

PHOTOSYNTHETIC CAPACITY AND LEAF LONGEVITY IN THE CANOPY OF A DRY TROPICAL FOREST

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ABSTRACT. Assimilation capacity and leaf longevity were documented for a stand of trees in a neotropical dry forest near Panama City, Panama. A construction crane was used to select leaves from exposed locations of the upper canopy of the seven most abundant species in this stand. A general negative relationship exists between mean A_{\max} and mean leaf longevity among the seven species, but this is statistically significant only for leaves produced in the late dry season.

Because photosynthesis is the sole mechanism for carbon assimilation in most higher vascular plants, we expect the investment of nutrients and carbon in this process to strongly reflect the opportunity for carbon gain over the lifetime of a leaf. The relationship between leaf functional characters and photosynthesis has been called the functional convergence hypothesis (Field 1990), which identifies a suite of interdependent characters that reflect past selection to maximize carbon gain over the lifetime of the leaf relative to the investment in the machinery of photosynthesis. Central to this idea is the hypothesis that leaf lifespan should be negatively related to photosynthetic capacity (Chabot & Hicks 1982). Reich *et al.* (1992) showed that there is a strong negative relationship between leaf longevity and mass-based assimilation capacity ($r^2=0.91$) for a wide range of tropical forest trees. Other characters that vary with assimilation and leaf longevity include leaf nitrogen content, construction costs, and mass per unit area. Components of this suite of features have been characterized as “mutually supporting, interdependent” and “causally interrelated” (Reich *et al.* 1992). Despite the expected tight linkage, the relationship between leaf lifespan and photosynthetic capacity is weak for broad-leaved temperate trees (Koike 1988), and virtually nonexistent for herbs of lowland and alpine meadows (Diemer *et al.* 1992).

One explanation for the absence of a strong relationship between assimilation capacity and leaf longevity in these studies is that species of similar life form from similar communities tend to have about the same opportunity for carbon gain during the growing season, and thus show little variation in leaf lifespan. It is only when we look at leaf lifespans over the range of a few days to many years, including species from con-

trasting habitats that we see the predicted relationship (Reich *et al.* 1992, Reich 1993). In contrast to the narrow range of leaf lifespans found in temperate deciduous forests, plants of tropical forests show wide variation in leaf longevity. Here we examine this relationship for leaves from a stand of second-growth neotropical trees including species characteristic of early through late-stage forest development. Pioneer tropical trees often have higher photosynthetic capacity, shorter leaf lifespans, and complete their life cycle faster than trees later in succession (Bazzaz & Pickett 1980). Moreover, within most tropical forest communities, the opportunity for carbon gain varies with respect to the availability of light and water during the wet season and dry season, respectively. The goal of this work was to examine the assimilation-longevity relationship for leaves of species with contrasting successional status and leaf production phenology. This is in contrast to previous studies of this relationship within a community which have focused on species of similar successional status (Koike 1988), or on species with very similar phenologies (Diemer *et al.* 1992).

METHODS.

STUDY SITE AND CANOPY ACCESS. The forest is 75–150 year-old second growth, including many pioneers as well as late-stage successional species typical of dry forest in Central America. Trees ranged in height from a few meters to 40 m. Total annual rainfall averages 1740 mm with heaviest rains during mid-May through mid-December. The dry season typically lasts between four and five months during which evapotranspiration exceeds mean rainfall by 431 mm. Global radiation averages 48% greater in February and March than in the cloudy wet season (Fig. 1). The upper canopy of this forest was accessed with a construction crane 42 m tall with an arm with 51 m radius

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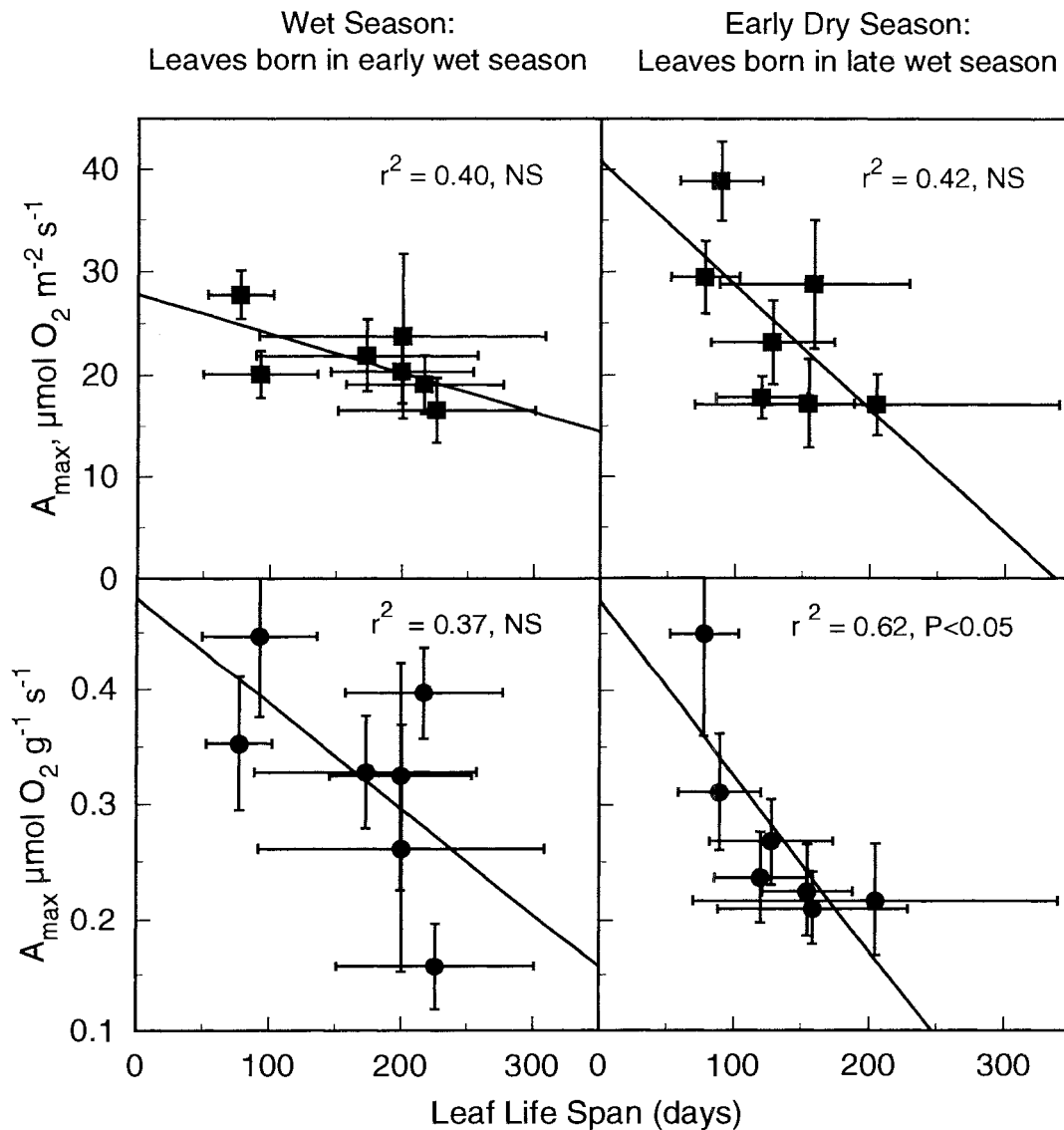


FIGURE 2. A_{\max} and leaf lifespan plotted for seven tree species near the canopy crane in Parque Nacional Metropolitan, Panama. Regressions are shown for mass-based and area-based A_{\max} derived from leaves born in the early wet season and leaves born in the late wet season. Error bars are the standard deviation. Regressions are based on the mean leaf lifespan and mean A_{\max} for each species.

capacity is reported here as the maximum stable assimilation rate achieved during the light response curves.

RESULTS

There was a negative relationship between mean A_{\max} and mean leaf life span, but this relationship was statistically significant only for

mass-based assimilation capacity for leaves born in the late wet season (Fig. 2).

DISCUSSION

Our results are consistent with community-wide studies of species with a narrow range of leaf lifespans (Diemer *et al.* 1992; Koike 1988). Although we found the predicted trend among

species, there is considerable unexplained variation in the dependent variable, A_{\max} . Certainly we would not conclude from these data that the relationship between these two phenotypic characters results from any strict causality. We obtained a similar result if the median leaf lifespan of each species was used, and in all cases this value was very close to the mean. The relationship did not improve if a grand mean lifespan was derived from all leaves produced over the year for each species. In contrast to Reich *et al.* (1992), we did not log-transformed our data because the relationship in our data was not curvilinear. In general, mass-based A_{\max} has been found to be more tightly related to lifespan than area-based A_{\max} (Reich *et al.* 1992). In our data a significant relationship was found for mass-based A_{\max} , but only during the early dry season (Fig. 2).

Two arguments suggest that assimilation and leaf longevity should not be viewed as tightly linked and "causally interrelated". First, few complex traits show such tight linkage because their phenotypic expression is always partly a consequence of the environment, which can be variable during development (Via 1985; West-Eberhard 1989). Assimilation capacity and leaf longevity are each the result of the complex quantitative expression of many genes, and thus we would expect variation in this relationship among individuals of any population, even when both characters are highly heritable. Indeed, in some populations A_{\max} has a heritability close to zero and is substantially determined by environment (Gurevitch 1992).

Secondly, is the question of how selection could act to link these two features. One can argue from an adaptationist perspective that the opportunity for carbon gain is constantly changing in time and space, and thus it is difficult for selection to finely tune the assimilation-longevity relationship. If A_{\max} is the "master integrator" (Field 1990) of past selection to maximize carbon gain over the lifetime of the leaf, then selection must have acted to coordinate several processes that compete for the same carbon during leaf development, maturity, and senescence. Leaf lifespan is merely one of several characters that may be functionally convergent, and others, such as nitrogen content, may be more directly causally related to A_{\max} . The schedule of leaf senescence may be only weakly related to these other factors if the cost of carbon gain is not strongly linked to how long a leaf exists. For the trees described here, we speculate that the assimilation-longevity relationship is tightest during the early dry season because leaves produced during this period have the highest potential return on carbon

invested in photosynthesis due to relatively continuous, direct sunshine over their lifetime.

In some species, leaf lifespan is partially determined by proximal environmental factors. Plants of three species of *Psychotria* that were irrigated for the entirety of the dry season over four consecutive years showed as much as a doubling of leaf longevity relative to plants in control sites (Mulkey *et al.* 1993). In contrast, irrigation had no effect on leaf longevity of two broad-leaved understory herbs (Mulkey *et al.* 1991). Our results suggest that such proximal factors should be more completely explored for canopy trees. We standardized the environment during leaf development by sampling only leaves from the uppermost branches that were exposed to sunlight for most of the day. Yet, the variation in leaf lifespan and assimilation within each species was much greater than many previous studies have assumed. This points to a need to relate fine-scale variation within a canopy to leaf functional syndromes.

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