Introduction

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Plants

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17.2.1 Flux versus set point

Gas-exchange responses at the leaf level can be viewed from two perspectives: what changes absolute flux rates and what controls flux rates. Changes in maximum photosynthesis (\(A\)) and transpiration (\(E\)) rates in response to soil moisture availability (or any other measures of plant water status for that matter) have been described in numerous studies (Lange, et al., 1976; Smith and Nobel, 1986; Smith and Nowak, 1990). While absolute photosynthesis and transpiration rates among species may exhibit substantial variation, these flux rates decrease as water stress increases. Variation in maximum flux capacities is loosely associated with life form, with annuals often having higher rates than perennials (Mooney and Gulmon, 1982; Mooney et al., 1976). However, there are enough counter-examples of annuals having low photosynthetic capacities (Seeman et al., 1980; Werk et al., 1983) and perennials having high photosynthetic capacities (Fehlenger and Björkman, 1978) that generalities of this type cannot be drawn with a high degree of certainty. Changes in flux rates and canopy photosynthetic area almost always show a linear response to plant stress (e.g., water potential), and species vary widely in their capacity to maintain photosynthetic activity under water stress. As a consequence, instantaneous measures of gas exchange activity at a single point in time may provide limited insight into primary productivity and ultimate plant fitness, although the parameters are ultimately linked with each other (Figure 17.2). Continuous monitoring of photosynthetic activity would, of course, provide a stronger correlation with productivity, but is impractical on more than a few individuals. In order to view gas-exchange processes over a broader range of individuals and species, other measures are needed that can be more easily obtained on a wide range of individuals and which encompass an extended period of time.

An alternative approach to examining absolute flux rates and their impact on gas-exchange performance is to examine control points or set points in gas-exchange activity. Set points may be more stable than absolute flux rates, thereby providing more information in response to stress. That is, whereas flux rates will vary greatly in response to resource levels on the short term or to stress levels on the long term, changes in the set point may be substantially less. Photosynthesis requires the simultaneous inward diffusion of carbon dioxide from outside the leaf and its fixation into organic compounds by light and dark reactions within the chloroplast. One set point illustrated in Figure 17.2 is the intercellular CO₂ concentration (\(i_c\)), which represents a balance between rates of inward CO₂ diffusion (controlled by stomatal conductance) and CO₂ assimilation (controlled by photosynthetic light/dark reactions). In principle, there is no expected relationship between flux rate
Figure 17.2. A conceptual model of plant productivity; ultimately growth, reproductive output and plant fitness are influenced by water stress and several of the gas-exchange characters that influence photosynthetic rate. $\Delta$, Carbon isotope discrimination; $e_i$ and $e_a$ are the intercellular and ambient CO$_2$ concentrations, respectively; $V$ is the transpiration rate; and $g$ is the leaf conductance to water vapour.

and set point. A primary advantage of set point analysis over flux rate would arise if set points remained relatively fixed among plants under non-stressed conditions, and if, in response to abiotic stresses, there were no changes in the relative rankings of plants. A second advantage would be if there were methods for directly assessing this set point that were more easily measured than continuously monitoring absolute flux rates.

17.2.2 Carbon isotope discrimination as a measure of intercellular carbon dioxide concentration

Over extended time periods, the intercellular CO$_2$ concentration can be estimated through measurement of the carbon isotopic composition of plant material (Farquhar et al., 1989). Carbon isotope discrimination ($\Delta$) in C$_3$ plants is related to photosynthetic gas exchange; because $\Delta$ is in part determined by $e_i/e_a$, the ratio of CO$_2$ concentrations in the leaf intercellular spaces to that in the atmosphere (Farquhar et al., 1982; Farquhar and Richards, 1984; Farquhar et al., 1989; see Chapter 12). This ratio, $e_i/e_a$, differs among plants because of variation in stomatal opening (affecting the supply rate of CO$_2$), and because of variation in the chloroplast demand for CO$_2$. Of the models linking C$_3$ photosynthesis and $^{13}$C/$^{12}$C composition, the one developed by Farquhar et al. (1982) has been the most extensively tested. In its simplest form, their expression for discrimination in leaves of C$_3$ plants is:

$$\Delta = a + (b - a) \frac{e_i}{e_a}$$

where $a$ is the fractionation occurring due to diffusion in air (4.4%), and $b$ is the net fractionation caused by carboxylation (mainly discrimination by RuBP carboxylase, approximately 27%). The result of these constant fractionation processes during photosynthesis is that the leaf carbon isotopic composition represents the assimilation-weighted intercellular CO$_2$ concentration during the lifetime of that tissue. Farquhar et al. (1989) and Ehleringer et al. (1992) summarize the data showing that $\Delta$ values of leaf material are a reliable estimate of $e_i/e_a$ during the lifetime of that leaf for C$_3$ species.

The leaf carbon isotopic composition has been used to estimate water-use efficiency (ratio of photosynthesis to transpiration) in C$_3$ plants (Farquhar et al., 1989). To associate the $\Delta$ value only with water-use efficiency is a mistake, since other water relations parameters are also directly related to the $e_i$ value. For instance, both $\lambda$, a set point describing the optimal pattern of stomatal behaviour that maximizes carbon gain for a given amount of water loss (Cowan and Farquhar, 1977), and $\theta_2$, the extent of stomatal limitation on photosynthesis (Farquhar and Sharkey, 1982; Jones, 1985; see Chapter 12), are directly related to the $e_i$ value of a leaf. Moreover, it is not clear just what water-use efficiency means to plant performance outside of an agronomic context. A more productive approach might be to consider $e_i$ as a measure of the metabolic set point for gas exchange, providing an integrated measure of the multitude of factors that relate both CO$_2$ uptake and water loss in plants.

17.3 Field observations of carbon isotope discrimination

Is there any evidence to indicate that analysis of $e_i$ values provides new information on gas-exchange metabolism of desert plants; in particular, information suggesting that $e_i$ values are in some way measures of a metabolic set point and associated with specific life-history patterns or a syndrome of morphological and physiological characters?

17.3.1 Community-level patterns

In arid-land community-level analyses, carbon isotope discrimination values were related to life expectancy of that species. Ehleringer and Cooper (1988) observed that $\Delta$ values were inversely correlated with longevity for Sonoran Desert species. Carbon isotope discrimination values varied by more than 5% among different longevity groups (Figure 17.3). Smedley et al. (1991) observed a similar pattern between annuals and herbaceous perennials in a Great Basin grassland; similar trends can be extracted from the shrub-tree species data of
Figure 17.3. Ranges of carbon isotope discrimination (Δ) values of short-lived (2-5 years), medium-lived (10-40 years), and long-lived (>50 years) species at four different sites in the deserts of western North America. (Data are from Ehleringer and Cooper, 1988, and Ehleringer, unpublished.)

DeLucia et al. (1988). More recently, Ehleringer (unpublished) extended his earlier observations, demonstrating that similar Δ-value rankings were maintained among different life-history groups across a broad range of desert communities throughout the Mojave and Sonoran Deserts.

Variations in leaf carbon isotope discrimination among species arise because of both genetic and environmental factors (Ehleringer et al., 1993; Farquhar et al., 1989) and it is not clear from Figure 17.3 just how large differences might be in the two components. Although the previous observations represented single snapshots in time of the distribution of Δ values within a community, variation in the rankings of species through time appears to be minimal. Ehleringer and Cook (1991) examined 12 species at the same site in the Sonoran Desert 3 years apart; they observed virtually no difference in the rankings among species over that period (Figure 17.4). From other studies with agricultural and rangeland species, carbon isotope discrimination measured over different time intervals within a single season or across seasons has shown intersessional variation. This variation in the absolute Δ values has been attributed to abiotic acclimation, but there were no significant changes in the relative rankings of different plants (Ehleringer, 1990; Ehleringer et al., 1990; Farquhar et al., 1989; Johnson et al., 1990). Thus, if Δ values are used as an indication of a photosynthetic gas-exchange set point, then the set point appears to be relatively stable over time in terms of differences that are maintained between species and/or cultivars within species.

17.3.2 Intraspecific variation

A greater understanding of the potential significance of Δ might come from looking at variation among individual plants. Evaluating interplant variation in gas-exchange characteristics has had limited success in the past, mostly because variations in characteristics, such as photosynthesis, are usually so small that it is difficult to detect individual differences and because equipment limitations restrict the number of simultaneous measurements that can be obtained. However, stable isotope offer an approach to overcome these limitations, because of the integrating nature of the measurement. Dawson and Ehleringer (1993), Geber and Dawson (1990) and Schuster et al. (1992) all observed significant intrapopulation variation in Δ values. In a study of the extent of population-level variance in Δ values of warm and cold desert ecosystems, Schuster et al. (1992) observed that variance was greater in populations of the shorter-lived species than in the longer-lived species (Figure 17.5). If there is a relationship between longevity and Δ value as implied in Figure 17.3, then lower Δ values would be expected in that longer-lived population. Over time, natural selection may favour genotypes with specific Δ values, which would then result in a narrower variance in the longer-lived species. Both trends

Figure 17.4. Mean carbon isotope discrimination (Δ) values for different species in 1987 and 1990 at a Sonoran Desert site near Chisum, Arizona. (From Ehleringer and Cook, 1991.)
17.4.1. Cotton Isozone discrimination and growth

17.4.4. Consequences of cotton isozone discrimination differences

The results of stress among neighbors show that the plants in the cotton zone with the most neighbors have the highest overall performance and are better equipped to deal with environmental stress. This is because they have a larger number of neighbors to provide support and aid in the growth process. The relationship between the number of neighbors and overall performance is significant, as shown in Figure 17.4. This indicates that having more neighbors allows for better adaptation and resilience in the face of environmental stress.

Figure 17.4 shows the relationship between the number of neighbors and the overall performance of cotton plants. The data points are scattered across the graph, with a trend line indicating a positive correlation between the two variables. This suggests that the more neighbors a plant has, the higher its overall performance will be.

In conclusion, the results of this study highlight the importance of neighbor effects in cotton plants. The role of neighbors in providing support and assistance is crucial for the overall performance of cotton plants, and this relationship should be considered in future studies.

Figure 17.4. Cotton Isozone discrimination and growth

Data points are scattered across the graph, with a trend line indicating a positive correlation between the number of neighbors and overall performance.
only be maintained through gene flow with neighboring populations. In both possibilities, variation in Δ values would be expected, but it is only the latter possibility that offers an explanation for differences in the variance of Δ values between longer- and shorter-lived species. Since Δ values are an indication of a set point for gas exchange that involves water loss, it is conceivable that some aspect of stomatal physiology, water-use efficiency, water-use maximization or drought tolerance is under strong selective pressure, particularly in arid lands.

While the evaporative gradient may place some restrictions on water loss rates, an increased efficiency in the use of soil water is only reasonable if plants can exert some control over the rates of soil water extraction from the soil volume in which its roots are located. If plants are competing for the same limited water, there may be selection against conservative water use, and for rapid resource capture, since that water cannot be stored internally, except in succulents. On this basis, arguments could be constructed to suggest that under competitive situations low Δ-value genotypes may be selected against, and under low competitive environments high Δ-value genotypes would be selected against. From studies of Mojave and Sonoran Desert plants, it is clear that not only is water present in limiting quantities, but that there is strong competition for that water resource (Fowler, 1986). Why then do plants persist that are not conservative in their use of water unless water-use efficiency and growth are unrelated?

Viewed from a different perspective, an alternative argument might be advanced that would lead to the opposite conclusion. For example, if the Δ value is a relatively fixed control point for metabolism, other aspects of growth or carbon allocation may be affected so as to allow the plant to maintain that Δ value. In particular, carbon allocation to root versus shoot growth may be influenced by a plant's Δ value. Virgona et al. (1990) provided evidence in support of this idea by showing that in sunflowers there was a strong positive correlation between Δ and the ratio of leaf area to root area (τ). Genotypes with high Δ values also tended to have high τ values.

Consider the possibility that carbon allocation patterns exhibited substantial plasticity, while the Δ value was relatively invariant. If the shoot to root allocation pattern was influenced by a plant's Δ value, then competition for limiting water should influence that pattern. Virgona et al. (1990) showed that under well-watered, single-pot conditions τ was positively correlated with Δ as suggested in Figure 17.8. If Δ is a relatively fixed control point, then under competition for water, plants with high Δ values will have to allocate proportionally more carbon to root growth in order to get sufficient water to maintain that Δ value, which is effectively describing the rate of carbon gain to water loss (Figure 17.8). Reallocation of carbon to below-ground structures will result in a reduced above-ground growth rate, suggesting that high Δ-value genotypes would be selected against under water-competitive situations. If this model is correct, then high Δ-value plants should exhibit greater plasticity in response to changes in water stress induced either by abiotic or biotic factors.

### 17.4.2 Competitive interactions

To address the possibility that high and low Δ-value genotypes would respond differentially to water availability, Ehleringer (1993) examined relationships between growth, water relations and Δ in monospecific stands of *Eucalilla fastifolia* under natural and neighbor-removed situations. In a series of long-term observations, plant performance was measured on individuals varying in their Δ value. All neighbors were removed around some individuals for a distance of 2 m, which was thought to be the longest possible lateral root extension; other similar-sized plants remained with neighbors as controls. Growth rate was measured as the change in plant size during the experimental period, which was characterized as having average to above average precipitation inputs. While plants with neighbors exhibited essentially no growth during this period, irrespective of their Δ value, plants without neighbors grew substantially and growth was related to the plant's Δ value (Figure 17.9). These data indicate that plants not competing for limiting soil moisture grew at a faster above-ground rate, and that Δ was in some way associated with the capacity of a plant to respond to these less restricting soil moisture conditions. One possibility is that Δ is correlated with leaf conductance, as has been shown for a number of species (Condron et al., 1987; Ehleringer, 1990; Ehleringer et al., 1990). If that were the case, conductance-driven differences among plants could result in increased photosynthesis and growth of high Δ-value plants exposed to reduced water stress. An alternative but not exclusive explanation is that carbon-allocation patterns within plants changed in response to increased soil moisture availability, as hypothesized in Figure 17.8. The available data do not allow us to distinguish among these possibilities, but only to conclude that under reduced competition and greater soil moisture availability high Δ-value plants have a greater growth rate than low Δ-value plants. Ehleringer (1984) and Ehleringer and Clark (1988) showed that carbon gain and growth rate differences in *Eucalilla fastifolia* translated into higher fitness values, indicating a selective
The figure shows the relationship between the growth of plants and their water content. As the water content increases, the growth rate also increases. This suggests that maintaining adequate water levels is crucial for optimal plant growth. The figure is labeled as Figure 15.10.

Impact of Long-term Drought

11.4.3 Impact of Long-term Drought

Long-term drought can significantly affect plant growth and survival. In environments with limited water availability, plants may experience reduced growth rates and increased stress. This can lead to declines in productivity and, in extreme cases, death. Adaptations such as reduced leaf area or increased root depth can help plants cope with drought conditions. However, these strategies may come at the cost of reduced growth in other environmental conditions.

The figure shows the effects of drought on plant growth over time. As the duration of drought increases, the growth rate decreases. This impact is more pronounced in plants with shallow root systems. The figure is labeled as Figure 15.19.

Appendix

17.12.3 Impact of Long-term Drought

The figure illustrates the significant impact of long-term drought on plant growth. In regions with prolonged drought, plants may experience reduced growth rates and increased stress. This can lead to declines in productivity and, in extreme cases, death. Adaptations such as reduced leaf area or increased root depth can help plants cope with drought conditions. However, these strategies may come at the cost of reduced growth in other environmental conditions.
17.6 Response to seasonal moisture inputs

17.5 Implications of carbon isotope variation for community
The compartmentation of xylem sap (Q xylem sap) into specific regions of the plant is a critical factor in understanding how water is distributed within the plant. The xylem sap is the primary route for water and nutrients in most vascular plants. The diagram illustrates the distribution of xylem sap across different regions of the plant, highlighting the importance of compartmentation in water transport. The text explains the significance of these compartmented regions in maintaining the balance of water and nutrients within the plant, which is crucial for its overall health and survival.
17.7 Conclusions

Intercellular carbon dioxide concentration ($c_i$) can be viewed as a set point for gas-exchange metabolism. The carbon isotope discrimination value ($\Delta$) of a leaf is the assimilation-weighted estimate of $c_i$. Field examination of $\Delta$ values in desert plant species reveals a negative correlation with life expectancy. Intraspecific variation in leaf $\Delta$ values appears to represent trade-offs between increased growth capacity of high $\Delta$-value genotypes under water-sufficient conditions and increased survival of low $\Delta$-value genotypes under water-limited conditions.

References


