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Carbon Isotope Discrimination in Coffee Genotypes Grown under Limited Water Supply[1]

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ABSTRACT

Photosynthetic gas exchange, plant-water relations characteristics, and stable carbon isotope discrimination (Δ) were evaluated for five *Coffea arabica* L. genotypes growing under two soil moisture regimes in the field. The Δ of leaf tissue was strongly correlated ($r = -0.95$) with inherent water use efficiency (ratio of assimilation to stomatal conductance; A/g). The variation in inherent water use efficiency (WUE) among genotypes was 30% for plants irrigated weekly. The higher WUE exhibited by some of these plants resulted from reduced g rather than increased photosynthetic capacity at a given g. Withholding irrigation for 1 month caused Δ to decline substantially in expanding leaf tissue of all genotypes. A strong correlation ($r = 0.92$) was found between Δ and plant hydraulic efficiency estimated as the ratio of g to the diurnal range in leaf water potential (Ψ_L). The Δ values for plants irrigated weekly adequately predicted drought-induced changes in Δ ($r = 0.99$) and midday Ψ_L ($r = 0.95$). The results indicated that Δ might be used to evaluate several aspects of plant performance and response to specific environmental conditions, once suitable background physiological data have been gathered.

Discrimination (Δ^2) against the naturally occurring stable isotope ^{13}C during photosynthetic CO_2 fixation in C_3 plants is largely determined by the ratio of the intercellular to atmospheric partial pressure (p_i/p_a) or CO_2 (7, 8, 10). This ratio is also directly related to the ratio of the instantaneous A and transpiration (9, 11), a measure of WUE. These relationships have been exploited to establish correlations between Δ in leaf tissue and WUE for several crop (3, 11, 15, 18) and native (4, 6, 13) species.

Variation in Δ among genotypes grown under identical conditions has been evaluated for its potential use as a means of selecting for improved WUE and yield in C_3 crop species (3, 11, 15, 18, 24). Leaf tissue Δ is an integrated measure of internal plant physiological and external environmental properties influencing photosynthetic gas exchange. Thus, variations in Δ within and among genotypes may prove useful for assessment and prediction of several aspects of plant performance under different environmental conditions once appropriate baseline physiological data have been gathered.

In recent years, several workers have called attention to the relationship between the operational range of g and the photosynthetic capacity of C_3 plants (12). In a number of species, changing environmental conditions have been reported to cause A and g to change proportionally in a linear relationship which passes through the origin of a plot of these two variables (16, 22, 23). A consequence of this would be that p_i, and therefore Δ, should remain constant. WUE would thus remain constant over the range of environmental conditions and values of A and g, provided the leaf-to-air vapor pressure gradient did not change. However, evidence obtained from carbon isotopic composition of leaf tissue from water-stressed plants suggests that drought-induced changes in A and g may lead to reduced p_i (5, 18).

In the present study we examined the relationship among leaf gas exchange characteristics, plant-water relations, and Δ for five coffee genotypes growing under different irrigation regimes in the field.

MATERIALS AND METHODS

Plant Material and Growing Conditions

The following five *Coffea arabica* L. genotypes were used: Catuai, Guatemalan, Moka, San Ramon, and Yellow Caturra. Seedlings were planted on November 12, 1987, in a field near Waipahu, Hawaii (lat. 21°21″ N, long. 158°02″ W, alt. 100 m) at a spacing of 1 m between plants and 3.7 m between rows. The field was irrigated weekly through drip emitters placed along the center of each row. Plants were grown in full sunlight, with 1.5 m-tall grass windbreaks planted halfway between the rows.

Irrigation was discontinued to five individuals of each genotype on May 9, 1988, and resumed 1 month later. An additional five individuals of each genotype continued to receive irrigation. Individuals of all genotypes except San Ramon were approximately 90 cm tall when the experiment began. The growth habit of San Ramon was atypical in that its extremely shortened internodes resulted in plants of low stature (about 30 cm tall) with dense, hemispherical crowns.

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[2] Abbreviations: Δ, stable carbon isotope discrimination; p_i and p_a, intercellular and atmospheric partial pressure of CO_2, respectively; A, rate of CO_2 assimilation; E, transpiration rate; WUE, water use efficiency; g, stomatal conductance; $\delta^{13}C$, ratio of $^{13}C/^{12}C$ relative to the PeeDee belemnite standard; Ψ_L, leaf water potential; Ψp, bulk leaf turgor.

Gas Exchange

Daily courses of A, g, and p_i/p_a were determined on the first fully expanded leaves on lateral branches with a portable photosynthetic gas exchange system (LI-6200; LI-COR, Inc., Lincoln, NE)[3] at 14, 22, and 25 d after irrigation was discontinued. The daily courses, determined between 0900 and 1600 h when light levels were above saturation for photosynthesis, were used to obtain average daily values of gas exchange parameters. These daily averages thus favored the portion of the day during which most of the leaf carbon was assimilated. A single set of 40 premarked leaves, representing two leaves on each of two individuals per genotype per treatment, was monitored throughout the experiment. Leaf chamber CO_2 concentration was allowed to return to the ambient level (about 347 μL/L) between measurements.

Stable Carbon Isotope Composition

Several expanding leaves, less than 40% of their final size, were collected from each individual at the end of the experiment when irrigation was resumed. This was done to ensure that most of the leaf carbon analyzed was assimilated during the experiment. Since nearly all leaf carbon is contained in cellulose, leaves that were mature at the beginning of the experiment were expected to show little, if any, change in their own carbon isotope composition resulting from alterations in their gas exchange behavior. To test this assumption, the mature leaves used for gas exchange measurements were also harvested at the end of the experiment and their carbon isotope composition determined.

Leaf samples were pooled according to genotype and treatment, oven-dried at 70°C, and finely ground. Subsamples were combusted and the relative abundance of ^{13}C and ^{12}C in the CO_2 produced was analyzed by mass spectrometry using the isotope ratio mass spectrometer facilities of the Department of Biology at the University of Utah. Stable carbon isotope composition was expressed as the $^{13}C/^{12}C$ ratio relative to that of the PeeDee belemnite standard with a precision of $\pm 0.20‰$. The resulting $\delta^{13}C$ values were used to estimate isotopic discrimination as

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p}$$

where δ_p is the isotopic composition of the plant material and δ_a is the isotopic composition of the air (8). The $\delta^{13}C$ value of the air was taken as $-8‰$, the value at Mauna Loa, Hawaii (1).

Water Relations

Predawn and midday leaf water potential (Ψ_L) were determined with a pressure chamber at 14, 18, 22, and 25 d after irrigation was discontinued. Additional twigs, each containing a pair of opposite leaves, were excised at dawn for determination of leaf water relations characteristics in the laboratory by the pressure-volume method as described previously (19). These data permitted leaf turgor (Ψ_P) and relative water content to be estimated from field measurements of Ψ_L.

RESULTS

Plant Water Status

Midday Ψ_L differed by less than 0.1 MPa among well-irrigated individuals of the five genotypes studied (Table I). Predawn water status of well-irrigated San Ramon plants was slightly higher than that of the other four genotypes. As expected, withholding irrigation for 1 month caused both predawn and midday Ψ_L of all genotypes to decline, although the magnitude of the decline differed considerably among genotypes. For example, the 30 d drought caused predawn and midday Ψ_L of Moka to decrease by about 1.0 MPa, while Ψ_L for individuals of Guatemalan exhibited a difference of only 0.2 MPa at midday and 0.13 MPa prior to dawn. Predawn Ψ_P, estimated from pressure-volume curves and Ψ_L, differed by 0.2 MPa or less among well-irrigated plants. Maintenance of predawn Ψ_P when irrigation was withheld was nearly complete in all genotypes except Moka, in which Ψ_P declined by 0.55 MPa.

Carbon Isotope Discrimination

Expanding leaves of coffee plants receiving irrigation weekly exhibited a 1.80×10^{-3} genotypic range in Δ (Table II). Withholding irrigation caused Δ of expanding leaves to decline noticeably in all genotypes. The drop in Δ associated with a decreased water supply ranged from 4.0×10^{-3} in Moka to 1.85×10^{-3} in Guatemalan. Mature leaves, whose cellulosic carbon was assimilated prior to the initiation of the

Table I. *Leaf Water Relations of Irrigated (I) and Droughted (D) Coffee Plants*

Values of Ψ_L and Ψ_P are means of 12 and 8 determinations, respectively. Predawn Ψ_P was estimated from pressure-volume curves determined for leaf samples excised at dawn.

Genotype	Predawn Ψ_L		Midday Ψ_L		Predawn Ψ_P	
	I	D	I	D	I	D
			MPa			
San Ramon	−0.09	−0.37	−1.03	−1.34	1.34	1.20
Moka	−0.21	−1.23	−1.07	−2.02	1.35	0.80
Yellow Caturra	−0.22	−0.44	−1.09	−1.66	1.14	1.13
Guatemalan	−0.23	−0.36	−1.01	−1.22	1.27	1.26
Catuai	−0.25	−0.38	−1.10	−1.53	1.23	1.18

Table II. *Carbon Isotope Discrimination in Leaves of Irrigated (I) and Droughted (D) Coffee Plants*

Genotype	Expanding Leaves			Mature Leaves		
	I	D	I-D	I	D	I-D
			$10^3 \times \Delta$			
San Ramon	20.29	17.98	2.31	19.41	18.78	0.63
Moka	20.06	16.05	4.01	19.33	18.05	1.28
Yellow Caturra	19.38	16.10	3.28	18.89	18.60	0.29
Guatemalan	18.49	16.65	1.85	18.67	18.97	−0.30
Catuai	18.53	16.29	2.24	18.22	18.38	−0.16

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[3] Mention of commerical products does not imply endorsement by the USDA/ARS or the HSPA Experiment Station.

experiment, showed only a slight difference in Δ between irrigation treatments (Table II). Values of Δ for mature leaves of well-irrigated plants averaged 0.45×10^{-3} lower than those for expanding leaves from the same plants.

Gas Exchange

Carbon isotope discrimination was highly correlated with average A/g across all genotypes and irrigation treatments (Fig. 1). The A/g ratio is a measure of inherent WUE and determines p_i/p_a, which has been shown largely to determine Δ (6). The 1.80×10^{-3} range in Δ among well-irrigated genotypes (Table II) represented a 30% genotypic variation in inherent WUE (Fig. 1).

Both the slope and the intercept of the theoretical relationship between Δ and A/g at $p_a = 347$ μbar were within the 95% confidence interval for these parameters calculated from combined measurements for well-irrigated and droughted plants (Fig. 1). Computation of separate regressions for the two treatments yielded an intercept and slope of 27.04 and −0.114 for well-irrigated plants and 23.08 and −0.076 for droughted plants, respectively.

Average A and g were both positively correlated with Δ (Fig. 2). These correlations were higher within the group of well-irrigated plants (Fig. 2, open symbols) than in the combined group of droughted and well-irrigated plants. A single linear function appeared to describe adequately the relationship between average A and g for all coffee genotypes and levels of water availability (Fig. 3); however, the regression line did not pass through the origin.

Selected physiological variables and their coefficients of determination with respect to Δ are shown in Table III. Although Δ was significantly correlated with all the measures of leaf water status selected, a measure of plant hydraulic efficiency was most effective in accounting for the variation in Δ observed. Plant hydraulic efficiency was calculated as g divided by the difference between predawn and midday Ψ_L, which is analogous to an apparent hydraulic conductance when g is multiplied by the prevailing leaf-to-air vapor pressure gradient to obtain transpiration. The relationship between Δ and hydraulic efficiency is shown in Figure 4.

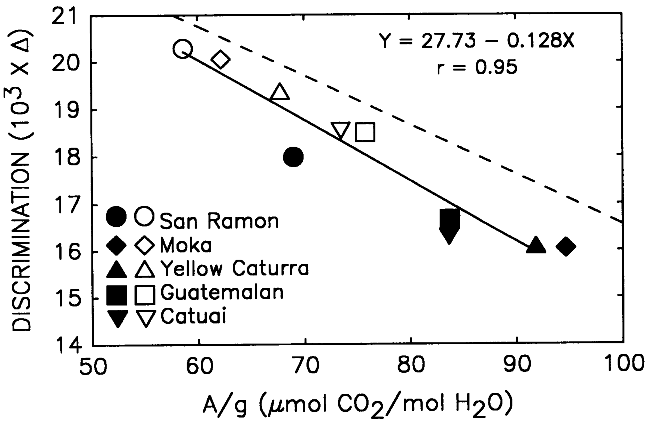

Figure 1. Relationship between carbon isotope discrimination in leaves and inherent water use efficiency (A/g) for five coffee genotypes. Open symbols represent plants irrigated weekly and closed symbols represent plants from which irrigation was withheld for 1 month. Dashed line represents the theoretical relationship between discrimination and A/g at constant $p_a = 347$ μbar ($\Delta = 27 - 0.104A/g$).

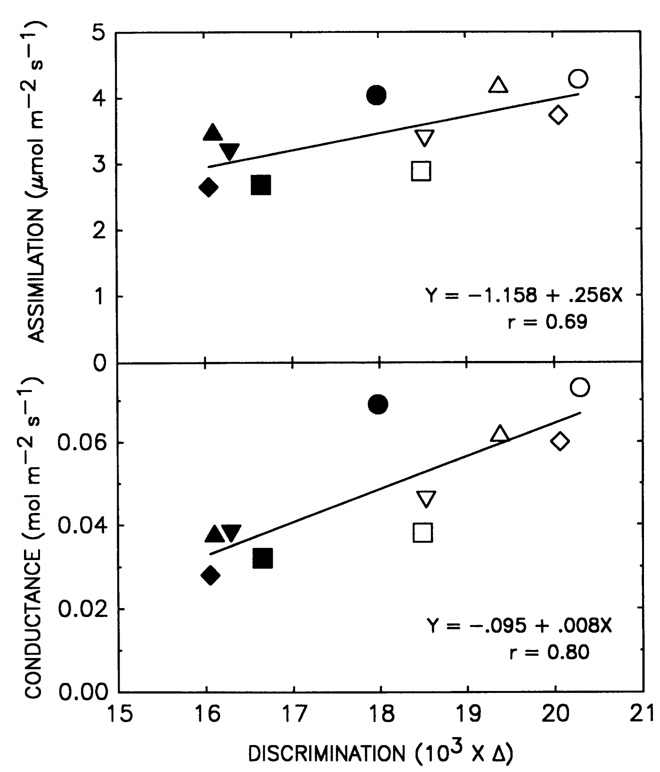

Figure 2. Assimilation and stomatal conductance in relation to carbon isotope discrimination in leaves of five coffee genotypes. Symbols are as defined in Figure 1.

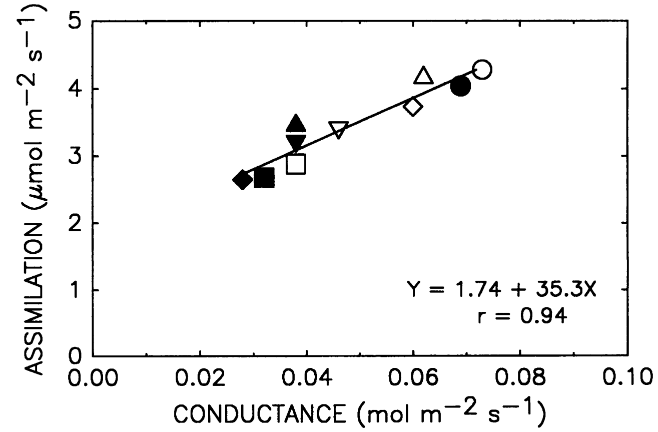

Figure 3. Relationship between average assimilation and stomatal conductance for five coffee genotypes. Symbols are as defined in Figure 1.

The relationship between g and Δ (Fig. 2) suggested that Δ of well-irrigated plants might serve as a useful predictor of genotype performance under reduced water supply. To test this hypothesis the change in Δ and the change in midday Ψ_L caused by withholding irrigation were plotted against Δ values

Table III. *Correlation of Carbon Isotope Discrimination with Selected Physiological Variables*

Variable	r^2	Significance
Predawn water potential	0.45	$p < 0.05$
Midday water potential	0.66	$p < 0.005$
Predawn turgor	0.40	$p < 0.05$
Relative water content	0.51	$p < 0.05$
Plant hydraulic efficiency	0.84	$p < 0.001$

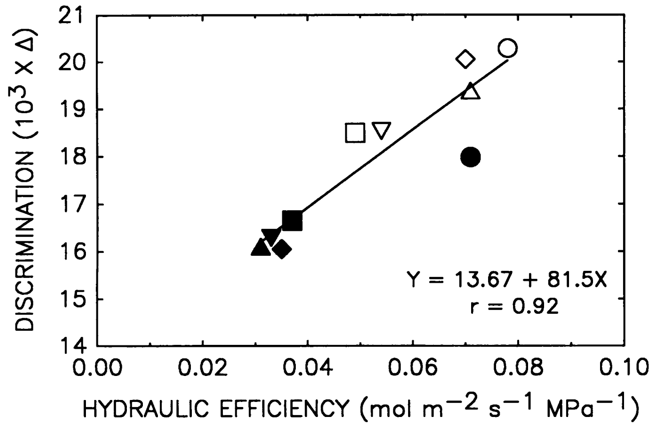

Figure 4. Relationship between carbon isotope discrimination in leaves and hydraulic efficiency, the ratio of stomatal conductance to the difference between predawn and midday Ψ_L (g/predawn Ψ_L − midday Ψ_L). Symbols are as defined in Figure 1.

of the same genotypes under irrigated conditions (Fig. 5). The correlations in both cases were highly significant, indicating that genotypes with higher Δ values became water-limited more rapidly because of their higher levels of g and therefore higher rates of water use. San Ramon was not included in this analysis because its atypical crown morphology and resultant canopy boundary layer properties prevented it from having a transpiration rate similar to that of the other genotypes at a given level of g.

DISCUSSION

The five coffee genotypes studied exhibited substantial variation in inherent WUE at the leaf gas exchange level. This was reflected in their leaf tissue carbon isotope composition. When gas exchange is measured in leaf chambers in the same field location, A/g should provide more consistent estimates than A/E of the relative ranking of WUE among genotypes. This is because a difference in evaporative demand between the inside of the leaf chamber and that which prevailed before sealing the leaf inside will immediately be reflected in E, but not in g. Since A/g, and not A/E, essentially determines p_i/p_a and therefore Δ, A/g was used to confirm the relationship between instantaneous gas exchange behavior and Δ. Measurements from droughted plants exhibited greater deviation from the theoretical relationship than those from well-irrigated plants. Among the factors responsible for this may have been fixation of a larger fraction of CO_2 via phosphoenolpyruvate carboxylase and production of leaves from stored carbohydrate in droughted plants (9).

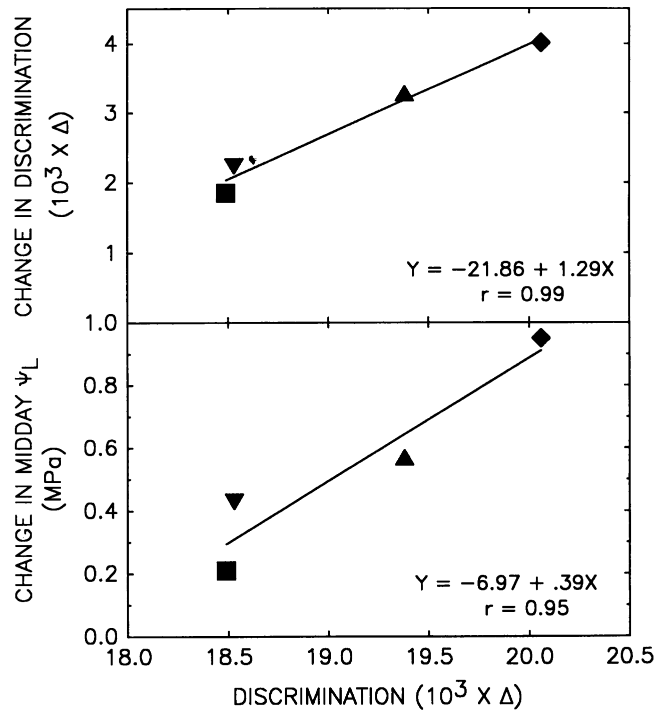

Figure 5. Changes in carbon isotope discrimination in leaves and in midday Ψ_L during a 1-month drought, as functions of carbon isotope discrimination in leaves of plants irrigated weekly. Symbols are as defined in Figure 1.

Intensive field gas exchange measurements made for 3 d during the final 2 weeks of the experiment were sufficient to characterize adequately the relationship between Δ and leaf gas exchange components. The high degree of environmental stability at the site where the plants were grown and the judicious choice of leaf material for carbon isotope analysis contributed to the success of this approach.

Under adequate irrigation, higher WUE in these coffee genotypes resulted from reduced stomatal aperture rather than increased photosynthetic capacity at a given stomatal conductance (Figs. 2 and 3). This suggests that high water use efficiency in coffee may restrict yield when water supply is nonlimiting. Behavior consistent with this idea has been observed in wheat genotypes, in which g was found to covary with photosynthetic capacity, with the relative change in g being greater (11). In a later study of wheat, Δ, g, and productivity were shown to be positively correlated for well-irrigated genotypes grown in the field (3). Apparently contrasting behavior has been reported for well-irrigated peanut genotypes in which productivity and Δ were negatively correlated (15, 24), suggesting that variations in Δ were the result of variations in photosynthetic capacity, and therefore p_i/p_a, at similar levels of g. These contrasting observations indicate that appropriate background physiological data must be acquired before the results of leaf carbon isotopic analyses can be fully interpreted.

Coffee genotypes with higher Δ under well-irrigated conditions depleted soil water more rapidly and experienced symptoms of physiological stress more rapidly (Fig. 5) when water was withheld, suggesting that Δ of well-irrigated coffee plants can be used to predict genotype performance under water-limited conditions. Potentially confounding factors such as genotypic differences in leaf area, root/shoot ratio, and soil volume explored by root systems did not interfere with this relationship as long as the analysis was restricted to the four genotypes with similar crown morphology. This pattern accounts for the change in the WUE ranking of the genotypes under water-limited conditions (Table II; Fig. 1). For example, the Δ values of Guatemalan and Catuai were among the lowest under well-irrigated conditions, but among the highest after a 1-month drought (Table II). In contrast, WUE rankings of wheat, peanut and tomato genotypes grown under different soil moisture regimes were reported to be stable (11, 18, 24).

The results described above imply that genotypes such as Guatemalan and Catuai may exhibit more satisfactory performance than Yellow Caturra and Moka under rainfed conditions. The reverse may be true under a regime of frequent, ample irrigation, since Yellow Caturra and Moka exhibited higher rates of gas exchange under these conditions. Yield data were not gathered in the present study, but there is a large body of literature demonstrating a positive correlation between total water use (gas exchange) and yield in a variety of crop species (14).

The ability of a single linear function to adequately describe the relationship between prevailing A and g over a range of contrasting genotypes and soil water contents suggests that the degree of coupling between g and A (21, 22) is highly conserved among coffee genotypes. It is likely that in droughted plants coupling between A and g was maintained through changes in the response of photosynthesis to p_i, as well as in stomatal limitations to photosynthesis. Typical values of p_i estimated under high irradiance in the field ranged from a low of 170 μbar in droughted Yellow Caturra plants to a high of 235 μbar in well-irrigated San Ramon plants. This corresponds to the range over which the response of A to p_i is strongly curvilinear in most C_3 plants during short-term experiments in which variations in p_i are attained by varying p_a or g (*e.g.* 2). The linear relationship between A and g, and its nonzero intercept, observed in the present study thus provides indirect evidence for adjustments in both biochemical and stomatal limitations to photosynthesis.

It is noteworthy that a measure of plant hydraulic efficiency, the ratio of g to the apparent soil/leaf Ψ_L gradient, was more effective than either g or Ψ_L alone in accounting for the variation in Δ observed (Table III, Figs. 2 and 4). Stomatal and liquid phase conductances have been reported to change in parallel in a number of species (17, 20, 21). Since Δ represents an integrated measure of both stomatal and photosynthetic properties, the results of the present study suggest that both g and photosynthetic capacity may have changed in a coordinated manner with hydraulic conductance in the soil/root/leaf pathway. This suggestion is supported by similar observations of seasonal changes in plant hydraulic conductance and WUE of woody species in a European hedgerow (17). Water use efficiency in coffee may thus be a function of the hydraulic capacity of the soil and stem to supply the leaves with water (Fig. 4).

We conclude that leaf carbon isotope analysis shows promise as a rapid means of evaluating multiple aspects of plant performance and responses to specific environmental conditions.

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