VARIATION AMONG YELLOW BIRCH POPULATIONS IN PHOTOSYNTHETIC RESPONSE TO VARYING LIGHT INTENSITY AND TEMPERATURE

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Abstract .--Yellow birch seedlings from 6 populations were grown indoors and examined at 4 and 12 weeks to determine if these populations differed in photosynthetic response to changing light intensity and temperature. On average, photosynthetic efficiency decreased with increasing temperature and increased with increasing light intensity. There were no differences in average photosynthetic efficiency among populations, primarily because of large population interactions with light intensity and temperature. The magnitude of photosynthetic response to changing light intensity and temperature decreased with seedling development. However, there were no apparent geographic or elevational patterns to differences in the responses to either light intensity or temperature, suggesting random as opposed to adaptive population variation.

INTRODUCTION

Large amounts of genetic diversity still exist in many woody species, and this makes these populations a unique resource. Comparatively few types of organisms remain which have large populations with substantial genetic variation, and which have not become subject to manipulation of gene frequencies based on artificial selection. Thus, woody plants are ideal subjects for study of genetic variability and adaptive differentiation.

Because of its high survival value, photosynthesis, and its relationship to environmental parameters, should be subject to relatively intense natural selection pressures. If these selection pressures are great enough to offset gene migration, genetic differentiation in the photosynthetic apparatus should result. Photosynthesis, and the photosynthetic response to changes in environmental variables, should be excellent parameters for characterizing genetic variability and adaptational differentiation within a species. However, photosynthesis is time-consuming and comparatively difficult to measure accurately, and studies of adaptational patterns of genetic variation in photosynthesis are relatively rare. In fact, they are almost non-existent for woody angiosperms.

The research reported herein examines population variation in photosynthetic rate and the nature of changes in photosynthetic rates with changes in light intensity, temperature, and age in seedlings of *Betula alleghaniensis* Britt., an important component of the Northern Hardwoods forest biome.

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MATERIALS AND METHODS

Plant Material

Six populations of yellow birch were selected to encompass a major portion of the latitudinal extent of the species' range (West Virginia to Vermont), and the elevational distribution of the species at a specific latitude (67 m to 732 m) (Table 1). Open-pollinated seeds were collected from 5 trees per population and 2000 seeds from each tree within each population were bulked by population and used to grow seedlings.

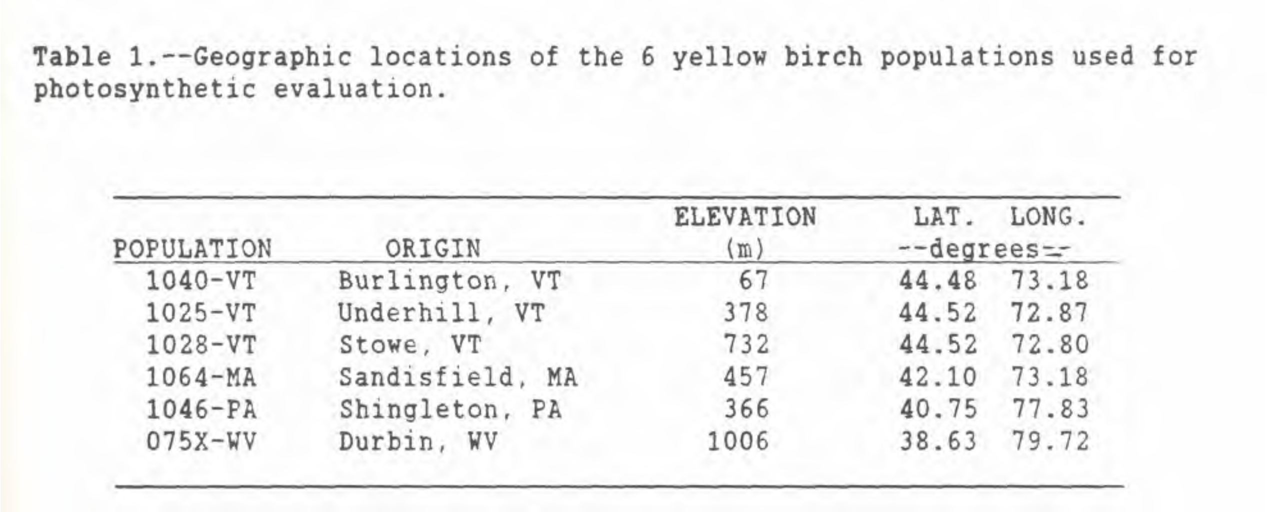


Table 1.--Geographic locations of the 6 yellow birch populations used for photosynthetic evaluation.

POPULATION	ORIGIN	ELEVATION (m)	LAT.	LONG.
			--degrees--	
1040-VT	Burlington, VT	67	44.48	73.18
1025-VT	Underhill, VT	378	44.52	72.87
1028-VT	Stowe, VT	732	44.52	72.80
1064-MA	Sandisfield, MA	457	42.10	73.18
1046-PA	Shingleton, PA	366	40.75	77.83
075X-WV	Durbin, WV	1006	38.63	79.72

Seedlings representing each population were grown to 4 and 12 weeks of age. For both ages, seedlings were grown in 25 cm diameter pots containing a standard greenhouse soil mix (1/3 peat, 1/3 perlite, 1/3 sandy loam). Pots were located in a controlled-environment growth room with temperatures ranging from 23°C to 26°C, under an 18-hour photoperiod. Light was provided by a combination of cool and warm white fluorescent bulbs yielding a light intensity of 8070 lux. Following germination, pots were thinned to leave either 3 (age 4 weeks) or 2 (age 12 weeks) seedlings evenly spaced within the pot.

In order to comply with the statistical assumption of independence of observations, a different group of seedlings representing each population were used to generate photosynthesis measurements at each age. Space limitations prevented the simultaneous growth of seedlings of the 2 ages. Thus, seedlings for analysis at each age were grown sequentially. Seedlings representing each population were grown to a randomly chosen age (either 4 or 12 weeks), subjected to photosynthetic measurement, and the procedure repeated for the remaining age.

Measurement of Photosynthesis

Photosynthesis was measured by CO_2 depletion using an infrared gas analyzer operating in a closed-cuvette system. Net photosynthetic rates were determined from the time required to reduce CO2 concentrations within the cuvette from 320 to 280 ppm CO_2. Prior to photosynthetic measurement, seedlings to be analyzed were removed from the growth room and placed in an acclimation chamber with light intensity and temperature set to duplicate cuvette conditions. Seedlings were allowed to acclimate to these conditions for 30 minutes prior to analysis (a duration we previously determined to be adequate for acclimation). Before being placed into the cuvette, pots were sealed with plastic to prevent gas exchange with soil microbes. Immediately following measurement of photosynthesis, leaf area was determined for seedlings in each pot; these measurements were used to express photosynthesis on a per unit leaf area basis ($mgCO_2 \cdot hr^{-1} \cdot dm^{-2}$), i.e., photosynthetic efficiency (PE).

Study Design and Statistical Analyses

The study followed a split-split plot design with a factorial arrangement of treatments, and 3 replications. Temperatures, light intensities, and populations were treated as main plots, sub-plots, and sub-sub plots, respectively, and each population was represented by 27 pots (3 temperatures X 3 light intensities X 3 replications)at each age. Photosynthetic rates were determined at all 9 combinations of 3 light intensities (8070, 29590, and 51110 lux) and 3 temperatures (20°C, 25°C, and 30°C) .

On the first measurement day, for a given seedling age, the cuvette was set to 1 of the 3 temperatures, chosen at random. A light intensity was randomly chosen, and photosynthesis was measured for 1 pot per population. This process was repeated for the remaining 2 light intensities. On the following 2 days, the cuvette temperature was changed, and the procedures repeated in the same fashion, using separate pots for each population at each light intensity-temperature combination. Since 3 days were required to complete the photosynthetic measurements for each replication, it took 9 days around each nominal measurement date to complete the photosynthetic measurements at each age. Seedling growth during this 9-day interval was blocked by replication into 3-day periods. Thus, to a large extent, any variability introduced by the extended measurement period was accounted for in the statistical design.

Photosynthetic rates were subjected to analyses of variance, following the split-split plot design, both at the individual ages and combined over the 2 ages, with pot means as observations. Significant interactions were partitioned into proportions contributed by each population through orthogonal techniques described by Shelbourne (1972).

RESULTS AND DISCUSSION

Age Effects

Yellow birch seedlings had significantly (p=0.05) lower PE at 12 weeks (3.42 mg $CO_2 \cdot hr^{-1} \cdot dm^{-2}$) than at 4 weeks (4.38 mg $CO_2 \cdot hr^{-1} \cdot dm^{-2}$). Decreased FE with increasing age has been reported for a number of species, and has been attributed to a variety of factors. Increased self-shading in the older and larger seedlings could be partly responsible for decreasing PE with age. Another likely explanation for this pattern was advanced by Ledig et al

(1977), who speculated that decreasing PE with increased seedling age might result from an increase in the ratio of respiring tissue (stems) relative to photosynthetic tissue (leaves) with seedling development.

Temperature Effects

Seedling PE decreased significantly with increases in temperature at age 4 weeks; at age 12 weeks, PE differences among temperature treatments were not significant (Figure 1). Thus, the major effect of temperature variation on PE was an overall decrease in PE at higher temperatures for 4 week old seedlings; a response which disappeared by age 12 weeks. Respiration rates are known to be influenced by temperature (Kramer and Kozlowski 1979), and lower PE at higher temperatures most likely resulted from increased respiration rates at these temperatures. Reasons for the higher PE at 20°C and 25°C in the 4 week seedlings compared with the 12 week values are unknown. However, McNaughton (1973) also found that PE of some *Typha latifolia* populations exhibited a strong temperature dependence when young, which then moderated with age.

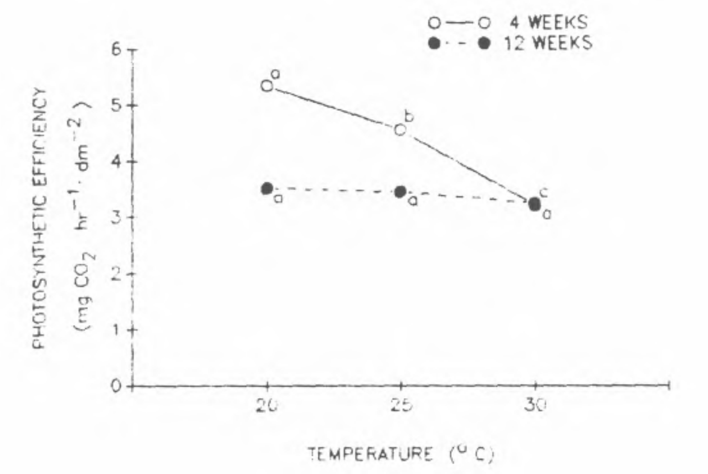


Figure 1.-- Photosynthetic efficiency of yellow birch seedlings (averacr of 6 populations) at 2 seedling ages plotted against temperature. Each value is a mean of 54 "pot-mean" observations. Values at a given age followed by a different letter are statistically different (p=0.05).

Light Intensity Effects

As expected, there were significant increases in PE with increases in light intensity for both 4 and 12 week old seedlings (Figure 2). PE was slightly higher at all light intensities for seedlings at age 4 weeks than at age 12 weeks, but the 4 and 12 week curve shapes were quite similar and there was no light intensity interaction with age.

Seedlings did not reach a light saturation point within the range of light intensities employed. Logan (1970) reported saturation light intensities for 4-year old yellow birch grown outdoors in both shade and full sun. In his study, sun-grown yellow birch had a light saturation of about 26900 lux; light saturation of shade-grown yellow birch was about 12912 lux. It is interesting that seedlings in the present study continued to increase their PE with increasing light intensity even though they were grown at a relatively low light intensity (8070 lux). It is possible that relatively young, indoor- and continuously-grown seedlings have higher light saturation values than plant material grown in outdoor environments.

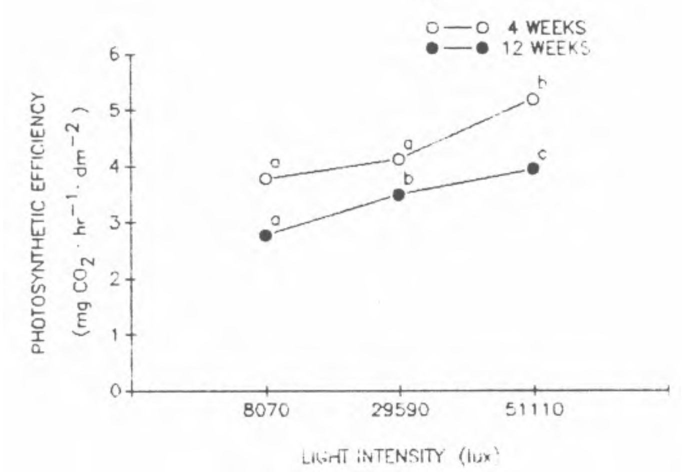


Figure 2.-- Photosynthetic efficiency of yellow birch seedlings (average of 6 populations) at 2 seedling ages plotted against light intensity. Each value is a mean of 54 "pot-mean" observations. Values at a given age followed by a different letter are statistically different (p=0.05).

Population Effects, and Interactions of Populations with Light Intensity and Temperature

There were no significant differences in PE among populations for seedlings at both 4 and 12 weeks of age (Table 2). The lack of population differences is due, at least in part, to the large and significant interactions of population with both light intensity and temperature which occurred at both 4 and 12 weeks of age.

Table 2.-- Photosynthetic efficiency of each of the 6 yellow birch populations at each of 2 ages. Each value is the mean of 27 'pot-mean' observations. Differences in PE among populations at both ages were not statistically significant (p=0.05).

POPULATION NUMBER AND ORIGIN	PHOTOSYNTHETIC EFFICIENCY (mg CO2.hr-1.dm-2) 4 WEEKS	12 WEEKS
1040-VT	4.836	3.461
1025-VT	4.730	3.407
1028-VT	4.393	3.262
1064-MA	4.093	3.588
1046-PA	4.210	3.608
075X-WV	3.994	3.171

<u>Population interactions with temperature</u> -- There were large and significant population X temperature interactions at both ages. Individual population responses to temperature are plotted for both ages in Figure 3.

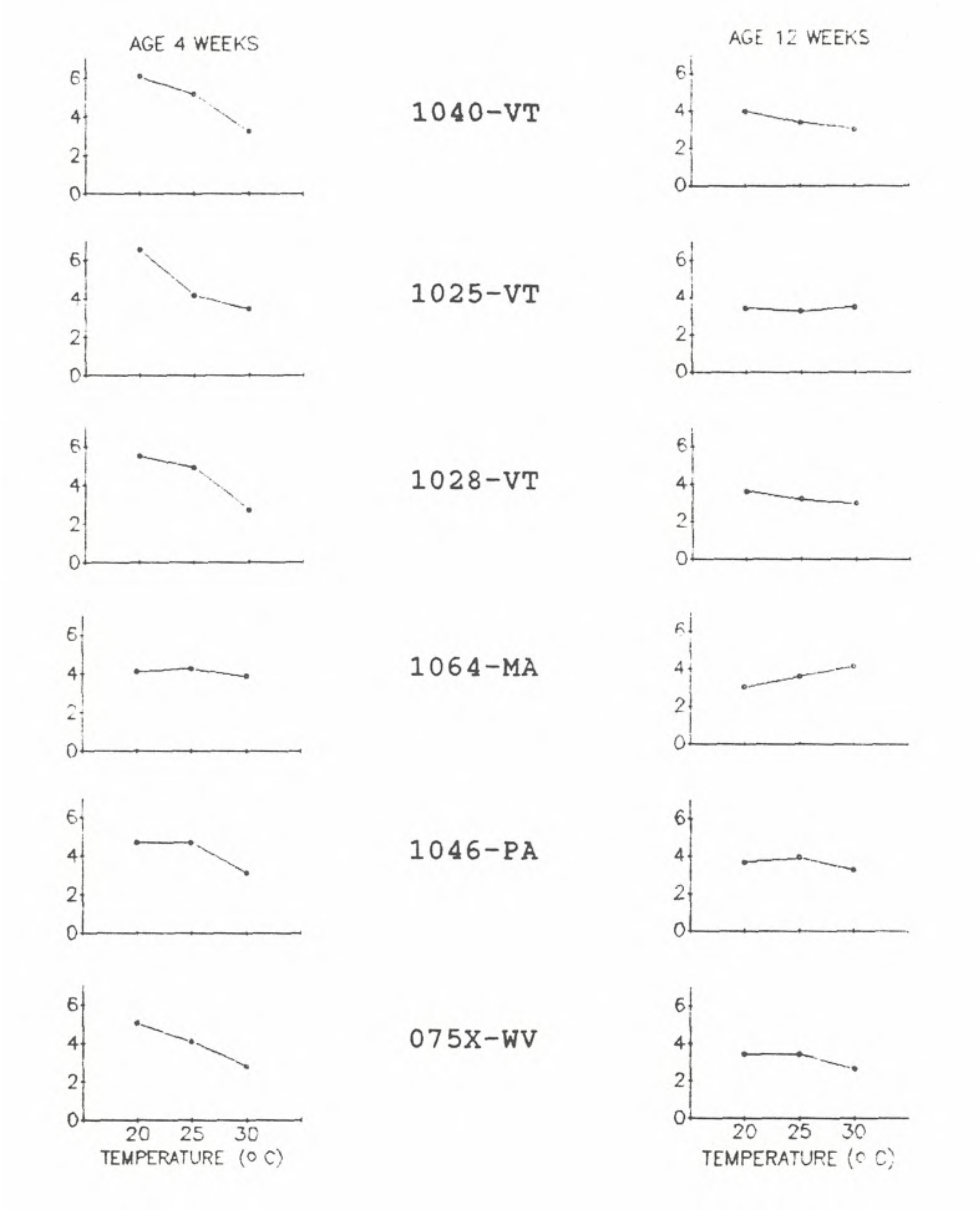
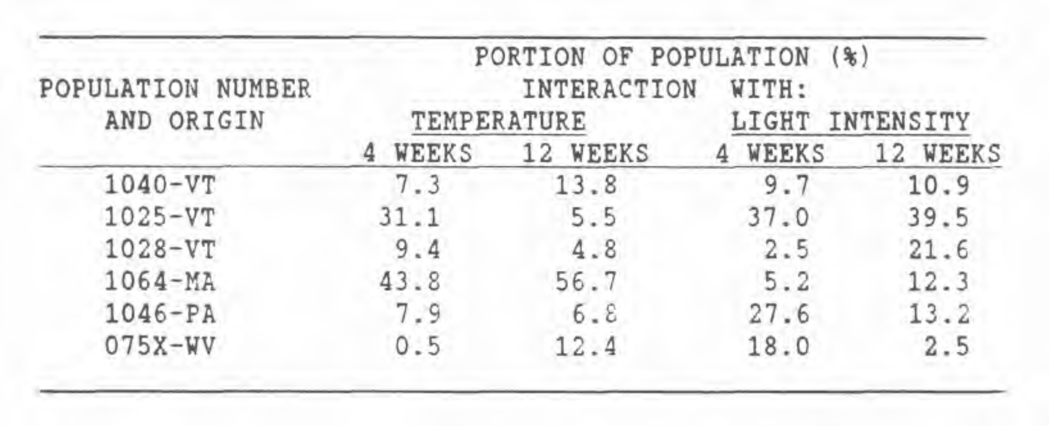


Figure 3.-- Photosynthetic efficiency plotted against temperature for each of the 6 yellow birch populations at each seedling age. Plotted values are means of 9 "pot-mean" observations.

Although for most populations there was a general decline in PE with increasing temperature, populations differed in the magnitude and pattern of their temperature responses. And, populations generally changed their temperature response with age. Partitioning of the population X temperature interaction at both ages yields the contribution of each population to the interaction (Shelbourne 1972). These interaction components are shown in Table 3. The greatest difference among populations in response to temperature at both ages was attributed to population 1064-MA (Table 3, Figure 3). At age 4 weeks, when other populations exhibited decreased PE with increasing temperature, this population was essentially homeostatic in response to temperature. At 12 weeks, population 1064-MA increased PE with increasing temperature, while other populations were either homeostatic or decreased PE with increasing temperature. Reasons for the consistent anomalous behavior of this population are unknown.

Table 3.-- Partitioning of sums of squares attributable to population interactions with temperature and light for seedlings grown for 4 and 12 weeks.



POPULATION NUMBER AND ORIGIN	PORTION OF POPULATION (%) INTERACTION WITH: TEMPERATURE		LIGHT INTENSITY	
	4 WEEKS	12 WEEKS	4 WEEKS	12 WEEKS
1040-VT	7.3	13.8	9.7	10.9
1025-VT	31.1	5.5	37.0	39.5
1028-VT	9.4	4.8	2.5	21.6
1064-MA	43.8	56.7	5.2	12.3
1046-PA	7.9	6.8	27.6	13.2
075X-WV	0.5	12.4	18.0	2.5

Although there were no general geographical patterns to population response to temperature, there was a tendency at age 4 weeks for Vermont populations (1040-VT, 1025-VT, 1028-VT) to exhibit the most abrupt decline in PE with increasing temperature. By 12 weeks, Vermont populations were not distinct as a group.

<u>Population interaction with light intensity</u>--There was a large and significant interaction between population and light intensity at both age 4 and 12 weeks. Individual population responses to changing light intensities are plotted for both ages in Figure 4. Although populations generally increased PE with increases in light intensity, there were differences among populations in the pattern and magnitude of their PE-response to light intensity, and most populations changed their pattern of response with age. Partitioning of the population X light intensity interactions at each age (Shelbourne 1972) yielded the interaction components shown in Table 3. At both ages, the largest contribution to the interaction sums of squares was made by population 1025-VT. This population exhibited a very large relative increase in PE with increases in light intensity above 29590 lux at both 4 and 12 weeks (Figure 4).

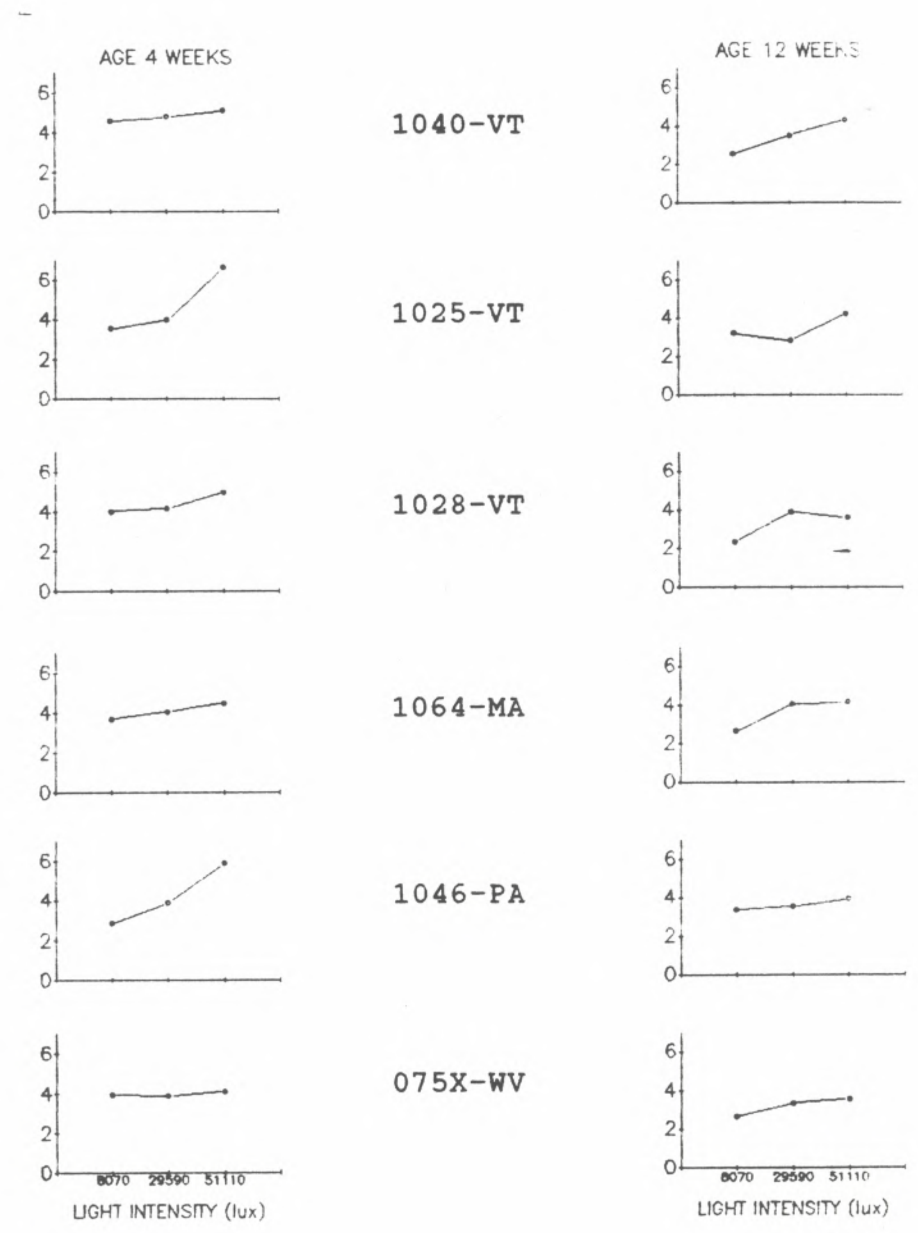


Figure 4.-- Photosynthetic efficiency plotted against light intensity for each of the 6 yellow birch populations at each seedling age. Plotted values are means of 9 "pot-mean" observations.

In contrast to seedlings from population 1025-VT, seedlings from populations 1028-VT, 1064-MA, and 075X-WV showed little or no increase in PE between 29590 and 51110 lux at age 12 weeks (Figure 4). Although, when averaged for all populations, seedlings did not appear to reach light saturation, these individual population curves indicate that light-saturation may have been reached for these 3 populations at age 12 weeks. It is interesting that some populations apparently reached light saturation at age 12 weeks and not at age 4 weeks, even under the same light intensities. Although the adaptive significance of this is not readily apparent, the developmental changes in PE response to light intensity seem to be sufficiently great to alter not only the general magnitude of these responses, but to shift saturation light intensities.

Population interactions with light intensity and temperature -- There were significant population X temperature X light intensity interactions at both seedling ages (Figure 5). It is apparent that populations differ in their response to temperature, and that the temperature responses themselves differ with light intensity. A few apparent trends are discernable. Comparison of the 4 week and 12 week curves in Figure 5 reveals a tendency toward stabilization of population PE-response to environmental change with increasing age. That is, the magnitude of population responses to changing light intensity and temperature decreased during development. And, for a given population, the individual light intensity-PE response curves plotted over increasing temperature are more similar in shape to one another at age 12 weeks than at 4 weeks. For population 1040-VT, for example, at age 4 weeks there is a complete reversal in PE rankings for light intensities at 20°C when compared with 300 values, while at age 12 weeks, curve shapes for all 3 light intensities are similar.

The general trend toward more homeostatic responses to light intensity and temperature with increasing age was the strongest developmental pattern to emerge from this study, and this developmental pattern has been documented in other species. For example, Pinus rigida seedlings decreased their PE response to changing light intensity and temperature with age (Ledig and Clark 1977; Ledig et al 1977), and McNaughton (1973) found that Quebec ecotypes of Typha latifolia broadened their PE response to differing temperatures with increasing leaf age. This broadening of response was interpreted by McNaughton as a method of integrating assimilation with increasing temperatures in spring. According to this interpretation, young leaves are physiologically organized to achieve maximum assimilation in a relatively narrow and cooler range, while older leaves broaden the temperature range under which maximum assimilation occurs, sacrificing some peak efficiency for a wider temperature optima.

It is possible that this explanation holds true for other northern plant species. These arguments, if true, would be equally applicable to most species which occupy regions with low spring temperatures, including yellow birch. However, we found no geographical patterns relative to developmental broadening of environmental response, at least within the latitudinal and altitudinal extent of populations included in this study. This implies that either the environment is functionally cool enough within the sampled portion of the latitudinal/elevational range of yellow birch so that the broadening of PE response is common to most populations, or that the observed broadening of the PE response with age is a generalized developmental phenomenon unrelated to northern environments. Studies which generate the type of data needed to address this issue are rare, and there have not been sufficient photosynthetic data collected across differing plant ages to resolve the question of adaptive significance of the broadening of PE response to environmental variation with age.

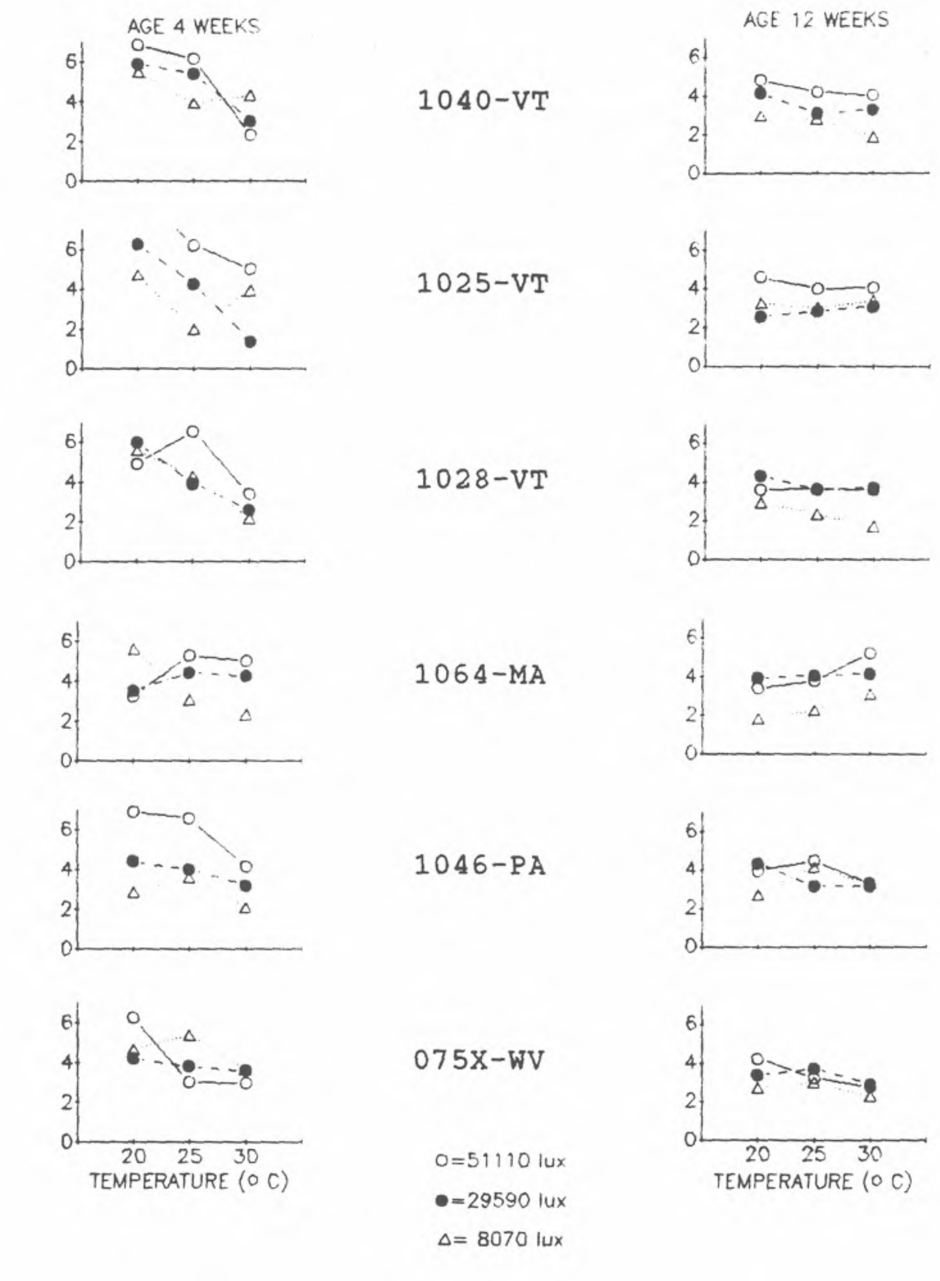


Figure 5.-- Photosynthetic efficiency as a function of light intensity and temperature for the 6 yellow birch populations at each seedling age. Each value is a mean of 3 "pot-mean" observations.

Although there are no apparent adaptational explanations for the differential responses of these seedlings to light intensity/temperature conditions, large developmental changes in PE response to light intensity and temperature in yellow birch seedlings emerged from this study. Yellow birch seedlings are developmentally dynamic in terms of their photosynthetic responses to changing light intensity and temperature. The possibility of large qualitative and quantitative developmental changes in physiological responses should be recognized in investigations using young woody plant material.

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