

## CHAPTER 7

### CONCLUSION

#### **Leaf water $\delta^{18}\text{O}$**

Nearly all aspects of oxygen isotope research in plant processes, from leaf-level physiology to global carbon budgets are affected by the leaf-water  $\delta^{18}\text{O}$  signal (Yakir 1998). Therefore, a coherent understanding of leaf-water enrichment across dominant plant functional-types is essential. Grasses display a fundamentally different pattern of leaf-water  $^{18}\text{O}$ -enrichment than dicots (Chapter 1), which is attributable to the progressive evaporative enrichment along parallel veins.  $\text{C}_4$  grasses have smaller interveinal distances and as a result experience greater mixing of enriched water at the stomatal complexes and unenriched vein water. This process, integrated over the whole leaf, resulted in  $\text{C}_4$  grasses being more enriched than  $\text{C}_3$  grasses.

For the first time, the Gat-Bowser (1991) model was applied to plants and was shown to be capable of explaining observed enrichment that was greater than the Craig-Gordon (1965) model predictions (Chapter 2). This was largely

because the evaporative flux profile along the grass leaf can change, and as it changes the  $\delta^{18}\text{O}$  of bulk leaf water also changes. It is hypothesized that the level of evaporative enrichment in a grass leaf will vary as drought stress varies. The basic concept behind this is that when a grass is well-watered, the tips of the leaves should transpire proportionally more than the base due to higher irradiance (Meinzer and Saliendra 1997). As a leaf becomes stressed the water potential in the tip of the leaf will decrease first, either to avoid xylem cavitation or because of xylem cavitation. This change in the flux profile should, according to the Gat-Bowser model, result in a large change in bulk leaf  $\delta^{18}\text{O}$ . There is currently only one data set to support this hypothesis (Chapter 2), and concomitant water status parameters were not measured.

### **Leaf cellulose $\delta^{18}\text{O}$**

At the onset of this dissertation research, there were several unknowns in the relationship between leaf water  $\delta^{18}\text{O}$  and cellulose  $\delta^{18}\text{O}$ . In Chapters 3 and 4, these unknowns were clarified by taking into account the developmental patterns of grasses and the  $\delta^{18}\text{O}$  signature associated with the water pools in which sucrose and cellulose were synthesized. Importantly, five  $\text{C}_3$  grass species and five  $\text{C}_4$  grass species were explained equally well by the tree-ring model, which suggests broad applicability to all grass species, both natural and agricultural.

The results in Chapter 4 show that the  $\delta^{18}\text{O}$  signature can change along the leaf as environment changes during leaf expansion. This is an important finding as it shows that grass blades are analogous to tree-rings (Roden et al. 2000) and that grass blades may offer climatic reconstruction on an inter-seasonal basis. Additionally, it has been shown that the  $\delta^{18}\text{O}$  of bulk leaf cellulose is correlated with stomatal conductance (Barbour and Farquhar 2000). The results presented here suggest that the  $\delta^{18}\text{O}$  of grass blades may offer insight to smaller scale physiological changes as grass blades develop throughout the season.

Future studies must determine if smaller scale environmental changes, on the order of 5- 10 % relative humidity, can be detected in the cellulose  $\delta^{18}\text{O}$  along a grass blade. Furthermore, more tests must be performed to determine why grasses grown in relative humidity above 90 % do not respond in the same linear fashion as grasses grown at lower relative humidity (Figure 4.7).

### **$\delta^{18}\text{O}$ of atmospheric $\text{CO}_2$ .**

As  $\text{CO}_2$  diffuses into a leaf during photosynthesis, a large proportion of that  $\text{CO}_2$  retrodiffuses from the leaf without being fixed by the photosynthetic machinery (Francey and Tans 1987). Upon entering the leaf,  $\text{CO}_2$  molecules are subject to rapid oxygen exchange with leaf-water due to carbonic anhydrase activity. This process labels atmospheric  $\text{CO}_2$  with the oxygen isotope ratio of leaf-water. It

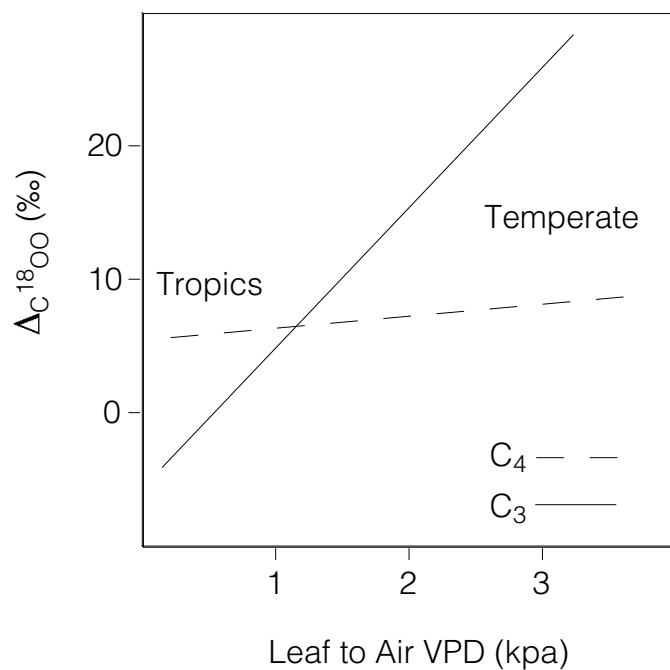
has been estimated that 45 % of atmospheric CO<sub>2</sub> has been through this process (Keeling 1993). The isotope ratio of leaf water is determined by initially by geography (source water  $\delta^{18}\text{O}$ ) and secondly by environmental factors (Craig and Gordon 1965, Flanagan et al. 1991). Hence, CO<sub>2</sub> retrodiffusion from leaves represents a powerful tool for partitioning carbon fluxes from local to global scales.

The C<sub>4</sub> grass *Andropogon gerardii* displayed low discrimination and low variability in discrimination against C<sup>18</sup>OO, through both low C<sub>cs</sub>/C<sub>a</sub> and low carbonic anhydrous activity (Chapter 5). These results were similar to those of Gillon and Yakir (2000) and suggest that the CO<sub>2</sub> retrodiffused flux from C<sub>4</sub> dominated ecosystems should be unique, and allow for the partitioning of C<sub>4</sub> contributions to global net primary productivity.

Over the past decade, the global mean  $\delta^{18}\text{O}$  of atmospheric CO<sub>2</sub> has decreased by 0.08 ‰ per year (NOAA/IAAR 2000). There will, undoubtedly, be a large effort among atmospheric CO<sub>2</sub> researchers to determine the cause of this decrease. To date, only one hypothesis has been put forth to explain this phenomenon. Throughout the tropics, vast areas are being deforested and replaced by pasture systems. Due to the high mean annual temperatures in the Tropics, these forest are being replaced by C<sub>4</sub> grasses (Ehleringer 1978). Gillon and Yakir (2001) hypothesized that this C<sub>4</sub> expansion, and with it the low discrimination against C<sup>18</sup>OO, may be a contributing factor to the global decrease in the  $\delta^{18}\text{O}$  of atmospheric CO<sub>2</sub>.

A contrary hypothesis offered here is that the change in energy budget that would occur in a transformation from forest to grassland should actually result in  $C_4$  pastures discriminating more (or increasing the  $\delta^{18}\text{O}$  of atmospheric  $\text{CO}_2$ ) than the surrounding forest. Figure 7.1 shows a simple modeling procedure (using the equations and results from Chapter 5) to predict  $C_3$  versus  $C_4$   $\Delta_{\text{C1800}}$  in forest-to-grassland changes from temperate to tropic systems. The only parameter changing from temperate to tropic in the modeling analysis was VPD. The difference between  $C_3$  and  $C_4$  systems are  $C_{\text{cs}}/C_{\text{a}}$ ,  $\theta$ , and leaf temperatures. This modeling procedure suggest that  $C_4$  expansion in the tropics probably does not account for the global decrease in the  $\delta^{18}\text{O}$  of atmospheric  $\text{CO}_2$ .

While there is little empirical support for either hypothesis, two such largely contrasting hypothesis stress both the global impact that  $\Delta_{\text{C1800}}$  in  $C_4$  grasses may have, and the need for more research on  $\Delta_{\text{C1800}}$  in  $C_4$  grasses.



**Figure 7.1** Predicted  $\Delta_{C^{18}O_0}$  for C<sub>3</sub> forest and C<sub>4</sub> pasture versus vapor pressure deficit.  $\delta^{18}O_{atmwv} = -20$ ,  $\delta^{18}O_{atmco2} = -1.5$ ,  $\delta^{18}O_{s. water} = -8$ ,  $T_{leaf} = 30, 33$  °C for forest and pasture, respectively;  $C_{cs}/C_a = 0.7, 0.3$  and  $\theta = 1, 0.4$  for forest and pasture, respectively.

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