

## Changing Photosynthetic Capacity during Leaf Ontogeny in Juvenile and Mature *Metrosideros polymorpha* Trees<sup>1</sup>

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**ABSTRACT:** Net CO<sub>2</sub> uptake at light saturation ( $P_{\max}$ ) was measured (both area and weight basis) for leaves of four categories based on leaf age and branch position in juvenile and mature trees of *Metrosideros polymorpha*, a tropical, dicot evergreen species. Conductance, weight/area, and N and P concentrations were also measured. In both juvenile and mature trees,  $P_{\max}$  was higher in terminal leaves 6–14 months old than in younger or older leaves. Low  $P_{\max}$  of leaves less than 6 months old was related to factors of immaturity, including low weight/area and low N concentration. Low  $P_{\max}$  of older and subterminal leaves was correlated with low N concentration related to withdrawal during leaf aging. This correlation was stronger in mature than in juvenile trees.  $P_{\max}$  was significantly lower, and nitrogen concentration and specific leaf weight were higher, in the sample of mature trees than in the juvenile tree sample ( $P_{\max}$  5.89 and 4.99  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in juvenile and mature trees, respectively).

THIS PAPER REPORTS measurements of apparent photosynthesis at light saturation ( $P_{\max}$ ) made in leaves of different ages from both juvenile and mature *Metrosideros polymorpha* Gaud. var *polymorpha* (Myrtaceae) trees. This work is part of an investigation of physiological differences between juvenile and mature trees, guided by the hypothesis that senescence in *M. polymorpha* trees is related to the declining carbon balance that accompanies increasing size (Gerrish 1988, 1989, 1990; also see Mueller-Dombois 1987). Rates of photosynthesis are used in models of growth and carbon balance.

Molisch (1938) reported that younger leaves and younger plants have higher rates of photosynthesis than older leaves and plants and suggested that auto-toxication is the fore-

most cause of senescence in leaves and in organisms.  $P_{\max}$  is lower in older than in young trees in some conifer species. In *Picea abies* (Norway spruce) the older trees lack the developmental flexibility that allows younger trees to produce needles morphologically optimal for the ambient light conditions (Kull and Koppel 1987).

Changes in  $P_{\max}$  associated with the development of leaves are well documented. In many kinds of plants,  $P_{\max}$  increases until the leaf is fully expanded, then declines from that peak (Chabot and Hicks 1982). In fast-growing herbaceous plants the decline may be fairly rapid, soon terminating in a distinct phase of leaf senescence (Hopkinson 1964). In trees, the decline in  $P_{\max}$  is slower, with leaves maintaining an appreciable percentage of their peak photosynthetic capacity throughout most of their life span. This pattern is described in temperate deciduous trees with a terminal phase of leaf senescence (Jurik 1986) and in conifers with leaves that function for several years (Freeland 1952). In *Coffea arabica*, a tropical evergreen tree,  $P_{\max}$  peaked at a leaf age of 90 days, then declined. Leaves were followed for 140 days, but not through senescence (Yamaguchi and Friend 1979). In a 2½-month study of *Hevea brasiliensis*, an-

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other tropical evergreen tree,  $P_{\max}$  fell after an early peak but then stabilized (Samsuddin and Impens 1979).

Although the anatomical and biochemical changes of the chloroplast that occur during leaf senescence are well described (Woolhouse 1974), causes of the less-drastic changes in  $P_{\max}$  associated with aging before senescence are poorly known. A widely observed decrease in nitrogen content and a concomitant decline in  $P_{\max}$  is attributed to the translocation of nitrogen from older leaves to actively growing younger leaves (Chabot and Hicks 1982). Because a large part of the nitrogen in leaves is a constituent of the carboxylase enzymes, the correlation of  $P_{\max}$  with nitrogen concentration may be causative. Phosphorus concentration is not generally correlated with  $P_{\max}$  and, in some species, begins to decline before leaf growth and expansion is completed (Hopkinson 1964).

Changes in apparent photosynthesis during leaf ontogeny are also caused by differential losses of carbon due to dark (mitochondrial) respiration associated with growth and biosynthesis in expanding leaves (Hopkinson 1964, Salin and Homann 1971, Samsuddin and Impens 1979, Yamaguchi and Friend 1979, Reich 1984, Jurik 1986) and by photorespiration (peroxisomal respiration). In *Citrus* spp. and some herbaceous plants, photorespiration was higher in old leaves than in young leaves, thus partially accounting for low apparent photosynthesis of older leaves (Salin and Homann 1971).

## MATERIALS AND METHODS

### Experimental Design

*Metrosideros polymorpha* is a tropical, broadleaf evergreen tree that dominates the Hawaiian montane rainforests (Mueller-Dombois et al. 1981). The study sites are 1190 m above sea level near Thurston Lava Tube within Hawaii Volcanoes National Park on the island of Hawaii. The study area has an annual rainfall of 2.5 m; the well-drained soil has an average depth of 30 cm overlying a pahoehoe lava flow. The *M. polymorpha* trees

used in this study were identified as var. *polymorpha* based on the rounded leaf shape, cordate leaf base, and especially the rolled leaf margins (Dawson and Stemmermann 1990).

Porter (1972) found the average life span of leaves of trees in the locale of my study area (which he identified as var. *incana*) to be 2 yr. Leaf flushing and leaf fall occur throughout the year, with broad peaks in activity and periods of relative quiescence (Porter 1972, Gerrish 1989). Bud break is followed by a period of twig extension and leaf development; the apical meristem then forms bud scales and becomes dormant. Each of these proleptically formed twigs is clearly distinguished from the supporting twig by bud scale scars and other morphological features. However, the timing of bud break of neighboring twigs is random; terminal twigs on a branch are of many different ages (Gerrish 1989).

The trees used for gas-exchange measurements had been selected for a study of crown development (Gerrish 1989). Each terminal twig in randomly selected branchlets of the upper crowns of mature trees and all the terminal twigs of saplings had been marked with colored wire. Every three months, all newly flushed twigs were marked with a wire of a different color. Thus, twigs and leaves of known age ranges were available for gas-exchange measurements.

The tops of the crowns of three mature trees, 12–14 m tall, were reached with a scaffold. Characteristics of these trees that identify them as mature are their height, presence of flowers and seed capsules, and having foliage clustered at the ends of a sympodial branching system so that most of the leaves occur in a shallow layer at the highest level of the canopy (Gerrish 1989, 1990). These trees are approaching the maximum height and crown development seen on this site. Based on these characteristics, I consider these trees to be fully mature. There is no crown dieback or any other visible sign of tree senescence or overmaturity. All three of these mature trees have dominant positions in the stand, with no shading from neighboring trees. The branches chosen for gas-exchange measurements were from the top-

most parts of the crown where the leaves had developed in full sun.

I used juvenile trees (saplings) 2–3.5 m tall that were reinvading a nearby clearing created during road construction. These juvenile trees have long crowns with the foliage borne along a monopodial axis and have not yet flowered. Five of these with dominant positions had been randomly selected for the crown-development study and had had their terminal twigs marked as described above. I chose the three largest of these to ensure that there would be enough twigs for gas-exchange measurements. These juvenile trees were the tallest in the clearing; leaves at the top of their crowns had grown and developed in full sunlight.

Leaves were sampled according to their age and the position of the leaf-bearing twig on the branch (Table 1). All twigs and leaves on a *M. polymorpha* tree are first formed in the terminal position. Twigs are reclassified as “subterminal” when the terminal bud grows, overtopping the original twig. The four categories compare leaves across the maximum age range of marked twigs, and compare the effect of branch position on leaves of the same age. Five replicates of each of the four categories of leaves were sampled in each of the three saplings and three mature trees (i.e., 15 measurements of each leaf category divided equally among three trees, making 60 measurements on saplings and 60 on mature trees). The sequence of measurements at each stand was determined by random draw. The total 120 gas-exchange measurements required 7 days of sampling between 29 April and 13 May 1987.

TABLE 1

BRANCH POSITION AND AGE OF LEAVES OF THE FOUR CATEGORIES OF LEAVES SAMPLED

CATEGORY DESIGNATION	DESCRIPTION
T1	Terminal, 0–6 months old
T2	Terminal, 6–14 months old
S2	Subterminal, 6–14 months old
S3	Subterminal, > 18 months old

The attributes determined for each leaf sample were two measures of  $P_{\max}$ : ( $P_w$ ) net uptake  $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$  and ( $P_a$ ) net uptake  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ; stomatal conductance:  $\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ; leaf weight/area (W/A): dry weight  $\text{g cm}^{-2}$ ; the concentration of phosphorus ( $P_a$ ):  $\text{mmol g}^{-1}$ ; and two measures of nitrogen content: ( $N_w$ )  $\text{mmol g}^{-1}$  ( $N_w$ ) and ( $N_a$ )  $\text{mmol m}^{-2}$ . Data were analyzed using the Statistical Analysis System (SAS Institute 1982) statistical programs at the University of Hawaii at Manoa Computing Center.

### Gas-exchange Measurements

The uptake of carbon dioxide by leaves was measured in the field with a LI-COR LI-6000 Portable Photosynthesis System. This micro-processor-controlled instrument uses an infrared gas analyzer (IRGA) to measure change in the concentration of  $\text{CO}_2$  in a closed chamber in which the operator has placed a leaf or leaves. Transpiration rate is calculated from the increase of humidity in the system.

Preliminary studies with the IRGA showed that leaves on detached twigs maintain unchanged rates of photosynthesis and transpiration for at least 5 min. All subsequent measurements were made on detached twigs. The photosynthetic response to irradiance was measured for detached young leaves from three vigorous, reproductively mature *M. polymorpha* trees. A range of light levels was obtained by using multiple layers of shade cloth. Leaves reached light saturation at about  $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$  (Figure 1). The mean photosynthetic rate ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ), sample standard deviations, and number of twigs sampled at light levels above  $600 \text{ mmol m}^{-2} \text{ s}^{-1}$  for each of the three trees were 8.6, 1.97, 8; 8.4, 0.72, 4; and 5.4, 2.28, 5, respectively. These measurements were made with the air and leaf surface temperatures within the gas-exchange chamber between 24 and  $30^\circ\text{C}$  and relative humidity between 43 and 66%. This response is within the range normal for tropical trees (Sestak et al. 1971).

A workbench was built that could be used atop the scaffold or at ground level to support the IRGA and an electric lamp needed to

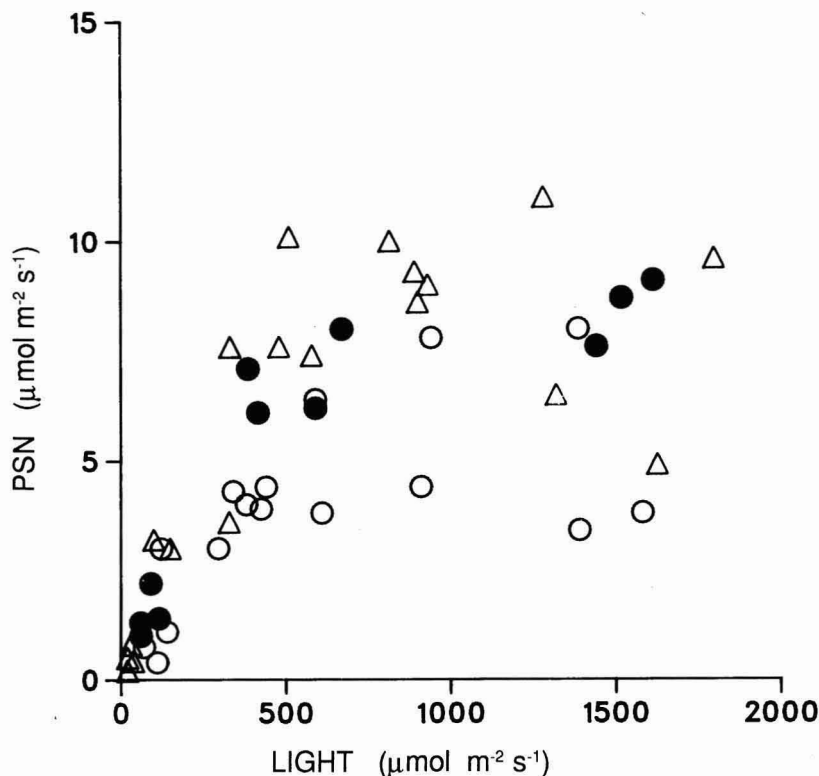


FIGURE 1. The response of apparent photosynthesis (PSN) to photosynthetically active radiation (LIGHT) measured on sun leaves from three trees (represented by triangle, open circle, and filled circle).

deliver a standard beam of light. A stand on the workbench held the lamp in a fixed position with a cooling water bath between the lamp and the gas-exchange chamber. The light source was one 120-watt floodlight (General Electric "Miser Floodlight," order code 150 PAR/FL/120WM) powered by a portable gasoline-powered 115-volt, alternating current electrical generator. Ambient light was excluded by covering the stand with a hood of black plastic. A cradle was fixed beneath the stand that held the gas-exchange chamber in a constant position relative to the light.

The IRGA was calibrated by the manufacturer's prescribed methods using a test gas of 500 ppm  $\text{CO}_2$  and using the atmospheric  $\text{CO}_2$  concentration as 350 ppm. Light calibration was performed with a LI-COR quantum sensor at the level that leaves are held in the gas-exchange chamber to ensure that the

irradiance at all points was at least  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  of photosynthetically active radiation. The IRGA and the light source were calibrated after every five measurements. Measurements of  $\text{CO}_2$  uptake were made between 0830 and 1130 hours only. I made measurements only on days when no rain fell during these morning hours. Air temperature in the gas-exchange chamber ranged between 15 and  $25^\circ\text{C}$ , leaf-surface temperatures between 17 and  $30^\circ\text{C}$ , and relative humidity within the chamber ranged between 40 and 85%. These ranges reflect the normal variations in atmospheric conditions between 0830 and 1130 hours on the 7 days sampled between 29 April and 13 May 1987.

It was not feasible to select leaf pairs randomly from the same-age cohorts of marked twigs. These criteria were used to choose samples: (1) apical position on the tree—

leaves at the ends of branches at the top of the tree's crown that would have had maximum sun exposure during development (sun leaves); (2) condition—leaves with the least possible amount of herbivore damage, dirt, or other discoloration of the upper surface; and (3) size—the largest leaves available to maximize the ratio of leaf area to the volume of the gas-exchange chamber. Thus the sample was representative of large, clean, sun leaves.

Measurements were made in the following manner. A suitable twig representing the randomly drawn leaf category was found on the appropriate tree. The twig was clipped from the branch at the junction. The basal pair of leaves on the removed twig was saved; all others were removed from the twig. The sample placed in the chamber consisted of this basal pair of leaves still attached to 2–3 cm of the twig. The chamber held the leaves perpendicular to the direction of the light beam. The chamber was slid into the cradle and the light was turned on. Gas-exchange measurements were made over a 100-sec interval in the manner prescribed by the IRGA manufacturer.

After each morning's work, the area of each sample of two leaves was determined with an electronic area meter (Delta T area meter, Decagon Devices, Inc.). The leaves were dried at 70°C for 72 hr to determine dry weight and for nutrient analysis. Leaf nitrogen concentration was measured with a continuous flow analyzer after sulfuric acid–mercuric oxide digestion.

## RESULTS

In both the juvenile and mature trees,  $P_{\max}$  of the terminal 6–14-month-old leaves (T2) was higher than for leaves of any other category (Figure 2). Differences in  $P_{\max}$  among leaf categories are statistically significant only in the juvenile trees (Table 2), but with W/A as a covariate, differences in  $P_w$  are significant in both mature and juvenile trees (Table 3). This rise and fall of  $P_{\max}$  during the life cycle of leaves of *M. polymorpha* is consistent with developmental patterns described for other

plants. As in other evergreen trees,  $P_{\max}$  remained at an appreciably high level throughout much of the leaf life span. I did not sample leaves that could be characterized as senescent.

Some of the patterns of variations in the other leaf attributes were statistically significant (Table 2) and some were correlated with  $P_{\max}$  (Table 4). W/A was only very weakly or not at all correlated with  $P_{\max}$  across all the leaf categories (Table 4), but, as mentioned above, as a covariate with a significant interaction effect, W/A sharpened the differences in  $P_{\max}$  between leaf categories (Table 3). The nitrogen content of the leaves also varied significantly between the leaf categories in a pattern similar to that of  $P_{\max}$  (Figure 2). In the juvenile trees, the correlation of  $P_{\max}$  with nitrogen was weak (Table 4), but when used as a covariate, rendered differences in  $P_{\max}$  associated with leaf category not significant (Table 3). The correlation of  $P_{\max}$  with nitrogen content was stronger in the leaves of mature trees (Table 4). Although nitrogen concentration was useful as a predictor of  $P_{\max}$  in the mature trees, the relatively low correlation coefficients indicated that other factors must be involved.

The mean concentrations of phosphorus in leaves of juvenile and mature trees were, respectively,  $0.0151 \pm 0.0006$  (standard error of the mean) and  $0.0169 \pm 0.0007$  mmol  $g^{-1}$ . As has been reported for other plant species, phosphorus concentration was highest in the youngest leaves and then remained constant at a lower level in older leaves. Differences between young and old leaves were significant in both life states (Table 2), but phosphorus content was not positively correlated with  $P_{\max}$  (Table 4) and will not be discussed further.

None of the differences in conductance between leaf categories were significant (Figure 2 and Table 2), nor did the use of conductance as a covariate alter the significance of differences in  $P_w$  among the various leaf categories (Table 3). The results of the analysis of covariance of conductance with  $P_a$  (not shown) are identical to those just described. Conductance was significantly correlated with  $P_{\max}$  only in the youngest category of leaves in juvenile trees (Table 5). This general lack of

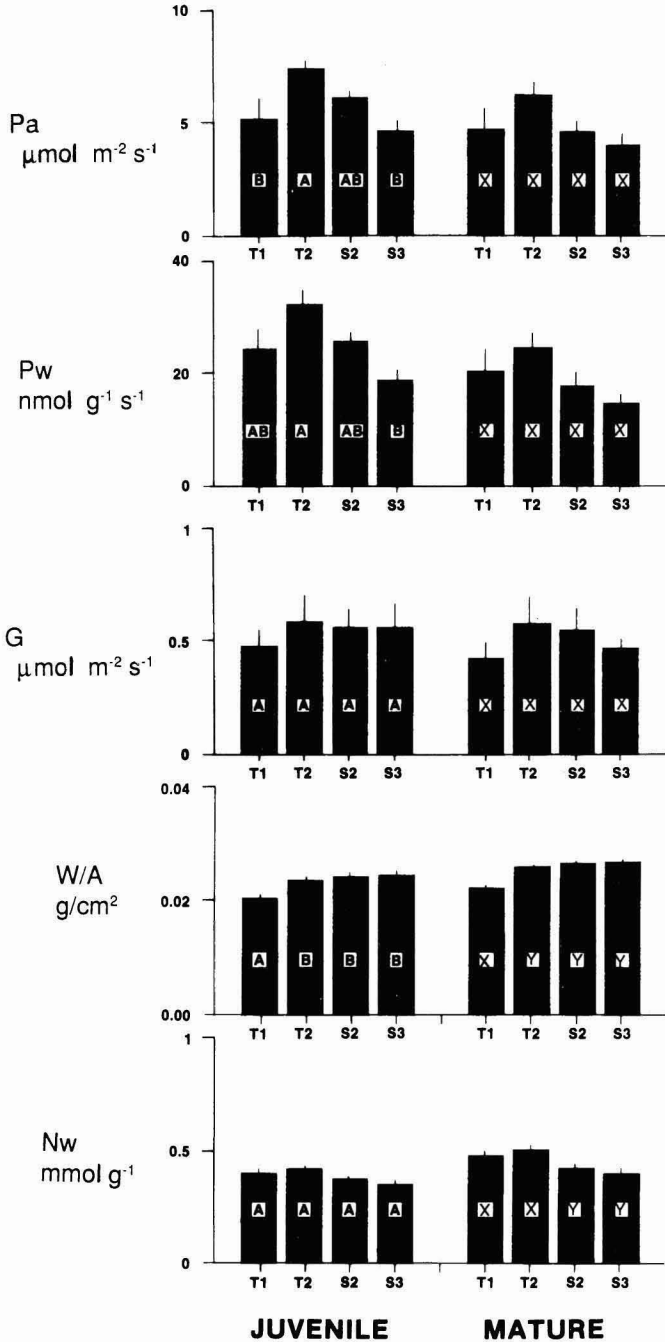


FIGURE 2. Mean  $P_{\max}$  ( $P_a$  and  $P_w$ ), conductance ( $G$ ), weight/area ( $W/A$ ), and nitrogen concentration ( $N_w$ ) of leaves of four age-and-position leaf categories in juvenile and mature trees. Vertical lines indicate the standard error of the mean;  $n = 15$  in each category. Leaf categories are as follows: T1 = terminal, 0–6 months; T2 = terminal, 6–14 months; S2 = subterminal, 6–14 months; S3 = subterminal, > 18 months. Capital letters within bars show results of ANOVA and Student-Newman-Keuls means separation done separately for juvenile and mature trees. Bars labeled with the same letter are not significantly different (.05 confidence level).

TABLE 2  
ANOVA OF LEAF ATTRIBUTES BY LEAF CATEGORY

ATTRIBUTE	df	JUVENILE			MATURE		
		AP 3	TREE 2	MODEL 5	AP 3	TREE 2	MODEL 5
$P_a$		.005*	.060	.004	.120	.437	.188
$P_w$		.003*	.077	.003	.067	.326	.097
G		.484	.449	.539	.349	.442	.425
W/A		<.001*	<.001	<.001	<.001*	.006	<.001
$N_w$		.083	.015	.013	<.001*	<.001	<.001
$N_a$		.001*	<.001	<.001	<.001*	.006	<.001
P		<.001*	.002	<.001	<.001*	.193	<.001

NOTE: Two-way ANOVAS of leaf attributes by age-and-position category and tree for juvenile and mature trees. Values in table are the probabilities that the ANOVA (MODEL) and the differences associated with age-and-position category (AP) and TREE are not significant. df = degrees of freedom,  $P_a = P_{max}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $P_w = P_{max}$  ( $\text{mmol g}^{-1} \text{s}^{-1}$ ), G = stomatal conductance ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), W/A = leaf weight per unit area ( $\text{g cm}^{-2}$ ),  $N_w$  = nitrogen concentration ( $\text{mmol g}^{-1}$ )  $N_a$  = nitrogen content ( $\text{mmol m}^{-2}$ ), P = phosphorus concentration ( $\text{mmol g}^{-1}$ ). All mean squares tested against error mean square with 54 df.

\* Both model and effect of AP significant at .05 confidence level.

TABLE 3  
ANALYSIS OF COVARIANCE

COVARIATE IN MODEL	df	JUVENILE				MATURE			
		AP 3	COV 1	INT 3	MODEL 7	AP 3	COV 1	INT 3	MODEL 7
G		<.001	.051	.007	<.001	.268	.402	.436	.209
W/A		<.001	.561	<.001	<.001	.003	.726	.003	.002
$N_w$		.115	.649	.154	.007	.234	.021	.185	.025

NOTE: Analysis of covariance of  $P_{max}$  ( $P_w$ ) with stomatal conductance (G), leaf weight/area (W/A), and nitrogen concentration ( $N_w$ ). Units as in Table 2. Values are the probabilities that the statistical model (MODEL), the differences associated with leaf age-position category (AP), the correlation of the covariate with  $P_w$  (COV), and the interaction of AP and the covariate (INT) are not statistically significant. df = degrees of freedom. All mean squares tested against error mean square with 52 df.

correlation of conductance with photosynthesis implies that  $P_{max}$  was not limited by conductance at the time of the measurements and that all measurements can be considered comparable without concern that water availability was differentially limiting.

#### DISCUSSION

The variation of  $P_{max}$  among leaf categories was very similar in both mature and juvenile trees, suggesting common developmental processes during leaf ontogeny. The analysis of covariance (Table 3) shows that the interaction between W/A and leaf age-and-position

category was significant, meaning the relationship between W/A and  $P_w$  was not the same in every leaf category. Changes in  $P_{max}$  can be better understood by dividing the leaf life cycle into a phase of leaf growth and a phase of leaf aging. Leaves of *M. polymorpha* are formed in the dormant bud (Porter 1972), but for practical purposes, the leaf growth phase extends from bud break through leaf expansion to the time when maximum W/A is approached and maximum nitrogen concentration is attained.  $P_{max}$  and nitrogen concentration peaked in the 6–14-month-old leaves, indicating that they were mature while leaves less than 6 months old were not.

TABLE 4  
CORRELATIONS OF LEAF ATTRIBUTES FOR JUVENILE  
AND MATURE TREES

ATTRIBUTE	$P_w$		$P_a$	
	$r$	prob	$r$	prob
Juvenile				
G	.104	.431	.131	.317
W/A	.027	.839	.292	.024
$N_w$	-.016	.903	.021	.874
$N_a$	.050	.706	.287	.026
P	-.274	.034	-.294	.023
Mature				
G	.055	.682	.054	.686
W/A	.024	.855	.167	.202
$N_w$	.386	.002	.332	.010
$N_a$	.395	.002	.425	.002
P	-.127	.333	.034	.797

NOTE: Correlation of leaf attributes with two measures of  $P_{max}$ .  $r$  = Pearson correlation coefficient, prob = probability that  $r$  is not significantly different from zero; symbols and units as in Table 2.

TABLE 5  
CORRELATIONS OF LEAF ATTRIBUTES  
WITHIN LEAF CATEGORIES

ATTRIBUTE	AP	$P_w$		$P_a$	
		$r$	prob	$r$	prob
Juvenile					
G	T1	.587	.021	.649	.009
W/A	T1	.602	.018	.690	.004
	T2	-.718	.003	-.416	.123
$N_w$	No significant differences				
$N_a$	T2	-.580	.023	-.276	.319
Mature					
G	No significant differences				
W/A	T1	.552	.033	.618	.014
	S3	.530	.042	.595	.019
$N_w$	S2	.632	.012	.587	.022
$N_a$	T1	.607	.017	.665	.007
	S2	.534	.040	.537	.039

NOTE: Significant correlations of leaf attributes with two measures of  $P_{max}$  within each leaf category. AP = leaf age-position category,  $r$  = Pearson correlation coefficient, prob = probability that  $r$  is not significantly different from zero; symbols and units as in Table 2. Correlations between  $P_{max}$  and leaf attributes not shown for leaf categories where correlations were not significant.

The correlations of conductance,  $W/A$ ,  $N_w$ , and  $N_a$  with  $P_w$  and  $P_a$  within each leaf category were calculated to see if such correlations could be useful in predicting the variation of  $P_{max}$  within each leaf category (Table 5). These correlations were generally low and not consistent between juvenile and mature trees or between the leaf categories. Only in the youngest leaves was correlation with  $W/A$  significant and relatively high, as was  $N_a$  and conductance in the youngest leaves of mature trees. These results support the observation that, in the growing phase,  $P_{max}$  is limited by immaturity of leaves that are not fully developed.

The differences in  $P_{max}$  between growing and mature leaves was less with  $P_w$  than with  $P_a$  because  $P_w$  eliminates differences due directly to low  $W/A$  in growing leaves. As such,  $P_w$  is a measure of "mass use efficiency." However, in young leaves of both juvenile and mature trees,  $P_w$  was significantly correlated with  $W/A$  (Table 5), meaning that photosynthesis was limited by two facets of leaf immaturity in young leaves:  $P_a$  was limited by the low  $W/A$ , and  $P_w$  was limited by low mass use efficiency at low  $W/A$ . This latter limitation may be linked to the lower concentration of nitrogen in the leaf tissue of young leaves (Figure 2).

The significant correlation between nitrogen concentration and  $P_{max}$  in mature trees (Table 4), especially during the aging phase (Table 5), suggests a causative relationship. In mature trees, nitrogen concentration was also significantly lower in leaves that had been overtopped by new growth (S2) than in leaves of the same age that had remained in the terminal position (T2) (Figure 2). This reduction in nitrogen concentration may have been due to the translocation of nitrogen to the overtopping twig, or the lower  $P_{max}$  and nitrogen content might both have been initiated by shading by the overtopping twig (Leverenz and Jarvis 1980). However, in juvenile trees  $P_{max}$  and nitrogen concentration were only very weakly correlated, and the differences in nitrogen concentration between leaf categories were small and not significant. The poor correlations of  $N_w$  and  $N_a$  with  $P_w$  and  $P_a$  in

TABLE 6

ANOVA COMPARISONS OF JUVENILE AND MATURE TREES

ATTRIBUTE	STATE	AP	TREE	MODEL
	df 1	3	5	9
$P_a$	.040*	<.001*	.052	<.001*
$P_w$	.001*	<.001*	.002*	<.001*
G	.893	.173	.643	.492
W/A	<.001*	<.001*	<.001*	<.001*
$N_w$	<.001*	<.001*	<.001*	<.001*
$N_a$	<.001*	<.024*	.166	<.001*

NOTE: Three-way ANOVAS of  $P_{max}$  and other leaf attributes by STATE (juvenile or mature), leaf category (AP), and TREE. Values shown are the probabilities that the ANOVA (MODEL), and the differences due to STATE, AP, and TREE are not significant; other symbols and units as in Table 2. All mean squares tested against error mean square with 110 df.

\*Significant at .05 confidence level.

the juvenile trees imply that  $P_{max}$  was not closely tied to leaf nitrogen concentrations in these trees. The same correlations were stronger, and statistically significant, in the mature trees, leading to the opposite conclusion.

This study, designed to characterize changes in  $P_{max}$  during leaf development, found similar patterns of change in both juvenile and mature *M. polymorpha* trees (Figure 2). However, the mean rates of  $P_{max}$  for juvenile and mature trees, 5.89 and 4.99  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  ( $P_a$ ) or 25.2 and 19.5  $\text{nmol g}^{-1} \text{ s}^{-1}$  ( $P_w$ ), respectively, were significantly different (Table 6). It cannot be concluded that the differences in  $P_{max}$  or any other leaf attributes are the effects of tree maturity because the differences could be due to site variation. However, these data do not contradict a hypothesis that mature trees have lower rates of photosynthesis than juvenile trees. Both samples were from sites less than 1 km apart that were selected because of their similar soil and climate conditions.

Unlike the difference in  $P_{max}$  due to age-and-position categories, the lower  $P_{max}$  of the mature tree sample cannot be explained by lower nitrogen concentration or lower W/A, because both of these properties are higher in mature trees (Figure 2).

Differences in mean  $P_{max}$  between the juve-

nile and mature trees might have resulted from growth of the leaves under different light regimes. Leaves of some conifer species have higher  $P_{max}$  and higher leaf nitrogen concentrations when the entire tree has grown in shaded conditions compared to trees grown in the open (Leverenz and Jarvis 1980, Kull and Koppel 1987). This phenomenon is interpreted as homeostatic flexibility, allowing low-light phenotype trees to form high-capacity leaves while allowing trees that are not light limited to refrain from investing unnecessary levels of nitrogen in the leaves. I found a different pattern in *M. polymorpha*.  $P_{max}$  was higher in juvenile than in mature trees, but nitrogen content and W/A were lower (Figure 2). It is the low- $P_{max}$  leaves of mature trees that contain high investments of mass and nitrogen. This is not the pattern found in low-light phenotypes.

I believe that these differences in  $P_{max}$  are most reasonably explained as the effect of different tree maturity. Further measurements of  $P_{max}$  and other leaf attributes of juvenile and mature trees from a range of habitat types are needed to confirm that these leaf properties change predictably as trees age. The confirmation of lower mass use efficiency and lower nitrogen use efficiency in leaves of mature trees would indicate an important physiological decline not directly linked to size or shape in aging trees and might be a key to understanding physiological senescence in *M. polymorpha*.

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