

ADAPTATION OF SUGAR MAPLE POPULATIONS ALONG ALTITUDINAL GRADIENTS: PHOTOSYNTHESIS, RESPIRATION, AND SPECIFIC LEAF WEIGHT¹

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ABSTRACT

Sugar maple seeds were collected from populations spaced along two altitudinal gradients in the White Mountains of New Hampshire. When grown in a uniform environment, progeny of stands less than 0.8 km apart differed significantly in photosynthesis, respiration, and leaf characteristics, despite a lack of physical barriers to gene migration. Sugar maple is a long-lived (200–300 yr) species with continuous distribution, but adaptive adjustment along the altitudinal gradient has occurred in only 8,000 yr, the time since colonization of the White Mountains in the wake of glacial melting. Photosynthesis was highest in progeny from high-altitude populations, representing the species' ecological margin. High-altitude populations also had the lowest specific leaf weight (SLW), the ratio of leaf weight to leaf area, providing a highly cost-effective photosynthetic system, probably the result of natural selection in a short growing season. Respiration rates were also highest in populations native to high altitudes and constitute the cost of maintaining the photosynthetic machinery at high capacity. Photosynthesis tended toward a minimum and SLW to a maximum at mid-elevations. There were parallel patterns on both gradients, suggesting parallel evolution. There were no differences among sugar maple populations in photosynthetic response to temperature, in contrast to observations on balsam fir in the same locality.

ALTITUDINAL GRADIENTS are ideal situations in which to study physiological adaptation with a minimum of confounding biogeographic influences, and, therefore, a maximum of interpretability. Along altitudinal gradients, the environment changes rapidly over short distances. Temperature, growing season, barometric pressure, and soil depth decrease with altitude while radiation flux density, precipitation, wind speed, and snow cover generally increase.

Adaptation to altitudinal gradients has been well documented, particularly in the early work of the Carnegie Institution (e.g., Clausen, Keck and Hiesey, 1940, 1958; Milner and Hiesey, 1964a, b). But in most investigations, populations were separated by many miles, limiting gene migration and facilitating differentiation. Whether adjacent populations on the same slope could adapt to climatic differences along

the altitudinal gradient was left unanswered. However, local differentiation has occurred in grasses as a response to heavy metal pollution (see Antonovics, Bradshaw and Turner, 1971 for a review), in several herbaceous species at the boundary between serpentine and granitic soils (Kruckeberg, 1951), and in forest trees in montane environments (e.g., Rehfeldt, 1974; Squillace and Bingham, 1958).

Populations of balsam fir (*Abies balsamea* [L.] Mill.), distributed from 731 m to 1,463 m mean sea level (msl) along a continuous altitudinal gradient in the White Mountains of New Hampshire, have differentiated with respect to their temperature optimum for photosynthetic CO₂-uptake (Fryer and Ledig, 1972). In balsam fir, evolution of a clinal series of "temperature races" occurred despite the fact that it is an outbreeding, anemophilous species and that species distribution is essentially continuous along the gradient. Distances between sampled populations averaged less than 0.8 km. A similar pattern in snow gum (*Eucalyptus pauciflora* Sieb. ex Spreng.) was documented in an elegant series of papers by Slatyer and coauthors (see Slatyer, 1978 and earlier).

Our objective in the present study was to test the hypothesis that sugar maple (*Acer saccharum* Marsh.) populations had differentiated along altitudinal gradients. We compared photosynthesis, respiration, and gross leaf mor-

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phology in the progeny of trees of different altitudinal origin grown in a uniform environment. In particular, we sought to determine whether altitudinal populations of sugar maple, like balsam fir, had differentiated in temperature response. In an earlier study, Ledig (1971) found that sugar maple populations distributed from 174 m to 783 m msl in the White Mountains differed in many aspects of leaf morphology, but it was impossible to separate environmental and genetic effects.

MATERIALS AND METHODS—Materials—In October 1971, seeds were collected from sugar maples distributed along two altitudinal transects in the White Mountains National Forest. For the first transect, seeds were collected at five elevations along a single drainage in and adjacent to the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. All stands were located on a southeastern aspect. At each altitude, seeds were collected from seven trees. Sugar maple, beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton), were codominants in the forest, and sugar maple was more or less continuous along the gradient. Collection points were equispaced along the altitudinal axis at intervals of 152 m (500 ft) ranging from base elevation on the Pemigawasset River (174 m) to the highest altitude (783 m) at which sugar maple could be found. The total horizontal distance was only 5.23 km (3.25 miles) and the distance between collections became progressively shorter at higher altitudes. There was less than 0.8 km (0.5 miles) between collection points at 783 m and 631 m msl.

The second transect was located along Route 118, called the Sawyer Highway, running southwest from North Woodstock, New Hampshire above Jackman Brook. The Sawyer Highway lies ca. 4 to 10.5 km (2.5 to 6.5 miles) north of the Hubbard Brook transect. Seeds were collected from seven trees at each of five altitudes. Collection points were at equal intervals of 113 m (375 ft) from 305 m (1,000 ft) to 762 m (2,500 ft) msl. The lower altitude was essentially at base for the locality and the upper altitude was the highest at which sugar maple occurred. Slope aspect on the Sawyer Highway transect was more easterly than that at Hubbard Brook. Total distance from top to bottom was 7.1 km (4.4 miles).

Climate of the forest is humid continental. Annual precipitation in the study area is 123 cm. The high altitudes are characterized by cooler summers, colder winters, deeper snowpack, and shorter growing seasons than low altitudes. Based on phenological observations,

Mahall and Bormann (1978) estimated there was a 5-day difference in length of growing season between 500 and 800 m msl. Details of the climate, soils, and cutting history of the Hubbard Brook watershed can be found in Likens et al. (1967) and Bormann and Likens (1979), and vegetation analyses of a portion of the Hubbard Brook transect were presented by Bormann et al. (1970) and Siccama, Bormann and Likens (1970).

Seeds were stratified for several months and then sown in clay pots ca. 10 cm diameter on May 22, 1972. Because of failures in germination, mostly among high-altitude populations, some replacements were sown July 24, 1972. For purposes of this experiment, seeds from each of the seven trees per elevation were mixed in equal proportion; i.e., family identity within elevation was not retained. Pots were placed in a greenhouse at New Haven, Connecticut, and seedlings grown with supplemental illumination to provide a 20-hr photoperiod. The potting mix was soil, peat, sand, and perlite in a 2:2:1:1 ratio. Seedlings were fertilized with a soluble NPK fertilizer at 3-wk intervals. Day temperature peaked at ca. 25 C and night temperature was maintained at 20 C. Light flux density on clear days varied with location on the bench from 390 to 780 $\mu\text{E m}^{-2} \text{sec}^{-1}$ (400 to 700 nm), with most readings from 390 to 585 $\mu\text{E m}^{-2} \text{sec}^{-1}$, measured with a Lambda Instruments model LI-190SR quantum sensor. Seedlings were rotated among positions on the bench at frequent intervals. At the time of photosynthetic measurement, seedlings varied in age because of differences in sowing date, but all had ceased stem elongation and formed resting buds. A few had produced a second, small flush of immature leaves and stem.

Methods—During the period September 19 to 28, pots were removed from the greenhouse and seedling CO_2 -exchange rates measured using infrared gas analyzers (IRGA). The above-ground portions of the seedlings were sealed in cylindrical, plexiglass cuvettes. The rate of CO_2 -exchange, determined over the range 280 to 320 ppm with an IRGA operated in a closed system, represented simultaneous CO_2 -exchange of 1, 2, or 3 seedlings, depending upon the number of survivors per pot. The mean number was 1.9 and averaged nearly the same for each population. Procedures were similar to those described by Ledig and Clark (1972), except the light source was a bank of 36, 150-w Sylvania Cool-lux PAR2, wide-flood lamps.

The cuvettes were enclosed in a temperature-

controlled chamber, and solenoid valves switched seedlings from standby, during which humidified air was passed through the cuvette, to the IRGA circuit. Air flow rate was 6.5 l min^{-1} . Given cuvette diameter, this would correspond to a minimum air speed of 51.3 cm min^{-1} . However, the cuvettes were constructed to achieve turbulent flow, and observations with a hot wire anemometer indicated actual flow was highly turbulent with air speeds varying from 0.3 to over 1.8 km hr^{-1} in an empty cuvette. Smoke tests indicated no dead spots within the cuvette.

Three series of measurements were made: 1) a temperature series at 5, 10, 15, 20, 25, 30, 35 C measured at $260 \mu\text{E m}^{-2} \text{ sec}^{-1}$, which was just below saturating light flux densities for 3-yr-old seedlings and single leaves according to previous reports (Logan and Krotkov, 1969; Hesketh, 1963); 2) a temperature series in the dark over the same range of temperatures; and 3) a light series at 0, 65, 135, 260, and $730 \mu\text{E m}^{-2} \text{ sec}^{-1}$ at both 15 C and 25 C. There were four replications in each case. Seedlings from the Hubbard Brook and Sawyer Highway transects were measured and analyzed separately. All measurements on five populations, representing one complete replication of an altitudinal transect, were made on the same day. The order of measurement was from low to high temperature and from high to low light. At any given temperature, measurement of dark respiration followed measurement of photosynthesis after an adjustment period. Temperature refers to exit air temperature measured by copper-constantan thermocouples. Temperature never deviated from the desired value by more than 1.5 C. Within a cuvette the temperature was virtually constant during the period of adjustment and measurement. Light flux density was measured at pot height with a Weston illumination meter calibrated against Lambda Instruments LI-190SR quantum sensor. Seedlings were allowed 20 min at a new light or temperature before measurement. Preliminary work indicated no changes for at least several hours.

Seedlings were harvested following measurement of CO_2 -exchange. Leaf area was determined immediately with a leaf area meter constructed on the capacitance-shading principle (improved from an original designed at Brookhaven National Laboratory). Leaf and stem weight were measured after several days drying at 90 C. Specific leaf weight (SLW) was calculated as $\text{mg leaf weight cm}^{-2} \text{ leaf area}$.

Analyses of photosynthesis were made on the basis of leaf dry weight and leaf area. Respiration was analyzed on a shoot dry weight

(i.e., leaf plus stem dry weight) basis. For both the temperature series in the light and in the dark, data for each transect were analyzed as factorials with 4 blocks $\times$ 5 populations $\times$ 7 temperatures. For the light series, data were analyzed as a factorial with 4 blocks $\times$ 5 populations $\times$ 2 temperatures $\times$ 5 light intensities. Temperature and light were considered fixed effects. In the temperature series at $260 \mu\text{E m}^{-2} \text{ sec}^{-1}$, one observation at 10 C was missing for the Hubbard Brook transect. For the temperature series in the dark, total shoot weights were unavailable for one population in one replication of the Sawyer Highway transect. For the analysis of variance, these missing values were estimated by interpolation, but the estimates did not change the outcome because of the high precision of the analysis. Regression analyses were used to investigate the relationships of photosynthesis, respiration, and SLW to altitude and the interrelationships of these variables with each other.

RESULTS—Photosynthetic response to temperature—Inspection of mean rates indicated that nearly all populations have an optimum for photosynthesis at 25 C; i.e., the maximum rate of photosynthesis occurred at 25 C for 9 of the 10 populations. In the single exception, the maximum rate occurred at 20 C but was not significantly higher than the rate at 25 C (Fig. 1). For most populations, rates of photosynthesis at 20 and 25 C were not greatly different. When rates for individual observations were examined, there was some variation in the temperature optima, but differences were not significant. Analysis of variance indicated no population $\times$ temperature interaction, indicating that photosynthetic response to temperature was similar in all populations. Differences among populations in mean rate were highly significant, and were due in part to the high rates of the high-altitude populations; however, the mid-altitude population on the Hubbard Brook transect had a significantly lower photosynthetic rate than any of the other populations.

Respiratory response to temperature—Rate of respiration increased rapidly with temperature (Fig. 2). Q_{10} was high, decreasing from 3.3 between 5 and 10 C to 2.8 between 25 and 30 C. There were no population $\times$ temperature interactions for Sawyer Highway, indicating that all populations responded in the same way to increasing temperature. For Hubbard Brook, interactions were significant; the high-altitude population was more responsive to increasing temperature than mid-altitude populations.

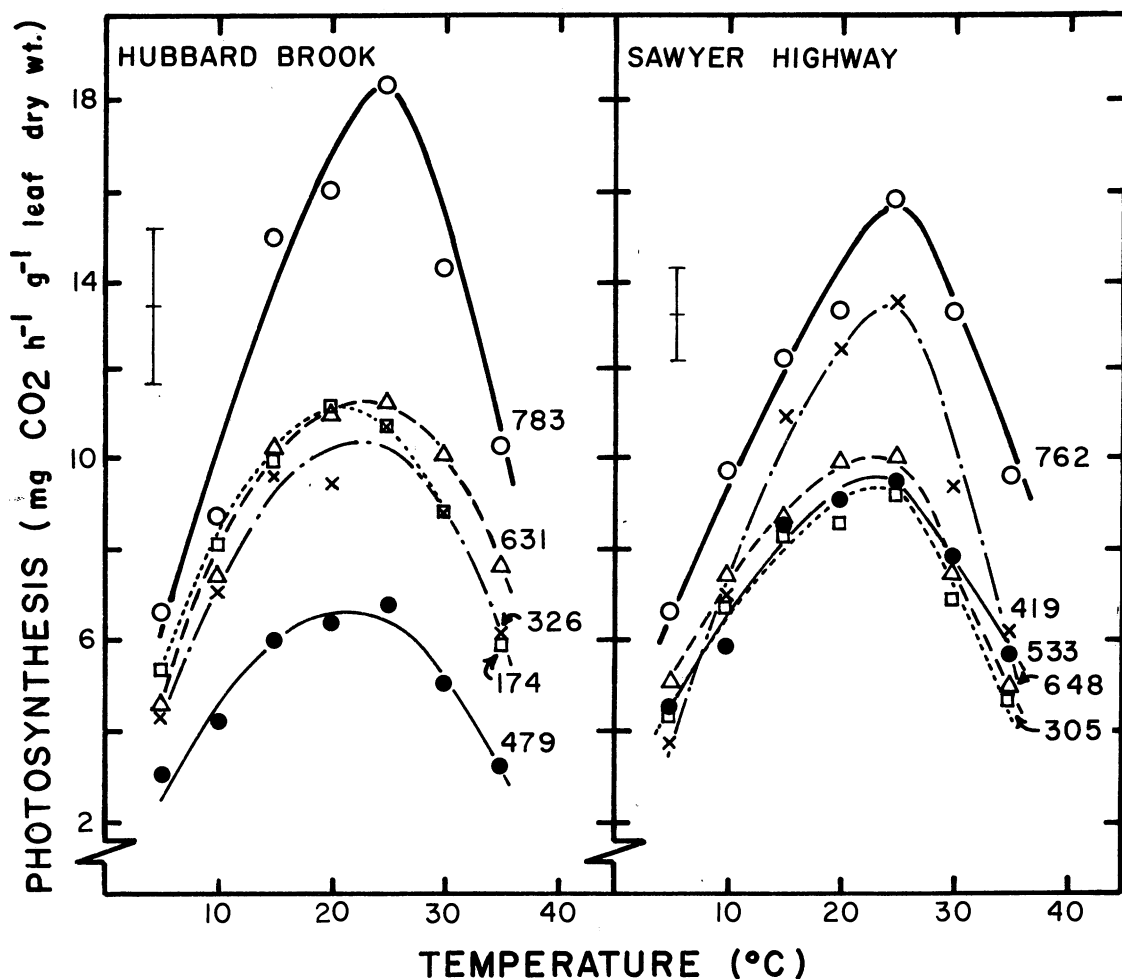


Fig. 1. Photosynthesis at $260 \mu\text{E m}^{-2} \text{sec}^{-1}$ in relation to temperature for progeny of sugar maple from two altitudinal transects in the White Mountains, New Hampshire. Altitude is indicated in meters. Vertical bars are 2 S.E. ($n = 4$).

The difference among populations was a result of the markedly higher rate of respiration of the high-altitude populations on both transects, according to Duncan's new multiple range tests.

Photosynthetic response to light at 15 and 25 C—There was no interaction effect between light flux density and temperature; i.e., light response at 15 C was essentially the same as at 25 C. Neither were there any differences in population response to light flux density on a leaf area basis, but there were differences on a leaf dry weight basis. The interaction may have resulted from differences either in the initial slope of the light response curve or in the saturation point (Fig. 3). More observations are needed at low light to determine the nature of the interaction. Several populations showed a

slight increase in photosynthetic activity between 260 and $730 \mu\text{E m}^{-2} \text{sec}^{-1}$, but differences were not significant. At $260 \mu\text{E m}^{-2} \text{sec}^{-1}$ and either 15 or 25 C, rates of photosynthesis were already 90% of rates at $730 \mu\text{E m}^{-2} \text{sec}^{-1}$ and in fact, rates at $65 \mu\text{E m}^{-2} \text{sec}^{-1}$ were already 80% of rates at $730 \mu\text{E m}^{-2} \text{sec}^{-1}$.

Relation of photosynthesis and respiration to altitudinal origin—In both the temperature (Fig. 1) and the light series (Fig. 3), rates of photosynthesis on a leaf weight basis were highest in the high-altitude populations of both the Hubbard Brook and the Sawyer Highway transects. On the Hubbard Brook transect, the mid-altitude population had significantly lower rates of photosynthesis than any other population, and rates of photosynthesis increased again toward lowest altitudes. Maximum rates

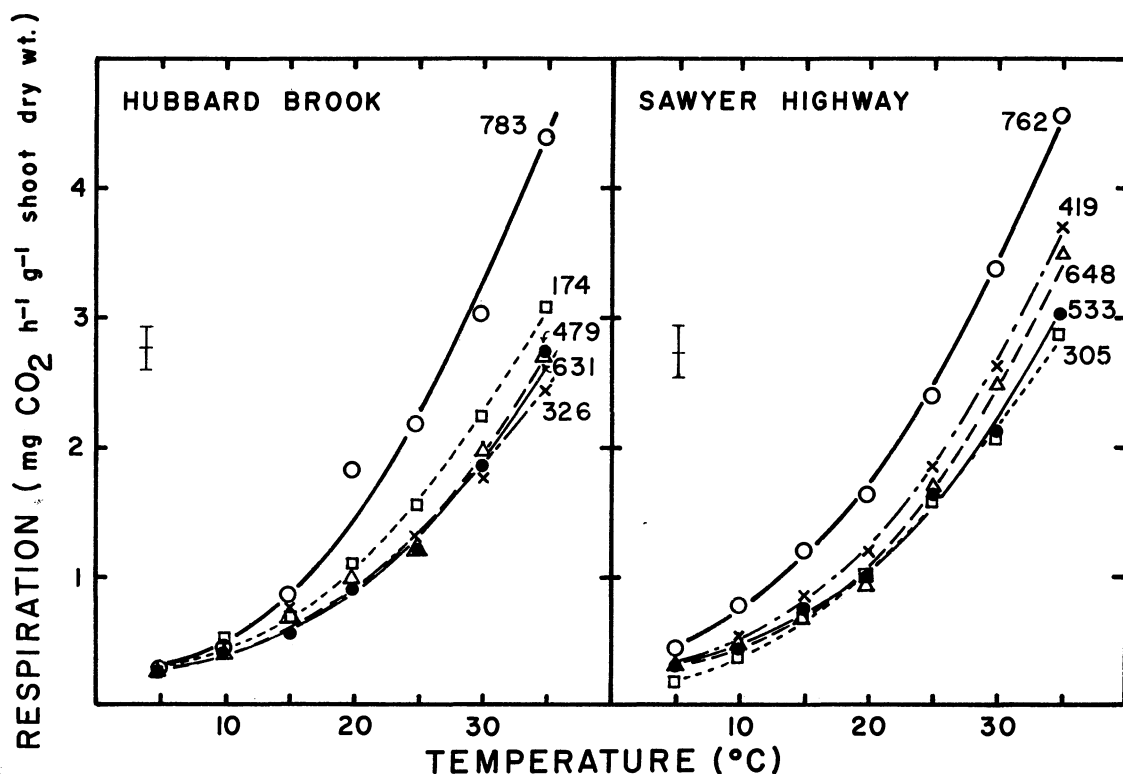


Fig. 2. Dark respiration in relation to temperature for progeny of sugar maple from two altitudinal transects in the White Mountains, New Hampshire. Altitude is indicated in meters. Vertical bars are 2 S.E. ($n = 4$).

of photosynthesis (i.e., rates at 25 C and 730 $\mu\text{E m}^{-2} \text{sec}^{-1}$) were also related to altitude (Fig. 4). The pattern was consistent for both transects, with the exception of the population from 419 m on Sawyer Highway. Using Bliss's (1967) technique for testing aberrant observations, this population was rejected as a statistical outlier. R^2 for the quadratic regression of photosynthetic rate on altitude, omitting the population from 419 m, was 0.96.

When photosynthesis was expressed on a leaf area basis, differences among populations were not significant and the relationship to altitude was not as clear. Nevertheless, high-altitude populations still had the highest or near highest rates of photosynthesis and mid-altitude populations the lowest or near lowest rates (Table 1).

High-altitude populations had highest rates of respiration at all temperatures, but the tendency for a relative minima at mid-altitudes was not as obvious as that for photosynthesis (Fig. 5). The quadratic regression of respiration at 20 C, which was approximately the mean night temperature in the greenhouse, on altitude had a coefficient of determination of 0.81.

Respiration was positively correlated with photosynthesis ($r = 0.90$; Fig. 6), which would be expected if both respiration and photosynthesis followed the same pattern in relation to altitude.

Specific leaf weight—The pattern of SLW was the inverse of that found for photosynthesis (Fig. 7). SLW was lowest in high-altitude populations, indicating thinnest leaves, increased to maximum values for the mid-altitude populations, indicating thickest leaves, and then decreased significantly in low-altitude populations. Though the pattern was the same within both transects, they did not seem to share the same relationship with respect to altitude.

Values of SLW of leaves collected in the field from the top of mature trees were available for the Hubbard Brook transect (Ledig, 1971). Except for the difference in absolute value, which is partly the result of differences in technique (i.e., air drying for the leaves collected in the field vs. oven drying for the greenhouse-grown seedlings), the leaves collected in situ and those grown in the uniform environment revealed the same pattern. Predictions based on the field

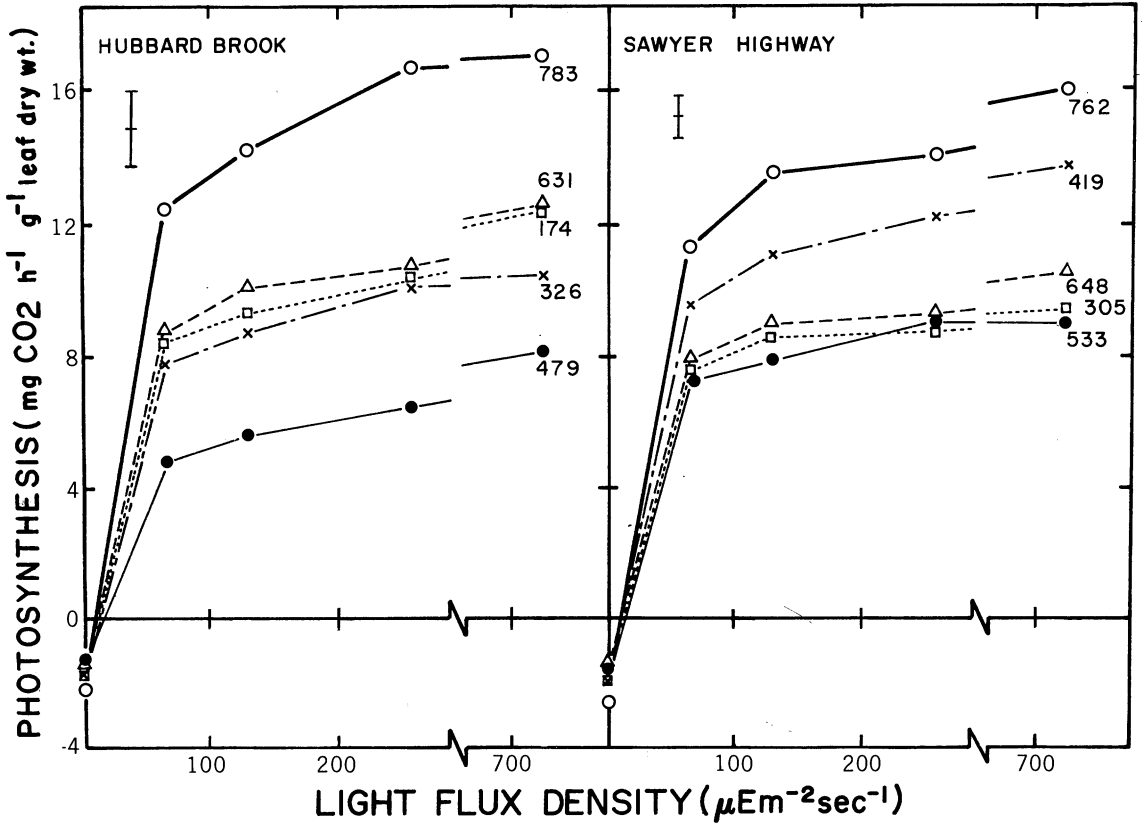


Fig. 3. Photosynthesis (means of rates at 15 and 25 C) in relation to radiation flux density for progeny of sugar maple from two altitudinal transects in the White Mountains, New Hampshire. Altitude is indicated in meters. Vertical bars are 2 S.E. ($n = 8$).

samples were accurate descriptions of SLW for the Hubbard Brook transect in the present trial ($r = 0.92$ for correlations of SLW in the field with SLW in the greenhouse study).

As would be anticipated from the altitudinal trends, net photosynthesis g^{-1} leaf dry weight was negatively correlated with SLW ($r = -0.78$; Fig. 8). There was no relationship between net photosynthesis on a leaf area basis and SLW.

DISCUSSION—If the observed differences are genetic, they are maintained over distances of less than 5.23 km. In fact, populations less than 0.8 km apart differed significantly in rates of photosynthesis and respiration, photosynthetic light response, and SLW. We believe that the pattern of variation was continuous or clinal with respect to some underlying environmental factor associated with altitude. More intensive sampling might reveal discontinuities. For example, the population from 419 m msl on Sawyer Highway deviated from the general pattern. In contrast to other populations, this stand was right on the banks of Jackman

Brook, had a high component of balsam fir, and may be a frost pocket, explaining its similarity to populations from higher altitudes.

TABLE 1. Rate of CO_2 -uptake measured at 25 C and 730 $\mu\text{E m}^{-2} \text{sec}^{-1}$ on leaf weight and leaf area bases

Transect and elevation (m)	Rate of CO_2 -uptake ($\text{mg CO}_2 \text{ hr}^{-1}$)	
	$\text{g}^{-1} \text{ leaf}^a$	$\text{dm}^{-2} \text{ leaf}$
HUBBARD BROOK		
783	17.98 a	4.37
631	13.26 ab	4.84
479	8.32 b	3.21
326	10.59 b	4.35
174	13.05 ab	4.28
SAWYER HIGHWAY		
762	18.79 a	5.27
648	11.43 bc	4.17
533	10.12 c	3.63
419	15.15 ab	4.80
305	10.13 c	3.11

^a Values followed by the same letter are not significantly different by Duncan's new multiple range test.

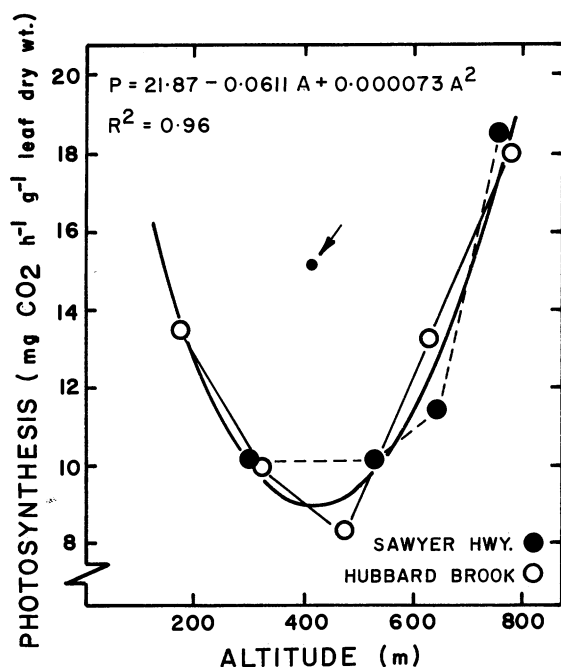


Fig. 4. Photosynthesis under optimum conditions (25 C and $730 \mu\text{E m}^{-2} \text{sec}^{-1}$) in relation to altitude for progeny of sugar maple from two transects in the White Mountains, New Hampshire ($n = 4$). Arrow indicates an outlier which does not fit the general pattern and which was rejected as belonging to a different statistical population using techniques described by Bliss (1967).

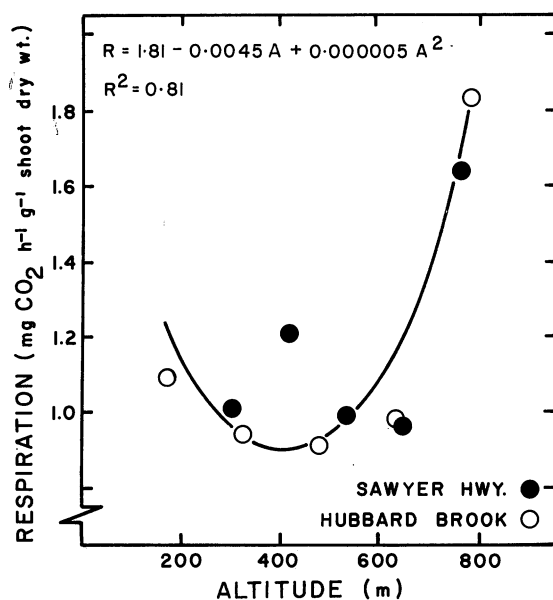


Fig. 5. Dark respiration (at 20 C) in relation to altitude for progeny of sugar maple from two transects in the White Mountains, New Hampshire ($n = 4$). The deviant point at 419 m was included in this regression, but rejected as an outlier in comparisons of photosynthetic rate (Fig. 4).

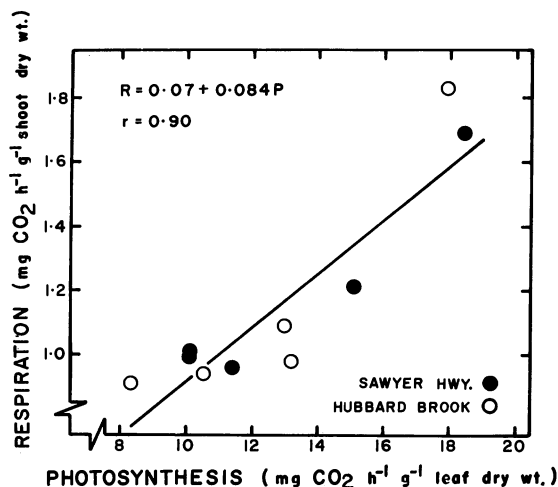


Fig. 6. The relationship between dark respiration and photosynthesis for progeny of sugar maple distributed along two altitudinal transects in the White Mountains, New Hampshire and measured under conditions approximating those under which seedlings were grown (i.e., 20 C for respiration and 25 C, $730 \mu\text{E m}^{-2} \text{sec}^{-1}$ for photosynthesis; $n = 4$). Correlations at other temperatures were as high or higher.

The altitudinal patterns are the resultant of at least two forces, natural selection and gene migration. Because sugar maple is largely entomophilous (Kriebel and Gabriel, 1969), gene migration among populations is probably less than that in anemophilous tree species. Parallel patterns of variation on two altitudinal transects suggest parallel evolution by natural selection for adaptive characteristics. Parallels between the transects increase confidence and suggest that the observed trends may be a general phenomenon in the White Mountains.

In ecologically marginal habitats, assimilation may limit survival (e.g., Mooney, West and Brayton, 1966); so at high altitudes, characterized by short growing seasons, high rates of carbon assimilation per unit of energy invested in leaf structure would be favored by natural selection. In climatically unfavorable years with late springs, dry summers, or early autumns, the balance between surviving and failing-to-survive could depend on the capacity to produce and store carbohydrates during relatively short periods or good years. The reason for observed differences in photosynthesis in sugar maple are not known, but could be the result of variation in stomatal frequency, pore size, mesophyll resistance, or carboxylation capacity.

Photosynthetic patterns similar to those in sugar maple have been observed in cattail (*Ty-*

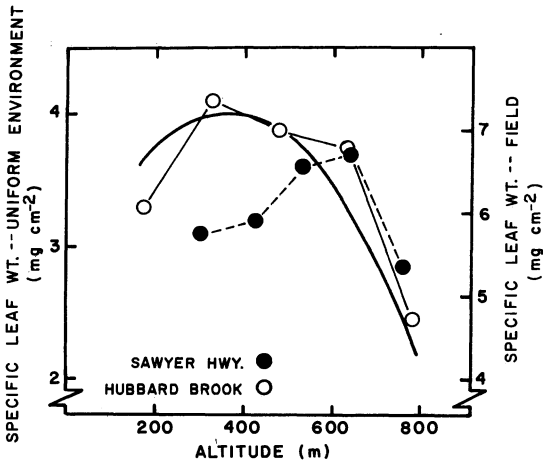


Fig. 7. Specific leaf weight in relation to altitude for sugar maple populations distributed along two transects in the White Mountains, New Hampshire ($n = 4$). The scale on the right refers to the smooth curve which is the fitted relationship ($n = 10$) for leaf samples collected in the field along the Hubbard Brook transect (Ledig, 1971); it closely describes the pattern of specific leaf weight in Hubbard Brook progeny raised in the uniform environment. For Sawyer Highway progeny, the pattern is similar in form, but not coincident. There were no field measurements for the Sawyer Highway transect.

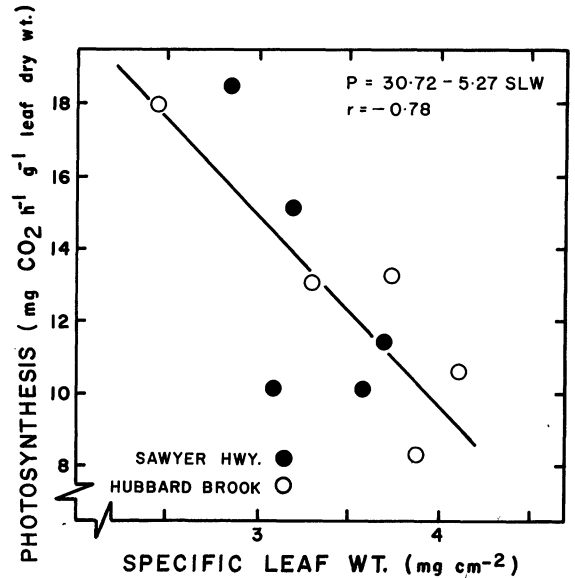


Fig. 8. The relationship between photosynthesis under optimum conditions (25°C , $730 \mu\text{E m}^{-2} \text{sec}^{-1}$) and specific leaf weight for progeny of sugar maple distributed along two altitudinal transects in the White Mountains, New Hampshire ($n = 4$).

pha latifolia L.). Cattail native to Quebec, which has a short growing season, had higher rates of CO_2 -uptake between 20 and 30°C than cattail from an area in California with a long growing season (McNaughton, 1973), and high-altitude populations from California and Colorado had higher rates than low-altitude populations from California (McNaughton et al., 1974). Comparison with other studies is difficult because objectives differ and most investigators were interested in comparisons between different species (e.g., Wright, 1970; Mooney, Wright and Strain, 1964; Anderson and McNaughton, 1973) or have confounded the effects of altitude with other biogeographical influences by comparing populations from widely separated localities (Billings et al., 1971). The effect of altitude on climate may vary significantly from transect to transect even locally, particularly if slope and/or aspect differ.

Frequently, both inter- and intraspecific comparisons indicate that populations native to high altitudes have higher rates of dark respiration than those from low altitudes (Björkman, 1966; Björkman and Holmgren, 1958, 1961; Mooney, Wright and Strain, 1964; Stewart and Bannister, 1974). Respiration in sugar maple was highest at high altitudes. Rates were a minimum in the zone in which the species makes optimum growth and achieves greatest

importance (Bormann et al., 1970). Generally, low rates of respiration are coincident with a low light compensation point (the light intensity at which respiration and photosynthesis are in balance), but for sugar maple the pattern may be reversed, if Fig. 1 represents the true light response curves.

The responses of high-altitude and mid-altitude populations were typical of shade- and sun-plants respectively (e.g., Logan and Krotkov, 1969). Light saturation for sugar maple seedlings was $21,600 \text{ lux}$ (ca. $390 \mu\text{E m}^{-2} \text{sec}^{-1}$ for sunlight) and for excised leaves at 0.34 ly min^{-1} (ca. $450 \mu\text{E m}^{-2} \text{sec}^{-1}$ for sunlight) according to Logan and Krotkov (1969) and Heskestad (1963). Rates of photosynthesis reported by previous investigators were similar to those reported here.

Low SLW is usually considered a morphologic response to shading, but in sugar maple it was also a feature of high-altitude populations, and to a lesser extent, low-altitude populations, both of which, paradoxically, occupied more exposed habitats than those at mid-altitude. SLW in uniform environments paralleled that observed in the field ($r = 0.92$). High SLW is often associated with high rates of photosynthesis per unit leaf area (e.g., Jones, Ford and Plumley, 1975; Pearce et al., 1969), but that was not true for sugar maple. Photosynthesis on a leaf weight basis was nega-

tively associated with SLW. High-altitude populations with the lowest SLW had highest rates of photosynthesis on a leaf area basis, but the overall correlation between photosynthesis on a leaf area basis and SLW was not significant. High rates of photosynthesis combined with low SLW provides a highly cost-effective system for populations in which assimilation is restricted to a short season. Low SLW means a low investment of energy required to produce a unit of leaf area. Due to temperature gradients, actual dark respiration of high-altitude populations would be roughly equivalent to that of low-altitude populations. Combined with low SLW, respiratory losses per unit leaf area would be minimal for high-altitude populations. It may also be that leaves of low SLW can be deployed more rapidly in the spring than those of high SLW. All of these factors are adaptive in a short growing season.

Surprisingly to us, there were no differences in temperature response among sugar maple populations, in contrast to results for balsam fir (Fryer and Ledig, 1972). Sugar maple may be incapable of evolving "temperature races." Its relatively restricted altitudinal range (sea level to 800 m) compared to balsam fir (sea level to timberline at 1,460 m), may in part reflect a limited capacity for adaptation to temperature regimes. Because sugar maple is deciduous, its leaves are not exposed to the full temperature range experienced by balsam fir, an evergreen. Slatyer (1978) hypothesized that large, perennial evergreen species might show a high degree of adaptation to temperature, whereas herbaceous species would not because they utilize only a short growing season. We suspect deciduous perennials like sugar maple may be analogous to herbaceous species.

Sugar maple populations did differ in photosynthetic response to light, while no differences with respect to light response were apparent in balsam fir (Fryer, Ledig and Korbobo, 1972). Further research will be necessary to determine why balsam fir and sugar maple differ in their adaptive response to the altitudinal gradient, and it will not be possible to generalize about response along altitudinal gradients until more species are tested.

There are at least three hypotheses to explain the origin of adaptive intraspecific diversity in sugar maple. 1) Populations could have differentiated in situ by selection and recombination operating in an initially heterogeneous population distributed along the altitudinal gradient. It seems possible that populations could differentiate in situ, because Mulcahy (1975) has shown that even cohorts differing in age by only a few years can be distinguished

in sugar maple, presumably as a result of selection pressures imposed by climatic events operating in the year of their establishment. 2) The first sugar maples to reach the White Mountains following glacial recession may have been descendants of the northernmost populations and perhaps similar to those now found at high altitude. With time and a moderating climate, the progeny of the original immigrants could have colonized higher altitudes, being better adapted to cool temperatures and short growing seasons, while new immigrant genes and individuals from the south began to occupy the lower slopes. 3) When sugar maple reached the White Mountains 8,000 years ago (i.e., during the hypsithermal; Davis, Spear and Shane, 1980), climate was warmer than at subsequent periods. Therefore, low-altitude rather than high-altitude populations may be relict. However, it seems unlikely that warm-climate adapted, southern populations could have reached the White Mountains before the northernmost populations. More exact knowledge of the genetic structure of sugar maple and of post-Pleistocene climates is necessary to evaluate the alternative hypotheses.

Sugar maple is long-lived (200–300 yr), it has occupied slopes in the White Mountains for only 8,000 years following recession of the Wisconsin glacial front, and there are no physical barriers to gene flow along the transects reported here. Nevertheless, differentiation has occurred over short distances (e.g., less than 0.8 km), suggesting that selection is strong relative to gene migration, and demonstrating the capacity of trees for rapid evolutionary adjustments.

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