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Internal respiration of Amazon tree stems greatly exceeds external CO_2 efflux

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Abstract

Respiration in tree stems is an important component of forest carbon balance. The rate of CO_2 efflux from the stem has often been assumed to be a measure of stem respiration. However, recent work in temperate forests has demonstrated that stem CO_2 efflux can either overestimate or underestimate respiration rate, because of emission or removal of CO_2 by transport in xylem water. Here we used the ratio between CO_2 efflux and O_2 influx in stems of tropical forest trees to better understand respiration in an ecosystem that plays a key role in the global carbon cycle. This ratio, which we defined here as apparent respiratory quotient (ARQ), is expected to equal 1.0 if carbohydrates are the substrate for respiration, and the net transport of CO_2 in the xylem water is negligible. However, using a stem chamber approach to quantifying ARQ we found values of 0.66 ± 0.18. These low ARQ values indicate that a large portion of respired CO_2 ($\sim 35\,\%$) is not emitted locally, and is probably transported upward in the stem. ARQ values of 0.21 ± 0.10 were found for the steady-state gas concentration within the tree, sampled by in-stem equilibration probes. These lower values may result from the proximity to the xylem water stream. In contrast, we found ARQ values of 1.00 ± 0.13 for soil respiration. Our results indicate, for the first time, the existence of a considerable internal flux of CO_2 in the stem of tropical trees. If the transported CO_2 is used in the canopy as a substrate for photosynthesis, it could account for several percent of the C fixed by the tree, and perhaps serve as a mechanism that buffers the response of the tree to changing CO_2 levels. Our results also indicate, in agreement with previous work, that the widely used CO_2 efflux approach for determining stem respiration is unreliable. We demonstrate here a field applicable approach for measuring the O_2 uptake rate, which we suggest to be a more appropriate method to estimate stem respiration rates.

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1 Introduction

Respiration in tree stems is an important component of the terrestrial carbon cycle, and the emission of CO_2 from tree stems amounts to ~ 16 % of the forest annual gross photosynthesis flux (Litton et al., 2007; Ryan et al., 1997; Waring et al., 1998). In a Central Amazon forest, woody tissue respiration as estimated from stem efflux accounted for ~ 20 % of total autotrophic respiration (Chambers et al., 2004b). Aerobic respiration results in the production of CO_2 and the consumption of O_2, thus measurements of both gases can be used to quantify the rate of respiration. While measurements of O_2 are technically demanding, mainly because of the high natural background level that makes it difficult to detect changes, measuring CO_2 directly in the field (in situ) is both easy and affordable. Hence, it has become a common approach to measure the emission of CO_2 from a stem to the atmosphere as a proxy for the stem's respiration (Sprugel, 1990; Tranquillini, 1959). Lately, however, the assumption that stem CO_2 efflux provides a good measure of stem respiration has been questioned, and the question of how to correctly quantify stem respiration is still open (Teskey et al., 2008).

Any CO_2 respired by living cells inside a tree's stem has first to pass barriers to diffusion in the bark and/or the xylem before it is emitted into the atmosphere. Lenticels can probably facilitate this diffusion, but the diffusivity of stems for gases is somewhat limited (Hook et al., 1972). As a result, the concentration of CO_2 within stems builds up due to diffusive limitation. High internal CO_2 mixing ratios (up to 25 %) have been reported for a range of tree species (Teskey et al., 2008). These values are usually measured within the gas phase, which is presumed to be in equilibrium with the water that is lifted towards the crown in the transpiration stream. How much gas actually dissolves in or exsolves from the transpiration stream depends on several factors, such as pH and temperature, the concentration in the gas phase, and degree of saturation in the xylem water (Stumm and Morgan, 1995). It can be assumed that any gas that dissolves in the transpiration stream will be transported upward in the xylem, possibly all the way up to the crown. Alternatively, it will be lifted to any point within the stem

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where the CO_2 concentration within the gas phase is lower, and hence CO_2 from the liquid phase will escape back into the gas phase.

The degree to which CO_2 produced within the stem by respiration is emitted to the atmosphere versus transported in dissolved form likely varies and is a subject of current debate. Some findings suggest that xylem CO_2 transport is considerable (Teskey et al., 2008), and that the source of CO_2 diffusing out of the stem also includes CO_2 produced by respiration in other parts of the plant, such as roots (Aubrey and Teskey, 2009).

The main argument supporting the importance of CO_2 transport in the transpiration stream has been an observed correlation between sap flow velocity and stem CO_2 efflux (Levy et al., 1999; McGuire and Teskey, 2004). Additional support for this theory came from an experiment in which isotopically labeled carbonate was injected directly in the transpiration stream (Powers and Marshall, 2011). Apart from internal transport of tree-produced CO_2, some authors claim that CO_2 respired by soil microorganisms might be taken up by roots and then transported upwards (Ford et al., 2007; Vapaavuori and Pelkonen, 1985). In contrast, other authors have found no relationship between sap flow and stem CO_2 efflux (Maier and Clinton, 2006; Ubierna et al., 2009a). A field study in which trees were watered with isotopically labeled dissolved CO_2 found clear evidence for the uptake of the water, but no evidence for uptake of the dissolved CO_2 from the soil (Ubierna et al., 2009a). A possible explanation for these contrasting results might be differences in wood anatomy (e.g. diffuse porous, ring porous, and tracheid trees) or other traits among species. To summarize, we can say that the question "To what extent does CO_2 efflux from a given portion of tree stem reflect transport versus in situ respiration?" remains unanswered.

To further add to the complexity of this situation, it has recently been reported (Berveiller and Damesin, 2008; Hibberd and Quick, 2002) that C3 plants can use a mechanism typically associated with C4 metabolism to take up and transport CO_2. By using the enzyme phosphoenolpyruvate carboxylase (PEPC), trees can bind CO_2 to phospoenolpyruvate, resulting in the formation of oxalacetate, which is then quickly transformed into malate that will also be dissolved and transported in the transpiration

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stream. By using the enzyme malate dehydrogenase, this process can be reversed, re-releasing the CO_2, presumably at a location where the CO_2 is needed (photosynthetically active tissue). It is not yet known to which extent this mechanism is used within trees, but in 9 temperate tree species, tested by Berveiller and Damesin (2008), all species had significantly increased ratios of PEPC activity in stem wood compared to what is usually reported for C3 metabolism.

It should be noted that none of the studies mentioned above were conducted in tropical forest, and many of methods to study internal carbon transport are not applicable in remote locations. Recently, Angert and Sherer (2011) demonstrated that the combined measurement of O_2 uptake in addition to CO_2 efflux can potentially separate transport from respiration fluxes, because the lower solubility of O_2 in water (28 times lower than that of CO_2 at 20 °C) should limit the contribution due to gas exchange with xylem water. In addition, in contrast to O_2, the dissolved CO_2 forms additional chemical species (bicarbonate, carbonate). These reactions are pH-dependent and can increase the total inorganic-carbon capacity. These differences between CO_2 and O_2 have been used at the global scale to separate the land and the ocean carbon sinks (Keeling et al., 1996). Here, we will use the method developed by Angert and Sherer (2011) to measure for the first time the ratio between CO_2 efflux to respiration in tropical forests.

This method is based on the ratio of CO_2 emission to O_2 uptake in respiration, which is known as the Respiratory Quotient (RQ). The RQ is 1.0 when carbohydrates are the substrate for respiration, but it is for example ~ 0.7 for fats, and ~ 1.3 for malic acid (Stiles and Leach, 1933). Nitrate assimilation in roots can also cause RQ values above 1.0 (Bloom et al., 1989). We will define the ratio between the stem's CO_2 efflux to O_2 influx as ARQ (Apparent Respiratory Quotient). If the emissions from a stem are controlled only by respiration, then the value of ARQ will be equal to RQ and ARQ = 1.0 (assuming that carbohydrates are the main substrate for stem respiration). Alternatively, if net transport of CO_2 from outside the region where the measurement is made contributes significantly to CO_2 stem efflux (Aubrey and Teskey, 2009), we would expect to measure local ARQ > 1.0. Conversely, if there is net removal of locally produced

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CO_2 by the xylem sap or by PEPC, we would expect to measure ARQ < 1.0 in the part of the stem where this occurs. Here, we applied this approach to tropical forest trees, which are responsible for ~ 40 % of global terrestrial GPP (Beer et al., 2010). In addition to fluxes emitted from the stem surface, we also measured the concentrations of CO_2 and O_2 inside the stems and in the soil, which help to better constrain the CO_2 sources and sinks.

2 Methods

2.1 Site description

The study was carried out 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 at 3°49′53.8″ N, 73°22′28.2″ W, encompassing a forested area of 1300 ha and managed by the Faculty of Forest Engineering (FCF)-UNAP. Landforms in this area include plateaus, slopes and small valleys associated with perennial streams. The average canopy height in this area is 30 m and the most abundant taxonomic families include *Lauraceae*, *Apocynaceae*, *Lecythidaceae*, *Fabaceae*, *Lauraceae*, *Burseraceae*, *Symaroubaceae*, *Myristicaceae*, *Simaroubaceae*, and *Annonaceae*. More than 250 tree species are found in this area, and some common species include *Hymenolobium pulcherrimum* Ducke (Mari Mari), *Tachigali paniculata* Aublet (Tangarana), *Simarouba amara* Aublet (Marupa), *Euterpe precatoria* C. Martius (Huasai), and *Guarea glabra* M. Vahl (Requia).

The meteorological station at CIEFOR, under the responsibility of SENAMHI (Meteorological and Hydrological National Service of Peru), reports a climatological annual rainfall of 2979 mm and maximum, average and minimum temperatures of 31.6 °C, 26.7 °C, and 21.6 °C, respectively. There is a dry season with reduced monthly averaged rainfall, which usually extends from May to October. The 2010 dry season

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was characterized by a widespread drought in the Amazon Basin (Lewis et al., 2011; Marengo et al., 2011), and rainfall deficits were observed in this site from May 2010 to February 2011. The rainfall was especially low in August (43 mm) and September (102 mm). These values correspond to 20 % and 41 % of the climatology values for those months (www.senamhi.gob.pe).

We sampled stem CO_2/O_2 fluxes in both in the dry (27–30 September 2010) and wet (April 2011) seasons. We sampled in-stem gases twice, in October and December 2010. 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. (MariMari) from the *Fabaceas* family, with typical wood density values of 0.53 and 0.65 g ml^{-1}, respectively, and *Simarouba amara* (Marupa) from the *Simaroubaceae* family with wood density of 0.35 g ml^{-1} (Chambers et al., 2004a). These three species have diffuse-porous xylem anatomy. The stem chambers and in-stem probes were attached at heights of ∼ 1.6 to ∼ 2 m. Description of tree dimensions for the individuals sampled are summarized in Table 1.

2.2 Stem chambers, in-stem probes, and soil air sampling

Different stem chamber designs were used for each season. The stem chambers used for the dry season campaign 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, with its bottom part was sawed-off to allow decreasing of the system's volume while taking an air sample. The total volume of the system was ∼ 550 ml. The chamber was sealed to the stem by hot-glue. For installation on trees with rough bark surfaces that complicated air-tight sealing, we first removed some bark, and then smoothed the surface with a file, while being careful not to damage the phloem and the cambium. In case of trees with smooth bark, we only removed loose bark and lichen before installing the chambers. After closing the lid, we checked that the seal was air-tight by pulling the piston of the bottomless syringe attached to the lid. In all

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trees except “Tangarana 2” (see below) the piston returned in after releasing it, while in that tree there was only some resistance to the pull, even after adding more hot-glue. Hence, it seems that air could still enter the chamber through small pores in the bark, but only at low rates. We conclude that for all trees, in the absence of strong winds (which were not present during our field campaign), the mixing between the chambers and the atmosphere was dominated by diffusion rather than by mass-flow. Samples of the air in the chamber were collected in two pre-evacuated ~ 3.6 ml glass flasks with a Louwers-Hapert O-ring valve (one for O_2 analysis and one for CO_2). Before sampling, the dead volume in the tubing and flask necks were purged with 30 ml of air from the chamber. Each chamber was sampled twice: the first sampling occurred 2–3 h after the start of the experiment (sealing of the chamber), while the second one occurred the following morning, at least 17 h later.

In the wet season sampling (April 2011) we used chambers, based on the design reported in Ubierna et al. (2009b). The new chambers were custom-built from polypropylene (PP) tubing material (11 cm OD). We used T-pieces (Ostendorf Kunststoffe GmbH, Vechta, Germany, HTRE DN 110) that are originally equipped with a threaded lid to close the third opening. 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 initially attached by using two sets of lashing straps. To further stabilize the chambers and provide a gas-tight seal, the outline of the chamber was then glued to the stem with hot glue. As soon as the hot glue was hardened, the chambers were tested for leaks (and sealed again if necessary, until no leaks were found). Leak-testing was performed by measuring CO_2 inside the chamber and blowing respiratory air through a piece of tubing on all potentially leaky spots. Due to the high concentration of CO_2 in respiratory air, this method is both easy and highly sensitive.

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The wet season chambers provided a permanently installed plastic chamber that could be closed for incubation, or opened for ventilation between measurements dates. To avoid insect infestation, the chambers were covered with stainless steel mesh whenever opened for ventilation. These chambers were also used to measure the CO_2 efflux rate from the trees by attaching an Infra Red Gas Analyzer (IRGA, LI-820 LI-COR, Lincoln NE, USA). Gas from the chamber was pumped through a water trap filled with Drierite into the IRGA at a constant flow rate of $\sim 600\,ml\,min^{-1}$, and then pumped back into the chamber (closed dynamic chamber measurements, Pumpanen et al., 2004). Data was logged on a portable computer, using the Li-820 software. A linear regression was performed on the $[CO_2]$ data as a function of time to determine a flux rate, which was corrected for atmospheric pressure and temperature.

Using a modified lid, four flasks could be connected simultaneously to each chamber. Leaving the flasks' valves open allowed for CO_2 and O_2 to diffuse in and out from the chamber. Two 3.6 ml flasks (one for O_2 analysis and one for CO_2) were closed ~ 6 h after the beginning of the experiment, and then removed. The second pair of 3.6 ml flasks was closed 10 days after the experiment has begun.

The probes used to sample in-stem air were inspired by the design of Ubierna et al. (2009b). This approach is based on drilling a 6 cm deep hole into the stem after the removal of cracked bark, and hammering in a stainless steel tube (the probe), with an outer diameter that slightly exceeds that of the hole (we have used a 6 mm drill bit and a 1/4″ OD tube). The probe was then connected to a flask filled with air and left for several days to weeks to equilibrate with the gases inside the stem. In our design, the equilibrium volume was two 3.6 ml sampling flasks, which were connected to the probe by a plastic T connector and rubber tubing (10 ID mm 20 OD mm). This approach is simpler than the original design of Ubierna et al. (2009b), which required injecting acidified water into the equilibration volume, while collecting the sample. In the current design, sampling is simply done by closing the valves of the flasks and removing them from the probe.

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Since the probe installation could potentially invoke a wound response, we installed the probes only after the chamber measurements ended, and left the equilibrating flasks connected to trees for extra 2 weeks in the probe sampling time "A". The flasks were closed and removed on 29 October. Probe sampling time "B" started on the same day, and ended on 6 December, allowing ample time for the air in the flasks to equilibrate.

Soil air was sampled, during the dry season, using a stainless steel tube (10 mm ID, 12.5 mm OD) that was hammered into the soil, as in Angert et al. (2001). The tube end was pointed to ensure easy insertion, and 2-mm-diameter holes were drilled above the pointed end for soil air collection. An 8-mm-diameter plastic rod inserted inside the tube reduced its dead volume. For the sampling of soil air, we used the same connectors and flasks used to sample the dry-season chambers.

2.3 Analytical methods

The CO_2 concentrations in the 3.6 ml flasks were measured in the lab by an IRGA (Li-840A) connected to a circulating system, as described in Angert and Sherer (2011). In addition to the measurements of CO_2 in flasks sent to the lab, we also conducted measurements in the field during the dry season campaign. In these chamber experiments, 10 ml of chamber air were sampled into 60 ml syringe, containing 50 ml of CO_2-free air. The diluted sample was then immediately introduced to the IRGA. To determine CO_2 concentrations in the soil air, we connected the IRGA by a three-way valve to the syringe used for flushing the soil tube and the flasks' necks. Good agreement was found between the measurements made in the lab and in the field. The relative error of the [CO_2] field measurements, based on the difference between duplicates, averaged 2.5 %, which is similar to that achieved in measuring the flasks in the lab. The oxygen concentrations were calculated from the O_2/Ar ratio (expressed as δO_2/Ar) determined by mass-spectrometric analysis, under the assumption of constant Ar concentration. Sample preparation and mass spectrometry were according to Barkan and Luz (2003),

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which gives an accuracy of 0.02 % in O_2 concentrations (which translates to a relative accuracy of ~ 0.1 %).

3 The Models for stem and chamber gases

3.1 Analytical 1-box model

Estimating the ratio between the stem's efflux of CO_2 and influx of O_2 from the concentration measurements requires some simple modeling. Our 1-box analytical model follows the one we have presented earlier (Angert and Sherer, 2011). In this model, a box represents the chamber and the top layer of the stem, which are assumed to have the same gas concentrations and to be in steady-state on the timescale integrated by our sampling. For CO_2 this steady-state results from a balance between CO_2 emitted from deeper layers of the stem to this box, and the CO_2 that diffuses out of the box to the atmosphere (Fig. 1). This balance can be described by the following equation:

$$E_C = g_C \Delta_C \quad (1)$$

where E_c is the CO_2 efflux to the box ($\mu mol\, CO_2\, m^{-2}\, s^{-1}$), g_C is CO_2 conductance in the wood between the box and the atmosphere ($mol\, m^{-2}\, s^{-1}$) and Δ_C is the difference between the box and the atmosphere CO_2 partial pressures ($\mu mol\, mol^{-1}$).

We can write similar equation for O_2 by replacing the subscript "C" with "O" (here both E_O and Δ_O are negative):

$$E_O = g_O \Delta_O \quad (2)$$

Dividing Eq. (1) by Eq. (2) yields:

$$\frac{E_C}{E_O} = \frac{g_C}{g_O}\frac{\Delta_C}{\Delta_O} \quad (3)$$

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The term $(-E_C/E_O)$ is, by definition (see introduction), equal to ARQ, and is controlled by both the stem's RQ, and by processes that remove or import CO_2 to the portion of the stem sampled by the chamber.

The conductance (g) for each gas depends on its diffusivity in air, on the length and area of the conduction wood section, and on the structure of the air-filled pore spaces. (Millington and Shearer, 1971). In most trees, lenticels in the stem provide the necessary aeration pathways (Hook et al., 1972). This structure determines the length of the conducting elements, which largely control the effective diffusivity in tree stems (Sorz and Hietz, 2006). Since the structure, the length, and the area, are identical for both gases, the ratio g_C/g_O in Eq. (3) is controlled only by the ratio of diffusivity of the two gases in air. For CO_2/O_2 this ratio of diffusivity in air is 0.76 ($0.138\,cm^2\,s^{-1}/0.182\,cm^2\,s^{-1}$ at STP) and is independent of temperature, since for different temperatures both diffusivity coefficients will change by the same factor (Massman, 1998). Thus, Eq. (3) becomes:

$$ARQ = -0.76(\Delta_C/\Delta_O) \quad (4)$$

3.2 Numerical 1-box model

To deal with non-steady-state cases we employed a simple numerical model. This 1-box numerical model is based on the same box and flux definitions as the analytical model above. The main difference is that no steady-state is assumed between the box and the atmosphere. 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-differences approach. An example of a model run with a RQ = 1.0 (and arbitrary respiration and conductance values) is presented in Fig. 2.

After this time (~ 10 h in the model run pictured in Fig. 2) the gas concentrations approach their steady-state values. The time required to achieve steady-state is a function of the value chosen for conductance. However, previous experiments with the same

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stem chambers on trees have shown that steady-state is achieved in ~ half day (Angert and Sherer, 2011).

As predicted by the analytical model, the value of $-0.76(\Delta_C/\Delta_O)$ approaches 1.0 as the model approaches steady-state. In contrast, at the beginning of the run, before there was sufficient time to establish diffusive steady-state, this value is 0.76, so the value of $-\Delta_C/\Delta_O$ is 1.0 (i.e. it is equal to the ratio of E_C to E_O, which for the purpose of the model was set to be 1.0). Thus, in our chamber experiments the ARQ can be estimated from the value of $-\Delta_C/\Delta_O$ for samples taken shortly after sealing the chambers, and from the value of $-0.76(\Delta_C/\Delta_O)$ for samples taken when the system is close to steady-state.

In order to investigate how the simplification of a 1-box model affects our estimate of the ARQ, we have also employed a 2-box numerical model (Fig. 1b). In this model, one box represents the air in the stem, while the other box represents the chamber air. The chamber air exchanges O_2 and CO_2 with the stem by diffusion, while both the stem and the chamber exchange gases with the atmosphere. The stem box also loses O_2 and gains CO_2 from respiration. In this model run, we allowed the stem to achieve steady-state in terms of O_2 and CO_2 concentrations, while the chamber was assumed to be ventilated with atmospheric air ("open"). After the stem achieved steady-state, the chamber was "sealed", to simulate a chamber experiment in the field. The resulting increase in CO_2 and decrease in O_2 were similar to the results of the 1-box model, and again the value of $-\Delta_C/\Delta_O$ was 1.0 at the beginning of the simulated experiment, while later the value of $-0.76(\Delta_C/\Delta_O)$ approached 1.0.

Additional complexity can be introduced if the rate of oxygen uptake by the stem exceeds the rate of CO_2 emission. This would be accompanied by a reduction in pressure with a consequent mass flow of atmospheric air into the box. This will not only bring in O_2, but also N_2 and Ar. As a result, N_2 and Ar concentrations in the stem will increase, and the O_2/Ar ratio will not simply indicate O_2 concentrations. Further, the assumption of transport only by diffusion will not be valid in such a situation. However, including this effect of pressure induced mass-flow in the model has shown that even

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in an extreme case with RQ = 0.5 and O_2 decrease to less than 15 %, the effect on the estimated value of ARQ is in the order of only few percent. This small effect results from the fact that the diffusion of Ar and N_2 tends to cancel the concentration gradients, and because the effect on the O_2/Ar ratio tends to cancel the effect of non-pure diffusion transport.

We have also considered the "water vapor flux fractionation effect", which is driven by the diffusion of water vapor (Severinghaus et al., 1996). If a gradient in the concentration of water vapor is present in the outer bark layer, this effect can have some impact on the gas concentrations. However, even if we assume that water vapor concentration changes from 4 % to 1 % within the bark, it will only change the CO_2/O_2 ratio by ~ 1 % and the O_2/Ar by 0.15 ‰. Thus, even under extreme water vapor gradients this effect will not have a measurable impact on our results.

3.3 Calculating O_2 respiration rates

The respiration rate can be calculated from the change in the $[O_2]$ in the chamber headspace with time. The simplest approach is to use the first sampling time, and assume that $[O_2]$ linearly decreased with time. This approach, which we call a "1-point approach", neglects the increased diffusion of O_2 into the chamber as the concentration inside drops. Another approach is to solve the following differential equation, which describes the changes in $[O_2]$:

$$\frac{\mathrm{d}[O_2]}{\mathrm{d}t} = g\Delta O - R \tag{5}$$

The solution of this equation is:

$$R = -V(O_0 - O_{ss})\ln\left(\frac{O_t - O_{ss}}{O_0 - O_{ss}}\right)/t \tag{6}$$

Where R is the respiration rate (O_2 consumption rate in $l\,O_2\,s^{-1}$), V is the chamber volume (l), O_0 is the atmospheric concentration (20.95 %), O_{ss} is the concentration in

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steady-state (which is assumed to be the concentration of the second sampling), and O_t is the concentration at time t, which will be the time of the first sampling. The built-in assumption of this approach, which we call a "2-point approach", is that respiration rate does not vary with time.

4 Results

4.1 Soil air measurements

The CO_2 concentrations in the soil air ranged from 0.57 % to 2.60 %, while the O_2 concentrations ranged from 19.22 % to 20.57 % (Table 2). The ARQ can be estimated from $-0.76\Delta_C/\Delta_O$ and varied from 0.83 to 1.14, with an average of 1.00.

4.2 Stem chamber measurements

In the dry season, 2–3 h after the chambers were installed, the CO_2 concentrations were in the range of 0.77–2.51 %. After ~ 20 h, they had increased to 1.45–8.67 % (Table 3). The O_2 concentrations were in the range of 16.22–19.68 % (after 2–3 h) and 7.91–18.41 % after ~ 20 h. The ARQ ratio, which we estimated as $-\Delta_C/\Delta_O$ for the first sampling time, when the chamber headspace was far from steady-state, ranged from 0.51–0.93. The ARQ estimated from $-0.76\Delta_C/\Delta_O$ at the second sampling time (~ 20 h), when we assumed the chamber headspace air was at steady-state, ranged from 0.23–0.89. The average estimates of ARQ agreed well between the two calculation methods, 0.65 using the non-steady state approach (first sampling) and 0.57 using the steady state approach (second sampling) (Table 3).

In the wet season, the chamber headspace had CO_2 concentrations ranging from 0.30–1.49 % after 6–8 h (first sampling), which increased to 1.23–4.26 % by the time of the second sampling (10 days). The corresponding O_2 concentrations were 18.63–20.71 % and 16.15–19.57 %, respectively. The ARQ estimated from $-\Delta_C/\Delta_O$ for the first sampling ranged from 0.47–1.09, again in good agreement with those calculated

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assuming steady-state ($-0.76\Delta_C/\Delta_O$) at the second sampling, 0.47–0.90. The average estimate of ARQ was 0.73 in the first sampling and 0.69 in the second (Table 3).

4.3 In-stem probe measurements

The CO_2 concentrations for air sampled by the in-stem probes ranged from 1.12–9.68 % for the month following the dry season chamber sampling (A in Table 4), and increased slightly in the following month 1.40–10.4 % (B in Table 4). The corresponding O_2 concentrations decreased from 3.53–18.06 % (A) to 0.0–17.98 % (B). The ARQ values estimated for sampling period A and assuming steady state (i.e. $ARQ = -0.76\Delta_C/\Delta_O$) ranged from 0.13–0.88, in good agreement with the subsequent sampling period (B) with ARQ of 0.14–0.77. Excluding tree "Marupa 3", which gave constantly higher values, the average ARQ was 0.29 in experiment A and 0.17 in experiment B. Some of the equilibrating flasks filled with water which prevented measurements of air O_2 and CO_2, but allowed for measurements of water pH (using pH strips with ±0.5 units resolution). The pH of the xylem sap was 4.5 for trees "Tangarana 2" and "Mari Mari 3", and 7.0 for trees "Mari Mari 2" and "Tangarana 3".

5 Discussion

5.1 Explaining the measured ARQ values

We found average ARQ values (± standard deviation) of 1.00 ± 0.13 for the soil pore space, but considerably lower values in all measurements for tree stems: 0.21 ± 0.10 in the air sampled by in-stem probes (excluding tree "Mari Mari 3"), and 0.66 ± 0.18 in the chamber experiments (Fig. 3). These low ARQ values were found in all tree species studied, and in both the dry and wet seasons. The variability in ARQ is higher than expected from propagation of the analytical uncertainties for $[CO_2]$ and $[O_2]$ measurements, which result in uncertainties of 0.05 in the value of ARQ for the soil air

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pore space samples, 0.02–0.03 for the chamber headspace gases, and 0.01 for the gases sampled within stem probes. Thus, the observed variability could represent (1) differences in the RQ of the substrates used for respiration, (2) small deviations from steady-state, or (3) processes other than respiration that affect $[CO_2]$ and $[O_2]$ differently. The low ARQ values, which are considerably below the expected value of 1.0, need to be explained.

First, the low ARQ values may be the result of some artifact associated with the assumptions we used in the calculations of ARQ. However, results for samples taken many hours after the chamber headspace was isolated and therefore including the 0.76 factor associated with the assumption of steady-state gas-phase diffusion, yielded similar ARQ values to that of samples taken a few hours after chamber closure, where no diffusion correction was necessary ($ARQ = -\Delta_C/\Delta_O$). We thus conclude that the finding of low ARQ values (0.66 averaged across all chamber measurements and all trees) is robust. Further confidence that we have no systematic sampling or analytical errors comes from the soil pore space samples, which give the expected ARQ of close to 1.0.

A second possibility is that the low ARQ values actually represent low RQ values. However, in order to explain RQ values of around 0.6 this way, fats would have to be the main substrate for respiration in both the dry and wet seasons, which is extremely unlikely. Moreover, ARQ values of around 0.5, as found for some of our trees in the stem chambers experiments, and 0.3, as found in the in-stem probe experiments, cannot be explained by the known range of substrate dependent RQ. Corticular photosynthesis will not cause deviations in the ARQ since the photosynthetic exchange of CO_2 and O_2 is with a ratio of about 1 : 1, and photorespiration will be inhibited by the high CO_2 concentration in the stem. As a result, we conclude that the low ARQ values are not the result of low RQ.

A third possibility is that some of the O_2 uptake is not driven by respiration but by dissolution in the xylem water. However, even if we assume that the water arrives at the base of the stem with no O_2, this water could take up dissolved O_2 up to a concentration

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in equilibrium with atmospheric air (~0.25 m mol l^{-1}). For a tree with a stem diameter of 0.5 m, a respiration rate of 200 mg C m^{-2} h^{-1}, and a xylem water flux of 500 l per day, this removal of O_2 by dissolution will amount to only 10 % of the O_2 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 O_2. A more reasonable assumption is that the water O_2 was equilibrated in the roots, and hence, was close to equilibration with the stem O_2 and can take up even smaller amounts of O_2. We conclude that O_2 dissolution and transport is not a large contributor to the fluxes we observe.

The fourth possibility, which is the only one left after rejecting the other three, is that a large portion of the respired CO_2 is removed from the stem sections studied, as was shown by previous studies in temperate forests (Teskey et al., 2008). It was also suggested (Teskey and McGuire, 2002, 2007) that storage and transport of dissolved CO_2 and bicarbonate in the xylem play an important role in controlling the CO_2 efflux from the stem. In our case, the storage option is ruled out, since storage effects would be averaged out in our longer experiments, like the 10 day chamber deployment, and the stem probe flasks that were left on for a few weeks time.

Given the high concentrations of CO_2 we measured at the chambers, it can be expected that a substantial amount of CO_2 will be dissolved in the xylem water. Hence, it seems plausible that xylem transport of DIC (Dissolved Inorganic Carbon) upward from the chambers, can at least partly explain our results. However, the flux of DIC upward in the xylem depends on the sap flow rate (which we have not measured), and is very sensitive to the pH of the sap, which we find for four of our trees to vary from 4.5 to 7.0. At this range of pH values, the DIC concentration varies by a factor of 6 (for a given P_{CO_2}). Hence, at present we do not have sufficient data to conclude if DIC transport in xylem water can be solely responsible for the low ARQ values we observed. Conversion of CO_2 into malate by PEP-carboxylase, and a transport of this malate in the xylem water represents another possible pathway for transporting CO_2 away from the site of respiration (Berveiller and Damesin, 2008; Hibberd and Quick, 2002).

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It has been suggested (Aubrey and Teskey, 2009) that in some tree species part of the CO_2 emitted by tree stems may originate from respiration taking place in the roots, and imported to the stem by transport in the xylem water. Aubrey and Teskey (2009) suggest that such transport could result in underestimation of root respiration from studies that use soil respiration measurements, since some of the root-respired CO_2 bypasses the soil and is instead emitted from tree stems. Such transport should result in ARQ values of stems that are above 1.0 and ARQ values for soil that are below 1.0, both of which are inconsistent with our observations which point to the removal of stem CO_2 in the trees we studied.

The in-stem gas measurements present an additional challenge. The ARQ values found in these experiments were especially low (averaging 0.21 versus 0.66 for the chamber headspace samples). In general, we saw no big differences between tree species in our study. However, one individual tree ("Marupa 3") had higher ARQ values in both probe experiments (0.77 and 0.88). The other two Marupa trees had low ARQ values in the stem gases sampled with probes, but did show high values of ARQ (0.90–1.09) in some of the chamber headspace samples. Thus, it is possible that this species, which belongs to a different family than the other two studied species, has different characteristic related to the "removal" of CO_2. In any case, a more important question is why are most of the ARQ values obtained for in-stem gases so much lower than those sampled using chambers at the stem surface? One possible answer is that the O_2 and CO_2 pools in the deeper parts of the stem have poor contact with the outer parts. As a result, the processes taking place in those deeper layers and sampled by the probes, have only a small impact on the stem's CO_2 efflux and O_2 influx, which are sampled by the chambers. Alternatively, the lower ARQ deeper in the stem may be the result of the proximity to the xylem water, which removes the CO_2 and locally reduces the ARQ.

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5.2 Implications of the low ARQ values

The respired CO_2 that is not emitted from the stem is most probably transported upward in the transpiration stream, as either dissolved CO_2 or bicarbonate, and maybe as malate as well. This CO_2 can be emitted to the atmosphere higher in the stem, or in the canopy. While a shift in the height in which CO_2 is emitted from the stem will not affect the entire tree carbon balance, this shift is important for the following reasons: First, measurements of stem CO_2 efflux are normally made at ~ 1.3 m height and then extrapolated to the surface area of the rest of the tree. The upward transport of CO_2 we report would creates a systematic error in such extrapolated stem respiration rates. Indeed, a recent study (Cavaleri et al., 2006) at a wet tropical forest found that most of the CO_2 efflux came from the smallest branches (perhaps from outgassing of transported CO_2). The implications of such systematic error, is that our models will fail to predict the response of trees to novel conditions like climate change and increasing CO_2.

Moreover, at least part of the CO_2 transported up the stem could potentially be re-fixed by photosynthesis. Given the high concentration of CO_2 within stems, which reaches above 8.5 % in the current study, in contrast to the 0.039 % currently in the atmosphere, and given the low affinity of Rubisco to CO_2, there is a clear advantage for plants to use this internal CO_2 for photosynthesis. Indeed, there is evidence for such re-fixing or internal recycling of carbon. For example, Hibberd and Quick (2002) found that ^{14}C labeled bicarbonate and malate added to the xylem water of celery and tobacco were fixed in bundle-sheath cells in the stem and leaves. Similarly, Stringer and Kimmerer (1993) found that excised leaves of *Populus deltoides* trees which transpired ^{14}C labeled bicarbonate, fixed 99.6 % of the label. Similar ^{13}C labeling of the bicarbonate in water transpired by *Platanus occidentalis* L. branches showed that 35 % of the label was fixed (McGuire et al., 2009). Recently, Powers and Marshall (2011) showed that introducing ^{13}C labeled bicarbonate to a tree xylem resulted with the label appearing in the phloem contents within a few days. This experiment provides a clever

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demonstration that such internal carbon recycling mechanism is active in trees. However, the question of what is the relative contribution of this mechanism to forest primary productivity is still open. Based on our results, we can only estimate the maximal possible contribution of this process to canopy photosynthesis.

When assuming that (1) the actual RQ value for respiration in the stem is 1.0, and (2) that $[O_2]$ is affected only by respiration, we can use measurements of $[O_2]$ to estimate how much CO_2 is produced locally by respiration. This approach suggests that on average about 35 % of the respired CO_2 has to be taken up by the transpiration stream to explain our observed ARQ values. This estimate is in accord with previous estimates based on other methods (McGuire and Teskey, 2004), and with previous implementation of the current method on different trees species (Angert and Sherer, 2011). If this estimate holds true for the entire stem, and if all of the transported CO_2 is re-fixed in the canopy, and based on the estimate that the emission of CO_2 from tree stems amounts to $\sim$ 16 % of the gross photosynthesis flux (Litton et al., 2007; Ryan et al., 1997; Waring et al., 1998), carbon originally respired within the tree stem could at the very maximum contribute 10 % to a tree's gross productivity. Internal CO_2 recycling would be even higher if root-respired CO_2 also enters the transpiration stream (Aubrey and Teskey, 2009). Assuming that 35 % (i.e. the same proportion as for stem-respired CO_2) of the root-respired CO_2 is also transported to the canopy to be re-fixed, then the internal transport and re-fixing mechanism can contribute to a maximum of 20 % of the tree productivity. The re-fixing of internal carbon is insensitive to the atmospheric CO_2 concentration, and hence, will show no "carbon fertilization" effect. In addition, this re-fixation is expected to increase the plant resilience to drought, since partial closer of the stomata, which lowers the leaves internal CO_2 concentration and slows down photosynthesis, has only limited effect on the CO_2 concentration in the bundle sheath cells.

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5.3 Estimating stem respiration from the consumption of O_2

Regardless of the nature of the processes that remove CO_2 from the stem, our results agree with previous studies showing that the CO_2 efflux does not correctly capture the stem respiration rate. This is not only because a fraction of the CO_2 respired is not emitted, but also because this fraction is highly variable and covers the range of 0–50 % of the respired CO_2. Understanding the processes that control stem respiration is thus impossible to make based solely on CO_2 efflux measurements. We suggest here that measurements of the O_2 influx are a better indicator of stem respiration at the field, as was previously suggested for respiration measurements in the lab (e.g. Davey et al., 2004).

Calculated respiration rates based on the two approaches discussed in Sect. 3.3 are presented in Table 5. As expected, the respiration estimated using the 2-point approach is higher than the one calculated by the 1-point approach. The 2-point respiration is also higher than the CO_2 efflux estimated by monitoring the CO_2 concentration change in the headspace of the chamber. This result agrees with our finding of ARQ values below 1.0 (based on the flux ratios in Table 5, they range between 0.35 and 1.0). Since it is not possible, at present, to measure the small O_2 changes created only a few minutes after sealing the chamber, the diffusion into the chamber will always bias the 1-point approach estimates. As our calculations show, the correction for that bias is not negligible. Thus we recommend using the 2-point approach to estimate O_2 uptake, and hence respiration. Simplifying the $[O_2]$ measurements technique (e.g. by adapting fuel-cell-based O_2 analyzers for this task) is necessary to make this method widely applicable.

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6 Conclusions

The average ratio between the CO_2 efflux and O_2 influx, which we defined here as ARQ, was found to be 0.66 ± 0.18 for three species of tropical forest trees, using the gases sampled with stem chambers. For the in-stem gases we found ARQ values of 0.21 ± 0.10. The low ARQ values in both the in-stem and chambers measurements indicate that a large portion of the CO_2 respired ($\sim 35\%$) in these tropical trees is transported upward in the stem by the xylem water. This CO_2 can be transported in both inorganic and organic forms. If the transported carbon is later fixed in the canopy, then a potentially important photosynthesis flux is also missing from current carbon balance estimates. Future work should reveal the fate of this transported carbon, and estimate the effect of this "recycled" photosynthesis flux on the sensitivity of forests to atmospheric CO_2 changes, and to drought stress. The removal of CO_2 by the xylem water causes an underestimation of the stem respiration flux by the standard CO_2 efflux techniques in the tropical trees we studied. We thus conclude that measuring O_2 consumption provides a better way to quantify stem respiration rates. Although these kinds of measurements are technically more demanding, we show here a field applicable approach to perform it.

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Table 1. Trees dimensions.

Tree	diameter (m)	estimated height (m)
Mari Mari 1	1.34	25
Mari Mari 2	0.39	18
Mari Mari 3	1.13	30
Marupa 1	0.33	15
Marupa 2	0.43	18
Marupa 3	0.38	16
Tangarana 1	0.71	23
Tangarana 2	0.42	20
Tangarana 3	0.88	23

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Table 2. Results of soil air sampling in the dry season. The analytical error in ARQ estimate is 0.05 on average.

sampled next to tree	soil [CO_2] %	soil [O_2] %	ARQ
Mari Mari 1	n.a.	20.05	n.a.
Mari Mari 2	n.a.	n.a.	n.a.
Mari Mari 3	1.35	19.92	0.99
Marupa 1	1.09	20.03	0.90
Marupa 2	0.6	n.a.	n.a.
Marupa 3	0.73	20.28	0.83
Tangarana 1	n.a.	20.36	n.a.
Tangarana 2	0.57	20.57	1.14
Tangarana 3	2.6	19.22	1.14
Average			1.00

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Table 3. Results of the stem chambers experiments. First sampling: 2–3 h after the start of the experiment in the dry season, 6–8 h on the wet season. Second sampling: ~ 20 h on the dry season, 10 days on the wet season. The ARQ values are calculated in the two ways explained in the text. The analytical error in ARQ estimate is 0.02 on average on the dry season and 0.03 on the wet season.

Tree	season	first sampling $[CO_2]$ %	first sampling $[O_2]$ %	ARQ	second sampling $[CO_2]$ %	second sampling $[O_2]$ %	ARQ
Mari Mari 1	dry	0.77	19.51	0.51	5.75	16.05	0.89
Mari Mari 2	dry	1.13	n.a.	n.a.	1.50	n.a.	n.a.
Mari Mari 3	dry	1.34	19.55	0.93	1.45	18.41	0.42
Marupa 1	dry	n.a.	19.68	n.a.	2.56	12.62	0.23
Marupa 2	dry	0.81	n.a.	n.a.	2.80	15.61	0.40
Marupa 3	dry	1.36	19.06	0.70	4.83	16.07	0.75
Tangarana 1	dry	2.51	16.22	0.52	8.67	7.91	0.51
Tangarana 2	dry	1.14	19.16	0.61	5.87	12.59	0.53
Tangarana 3	dry	2.21	17.42	0.62	7.79	13.55	0.80
dry season average				0.65			0.57
Mari Mari 1	wet	0.54	20.16	0.63	1.40	19.55	0.74
Mari Mari 2	wet	0.55	19.87	0.47	1.23	19.57	0.66
Mari Mari 3	wet	0.63	20.08	0.68	2.06	18.83	0.73
Marupa 1	wet	1.16	19.86	1.03	4.26	17.37	0.90
Marupa 2	wet	0.62	20.12	0.70	3.86	16.76	0.69
Marupa 3	wet	0.30	20.71	1.09	2.46	18.36	0.71
Tangarana 1	wet	1.16	19.47	0.76	1.40	19.48	0.71
Tangarana 2	wet	0.69	19.86	0.60	3.01	16.15	0.47
Tangarana 3	wet	1.49	18.63	0.63	2.66	17.70	0.61
wet season average				0.73			0.69

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Table 4. Results of in-stem probe sampling. During sampling period A the gas samplers attached to the probes were opened on 30 September and closed on 29 October 2011. In sampling period B, the gas flasks were attached and opened on 29 October and closed on 6 December 2011. The analytical error in ARQ estimate is 0.01.

Tree	period	$[CO_2]$ %	$[O_2]$ %	ARQ
Mari Mari 1	A	n.a.	3.53	n.a.
Mari Mari 2	A	9.68	n.a.	n.a.
Mari Mari 3	A	n.a.	n.a.	n.a.
Marupa 1	A	2.89	3.66	0.13
Marupa 2	A	1.12	18.06	0.29
Marupa 3	A	3.37	18.05	0.88
Tangarana 1	A	8.29	6.42	0.43
Tangarana 2	A	5.03	n.a.	n.a.
Tangarana 3	A	8.12	n.a.	n.a.
Mari Mari 1	B	10.4	n.a.	n.a.
Mari Mari 2	B	5	0.47	0.19
Mari Mari 3	B	n.a.	0.13	n.a.
Marupa 1	B	2.8	7.45	0.16
Marupa 2	B	1.4	14.6	0.17
Marupa 3	B	3	17.98	0.77
Tangarana 1	B	2.6	10.33	0.18
Tangarana 2	B	3.8	0	0.14
Tangarana 3	B	5	0.01	0.18
average (excluding “Marupa 3”)				0.21

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Table 5. Stem respiration rate (R) based on O_2 (1-point and 2-points approaches) and CO_2 efflux (dynamic chamber). The units for all columns are $\mu mol\, m^{-2}\, s^{-1}$.

species	season	R (1-point)	R (2-points)	CO_2 efflux
Mari Mari 1	dry	5.9	7.0	6.3
Mari Mari 2	dry	n.a.	n.a.	3.5
Mari Mari 3	dry	3.6	5.0	2.7
Marupa 1	dry	3.5	3.8	3.1
Marupa 2	dry	n.a.	n.a.	2.8
Marupa 3	dry	n.a.	n.a.	2.5
Tangarana 1	dry	17.7	21.9	7.7
Tangarana 2	dry	n.a.	n.a.	2.2
Tangarana 3	dry	7.6	10.5	5.7
Mari Mari 1	wet	1.9	2.8	n.a.
Mari Mari 2	wet	2.7	5.3	n.a.
Mari Mari 3	wet	2.1	2.8	n.a.
Marupa 1	wet	2.6	3.1	n.a.
Marupa 2	wet	2.1	2.3	n.a.
Marupa 3	wet	0.6	0.6	n.a.
Tangarana 1	wet	n.a.	n.a.	n.a.
Tangarana 2	wet	2.6	3.0	n.a.
Tangarana 3	wet	5.9	10.3	n.a.

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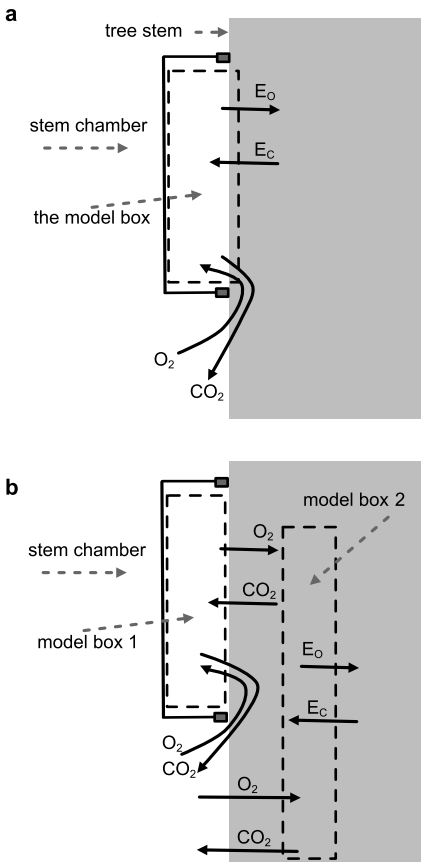

Fig. 1. Schematic drawing of the model boxes and fluxes, **(a)** 1-box model, **(b)** 2-box model. The O_2 and CO_2 diffusive fluxes, as well as the fluxes of O_2 consumption (E_O) and CO_2 release (E_C) are shown by solid lines.

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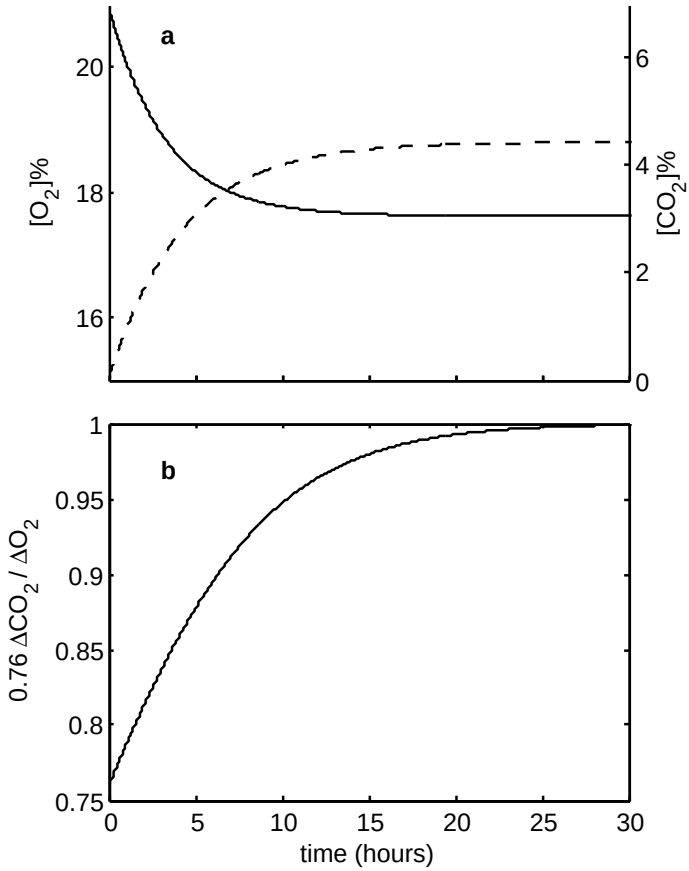

Fig. 2. Modeled **(a)** O_2 (solid line) and CO_2 (dashed line) concentrations, and **(b)** the relationship between the increase in CO_2 and the decrease in O_2 (multiplied by the ratio of these gases diffusivities in air, which is 0.76), as produced by a 1-box numerical model.

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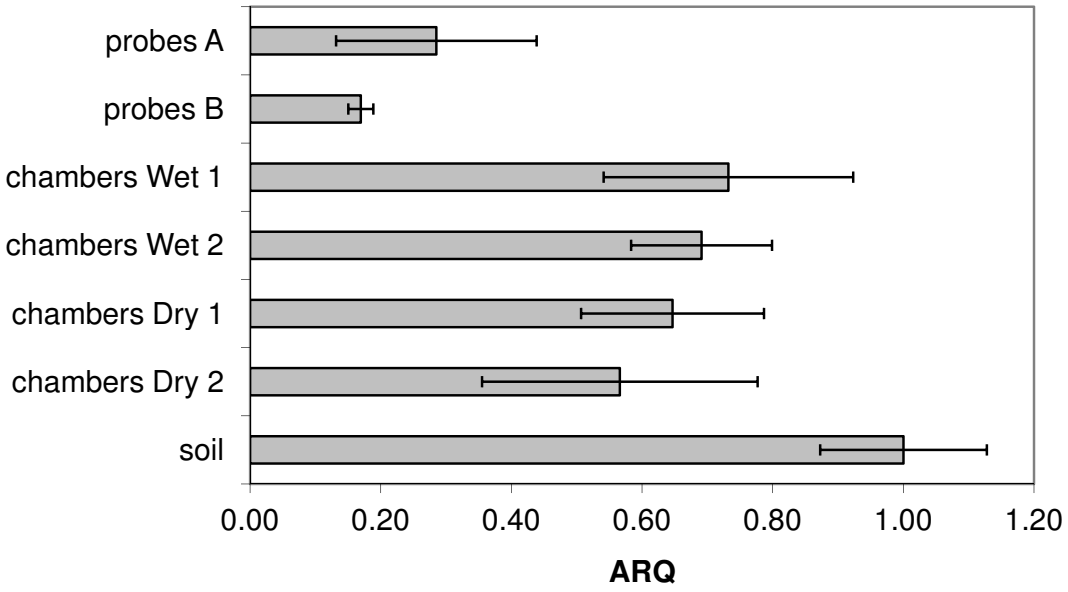

Fig. 3. The average ARQ for the gases sampled from in-stem probes, chamber headspace, and soil pore space. The error bars represent one standard deviation. The average for in-stem probes does not include tree "Marupa 3", which gave a value of 0.88 in sampling period A and 0.77 in sampling period B (Table 4).

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