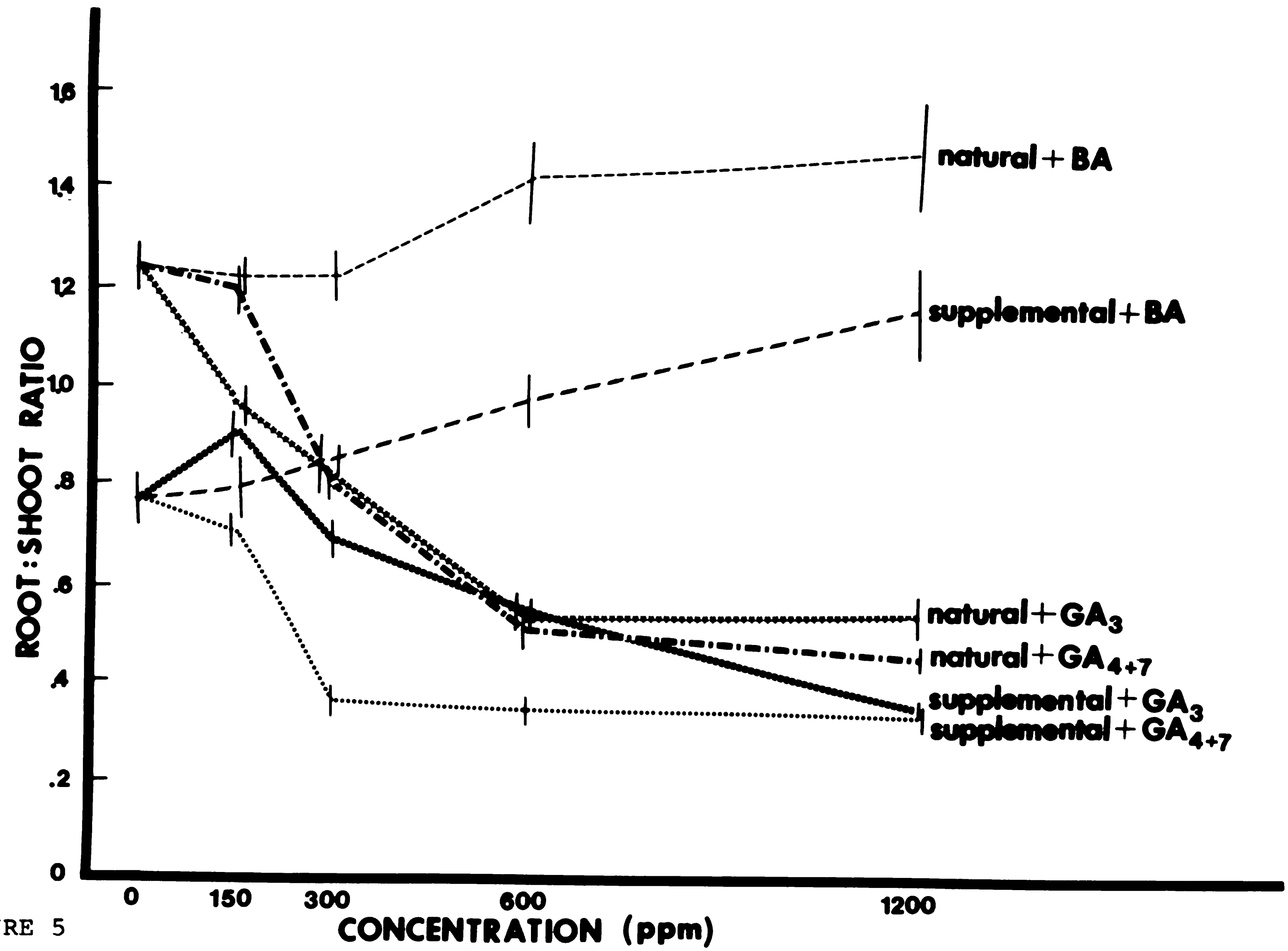

ROOT:SHOOT RATIO
1.6
1.4
1.2
1.0
.8
.6
.4
.2
0
0
150
300
600
1200
CONCENTRATION (ppm)
natural + BA
supplemental + BA
natural + GA_3
natural + GA_{4+7}
supplemental + GA_3
supplemental + GA_{4+7}

FIGURE 5

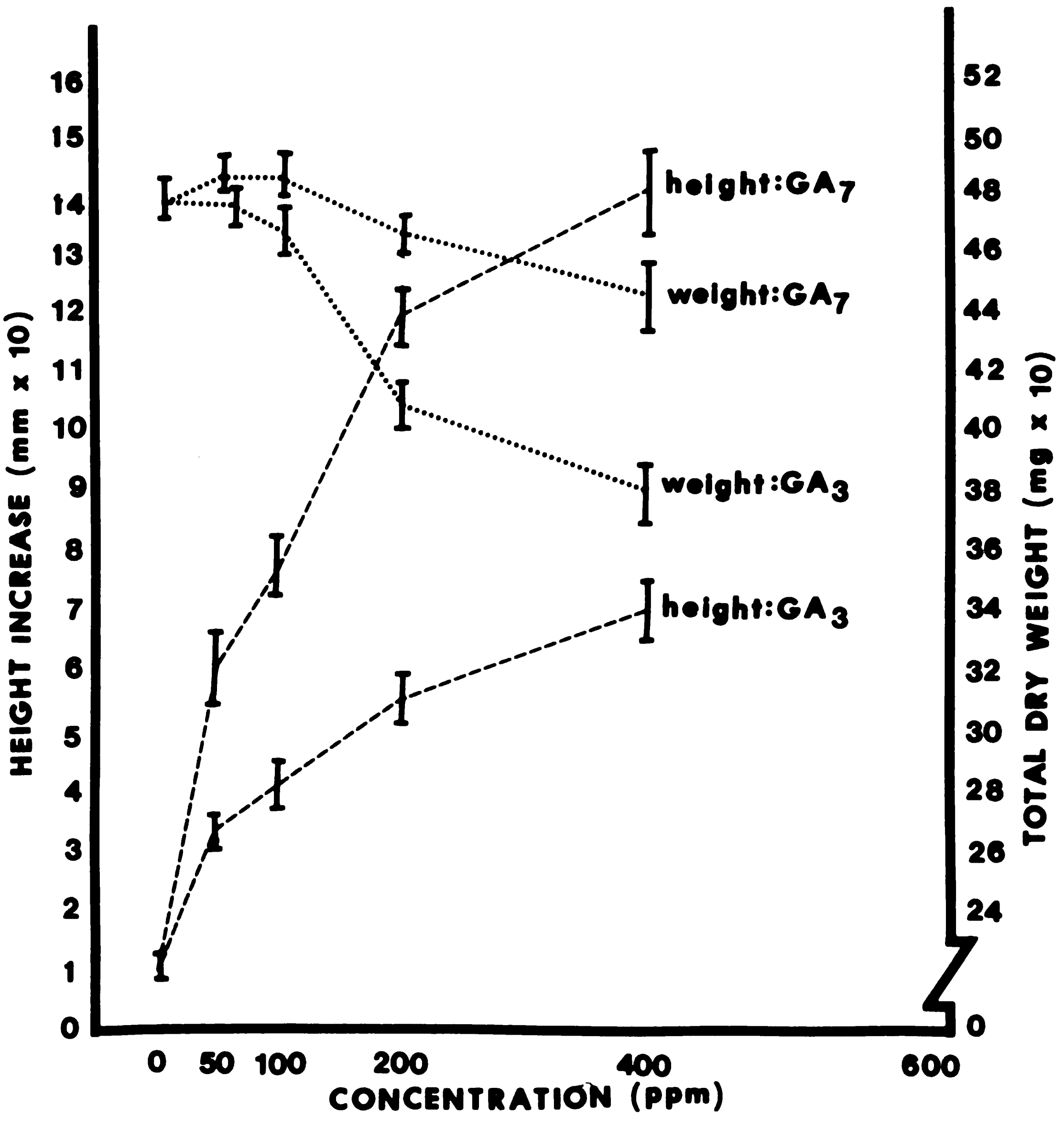
The results indicate that the gibberellines and BA can be of practical value in manipulating growth of seedlings when they are used at the proper concentrations. They can be especially useful for manipulating the root: shoot ratio of seedlings. Seedlot-GA concentration interactions indicate that these hormones must be used with caution, otherwise growth of some seedlots can be adversely affected.

Experiment 2. Comparative effectiveness of GA_3 vs. GA_7. Experiment 1 indicated that GA_{4+7} increased shoot growth rate and dry weight accumulation more than GA_3. The trees treated with GA_{4+7} and GA_3 were generally too spindly for good survival and growth after outplanting due to frequent spray with high GA concentrations. Experiment 2 was an attempt to accelerate both height and weight growth of seedlings by treating with optimal concentrations and to determine which GA was more effective.

All GA treatments greatly increased height, and GA_7 was twice as effective as GA_3 at each concentration (Figure 6). The effect of GA was due to an increase in both number of nodes and internode length. The differences between GA types and concentrations were due to increases in internode length.

Dry weight did not parallel height in GA treatments. Total seedling dry weight generally decreased

FIGURE 6. Comparisons between GA_7 and GA_3 with respect to height increase and dry weight of sugar maple seedlings. Vertical lines equal the standard error of the mean.



16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
HEIGHT INCREASE (mm x 10)
52
50
48
46
44
42
40
38
36
34
32
30
28
26
24
0
TOTAL DRY WEIGHT (mg x 10)
height:GA7
weight:GA7
weight:GA3
height:GA3
0
50
100
200
400
600
CONCENTRATION (ppm)

FIGURE 6

as GA concentration increased. Trees treated with GA_7 were taller and had a greater dry weight than those treated with GA_3. Dry weights did not differ from the control at concentrations of 100 ppm and 200 ppm or lower for GA_3 and GA_7, respectively. Thus, a 3-fold increase in height was obtained by treatment with GA_3 without decreasing total dry weight, while a 12-fold increase was possible with GA_7. This suggests that gibberellins can be very useful for accelerating tree growth and that the degree of response is dependent upon type of GA. The difference in response between GA_7 and GA_3 suggests that GA_7 may naturally occur in sugar maple or that GA_7 is readily metabolized to the endogenous GA.

Root dry weight generally decreased with increasing GA concentration (Figure 7). Although GA_7 increased shoot weight at all concentrations, GA_3 decreased it at concentrations above 100 ppm. The root:shoot ratio generally decreased for both hormones but the decrease was greater with GA_3. Thus, the GAs alter the normal distribution of photosynthate. GA_3 alters distribution of photosynthates in various species (Little and Loach 1975), but this experiment shows that GA_3 is not nearly as effective as GA_7.

Both GAs increased leaf area and number (Figure 8). GA_7 more effectively increased leaf area than did GA_3, but there was no difference in leaf number except at the

FIGURE 7. Component dry weights and root:shoot ratio of sugar maple seedlings treated with GA_7 and GA_3. Vertical lines equal the standard error of the mean.

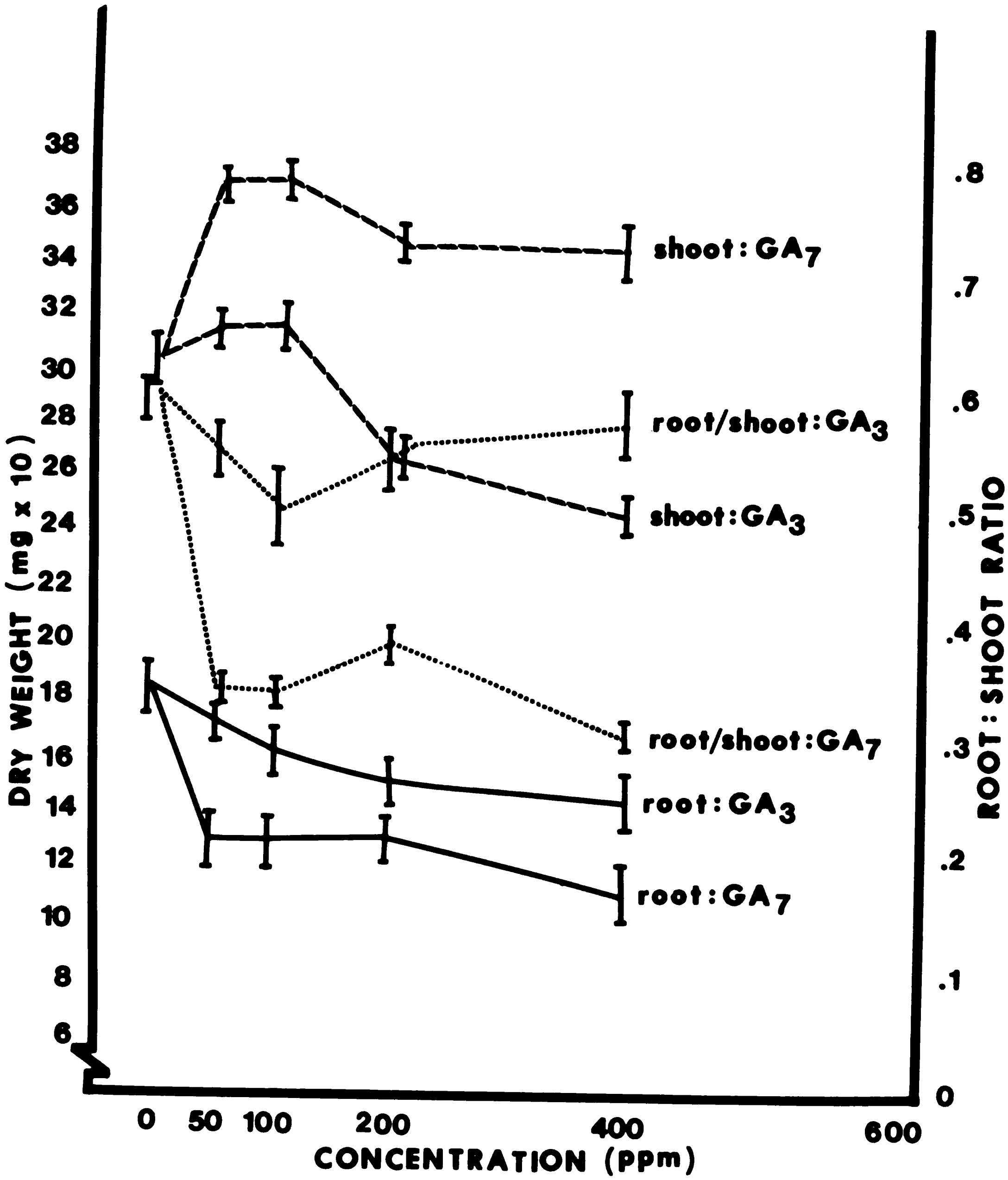
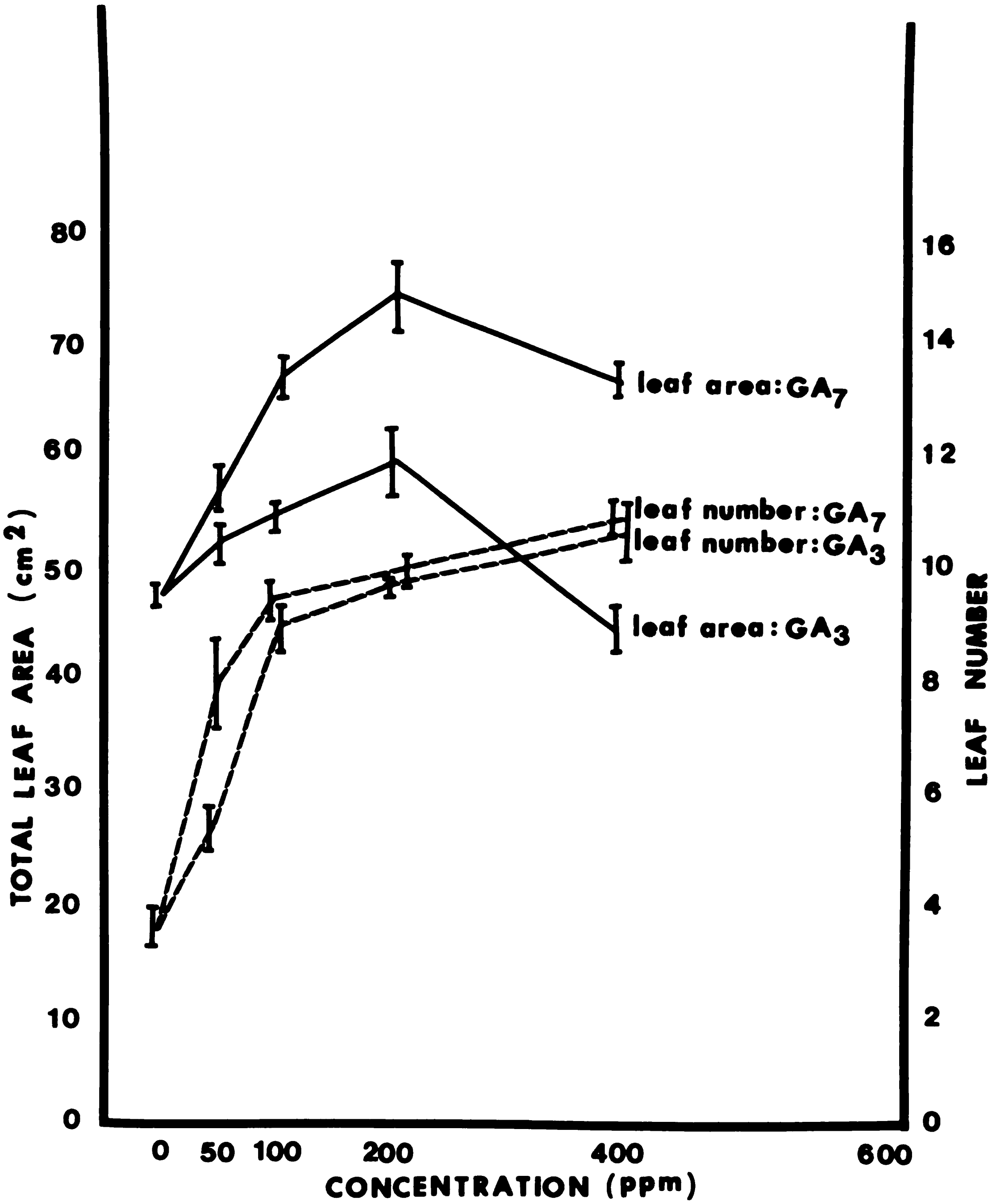

38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
DRY WEIGHT (mg x 10)
.8
.7
.6
.5
.4
.3
.2
.1
0
ROOT: SHOOT RATIO
shoot: GA7
root/shoot: GA3
shoot: GA3
root/shoot: GA7
root: GA3
root: GA7
0
50
100
200
400
600
CONCENTRATION (ppm)

FIGURE 7

FIGURE 8. Relative effects of GA_7 and GA_3 treatments on total leaf area and leaf number of sugar maple seedlings. Vertical lines equal the standard error of the mean.



80
70
60
50
40
30
20
10
0
TOTAL LEAF AREA (cm²)
16
14
12
10
8
6
4
2
0
LEAF NUMBER
leaf area: GA_7
leaf number: GA_7
leaf number: GA_3
leaf area: GA_3
0
50
100
200
400
600
CONCENTRATION (ppm)

FIGURE 8

50 ppm levels. The difference in leaf area probably accounts for the large differences in shoot and root dry weights. GA_3 appears to inhibit leaf expansion, thus decreasing average leaf area and the amount of total photosynthate produced by the seedling.

These growth responses generally agree with those previously reported (Little and Loach 1975; Einspahr and van Buijtenen 1961; Roberts et al. 1963; Bachelard 1968). They are generally unfavorable for survival except under protective conditions; however, biweekly treatments with GA_7 at 100 ppm might greatly increase sugar maple height without decreasing total, root, or stem dry weight. This could be very beneficial in accelerating tree growth.

Experiment 3. Effects of hormones and defoliation on budbreak. Budbreak was stimulated by topical application of hormones to the terminal bud and by complete defoliation (Table 1). After 2 months in rest, terminal buds were induced to flush by all 4 GA treatments by high IAA levels and by defoliation. Both GA_7 and GA_3 were far more effective than IAA, but not as effective as defoliation. Response to GA was not concentration-dependent, 400 ppm being adequate to induce budbreak. Seedlings broke bud about 2 weeks after GA and IAA treatments, but only 1 week after defoliation. The data support the results of other investigators (Pharis and Kuo 1977) in suggesting that both GA_7 and GA_3 are capable

TABLE 1. Effects of defoliation and hormone applications to buds on budbreak in sugar maple seedlings experiencing budset for different periods of time.

Treatment and Concentration (ppm)	Percentage of Seedlings Breaking Bud after Period Indicated		
	2 months	4 months	6 months
GA_7			
800	95 c[1]	0	0
400	90 c	0	0
GA_3			
800	85 c	0	0
400	80 c	0	0
BA			
800	0 a	0	0
400	0 a	0	0
IAA			
800	20 b	0	0
400	0 a	0	0
Defoliated	100 d	100	100
Foliated	0 a	0	0
Foliated + ethanol	0 a	0	0

[1]Values within a column followed by the same letter are not significantly different at the 5% level.

of either directly or indirectly regulating bud dormancy. GA_7 was somewhat more active than GA_3. Perhaps GA_7 is absorbed and translocated by the bud more readily than GA_3. Alternatively, GA_7 could be the natural promoter or it may be metabolically closer to the promoter than GA_3. Since the GAs were applied exogenously, the data do not provide conclusive evidence that GAs regulate bud dormancy of sugar maple directly. However, these compounds are at least indirectly involved and this regulatory potential can be used as a cultural treatment for regulating shoot growth, thus becoming a practical component of the AOG concept (Hanover 1976).

A limitation to the use of hormones for controlling bud dormancy is that the time of treatment is crucial. None of the hormones were able to induce budbreak 4 to 6 months after budset (Table 1), while defoliation was completely effective at all times. The amount of gibberellin reaching the apex may be insufficient of the bud's requirements for budbreak may have changed.

The growth response of seedlings whose buds were treated with GAs 2 months after budset was about 4 times (29mm vs. 115mm) as great as the response of similar seedlings which were defoliated (Table 2). There was no difference between GAs or concentrations. The new growth flush induced by the GAs contained slightly more nodes than did growth induced by defoliation. New shoot growth

TABLE 2. The effects of defoliation and application of GA_7 and GA_3 to buds on growth following budbreak.

Treatments	Increase in Height (mm)	Increase in Node Number
GA_7		
800 ppm	136 b[1]	3.6 b
400 ppm	111 b	3.6 b
GA_3		
800 ppm	91 b	3.7 b
400 ppm	120 b	3.9 b
Defoliated	29 a	3.0 a

[1]Values within a column followed by the same letter are not significantly different at the 5% level.

appeared completely normal with the exception of differences in leaf morphology. Etiolation was not apparent as was the case following repeated foliar application. Shoots appeared strong and with normal diameters. Leaves were well developed but appeared to differ slightly in morphology, with greater length:width ratios.

The dramatic difference in stem growth between GA and defoliation treatments means that GA induced a major redistribution of photosynthate relative to defoliation. This may be evidence of the ability of GAs to mobilize organic substrates to the new shoot. Enhancement of mobilization by GAs has been reported (Harris et al. 1969; Quinlan and Weaver 1970) and may occur in trees (Pharis and Kuo 1977). The relatively small height increase following defoliation possibly reflects low endogenous GA levels relative to seedlings treated with GAs.

The limited growth of defoliated seedlings possibly represents a survival mechanism. A seedling that utilizes most of its stored photosynthate in reflushing after defoliation in the latter part of summer could expect to be at a selective disadvantage because an early frost or lack of sufficient stored photosynthate for vigorous spring growth could result in death. On the other hand, if the seedling is defoliated relatively early in the growing season, it may also be at a selective disadvantage if it does not reflush and capitalize on the remaining growing season. Apparently the seedling responds by limited reflushing, and perhaps low GA levels are the key to this behavior. A seedling growing under AOG conditions does not need this conservative mechanism. Consequently, manipulating seedling growth with GAs should be useful, especially with species such as sugar maple which exhibit a relatively strong determinate growth pattern and naturally require a long exposure to cold temperatures for release of bud dormancy.

Experiment 4. Effects of partial defoliation on budbreak. The observation that total defoliation of seedlings induces budbreak raises questions as to the degree of defoliation necessary to obtain this response and whether specific leaves are controlling the response. Only complete defoliation induced budbreak (Table 3), the presence of a single leaf at any position on the stem being enough to maintain dormancy. This suggests that the inhibitor(s) produced by the leaves is either active at low levels or is produced in large amounts. The fact that a single leaf prevents budbreak indicates a very conservative growth strategy. Seedlings used in this experiment had set bud 2 months earlier; this relationship may not hold for seedlings which have experienced bud dormancy for less than 2 months. The data show that if height growth of sugar maple seedlings is to be controlled by defoliation, all leaves must be removed.

TABLE 3. Effects of degree of defoliation on budbreak of sugar maple seedlings.

Defoliation Treatments (Leaves Removed)	Seedlings Breaking Bud (Percentage)
None	0
All	100
Top two leaves	0
Single top leaf	0
Lower two leaves	0
Single lower leaf	0
Middle two leaves	0
Single middle leaf	0

CHAPTER III

A HYDROPONIC SYSTEM FOR STUDYING ROOT GROWTH OF SUGAR MAPLE SEEDLINGS

Abstract

Sugar maple (*Acer saccharum* Marsh.) seedlings were grown in an irrigation-type hydroponic system to determine the effects of photoperiod (natural vs. continuous) and gibberellin (GA_7) treatment (0 vs. 200 ppm) on root and shoot growth. The system allowed for well-developed and apparently normal root growth and development. Continuous light did not affect root number or growth rates. Application of GA_7 to shoots reduced growth of secondary roots and number of secondary and secondary roots, while not affecting tap root growth. Supplemental photoperiod and GA_7 increased incidence of budbreak and shoot growth. Caution must be observed in using GA_7 for regulating shoot growth because root growth and development can be greatly altered.

Introduction

Even though roots are an essential plant organ, relatively little is known about their growth and development. The lack of knowledge concerning root physiology, ecology, and genetics is especially true for forest tree species and is primarily due to technical difficulties inherent in the methods used to study root growth. An ability to manipulate the root system by genetic and environmental or cultural means would offer potential for improvement of tree growth and productivity. The root systems of many species are genetically variable (Ledig and Perry 1965; Vose 1962) and are affected by many environmental factors (Tew et al. 1963; Kramer and Kozlowski 1960; Whalley and Cockshull 1976; Lyr and Hoffman 1969). Optimal environmental conditions for root growth is as important for high productivity as are favorable conditions for shoot growth.

Accelerated-optimal-growth (AOG) is a relatively new concept of tree seedling production that utilizes environmental variables for the manipulation and acceleration of seedling shoot and root growth (Hanover 1977, 1976; Hanover et al. 1976). Two important factors of the AOG concept are supplemental light during the night to provide a long day for continuous shoot growth conditions and the use of growth regulators such as the gibberellins on certain species for control of bud dormancy. For sugar maple seedlings, both factors are important in the manipulation and acceleration of shoot growth. However, very little is known of their influence on root growth and development. To determine this influence it is desirable to have a relatively homogenous root environment that provides a well-formed and media-free root system that is easily accessible for periodic growth measurements. The purposes of this study were to determine if a modification of the irrigation-type waterculture system developed by De Stigter (1969) could be practical for studying roots of tree seedlings and to determine the relative effects of various photoperiod and gibberellin A_7 shoot treatments on the root system.

Materials and Methods

Hydroponic System

The hydroponic system used in this study is a modification of the versatile irrigation-type system for root-growth studies developed by De Stigter (1969). Our modified system consists of two rows of shallow root trays placed at a 20° angle on greenhouse tables (Figure 1). Trays have removable lids for easy root viewing. Tray bottoms are lined with black nylon cloth which is continuously bathed in a nutrient solution which drips from 0.05 mm diameter tubing at the upper end of the tray. Solution is continuously drained from the bottom of the tray into a 200 liter reservoir. Solution is then pumped to another 200 liter reservoir located above the root trays. Nutrient solution is gravity fed to root trays by dripping from polyvinyl

FIGURE 1. A hydroponic system for growing forest tree seedlings for root observation.

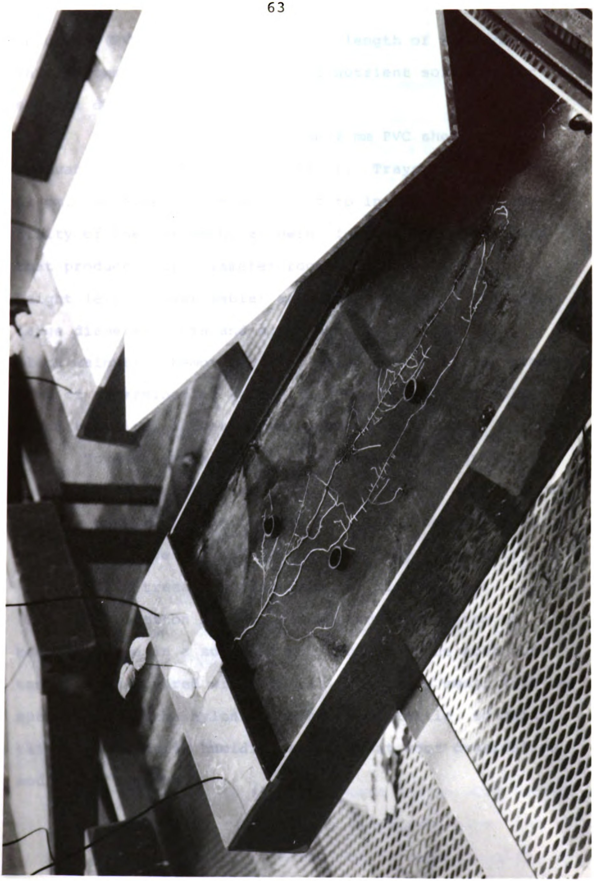


FIGURE 1

chloride (PVC) tubing running the length of the system. This allows for recirculation of nutrient solution for several days.

Root trays are made from 2 mm PVC sheets with removable aluminum lids (Figure 1). Trays are 10 x 30 x 61 cm. A false bottom was found to increase the versatility of the system by allowing for the study of trees that produce small diameter roots and grow slowly in height (e.g., sugar maple) as well as trees that produce large diameter roots and grow rapidly in height (e.g., black walnut). Removal of the false bottom allows placement of a germinating walnut in the system, especially since the first leaves appear several centimeters up the stem. However, with sugar maple, stem height growth is relatively slow during the time of expansion of the first leaves, thus requiring the use of a false bottom to raise the leaves above the lid of the root tray (Figure 1).

When trees are placed in the plant holder (Figure 1), cotton must be packed around the stem to keep the tree in a suitable position, and the root system must be covered with plastic, keeping a small (0.5 cm) space between the nylon cloth and the plastic, to maintain high relative humidity and prevent root dessication and root "humping."

Plant Material and Experimental Design

Sugar maple seed from a single seedlot were air-dried at room temperature to 30% moisture. They were stratified in moist perlite at 3° C for 4 months, then germinated and sown (January 24) in the trays, using 6 trees per treatment. Treatments were natural light, natural light plus gibberellin A_7 (GA_7), continuous light, and continuous light plus GA_7. Supplemental light (100 $\mu Ecm^{-2}s^{-1}$) was provided by fluorescent tubes during the night to provide a continuous photoperiod. GA_7 treatments were applied as a foliar spray at biweekly intervals for 8 weeks beginning at 5 weeks of age. GA_7 was applied at 200 ppm in a water, ethanol, and 0.1% Tween-80 solution. A quarter strength general purpose nutrient solution, pH 5.5-6.0, was supplied. Root and shoot growth and development were monitored by weekly photographs from which measurements of growth were made. The data were analyzed using analysis of variance, and differences among treatment means were evaluated with Duncan's Multiple Range Test.

Results and Discussion

Performance of the Hydroponic System

Root systems in the hydroponic system were better developed than those of equal age greenhouse-grown and one-year-old nursery-grown seedlings (Figure 2), although

FIGURE 2. Comparison of root development of sugar maple seedlings grown 3 months in paper plant containers containing an artificial soil mix, 3 months in an irrigation-type hydroponic system, and 1 year in an outdoor nursery.

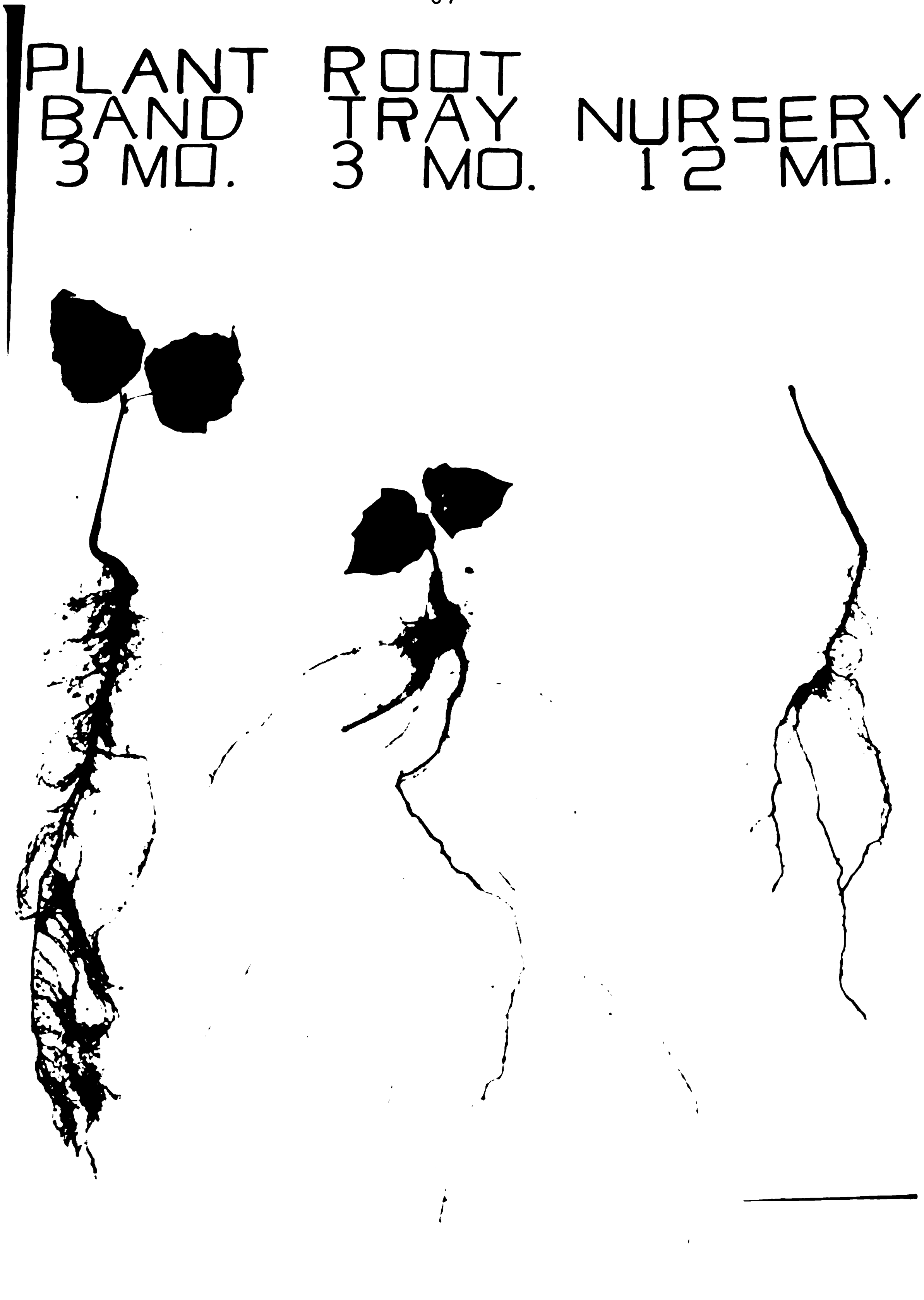


FIGURE 2

root development in greenhouse-grown and hydroponic-grown seedlings were about a third taller than those in root trays. Of particular interest was the observation that one-year-old nursery-grown seedlings had relatively poorly developed root systems with respect to both root length and number. Obviously, the 3 different environments have influenced the intensity and course of root growth. This observation is common when comparing root development between heterogenous root and shoot environments (Lyr and Hoffmann 1969).

Stem height growth followed the pattern often observed for sugar maple seedlings in greenhouse and nursery environments (Figure 3), being most rapid during the first week after germination and ceasing by the fourth week, with formation of a resting bud that will usually not reflush without cold treatment. Root and shoot growth rates were parallel during the first 3 weeks following germination, although root growth was about 50% greater than shoot growth during the first week. This suggests the adaptive importance to a young seedling of establishing a root system capable of supplying support, nutrient elements, and water very soon after germination. Growth in height ceased after 3 to 4 weeks, and primary root (tap root) growth dropped to half the first week's rate. During this time secondary roots were developing, but their growth rate was also decreasing. This general

FIGURE 3. Root and shoot growth rates of sugar maple seedlings grown under a natural photoperiod in a hydroponic system. Week 0 = January 24. Vertical lines equal the standard error of the mean. Primary root equals tap root. Secondary roots refers to the 6 longest secondary roots.

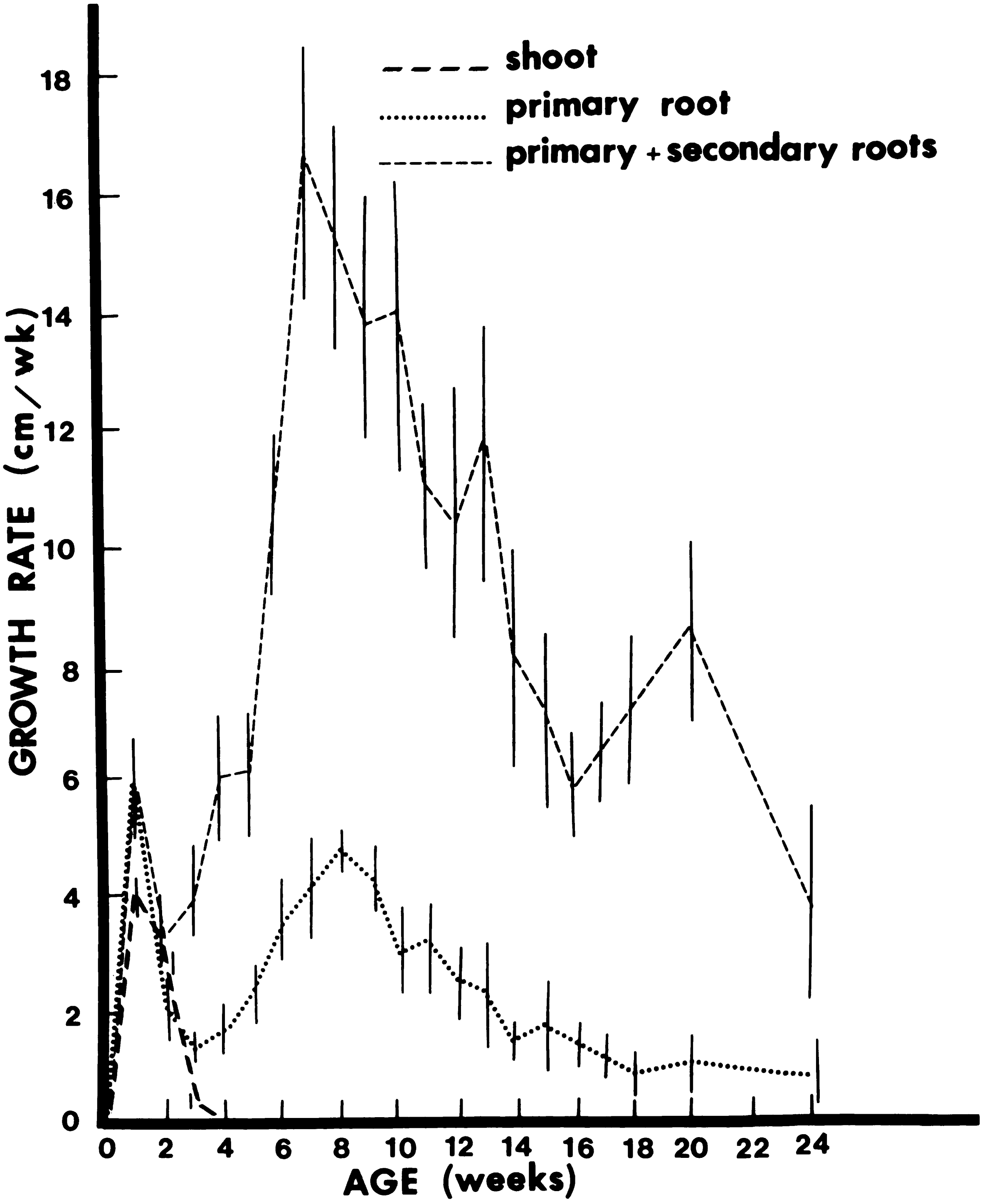

shoot
primary root
primary + secondary roots
GROWTH RATE (cm/wk)
AGE (weeks)
0
2
4
6
8
10
12
14
16
18
20
22
24

FIGURE 3

decline in stem height and root growth rates possibly reflects the transfer of photosynthate to expanding leaves and the thickening stem. The primary root and total root system (primary root plus major secondaries) resumed rapid growth after the third week and continued without declining for 4 additional weeks. During this time, growth rate of the root system was not only much greater than that of the primary root but was accelerating, suggesting that development of the major secondary roots has priority over primary root growth during this stage of seedling development.

After about 8 weeks of age, growth rates of both the primary and the major secondaries declined steadily with intermittent spurts of increased growth (Figure 3). The greater decline in growth rate of major secondaries relative to that of the primary root suggests that primary root growth is more important at this stage of development. After 6 months, mean primary root growth had stabilized at about 1 cm per week. However, primary root growth in some trees had completely ceased by this time, even though leaves were green and apparently photosynthetically active. Perhaps the basal metabolism of the seedling required most of the photosynthate, leaving very little for new growth, or photosynthate was going into root storage products rather than growth. If the latter were true, then longitudinal root growth may not be as important as radial growth at a certain point in development. Roots of trees in temperate latitudes experience a period of rest in winter. The beginning of this period depends upon the species and upon the environment (Lyr and Hoffmann 1969). Rest may be responsible for cessation of root growth, even though the foliage is still apparently actively photosynthesizing.

A second flush of root growth occurred 4 months after germination (Figure 3), corresponding with the natural second flush that most trees experience in autumn (Lyr and Hoffmann 1969). This so-called "autumn" peak occurred in major secondary roots but not in the primary root, suggesting that development of the entire root system is more important than development of only the primary root during this second period of activity.

Shoot and root growth rates resulting from the hydroponic technique paralleled very closely the reported growth pattern exhibited by trees growing under natural environments. This means that the technique probably provides an environment suitable for root growth which is close to that of the outdoor environment, thus allowing experimental manipulation. The hydroponic system is, therefore, useful for studying many aspects of root physiology and genetics since it allows continuous and simultaneous observation or measurement of root growth and development.

Root growth rates indicated correlative reciprocal effects between roots. Certain major secondary roots grew at rates highly correlated with primary root rates, while others did not. Perhaps this reflects a balance in roots just as there is an optimal balance in root/shoot ratios (Kramer and Kozlowski 1960). This is supported by the observation that on several occasions either primary root or major secondary roots would cease growth for several weeks and then resume growth. This renewed growth was often rapid, commonly doubling its length within 2 or 3 weeks.

Secondary roots forming near the base of the primary root during the first 2 or 3 weeks after germination generally did not develop into major secondary roots. They grew very rapidly for 2 or 3 weeks then either ceased growth or died.

Secondary roots were initiated about 1 week after primary root emergence, while tertiary roots about 2 weeks later (Figure 4). Tertiaries did not exceed secondaries until after 20 weeks. After 6 months the major roots had almost ceased growth; however, a very large increase in the number of minor secondaries occurred at this time, resulting with 70% more secondaries than tertiaries. At 6 months of age, seedlings had an average of 341 roots.

There was a large amount of variation in root morphology between seedlings. The root system ranged

FIGURE 4. Cumulative root number and ratio of tertiary to secondary roots in sugar maple seedlings grown under a natural photoperiod in a hydroponic system. Week 0 = January 24. Vertical lines equal the standard error of the mean.

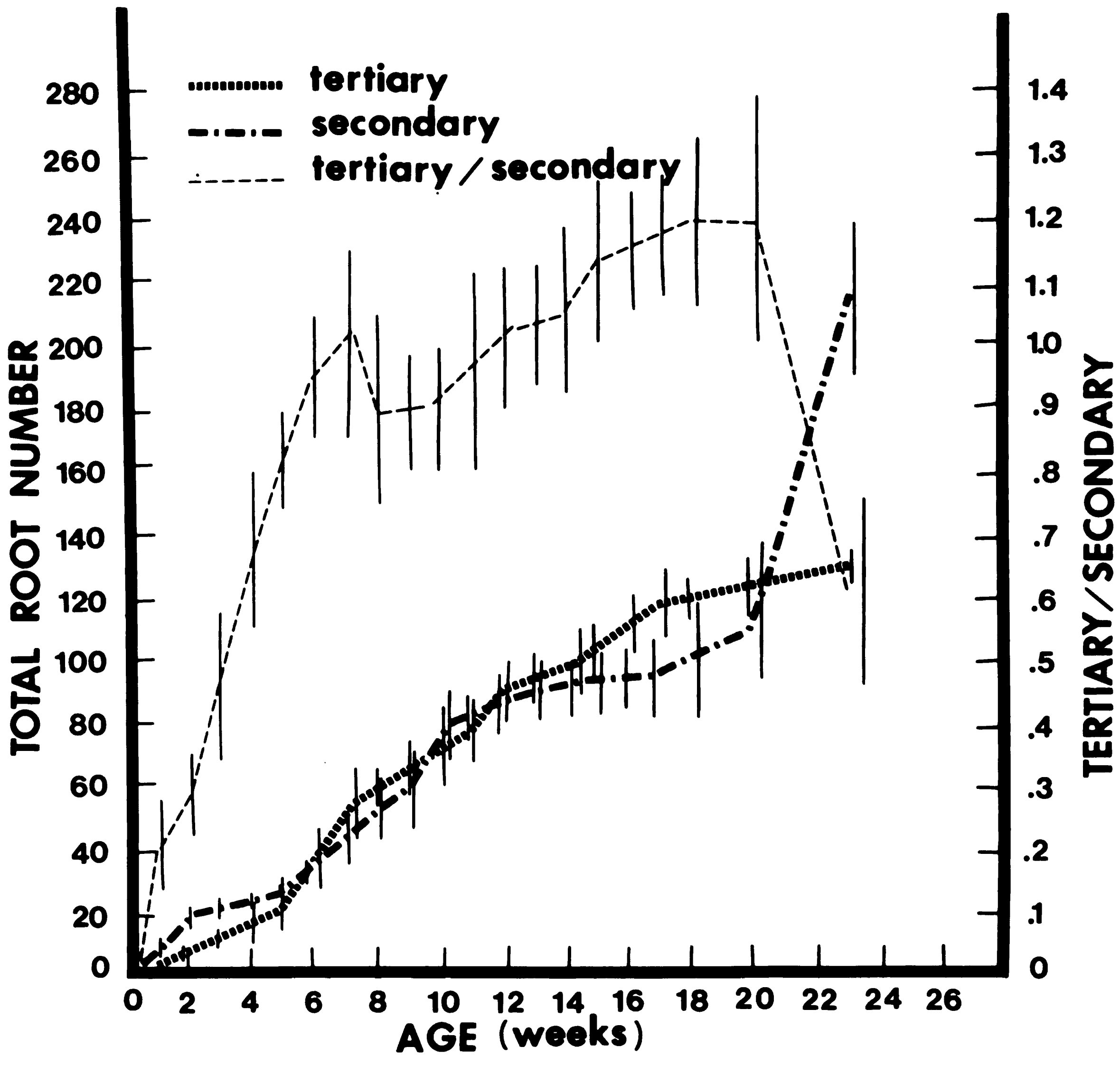

tertiary
secondary
tertiary / secondary
TOTAL ROOT NUMBER
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
TERTIARY/SECONDARY
1.4
1.3
1.2
1.1
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26
AGE (weeks)

FIGURE 4

from trees with a very strong primary root with few major secondaries to trees with essentially no primary root and many secondaries. Thus, there is either a large amount of genetic variation in root morphology and/or root morphology is easily affected by small changes in root environment. If these differences are primarily genetic, then much potential should exist for selecting and breeding and tailoring root systems for the environment in which trees are to be grown. This possible wide variation in root form suggests the potential for using intergenotypic interactions to increase unit area yields of forest products. Allard and Adams (1969) have successfully used this technique to increase the yield of similar grain varieties by 6%. Use of more diverse varieties could result in yield increases of 25%. In light of the possible genetic variation observed in sugar maple, genetics of competition with respect to intraspecific root differences warrants investigation.

Upon defoliation of a single seedling at about 16 weeks, an immediate cessation of root growth was observed. This supports the observation of Webb (1976) who found that root elongation rates of first-year sugar maple seedlings appeared to be dependent on current photosynthate production by the shoot.

Effects of Photoperiod and GA_7

Photoperiod did not affect cumulative growth of the primary root and major secondaries; however, GA_7 treatment inhibited root growth (Table 1) within 3 weeks of initial treatment (Figure 5), primarily by reducing growth rates of major secondary roots. There was no effect on primary root elongation rates (Table 1). GA_7 also greatly decreased the number of secondary and tertiary roots, while photoperiod had no effect. There were no photoperiod-GA_7 interaction effects on any measured variable.

Supplemental light and GA_7 treatments induced various degrees of budbreak (Table 1), and the effects were additive. The resulting increases in shoot growth reduced root-shoot ratios significantly.

TABLE 1. Effects of photoperiod and gibberellin A_7 treatments on root and shoot growth of sugar maple seedlings grown in an irrigation-type hydroponic system.

Treatment	Total[1] Growth	Growth Rate		Root Type			Tertiary to Secondary Ratio	Bud Break	Shoot Height	Root to Shoot Ratio
		Tap Root	Root[2] System	Total	Secondary	Tertiary				
	cm	cm/wk	cm/wk	Number	Number	Number		%	cm	
Photoperiod										
Natural	136 a[3]	2.5 a	43.0 a	109 a	54 a	54 a	1.0 a	16	7.2 a	1.1 b
Supplemental	144 a	2.2 a	45.7 a	105 a	46 a	52 a	1.2 a	42	7.6 b	0.7 a
Gibberellin A_7										
0 ppm	172 b	2.5 a	54.6 b	128 b	59 b	68 b	1.1 a	8	7.1 a	1.0 b
200 ppm	108 a	2.2 a	34.2 a	86 a	42 a	43 a	1.0 a	50	7.7 b	0.8 a

[1]Tap root and 6 longest secondary roots.

[2]Tap root and 6 longest secondary roots

[3]Values within a column and within photoperiod or gibberellin A_7 treatments which are followed by the same letter are not significantly different at the 5% level of probability using Duncan's Multiple Range Test.

FIGURE 5. Cumulative root growth (tap root and 6 longest secondary roots) of sugar maple seedlings grown under 2 photoperiods (natural vs. continuous with supplemental fluorescent light during the normal dark period) and 2 gibberellin A_7 (0 ppm vs. 200 ppm as a foliar spray at biweekly intervals) treatments. Week 0 = January 24. Vertical lines equal the standard error of the mean.

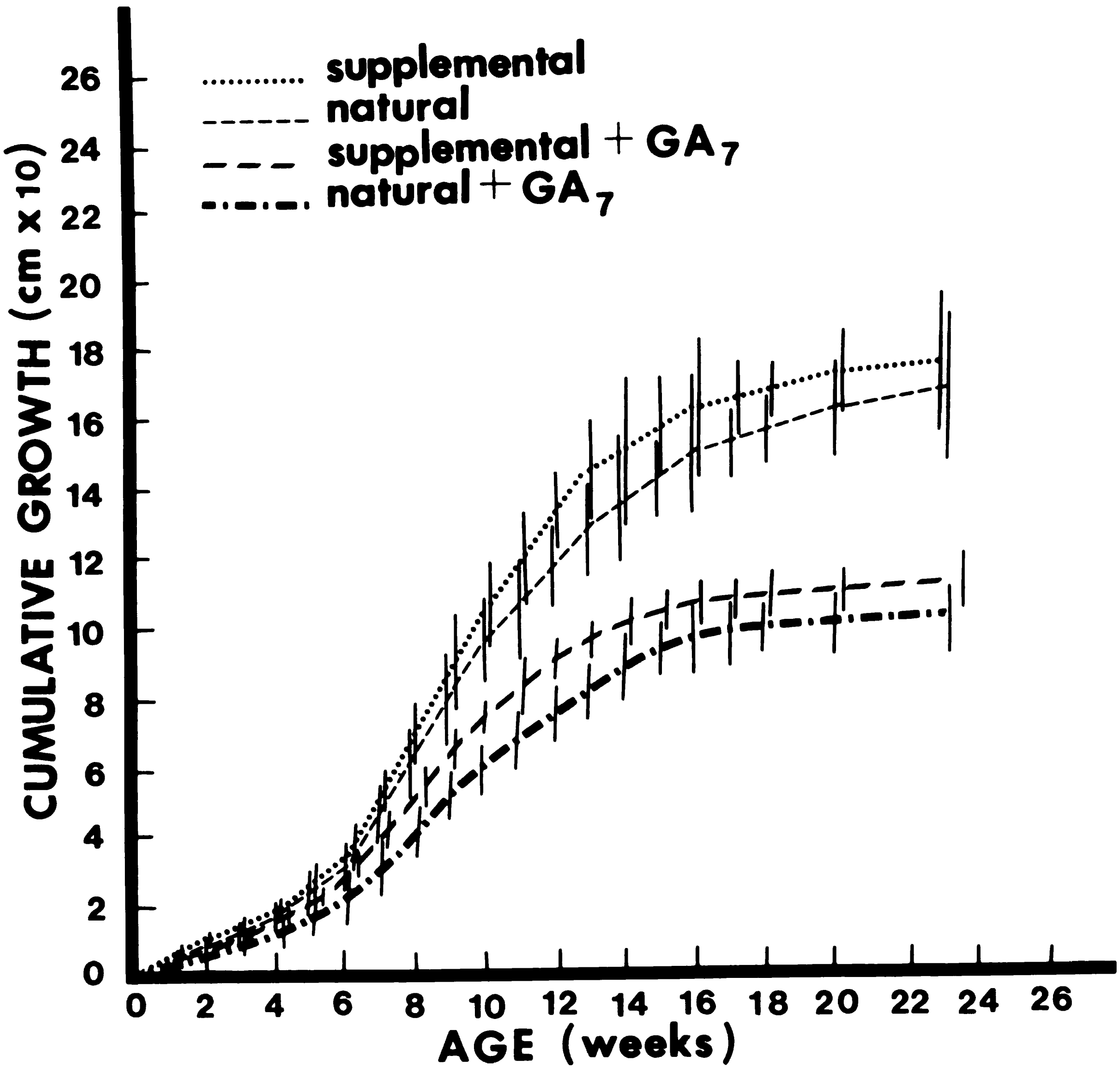

supplemental
natural
supplemental + GA_7
natural + GA_7
CUMULATIVE GROWTH (cm x 10)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
AGE (weeks)

FIGURE 5

CHAPTER IV

LACK OF EFFECT OF TRIACONTANOL ON GROWTH OF SUGAR MAPLE SEEDLINGS

Abstract

Triacontanol, a 30-carbon primary alcohol, with growth-promoting effects in some plant systems, was evaluated to determine if it has potential for accelerating and/or altering sugar maple (*Acer saccharum* Marsh.) seedling growth. Foliar spray applications of 0, 1, and 10 ppm triacontanol applied as both single and repeated weekly treatments did not significantly promote or inhibit height growth, total leaf area, root to shoot ratio, total dry weight, component dry weights, or bud dormancy.

Introduction

Triacontanol is a naturally occurring straight-chain 30-carbon saturated alcohol ($CH_3(CH_2)_{28}CH_2OH$) which promotes growth and markedly increases harvest yields in several horticultural and agronomic crop species (Ries and Wert 1977; Ries et al. 1977; Ries et al. 1978; Hangarter et al. 1978; Bittenbender et al. 1978). Most of the tested species have been either annuals or biennials. Their response warrants an evaluation of triacontanol's effectiveness on perennial woody species such as fruit and forest trees. Our objective was to determine if triacontanol would promote growth of sugar maple (*Acer saccharum* Marsh.) seedlings.

Materials and Methods

Sugar maple seed for this study was collected from several Michigan sources and bulked. Seeds were air-dried at room temperature to about 30% moisture and stratified 4 months at 3° C in moist perlite. Germinated seedlings were sown in 5 X 5 X 28 cm polycoated paper plant bands filled with a peat-vermiculite-perlite (1:1:1) potting mix and contained in plastic cases. Seedlings were grown in a greenhouse under natural daylight supplemented with 100 $\mu Ecm^{-2}s^{-1}$ of continuous fluorescent light during the night. Greenhouse temperatures ranged from 20° to 30° C. Seedlings were grown at near optimum moisture and nutrient levels. They were fertilized with 25-0-25 Peters solution every two to three weeks.

Seedlings were planted in a randomized complete block design with 4 replicates. Triacontanol was applied in 3 concentrations and 2 modes of application. Plot means were composed of 12 trees. Triacontanol was applied at 0, 1, or 10 ppm in a water emulsion with 0.1%

Tween-20, either as a single foliar spray to runoff or 10 consecutive weekly sprays. Treatment began 3 weeks after germination when leaves of the first node were about 75% expanded. Sprays were applied in early morning when the greenhouse temperature was generally near 20° C. Solutions were refrigerated between sprayings and allowed to warm to room temperature before application. The seedlings were measured in October after 4 months of growth, and the data analyzed by analysis of variance, using Duncan's Multiple Range Test to test the significance of treatment differences.

Results and Discussion

Triacontanol had no promotive or inhibitory effect of height growth, total leaf area, root to shoot ratio, total dry weight, or component dry weights. Visual observation did not suggest any differences in leaf morphology (Table 1).

Thus, triacontanol does not act as a growth regulator in sugar maple seedlings, at least under the experimental conditions imposed here. Possibly the concentration of triacontanol was not high enough to induce a growth response, although the same concentrations are effective in promoting growth in several horticultural and agronomic species (Ries et al. 1978; Ries et al. 1977). The relatively high daytime temperature at which the seedlings were grown resulted in poorer seedling growth than that

TABLE 1. Growth responses of sugar maple seedlings to foliar applications of triacontanol.[1]

Method of Application	Dry Weight				Root:Shoot Ratio	Leaf Area	Height
	Root	Stem	Leaves	Total			
	g	g	g	g		cm^2	mm
Single spray							
0 ppm	2.868	.572	1.205	4.645	1.614	262	104
1 ppm	2.406	.717	1.243	4.366	1.228	264	118
10 ppm	2.297	.748	1.253	4.298	1.148	285	126
Repeated sprays							
0 ppm	2.452	.689	1.176	4.317	1.317	277	114
1 ppm	2.428	.838	1.197	4.463	1.193	288	121
10 ppm	2.897	.703	1.251	4.851	1.483	285	115

[1]No differences significant at the 5% level of probability.

observed at cooler temperatures. This may have prevented action of triacontanol, assuming it is active in sugar maple. If true, there may be a triacontanol-temperature interaction.

Triacontanol may exist in the xylem sap of sugar maple trees (Robert Haus, personal communication). It increased to a very low concentration just prior to spring budbreak and later decreased. This observation suggests that triacontanol may play a role in regulating budbreak. However, the seedlings in our study were treated before, during, and after budset, and there was no apparent effect of triacontanol on date of budset or on budbreak. This suggests that either triacontanol is not involved in budbreak or it acts in conjunction with another growth promoters or inhibitors.

This study indicates that under the described set of experimental conditions triacontanol does not stimulate growth of sugar maple seedlings, and therefore has no potential for accelerating and/or altering tree seedling growth such as described by Hanover (1976). However, it may be effective on other tree species either as a spray or as a seed oak (Ries et al. 1978).

CHAPTER V

CARBON DIOXIDE, TEMPERATURE, AND AGE EFFECTS ON GROWTH, PHOTOSYNTHESIS, AND DARK RESPIRATION OF SUGAR MAPLE SEEDLINGS

Abstract

Sugar maple (*Acer saccharum* Marsh.) seedlings grown 4 months at elevated atmospheric carbon dioxide levels (700, 1400, and 2100 ppm) elevated levels resulted in substantial increases in height, organ dry weights, and leaf area with increasing carbon dioxide concentrations. The photosynthetic mechanism of these seedlings was adapted to the environment in which they developed, but respiration was not. When seedlings preconditioned at either 1400 or 2100 ppm carbon dioxide were grown in a 700 ppm environment for 2 weeks, net photosynthesis decreased by 25%.

Seedlings grown continuously at 20° C were 94% taller and had 2.5 times more nodes than those at 30° C. The photosynthetic system apparently adapted to the temperature at which the seedlings developed. Photosynthetic measurements of seedlings preconditioned at 20° and 30° C and subsequently exposed to 30° and 20° C,

respectively, showed an 18% decrease in net photosynthesis. The photosynthetic mechanism was capable of readapting at least twice to new temperature environments.

Rates of photosynthesis and dark respiration in greenhouse-grown seedlings generally were highest early in development and decreased with leaf age, regardless of leaf types. A large increase in net photosynthesis always followed budset. At 22 weeks after germination, sharp decreases in both photosynthesis and dark respiration occurred in all seedlings, regardless of leaf type. At 32 weeks, rate of respiration exceeded that of net photosynthesis.

Introduction

Accelerating and manipulating growth by controlling environmental factors is advantageous in the production of forest tree seedlings for both research and commercial purposes (Hanover 1976, 1977; Logan and Pollard 1976). Atmospheric carbon dioxide level and temperature are 2 factors that greatly influence seedling growth and development and may affect growth even after outplanting due to acclimation or adaptation to the greenhouse environment. Exposure of seedlings to higher or lower temperatures may result in a decrease in photosynthetic rates and change the point of optimal photosynthetic temperature. Many woody species experience temperature-related adaptive changes in both photosynthesis and respiration (Mooney and West 1964; Rook 1969; Strain 1969; Strain et al. 1976; Strain and Chase 1966).

Photosynthesis of forest tree seedlings in outdoor or greenhouse atmospheres is almost always below optimal levels because of low CO_2 concentrations (Salisbury and Ross 1969). CO_2-enriched atmospheres are used in greenhouse production of horticultural and field crops (Wittwer and Robb 1964; Ford and Thorne 1967). Growth of many tree species is stimulated by CO_2 enrichment (Funsch et al. 1970; Yeatmen 1970; Zimmerman et al. 1970; Stanley 1971; Tinus 1976; Wood and Hanover 1979). This technique might accelerate tree seedling growth and development for physiological and genetic evaluation but has received very little attention. It may be possible that CO_2 levels can also induce adaptive responses in forest trees.

Sugar maple seedlings typically exhibit a determinate growth habit and grow relatively slowly under conditions that greatly accelerate growth of seedlings of many other forest tree species. An understanding of the developmental patterns of photosynthesis and respiration in leaves might aid in overcoming this problem. Knowing how long the leaves can be expected to produce significant levels of photosynthate is also important.

The objectives of this study with greenhouse-grown sugar maple seedlings were to determine: (a) the influence of CO_2 and temperature on growth, net photosynthesis, and dark respiration; (b) adaptation of the photosynthetic and respiratory mechanisms to certain CO_2 and temperature levels; and (c) age differences in photosynthesis and dark respiration of leaves from seedlings in different developmental states but of equal age.

Materials and Methods

Seeds were collected from natural forest in Michigan and kept separate by seedlot. They were air-dried at room temperature to about 30% moisture and stratified 4 months at 3° C in moist perlite. Germinated seedlings were then bulked and planted in 5 X 5 X 28 cm polycoated paper plant bands containing a topsoil-peat-perlite (1:1:1 v/v) potting mix.

Experiment 1. The purpose of this experiment was to investigate the potential for accelerating seedling growth by CO_2 enrichment of the atmosphere and to determine if the photosynthetic and dark respiratory mechanisms become adapted to these elevated CO_2 levels. Seedlings were grown in air-tight transparent fiberglass chambers within a greenhouse and were exposed to normal light during the day and to 100 $\mu Ecm^{-2}s^{-1}$ of continuous supplemental fluorescent light during the night. Continuous light was used to prevent budset due to imposition of long nights from becoming a limiting factor in height growth. Temperature within the chambers ranged from 20° C at night to 35° C during the day. Experimental design consisted of 3 blocks, each with 3 CO_2 concentrations--700, 1400, and 2100 ppm, and 36 trees per treatment. These levels were monitored daily with a Beckman 864 infared gas analyzer and maintained at ± 100 ppm by bleeding in CO_2 gas. Chambers were opened to the greenhouse atmosphere for a few minutes every 3 or 4 days to allow fresh air to replace air within the chambers. Fans in each chamber provided continuous air movement.

After growing 4 months in CO_2-enriched atmospheres, growth measurements were made and healthy appearing seedlings were transported into the laboratory for photosynthesis and dark respiration measurements. After removal from the CO_2 environment in which they were grown, seedlings were exposed to greenhouse ambient CO_2 levels (approx. 700 ppm) for 2 weeks, then preconditioned in each of the 3 test environments for 1 hour, then tested at each CO_2 level used in the growth phase. Initial CO_2 level was established by exhaling small amounts of CO_2-enriched air in the vicinity of the uptake tubing from the pump to the chamber. The attached leaves of 3 seedlings (3 trees per plot mean and 3 replicates) were sealed in a water-jacketed plexiglas chamber (0.95 l). Illumination was provided by one 400-watt color-improved mercury vapor lamp positioned above and perpendicular to the leaf surface. Photon flux density at the leaf surface was 500 $\mu Ecm^{-2}s^{-1}$ (3,200 ft. c.), as determined by a Lambda quantum sensor. Temperature was maintained at 25° ± 0.5° C by circulating water from a constant temperature bath through the plexiglas water jackets. Air flow was at 400 cc $min.^{-1}$. Net photosynthesis and dark respiration were determined by measuring the rate of CO_2 change ($mg/dm^2/m$) in a closed system between 670-730 ppm, 1370-1430 ppm, and 2070-2130 ppm. Dark respiration was measured after each photosynthetic measurement by placing a black cloth over the leaf chamber. Leaf area was then measured with a Lambda LI-300 portable area meter.

Experiment 2. In this experiment, we wanted to investigate the sensitivity of sugar maple seedling growth to temperature and to determine if the photosynthetic and respiratory mechanisms of sugar maple can become adapted to the temperature conditions in which they are grown. Three blocks of seedlots (from 12 bulked sources) were germinated and grown for 2 months in the greenhouse under continuous light. They were then transferred to growth chambers at constant 20° or 30° C.

Height and node number were recorded after 2 months under these conditions. Photon flux density was 100 $\mu Ecm^{-2}s^{-1}$ from an arrangement of fluorescent and incandescent light bulbs. The vapor pressure deficit in both chambers was 12.5 mmHg.

To determine whether or not temperature adaptation occurs in sugar maple, seedlings were moved to growth chambers after 3 months in a greenhouse under continuous light. They were placed in a split-plot design with 6 blocks of 2 growth temperatures and 2 measurement temperatures. Growth and measurement temperatures were 20° ± 0.5° and 30° ± 0.5° C. Means for CO_2 exchange rates were composed of 3 trees. At the end of 3 months photosynthesis and respiration were measured at each of the test temperatures and the seedlings were then transferred to another chamber and grown for 1 month at 25° C (a neutral temperature). Photosynthesis and respiration were then measured at each of the test temperatures.

Photosynthetic and respiratory measurements were the same as in the previous experiment with respect to instrumentation and light conditions. Attached leaves of 3 trees were placed in the leaf chamber at the test temperatures and allowed to precondition for about 1 hour. CO_2 exchange rates were measured at both 20° and 30° C for trees grown at these 2 temperatures, with sequence random. Only seedlings with 2 leaves (1 node) were used.

Experiment 3. To determine developmental differences in photosynthesis and dark respiration of greenhouse-grown trees, bulked seedlings (from 20 Michigan sources) were grown 32 weeks (from germination) in a greenhouse where temperatures ranging from 20° to 40° C. Supplemental fluorescent light at 100 $\mu E cm^{-2} s^{-1}$ during the night provided continuous photoperiod. Trees were planted in 4 blocks with 3 tree classes (single node, double node, and triple node: totaling 6 leaf types), and measurements were made 20 times over a period of 32 weeks. The plot mean for the CO_2 exchange measurements consisted of 3 trees and this was replicated 3 times. Sugar maple seedlings grown in the greenhouse typically produce 1 leaf node and then promptly set bud; a few weeks later they may break bud and produce 1 or more new nodes before setting a resting bud. Therefore, trees are produced having 1, 2, 3 nodes, etc.

Instrumentation and light and temperature treatments for the CO_2 exchange measurements were the same as in Experiment 1. Seedlings were watered to field capacity 2 days prior to measurement. They were preconditioned to the test conditions for 15 minutes. Leaves were then cut from the shoot and the petiole immersed in a small test tube containing distilled water. Measurements were completed within 20 minutes. CO_2 exchange rates were measured between 300 and 360 ppm. Preliminary studies showed that CO_2 exchange rates were not affected until 45 minutes after detachment.

Results and Discussion

Experiment 1. Height, leaf area, and organ dry weights of sugar maple seedlings were greater in enriched CO_2 atmospheres (Table 1). These responses increased with increasing CO_2 levels, although growth increase per unit CO_2 added declined. Seedlings at the 2100 ppm level had 62% more dry weight and a reduced root:shoot ratio relative to the controls (700 ppm). This ratio difference was primarily due to an increase in stem weight.

Diminishing returns for dry weight gain increase per unit increase of CO_2 may be attributed to (a) CO_2 saturation of the photosynthetic reactions and (b) the known interaction between light intensity and CO_2 may occur (Salisbury and Ross 1969). CO_2 is generally the limiting factor in photosynthesis; however, at high CO_2 levels light intensity becomes limiting. This is illustrated in Figure 1 by the observation of diminishing returns of net photosynthesis with increasing CO_2 levels at a constant photon flux density. A plant can more efficiently use CO_2 at high atmospheric levels when light intensity is high. When intensity is low, efficiency of CO_2 utilization is greatly diminished (Salisbury and Ross 1969). This means that a grower can use CO_2 more

TABLE 1. Effects of carbon dioxide levels on growth of sugar maple seedlings.

Carbon Dioxide Growth Environment	Height	Total Leaf Area	Dry Weight				Root/shoot
			Total	Root	Stem	Leaves	
	(mm)	(cm^2)	---------------mg---------------				
700 ppm	86 a[1]	29 a	1040 a	700 a	245 a	95 a	2.06 b
1400 ppm	92 b	37 b	1430 b	990 b	340 b	100 a	2.25 b
2100 ppm	103 c	43 b	1680 c	1060 b	506 c	114 b	1.71 a

[1]Values within a column and not followed by the same letter are significantly different at the 5% level by Duncan's Multiple Range Test.

FIGURE 1. The effects of carbon dioxide concentration on net photosynthesis and dark respiration of sugar maple seedlings preconditioned in 700, 1400, and 2100 ppm carbon dioxide atmospheres. Vertical lines equal the standard error of the mean.

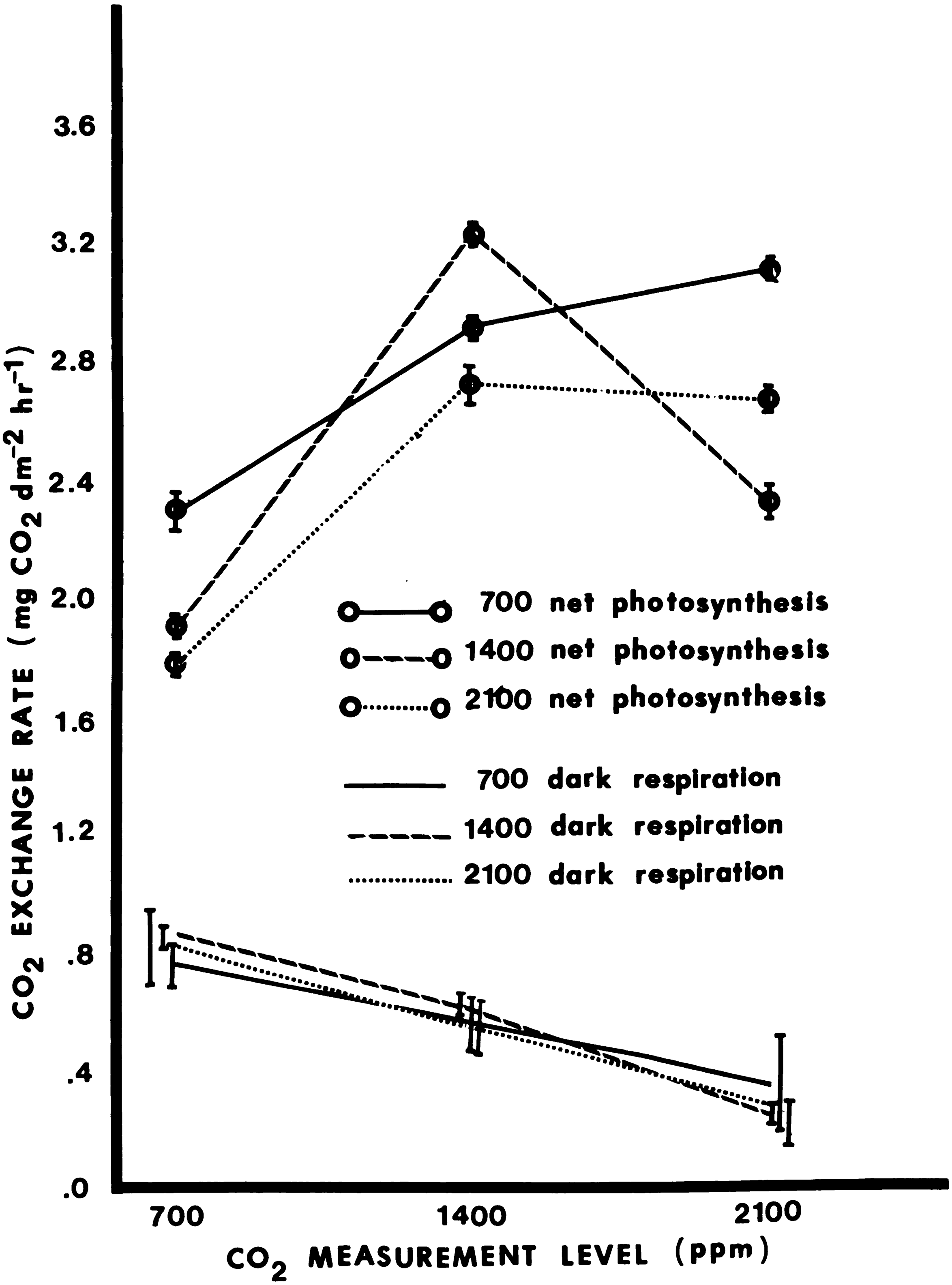

3.6
3.2
2.8
2.4
2.0
1.6
1.2
.8
.4
.0
CO_2 EXCHANGE RATE (mg CO_2 dm^{-2} hr^{-1})
700 net photosynthesis
1400 net photosynthesis
2100 net photosynthesis
700 dark respiration
1400 dark respiration
2100 dark respiration
700
1400
2100
CO_2 MEASUREMENT LEVEL (ppm)

FIGURE 1

effectively by tailoring the CO_2 level to the light intensity in the greenhouse. CO_2 levels should be relatively high during the day but should be allowed to decrease to the ambient level during the night.

Our observations indicate that growth of sugar maple seedlings can be increased by the incorporation of CO_2 into the cultural system. As a result of such a practice trees should be more vigorous for outplanting and other uses.

The photosynthetic mechanism was affected by the environment in which seedlings were grown (Figure 1). Trees grown in 700 ppm CO_2 produced more net photosynthate when measured at the 700 or 2100 ppm level than did seedlings grown at higher CO_2 levels. Trees grown at 2100 ppm produced the least net photosynthate when measured at the 700 or 1400 ppm level but were intermediate in production at the 2100 level. These observations indicate that the photosynthetic mechanism of seedlings is affected by the CO_2 environment in which they are grown. Enzyme or isoenzyme changes in the reductive pentose phosphate pathway may occur. CO_2 adaptation in _Chlorella_ has been attributed to changes in the activity of at least one of these enzymes (Reed and Graham 1977).

Dark respiration was not affected by the CO_2 level in which seedlings were grown (Figure 1). Increasing CO_2 levels decreased dark respiration for all 3 treatments.

Dark respiration rates at 1400 and 2100 ppm were only 75 and 38%, respectively, of that at 700 ppm CO_2.

This study illustrates the potential usefulness of CO_2 fertilization of greenhouse-grown trees. The photosynthetic mechanism of seedlings can be expected to be adapted to the CO_2 concentration in which they develop. Seedlings grown at a relatively constant high CO_2 level may experience a reduction in net photosynthesis of 25% or more for at least 2 weeks after outplanting. Whether the photosynthetic mechanism will readapt to the ambient outdoor CO_2 environment is unknown; however, it seems likely. If leaves are unable to readapt to the outdoor level, then chances of survival after outplanting may be affected; but if readaptation is possible, it should be done before outplanting. This could be accomplished in either of two ways: First, they could be moved to the outdoor environment and allowed to readapt before outplanting; second, a period of growth at a lower CO_2 level could be imposed on the seedling prior to removal from the greenhouse. This might produce seedlings that are adapted to both high and low CO_2 levels.

Experiment 2. After 2 months at constant temperature sugar maple seedlings were 94% taller and had 2½ times as many nodes at 20° than at 30° C (Table 2), and growth was active only at 20° C. A cool environment

TABLE 2. Effects of temperature on growth of sugar maple seedlings.

Growth Temperature	Height (cm)	Nodes
30° C	6.8 a[1]	2 a
20° C	13.2 b	5 b

[1]Values within a column and not followed by the same letter are significantly different at the 5% level.

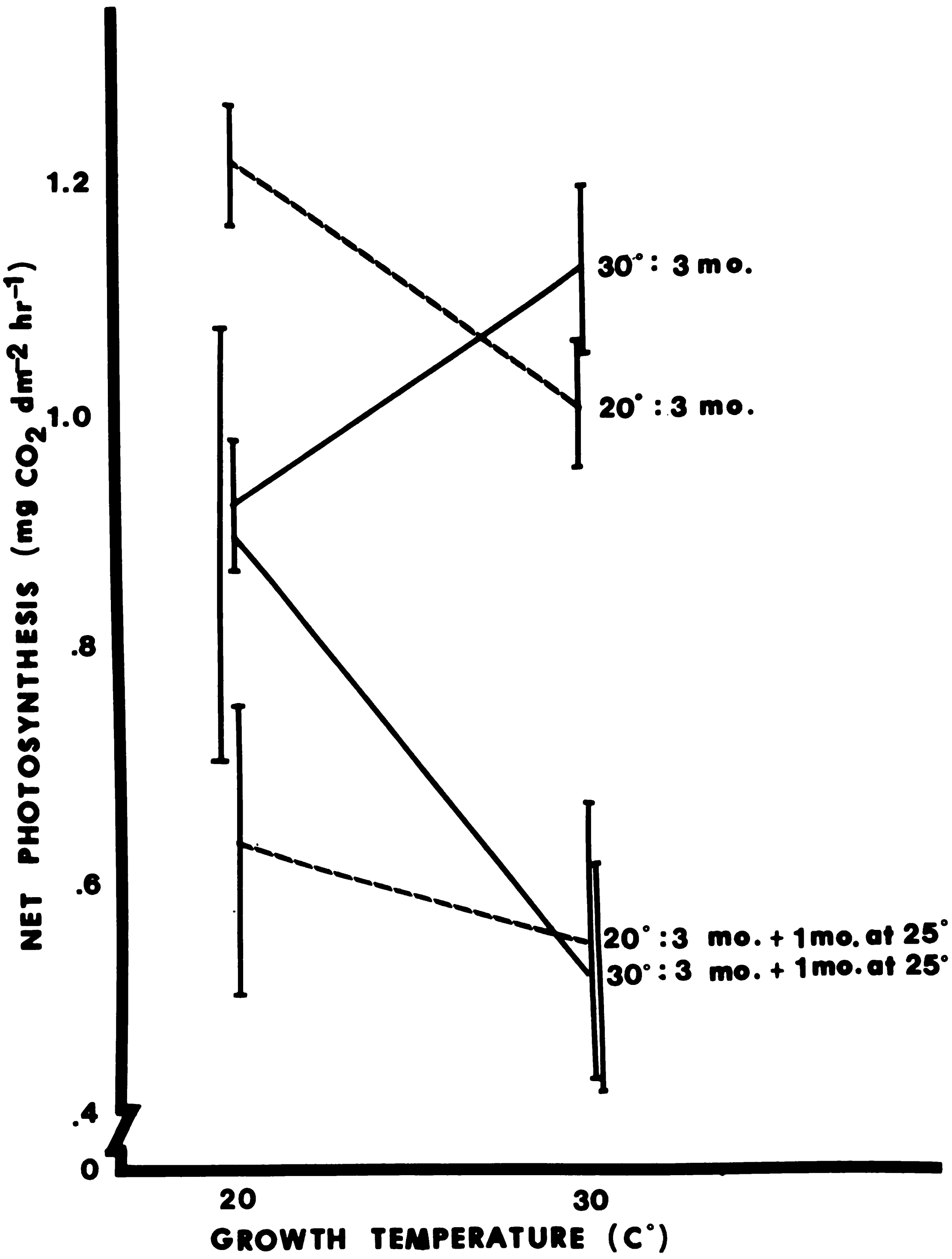
appears to be essential for growing large sugar maple seedlings in greenhouses.

Under natural conditions, height growth of sugar maple seedlings occurs in early spring when temperatures are relatively low. By late spring or early summer, when temperatures are relatively high, seedlings have set a resting bud which generally does not break until exposed to about 2000 hours of temperatures 5° C or lower (Taylor and Dumbroff 1975). This determinate growth may be largely controlled by relatively high temperatures experienced in late spring or summer. Previous observation of greenhouse photoperiod studies with sugar maple showed that exposure to continuous light and warm (23° to 35° C) temperatures increased height growth and node formation slightly in comparison with natural photoperiod controls. This effect could be either photoperiodic or photosynthetic. Certain forest tree species have been shown to be photoperiodically sensitive with respect to dormancy (Young and Hanover 1977; Butler and Downs 1960; Nitsch 1957; Williams et al. 1972). If sugar maple is photoperiodic sensitive, then these observations suggest that phytochrome may be a switching system for regulating height growth and bud formation, while temperature controls expression of the phytochrome response. Temperature could conceivably affect the relative levels of growth promoters and inhibitors, with promoter levels being higher and inhibitor levels lower under long days and cool temperatures (20° C).

After seedlings had grown 3 months at either 20° or 30° C, net photosynthesis and dark respiration were well conditioned to these temperatures. Net photosynthesis of seedlings grown in both environments decreased when measured at the other growth temperature (Figure 2). Dark respiration of trees grown at 20° C increased twofold at 30° C; however, temperature did not affect dark respiration of trees grown at 30° C (Figure 3). These differences were probably not due to inadequate preconditioning, because there was no difference between measurements made at preconditioning periods of 30 minutes or 24 hours.

Growing temperature did not significantly effect net photosynthesis when measured at the temperature at which the seedlings were grown, i.e., net photosynthesis of trees grown at 20° and measured at 20° C did not differ from trees grown at 30° and measured at 30° C (Figure 2). This was also true when measured at the temperature in which they were not grown, although net photosynthesis decreased 18% in both treatments. This indicates that changes occurred in both cool and warm adapted seedlings that allowed them to maximize photosynthetic rates under each temperature environment. This adaptation of CO_2 exchange to temperature has also

FIGURE 2. Effects of cool and warm temperatures on net photosynthesis of sugar maple seedlings grown in constant cool or warm environments. Vertical lines equal the standard error of the mean.



NET PHOTOSYNTHESIS (mg CO_2 dm^{-2} hr^{-1})
1.2
1.0
.8
.6
.4
0
20
30
GROWTH TEMPERATURE (C°)
30° : 3 mo.
20° : 3 mo.
20° : 3 mo. + 1 mo. at 25°
30° : 3 mo. + 1 mo. at 25°

FIGURE 2

FIGURE 3. Effects of cool and warm temperatures on dark respiration of sugar maple seedlings grown in constant cool or warm environments. Vertical lines equal the standard error of the mean.

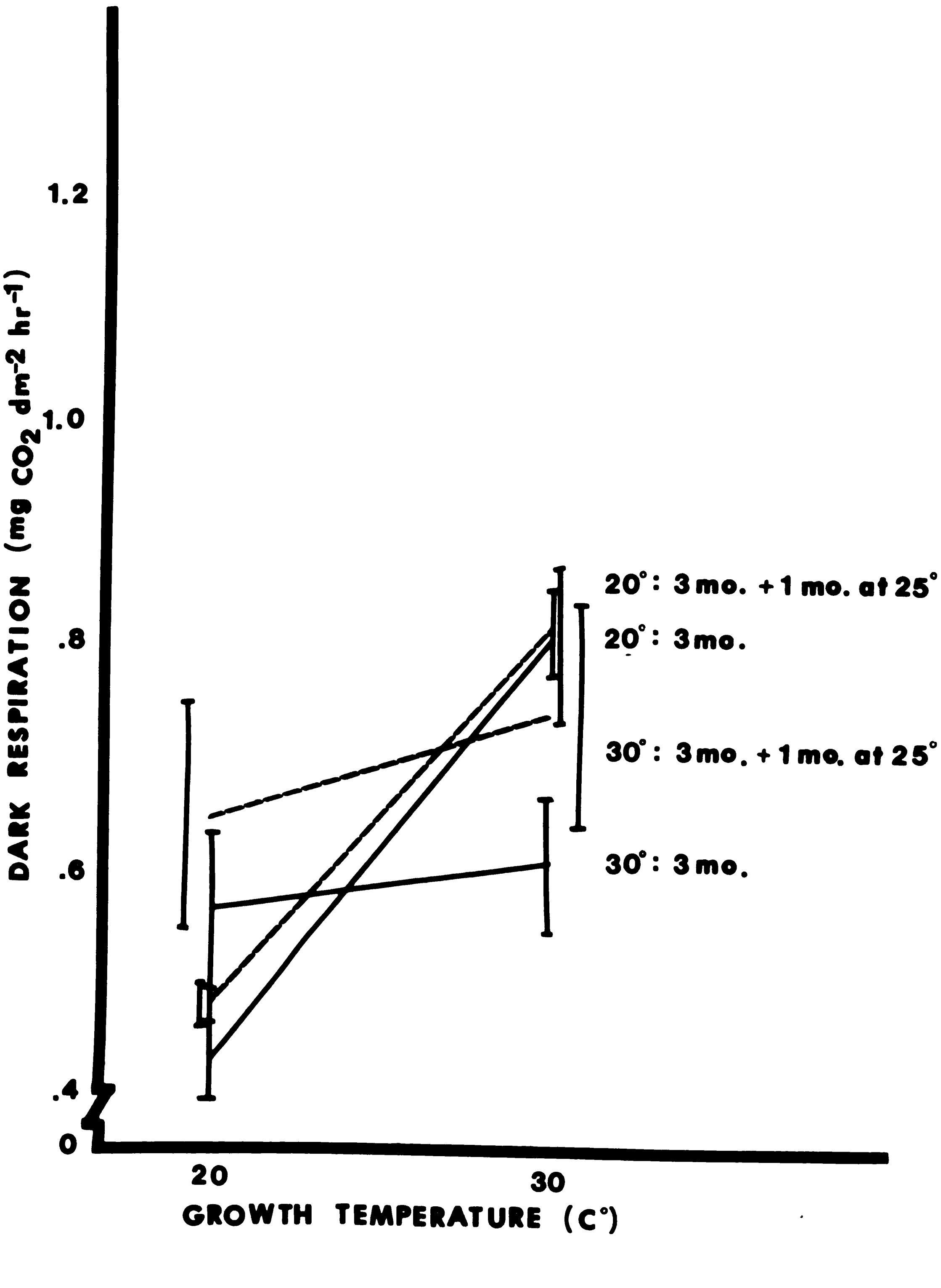

1.2
1.0
.8
.6
.4
0
DARK RESPIRATION (mg CO_2 dm^{-2} hr^{-1})
20°: 3 mo. + 1 mo. at 25°
20°: 3 mo.
30°: 3 mo. + 1 mo. at 25°
30°: 3 mo.
20
30
GROWTH TEMPERATURE (C°)

FIGURE 3

been observed in a number of other species (Mooney and West 1964; Rook 1964; Strain 1969; Strain and Chase 1966; Strain et al. 1976). The ability to adapt to temperature probably provides a distinct selective advantage which increases survival under a wide range of temperature conditions. This characteristic may be a major factor contributing to the ability of sugar maple to occupy such a wide natural range (Fowells 1965).

Seedlings of both treatments were grown in a common greenhouse environment with temperatures ranging from 20° to 35° C for 2 months then transferred to growth chambers and exposed to either constant cool or warm conditions for 3 months. Thus, any differences were induced within this 3-month period. To better understand the ability of these seedlings to readapt to temperature, they were grown at a constant neutral (25° C) temperature for 1 month after the initial measurement. No difference in net photosynthesis of the cool adapted trees was evident at either 20° or 30° C. Net photosynthesis of warm adapted trees was much greater (equal to 20° C trees measured at 20° C) at 20° than at 30° C (Figure 2). Perhaps this latter response is due to accelerated senescence resulting from 3 months of growth at 30° C. This may also account for the lack of difference in net photosynthesis of seedlings grown at 30° for 3 months and measured at 20° C with the same seedlings when measured at 20° after growing at 25° C for 1 month. Dark respiration patterns differed little from the 3-month measurements (Figure 3), escept for an increase in trees transferred from 20° to 25° C. These observations suggest that the dark respiration mechanism of leaves is not as easily adapted as is the photosynthetic mechanism, which adapts fairly rapidly and readapts to the original temperature. Readaptation occurred after leaves were 6 months old and senescing, hence temperature adaptations are not restricted to young foliage.

This study shows that growth of sugar maple seedlings can be greatly accelerated by growing at cool, rather than warm, temperatures. Photosynthetic and respiratory mechanisms of seedlings grown in a greenhouse at a relatively constant temperature adjust to that temperature.

When outplanted at a temperature differing from that to which they are adapted, net photosynthesis decreases and respiration may increase. Readaptation to normal outdoor temperature can be expected within a month or two. Therefore, a delayed temperature adaptation might cause a loss in growth for the first few weeks after outplanting. This may be a factor contributing to the difficulty of establishing sugar maple plantings (von Althen 1971, 1972, 1974).

Experiment 3. Photosynthetic and respiratory rates for all seedlings were highest in very young expanding leaves (Figures 4, 5, and 6). These rates declined rapidly until budset (4 weeks old). Net photosynthesis increased dramatically 5 weeks after germination, while dark respiration continued to decrease. This response was correlated with budbreak. It was observed in both seedlings that were about to form new nodes and in seedlings which did not experience a second budbreak. In leaves on seedlings with 2 or 3 nodes, this increase in photosynthesis was soon followed by a sharp rise in dark respiration rate. Presumably this was a response to the actively expanding newly formed leaves because it did not occur in single node seedlings. Both photosynthetic and respiratory rates then decreased in all seedlings until budset at 10 weeks of age. During the 2-week period following budset, there was a second large increase in net photosynthesis in almost all leaf types, even though the 1-node seedlings did not reflush after the initial budset. However, this increase did not occur in leaves at the lower node of 3-node seedlings.

The peak in net photosynthesis just after budset, even in 1-node seedlings, suggests a nonrandom relationship. The leaves were fully expanded at this time, consequently maximum export would be expected to be occurring at this time (Thrower 1964). Something may be preparing

FIGURE 4. Changes in net photosynthesis and dark respiration with development of greenhouse-grown sugar maple seedlings with 1 leaf node. The states of development are as follows: (A) leaves 1/3 expanded, (B) leaves 2/3 expanded, (C) leaves fully expanded and has set bud, (D) time of bud-break on trees with 2 or 3 nodes, (E) time of second budset for trees with 2 and 3 nodes. Vertical lines equal the standard error of the mean.

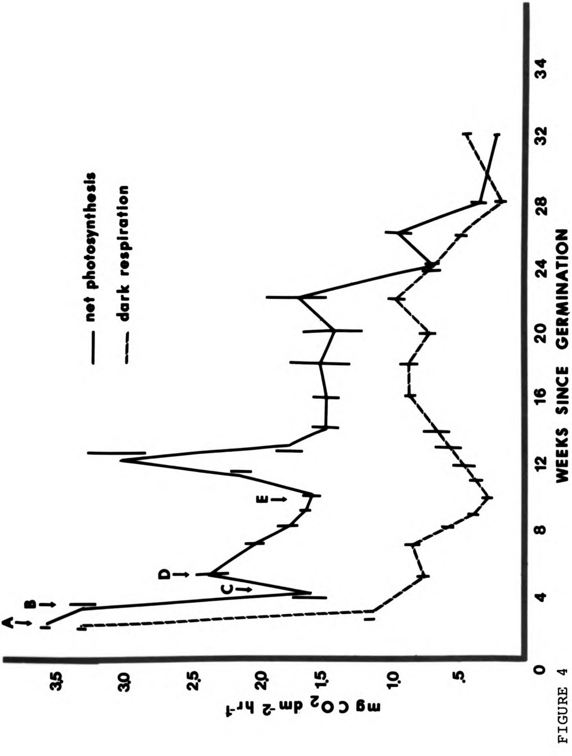
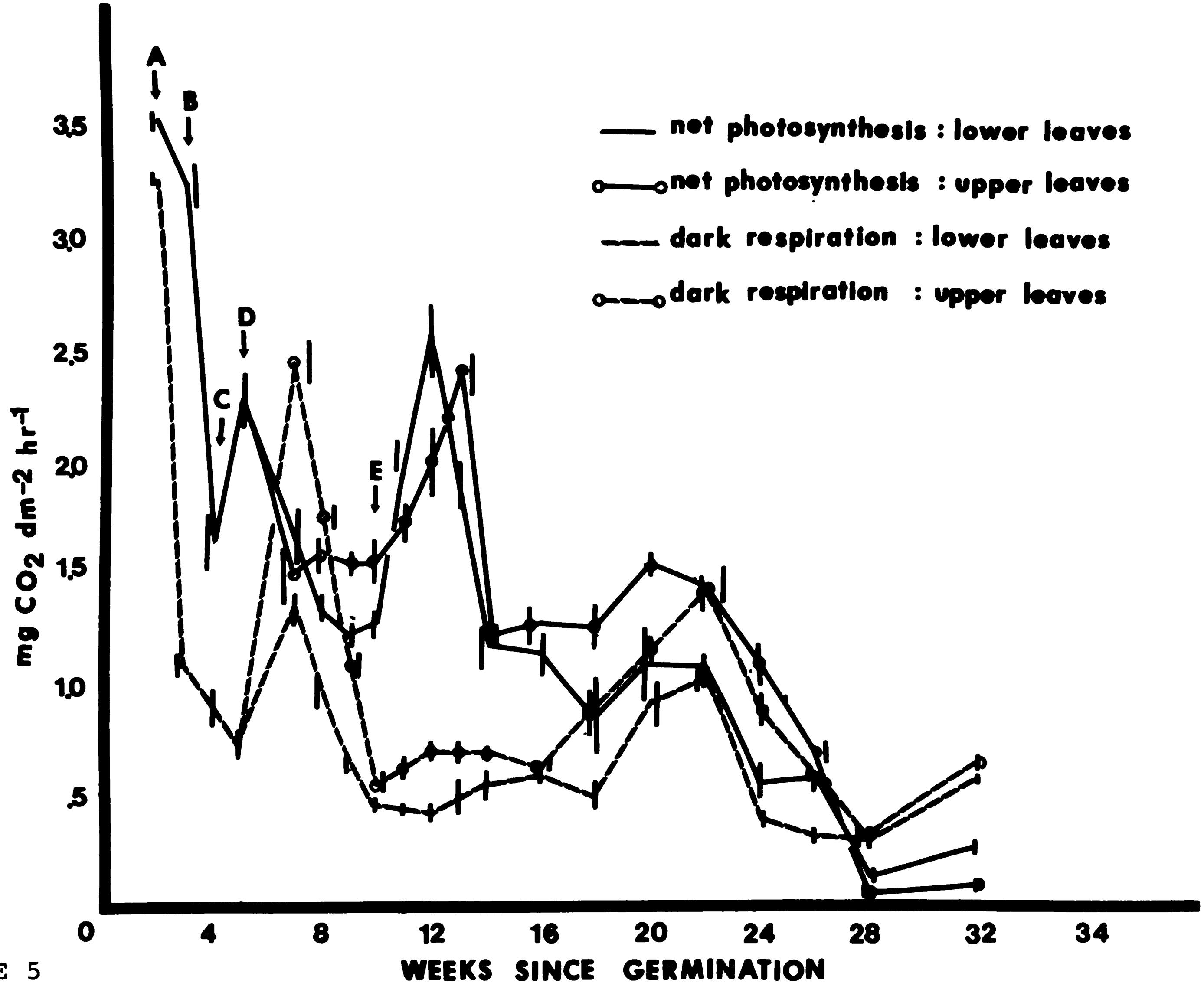

net photosynthesis
dark respiration
A
B
C
D
E
3.5
3.0
2.5
2.0
1.5
1.0
.5
0
mg CO2 dm-2 hr-1
4
8
12
16
20
24
28
32
34
WEEKS SINCE GERMINATION

FIGURE 4

FIGURE 5. Changes in net photosynthesis and dark respiration with development of greenhouse-grown sugar maple seedlings with 2 leaf nodes. The states of development are as follows: (A) leaves 1/3 expanded, (B) leaves 2/3 expanded, (C) leaves fully expanded and has set bud, (D) time of budbreak on trees with 2 or 3 nodes, (E) time of second budset for trees with 2 and 3 nodes. Vertical lines equal the standard error of the mean.



net photosynthesis : lower leaves
net photosynthesis : upper leaves
dark respiration : lower leaves
dark respiration : upper leaves
A
B
C
D
E
mg CO_2 dm-2 hr-1
3.5
3.0
2.5
2.0
1.5
1.0
.5
0
4
8
12
16
20
24
28
32
34
WEEKS SINCE GERMINATION

FIGURE 5

FIGURE 6. Changes in net photosynthesis and dark respiration with development of greenhouse-grown sugar maple seedlings with 3 leaf nodes. The states of development are as follows: (A) leaves 1/3 expanded, (B) leaves 2/3 expanded, (C) leaves fully expanded and has set bud, (D) time of budbreak on trees with 2 or 3 nodes, (E) time of second budset for trees with 2 or 3 nodes. Vertical lines equal the standard error of the mean.

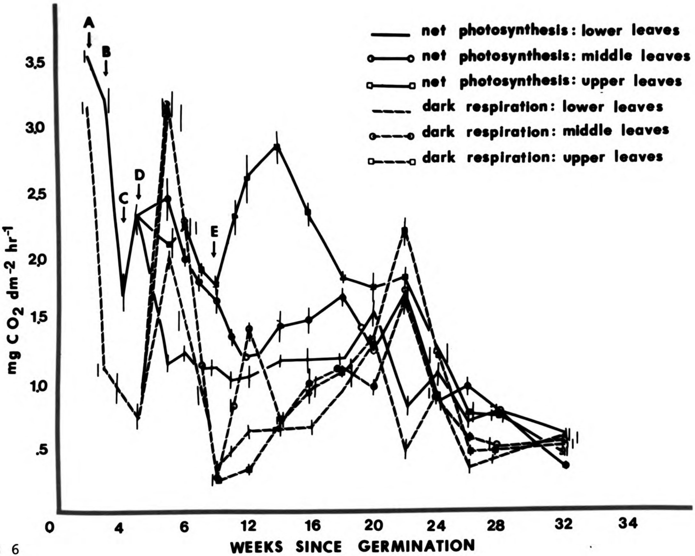

net photosynthesis: lower leaves
net photosynthesis: middle leaves
net photosynthesis: upper leaves
dark respiration: lower leaves
dark respiration: middle leaves
dark respiration: upper leaves
A
B
C
D
E
mg C O2 dm-2 hr-1
3.5
3.0
2.5
2.0
1.5
1.0
.5
0
4
6
12
16
20
24
28
32
34
WEEKS SINCE GERMINATION

FIGURE 6

the leaves for a new budbreak phase by stimulating photosynthesis. Perhaps this is due to increases in growth promoters, such as gibberellins or cytokinins, by the newly expanded leaves. Both gibberellin and cytokinin have been observed to increase photosynthetic rates of treated plants (Treharne et al. 1970; Meicher 1967). During the last photosynthetic peak, something apparently happened that prevented budbreak. Warm temperature is capable of acting in this manner (see Experiment 2). During the growth of these seedlings, greenhouse temperatures were often as high as 35° C.

After this second peak, net photosynthetic rates declined to about one-half their maximum level, remained relatively constant for about 2 months (to 22 weeks), then rapidly decreased. Respiration generally increased between 14 and 22 weeks, then rapidly decreased coincident with the sharp decrease in both net photosynthesis and dark respiration rates. This CO_2 exchange pattern corresponds with that which is normally observed in Populus (Hernandez-Gil and Schaedle 1973). By 32 weeks after germination, leaves of all seedlings had aged sufficiently to exhibit dark respiration rates greater than those for net photosynthesis. By this time leaves are of little value as far as photosynthate production.

Leaves on greenhouse-grown seedlings were photosynthetically active for 8 months, whereas in the outdoor environment they would probably be active for only about 5 to 6 months. In order to maximize sugar maple seedling growth, any growth beyond the 22-week phase is minor at which time they should be esposed to a cold treatment sufficient to induce budbreak. Alternatively they could be treated with GA_7 to induce budbreak and permit continued growth (Wood and Hanover 1979).

Sugar maple seedlings grown at cool temperatures and in an enriched CO_2 environment can be expected to grow much better than seedlings grown at warm temperatures and anbient CO_2 levels. The control of these 2 environmental factors in greenhouses can result with the production of seedlings that are probably much better suited for outplanting than outdoor nursery-grown seedlings and can be produced in a shorter period of time. However, survival and growth upon outplanting may be reduced relative to outdoor-produced seedlings due to adaptation of the photosynthetic and respiratory systems of greenhouse-grown seedlings to different CO_2 and temperature environments than observed in nature. They need to be preconditioned to the outdoor CO_2 and temperature environment before outplanting.

The photosynthetic rates of leaves of greenhouse-grown sugar maple varied greatly with age and were essentially nonproductive after 22 weeks of age. The great increases in photosynthesis observed immediately after budset suggest the possibility of manipulating photosynthetic rates by applying growth-regulating chemicals.

SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

Application of the accelerated-optimal-growth (AOG) concept to greenhouse production of containerized seedlings has much potential for both researchers and commercial nurserymen. Its use for early genetic evaluation by forest geneticist is one such potential advantage. However, this remains to be proven. The AOG growth conditions offered an advantage over nursery-grown trees in that seed source differences were apparent under the AOG environment as early as 4 months after planting. Even though AOG and nursery treatments experienced equal growing seasons, there were no detectable provenance and few seedlot differences in nursery-grown sources after 16 months of age. This means that relative performance of sugar maple genotypes depends greatly upon the environment in which they are grown. Thus, one cannot assume that progeny testing and early evaluation of sources grown under AOG conditions is reliable without first determining the magnitude of these genotype-environment interactions. If there proves to be a difference in ranking between the AOG and nursery treatments, it could be due to any one of several genotype-environment interactions or to accelerated physiological aging of AOG trees. If rank changes do occur, then the use of AOG for early progeny evaluation with the assumption that seedlings will behave similarly when outplanted would probably be invalid. Otherwise, AOG may be an important tool for early progeny evaluation. Definite conclusions cannot be made until the plantings are established and observed for several years in a common environment and analyzed with rank and juvenile-mature correlations.

The height superiority experienced by AOG trees was manifested by increases in leaf nodes and internode length, rather than growth flushes. The observation that relatively high (30 C) temperatures inhibit budbreak suggests the possibility that there is a phytochrome response-temperature interaction effect on budbreak. This is probably worth further investigation from the AOG standpoint.

Variation patterns in growth characteristics exhibited by AOG-produced trees revealed the existence of Upper and Lower Peninsula races in Michigan. This conclusion was further supported by differences in seed morphology from parent trees. Correlations of height and budset date with growing season length, temperature, and latitude suggests that different selection pressures between the two peninsulas have resulted with the evolution of different sugar maple races. This evolutionary trend is probably enhanced by both the straits of Mackinac and the alternative long distance around the Great Lakes acting as barriers to gene flow between peninsulas.

If the variation pattern of seedlings observed by application of AOG techniques holds true after outplanting, then the AOG concept would have greatly reduced the time required to determine within and between peninsula and individual seedlot differences. If these results remain true after outplanting, then it may be best to use sugar maple seed sources from the LP for planting in the LP. The establishment of UP trees in the LP would likely result in much reduced height growth relative to LP trees and would consequently result with large decreases in lumber or fiber yields. It may also be advantageous to establish plantings in the UP with northern LP seed sources because they are generally faster growing and are likely well adapted to climatic conditions not too different than that found in the UP. This scheme should at least be advantageous in the eastern UP. Evaluation of outplanted UP and LP sources in both UP and LP environments is necessary before a sound conclusion can be drawn. If this pattern exhibited under AOG conditions remains true when outplanted in both peninsulas, then use of northern LP trees in the UP could also result with greater increases in lumber and fiber yield.

The great height variation observed in seed sources within a county suggests the potential for growth and yield increases by selection and breeding among these superior trees. Certain sources from Iron County which evolved under a relatively cold climate with a short growing season were as tall as the best sources from the fast growing northern LP sources; thus, there is potential for selecting and breeding fast growing genotypes from generally slow growing prevenances.

Application of either gibberellins or defoliation treatments proved to be effective for controlling determinate growth and manipulating height growth of maple seedlings. This discovery eliminates the need for exposing the resting bud of maple to approximately 2000 hours of chilling and allows the grower to produce larger seedlings in a much shorter time. A potential user of GAs for manipulating seedling growth must keep in mind the differences in effectiveness among GAs. GA_7 was more effective than GA_3 for increasing dry weight and height. This difference suggests that GA_7 is possibly more similar or metabolically closer to the natural endogenous active GA than is GA_3. There was also a strong GA-photoperiod interaction response, so the growth response depends upon the photoperiod condition in which seedlings are grown. Topical applications of GAs to resting buds to induce budbreak must be done within about 2 months after budset; however, complete defoliation will induce budbreak for at least 6 months after budset. These growth control techniques should allow increased production capabilities by nurserymen and possibly earlier genetic evaluation of seed sources. Before the above treatments can be applied toward early genetic evaluation, it is necessary to establish whether seed source-hormone or defoliation interactions exist. The use of several foliar sprays with GA_3 and A_{4+7} indicated that such interactions do exist. Possibly single bud or defoliation treatments will not interact with the genotypes. Even though these growth-inducing techniques were only tested on sugar maple, they are likely to be of value in other determinate hardwoods such as black walnut, oaks, hickories, black cherry, etc.

The ability to control root:shoot ratios and total dry weight with BA and GAs should allow the researcher and commercial nurseryman to tailor seedling growth and development to a particular need. Observations of root growth and development using an irrigation-type water-culture system revealed that the GA_7 component of the AOG program can greatly affect root growth and development. Treatment of shoots with GA_7 can inhibit secondary root growth and number. This must be taken into consideration when GA_7 or other GAs are used to increase height growth or possibly to induce budbreak. This inhibition followed several spray applications of GA_7 to the foliage;

perhaps fewer applications or only a single bud treatment will not have such inhibitory effects on root growth. Trees grown under a continuous light photoperiod should not be expected to be affected with respect to growth rate of the tap or secondary roots. GA_7 treatments may be a factor worthy of consideration when preparing trees for outplanting. Improper use could greatly reduce a seedling's chances for survival.

The waterculture system proved to be very useful for allowing continuous observation and measurement of root growth while not interfering with normal growth. Results obtained from observation of sugar maple root growth indicate that the system provides a technique for investigating compensitory root:shoot and root:root relationships, root pruning, translocation studies, environmental effects on roots, genetic variation in root growth, etc. of forest tree species. Observations of root growth patterns of ½-sib progeny under a relatively equal root environment suggest that there is opportunity for selecting root systems that are either fiberous or tap-rooted. The whole spectrum of root growth patterns were observed. They ranged from a single taproot with essentially no secondaries to no taproot with many fiberous roots. This apparent variation pattern needs to be studied in greater detail to determine its genetic basis. Different types of root systems may be developed that are best suited for a particular site or for minimizing root competition on a site by interplanting taprooted and fiberous rooted seedlings.

Triacontanol, as a means for accelerating or modifying sugar maple growth and/or development seems to have little, if any, importance. It did not affect growth and is, therefore, of no value unless there is an interaction response with some environmental factor such as light or temperature.

Manipulation of CO_2 and temperature provides an effective means of regulating seedling growth in the greenhouse environment. Height, dry weight, and leaf area of seedlings grown in enriched CO_2 atmospheres are increased relative to seedlings in ambient CO_2 level. CO_2 levels of at least 2,100 ppm had no apparent detrimental effect on growth. It may be safe to use even higher levels. When CO_2 fertilization is used in the greenhouse, it is important to keep in mind that high CO_2 levels are of no value unless the light intensity is not limiting. Therefore, a high CO_2 level during the night (even under a continuous light photoperiod) is of no value because there is not enough light energy to allow CO_2 fixation.

Growth of sugar maple at relatively cool temperatures (20° C vs 30° C) will increase height growth, leaf nodes, and possibly dry weight. Growth at higher temperatures will usually be very poor; perhaps only 1 leaf node being produced before budset. High temperatures inhibit budbreak of maple. This situation may also be true for other difficult to grow hardwoods.

The production of sugar maple seedlings under a constant CO_2 level or temperature will probably result in the photosynthetic and respiratory mechanisms being adapted to those conditions. If trees are grown under strictly high CO_2 levels or high (or low) temperature and then outplanted in a normal (300 ppm) CO_2 and temperature environment, subsequent growth will likely be considerably reduced. Photosynthesis and respiration will probably readapt to the new temperature environment within 1 to 2 months, thus the growth loss may not be significant. This may not be true for CO_2-adapted trees because it is not known how much time the readaptation response requires. This potential problem could likely be avoided by growing trees under several CO_2 environments before outplanting, i.e., high during the day and low at night. Trees then may be adapted to a wide temperature range.

The regulation of temperature, CO_2, photoperiod, and plant growth regulators proved to be important in accelerating and manipulating sugar maple seedling growth in a greenhouse environment. Consequently, these factors should be considered for use by both researchers and commercial nurserymen. AOG also shows potential for enabling forest geneticists to make earlier genetic evaluations of sugar maple. Although this study was conducted on sugar maple, the results can probably be applied to most tree species in general and especially for determinate hardwoods.

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