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The contribution of respiration in tree-stems to the Dole Effect

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Abstract

Understanding the variability and the current value of the Dole Effect, which has been used to infer past changes in biospheric productivity, requires accurate information on the discrimination associated with respiratory oxygen consumption in each of the biosphere components. Respiration in tree stems is an important component of the land carbon cycle. Here we measured, for the first time, the discrimination associated with tree stem oxygen uptake. The measurements included tropical forest trees, which are major contributors to the global fluxes of carbon and oxygen. We found discrimination in the range of 12.6–21.5 ‰, indicating both diffusion limitation, resulting in O_2 discrimination values below 20 ‰, and alternative oxidase respiration, which resulted in discrimination values greater than 20 ‰. Discrimination varied seasonally, between and within tree species. Calculations based on these results show that variability in woody plants discrimination can result in significant variations in the global Dole Effect.

1 Introduction

The Dole Effect is defined as the difference between the average isotopic composition of oxygen in seawater (H_2O), and the oxygen in atmospheric O_2. The magnitude of the Dole effect depends mainly on three factors: the isotopic composition of leaf water from which O_2 is produced on land (Farquhar et al., 1993; Gillon and Yakir, 2001), the possible isotopic discrimination during release of O_2 from H_2O during photosynthesis (Eisenstadt et al., 2010; Luz and Barkan, 2011); and the discrimination against the heavier isotope in respiratory oxygen consumption (Lane and Dole, 1956; Guy et al., 1989, 1993). The Dole Effect was suggested to be a useful tracer for paleo-changes in the ratio of ocean to land productivity (Bender et al., 1994; Blunier et al., 2002). However, this use is based on the assumption of significantly different isotopic effects of the land and the oceans. New findings, including indications for significant discrimination during marine photosynthesis and the effect of diffusion in soils on the effective

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respiratory discrimination, have resulted in a decreased estimated difference between the terrestrial and marine Dole Effects, making it easier to explain why there have not been large shifts in the Dole Effect between glacial and interglacial times (Luz and Barkan, 2011).

As shown by previous studies (Angert et al., 2003; Angert and Luz, 2001; Angert et al., 2001), when the diffusion of O_2 from the atmosphere to the consumption site inside roots and soil aggregates is restricted, the effective discrimination of the soil system depends not only on the intrinsic discrimination in the respiration processes, but also on the discrimination in diffusion, and on the internal oxygen concentration at the consumption site. This effect of diffusion on the discrimination in O_2 uptake is similar to the well known isotopic effect which takes place in CO_2 diffusion and uptake in leaves (Farquhar et al., 1982). Overall, the effect of diffusion tends to lower the effective discrimination of O_2 uptake in soils (Angert et al., 2003).

However, observations in temperate and boreal forest soils demonstrated that a second process must also act to explain the observed $\delta^{18}O$-O_2 in soil pore space. This process is respiration through the alternative oxidase pathway (AOX). The discrimination of AOX respiration is ~30 ‰, which is considerably higher than the ~20 ‰ discrimination in "normal" dark respiration through the cytochrome oxidase pathway (COX) (Ribas-Carbo et al., 1995). High discrimination values (22.5 ± 3.6 %) were found in boreal soils (Angert et al., 2003), and can be explained by a large fraction of respiration which goes through the AOX in plant roots.

The emission of CO_2 from aboveground woody tissues amounts to ~16 % of the forest annual gross photosynthesis flux (Litton et al., 2007; Ryan et al., 1997; Waring et al., 1998) while below ground woody tissues contribute similar amount. As a result, the discrimination in woody tissue O_2 uptake may have a significant impact on the global contribution of land to the Dole Effect. To date there have been no measurements of O_2 isotope discrimination in tree wood respiration processes. Here we report the first measurements based on stem O_2 influx for 6 tree species, representing 4 different plant families, including trees from tropical forests that contribute ~40 % of global land

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primary production (Beer et al., 2010). Our results suggest that, as with soil respiration, both the effects of diffusion on one hand, and AOX activity on the other, control the isotopic effects in stem O_2 uptake.

2 Methods

2.1 Sites and trees

Trees from two sites were sampled. The first site was the Givat-Ram campus of the Hebrew university of Jerusalem (HUJI, 31°46′15" N 35°11′51" E). In this site we have performed experiments on the following trees: one Apple (*Malus domestica*), one Stone Pine (*Pinus pinea* L.), and one Aleppo Pine (*Pinus halepensis* Mill.). Experiments in this site were conducted from April 2010 to March 2011. The second site was the UNAP site, located at the Center for Research and Forest Learning (CIEFOR) of the National University of the Peruvian Amazon (UNAP) in the community of Puerto Almendras, which is located 16 km southwest of the city of Iquitos, Peru. CIEFOR is centered over 3°49′53" N, 73°22′28" W, encompasses a forested area of 1300 ha and belongs to the Faculty of Forest Engineering (FCF)-UNAP. For the base period 1971–2000 the mean annual rainfall is ∼3000 mm (http://www.senamhi.gob.pe/), and the maximum, minimum, and average temperatures are 26.3 °C, 25.9 °C, and 25.2 °C, respectively (Brohan et al., 2006). All the experiments in this study were conducted on a total of nine trees from the following species (three each): *Tachigali Paniculata (*Tangarana) and *Hymenolobium* sp (Mari-Mari) from the fabaceae family, and *Simaroura Amara* (Marupa) from the Simaroubaceae family, with a typical wood density values of 0.53, 0.65 g, and 0.35 g ml^{-1}, respectively (Chambers et al., 2004). The experiments in the UNAP site were conducted during the local wet season, from April to May 2011.

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2.2 Stem chambers

The stem chambers used at the HUJI site are described in Angert and Sherer (2011). Each chamber was constructed from two rectangular clear Perspex parts: (1) a frame base equipped with closed-cell foam on the stem side, and (2) a lid equipped with plastic connectors for sampling and a 60 mL syringe directly connected to it to allow decreasing the system's volume while taking an air sample. The bottom part of the syringe was sawed-off to allow good diffusive mixing with the rest of the chamber. The chamber was sealed to the stem by hot-glue. For installation on trees where rough bark made it difficult to make an air-tight seal with the chamber base, we first removed some bark, and then smoothed the surface with a file, while being careful not to damage the cambium. In case of smooth-barked trees, we only removed loose bark and lichen before installing the chamber base. After closing the lid, we have checked the seal by pulling the piston of the bottomless syringe attached to the lid, and checking for resistance to the pull. This resistance indicates that air could only enter the chamber through small pores in the bark, and hence, in the absence of strong winds (which were avoided during our field campaigns), the mixing between the chambers and the atmosphere was dominated by diffusion. Samples of the air in the chamber were collected in pre-evacuated ~3.6 mL glass flasks with a Louwers-Hapert™ O-ring valve. Before sampling, the dead volume in the tubing and flasks' necks were purged with 30 mL of air from the chamber.

The chambers used in the UNAP site were made from polypropylene (PP) tube T-pieces (OD 11 cm, Ostendorf HTRE DN 110) that are equipped with a threaded lid to close one end. The other two ends were welded shut with PP disks. These completely closed T-pieces were then cut longitudinally, thus removing a segment of the tube opposite to the threaded lid, resulting in an opening along the whole length of the tubing (27.2 cm) and 7.0 cm wide. The chambers were fit to the shape of the tree stem at the exact spot of installation, and sealed to the stem by hot-glue. Leak-testing was performed by measuring the chamber CO_2 concentration while blowing respiratory air

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through a piece of tubing on all possibly leaky spots. The removable chamber lids were equipped with connectors that allowed the 3.6 mL flasks to be directly connected once the lid was sealed. The flask valves were left open to allow O_2 to diffuse freely between the sampling flask and the chamber headspace. These flasks were left open and attached for 10 days to ensure that the chamber air reached steady-state between the rate of "leakage" of O_2 from the atmosphere, and the rate of consumption of O_2 by the stem (see next section). The flasks were then closed and shipped for analysis. At both sites, the chambers were attached at heights of ~1.6 to ~2 m above the ground.

2.3 Analytical methods

Sample preparation and mass spectrometry were according to Barkan and Luz (2003). The preparation of the sample included cryogenic removal of water vapor and CO_2 and chromatographic separation of N_2 by a fully automated system. Elimination of N_2 prevented the need for correction for the effect of N_2 interference in the ion source of the mass spectrometer. The oxygen concentrations were calculated from the ratio of O_2 to Ar (expressed as $\delta O_2/Ar$), under the assumption of constant Ar concentration. All measurements were performed on a Finnigan-MAT Delta-Plus (Thermo Scientific,Waltham, MA, USA) dual-inlet mass-spectrometer. The precision in $\delta O_2/Ar$ was 1 ‰ (which translates to a precision of 0.02 % in O_2 concentration), and the precision in $\delta^{18}O$ determination was 0.03 ‰. All the results are presented with respect to atmospheric air standard (Barkan and Luz, 2003).

2.4 Models for stem and chamber gases

Estimating the discrimination associated with stem O_2 uptake from the $\delta^{18}O$ and $[O_2]$ data requires some simple modeling. Our 1-box analytical model follows a model originally developed for soils (Angert et al., 2003, 2001). In our model, a box represents the chamber and the top layer of the stem, which are assumed to have the same O_2 concentration and isotopic composition. The O_2 in the box is assumed to be in

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steady-state. This steady-state results from a balance between O_2 diffusion into the box through the bark and outer layer of the stem, and O_2 consumption by respiration in the tissues under the chamber.

We assume that advective transport of O_2 dissolved in xylem water transiting the area enclosed by the chamber, as well as possible dissolution or exsolution of O_2 in this water, can be neglected compared to respiration consumption of O_2. This assumption is reasonable because of the relatively low solubility of O_2 in water, which dictates relatively small rates of transport in the xylem water. Even if we assume that the water that arrives at the base of the stem has zero oxygen, this water, at the maximum, could take up dissolved O_2 until it is in equilibrium with atmospheric air, or a concentration of roughly 0.25 mmol L^{-1}. If we assume, for example, a tree with a stem diameter of 0.5 m, respiration rate of 200 mg C m^{-2} h^{-1}, and xylem water flux of 500 liters per day, the removal of O_2 by dissolution will amount to 10 % of the oxygen consumed by respiration up to the height of 1 m. However, above this height the water will be saturated and will not be able to take up more oxygen. We assume that in a more realistic case, the water arrives from the roots close to equilibration with the stem O_2 and can take up or lose only small amount of oxygen compared to respiration fluxes. This also means that O_2 produced by corticular photosynthesis outside of the chamber will have negligible effect on the chamber $\delta^{18}O$. We will also neglect here the possible effect of thermal diffusion, under the assumption that the temperatures at the stem surface and inside it are similar.

Hence, the temporal change in O_2 concentrations in the chamber is given by:

$$\frac{d[O_2]_c}{dt} = I - O - R \quad (1)$$

Where the "c" subscript designate the chamber, I is the incoming diffusion flux, O is the outgoing diffusion flux, and R is the consumption flux in the soil. The isotopic composition of the O_2 in the chamber will depend on the balance between the entrance of atmospheric O_2 which will be affected by discrimination in diffusion, which favors the entrance of light (low $^{18}O/^{16}O$) oxygen into the chamber headspace, and uptake of

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O_2 by the stem, which removes light oxygen from the chamber headspace. Temporal changes in the $\delta^{18}O$ value of the chamber O_2 ($\delta^{18}O_c$) can be approximated by:

$$\frac{d([O_2]_c \cdot \delta^{18}O_c)}{dt} = I \cdot (\delta^{18}O_{atm} - D_{diff}) - O \cdot (\delta^{18}O_c - D_{diff}) - R \cdot (\delta^{18}O_c - D_{stem}) \quad (2)$$

Where D_{diff} is the ^{18}O discrimination in diffusion in air, and $\delta^{18}O_c$ and $\delta^{18}O_{atm}$ are the $\delta^{18}O$ values of the chamber and atmospheric O_2 respectively. D_{stem} is the overall ^{18}O discrimination of the O_2 uptake by the stem. The D_{stem} parameter integrates over the combined effects of the diffusion in gas phase in the stem, possible diffusion in liquid phase to the consumption site within living cells, and the biochemical uptake by both COX and AOX. Since we are interested in the change in $\delta^{18}O$ relative to atmospheric oxygen (our primary standard), $\delta^{18}O_{atm}$ is zero and can be omitted, and we obtain (Angert et al., 2001; Farquhar et al., 1982) :

$$D_{stem} = \frac{\delta^{18}O_c}{(1 - [O_2]_c / 20.95\ \%)} + 14.1\ ‰ \quad (3)$$

Where the values of 20.95 % and 14.1 ‰ are the O_2 concentrations in air, and the discrimination associated with O_2 diffusion in air, respectively.

Another way to represent the balance between diffusion and uptake is by a numerical model. Our 1-box numerical model is based on the same box and fluxes as the analytical model above. The main difference is that steady-state is not assumed between the box and the atmosphere. Rather, the model is initialized to start with atmospheric air in the box, and the changes in the O_2 and CO_2 are solved by a finite-difference approach. An example of a model run (with D = 14.1 ‰) appears in Fig. 1. As the simpler analytical model predicts, discrimination of 14.1 ‰ is associated with a $\delta^{18}O$ value of 0 ‰ (i.e. identical to the atmosphere) in steady-state. However, the time-resolving model shows that $\delta^{18}O$ overshoots to values above 1 ‰ before reaching steady-state. Hence, using the analytical model for a sample taken before the chamber reached

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steady-state will yield an erroneous estimate of the discrimination value. With the arbitrary conductance used in this example, the steady-state values in isotopic composition are achieved in ~30 h. This isotopic equilibration time is much longer than that required for concentrations to come into equilibration, as has been observed in other systems. Based on previous experiments (Angert and Sherer, 2011) we have estimated that the time needed for the isotopic composition in the stem chamber to reach steady-state is about 24 to 48 h. Consequently, we calculated here the discrimination by Eq. (1), only from chambers' experiments lasting at least 48 h.

3 Results

The results of all the stem chambers experiments are summarized in Table 1. The discrimination values (D) ranged from 12.0 ‰ to 21.5 ‰. Discrimination in the range of 14–16 ‰ was the most common and was found in 9 out of the 21 experiments. Discrimination below 16.5 was found in almost all the Apple tree experiments, excluding the one conducted shortly after bud burst in April 2010. The Mari-Mari trees discrimination was 15.2–15.3 % on average, while the Tanagrana trees range was 16.6–18.1 ‰, and the range for the Marupa trees was the widest: 15.2–19.8 ‰.

4 Discussion

The estimate of the discrimination by Eq. (3) is based on the assumption that the gas transport to the chamber is dominated by gas-phase diffusion. In other words, we assume that O_2 did not enter the chambers by mass flow. Entrance of O_2 by mass flow is with no isotopic discrimination, and hence using the parameter of 14.1 ‰ in Eq. (3) will bias D_{stem} toward higher values, if the assumption of dominating diffusion gas exchange is not valid. However, this assumption is supported by two tests we have made. First, we have successfully tested the chambers for leaks (see methods). Second, we

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have conducted an experiment on the Apple tree especially to test the assumption of dominating gas-phase diffusion. In this test, we have flushed the chamber at the start of the experiment with N_2 gas. In this condition, the initial gas exchange between the chamber and the atmosphere brings in O_2 to the chamber. Oxygen entering by mass flow, will enter with the same isotopic value of the atmosphere oxygen ($\delta^{18}O$=0 ‰), while oxygen entering by diffusion, will have negative $\delta^{18}O$ values (versus the atmosphere), due to fractionation by diffusion. Thus, if diffusion transport dominates, the oxygen in the chambers is expected to have negative $\delta^{18}O$ values that will increase with time as a result of back-diffusion (also with a discrimination of 14.1 ‰) and as a result of uptake by the stem. The results of this experiment, already published (Angert and Sherer, 2011), showed negative $\delta^{18}O$ values of −3.15 ‰ and −2.58 ‰, 2 and 4 h after the start of the experiment, respectively. Based on these two lines of evidence, and based on the absence of strong winds or strong diurnal temperature changes (especially in the tropical forest), we conclude that mass flow to the chambers was negligible.

We found frequent occurrence of low discrimination values, in the range of 12–16 ‰ which is well below the known values for COX respiration in isolated plant mitochondria, which is ∼20 ‰, (Ribas-Carbo et al., 1995). The low values are most probably not related to variation in the COX in different plant species, since discrimination of ∼20 ‰ was also reported for the much more genetically-remote marine eukaryotes and marine bacteria (Kiddon et al., 1993). Hence, the low value we measured can be explained only by the effect of diffusion limiting the internal O_2 concentration. As was found for soils, limiting diffusion of O_2 to the consumption site makes the effective discrimination lower than the one involved in the enzymatic respiration process by itself with no limit to the supply of O_2. Again as in soils, we can suggest a conceptual model of "a box within box", in which oxygen first diffuses in gas phase through the stem ("outer box"), and then diffuses in liquid phase to the consumption site within living cells ("inner box"). The discrimination by the combined effects of diffusion into the inner box and enzymatic O_2

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consumption within it, is given by the following equation (after Farquhar et al. (1982)):

$$D' = D_{diff'} + (D_{con} - D_{diff'})C_i/C_a \quad (4)$$

Where D' is the overall discrimination of the inner box, D_{con} is the discrimination in consumption, $D_{diff'}$ is the discrimination in diffusion to the inner box, and C_a and C_i are the O_2 concentrations outside and inside the inner box, respectively. The discrimination of the entire stem (D_{stem}) will relate to the discrimination of the inner box (D') by a similar equation:

$$D_{stem} = D_{diff} + (D' - D_{diff})C_i/C_a \quad (5)$$

Where D_{diff} is the discrimination in diffusion through the stem, which is 14.1 ‰ assuming that this diffusion is in gas phase. According to Equations 4 and 5, the D_{stem} values below 14 ‰ can only be explained if the diffusion to the inner box is by liquid phase diffusion, in which the discrimination is close to zero ($D_{diff'}$ ~0).

The differences observed between tree species could reflect variations in structural barriers to diffusion. Indeed, Marupa, the tropical tree in which the highest discrimination was measured, has a reported wood density of only 0.35 g ml^{-1} versus 0.53 and 0.65 g ml^{-1} for Mari-Mari and Tangarana (Chambers et al., 2004). However, the diffusivity depends not only on the density (and hence porosity) of the stem, but also on the water content which may vary, and on the structure of the air-filled pore spaces (Sorz and Hietz, 2006). We currently do not have data on diffusivity values of the live tissue.

Variations in diffusivity (resulting in lower discrimination values) cannot explain the discrimination measurements that are greater than those expected for the cytochrome (COX) pathway respiration (20 ‰). The only known process that can result in higher discrimination values is the engagement of the AOX respiration pathway. Moreover, since it is reasonable to assume that the diffusion limitation always exists, the discrimination values above 19.5 ‰ as those in some of the Marupa trees, also indicate large contributions of the AOX pathway (relative to the COX), which shift the overall discrimination to higher values, and compensate for the effects of diffusion. The changes

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in discrimination in the Apple tree with time resemble variation in the range of 12.3 to 19.9 ‰ observed for the same root system in the course of few weeks (Angert and Luz, 2001), and are probably also related to changes in the relative contribution of AOX to total respiration O_2 consumption.

Our findings have implication both for estimating the average land contribution to the Dole Effect, and for estimating the variability and uncertainty in this value. The average of the stem experiments in the current study is 16 ‰. However, we observed large variability in discrimination values with season, between species, and within species, so this value cannot be assumed to be globally representative. If the value of globally averaged discrimination in stem uptake happens to be 16 ‰, then, assuming that stems respiration consists of 16 % (Litton et al., 2007) of the land respiration, the estimation of the land contribution to the Dole Effect will be lower in 0.3 ‰ relative to an estimate that uses a discrimination value of 18 ‰ for all land dark respiration (Blunier et al., 2002). This 0.3 ‰ value is small in comparison to other uncertainties in estimating the land Dole Effect (Luz and Barkan, 2011). However, the paleo data point to variability in the land Dole Effect in the order of only 0.5 ‰ (Severinghaus et al., 2009). If we assume a shift from an average stem discrimination of 15 ‰ to 19 ‰ (well within our measured range of 12.0–21.5 ‰), it will induce a shift of ~0.6 ‰ in the land Dole Effect. This effect is in similar magnitude to that resulting from possible changes in the discrimination by soils, which were suggested (Severinghaus et al., 2009) to partly explain past changes in the Dole Effect. This soils effect was suggested to result from variations in the activity of tropical soil respiration, shown to be diffusion limited and have low discrimination, relative to the activity of boreal forest, where engagement of AOX resulted in high discrimination. However, given that to date there is only one survey of the discrimination in various soil sites (Angert et al., 2003), and considering the variability reported here for stem discrimination, many more studies must be conducted before the variability in the Dole Effect can be reliably interpreted.

Another important implication of our findings is for estimating the contribution of the AOX to respiration and the carbon cycle. To the best of our knowledge, this study

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is the only one to date that has estimated AOX activity in intact plants in the field. Given the known relation between AOX and various types of stress (Vanlerberghe and McIntosh, 1997; Moore et al., 2002; Rachmilevitch et al., 2007), working with intact plants has a clear advantage over incubating desiccated plant tissue (Ow et al., 2008; Searle and Turnbull, 2011) that might exhibit a wound response. Using the approach demonstrated here, it is possible to trace how the AOX contribution in woody tissue of a single plant changes seasonally, and due to environmental conditions such as temperature and soil moisture. For example, we found highest discrimination in the Apple tree shortly after bud burst, which somewhat resemble the high discrimination reported for aquatic systems shortly after spring bloom (Luz and Barkan, 2011). These findings are with agreements with findings of increased AOX activity shortly after changes in environmental conditions, or before an increase in the rates of respiration through the COX (Moore et al., 2002; Rachmilevitch et al., 2007). As noted above, the AOX is also reported to be activated as a response to stress. We thus believe that more field studies of the AOX will improve the understanding of the carbon cycle and its sensitivity to climate induced changes in respiration.

5 Conclusions

We have measured, for the first time, the O_2 discrimination associated with respiration of intact tree stems. We have found, as predicted from theory, evidence for both the effect of slow diffusion that limits the internal O_2 concentrations and lowers the discrimination, and the effect of the AOX that increases it. As a result of these two contrasting processes, the discrimination in stem uptake is highly variable and covers the range of 12.6–21.5 ‰. Our findings have implications for understanding past variations in the Dole Effect, and for tracing the AOX activity in intact plants at the field.

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Table 1. Summary of the stem chamber experiments.

Tree	Site	Experiment month and year	Comments	Experiment duration (hours)	$[O_2]$ %	$\delta^{18}O$	D_{stem}
Aleppo Pine	HUJI	July 2010		141	19.67	0.06	15.2
Aleppo Pine	HUJI	December 2011		117	18.85	0.24	16.5
Aleppo Pine	HUJI	January 2011		48	19.30	−0.12	12.6
Aleppo Pine	HUJI	January 2011		48	19.30	−0.02	13.8
Stone Pine	HUJI	July 2010		141	18.56	0.21	16.0
Apple	HUJI	April 2010	after bud burst	51	17.89	1.06	21.4
Apple	HUJI	April 2010	after bud burst	51	17.80	1.11	21.5
Apple	HUJI	December 2010	green leaves	96	19.68	0.11	15.9
Apple	HUJI	December 2010	green leaves	117	19.68	0.09	15.5
Apple	HUJI	January 2011	green leaves	48	19.78	−0.06	13.0
Apple	HUJI	January 2011	green leaves	48	19.77	−0.12	12.0
Apple	HUJI	March 2011	no leaves	120	19.57	0.08	15.4
Apple	HUJI	March 2011	no leaves	144	19.44	0.03	14.5
Mari Mari 1	UNAP	April 2011	wet season	240	19.55	0.08	15.3
Mari Mari 3	UNAP	April 2011	wet season	240	18.83	0.11	15.2
Marupa 1	UNAP	April 2011	wet season	240	17.37	0.19	15.2
Marupa 2	UNAP	April 2011	wet season	240	16.76	1.08	19.5
Marupa 3	UNAP	April 2011	wet season	240	18.36	0.70	19.8
Tangarana 1	UNAP	April 2011	wet season	240	19.48	0.28	18.1
Tangarana 2	UNAP	April 2011	wet season	240	16.15	0.57	16.6
Tangarana 3	UNAP	April 2011	wet season	240	17.70	0.40	16.6

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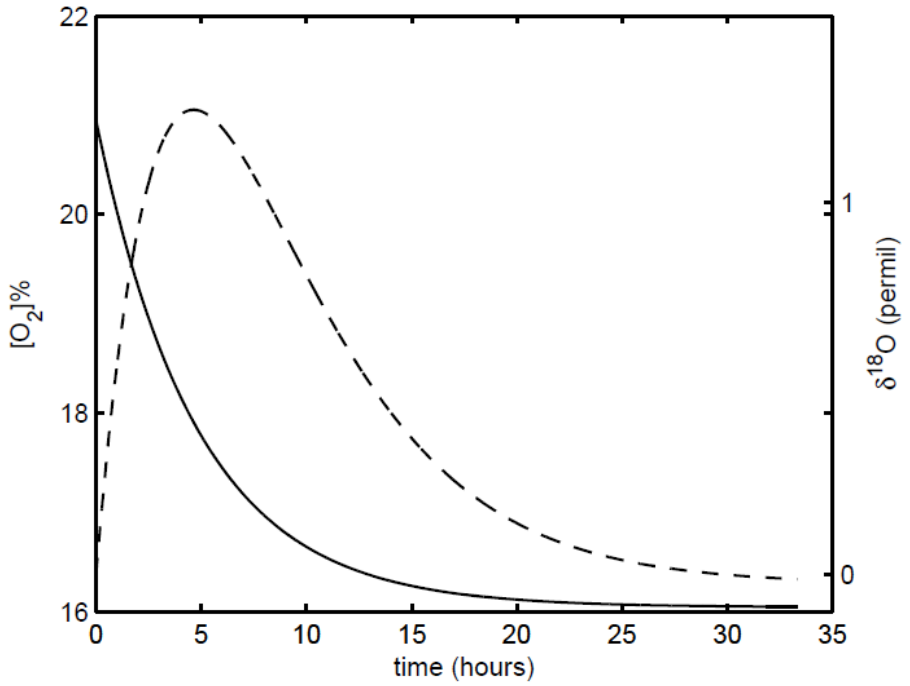

Fig. 1. Modelled O_2 concentrations (solid line) and $\delta^{18}O$ values (dashed line) in the stem chamber, for a model run with D_{stem}=14 %.

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