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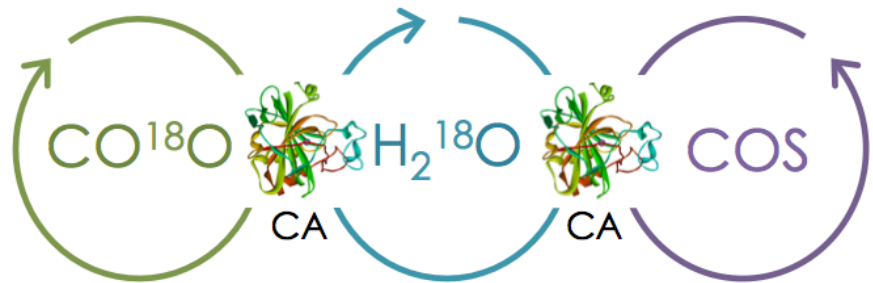
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MÉMOIRE POUR LE DIPLÔME D'HABILITATION À DIRIGER DES RECHERCHES

LISA WINGATE BSC. PHD.



CONSTRAINING THE IMPACT OF TERRESTRIAL BIOSPHERE ACTIVITY ON THE ATMOSPHERIC CONCENTRATION OF CO₂ AND OTHER CARBON CYCLE TRACERS: FROM ENZYME TO EARTH SYSTEM

Jury

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2 Novembre 2018

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First of all I would like to thank my jury Claude Plassard, Thierry Heulin, Dani Or, Stephen Sitch, Jaleh Ghashghaie and Pauline Defossez for taking the time to read this little memoir and come to Bordeaux for my 'soutenance'. I appreciate your time is precious and I am grateful you accepted to come and help me 'jump this hurdle'. I chose each of you with care as I genuinely hope that each of you might find something of interest in parts of my work and thoughts, thereby turning a bit of a chore into something you just might enjoy.

Anybody reading this thesis will quickly realise that this work represents many fruitful collaborations and positive interactions with many talented and innovative researchers and colleagues dispersed around the world, as well as those of my day-to-day work environment in Bordeaux. I have been particularly lucky to have shared time with a great team of young scientists that have passed through the lab over the past 10 years (Appendix II) and particularly the ECOFUN team that have been part of this wonderful and sometimes crazy journey building the lab from scratch and participating to some cool experiments. They have made my work extremely enjoyable and I have taken great pleasure and pride in watching them come together and work as an impressive team.

I have also benefited from the continuous input and support from key colleagues over the years in Bordeaux most notably Regis Burlett, Didier Bert, Alexandre Bosc, Cathy Lambrot and Valerie Savornin to whom I am extremely grateful for their endless patience, innovation and skills.

I have also been lucky to make some fantastic international collaborators over the years especially Matthias Cuntz, Bernard Genty, Laura Meredith and Ulli Seibt that have helped bring tremendous insights and tools to the table at various stages during my career.

I am also grateful to my scientific mentors Paul, Maurizio, John, Howard and Yves who have believed in me over the years and shown me the many different skills necessary to succeed in research.

Finally I acknowledge the support at work and home from Jérôme as we juggle and share our responsibilities day after day to enrich the lives of our little family and our colleagues that orbit in our gravity.

PART I : MY PAST RESEARCH

1.1 GRAND CHALLENGES IN EARTH SYSTEM RESEARCH

At around the time I began to imagine myself becoming an environmental scientist around 1992 the UN Framework Convention on Climate Change, historically known as the the Earth Summit, was being held in Rio de Janeiro. This summit served as the starting block for the first agreement between nations to curb greenhouse gas emissions, known as The Kyoto Protocol. By the time this agreement was signed in 1997 I was already in the 3rd year of my ecology and environmental sciences undergraduate degree, the atmospheric CO₂ concentration was around 360 ppmv and I had already encountered Professor Paul G Jarvis FRS. I first met Paul on an undergraduate field course at Firthush near Aberfeldy in Scotland. During this field course Paul somehow convinced me to do a 3-day ecology project in a young Sitka spruce plantation set against the tremendous backdrop of Schiehallion, where the mass of the Earth was famously determined in the late 18th Century. This forest was special, but not because of its proximity to Schiehallion or Paul's country house (!), but rather because it had a large tower that rose out of its canopy carrying with it an instrument that measured variations in the speed of sound. Paul explained that this instrument could help calculate the number of CO₂ and water molecules that moved into and out of the forest over the course of an hour, a day or a season. I was intrigued, as especially at the outset of my project it was not clear to me how with nothing more than a funny tape measure and a tree-borer I would eventually estimate the total stock of carbon stored in the above-ground biomass of that plantation¹ let alone relate this to variations in the speed of sound.

I would spend the following years of my life exchanging a lot of air with that spruce forest and I finally submitted a PhD in 2003. It took me a long time to develop my understanding of how conifer forests functioned. Being part of the Edinburgh University Biosphere Atmosphere Exchange group helped this process as I was exposed regularly to the latest advances in plant ecophysiology and soil biogeochemical processes in particular photosynthesis, stomatal conductance and soil respiration. With time I gradually became confident in the measurement and interpretation of ecosystem carbon and water feedbacks. With the continuous rise in CO₂ concentrations in the atmosphere it seemed timely back then to continue building my research career trying to understand better biosphere-climate feedbacks. Even now in 2018 the World Climate Research Programme (WCRP) emphasises that this particular field of research is as important today as it was back then during my early PhD years (Fig. 1.1).



<https://www.wcrp-climate.org/grand-challenges/grand-challenges-overview>

Figure 1.1 | Grand challenges identified by the World Climate Research Programme

¹ It was approximately 40 Mg C ha⁻¹

In particular, one of the recurring problems in understanding feedbacks in the carbon-climate system stems from a recurring difficulty the community face in measuring and describing confidently variations in the amount of CO₂ that is captured by an ecosystem via photosynthesis compared to the amount of CO₂ lost by the same ecosystem through the range of natural and/or management processes that can occur. This is because all of our methods measure the net effect of these processes on atmospheric CO₂ across every scale. However, these processes underpin the theoretical framework of current Land Surface Models (LSMs) and are required to predict how the terrestrial biosphere will respond in the future to changes in climate and CO₂ variability. As LSMs are one of the most powerful tools society has to provide guidance on present and future carbon-climate feedbacks, it is important that collectively we make efforts to perform experiments across a range of scales that validate the key processes within the LSM behave as we expect them to compared with current ecosystem function and ideally against experiments that create novel environmental constellations. Such critical evaluation of model performance is necessary to provide the intellectual feedback required to improve the representation of those key processes in LSMs that are highly sensitive to climatic change. However, testing Earth system models against ‘reductionist’ experiments, although unavoidable is obviously not ideal as scaling phenomenon from the microcosm to the Earth system is fraught with uncertainty especially when feedbacks at increasingly larger scales play a strong and unpredictable role. On the other hand, validation at larger and longer timescales is equally difficult because independent large-scale datasets are rare and commonly integrate multiple simultaneous processes that can be difficult to attribute to one particular process over another.

This grand challenge in Earth system science nicely sets the backdrop to my research over the past 20 years and has compelled me to channel my energy towards the development of tools and techniques that attempt to isolate and trace the key processes of photosynthesis, evapotranspiration and respiration within soil and plant communities. Since early in my PhD this has involved the development of (initially) field and (later) laboratory gas exchange techniques to measure the carbon and oxygen stable isotope fractionations of carbon dioxide and water during photosynthesis, evapotranspiration and respiration at different spatial and temporal scales (Fig. 1.2). Whilst more recently carbonyl sulphide (COS) has been added to my toolbox as an additional tracer that holds a lot of potential to interpret the impact of photosynthesis on the atmosphere when collected routinely over many years or within the bubbles of ice cores. These independent tracers can be used to build ‘bridges’ within LSMs allowing parallel mass balances to be constructed for each additional tracer. Thus when certain unique parameters common to all tracers within the modelling framework are varied to explore the sensitivity of an Earth system model to this particular parameter, very different responses in for example, the seasonal concentration change in atmospheric CO₂, CO¹⁸O and COS can be produced, with one or more of the simulations no longer resembling the atmospheric data (Fig. 1.2). This creates an opportunity to learn something about the optimal range of values for a given parameter in the LSM by deducing which (or set of) parameter values optimises best the pattern and/or magnitude of the seasonal cycle of all tracers simultaneously. Thus by using more tracers regulated by the same processes it should be possible to improve our parameterisation of key processes in carbon cycle models and overcome the problem of insensitivity in present

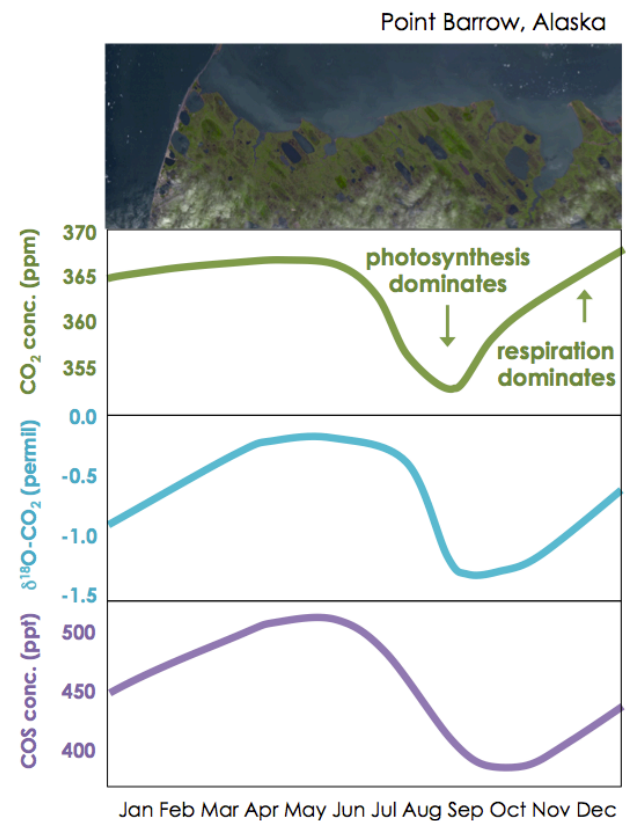


Figure 1.2 | Seasonal variations in the atmospheric concentrations of CO₂ and COS alongside the oxygen isotope composition of CO₂ (δ¹⁸O-CO₂). Data adapted from the NOAA CMDL archives.

carbon cycle model studies that only validate against atmospheric CO₂. Unfortunately, this latter approach typically results in models producing the same patterns in atmospheric CO₂ concentrations or net ecosystem CO₂ fluxes for very different process representation and parameterisation. Thus using a multi-tracer approach would be a bold step towards eliminating this problem of equifinality provided we have sufficient understanding about the key processes. Thus in the following chapters I will summarise and highlight a few of the incremental steps I have been making with collaborators over the past 20 years to build knowledge of certain key processes in LSMs whilst in parallel investigating critical gaps in the understanding that currently prevents us from using oxygen stable isotopes and COS routinely in LSMs to constrain carbon-climate feedbacks in large scale atmospheric inversions.

1.2 RESEARCH HIGHLIGHTS

Characterising leaf and soil gas exchange in temperate forests (Thesis, 1998-2003)

As described above at the start of my PhD I began to measure the exchange of CO₂ and water vapour between different ecosystem components and the atmosphere. However, after attending the Stable Isotope Ecology course in Utah (Class of 1999) I decided I wanted to try to measure the carbon and oxygen isotope discrimination of CO₂ exchange in the field using automated branch chambers (Fig. 1.3). Although Paul advised me that this idea would never work, I was convinced it could and promptly initiated a collaboration with Prof. Jon Lloyd at the time working at the Max Planck Institute of Biogeochemistry (Jena, Germany). Together we designed a flask sampling protocol and carried out our first field tests from branch and soil chambers at the Spruce forest in Aberfeldy. Shortly afterwards Dr Ulli Seibt (also a PhD student at the time) joined the experiment to study O₂ and together we made several field campaigns filling flasks with air captured from my chambers as well as simultaneous measurements of how the canopy air space varied over time. I was extremely reassured after the first experiment to see that the large CO₂ fluxes from the spruce trees made it possible to measure discrimination robustly and led to an experimental dataset that both Ulli and I could successfully write up and defend in our theses (Wingate, 2003; Seibt, 2003). As the branch-level data were highly novel at the time we went on to produce 5 peer-reviewed publications together (Seibt et al., 2004; 2007; 2006a; 2006b; Wingate et al., 2007) using the data. Furthermore, I shared the data to make further studies possible especially with Prof. Belinda Medlyn, whom I shared an office with as a PhD student (Ibrom et al., 2006; Lin et al., 2015; Medlyn et al., 2005; 2017; 2011). Rather than giving an exhaustive account of all the work involved in every paper, in the text that follows I will present a couple of results that were of particular personal interest.



Figure 1.3 | Chamber installed on Sitka spruce branches in Griffin Forest in Aberfeldy, Scotland

Spruce stomata remain open at night | We know that evapotranspiration and photosynthesis (gross primary productivity, GPP) impact the global land water and CO₂ budgets and are currently estimated with considerable uncertainty between 58,000-85,000 km³ of water yr⁻¹ and between 100-175 PgC yr⁻¹ (Beer et al., 2010; Welp et al., 2012). This uncertainty partly resides in the wide range of techniques used to construct large scale budgets (1) process-based land surface water cycle models (Friedlingstein et al., 2006; Sitch et al., 2008); (2) remote-sensing approaches using semi-empirical algorithms (Frankenberg et al., 2011), (3) eddy-covariance flux-based algorithms up-scaled with meteorological data (Jung et al., 2011; Keenan et al., 2013) or (4) stable isotope approaches using the oxygen and hydrogen stable isotopes of rainfall and terrestrial water pools (Jasechko et al., 2013). Another source of uncertainty lies in the parameterisation of key processes such as stomatal conductance in models (Medlyn et al., 2011). For example current LSMs tend to ignore stomatal opening in the dark and suffer from a crude description of the mechanisms controlling stomatal opening during drought, leaf development and in response to rising atmospheric CO₂ concentration (Lombardozzi et al., 2017).

This is partly because measuring low water fluxes during drought or at night (nocturnal stomatal conductance, $g_{s, \text{night}}$) is a challenge. Until recently, $g_{s, \text{night}}$ was often measured with conventional porometer gas-exchange techniques, for example using the Li-COR 6400. These porometers can measure CO₂ and H₂O exchange between the leaf and the atmosphere under a range of conditions. However, at night, vapour pressure deficits are extremely small and water vapour fluxes are often too low to derive accurate measurements of stomatal conductance using this technique (Barbour et al., 2005; Seibt et al., 2007). Thus very often it was assumed that stomata shut at night so these inconvenient technical limitations would bear little consequence to ecosystem water budget estimations. Nonetheless evidence for the nocturnal opening of stomata is growing and attempts have been made to assess the potential bias in LSM water budgets as a consequence (Barbour et al., 2005; Lombardozzi et al., 2017). However, for me the impact on the global water budgets are secondary compared to the impact that open stomata at night must have on the atmospheric composition (Gimeno et al., 2017; Seibt et al., 2007; Wingate et al., 2010a). This is because when stomata are open at night an isotopic exchange between the oxygen isotopes of CO¹⁸O and H₂¹⁸O in the leaf can occur rapidly (Ogée et al., 2018; Peltier et al., 1995). Using the first field data of night-time CO¹⁸O exchange from Sitka spruce foliage collected with my branch chamber technique, empirical evidence was obtained to support the hypothesis that stomata remained open at night, leading to extremely depleted oxygen isotope signatures in the CO₂ emitted from leaves that labelled the oxygen isotope composition of atmospheric CO₂ ($\delta^{18}\text{O}-\text{CO}_2$) in the canopy airspace dramatically (Seibt et al., 2007; 2006b)(Fig. 1.4). This nocturnal isotopic exchange was also observed in European Beech and Maritime pine using a similar approach (Seibt et al., 2007; Wingate et al., 2010a) and most recently inspired a recent Marie Curie fellowship project with Dr Teresa Gimeno to revisit nocturnal stomatal conductance (Gimeno et al., 2017).

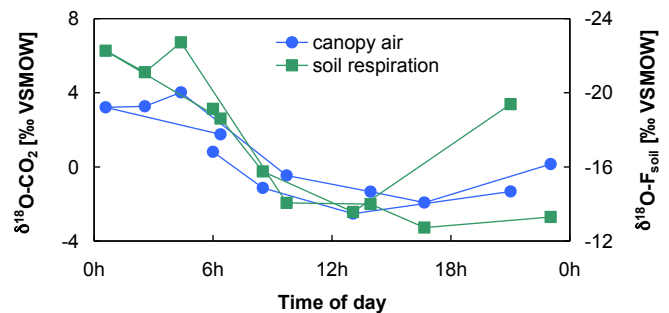


Figure 1.4 | Diurnal variations of the $\delta^{18}\text{O}$ of canopy air CO₂ and the soil CO₂ efflux, observed at Griffin forest in Sept. 2000 and July 2001.

CO₂ is strongly recycled in dense forest canopies | Strong variations in the oxygen isotopic composition of canopy CO₂ are also driven by shifts in the isotope composition of rainfall events in addition to changes in the amount of isotopic enrichment in ecosystem water pools driven by evaporation rates. As mentioned above when CO₂ and water interact they isotopically exchange oxygens. The dense canopy (leaf area index >6 m² m⁻²) of the Sitka spruce forest I studied fortuitously lent itself well to the investigation of CO₂ recycling within the canopy air space. The data clearly demonstrated that the oxygen isotope composition ($\delta^{18}\text{O}$) of leaf CO₂ gas-exchange caused the canopy air space to become increasingly enriched in CO¹⁸O because of the fast isotopic turnover of CO₂ reactions in leaf water pools and a lack of turbulent mixing at night within the canopy (Seibt et al., 2007; 2006b). Thus a strong enrichment in $\delta^{18}\text{O}-\text{CO}_2$ of canopy air was observed in this forest that also dynamically fed

back onto the $\delta^{18}\text{O}$ of the soil CO_2 flux (Fig. 1.4). This result had profound implications for the ability to model this particular isoflux correctly at larger scales (Seibt et al., 2006b). Specifically, this would mean that to capture this fast leaf-atmosphere-soil feedback and predict soil isofluxes with ecosystem or Earth system models either a turbulent transfer scheme would be necessary or the implementation of this isotopic feedback on atmospheric CO_2 in the lowest layer of the atmosphere. At the scale of the Earth system this process also contributes to the turnover of CO^{18}O molecules in the Earth's atmosphere measured by the atmospheric CO_2 network and calculated using the isotopic waves in the Earth's water composition produced by oscillations in El Nino events. Since my PhD I have been lucky to work with models (and modellers) that have implemented this feedback at different scales.

The importance of day respiration in ecosystem C budgets | As described above the size of GPP is large and highly uncertain. To estimate this flux the partitioning of gross photosynthetic and respiratory CO_2 fluxes during the day commonly relies on a relationship derived from the net ecosystem exchange of CO_2 (NEE) and air temperature measured at night (Wehr et al., 2016). Assuming this nocturnal relationship can be used to predict the rate of respiration from an entire ecosystem during the day, the amount of gross photosynthesis can be calculated adopting a mass balance approach and using the NEE measured during the day. However, reconciling this convenient mass balance approach with leaf scale respiration studies and stable isotope theory indicated that there was potentially an overestimation in the amount of respiration occurring during the day. If so this would lead to an overestimation in the amount of GPP that took place during the growing season.

This problem motivated me to measure the carbon isotope signatures of respired CO_2 ($\delta^{13}\text{C}$) from ecosystem components as well as the variability in photosynthetic carbon isotope discrimination $\Delta^{13}\text{C}$. Based on the observed $\delta^{13}\text{C}$ signatures of leaf CO_2 uptake, we identified an apparent isotopic fractionation effect, linked to differences in the isotopic composition of the gross CO_2 fluxes of photosynthesis and respiration at dawn and dusk, that had not been described previously. Prior to this it was assumed that the carbon isotope composition of respiration during the day was fuelled by recent assimilates and thus should not cause any net isotope effect (Farquhar et al., 1982). To interpret this effect, a new version of the classical theory of photosynthetic ^{13}C discrimination was developed (Wingate et al., 2007). This model was then used to predict over time how the different leaf fluxes varied over several days and how changes in day respiration would affect gross CO_2 fluxes and carbon isotope discrimination estimates at the canopy scale compared to those predicted from nocturnal NEE (Wingate, 2003). Unfortunately, at the time when I conducted my PhD study the only possibilities for measuring CO_2 isotopes in the field were with glass flasks and Isotope Ratio Mass Spectrometry. This limited the amount of data that could be collected and thus my capacity to confirm this hypothesis beyond a few days of stable isotope data. Nonetheless this work was well received by the research community and I was consequently invited to comment on breaking research articles (Bathellier et al., 2007) and give talks related to the topic of respiratory metabolism and the partitioning of C fluxes in high impact journals (Wingate, 2008), conferences and workshops (see list of communications). In addition key collaborations with the teams of Professors Nina Buchmann and Alexander Knohl at the ETH in Zurich investigating branch chamber fluxes would also evolve from this research front and resulted in the publication of two further papers on this subject (Gentsch et al., 2014a; 2014b) as well as a number of collaborative analyses and review papers with other teams around the world on this topic (Barbour et al., 2011; Werner et al., 2012). On reflection my frustrations with flask sampling constraints during these early PhD years definitely provided ample motivation to automate my chamber techniques, and eventually led me to

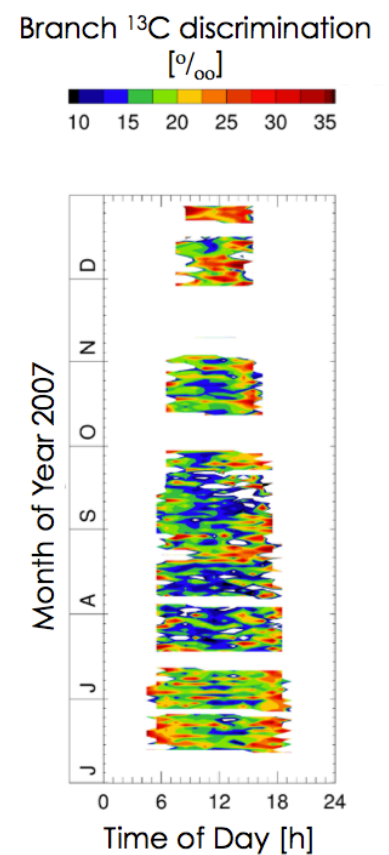


Figure 1.5 | Seasonal variability in measured photosynthetic ^{13}C discrimination (Wingate et al., 2009).

adopt the new laser spectrometer technologies that were gradually appearing on the horizon. These instruments would measure photosynthetic ^{13}C discrimination from branches (Wingate et al., 2010b) (Fig. 1.5) and ecosystems (Wehr et al., 2016) at a resolution never measured before and collect data to support the theory that inhibition of canopy day respiration may be significant and highly variable at the ecosystem scale during the growing season. Further recognition of my contribution to this technological advance in stable isotope ecology was nicely summarised in a glowing New Phytologist commentary (Subke and Ineson, 2010) (see end of my HDR p87).

Studying soil CO_2 flux response to drought in Mediterranean ecosystems (Post-doc MIND, 2003-2005)

After my PhD I continued working at the University of Edinburgh and became a postdoctoral fellow in the Forest Ecosystem Physiology Laboratory of Prof. Maurizio Mencuccini. Whilst writing my PhD, Maurizio and I co-authored a successful NERC grant to study the effects of aging on the exchange of CO_2 and water in Scots Pine across Scotland. The original idea was that after I had submitted my PhD I would continue to work on branch gas exchange with the funding from this project. However, Prof. Mencuccini had also recently obtained funding for an EU project called MIND (Mediterranean Terrestrial Ecosystems and Increasing Drought) and I deeply felt that I needed a bit of adventure and to work on a different system with different questions. Luckily Prof. Mencuccini was fine with this and I managed to contribute to both projects. Over the next years I made regular trips to Portugal and installed and co-ordinated a 2.5-yr soil respiration experiment in a Mediterranean oak forest at the Mitra CarboEurope flux site (Fig. 1.6). This brought me into regular contact with many of Europe's leading researchers in the field of Mediterranean ecophysiology and started my collaboration with Prof. Joao S. Pereira and colleagues at the Instituto Superior de Agronomia (Lisbon). Together we set up an experiment to monitor the changes in soil microclimate and gas exchange within large plot manipulations of rain exclusion or wetting treatments to investigate the impact of precipitation regime on belowground carbon cycling in droughted ecosystems (Fig. 1.6). I was also highly motivated to explore the isotopic soil signals from these droughted ecosystems and initiated further new collaborations with Prof. Jaleh Ghashghaie from the Université Paris-Sud, Paris and Prof. Dan Yakir and Dr Kadmiel Maseyk from the Weizmann Institute for Science, Israel. This work gave me a lot of experience in managing long-term experiments in another country and taught me many fascinating things about the physiology of soil microbes and how they have evolved to survive during drought. The data from my particular experimental work has so far appeared in 5 internationally peer-reviewed articles (Correia et al., 2012; Jarvis et al., 2007; Maseyk et al., 2009; Wingate et al., 2009; 2008b). Again rather than providing an exhaustive account of all the work involved in each of these papers, I will present a couple of key results that were of particular personal interest.



Figure 1.6 | Soil water manipulation conducted in a Mediterranean oak woodland in Evora, Portugal

Mediterranean regions are important drivers of atmospheric CO₂ variability | The total area of land occupied by Mediterranean and savannah regions (30-35 million km²) approximate the global area of wet and moist tropical, temperate and boreal forests combined (House and Hall, 2001). The latter forests are regarded as the terrestrial power-houses for atmospheric CO₂ removal, and contain the major reservoirs of global ecosystem carbon in their soils (Luyssaert et al., 2007). However, current LSMs predict that climate could increase the frequency and intensity of droughts, heatwaves, fires and flooding events in temperate and boreal ecosystems potentially contributing to an increase in the global extent of areas with Mediterranean and savannah climates at the expense of temperate and tropical forests. If this occurs CO₂ removal from the atmosphere is likely to be reduced and CO₂ emissions to the atmosphere may be increased (Jarvis et al., 2007). In this context, semi-arid regions have recently been identified as potential drivers of inter-annual variations in atmospheric CO₂ concentrations (Ahlstrom et al., 2015). However, state-of-the-art LSMs struggle to capture well the coupled dynamics of carbon and water exchange in Mediterranean ecosystems (Jung et al., 2007) because of an inability to simulate soil moisture conditions well (e.g. because of overestimation of evaporation and/or transpiration) or are too sensitive to variations in soil moisture. Moreover, because LSMs struggle to capture soil water dynamics well in semi-arid regions predicting the release of CO₂ from soils is a challenge. As shown in Fig. 1.7 just a few autumn rain events can have dramatic consequences for the flux of CO₂ from these ecosystems to the atmosphere resulting in considerable reductions in the cumulative C uptake by the ecosystem each year (Fig. 1.7).

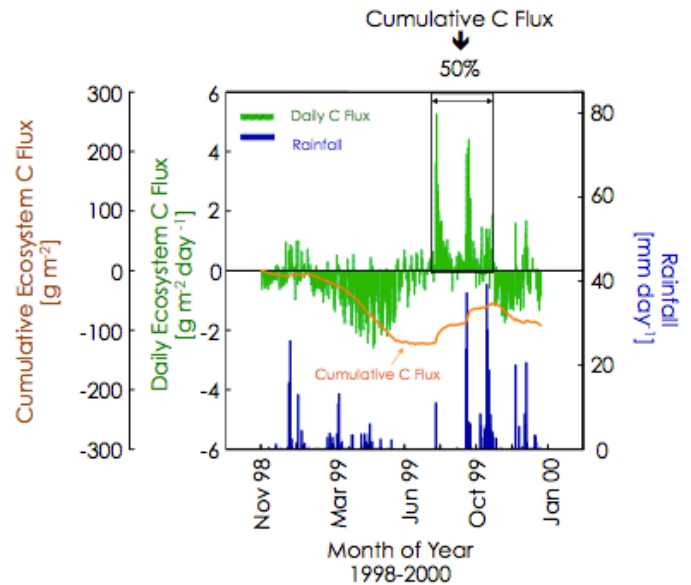


Figure 1.7 | Rainfall, daily ecosystem C flux and cumulative ecosystem C flux over 14 months in the Mediterranean forest site Mitra, Evora, Portugal Adapted from Jarvis et al., 2007

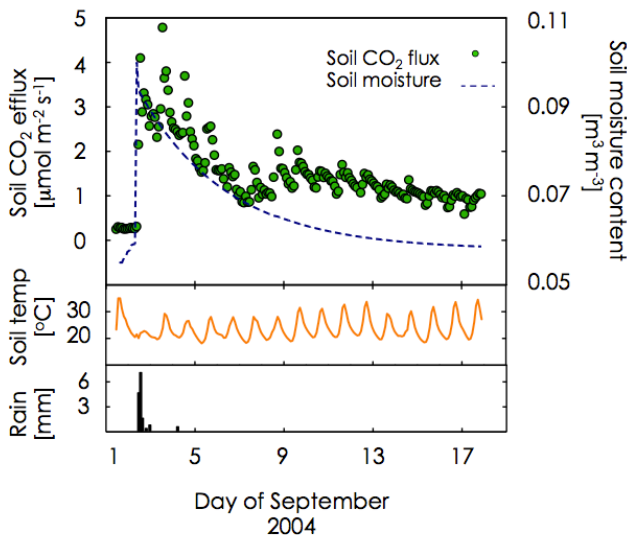


Figure 1.8 | Precipitation, soil CO₂ efflux and surface temperature and moisture variations in the Mediterranean forest site Mitra (Portugal). Diurnal variations of soil CO₂ efflux are controlled by soil temperature whilst synoptic variations are related to changes in soil moisture content and the extent of drought prior to the rain event.

Soil microbial respiration is strongly driven by the frequency and length of drought periods | Difficulties in the prediction of soil CO₂ emissions by LSMs in semi-arid regions are further complicated as microbial communities have evolved metabolic strategies to survive frequent and persistent soil drought. These metabolic strategies often give rise to soil CO₂ (and N₂O) fluxes after rain events that are much larger than fluxes predicted with empirical relationships constructed when soils are moist (Reichstein and Rey, 2003). This is a phenomenon observed at both the soil and ecosystem scale in Mediterranean and savannah systems, known as the 'Birch effect' (Birch, 2005) (Figs. 1.7 & 1.8). This process remains poorly represented in the current generation of ecosystem carbon models, despite it having a profound effect on the annual carbon balance in semi-arid ecosystems (Jarvis et al., 2007). However, recent models have been advanced to describe how the magnitude of CO₂ emissions can be linked to variations in the soil water potential experienced by soil communities (Manzoni et al., 2014). Using automated soil

chamber techniques deployed in the field, I collected an extensive and replicated dataset tracking the temporal and spatial variability of soil CO₂ fluxes to precipitation and drying events (Fig. 1.8, (Correia et al., 2012; Jarvis et al., 2007)). Although a number of papers have been published from this work my hope is to return to this dataset in the future with a modeller and explore how well the theoretical framework proposed by Manzoni et al. (2014) describes the high resolution field data I have collected. This could help identify the simplest model description of the Birch Effect that can be implemented in LSMs alongside global maps of key microbial and soil traits that could one day facilitate modelling of the Birch Effect at larger scales to explore its effect on the inter-annual variability of atmospheric CO₂ concentrations.

Soil CO₂ hydration rates are 300 times faster than the uncatalysed rate in Mediterranean ecosystems |
 During my PhD field work in Scotland interesting results obtained from the soil chamber stable isotope study indicated that the rate of CO₂ hydration in soils was much faster than that predicted from theory (Seibt et al., 2006b). We hypothesised that this was caused by the presence of carbonic anhydrase (CA) an enzyme that catalysed the rate of CO₂ hydration and the rate of oxygen isotope exchange between CO₂ and soil water pools. The soil chamber experiment in Portugal presented an opportunity to test this hypothesis further. To do this I initiated a collaboration with Prof. Dan Yakir and Dr Kadmiel Maseyk from the Weizmann Institute of Science to develop a new dynamic flask sampling method to measure the carbon and oxygen isotope composition of CO₂ (Maseyk et al., 2009; Wingate et al., 2008b). After three field campaigns testing the technique Kadmiel and I finally collected a beautiful set of data over three days and sleepless nights (Fig. 1.9). This dataset provided further evidence for the hypothesis proposed in (Seibt et al., 2006b), that the previously unknown role of the enzyme carbonic anhydrase (CA) in soils might have a substantial impact on the oxygen isotope composition of CO₂ exchanged with the atmosphere. Carbonic anhydrase is known to be present in microbes, plant roots, fungi and algae, and hypothesised to play a critical role in shaping the magnitude and variability of the oxygen isotope composition of the net soil CO₂ flux over time. This is because the enzyme CA accelerates the isotopic equilibration of oxygen atoms between soil CO₂ and water during the diffusion of CO₂ into and out of the upper soil layers ("atmospheric invasion") without affecting net soil CO₂ fluxes. Using δ¹⁸O measurements collected on the soil chamber plots set-up in Mitra coupled with a soil CO₂ isotope transport model, we demonstrated that a modest soil water evaporative enrichment and an enhanced CO₂ hydration rate *ca.* 300 times faster than the uncatalysed rate was needed to simulate the observed isotopic signals and their variability over time (Wingate et al., 2008b). This beautiful data and modelling study compelled me to advance current understanding of how this hydration rate enhancement varies between ecosystems and to explore the consequences of this process at larger scales (Wingate et al., 2009).

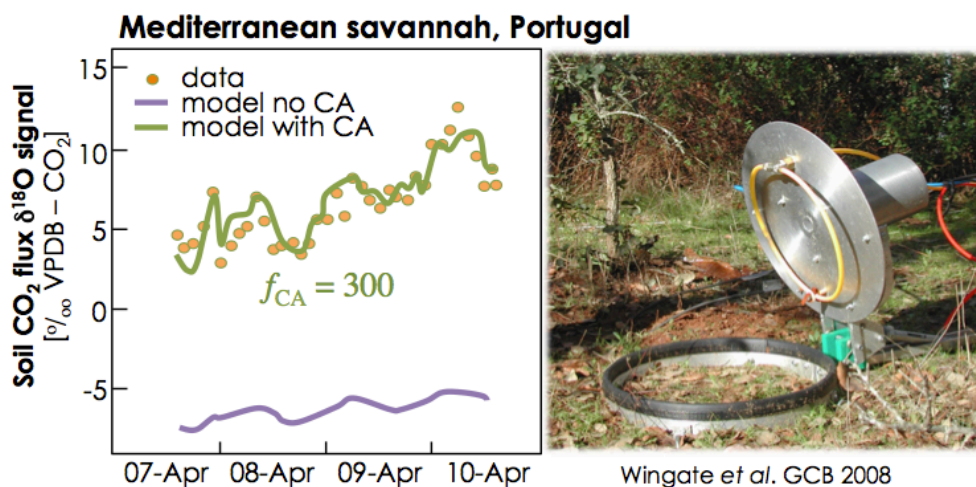


Figure 1.9 | Variations in the measured and modelled oxygen isotope composition of the soil CO₂ flux assuming either an uncatalysed or catalysed CO₂ hydration rate and isotopic exchange from soil chambers installed at the Mitra site, Evora, Portugal.

**Improving knowledge of the seasonal timing and optical sensing of photosynthesis using digital repeat photography at sites across Europe
(Post-doc CarboEurope-IP, 2005-2008)**

As part of my research trying to understand how climate change might affect primary productivity and ecosystem function I quickly appreciated that it was extremely important to maintain records of plant life cycle events. This is because the growth of new leaves every year is clearly signalled in atmospheric CO₂ concentration records and exerts a strong control on both spatial and temporal patterns of carbon (C) sequestration and water cycling (Keeling et al., 1996; Piao et al., 2008). Hence, for the purpose of understanding patterns and processes controlling C and water budgets across a broad range of scales, there are obvious advantages in creating explicit links between flux monitoring, phenological observation and biogeochemical studies (Ahrends et al., 2009; Baldocchi et al., 2005; Richardson et al., 2007; Wingate et al., 2008a).

In 2005 I was extremely lucky to obtain a 4-yr postdoc to develop my phenological understanding of plants as part of the EU project CarboEurope-IP mentored by Prof. John Grace FRSE. Within this new postdoc my brief was to participate to the Forest Synthesis and the Innovation work packages and thus one of my activities involved developing a very simple but effective phenology network across Europe. Although phenology networks have existed in the past this one was novel at the time as it used commercial cameras strategically mounted at long-term experimental flux sites across Europe <http://european-webcam-network.net>.

Since 2005 this digital camera network has grown and has been steadily archiving time-lapse images of European ecosystems that can now be used with novel algorithms to precisely determine the dates of leaf emergence and senescence for different land use types (Fig. 1.10) (Filippa et al., 2016; Mizunuma et al., 2011; 2014; Wingate et al., 2008a; 2015). I have also fostered links with other digital camera networks across the world especially in the USA and Japan (Filippa et al., 2016; Mizunuma et al., 2011; Nagai et al., 2018; Wingate et al., 2008a). As this method consists of simply taking digital images it can be a very powerful technique to communicate the impacts of climate change on biosphere function and crop production to the general public. Consequently this work was featured at a recent INRA exhibition targeting the general public at the Salon de Agriculture in 2016 (<https://www.youtube.com/watch?v=RTy1OJRuIXs>).

First synthesis results from this digital camera network indicate that variations in the Red, Green and Blue (RGB) fraction of images can be extracted routinely and used to identify key dates in canopy structural and physiological events, such as when maximum leaf area is attained and when maximum photosynthesis occurs (Plaza-Aguilar et al., in prep; Wingate et al., 2015). In addition, this work has demonstrated how variations in these colour signals are strongly related to the concentration of photosynthetic pigments in leaves (Fig. 1.11). In addition when this data is combined with a biochemical model of reflectance and radiative transfer in canopies, changes in important leaf traits can be detected in plant canopies. For example, differences in the concentration of secondary metabolites notably tannins between the crowns of different plant species and over time can be detected within the crowns of temperate European species such as Ash and Oak (Plaza-Aguilar et al., 2018). This technique can also provide valuable information on soil and vegetation responses to management practices such as mowing, harvesting and soil preparation in agricultural systems and may also provide a tool for the early detection of

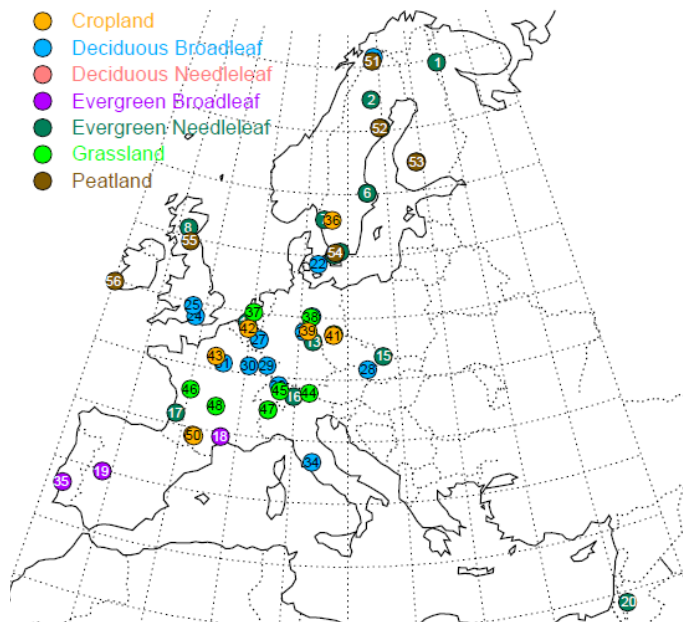


Figure 1.10 Map of the digital camera network located at European flux sites <http://european-webcam-network.net>

pathogen attack in forests and crops providing a cheap system to monitor colour changes whilst ‘keeping an eye’ on ecosystem health and function (Filippa et al., 2016; Wingate et al., 2015).

On this particular research theme I have co-supervised two PhD students Dr Toshie Mizunuma and Dr Andrés Plaza-Aguilar as well as two MSc students. I am also a participant of the French national phenology initiative SOERE-TEMPO and regularly train technicians, engineers and researchers from across France on the installation of digital cameras and processing of digital images at annual workshops. In addition, co-ordinating this network has strengthened my European research network and facilitated many collaborations and invited talks at a range of international meetings with the corresponding US and Asian digital camera networks. Finally, I have also been appointed as the ICOS working group leader for phenology camera measurements and have contributed as the senior author to the ICOS protocol to be published in the very near future. This work should continue to flourish over the next years, as I will work with an international postdoc Dr Koen Hufkens and a PhD student Ms Tania Fort as part of two currently funded Labex and Regional projects I co-manage with Dr Corinne Vacher (INRA BIOGECO) investigating the role of phenology and microclimate on the community structure and function of the microbial phyllosphere within forests.

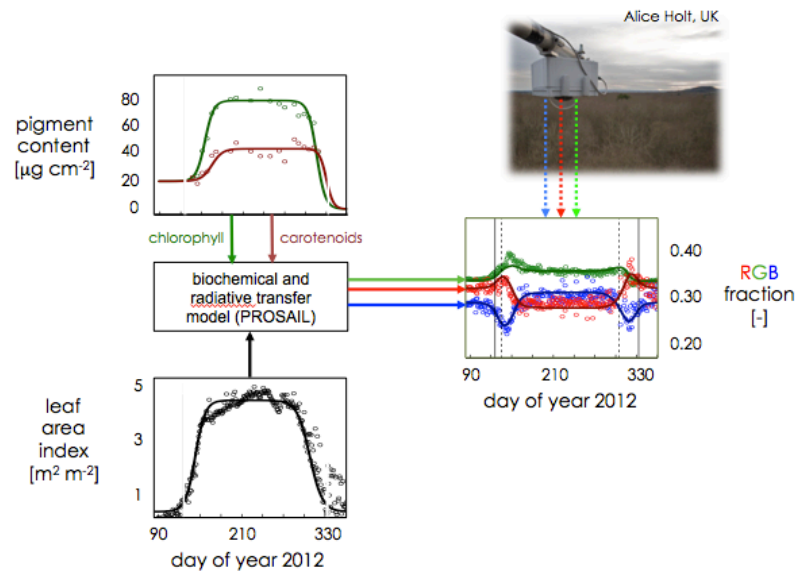


Figure 1.11 Schematic showing how measurements of pigment concentrations and leaf area index can be used to predict seasonal variations in RGB fraction that can also be estimated from digital images. Open symbols represent data whilst solid lines represent model estimates.

**Improving our knowledge of the seasonal timing of wood growth in trees and how this is linked mechanistically to plant function and climate
(Marie-Curie Fellowship 2009-2010, NERC Advanced Fellowship 2010-2011, INRA 2011-2013)**

Towards the end of my postdoc with John Grace I started to conduct experiments with the team at INRA Bordeaux and especially Dr Jérôme Ogée who had started to adapt his isotope-enabled ecosystem model MuSICA to work on tree rings. The motivation behind this was to explore how limitations in plant productivity might have occurred over the past decades to centuries, and to reconstruct past function and growth dynamics utilising plant archives. In particular, archives of cellulose in tree-rings, grass blades and moss bank cores can preserve a range of chemical signals that can be linked mechanistically to climate and physiological function. For example, within a single tree-ring, strong intra-annual variations in wood density and the carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope composition of cellulose can be observed (Ogée et al., 2009; Werner et al., 2012; Wilkinson et al., 2015) (Fig. 1.12). These seasonal variations in cellulose properties contain detailed information of plant carbon and water status over the growing season and between years (Maseyk et al., 2009; Voelker et al., 2016; Wilkinson et al., 2015; Wingate et al., 2010b; 2007) and are especially useful indicators of plant stress. This work became especially important for me when I moved to the University of Cambridge as a NERC fellow and started to work next door to the Godwin Laboratory full of Isotope Ratio Mass Spectrometers. I begin to visit a number of international research teams (University of Helsinki, Technische Universität Dresden, Weizmann Research Institute, DUKE Nicolas School of the Environment, Université Laval, Northern Arizona University and Université du Québec à Chicoutimi) to obtain tree-ring archives for model-bench-marking. These tree rings

were all sampled at flux sites where I knew it would be possible to obtain co-located climate and flux data that could drive and help validate MuSICA simulations. Again the idea was to draw from multiple independent datastreams that could be used to obtain unique insights on carbon allocation dynamics over past growing seasons and provide indications on the sensitivity of the different parameters linked to the carbon and water cycle in the model. In addition this work had the potential to resolve an ongoing problem about knowing when within the growing season a particular section of wood within an annual ring was deposited i.e substituting position with time. In fact this problem became the central focus of a number of my early research proposals most notably to the INRA CR Blanc concours in 2011 and the ERC call in 2008. Luckily I successfully obtained my permanent position with this project but did not have as good luck with the starting grant! Despite the lack of funding we still managed to combine a novel modelling and multi-proxy approach that can precisely date (to within ~10 days) when and at what rate carbohydrates are deposited in wood cellulose over the season opening up the possibility to reconstruct detailed weather events within tree ring chronologies and potentially changes in growing season length in the past (Fig. 1.12).

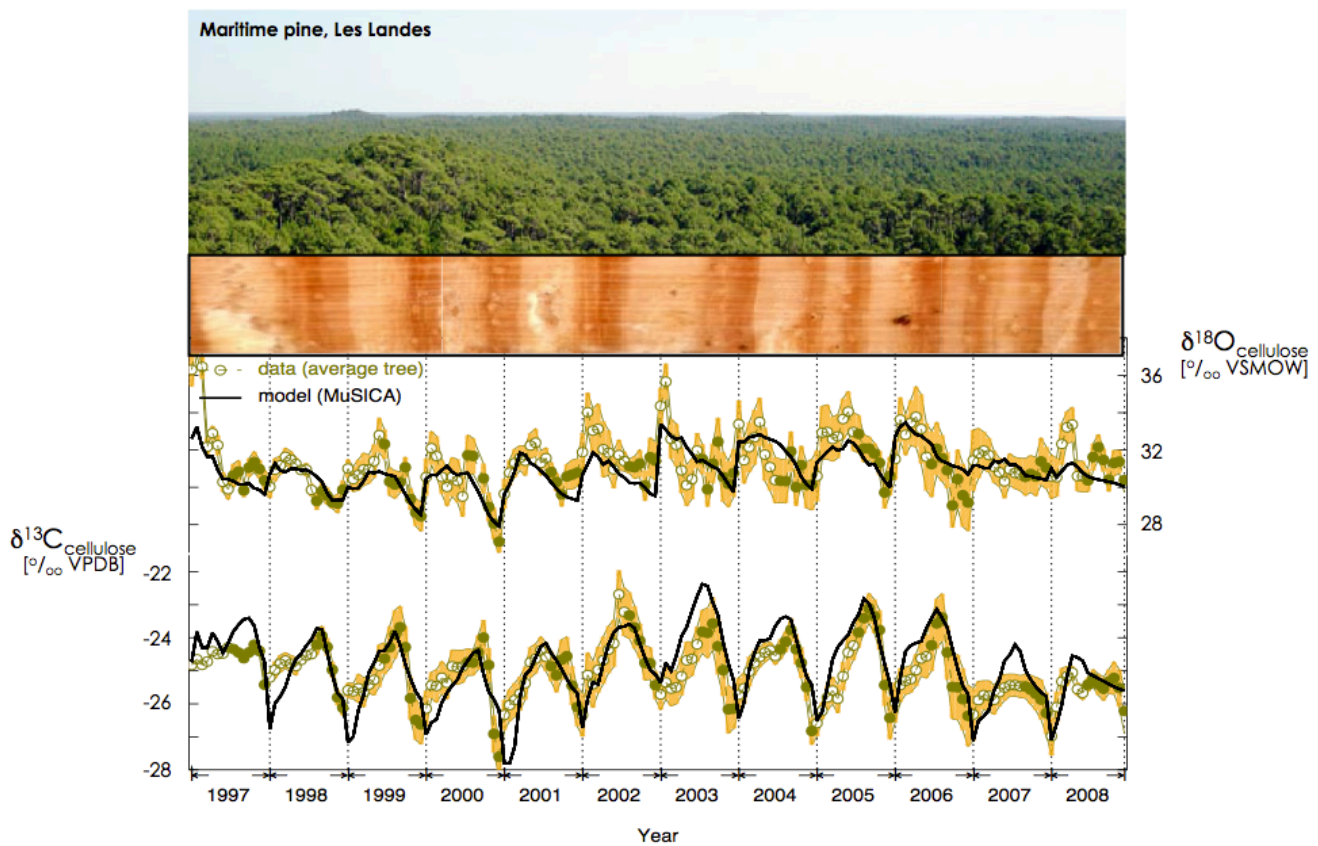


Figure 1.12 Intra-annual variability in the measured and modelled carbon and oxygen isotope composition of cellulose measured in Maritime pine sampled near Bordeaux.

This work so far has involved close collaborations within INRA including with Jérôme Ogée, Didier Bert, Cathy Lambrot and Jean-Christophe Domec and James Rolfe from the Godwin Lab in Cambridge. Furthermore, this topic has resulted in me co-supervising a PhD student (Mr Yann Cochet, Bordeaux Idex in co-tutelle with l'Université Laval) investigating the impact of elevated CO₂ and nitrogen fertilisation on tree-ring intra-annual density and stable isotope signals, in addition to supervising 3 MSc students on the topic. Furthermore, as grasses and moss bank deposits also exhibit sequential growth patterns the same tools developed for tree rings can be applied to interpret peat and grassland function in the past. For example, we have explored how photosynthesis rates varied in Antarctica over the past 3000 years using moss chrono-sequences with collaborators at the University of Cambridge (Royles et al., 2013; 2012) and more recently we are collaborating with researchers at the

Technical University of Munich interpreting cellulose stable isotope signals in managed grasslands (Hirl et al., in prep). Research on tree ring signals is also set to become more important over the next two years with the recent (or forthcoming) arrival of four postdoctoral fellows, Dr Camille Delvigne in collaboration with researchers from the Université Catholique de Louvain, Drs Adria Barbeta and Paula Martin Gomez, two Bordeaux IdEx fellows in the team and Dr Koen Hufkens, a Marie Curie Fellow that will start in 2019. Each of them will study stable isotope high-resolution signals in trees to understand better evapo-transpiration and climatic archives in a range of biomes. My hope is now that with a team of researchers growing around me interested in tree ring interpretation I will finally have the opportunity to write up and publish the high-resolution tree ring datasets that I have been collecting over the past 8 years.

**Linking the enzyme carbonic anhydrase to atmospheric carbon cycle tracers
(INRA ERC Starting Grant 2013-2019)**

As described above I have shown in past studies that the hydration rate of CO₂ in soils is highly variable but always much faster than the uncatalysed rate and can impact the δ¹⁸O-CO₂ (Wingate et al., 2008; 2009; 2010). However, utilising δ¹⁸O-CO₂ as a tracer of soil exchange at the large scale requires a theory that predicts how the spatial and temporal activity of the enzyme carbonic anhydrase varies. This problem motivated me to apply for an ERC Starting Grant (obtained in 2013) and this time the proposal was successful. This allowed me to bring together a great team of young scientists and engineers to address this problem. The project developed new techniques to measure CA activity from soils (Jones et al., 2017) and to survey a range of biomes across Europe to test enzyme kinetic theory in soils (Gangi et al., 2015; Sauze et al., 2018). In particular, we have now produced two benchmark datasets from Europe and the USA (encompassing >60 soils) that demonstrate how the spatial distribution of soil microbial biomass and pH can be used to model spatial variability in CA concentration and CA activity across different biomes (Sauze et al., 2018; Meredith et al., 2018b; Wingate et al., in prep). This now means that for the first time we can create a map of soil CA activity across the world (Fig. 3.5) and revisit our isotope-based estimates of global photosynthesis. In addition to establishing the key edaphic controls on soil CA activity, I have been collaborating with INRA researchers Dr. Pierre-Alain Maron and Dr. Olivier Crouzet and Dr Laura Meredith from the University of Arizona to develop molecular tools to look at the role of different community members and CA genes to the exchange of CO¹⁸O and COS between soils and the atmosphere (Sauze et al., 2017; Meredith et al., 2018a; 2018b). This functional genomic and transcriptomic approach is now providing strong clues regarding which organisms and CA genes co-vary (Fig. 1.13) with the CA activities we obtain from gas exchange studies pushing the scientific boundaries of our current knowledge on the links between CA gene expression and atmospheric chemistry.

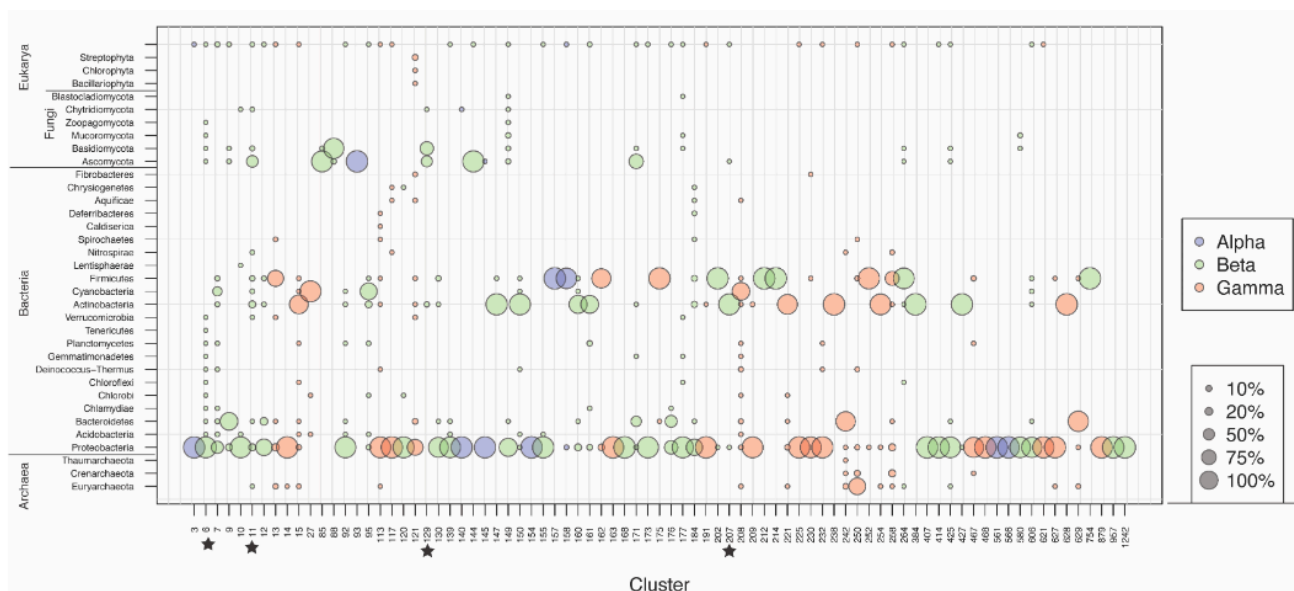


Figure 1.13 Taxonomic composition associated with CA clusters found in a range of soils (Meredith et al., 2018b)

PART II : PRESENT RESEARCH

CONSTRAINING THE ROLE OF SOILS ON ATMOSPHERIC COS CONCENTRATIONS AT LARGE SCALES

2.1 USING ATMOSPHERIC COS TO TRACE PHOTOSYNTHESIS

Carbonyl sulphide (COS) is the most abundant sulphur gas in the atmosphere (Andreae, 1997; Crutzen, 1976) with an atmospheric lifetime of about two years (Brühl et al., 2012). Interest in the seasonal variability of atmospheric COS (Fig. 1.2) has intensified as its use as an atmospheric tracer of global primary productivity has recently been demonstrated (Campbell et al., 2017; Montzka et al., 2007; Sandoval-Soto et al., 2005). This is because the enzyme carbonic anhydrase (CA) present in plants catalyses both the hydration of CO_2 and the hydrolysis of COS during leaf gas exchange (Gimeno et al., 2017; Ogée et al., 2018; Protoschill-Krebs et al., 1996; Sandoval-Soto et al., 2005; Seibt et al., 2010). Consequently the terrestrial biosphere is estimated to be a strong sink of COS, with around -0.24 to -1.4 Tg S y^{-1} taken up by plants (Fig. 2.1)(Berry et al., 2013; Campbell et al., 2017; Kettle, 2002; Launois et al., 2015; Whelan et al., 2018). As soil micro-organisms also contain the enzyme CA (Kesselmeier et al., 1999; Wingate et al., 2009), oxic soils have been estimated to take up a further -0.13 to -0.5 Tg S y^{-1} from the atmosphere (Berry et al., 2013; Campbell et al., 2017; Kettle, 2002; Launois et al., 2015; Whelan et al., 2018). However, soil COS flux datasets are scarce and restricted to a few studies focused on certain biomes and land use management (Van Diest and Kesselmeier, 2008; Whelan et al., 2016; Whelan et al., 2018). This problem leads to considerable uncertainty when determining the contribution of soils to atmospheric COS mass budgets and consequently uncertainties when trying to constrain global primary productivity using atmospheric COS variations (Berry et al., 2013; Campbell et al., 2017; Kettle, 2002; Launois et al., 2015; Whelan et al., 2018).

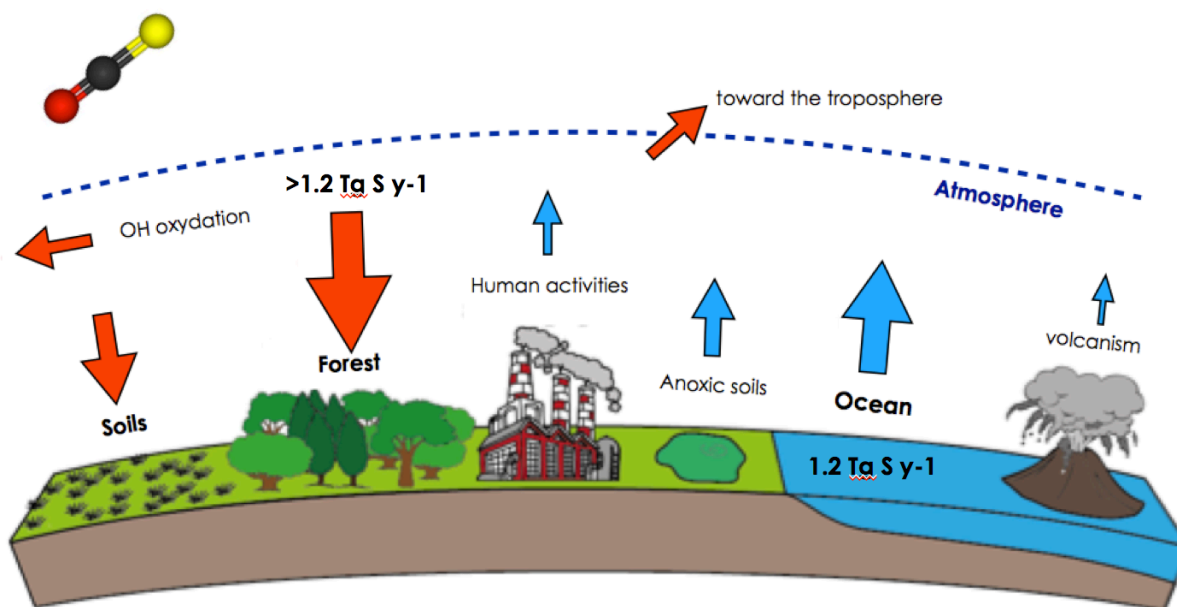


Figure 2.1 Representation of the major sources and sinks of COS to the atmosphere

2.2 DEVELOPING A MODEL DESCRIBING SOIL COS FLUXES

First attempts to assess the large-scale contribution of soil COS exchange were made by Kettle et al., (2002) using empirical relationships measured between soil COS uptake, soil water content and temperature derived by Kesselmeier et al. (1999):

$$F = F_0 \Phi_w(W) \Phi_T(T) \Phi_C(C_a), \quad (1)$$

where F is the modelled net soil-air COS exchange rate ($\text{pmol m}^{-2} \text{s}^{-1}$), F_0 is a reference exchange rate, and $\Phi_w(W)$, $\Phi_T(T)$ and $\Phi_C(C_a)$ are parametric functions describing how soil water content (W , in % volume), temperature (T , in K) and ambient COS mixing ratio above the soil surface (C_a , in pmol mol^{-1}), respectively modify the net COS exchange rate. Kettle et al. (2002) parameterised their model based on observations from only one soil type, a temperate arable soil, and used a unique value of F_0 across the globe ($F_0 = -10 \text{ pmol m}^{-2} \text{s}^{-1}$).² Using this empirical approach, Kettle et al. (2002) estimated for the first time a global COS sink from oxic soils of $-130 \pm 56 \text{ GgS yr}^{-1}$.

More recently, Berry et al. (2013) drew on empirical relationships by Yi et al. (2007) who observed that soil COS uptake seemed to be proportional to the rate of heterotrophic soil respiration:

$$F = k_{\text{soil}} F_{\text{CO}_2}, \quad (2)$$

where k_{soil} is a proportionality constant that relates the COS flux to heterotrophic respiration (F_{CO_2} , in $\mu\text{mol m}^{-2} \text{s}^{-1}$). This formulation was subsequently implemented in a version of the Simple Biosphere Model (Sellers et al., 1996) called SIB3 that estimates how F_{CO_2} varies across the land surface in response to soil water content and temperature (Berry et al., 2013). Simulations with this model, using a value of k_{soil} of about $-6 \text{ pmol(COS) } \mu\text{mol(CO}_2)^{-1}$, estimated a much stronger sink strength for soils globally than (Kettle, 2002) at -355 GgS yr^{-1} , highlighting a need for constraints on the contribution of soils to the global COS budget.³

The rationale behind Eq. 1 is mostly based on physical considerations where COS uptake by soils should depend on soil moisture and temperature because these variables act directly on the solubility and transport of COS to the CA reaction sites as well as on the reaction rates themselves (Fig. 2.2). In contrast, the rationale behind Eq. 2 is mostly based on ecological considerations that the uptake of COS should be proportional to the size and activity of the soil heterotroph community that could co-vary with heterotrophic respiration. Until recently these physical and ecological drivers had not been brought together in a unifying mechanistic framework describing COS exchange between soils and the atmosphere.

In 2014, our team set out to revisit these models and previously published datasets and construct a theoretical framework that would describe the patterns in COS fluxes observed across a range of soil types. For this we adopted the theoretical framework previously used to model soil CO^{18}O exchange (Wingate et al., 2010a; 2009; 2008b) and adapted it to describe the production, diffusion and hydrolysis of COS within re-packed soil microcosms (Ogée et al., 2016).

² They also considered W to be volumetric, not gravimetric, water content as originally presented in Kesselmeier et al. (1999).

³ [Note that the value for k_{soil} given by Berry et al. (2013) in their paper is actually much larger ($-120 \text{ pmol(COS) } \mu\text{mol(CO}_2)^{-1}$) and inconsistent with the results of Yi et al. (2007) and the value used in the actual numerical code that was used to produce the results in their study. The value of $-6 \text{ pmol(COS) } \mu\text{mol(CO}_2)^{-1}$ has been re-estimated here to be consistent with the value used in their global simulations and their total sink strength of -355 GgS yr^{-1} .]

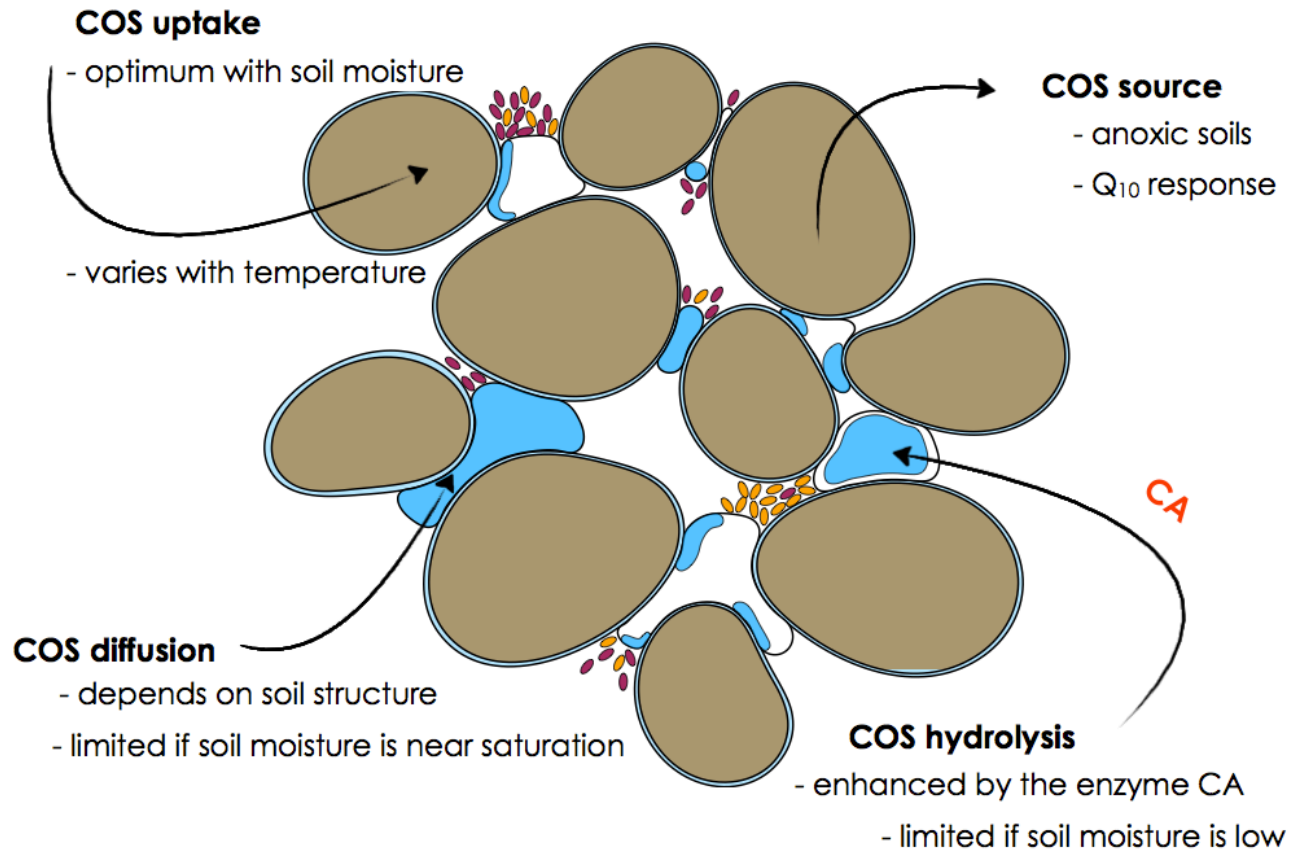


Figure 2.2 Pre-2016 understanding of soil COS exchange

This model was formally presented in a manuscript from our team (Ogée et al., 2016) and described for homogeneous soil columns how the soil COS flux should be related to soil moisture, temperature and microbial biomass according to:

$$F = \left\{ -\sqrt{kB\theta DC_a} + \sqrt{\frac{D}{kB\theta}} \rho_b P \right\} \tanh \left(z_{max} \sqrt{\frac{kB\theta}{D}} \right) \quad (3a)$$

where B is the solubility of COS in water ($\text{m}^3 \text{ air m}^{-3} \text{ water}$), θ is the soil volumetric water content ($\text{m}^3 \text{ m}^{-3}$), D is the effective diffusivity of COS through the soil matrix, k (s^{-1}) is the effective COS hydrolysis rate in soil water, C_a is the ambient COS mixing ratio above the soil surface (pmol mol^{-1}), ρ_b the soil bulk density, z_{max} the soil depth (m) and P represents the soil COS production rate ($\text{pmol m}^{-2} \text{ s}^{-1}$).

Different formulations relating the effective diffusivity and the soil moisture (and porosity) exist depending on whether the soil is repacked or not (Moldrup et al., 2003). Using only volumetric considerations we argued that the COS hydrolysis rate should be related to microbial biomass as:

$$k = k_{\text{uncat}} + \frac{B_v}{\theta} \left\{ k_{\text{uncat}} + [\text{CA}]_{\text{in}} \frac{k_{\text{cat}}}{K_m} \right\} \quad (3b)$$

where k_{uncat} (s^{-1}) is the uncatalysed rate of hydrolysis and k_{cat} (s^{-1}) and K_m (mol m^{-3}) are the (community-average) turnover rate and the Michaelis-Menten constant of the enzymatic reaction, $[\text{CA}]_{\text{in}}$ (mol m^{-3}) is the mean CA

concentration inside soil microbes and B_v (m^3 microbes m^{-3} soil) is the volumetric microbial biomass. The ratio k_{cat}/K_m was further assumed to respond to cytoplasmic pH according to:

$$\frac{k_{\text{cat}}}{K_m} = \frac{1}{1 + 10^{-pH_{\text{in}} + pK_{\text{CA}}}} \quad (3c)$$

where pH_{in} is the microbial cytoplasmic pH (Krulwich et al., 2011; Slonczewski et al., 2009) and $pK_{\text{CA}} = 7.1$ corresponds to the CA response to pH of *Arabidopsis thaliana* β -CA for CO_2 hydration (Rowlett et al., 2002; Sauze et al., 2018). This function was assumed appropriate for two reasons. The first is that most soils tend to be dominated by microbial β -CA (Fig. 2.3) (Elleuche, 2011; Meredith et al., 2018a; Smith et al., 1999) and the second is that Protoschill-Krebs et al. (1996) reported no pH optimum for β -CA extracted from *Pisum sativum* plants under a range of different pH values, but rather reported a steadily increasing COS consumption between pH 6 to 10. This reported pattern for COS hydrolysis is also consistent with the CO_2 hydration response to pH (Ogée et al., 2016). Nonetheless, this function still remains an uncertainty whilst the absence of experiments evaluating the pK_a value for COS persists.

In addition, a number of recent soil COS flux studies have also reported that oxic soils are not only sinks for COS, but can also be a source of COS to the atmosphere (Kitz et al., 2017; Maseyk et al., 2014; Rhew, 2015; Whelan et al., 2016). However, the mechanisms for these emissions are not clear. Initially it was thought that COS emissions were being driven directly by variations in soil redox potential and temperature especially in anoxic soils, whilst other studies showed that both temperature and light might be more important drivers of COS emissions in oxic soils (Kitz et al., 2017; Rhew, 2015; Whelan et al., 2016). A few studies also indicated that the rate of COS emission from soils can be described using a simple Q_{10} relationship with soil temperature (Maseyk et al., 2014; Whelan et al., 2016). Whilst other studies also indicate a potential abiotic component to this emission linked to changes in light intensity at the soil surface (Kitz et al., 2017; Rhew, 2015). However, mechanisms to explain these emissions of COS from oxic soils are currently putative and it remains difficult to prescribe in models how this relationship might vary with soil type or potential COS substrates.

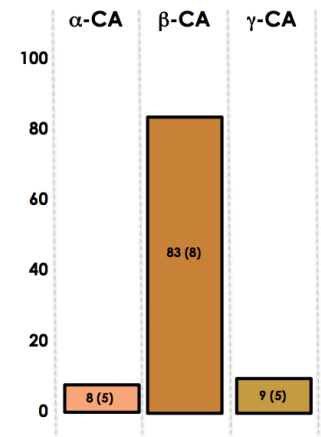


Figure 2.3 Distribution of CA classes within 7 different soil meta-transcriptomics (% of total CA) (Meredith et al., 2018)

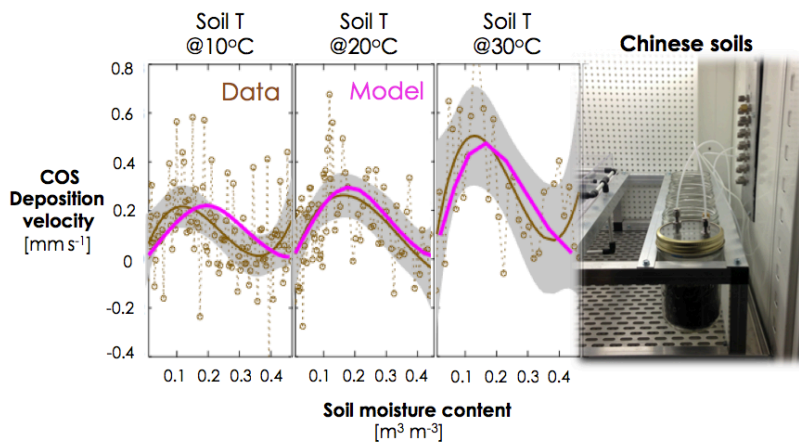


Figure 2.4 Relationship between observed and predicted COS deposition velocity as a function of soil moisture content for Chinese soil microcosms incubated at different soil temperatures (Ogée et al., 2016).

Despite our initial uncertainties in the mechanism of COS production from soils we decided to investigate how our model framework for the COS hydrolysis and diffusion in soils compared (Eq. 3) against a set of previously published data (Van Diest and Kesselmeier, 2008) assuming that the production term was negligible, a hypothesis that would require further investigation in our future studies. Initial results testing this novel mechanistic approach against soil flux datasets (Fig. 2.4) showed that the activity of the enzyme carbonic anhydrase (CA) known to catalyse the hydrolysis of COS (Kesselmeier et al., 1999; Protoschill-Krebs and Kesselmeier, 1992) was consistent with the range of soil CA activities previously obtained in published CO^{18}O studies on soils (Wingate et al.,

2010a; 2009; 2008b). In addition the model demonstrated clearly the important contribution of soil texture and diffusion in regulating the net COS flux (Fig. 2.4). Interestingly our representation of hydrolysis by CA generally explained the data well indicating that on the soil data we revisited COS production may have played a negligible role in determining the net COS flux.

2.3 PARTITIONING THE NET SOIL COS FLUX

As the mechanistic framework describing soil-atmosphere COS exchange was developing we felt it was increasingly important to challenge the various models (Eqs 1, 2 & 3) with new datasets and explore how each additional level of mechanistic complexity added to these models improved the description of patterns in COS exchange observed across a range of soils varying widely in biogeochemical properties. This step is especially necessary if we are to evolve models that can be parameterised robustly for different biomes or soil types whilst retaining a structure that can still be simply implemented in large-scale land surface models. With this in mind our team developed an experimental system to test a number of the hypotheses presented in the models above. However, it became clear that we would need to develop a method to isolate simultaneously COS hydrolysis

rates from COS production rates in soils. The first and most convenient method we explored was initially proposed by Whelan et al., 2016 and consisted of measuring net COS fluxes when the soil was moist then allowing the soil to dry out completely. Thereafter, the net COS flux would be re-measured from the exact same dry soils. By drying the soils it was assumed that the activity of CA would be negligible and thus any residual COS flux could be attributed to the production process. However, as it was still not clear whether the source of COS was caused by an abiotic or biotic mechanism we also developed another method that would allow the net COS flux to be partitioned even when soils were humid (Conrad and Meuser, 2000; Kaisermann et al., 2018b) (Fig 2.5).

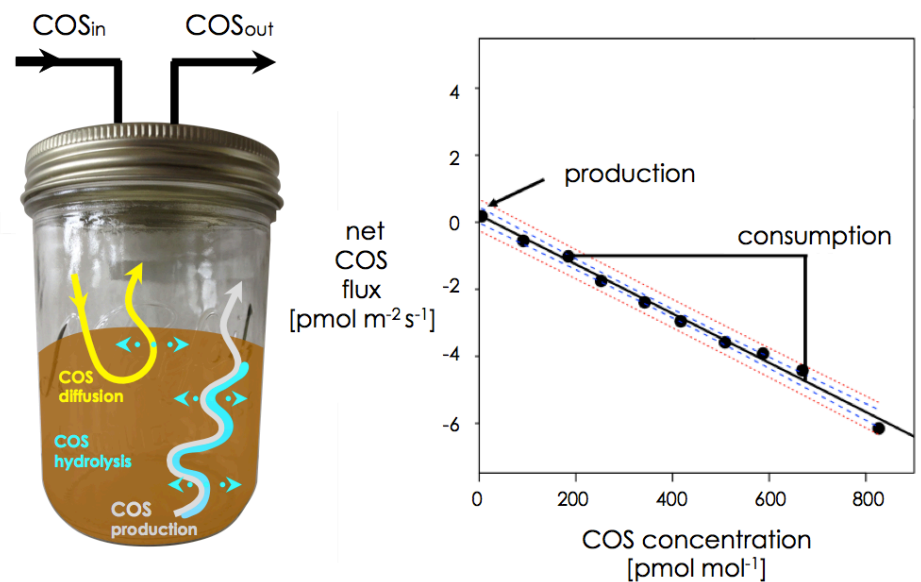


Figure 2.5 Relationship between the net COS flux and COS concentration measured in a soil microcosm demonstrating how the slope of this relationship yields an estimate of the hydrolysis rate whilst the production rate is estimated from the net COS flux measured or predicted at a COS concentration = 0 pmol mol⁻¹ (Kaisermann et al., 2018b).

To test these methods I became involved in two separate studies. The first study was conducted by our team in Bordeaux and involved measuring soils collected from a range of biomes and land uses across Europe and Israel (Fig. 2.6). In addition, I also began to collaborate with Drs. Laura Meredith and Mary Whelan on a second study being conducted across a range of sites in the USA and Cambodia. The European soil study partitioned COS production and hydrolysis rates using both approaches described above for dry and moist soils (Kaisermann et al., 2018b) (Fig. 2.7). Whereas the US study only employed the dry soil partitioning approach (Meredith et al., 2018a; 2018b). Results from these two studies first of all indicated that the COS production rates estimated using the two approaches (moist vs dry) were consistent with one another, strongly indicating that soil moisture did not appear to play a significant role in the COS production process (Fig. 2.7) (Kaisermann et al., 2018b).



Figure 2.6 Spatial distribution of soils measured to assess the spatial variability of soil COS hydrolysis, production and net COS flux (Kaisermann et al., 2018a; 2018b; Meredith et al., 2018a; 2018b).

On the other hand the soil COS hydrolysis rate was very sensitive to soil moisture content. Both datasets from the US and European studies indicated that soil net fluxes were highly variable across biome and land use. Both studies also confirmed that in general COS production rates were relatively smaller than the COS hydrolysis rates measured on the same soils (Fig. 2.8)(Kaisermann et al., 2018b; Meredith et al., 2018a). The only soils that did

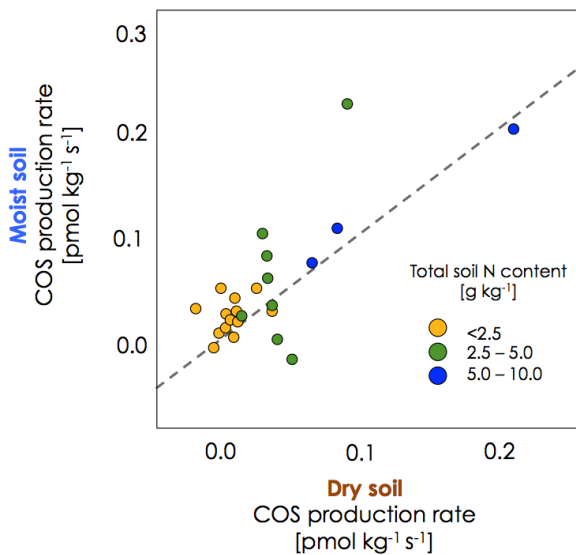


Figure 2.7 Comparison of COS production rates measured from dry or moist soils (Kaisermann et al., 2018b)

not emit detectable COS emissions were those collected from the deserts around Utah (Kaisermann et al., 2018b; Meredith et al., 2018a). Interestingly we also found that the temperature sensitivity of the COS production rate was similar in the two independent studies (mean $Q_{10} \sim 2.7$ for the dry soil only study ($n=20$) (Meredith et al., 2018a) and the moist soil experiment ($n=27$) (Kaisermann et al., 2018b). The temperature response of the soil COS production rate was much larger and more variable than for the COS hydrolysis rate measured on the same moist soils ($Q_{10} \sim 1.2$ ($n=27$) (Kaisermann et al., 2018b). Indicating that changes in soil temperature over the course of the day or season would have very different effects on the component fluxes. This also indicated that if soils were becoming droughted over the season often the case in Mediterranean and semi-arid regions they would most likely turn from being net COS sinks during the wet season to net COS emitters as hydrolysis rates decreased and soil temperatures increased. However, it became clear that it was also important to understand from this dataset what underpinned the variability in COS production and hydrolysis rates from site to site.

To investigate this each of the soils measured in the two studies for COS gas exchange were also analysed for a suite of other soil physical, chemical and biological characteristics. From these datasets we initially found that microbial biomass N was most strongly correlated with the COS hydrolysis rates measured across the 27 European soils whilst COS production rates were most strongly correlated to total soil N content (Figs. 2.7 & 2.9) (Kaisermann et al., 2018b). This was especially apparent at sites conducting *in situ* fertilisation manipulations such as at the grassland Laqueuille in France or in the Scots pine forests of northern Sweden (Fig. 2.9).

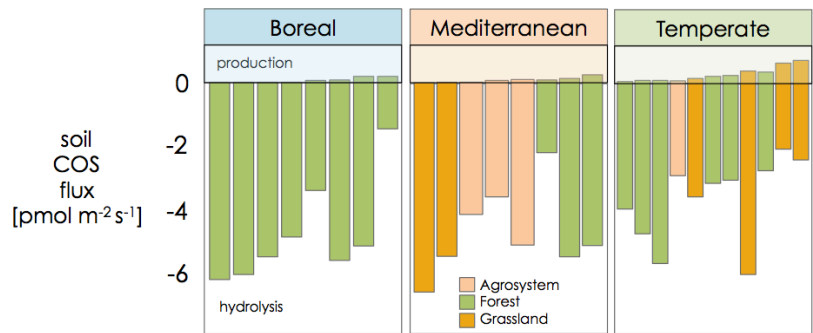


Figure 2.8 COS hydrolysis and production rates measured on moist soils (30% WHC) at 18°C collected from 27 European and Israeli flux sites (Kaisermann et al., 2018b).

2.4 THE IMPORTANT ROLE OF NITROGEN ON THE NET COS FLUX

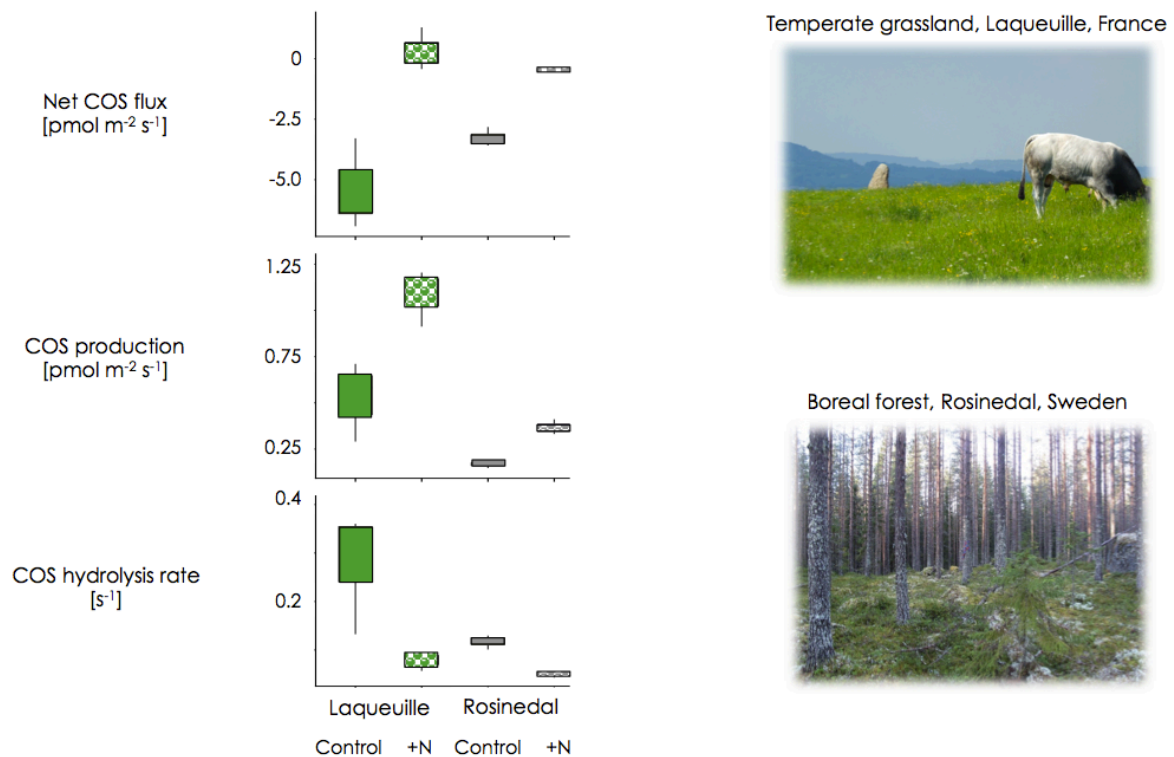


Figure 2.9 Variations in COS hydrolysis, COS production and net COS fluxes from soils collected from control and N fertilised plots in the same ecosystems (Kaisermann et al., 2018a).

Our survey results indicated that nitrogen fertilised sites tended to exhibit lower hydrolysis rates than control sites and relatively higher COS production rates in fertilised soils compared to control soils (Fig. 2.9). Overall this tended to reduce the sink strength of soils for atmospheric COS. We tested this further with additional experiments including a fertilisation experiment whereby NH_4NO_3 was added to sieved and re-packed soils and a greenhouse experiment that consisted of growing sapling trees of different species in the same artificial soils. The

lab study on soil microcosms confirmed that N fertilisation always caused COS hydrolysis rates to decrease whilst causing COS production rates to increase reducing the net COS flux significantly (Fig. 2.10). In the greenhouse study we also found that over time as the different plant species grew in the potted soils they differentially changed the inorganic N content of the soils and at the same time the net COS flux (Kaisermann et al., 2018a; in prep). Thus all of these studies indicate that in general changes in the COS hydrolysis and production rates are dependent on the N status of the soil. In addition, the COS response of any particular soil to further additions of inorganic N appears to be dependent on the amount of total inorganic N in the soil prior to fertilisation, such that soils very low in inorganic N tend to exhibit the largest relative change in their component COS fluxes, whilst soils that already contain large amounts of inorganic N are less responsive (Kaisermann et al., 2018a). The causes for these shifts in COS production or hydrolysis rates are not proven as yet. However, at least for the hydrolysis rate it is known that NO_3^- ions are inhibitors of CA activity in wide range of organisms (Del Prete et al., 2015; Peltier et al., 1995). This occurs as NO_3^- ions can bind to the active site of CA and thus inhibit enzyme regeneration and putatively COS hydrolysis.

In the case of COS production the mechanism linking the N and S cycling still remains cryptic. However, a recent study by Meredith et al. (2018a) may shed some light on this process. Using a novel metatranscriptomic approach, Meredith et al. (2018a) found that the Q_{10} of the COS production rate across a range of soils was strongly correlated to the number of cystine and methionine biosynthesis genes present in soils (Fig. 2.11). These amino acids have been identified previously as COS precursors and can represent a large fraction of the total soil S pool (11-31%) (Morra and Dick, 1985). Thus current interpretation of this experimental finding might indicate that as inorganic N concentrations in soils increases, an increase in S-containing amino acid biosynthesis

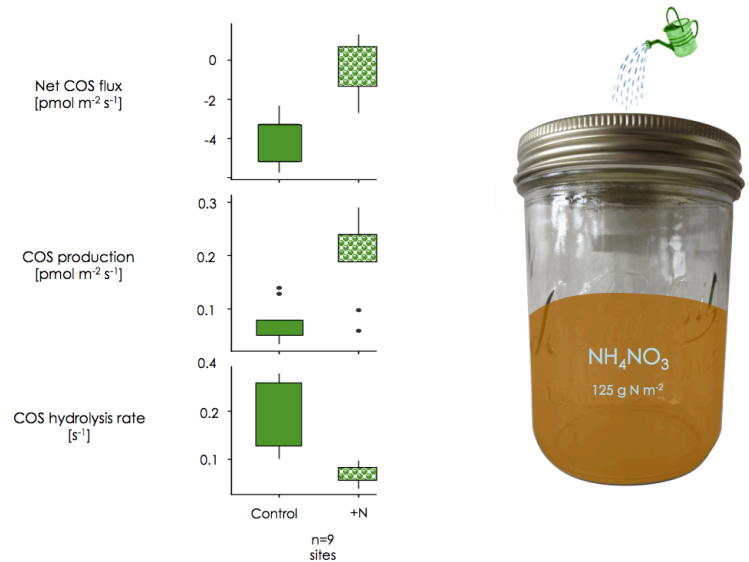
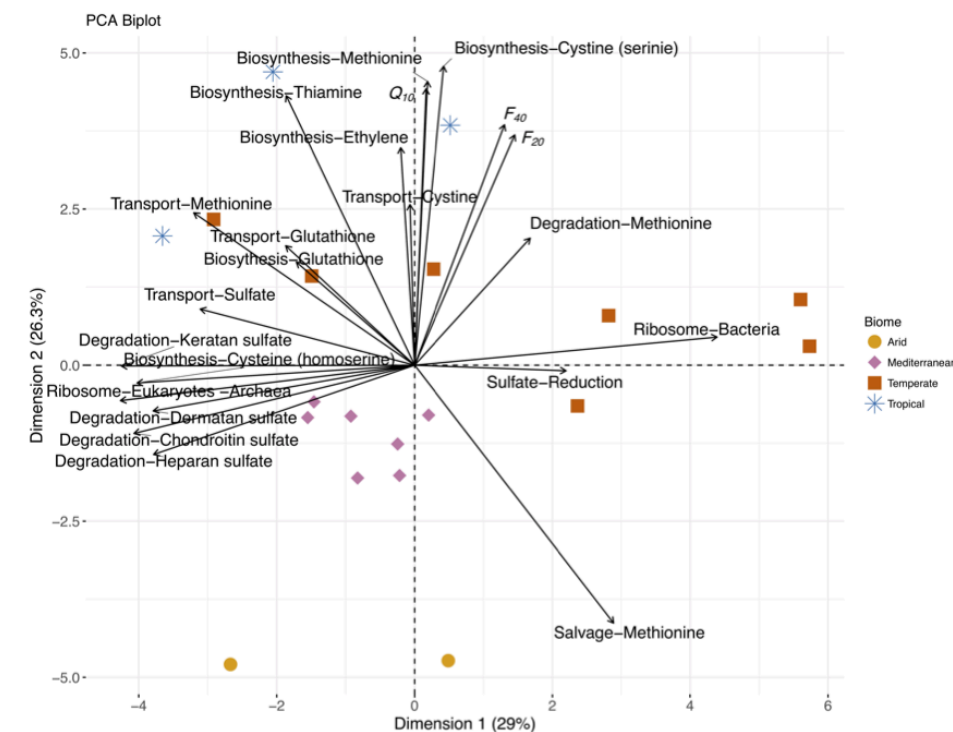


Figure 2.10 Variations in COS hydrolysis, COS production and net COS fluxes from soils collected from control and N fertilised plots in the same ecosystems (Kaisermann et al., 2018).



might be hypothesised. In turn as the concentration of S-containing amino acids increased, the pool of COS precursors would also become larger. Collectively, this would lead to an increased COS production rate as the precursor pools were either abiotically or biotically degraded. Ideally future studies designed to test this hypothesis directly and determine how the size of this precursor pool changes with N additions would present a logical next step.

Figure 2.11 Patterns of relatedness of S-cycling pathways and ribosomal phenotypes for each sample site PCA of predicted microbial sulphur pathways for each site (Meredith et al., 2018a).

From this body of experimental work presented above a clearer picture is now emerging of the main drivers of soil-atmosphere COS exchange. Synthesising all the existing studies that have measured both soil COS production rate and N content (Fig. 2.12), it is now possible to determine a pedotransfer function that will predict soil COS production rates with information on the total N content of a soil and its temperature. The next logical step will now consist of implementing this empirical knowledge to predict the soil-atmosphere exchange of COS across the land surface, however, this will first require knowledge of how soil N content varies across the soil surface. Working with colleagues amongst the carbon cycle research community should help achieve this goal in the near future.

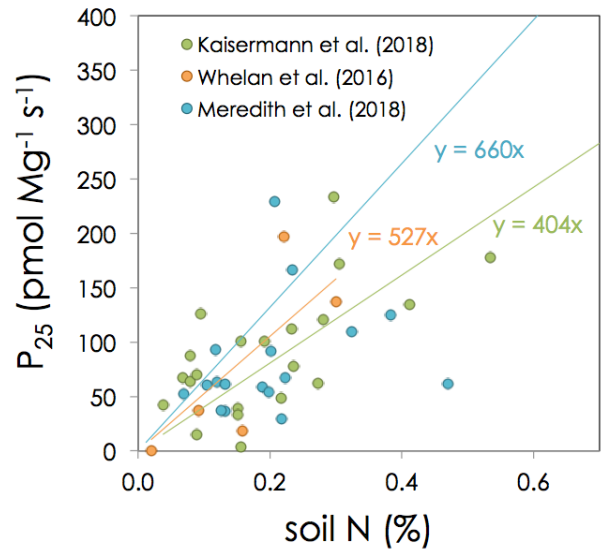


Figure 2.12 Relationship between the nominal COS production rate at 25°C with soil N content measured in three independent studies.

2.5 POTENTIAL TO MODEL SOIL COS FLUXES AT THE GLOBAL SCALE

Ultimately my aim will now be to test these newly developed empirical and mechanistic models of soil COS exchange in a COS-enabled global model. In this context we have been working with the MECBETH global model (Cuntz, 2003) (Fig. 2.13). We initially chose this model to work with, as it is one of the only isotope-enabled models that can also predict the oxygen isotope composition of atmospheric CO₂. As COS hydrolysis and the oxygen isotope exchange of CO₂ are both catalysed by the same enzyme CA this model was the most logical choice for running model experiments with new theories to provide constraints on the COS and CO₂ mass budgets at large scales. Thereafter, my long-term goal would see the tracer COS become fully integrated in the current generation of LSMs and used alongside CO₂ to monitor and predict changes in the function of the land biosphere C sink. Finally, with this new understanding we can now start to constrain with more confidence the role of natural and managed soils in the global COS mass balance and in turn reduce uncertainties on the magnitude of COS currently taken up by vegetation.

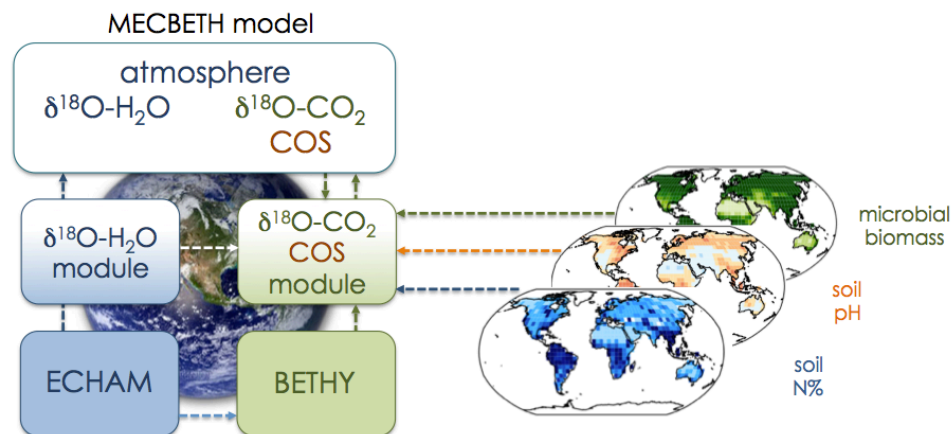


Figure 2.13 Next step to model COS exchange in the atmosphere using the MECBETH model and different fields describing the spatial distribution of microbial biomass, soil pH and soil N content across the land surface.

PART III : FUTURE RESEARCH

THE ROLE OF EARTH'S MYCELIAL COMMUNITY AND ENZYME ACTIVITY ON GLOBAL ATMOSPHERIC CO₂, COS AND CO¹⁸O BUDGETS

3.1 MYCORRHIZAL FUNGI AND THE TERRESTRIAL CARBON SINK

As CO₂ steadily accumulates in the planet's atmosphere many ecosystems are readily allocating carbon (C) to biomass whilst others display limited response (Ellsworth et al., 2017; Norby et al., 2017; Terrer et al., 2016). The ability of different ecosystems to store C is intimately coupled to the cycling of key nutrients such as nitrogen (N) and phosphorus (P) in soils facilitated by symbiotic relationships between plants and mycorrhizal fungi (Terrer et al., 2016). Presently it is understood that gymnosperms (~200 Mya) and more recently (~100 Mya) certain angiosperms (Fagales) evolved symbiotic relationships with ectomycorrhizal fungi (EM) (Maherali et al., 2016) that conferred these plants with an advantage when atmospheric CO₂ concentrations were higher than the present day (Franks et al., 2013) and in areas where soil organic matter has high C:N ratios with complex secondary metabolites such as lignins or tannins (Read, 1991). It has been shown that in these conditions EM-associated plants can more readily convert increasing atmospheric CO₂ into above and belowground biomass (Fig 3.1). In contrast, plants that form symbiotic relationships with arbuscular mycorrhizal fungi (AM), that usually grow in areas where soil organic matter (SOM) and litter C:N ratios are relatively low, tend to respond less readily to increasing CO₂, unless nutrients are available (Fig. 3.1)(Beerling et al., 2011; Read, 1991; Terrer et al., 2016). Based on this simplified EM/AM binary view, some studies suggested that boreal and temperate ecosystems, dominated by plants associated to EM fungi, should be more adapted to stock C in biomass in response to rising CO₂ than tropical regions where AM fungal associations dominate (Beerling et al., 2011; Terrer et al., 2016).

The ability to map variations in belowground mycorrhizal activity and biogeochemical cycling still represents a major challenge in the modelling of Earth system dynamics. This is probably the reason why, to date, the role of mycorrhizal associations on the future C cycle has not been evaluated in any of the IPCC Coupled Model Intercomparison Projects [see (Friend et al., 2014) for CMIP5 model descriptions and simulations]. **Given the growing evidence for a critical link between the capacity of certain ecosystems to sequester more C than others in response to rising CO₂ and mycorrhizal partnership, more studies are required to help implement the underlying mechanisms into current land surface models (LSM) and improve our future climate predictions.**

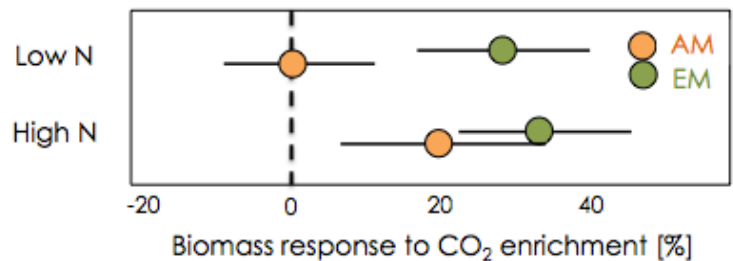


Figure 3.1 Growth response of ectomycorrhizal (EM) and arbuscular (AM) mycorrhizal associated plant total biomass to elevated CO₂ and nitrogen fertilisation (adapted from Terrer et al., 2016).

3.2 MYCORRHIZAL FUNGI DRIVE LARGE-SCALE CHANGES IN SOIL PH

The relationships between plants and mycorrhizal fungi also impact critical soil processes including soil aggregation (Berner, 2003; Rillig and Mummey, 2006) and chemical weathering rates (Berner, 2004; Taylor et al., 2011; 2012; 2009). In particular, the weathering rate of soil minerals such as silicates and carbonates are strongly controlled by soil pH that can be modified by root-fungal symbioses and variations in plant net primary productivity (NPP) (Beerling et al., 2011; Taylor et al., 2011; Thorley et al., 2014). Current theory posits that, as CO₂ concentrations in the atmosphere continue to build and photosynthetic activity is stimulated, plants should have more available C not only to invest in plant and fungal biomass but also to synthesise more organic acids and enzymes that could acidify soils and enhance soil mineral dissolution (Beerling et al., 2011; Berner, 2004; Read, 1991; Taylor et al., 2009). Ectomycorrhizal fungi are known to have a greater capacity than AM fungi to lower soil solution pH in the mycorrhizosphere *via* the exudation of organic acids, the exchange of protons during N uptake and the increase in belowground respiration degassing more CO₂ in the soil atmosphere (Raven and Smith, 1976; Taylor et al., 2009) (Fig. 3.2).

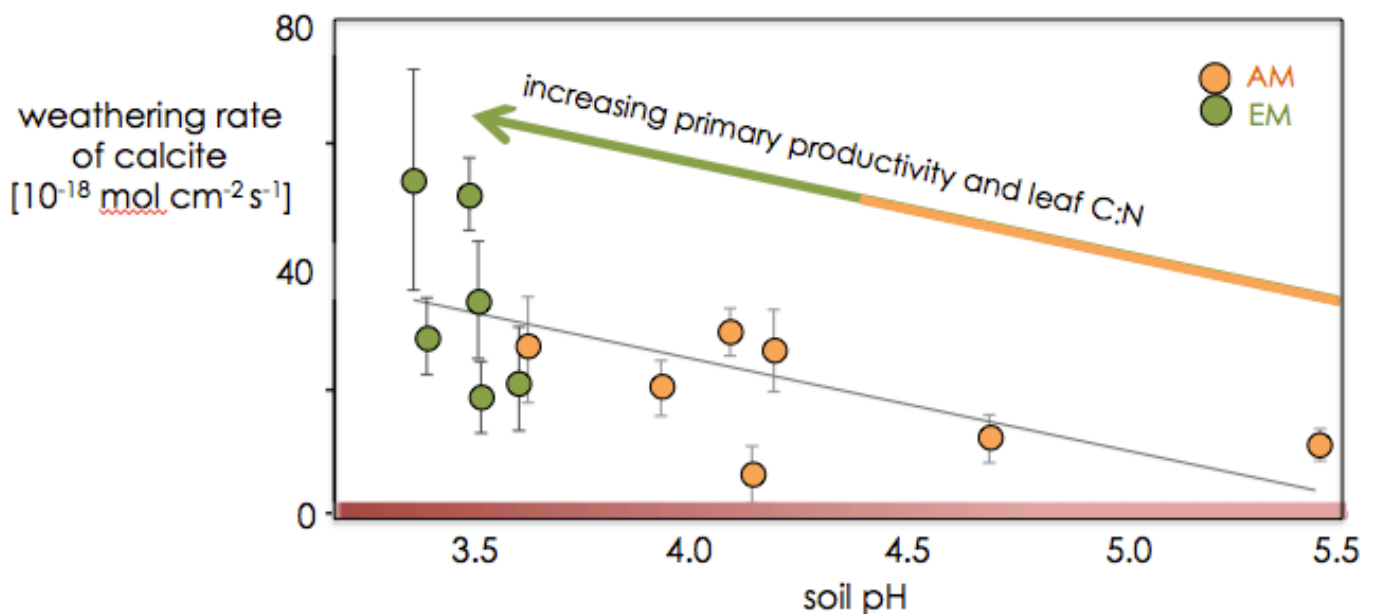


Figure 3.2 Rate of calcite weathering as soil pH varies with shifts in the dominance of ectomycorrhizae (EM) or arbuscular mycorrhizae (AM) in the hyphosphere community as CO₂, NPP and leaf C:N increases (adapted from Thorley et al., 2015).

Understanding why EM fungi have a greater ability to thrive in acidic conditions and exert higher weathering rates is thus important for C cycle studies (Pagani et al., 2009; Beerling et al., 2011). This is because the enhanced dissolution of continental carbonates and silicates by fungi and plants consumes atmospheric CO₂ and thus drives long-term feedbacks on atmospheric CO₂ concentrations (Berner, 2004; Taylor et al., 2009). For example, this mechanism has been advanced to explain variations in atmospheric CO₂ in the geological past and is thought to have maintained atmospheric CO₂ levels above ~200 ppm during the Miocene (18-5Mya) (Siegenthaler et al., 2005; Pagani et al., 2005; Luthi et al., 2008; Pagani et al., 2009). More recently, thought-experiments have indicated that enhancing this CO₂ sequestration mechanism through the use of mineral fertilisation might help reduce and stabilise future atmospheric CO₂ concentrations (Taylor et al., 2015). However, the logistics of implementing this CO₂ removal (CDR) scheme were initially deemed implausible as many of the Earth's basalt deposits are located in areas outside the regions of highest weathering potential i.e. the tropics. Nonetheless, a recent review detailing the advantages and disadvantages of this CDR scheme across temperate agricultural sites

demands reconsideration and a call for novel experimental evidence across temperate managed and natural systems (Beerling et al., 2018). In addition, I would add to this debate that for this CDR mechanism to be efficient there will be a need to understand better the optimal plant-mycorrhizosphere-enzyme composition that promotes the most efficient weathering rates.

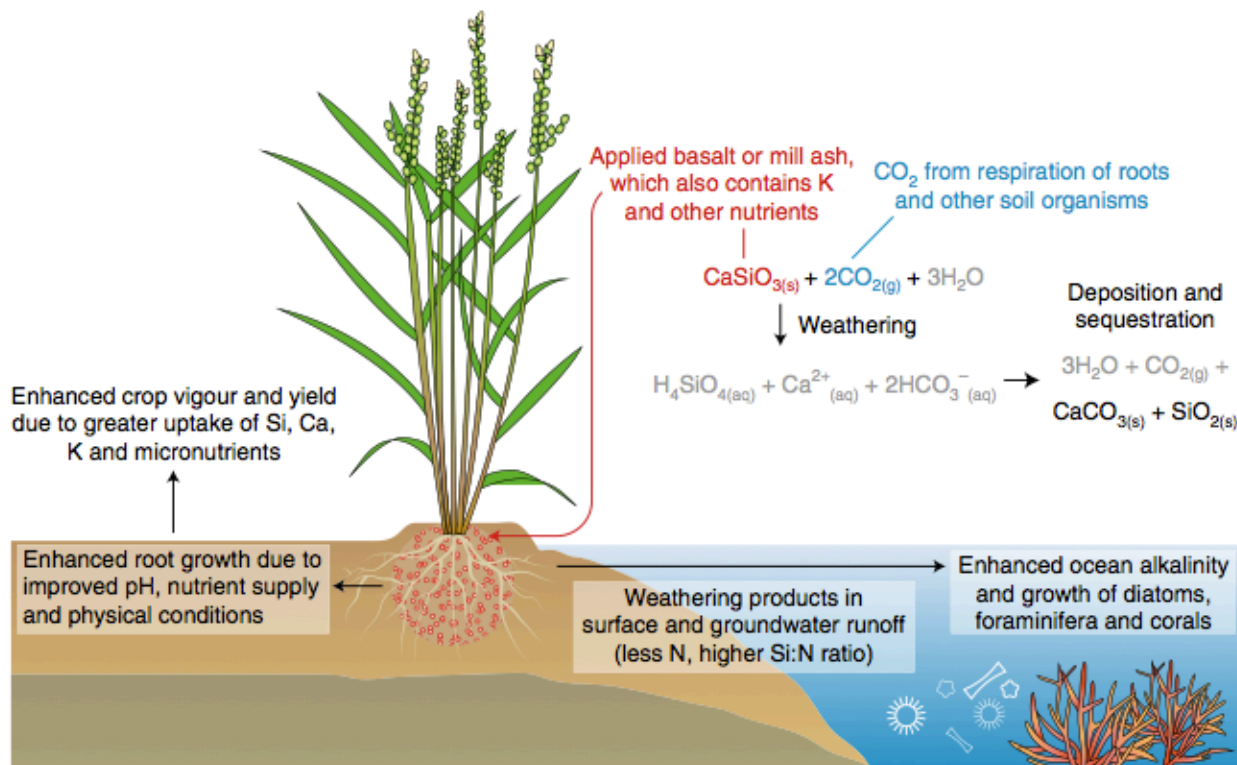


Figure 3.3 Summary of how fertilisation with silicate-rich wastes or basalts is hypothesised to improve crop nutrition, CO₂ removal from the atmosphere and ocean alkalinity (taken from Beerling et al., 2018).

3.3 WHAT IS THE ROLE OF CARBONIC ANHYDRASE DURING WEATHERING?

The acidification of the mycorrhizosphere is assisted by a suite of enzymes that promote the liberation of essential nutrients from soils whilst at the same time, protecting the micro-organisms from extreme variations in internal pH (Hesse et al., 2002; Krulwich et al., 2011; Penalva and Arst, 2002; Raven and F. A. Smith, 1976; Read, 1991; Sanders, 1982). In this respect, the carbonic anhydrases (CA) are a widespread family of metallo-enzymes as described previously (Fig 3.4) that play a crucial role in enabling certain phylum of bacteria and fungi to flourish in extreme pH environments (Krulwich et al., 2011; Sauze et al., 2018; Wingate et al., 2009) and potentially enhance the rate of soil mineral weathering (Li et al., 2005; 2008; Müller et al., 2013; Thorley et al., 2014; Wingate et al., 2008b). This is because rapid variations in CA activity can redress imbalances in C supply and pH within cells through the reversible interconversion of $\text{H}_2\text{O} + \text{CO}_2$ to $\text{HCO}_3^- + \text{H}^+$ (Krulwich et al., 2011; Smith and Ferry, 2000). Evidence from a growing number of fungal genome databases indicate that previously identified α - and β -CA gene sequences (and putative homologue genes) exist in a range of fungal species, with β -CAs being expressed in the cytosol and mitochondria of fungi and α -CAs in fungal secretions (Bahn et al., 2007; Elleuche, 2011; Elleuche and Pöggeler, 2009) (Fig. 3.4). However, although CA gene sequences exist in fungal genomes, there is no study reporting expression levels for these genes in the hyphosphere and how this varies with plant productivity and soil weathering. Obtaining empirical estimates of mycorrhizal CA activity is a necessary step to explore its role on the rates of soil acidification, mineral weathering and CO₂ uptake. At the

same time this could also help understand some of the functional differences between EM and AM fungal traits and perhaps shed light on the very process of mycorrhization itself.

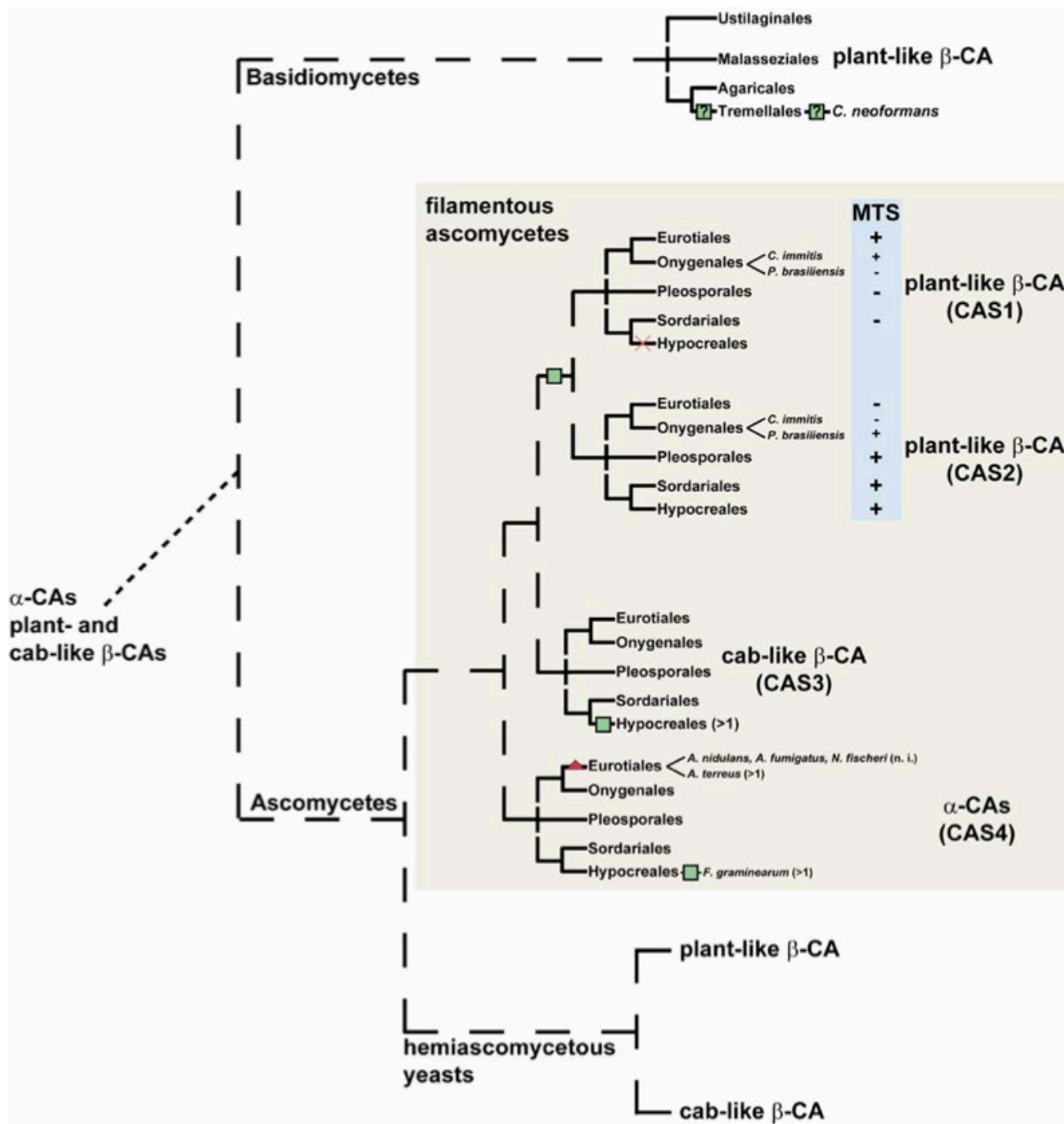


Figure 3.4 Distribution of different CA genes across the fungi. Green boxes represent gene duplications, red crosses represent gene loss events and red triangles represent putative horizontal gene transfers. Tree taken from Elleuche & Poggeler, 2009 and adapted from Hibbett et al. 2007

3.4 CAN FUNGI IMPACT ATMOSPHERIC TRACERS OF PHOTOSYNTHESIS?

As described previously, during CA-catalysed CO₂ hydration, an oxygen isotope exchange occurs between CO₂ and the different water pools within ecosystems (Jones et al., 2017; Meredith et al., 2018b; Sauze et al., 2018; Wingate et al., 2010a; 2009; 2008b). Atmospheric budgets of CO¹⁸O can thus be used to constrain the magnitude of land photosynthesis (GPP) at large scales, provided we understand the spatial and temporal variability of CA in soils (Welp et al., 2012; Wingate et al., 2009). Recently, our team has made a considerable breakthrough in developing a mechanistic framework to predict how soil CA activity varies across the land surface with variations in soil pH, moisture and microbial biomass (Jones et al. 2017; Sauze et al., 2017, 2018; Wingate et al., in prep) (Fig. 3.5). This novel understanding has now been implemented in an isotope-enabled global model to interpret variations in the atmospheric CO¹⁸O concentration (Wingate et al. in prep).

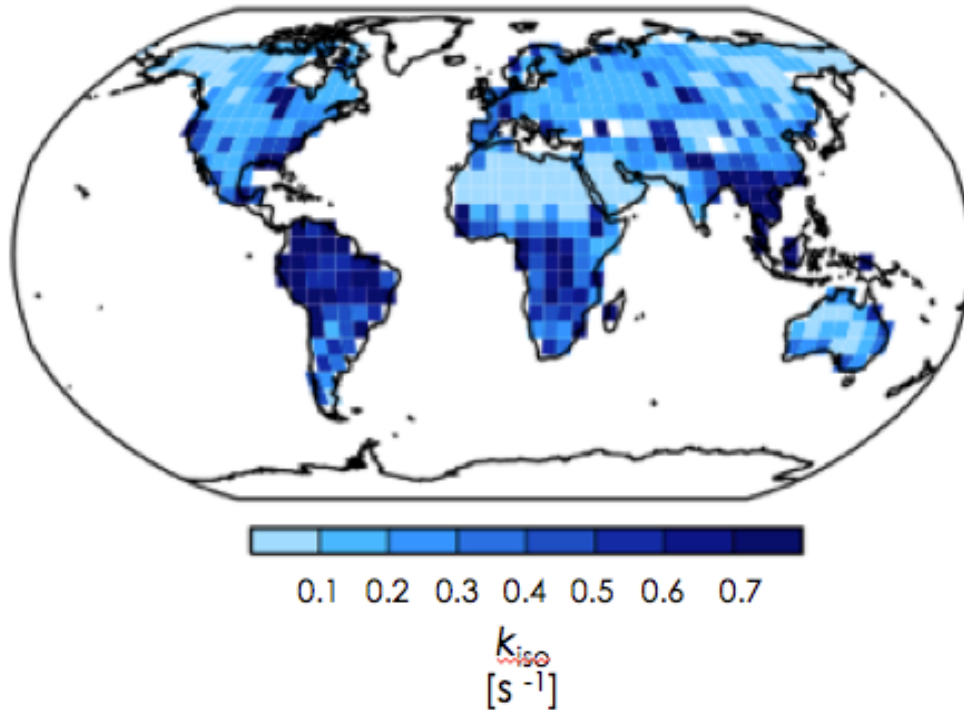


Figure 3.5 Variability in ‘soil community’ CA activity (k_{iso}) predicted across the land surface (Wingate et al., in prep).

However, although these new estimates of CA activity represent a significant advance in our ability to describe the enzymatic function of soil microbial communities, the current model may under-represent the contribution of mycorrhizal fungi to soil CA activity. This is because our new model is based on empirical evidence from sieved, re-packed soils primarily reflecting the function of bacterial, algal and saprotrophic fungal community members but not mycorrhizal fungi, as it is known that soil disturbance, sieving and mixing is detrimental to mycorrhizal hyphae (Jasper et al., 1989; Read, 1991). Thus there is a need to quantify the CA activity of soils containing ‘undisturbed’ mycorrhizal hyphae to complete our framework of how soil CA activity varies spatially in different ecosystems. Furthermore, it is currently unknown whether changes in the CA activity of mycorrhizal fungi in response to changes in CO₂ concentrations and net primary productivity will be significant enough to be imprinted on the atmosphere.

3.5 ARE MYCORRHIZAL FUNGI REGULATORS OF ATMOSPHERIC COS?

As described above carbonic anhydrases also catalyse the hydrolysis of carbonyl sulphide (COS) (Protoschill-Krebs and Kesselmeier, 1992) and drive the large seasonal removal of COS from the atmosphere during the summer months of the northern hemisphere (Fig. 1.2) (Montzka et al., 2007; Whelan et al., 2018). This seasonal variability in the atmosphere is dominated by the consumption of COS by CA in leaves (Campbell et al., 2017; Gimeno et al., 2017; Sandoval-Soto et al., 2005; Seibt et al., 2010; Whelan et al., 2018). However, an extensive survey of soils conducted by our team and collaborators in Europe and the US has shown that soils also represent an important sink for COS because many micro-organisms contain CAs and can metabolise COS (Kaisermann et al., 2018b; Meredith et al., 2018b; Ogée et al., 2016; Sauze et al., 2017; Whelan et al., 2018). In particular, there is growing evidence that soil fungi are important players of this COS uptake (Bunk et al., 2017; Masaki et al., 2016; Meredith et al., 2018b; Sauze et al., 2017). Recent soil microcosm experiments conducted by members of my team have observed that as the number of fungal 18S gene copies increased on a range of soils there was a significant increase in soil COS uptake and the associated soil CA activity (Fig. 3.6). This indicated that, at least for saprotroph-dominated fungal communities, an increase in fungal abundance led to a stronger uptake of COS from the atmosphere. So far no empirical dataset that quantifies the role of EM or AM fungi on soil-atmosphere COS exchange rates exist. However, based on current knowledge, mycorrhizal COS fluxes are likely an important missing component of the global COS budget. Thus it is now important to establish whether mycorrhizal fungi are strong consumers of COS and whether positive interactions between plant and hyphal biomass production enhance the consumption of atmospheric COS by soils.

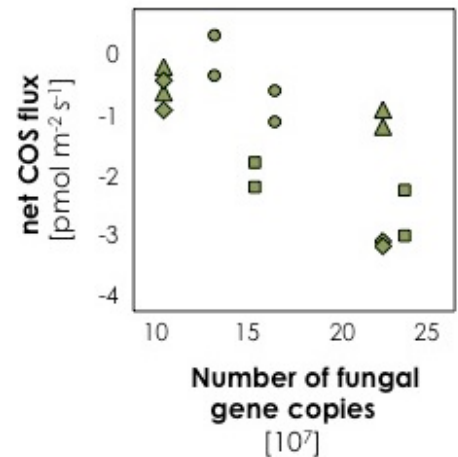


Figure 3.6 Variations in net COS flux and number of fungal (18S) gene copies (adapted from Sauze et al., 2017).

3.6 PREDICTING THE IMPACT OF FUNGAL CA ON THE ATMOSPHERE

In order to model the impact of hyphosphere CA on atmospheric tracers an estimate of the spatial distribution of AM and EM mycelial networks is required. There is growing evidence that mycorrhizal associations could be ‘trait integrators’ of above- and belowground community members and function (Austin et al., 2014; Fisher et al., 2016; Lin et al., 2016). For example leaf traits such as C:N ratio and lignin content are intimately coupled with the structure and metabolic activity of belowground decomposer consortia (Austin et al., 2014; Lin et al., 2016). This coupling may have evolved to ensure that the timing and quality of leaf litter inputs from the ‘host’ plant favours a particular belowground consortium, tailored to the needs of the host species, particularly nutrient exchange and protection from pathogens (Margulis, 1998; Read, 1991). In this context a recent study has indicated that remotely-sensed vegetation spectral reflectance indices and canopy growing season length are strongly correlated to mycorrhizal association and can be used to differentiate AM- from EM-dominated forest plots (Fig. 3.7) (Fisher et al., 2016). This study opens up an exciting opportunity to remotely-sense mycorrhizal associations from space and scale fungal-biogeochemical interactions within large-scale models spatially and temporally (Soudzilovskaia et al., 2017; Taylor et al., 2009; Terrer et al., 2017). However, it is currently not clear how stable these leaf spectral and phenological traits will remain in the face of rising temperatures, drought and atmospheric CO₂. For example, it is well known that interannual variability in air temperature and drought drive strong variations in the length of the growing season across the Earth’s surface (Pachauri et al., 2014; Wingate et al., 2008b).

Furthermore, increases in atmospheric CO₂ concentrations may increase leaf C:N ratios and leaf lignin and tannin contents (Gifford et al., 2000; Gill et al., 2002; Niklaus et al., 2003; Poorter et al., 2005). This not only makes leaf litter harder to breakdown, thus favouring EM fungi, but it also protects the plant from increases in insect herbivory also predicted to rise with CO₂ concentrations (Currano et al., 2008; DeLucia et al., 2008). Because tannins reflect wavelengths in 'brownier' spectral regions (Ferber et al., 2006; Lehmann et al., 2015), leaves may start to appear browner from space in the future if this effect is widespread and CO₂ concentrations and leaf herbivory increase. However, not all plant species synthesise tannins or lignin to the same extent. Many important AM forest species exhibit much lower tannin and lignin contents than EM plants (Harrison, 1971; Kubitzki and Gottlieb, 1984; Lin et al., 2016; Mole, 1993). Leaf lignin and tannin contents may thus be important leaf traits that could be used to map variations in AM and EM mycorrhizal associations and help develop an improved representation of mycorrhizal fungi and their function in dynamic vegetation and biogeochemical models.

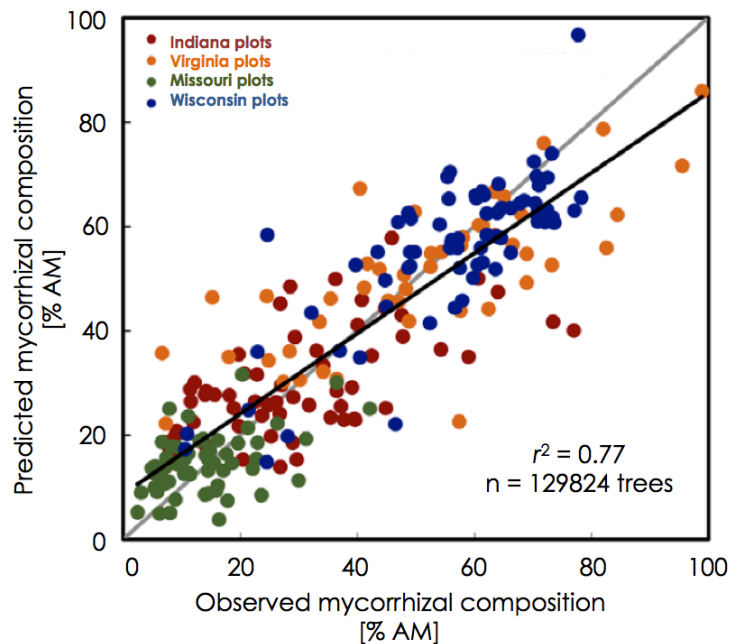


Figure 3.7 Predicted vs observed percentage of AM associated trees in a suite of 60m plots in 4 research forests located in the USA (adapted from Fisher et al., 2016).

3.7 RESEARCH OBJECTIVES AND HYPOTHESES FOR THE FUTURE

Based on the knowledge gaps described above the overall goal of my future research will be to quantify EM and AM fungal CA activity for the first time and characterise how changes in CO₂ levels and N fertilisation can drive changes in fungal CA activity and soil weathering.

- My **first hypothesis** is that putative CA gene sequences identified in saprotrophic and mycorrhizal fungal genomes can express CA proteins that result in detectable CA activities. Thus it is my aim to measure CA activity and gene expression levels of identified fungi under controlled conditions to test this hypothesis.
- My **second hypothesis** is that changes in plant productivity and hyphosphere pH are linked to variations in hyphosphere CA activity. By measuring CA activity on a range of inoculated AM and EM tree species with well-developed mycelial networks grown under different CO₂ concentrations I will challenge this hypothesis.
- My **third hypothesis** is that hyphosphere CA activity will be up-regulated in the presence of silicates in soils. Measuring hyphosphere CA activity, CA gene expression and pH for a range of AM and EM plant species grown with and without silicate aggregates will test this hypothesis.
- My **fifth hypothesis** is that leaf lignin and tannin contents and leaf spectral reflectance will vary in a predictive manner with CO₂ levels and EM or AM fungal associations. Meta-analysis of leaf chemical and spectral trait databases alongside manipulation measurements of leaf spectral reflectance and secondary metabolites on a range of plant species will test this hypothesis.

- A **final hypothesis** is that mycorrhizal fungi influence the global cycles of CO₂, CO¹⁸O and COS through variations in their CA activity. A theoretical framework based on soil characteristics, plant traits and biogeochemical understanding will be developed to test this hypothesis.

This modelling framework will improve the representation of plant-fungal relationships in global biogeochemical models describing the C cycle, its associated tracers (CO¹⁸O and COS) and the role of CA activity in soil weathering. Coupling such models with trait-based algorithms mapping the distribution of EM and AM fungi across the land surface, will provide a ground-breaking framework to predict and monitor changes in the function of the biosphere using atmospheric tracers and spectral signals measured at the Earth's surface.

3.8 REALISING THIS RESEARCH OVER THE NEXT 5 YEARS

To achieve this ambitious research project considerable funding and investment will be required. In addition a multi-disciplinary team working in collaboration will need to be constructed. For this reason I have submitted an ERC Consolidator Grant called COSMYCA with the hope that the project will be able to bring together a group of talented researchers and engineers to confront this challenge. Aspects of this research topic could also easily form the basis of a competitive ANR or Regional proposal with vital collaboration envisaged between several INRA research units. This is something I have already begun to discuss and build with the researchers and platforms identified in Figure 3.8.

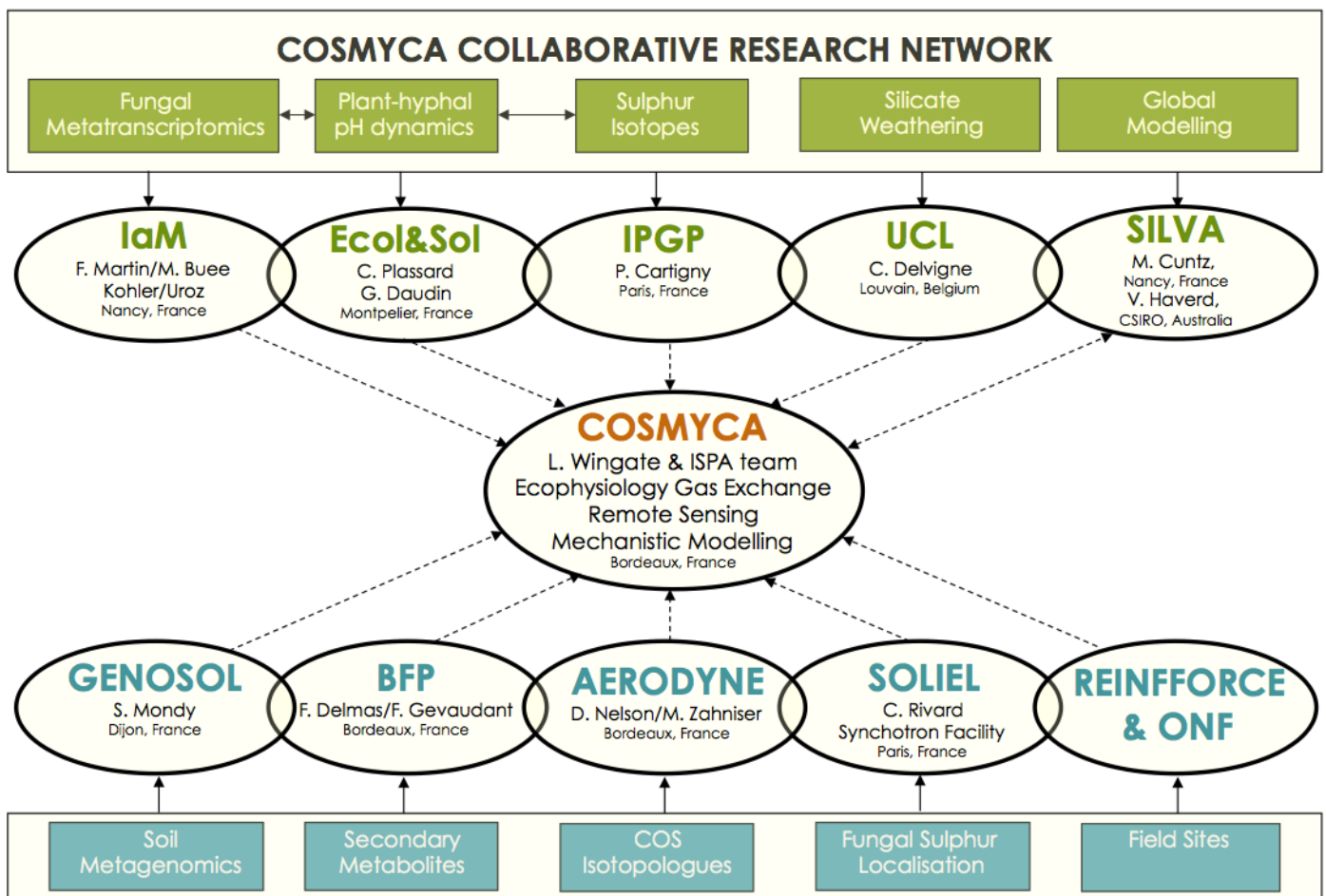


Figure 3.8 Research teams and infrastructures that I hope to interact and collaborate with on this research project.

This inter-disciplinary project will also draw on national and international expertise putting in place a number of new collaborations (Fig. 3.8). My future research project will aim to build a mechanistic bridge between the research fields of plant and fungal biochemistry, metagenomics, functional transcriptomics, biophysics, geochemistry, soil science, remote sensing, atmospheric physics and atmospheric chemistry. I furthermore believe this project is central to the mission of my host unit ISPA as the project touches many disciplines and is focussed on soil-plant-atmosphere interactions. I believe this research project and collaborative network is poised to make novel and state-of-the-art knowledge and models on topics that are of utmost political and intellectual relevance for today's society. In particular, I feel that this research could help advance our understanding of mineral weathering by trees and crops in temperate regions and help quantify the feasibility of fusing agroecology and geoengineering to reduce the CO₂ and GHG burden in the atmosphere.

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PART IV : CURRICULUM VITAE

4.1 PERSONAL INFORMATION

Lisa Wingate

Place of birth: Edinburgh, Scotland, UK
Date of birth: 13th March 1972
Nationality: Scottish
No. of children: 3 (Born 1993, 2007, 2012)

Researcher at INRA (**CR1**), UMR ISPA (formerly EPHYSE since 2012

UMR ISPA 1391, 71 Avenue Edouard Bourleaux, Villenave D'Ornon, 33140, France

Telephone : 33 (0)5 57 12 31

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Researchgate page: https://www.researchgate.net/profile/Lisa_Wingate

Web page: <https://www.bordeaux.inra.fr/ispa-ecofun/wordpress/index.php/people/lisa-wingate/>

Portrait:

French version: <http://jobs.inra.fr/A-la-une/Lauriers/Lauriers-2014/Lisa-Wingate-2014>

English version: <http://jobs.inra.fr/en/Headlines/INRA-Awards/2014-INRA-Awards/Lisa-Wingate-2014>

4.2 EDUCATION

Ph.D (2003) The University of Edinburgh, Edinburgh, Scotland

Supervisors : Prof. Paul Jarvis FRS & Prof. John Moncrieff

Subject: The contribution of photosynthesis and respiration to the net ecosystem exchange and ecosystem ¹³C discrimination of a Sitka spruce plantation.

B.Sc. (1998) The University of Edinburgh, Edinburgh, Scotland

Subject: **First Class Honours in Ecology and Environmental Science**

Thesis: Calibration of hemispherical photographic and beam transmittance techniques to measure leaf area index distribution in a *Picea sitchensis* (Bong.) Carr plantation.

4.3 PROFESSIONAL EXPERIENCE

European Research Council (ERC) Team Leader (2014-present), INRA-ISPA, Bordeaux, France

Subject: Carbonic anhydrase: where the global CO₂, H₂O and COS cycles meet

Chargée de Recherches 1ère classe (2012-present), INRA-ISPA, Bordeaux, France

Subject: Constraining the representation of photosynthesis and respiration in the terrestrial biosphere and its response to climatic change

Chargée de Conférences (2011-2015), Department of Plant Sciences, University of Cambridge, UK

Subject: Investigating environmental change and plant function using tree rings

Marie-Curie Intra-European Research Fellow (2011), INRA-Ephyse, Bordeaux, France/Project LATIS

Supervisor: Dr Yves Brunet

Subject: Linking the atmosphere and terrestrial biosphere carbon and water cycles using oxygen isotopes

NERC Advanced Research Fellow (2010-2011), Dept. of Plant Sciences, Univ. of Cambridge, UK

Subject: Linking the atmosphere and terrestrial biosphere carbon and water cycles using oxygen isotopes

Marie-Curie Intra-European Research Fellow (2009-2010), INRA-Ephyse, Bordeaux, France/Project LATIS

Supervisor: Dr Yves Brunet

Subject: Linking the atmosphere and terrestrial biosphere carbon and water cycles using oxygen isotopes

Postdoctoral Research Scientist (2009), INRA-Ephyse, Bordeaux, France/ANR Project MIST

Supervisor: Dr Jérôme Ogée

Subject: Modelling stable isotope signals in tree rings

Visiting Scientist (2007-2008), INRA-Ephyse, Bordeaux, France

Supervisors: Dr Jérôme Ogée (EPHYSE) & Prof. John Grace (Univ. of Edinburgh)

Subject: Measuring at high resolution the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of ecosystem CO₂ fluxes

Postdoctoral Research Fellow (2005-2008) School of GeoSciences, Univ. of Edinburgh/EU CarboEurope-IP

Supervisor: Prof. John Grace (Univ. of Edinburgh)

Subject: Assessment of the European Terrestrial Carbon Balance

Postdoctoral Research Fellow (2003-2005), School of GeoSciences, Univ. of Edinburgh/EU Project MIND

Supervisor: Prof. Maurizio Mencuccini (Univ. of Edinburgh)

Subject: Mediterranean terrestrial ecosystems and increasing drought

Visiting Scientist (2002), Max-Planck Institute for Biogeochemistry, Jena, Germany SPA¹³CE

Supervisor: Prof. Nina Buchmann (ETH, Zurich)

Subject: Investigating Soil-Plant-Atmosphere ¹³CO₂ exchange

4.4 ACADEMIC PRIZES AND DISTINCTIONS RECEIVED

Lauriers de l'INRA (2014), Prix de jeune chercheur

<http://jobs.inra.fr/A-la-une/Lauriers/Lauriers-2014/Lisa-Wingate-2014>

European Research Council Fellow (2014)

<http://jobs.inra.fr/A-la-une/Prix-et-distinctions/Bourse-ERC-2013-un-bon-millesime-pour-l-Inra>

INRA Fait Marquant (2011), INRA Dept. EFPA Fait Marquants for 2010

Subject: Suivi en temps réel des produits de la photosynthèse dans un écosystème forestier

<https://inra-dam-front-resources-cdn.brainsonic.com/ressources/afile/256190-d5d55-resource-faits-marquants-2010.html>

INRA Fait Marquant Majeur (2010), INRA Dept. EFPA Fait Marquants for 2009

Subject: Activité des micro-organismes du sol et bilan de CO¹⁸O

<https://inra-dam-front-resources-cdn.brainsonic.com/ressources/afile/256191-80d84-resource-faits-marquants-efpa-2009.html>

Natural Environment Research Council Advanced Fellowship Award (2009), University of Cambridge

<http://gtr.rcuk.ac.uk/project/F875FBFD-5B89-4765-BFC6-5E5EA5B2B6D6>

Honorary Fellowship Award (2009), School of GeoSciences, University of Edinburgh

<http://www.geos.ed.ac.uk/homes/lwingate/>

Marie Curie Intra-European Fellowship Award (2009), INRA-Ephyse, Bordeaux, France

http://ec.europa.eu/research/mariecurieactions/media-library/testimonials/index_en.htm

Best Conference Poster Award (2004), International SIBAE-BASIN Conference

Subject: Direct observations of environmental regulation on branch ¹³C and ¹⁸O discrimination in an old growth temperate forest (Prize: 1000 Swiss francs).

Outstanding Undergraduate Student Award (1996), University of Edinburgh

Subject: Climate and Water Resources (Prize: Medal)

Outstanding Undergraduate Student Award (1996), University of Edinburgh

Subject: Oceanography (Prize: Medal)

4.5 TEACHING ACTIVITIES

Chargée de Conférences (2015-2017), Sci. de la terre et environnement, écologie, Univ. of Bordeaux, France

Course: Spécialité Biodiversité et écosystèmes continentaux (MSc 2)

Subject: Investigating environmental change and plant function using tree rings

Chargée de Conférences (2014), Bordeaux Sciences Agro, Bordeaux, France

Course: Management forestier et logistique d'approvisionnement en bois (MSc 2)

Subject: Opportunities to investigate the functional phenology of ecosystems using a European Phenology Camera Network

Chargée de Conférences (2011-2015), Department of Plant Sciences, University of Cambridge, UK

Course: Responses to Global Change (Part II L2)

Subject: Investigating environmental change and plant function using tree rings

Invited lecturer (June 2014), Labex Côte International Summer School, Cadillac, France

Course: Transfer and Interactions between ecosystems

Subject: Using stable isotopes to link ecosystem processes to the global cycling of water and CO₂.

Invited lecturer (August 2010), The University of Gothenburg, Sweden

Course: European Stable Isotope Training Course

Subject: Principles of carbon isotope fractionation during photosynthesis and respiration.

Principles of oxygen isotope fraction during water cycling

Chargée de Conférences (2003-2009), School of GeoSciences, University of Edinburgh, UK

Course: Plant Ecophysiology (Hons. Course)

Subject: Using stable isotopes to study photosynthesis and respiration

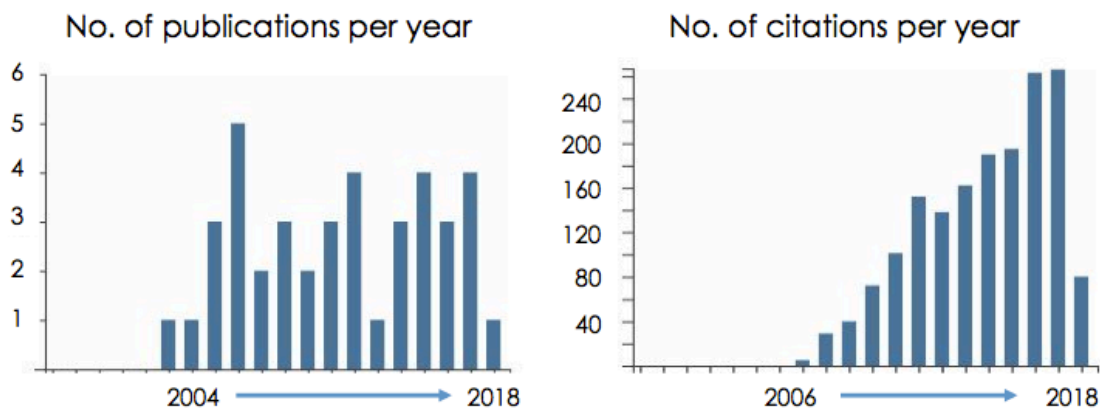
Course Demonstrator (1998-2003), School of GeoSciences, University of Edinburgh, UK

Subjects: Climate and Water Resources, Ecological Modelling, Plant Ecophysiology

Principles of Ecology, Environmental Science

4.6 PEER-REVIEWED PUBLICATIONS

Since obtaining my PhD I have published 45 scientific articles in a range of international peer-reviewed journals (ISI indexed) including Global Change Biology, PNAS, Nature Climate Change, ISME, New Phytologist, Biogeosciences, Tree Physiology, Global Biogeochemical Cycles, and JGR Biogeosciences amongst others and a peer-reviewed book chapter (Fig. 1.1 and Appendix I). For further details on my publications please refer to my complete list of scientific peer-reviewed publications at the end of this document in Appendix I.



(Sum of Citations 1693)

H index: 21

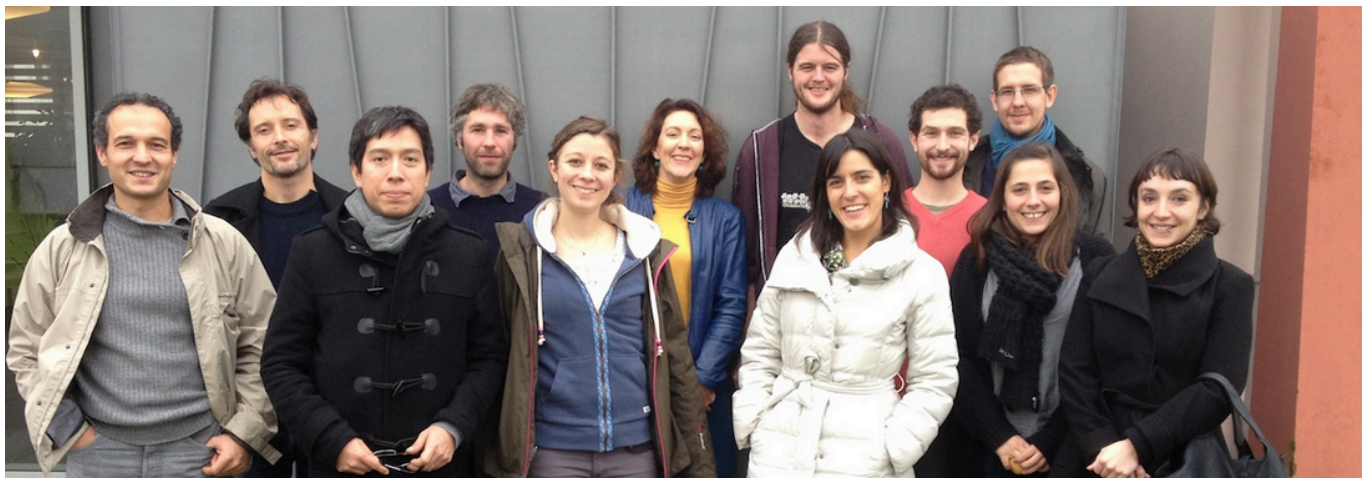
Figure 4.1 Publications in peer-reviewed indexed journals

4.7 STUDENT & STAFF SUPERVISION

Since January 2014 I have been a member of the ECOFUN team at the unit INRA UMR1391 ISPA. Within this new team I mentor a growing team of researchers that include the ERC SOLCA team and a number of Marie-Curie and Bordeaux Idex fellows (Figure 1.2) that study the interactions between water relations and ecosystem functioning. For further details on the research staff and students I have mentored please refer to Appendix II.



Figure 4.2 Organigramme of the ECOFUN team within the ISPA unit as at 1st August 2018 names in **bold** indicate those team mebers supervised by me.



In brief during the past 8 years, I have supervised 17 research staff and 20 students (6 PhD, 11 MSc & 3 BSc) on a range of research themes including:

- Linking photosynthetic activity to the anatomy and stable isotope composition of plants (Fig. 4.3)
- Understanding the activity of carbonic anhydrase in leaves and soils and its impact on predicting photosynthesis at large scales (Fig. 4.3)
- Using digital cameras to explore the climate-induced variability in phenological transitions and their link to photosynthesis and ecosystem CO₂ exchange (Fig. 4.3)

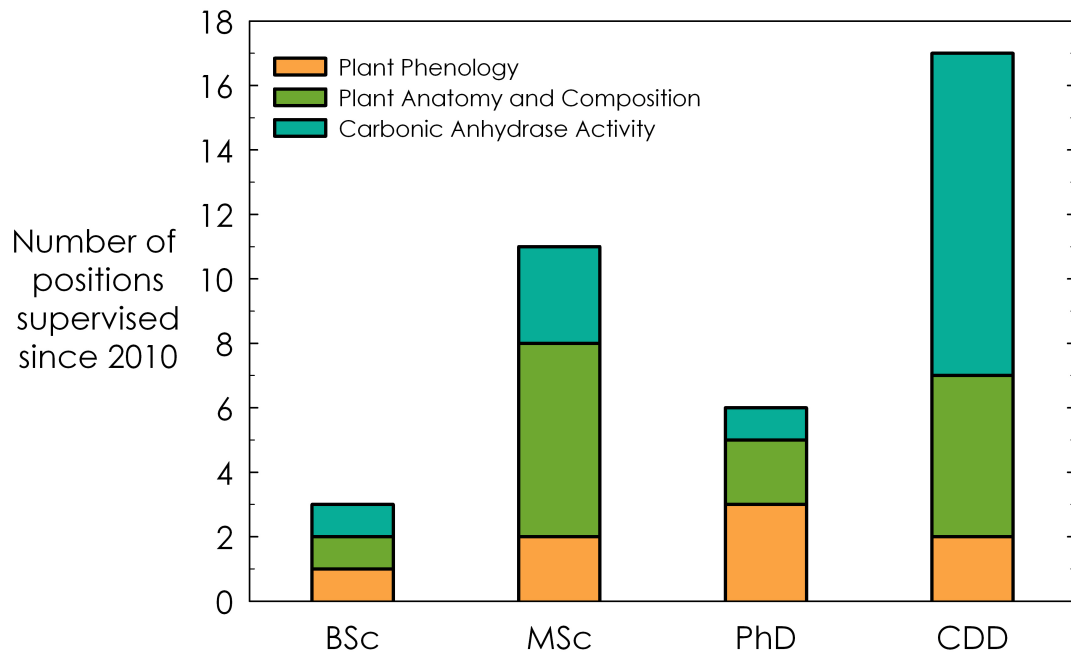


Figure 4.3 The contribution of supervised research staff and students to my priority research themes

4.8 RESEARCH FUNDING PROFILE

Over the past ten years I have also sourced independent funding for my research through a number of successful individual fellowships such as the EU-Marie Curie grants either as the fellow or now as the host PI to two Marie Curie and two Bordeaux Idex fellows. Previous to that I also obtained an advanced NERC fellowship to build a team at The University of Cambridge. Since then I have also obtained an EU-funded ERC starting grant that helped establish the ECOFUN ISPA team internationally. In total I have obtained more than **€3,462,291** in competitive funding as PI for research and a further **€1,765,782** on grants acting as either Co-PI or Work Package leader. For full details on the projects I have co-ordinated or co-authored please refer to Appendix III.

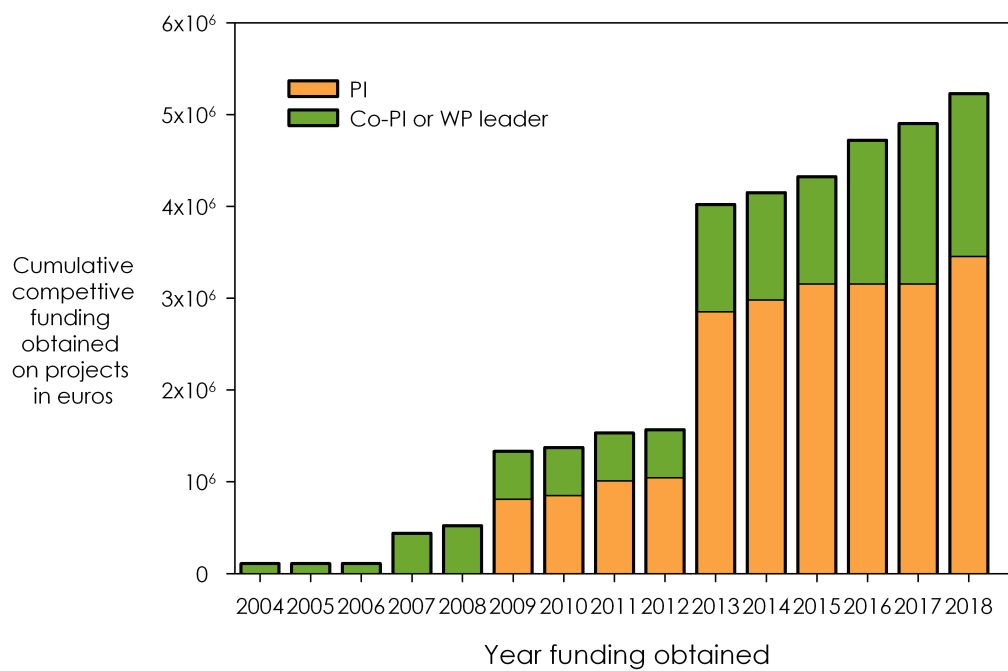


Figure 4.4 The cumulative competitive funding obtained on projects since obtaining my PhD

4.9 COMMISSIONS OF RESPONSIBILITY

Proposal **grant reviewer** for the National Science Foundation, USA and FWO, Belgium

Regular manuscript **reviewer** for a number of high impact scientific journals in relevant research fields including:

Nature, Nature Climate Change, Plant Cell and Environment, Global Biogeochemical Cycles, Global Change Biology, Journal of Geophysical Research, Tellus, Oecologia, New Phytologist, International Journal of Biometeorology, Rapid Communications in Mass Spectrometry, European Journal of Soil Biology, Agricultural and Forest Meteorology, Biogeosciences Discussions, Ecological Indicators, Proceedings of the Royal Society, ISME, Soils and the Journal of Hydrology.

Associate Editor for the *Vadose Zone Journal*.

International Referent for the INRA EFPA CR2 Recruitment Panel (3 profiles) [Paris, 2015]

Thesis Jury President for the PhD thesis of Mlle Silvia Poblador Lavergne at the University of Barcelona [Barcelona, 2018]

Thesis Jury Member for the PhD thesis of Mr Maximilian Larter at the University of Bordeaux [Bordeaux, 2016]

Thesis Jury Member for the PhD thesis of Mlle Aliénor Lavergne at the University of Versailles Saint-Quentin en Yvelines [Paris, 2016]

Thesis Jury Member for the Masters 2 - Spécialité Biodiversité et écosystèmes continentaux at the University of Bordeaux [Bordeaux, 2016]

Co-ordinator of a European Digital Camera Phenology Network (<http://european-webcam-network.net/>)

Co-ordinator of the ICOS Working Group Phenological Cameras (<http://gaia.agraria.unitus.it/icos/working-groups>)

French Co-ordinator (MC) and **Working Group Leader** (*WG3: Requirements for the development of a future cybernetic web of experimental structures*) for the European Cost Action on “Climate-smart forestry in Mountain Regions” CA15226 (http://www.cost.eu/COST_Actions/ca/CA15226)

Outreach Salon de Agriculture, Stage de Observation Lycee students, Enseignants dans Labo, Climate Music Project

Member of the European Geosciences Union (EGU), American Geophysical Union (AGU), Societe Francaise des Stable Isotopes (SFIS), British Ecological Society (BES), Association of Tree Ring research (ATR) and the INRA-MEM Phytobiome Working Group, SOERE-TEMPO Societe Francaise de la phenology, Young Academy of Europe (YAE)

Elected member of the Conseil d’Administration for the Societe Francaise des Stable Isotopes (2017 to present)

Participant of large-scale Earth system networks including:

ICOS (<http://www.icos-infrastructure.eu/>);

FLUXNET (<http://daac.ornl.gov/FLUXNET/>);

ESWN (<https://eswnonline.org/>);

BASIN network (<http://basinisotopes.org/Home>);

COSANOVA network (<http://www.cosanova.org/>);

COSIWAX network (<https://botanik.unibas.ch/en/botanical-research-groups/sustainable-land-use/projects/cosiwax/>);

IAEA-MIBA (http://www-naweb.iaea.org/napc/ih/MIBA/IHS_MIBA.html) and;

IAEA-GNIP (http://www-naweb.iaea.org/napc/ih/GNIP/IHS_GNIP.html).

4.10 NATIONAL AND INTERNATIONAL COLLABORATIONS

Since the start of my PhD I have been developing long-lasting and productive collaborations with plant physiologists, soil microbiologists, landscape ecologists, atmospheric chemists and Earth system modellers from across the world. This was facilitated early in my career by working regularly within the framework of large-scale European projects such as EUROFLUX, MIND and CARBOEUROPE investigating biosphere-atmosphere interactions across different ecosystems in Europe.



Figure 4.5 International Network of Co-Authors generated by the Web of Science [2017]

In addition, I have benefitted enormously throughout my career from a number of EU COST Actions in particular SIBAE, where I began to meet the wider research community working with stable isotopes. These early career interactions with the flux and stable isotope community in Europe led very quickly to collaborations in other networks across Australia, Japan and the USA. It is beyond the scope of this document to provide an exhaustive list of my collaborators but I have detailed a number of key past and present collaborators in Appendix IV.

4.11 INTERNATIONAL COMMUNICATIONS

Since my PhD I have contributed to a total of **116** oral communications, representing 97 at international workshops and conferences, 17 seminars at research institutes and universities across the world and teaching on 4 different courses. Of those 116 communications **I have orally presented 81**, of which **51 were invited (Fig. 4.6)**. In addition I have contributed to the preparation and presentation of 58 further oral communications. A selection of these invited talks are presented below and a comprehensive list of all my oral and poster communications can be found in Appendix V.

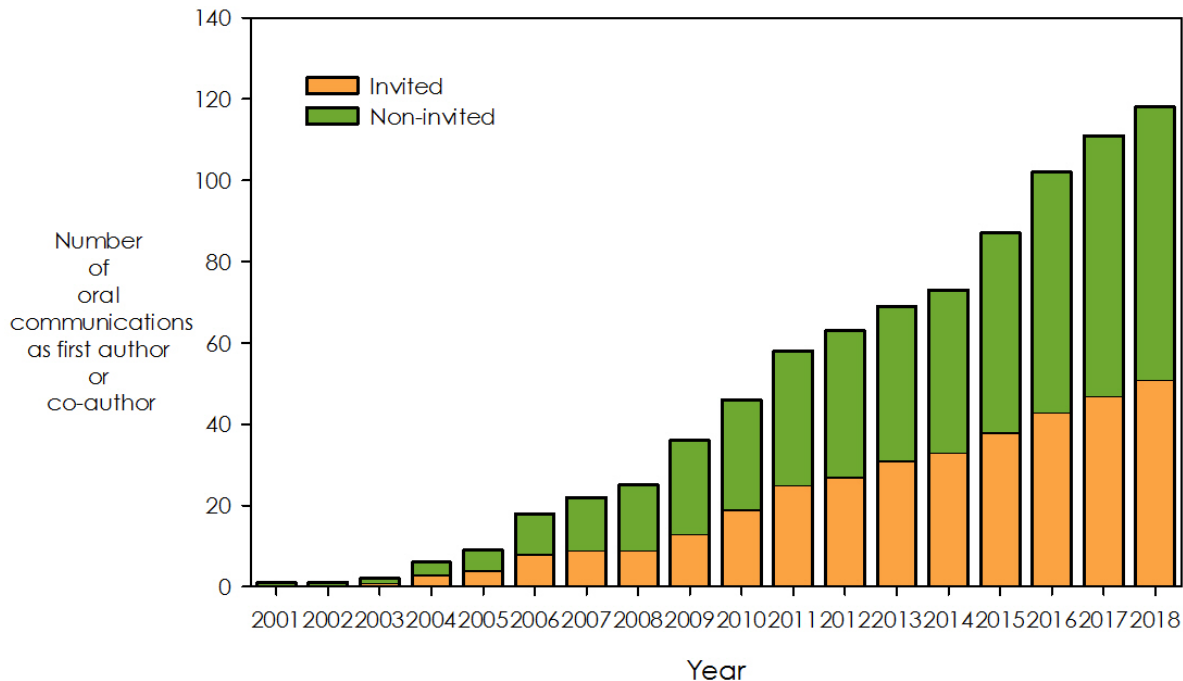


Figure 4.6 Cumulative number of oral communications also highlighting invited contributions.

Wingate, L. Promoting frontier Earth system research and female role models using dedicated geoscience symposiums. Geophysical Research Abstracts, Vol. 20, EGU2018-5132, Vienna, Austria, 9-13th April 2018 (**INVITED**)

Wingate, L. The impact of carbonic anhydrase on the atmospheric concentrations of CO¹⁸O and COS at large scales. Stable Isotope Society of France, Scientific Afternoon Series, National Natural History Museum, Paris, France 6th December 2016 (**INVITED**)

- Wingate, L.** Soil processes and climate models. Inaugural workshop for the International Soil Modelling Consortium, Austin, Texas, USA 29th March-1st April 2016 (**INVITED**).
- Wingate, L.** et al., The impact of Carbonic Anhydrase on the partitioning of leaf and soil CO¹⁸O and COS gas exchange across scales. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 13th December-17th December 2015 (**INVITED**).
- Wingate, L.** Investigating the impact of Carbonic Anhydrase on the atmospheric concentrations of CO¹⁸O and COS across scales. 8^{ème} journée thématique de l'Observatoire Aquitaine des Sciences de l'Univers, Bordeaux, France, 19th November 2015 (**INVITED**).
- Wingate, L.** and the European ICOS phenology camera network. Opportunities to investigate the functional phenology of ecosystems using a European Phenology Camera Network. French ICOS Infrastructure Inauguration, Pierroton, France, 24th Sept 2015 (**INVITED**).
- Wingate, L.** Impact of microbial carbonic anhydrase on the atmospheric concentrations of CO¹⁸O and COS at large scales. Joint meeting of the British Ecological Society's Plants, Soils, Ecosystems and Plant Environmental Physiology special interest groups: Carbon cycling: from plants to ecosystems, University of Manchester, UK 16th-17th October 2014 (**INVITED**).
- Wingate, L.** and Ogée, J. Seasonal contribution of soil CO₂ invasion to the total CO¹⁸O flux from a pine forest ecosystem, AGU Chapman Conference: Soil mediated drivers of coupled biogeochemical and hydrological processes across scales 2013, Biosphere 2, Arizona, USA 21st -24th October 2013 (**INVITED**).
- Wingate, L.** et al., Investigating high-resolution stable isotope signals of annual tree rings across a moisture gradient with the MuSICA model. COST-SIBAE Meeting: Challenges in the applications of stable isotopes across disciplines and scales, Wroclaw, Poland, 14th-19th May 2013 (**INVITED**).
- Wingate, L.** and the European FLUXNET webcam network. On Detecting Phenology with Digital Cameras, Hyperspectral Remote Sensing and Eddy Covariance Measurements across Europe, FLUXNET Specnet Open Conference 2011, Berkeley, California, USA 7th -9th June 2011 (**INVITED**).
- Wingate, L.,** Ogée, J., Burlett, R., Bosc, A. Tunable diode laser spectroscopy techniques for ecosystem CO₂ isotopologue exchange studies. Short Course on Laser-based Isotope Ratio Analyzers: From the User Perspective SC2/IG16, EGU 2011, Vienna, Austria, 3rd -8th April 2011 (**INVITED**).
- Wingate, L.** Using stable isotopes to determine the contribution of respiration to ecosystem carbon fluxes in forests. 24th New Phytologist Symposium: Plant respiration and climate change: scaling from mitochondria to the globe, Oxford, UK, 11th-14th April 2010 (**INVITED**).
- Wingate, L.,** Richardson, A., Mizunuma, T., Nasahara, K.N., Saigusa, N., Muraoka, Y., Nagai, S., Jacobs, N., Sanchez-Azofeifa, G.A., Wilkinson, M., Morison, J., Köstner, B., Grünwald, T., Braswell, R., Grace, J. and the FLUXNET webcam network. Keeping an eye on the carbon balance. 8th Asiaflux Workshop, Sapporo, Japan 27th-29th October, 2009 (**INVITED**).

Wingate, L., Seibt, U. and Ogée, J. An isotopic excursion through atmospheric and metabolic signals from conifer forests following a seasonal rhythm. SIBAE-BASIN Stable Isotope Meeting: Isotopes as tracers as ecological change, Tomar, Portugal, 13th-15th Mar 2006 (**INVITED**).

4.12 WORKSHOP PARTICIPATION

Lastly, I have participated actively to a range of different workshops over the years that have exposed me to many new ideas and created an environment to foster new collaborations and concepts for proposals. Through these workshops I have also become aware of the different funding mechanisms available at the national and European scale for bringing researchers together to discuss hot topics within and across different disciplines. Most recently I have also started to organise my own workshops and training events. Please find below a selection of the different workshops I have participated to.

COST ACTION workshop

- 29-30th November 2018 Developing sensor networks for climate smart forestry | Bordeaux, France
Organiser Lisa Wingate

Phenology method workshop

- 6th – 8th November 2017 SOERE-Tempo Workshop for the phenology | Bordeaux, France
Organiser David Alletru and Benedicte Wenden

ERC application workshop

- 7th March 2018 ERC Information, Outreach and Networking Event | Bordeaux, France
Organiser Lisa Wingate and Bordeaux Idex

Mentoring workshop

- 7th March 2018 Mentoring and networking skills for young researchers | Bordeaux, France
Organiser Lisa Wingate and Melanie Smith

Phenology method workshop

- 6th – 8th November 2017 SOERE-Tempo Workshop for the phenology | OHP, France
Organiser Frederic Jean and Nicolas Delpierre

Drought Response and Adaptation of Forests at their southern limit

- 10th – 14th June 2013 International Workshop for the INRA Metaprogramme ACCAF | Barsac, France
Organiser Jérôme Ogée

The significance of xylem hydraulic plasticity for ecological reconstruction

- 15th – 17th May 2012 European Science Foundation Workshop | Lötschental, Switzerland
Organisers Patrick Fonti and Steven Janssen

Stable isotopes in biosphere-atmosphere-earth system research summer school (INVITED LECTURER**)**

- 23rd – 27th Aug 2010 European Science Foundation Cost Action ES806, Workshop | Gothenburg, Sweden
Organisers Tobias Rütting

Stable isotopes in biosphere-atmosphere-earth system research

- 23rd – 25th Sept 2009 European Science Foundation Cost Action ES806, Workshop | Innsbruck, Austria
Organisers Daniel Epron and Thomas Wutzler

Diurnal- to century-scale controls on soil respiratory fluxes: Towards a new generation of integrated experimental and modelling approaches.

- 21st – 23rd Sept 2009 ESF Exploratory Workshop | Innsbruck, Austria
Organisers Michael Bahn, Markus Reichstein and Ivan Janssens

Disentangling abiotic and biotic effects on soil respiration

- 12th – 13th Mar 2007 ESF-funded “SIBAE Workshop” | Innsbruck, Austria
Organiser Michael Bahn

Stable isotopes in dendroclimatology – Current status and future prospects.

- 11th – 16th Feb 2007 ESF-funded “SIBAE Workshop” | Potsdam, Germany
Organisers Gerd Helle and Gerd Schleser

International workshop on isotopic effects in evaporation. Revisiting the Craig-Gordon model four decades after its formulation.

- 3rd – 5th May 2006 IAEA Workshop | Pisa, Italy
Organisers Pradeep Aggarwal, Joel Gat, Roberto Gonfiantini, Jean Jouzel, Piero Manetti and Kazimierz Rozanski

Aquaporins – Biophysical and molecular mechanisms for water transport.

- 28th Feb – 1st Mar 2005 | Turin, Italy
Organisers Andrea Schubert

Oxygen isotopes as a tracer linking global O₂, CO₂ and H₂O cycles.

- 19th – 22nd Oct 2004 Joint NSF-ESF-funded BASIN and SIBAE Workshop | California, USA
Organisers Diane Pataki and Jim Ehleringer

Stable isotopic signals of the terrestrial biosphere: linking ecosystem C fluxes to isotopic signals of plant components.

- 18th – 21st Nov 2003 ESF-funded “SIBAE Workshop” | Orvieto, Italy
Organisers Enrico Brugnoli

Methods for the detection of changes in soil carbon stocks under climate change.

- 29th – 31st Oct 2003 ESF-funded Workshop | Edinburgh, UK
Organisers Franz Conen, Maurizio Mencuccini and Argyro Zerva

APPENDIX I : PUBLICATIONS

PEER-REVIEWED PUBLICATIONS⁴

- [60] Sauze, J., Jones, S., Wohl, S., Ogée, J., Kaisermann, A. & **Wingate, L.** all site PIs (in prep) Pan-European variability in COS exchange between soils and the atmosphere. *Global Biogeochemical Cycles*
- [59] Jones, S., Kaisermann, A., Sauze, J., Wohl, S., Ogée, J., Launois, T., Cuntz, M., & **Wingate, L.** (in prep) Impact of soil nitrogen on soil microbial carbonic anhydrase and the oxygen isotope composition of atmospheric CO₂
- [58] Lacombe, L., Kaisermann, A., Gimeno, T., Wohl, S., Devert, N., Jones, S., Frejaville, B., Ogée, J. & **Wingate, L.** (in prep) Investigating the emissions of COS from *Alliaria petiolata* an isothiocyanate-producing plant species. *Frontiers in Plant Science*
- [57] **Wingate, L.**, Jones, S., Sauze, J., Meredith, L., Launois, T., Cuntz, M., Kaisermann, A., Wohl, S., Saavedra, N., Gutierrez, A., Fernandez, N., & Ogée, J., (in prep) The impact of pH on soil microbial carbonic anhydrase and the oxygen isotope composition of atmospheric CO₂.
- [56] Plaza-Aguilar, A., Ogée, J., Wilkinson, M., Filippa, G., Morison, J., Mizunuma, T., Griffiths, H. & **Wingate, L.** (in prep) Comparing seasonal differences in the phenology and physiology of oak and ash trees using canopy colour signals. *Tree Physiology*
- [55] Kaisermann, A., Jones, S., Wohl, S., Muñoz, N. G., Ogée, J. & **Wingate, L.** (in prep) Plant species influences soil carbonyl sulfide fluxes *Soils*
- [54] Kaisermann, A., Jones, S., Wohl, S., Ogée, J. & **Wingate, L.** (submitted) Nitrogen fertilization reduces the capacity of soils to take up atmospheric carbonyl sulphide. Preprints 2018, 2018080479 (doi: 10.20944/preprints201808.0479.v1) *Soil Systems*
- [53] Barbeta, A., Jones, S., Clavé, L., Wingate, L., Fréjaville, B., Gimeno, T.E. & Ogée, J. (submitted) Hydrogen isotopic fractionation affects the identification and quantification of tree water sources in a temperate deciduous forest. *HESS*
- [52] Preisler, Y., Grunzweig, J., Bert, D., Ogée, J., Wingate, L., Tatarinov, F., Rotenberg, E., Rohatyn, S., Her, N., Klein, T. & Yakir, D. (submitted) Mortality versus survival in drought affected Aleppo pine forest depends on the extent of rock cover and soil stoniness. *Functional Ecology*
- [51] Gimeno, T., Saavedra-Berlanga, N., Ogée, J., Medlyn, B.E. & **Wingate, L.** (submitted) Testing for non-stomatal limitations to optimisation behaviour under drought on contrasting plant functional types. *Journal of experimental Botany*.

⁴ Author names listed in blue indicate students and young researchers/engineers under my supervision.

- [50] [Hirl, R.](#), Schnyder, H., Ostler, U., Schäufele, R., Schleip, I., Vetter, S., Auserwald, K., **Wingate, L.**, Barbour, M. & Ogée, J. (submitted) The ^{18}O -ecohydrology of a grassland ecosystem – predictions and observations. *New Phytologist*.
- [49] Meredith, L., Ogée, J., Boye, K., Singer, E., **Wingate, L.**, von Sperber, C., Sengupta, A., Whelan, M., Pang, E., Keiluweit, M., Brüggemann, N., Berry, J.A. & Welander, P.V. (2018) Soil exchange rates of COS & CO^{18}O shift with the diversity of microbial communities and their carbonic anhydrase enzymes. *ISME*, doi.org/10.1038/s41396-018-0270-2
- [48] [Hufkens, K.](#), Filippa, G., Cremonese, E., Migliavacca, M., Brown, T., D'Odorico, P., Peichl, M., Gielen, B., Hortnagl, L., Soudani, K., Papale, D., Rebmann, C., Brown, T. & **Wingate, L.** (2018) Assimilating phenology datasets automatically across ICOS ecosystem stations. *International Agrophysics*
- [47] Franz, D., Acosta, M., Altimir, N., Arriga, N., Arrouays, D., Aubinet, M., Aurela, M., Ayres, E., López-Ballesteros, A., Barbaste, M., Berveiller, D., Biraud, S., Boukir, H., Brown, T., Brümmer, C., Buchmann, N., Burba, G., Carrara, A., Cescatti, A., Ceschia, E., Clement, R., Cremonese, E., Crill, P., Darenova, E., Dengel, S., D'Odorico, P., Filippa, G., Fleck, S., Fratini, G., Fuß, R., Gielen, B., Gogo, S., Grace, J., Graf, A., Grelle, A., Gross, P., Grünwald, T., Haapanala, S., Hehn, M., Heinesch, B., Heiskanen, J., Herbst, M., Hörtnagl, L., [Hufkens, K.](#), Ibrom, A., Jolivet, C., Joly, L., Jones, M., Kiese, R., Klemetsson, L., Kljun, N., Klumpp, K., Kolari, P., Kolle, O., Kowalski, A., Kutsch, W., Laurila, T., de Ligne, A., Linder, S., Lindroth, A., Lohila, A., Longdoz, B., Mammarella, I., Manise, T., Marañón Jiménez, S., Matteucci, G., Mauder, M., Meier, P., Merbold, L., Mereu, S., Herschlein, C., Metzger, S., Migliavacca, M., Mölder, M., Montagnani, L., Moureaux, C., Nelson, D., Nemitz, E., Nicolini, G., Nilsson, M.B., Op de Beeck, M., Osborne, B., Löfvenius, M.O., Pavelka, M., Peichl, M., Peltola, O., Pihlatie, M., Pitacco, A., Pokorný, R., Pumpanen, J., Ratié, C., Rebmann, C., Roland, M., Sabbatini, S., Saby, N.P.A., Saunders, M., Schmid, H.P., Schruppf, M., Sedláč, P., Ortiz, P.S., Siebicke, L., Šigut, L., Silvennoinen, H., Simioni, G., Skiba, U., Sonnentag, O., Soudani, K., Soulé, P., Steinbrecher, R., Tallec, T., Thimonier, A., Tuittila, E-S., Tuovinen, J-P., Vestin, P., Vincent, G., Vincke, C., Vitale, D., Waldner, P., Weslien, P., **Wingate, L.**, Wohlfahrt, G., Zahniser M. and Vesala, T. (2018) Towards long-term standardised carbon and greenhouse gas observations for monitoring Europe's terrestrial ecosystems. *International Agrophysics*
- [46] Ogée, J., **Wingate, L.** & Genty, B. (2018) Estimating mesophyll conductance from measurements of CO^{18}O photosynthetic discrimination and carbonic anhydrase activity. *Plant Physiology*
- [45] [Kaisermann, A.](#), Ogée, J., [Sauze, J.](#), [Wohl, S.](#) & **Wingate, L.** (2018) Disentangling the rates of carbonyl sulphide (COS) production and consumption across European soils. *Atmos. Chem. Phys.* 18, 9425-9440, doi.org/10.5194/acp-18-9425-2018
- [44] Nagai, S., Akitsu, T., Saitoh, T.M., Busey, R.C., Fukuzawa, K., Honda, Y., Ichie, T., Ide, R., Ikawa, H., Iwasaki, A., Iwao, K., Kajiwara, K., Kang, S., Kim, Y., Lip Khoon, K., Kononov, A.V., Kosugi, Y., Maeda, T., Mamiya, W., Matsuoka, M., Maximov, T.C., Menzel, A., Miura, T., [Mizunuma, T.](#), Morozumi, T., Motohka, T., Muraoka, H., Nagano, H., Nakai, T., Nakaji, T., Oguma, H., Ohta, T., Ono, K., Sylvester, R.A., Suzuki, R., Takagi, K., Takanashi, S., Tei, S., Tsuchida, S., Yamamoto, H., Yamasaki, E., Yamashita, M., Yoon, T.K., Yoshida, T., Yoshimura, M., Yoshitake, S., Wilkinson, M., **Wingate, L.** & Nasahara, K.N. (2018) Over 8 million phenological and sky images from 29 ecosystems from the Arctic to the tropics: the Phenological Eyes network. *Ecological Research* 10.1007/s11284-018-1633-x

- [43] Meredith, L., Boye, K., Youngermann, C., Whelan, M., Ogée, J., [Sauze, J.](#) & **Wingate, L.** (2018) Coupled biological and abiotic mechanisms driving carbonyl sulfide production in soils. *Soil Systems*, 2, 37 doi:10.3390/soilsystems2030037.
- [42] Stumpp, C., Bruggemann, N. & Wingate, L. (2018) Stable isotope approaches in vadose zone research *Vadose Zone Journal* 17:180096. Doi:10.2136/vzj2018.05.0096.
- [41] Whelan, M., Lennartz, S., [Gimeno, T.](#), Wehr, R., Wohlfahrt, G., Wang, Y., Kooijmans, L., Hilton, T., Belviso, S., Peylin, P., Commane, R., Sun, W., Chen, H., Kuai, L., Mammarella, I., Maseyk, K., Berkelhammer, M., Li, K-F., Yakir, D., Zumkehr, A., Katayama, Y., Ogée, J., Speilmann, F., Kitz, F., Rastogi, B., Kesselmeier, J., Marshall, J., Erkkila, K-M., **Wingate, L.**, Meredith, L., He, W., Bunk, R., [Launois, T.](#), Vesala, T., Schmidt, J., Fichot, C., Seibt, U., Saleska, S., Saltzman, E., Montzka, S., Berry, J. & Campbell, J.E. (2018) Reviews and Syntheses: Carbonyl sulfide as a multi-scale tracer for carbon and water cycles. *Biogeosciences*, doi:10.5194/bg-2017-427
- [40] [Sauze, J.](#), [Jones, S.](#), **Wingate, L.**, [Wohl, S.](#) & Ogée, J. (2018) The role of soil pH on soil carbonic anhydrase activity. *Biogeosciences* 15, 597-612 doi.org/10.5194/bg-15-597-2018
- [39] [Jones, S.](#), Ogée, J., [Sauze, J.](#), [Wohl, S.](#), [Saavedra, N.](#), [Fernandez-Prado, N.](#), [Maire, J.](#), [Launois, T.](#), Bosc, A., & **Wingate, L.** (2017) Non-destructive estimates of soil carbonic anhydrase activity and soil water oxygen isotope composition. *HESS* 21, 6363-6377 doi.org/10.5194/hess-21-6363-2017
- [38] [Sauze, J.](#), Ogée, J., Maron, P.-A., Crouzet, O., Nowak, V., [Wohl, S.](#), [Kaisermann, A.](#), [Jones, S.](#), & **Wingate, L.** (2017) The interaction of soil phototrophs and fungi with pH and their impact on soil CO₂, CO¹⁸O and OCS exchange *Soil, Biology and Biochemistry*, 115, 371-382, doi:10.1016/j.soilbio.2017.09.009
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- [36] [Gimeno, T.](#), Royles, J., Ogée, J., [Wohl, S.](#), [Jones, S.](#), [Sauze, J.](#), [West, J.](#), [Burllett, R.](#), Griffiths, H. & **Wingate, L.** (2017) Bryophyte gas-exchange dynamics along varying hydration status reveal significant COS emission in the light. *New Phytologist*.
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- [33] Voelker, S. L., Brooks, J.R., Meinzer, F.C., Anderson, R., Bader, M.K-F., Battipaglia, G., Becklin, K.M., Beerling, D., Bert, D., Betancourt, J.L., Dawson, T.E., Domec, J.C., Guyette, R.P., Körner, C., Leavitt, S.W., Linder, S., Marshall, J.D., Mildner, M., Ogée, J., Panyushkina, I., [Plumpton, H.J.](#), Pregitzer, K.S., Saurer, M., Smith, A.R., Siegwolf, R.T.W., Stambaugh, M.C., Talhelm, A.F., Tardif, J.C., Van de Water,

- P.K., Ward, J.K. & **Wingate, L.**, (2016) Carbon isotope discrimination reveals that leaf gas exchange regulation responds dynamically to CO₂ among woody angiosperms and gymnosperms. *Global Change Biology*, Vol. 22(2):889-902 doi: 10.1111/gcb.13102
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- [31] **Wingate, L.**, Ogée, J., Cremonese, E., Filippa, G., Mizunuma, T., Migliavacca, M., Moisy, C., Wilkinson, M., Moureaux, C., Wohlfahrt, G., Hammerle, A., Gimeno, C., Porcar-Castell, A., Galvagno, M., Nakaji, T., Morison, J., Kolle, O., Knohl, A., Kutsch, W., Kolari, P., Nikinmaa, E., Ibrom, A., Gielen, B., Eugster, W., Balzarolo, M., Papale, D., Klumpp, K., Kostner, B., Grunwald, T., Joffre, R., Ourcival, J-M., Hellstrom, M., Charles, G., Longdoz, B., Genty, B., Levula, J., Heinesch, B., Sprintsin, M., Yakir, D., Manise, T., Guyon, D., Ahrends, H., **Plaza-Aguilar, A.** & Grace, J. (2015) Observing canopy development and physiology using the EUROPhen camera network at flux sites. *Biogeosciences* doi:10.5194/bg-12-5995-2015
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PEER-REVIEWED BOOK CHAPTERS

- [1] Hemming, D., Loader, N., Marca, A., Robertson, I., Williams, D., **Wingate, L.** and Yakir, D. (2007) The Future of Large-Scale Stable Isotope Networks. In 'Stable Isotopes as Indicators of Global Change' Eds T. Dawson and R. Seigwolf, Elsevier, Academic Press pp 361-381.

THESES

- [1] **Wingate, L.** (2003) The contribution of photosynthesis and respiration to the net ecosystem exchange and ecosystem ¹³C discrimination of a Sitka spruce plantation. PhD Thesis, University of Edinburgh, Edinburgh, UK, pp. 268.
- [2] **Wingate, L.** (1998) Calibration of hemispherical photographic and beam transmittance techniques to measure leaf area index distribution in a *Picea sitchensis* (Bong.) Carr. plantation. BSc. Thesis, University of Edinburgh, Edinburgh, UK, pp. 45.

THESES SUPERVISED

- [1] Ludovic, L. (2018) The influence of *Alliaria petiolata*, L. on the soil-plant-atmosphere exchange of COS. **MSc** Thesis, Université de Bordeaux, Bordeaux, France.
- [2] Sauze, J. (2017) Identification des moteurs de l'activité de l'anhydrase carbonique dans les sols et son impact sur les échanges sol-atmosphère de CO¹⁸O et OCS, deux traceurs complémentaires du cycle du carbone. **PhD** Thesis, Université de Bordeaux, Bordeaux, France.
- [3] Daryono, R.N.H. (2017) The influence of earthworms on the soil-atmosphere exchange of COS and CO₂. **MSc** Thesis, Université de Bordeaux, Bordeaux, France.
- [4] Likiliki, E. (2017) Acclimation and seasonal coupling of photosynthesis, respiration and carbonyl sulfide exchange in bryophytes. **MSc** Thesis, Université de Bordeaux, Bordeaux, France.
- [5] Plaza-Aguilar, A. (2016) Investigating the link between phenology and ecosystem function of temperate tree species using colour signals. **PhD** Thesis, University of Cambridge, Cambridge, UK.
- [6] Maire, J. (2015) Linking digital image signals to the seasonal variations in photosynthetic pigments of different plant types. **MSc** Thesis, Université de Lorraine, Nancy, France.

- [7] Saavedra, N. (2015) Investigating the impact of drought on nocturnal stomatal conductance. **MSc** Thesis, Rey Juan Carlos University, Madrid, Spain.
- [8] Tyler, C. (2015) Implementation of a web-interface to visualise real-time imagery from a European Phenology Camera Network. **BSc** Internship, Queensland University of Technology, Queensland, Australia.
- [9] Mizunuma, T. (2014) Seasonal patterns of forest canopy and their relevance for the global carbon cycle. **PhD** Thesis, University of Edinburgh, Edinburgh, UK.
- [10] Plumpton, H. (2014) Investigating the effects of elevated CO₂ and N fertilisation on the inter-annual variability of cellulose on wood density and carbon and oxygen isotope signals in trees. **MSc** Thesis, University of Cambridge, Cambridge, UK.
- [11] Hirl, R. (2014) Modelling the impact of climate on the oxygen isotope composition of grassland water pools and cellulose signals **MSc** Thesis, Technical University of Munich, Munich, Germany.
- [12] Flatman, T. (2013) Effects of elevated CO₂ on tracheid anatomy in Loblolly pine trees. **BSc** Thesis, University of Stirling, Stirling, UK.
- [13] Markovic, T. (2011) Investigating the inter-annual variability of cellulose carbon isotope composition in trees. **MSc** Thesis, University of Belgrade, Belgrade, Serbia.
- [14] Wilkinson, S. (2011) Modelling the inter-annual variability in wood density and tracheid anatomy. **MSc** Thesis, Bangor University, Bangor, UK.
- [15] Philippe, P. (2010) Application of the use of digital photography to determine vegetation phenology. **MSc** Thesis, Université Henri Poincaré, Nancy, France.
- [16] Herfurth, D. (2010) Modelling carbon and oxygen isotope signals in Pine trees. **MSc** Thesis, Université de Bordeaux, Bordeaux, France.

APPENDIX II : SUPERVISION

RESEARCH STAFF

A synthesis of the research staff and students supervised or co-supervised by myself since my PhD are provided below.

Dr. Raphael Dulhoste (2010-2011), INRA-EPHYSE

Subject: Linking growing season length to tree-ring cellulose deposition and phenology

Ms. Murielle Misrachi (2011), The University of Cambridge

Subject: Linking growing season length to tree-ring cellulose deposition and phenology

Dr. Toshie Mizunuma (2010-2011), The University of Cambridge

Subject: Linking canopy phenology to net ecosystem exchange in temperate forests

Plaza-Aguilar, A., Ogée, J., Morison, J., Wilkinson, M., **Mizunuma, T.**, et.al (in prep) *Methods Ecol. Evol.*

Nagai, S.**Mizunuma, T.**,**Wingate, L.** et al., (submitted) *Ecological Research*

Wingate, L., Ogée, J., Cremonese, E., Filippa, G., **Mizunuma, T.** et al., (2015). *Biogeo. Disc.*

Mizunuma, T., Mencuccini, M., **Wingate, L.** et al., (2014) *Methods Ecol Evol.*

Mizunuma, T., Koyanagi, T., Mencuccini, M., Nasahara, K.N., **Wingate, L.** et al., (2011). *Plant Ecol.Div.*

Dr. Lydia Gentsch (2012-2013), INRA-EPHYSE

Subject: Carbon isotope discrimination during branch photosynthesis of *Fagus sylvatica*

Gentsch, L., Sturm, P., Hammerle, A., Siegwolf, R., **Wingate, L.**, et al., (2014). *J. Exp. Bot.*

Gentsch, L., Hammerle, A., Sturm, P., Ogée, J., **Wingate, L.** et al., (2014). *Plant, Cell and Env.*

Dr. Teresa Gimeno (2014-2018), INRA-ISPA Bordeaux Idex and Marie Skłodowska Curie Fellowship

Subject: Using stable isotopes and COS to track diurnal and nocturnal carbon and water fluxes under future climate scenarios

Gimeno, T., Saavedra, N., Ogée, J., Medlyn, B. & **Wingate, L.** (submitted) *J. of Exp. Bot.*

Whelan, M., Lennartz, S., **Gimeno, T.**, ...Launois, T., ...**Wingate, L.**...et al., (2018) *Biogeosciences*

Gimeno, T., Royles, Ogée, J., Wohl, S., Jones, S., Sauze, J., West, J., Burrett, R. & **Wingate, L.** (2017) *New Phyt.*

Lin, Y-S.,... **Gimeno, T.E.**, & **Wingate, L.** (2015) *Nature Climate Change*

Dr. Samuel Jones (2014-2018), INRA-ISPA

Subject: Identifying the spatial drivers of carbonic anhydrase activity in soils and its impact on soil-atmosphere exchanges of CO¹⁸O and COS

Gimeno, T., Royles, Ogée, J., Wohl, S., **Jones, S.**, Sauze, J., West, J., Burrett, R. & **Wingate, L.** (2017) *New Phyt.*

Sauze, J., Ogée, J., Maron, P-A, ...Wohl, S., Kaisermann, A., **Jones, S.**.....& **Wingate, L.** (2017) *Soil Bio.Biochem*

Sauze, J., **Jones, S.**, **Wingate, L.**, Wohl, S. & Ogée, J. (2017) *Bio. Disc*

Jones, S., Ogée, J., Sauze, J., Wohl, S., Saavedra, N.,....& **Wingate, L.** (2017) *Hydrology Earth System Sci*

Kaisermann, A., Ogée, J., Sauze, J., **Jones, S.**, Wohl, S., ...& **Wingate, L.** (2018) *Atm Chem & Phy*

Dr Thomas Launois (2014-2017), INRA-ISPA

Subject: Constraining global estimates of photosynthesis and respiration using a multi-tracer approach

Ogée, J, Sauze, J., Kesselmeier, J., Genty, B., Van Diest, H., **Launois, T.** & **Wingate, L.**, (2016) *Biogeosci.*
Whelan, M., Lennartz, S., Gimeno, T., ...**Launois, T.**, ...**Wingate, L.**...et al., (2018) *Biogeosciences*

Dr Aurore Kaisermann (2015-2018), INRA-ISPA

Subject: Linking the temporal and spatial variability of carbonic anhydrase activity of soils to soil community dynamics

Kaisermann, A., Ogée, J, Sauze, J., Jones, S., Wohl, S., ...& **Wingate, L.** (2018) *Atm Chem & Phy*
Sauze, J., Ogée, J, Maron, P-A, ... Wohl, S., **Kaisermann, A.**, Jones, S.....& **Wingate, L.** (2017) *Soil Bio.Biochem*

Mr. Steven Wohl (2014-2019), INRA-ISPA

Subject: Developing laser spectroscopy systems to measure soil-atmosphere exchanges of CO¹⁸O and COS in the lab and field

Kaisermann, A., Ogée, J, Sauze, J., Jones, S., **Wohl, S.**, ...& **Wingate, L.** (2018) *Atm Chem & Phy*
Gimeno, T., Royles, Ogée, J, **Wohl, S.**, Jones, S., Sauze, J., West, J., Burlett, R. & **Wingate, L.** (2017) *New Phyt.*
Sauze, J., Ogée, J, Maron, P-A, ... **Wohl, S.**, Kaisermann, A., Jones, S.....& **Wingate, L.** (2017) *Soil Bio.Biochem*
Sauze, J., Jones, S., **Wingate, L.**, **Wohl, S.** & Ogée, J. (2017) *Bio. Disc*
Jones, S., Ogée, J, Sauze, J., **Wohl, S.**, Saavedra, N.,....& **Wingate, L.** (2017) *Hydrology Earth System Sci*

Ms Juliette Maire (2015), INRA-ISPA

Subject: Developing a high-throughput cryogenic extraction line to estimate the δ¹⁸O of leaf and soil water pools and CO₂ exchange

Jones, S., Ogée, J, Sauze, J., Wohl, S., Saavedra, N., **Maire, J.**,....& **Wingate, L.** (2017) *Hydrology Earth System Sci*

Ms Noelia Saavedra (2016) INRA-ISPA

Subject: Developing a high-throughput cryogenic extraction line to estimate the δ¹⁸O of leaf and soil water pools and CO₂ exchange

Jones, S., Ogée, J, Sauze, J., Wohl, S., Saavedra, N., **Maire, J.**,....& **Wingate, L.** (2017) *Hydrology Earth System Sci*
Gimeno, T., Saavedra, N., Ogée, J., Medlyn, B. & **Wingate, L.** (submitted) *J. of Exp. Bot.*

Ms Noelia Fernandez (2016) INRA-ISPA

Subject: Performing high-throughput cryogenic extractions to estimate the δ¹⁸O of stem and soil water pools and CO₂ exchange

Jones, S., Ogée, J, Sauze, J., Wohl, S., Saavedra, N., **Fernandez, N.**,....& **Wingate, L.** (2017) *Hydro Earth Sys Sci*

Ms Ana Gutierrez (2016) INRA-ISPA

Subject: Linking microbial biomass measurements to the δ¹⁸O of soil CO₂ exchange.

Kaisermann, A., Ogée, J, Sauze, J., Jones, S., Wohl, S., **Gutierrez, A.** ...& **Wingate, L.** (2018) *Atm Chem & Phy*

Mr Bastien Frejaville (2017-2018) INRA-ISPA

Subject: Performing high-throughput cryogenic extractions to estimate the δ¹⁸O of stem and soil water pools and CO₂ exchange

Dr Koen Hufkens (2017-2020) INRA-ISPA Marie Skłodowska Curie Fellowship

Subject: Linking microbial community structure to canopy microclimate and function

Hufkens, K....& **Wingate, L.** (submitted) *International Agrophysics*

Franz, D., ...**Hufkens, K., Wingate, L.** (submitted) *International Agrophysics*

Dr Camille Delvigne (2018-2019) INRA-ISPA FNR Fellowship

Subject: Silicon isotopes in plants

Dr Paula Martin-Gomez (2018-2020) INRA-ISPA Bordeaux Idex Fellowship

Subject: Isotopic signals of embolism in trees

STUDENTS

POSTGRADUATE STUDENTS

Dr Toshie Mizunuma (2010 - 2014), University of Edinburgh, **PhD** Co-Supervisor

Subject: Investigating the link between phenology and ecosystem function of temperate tree species using colour signals

Nagai, S.**Mizunuma, T.,Wingate, L.** et al., (submitted) *Ecological Research*

Plaza-Aguilar, A., Ogée, J., Morison, J., Wilkinson, M., **Mizunuma, T.**, et.al (in prep) *Methods Ecol. Evol.*

Wingate, L., Ogée, J., Cremonese, E., Filippa, G., **Mizunuma, T.** et al., (2015). *Biogeo. Disc.*

Mizunuma, T., Mencuccini, M., **Wingate, L.** et al., (2014) *Methods Ecol Evol.*

Mizunuma, T., Koyanagi, T., Mencuccini, M., Nasahara, K.N., **Wingate, L.** et al., (2011). *Plant Ecol.Div.*

Dr Andrés Plaza-Aguilar (2011 - 2016), University of Cambridge, PhD Supervisor

Subject: Investigating the link between phenology and ecosystem function of temperate tree species using colour signals

Wingate, L., Ogée, J., Cremonese, E., Filippa, G., **Mizunuma, T.** et al., (2015). *Biogeo. Disc.*

Plaza-Aguilar, A., Ogée, J., Morison, J., Wilkinson, M., et.al **Wingate, L.** (in prep) *Methods Ecol. Evol.*

Dr Joana Sauze (2013-2017), INRA-ISPA, **PhD** Co-Supervisor

Subject: Investigating the relationship of carbonic anhydrase activity in soils to environmental drivers using a multi-tracer approach

Ogée, J., **Sauze, J.**, Kesselmeier, J., Genty, B., Van Diest, H., Launois, T. & **Wingate, L.**, (2016) *Biogeosciences*

Gimeno, T., Royles, Ogée, J., Wohl, S., Jones, S., **Sauze, J.**, West, J., ...& **Wingate, L.** (2017) *New Phyt.*

Sauze, J., Ogée, J., Maron, P-A, Nowak, V., Wohl, S., Kaisermann, A....& **Wingate, L.** (2017) *Soil Bio.Biochem*

Sauze, J., Jones, S., **Wingate, L.**, Wohl, S. & Ogée, J. (2017) *Biogeosciences*

Kaisermann, A., Ogée, J., **Sauze, J.**, Jones, S., Wohl, S., ...& **Wingate, L.** (2018) *Atm Chem & Phy*

Meredith, L.,**Sauze, J.,....& Wingate, L.** (submitted) Soil Systems

Mr Yann Cochet (2016-present), INRA-ISPA, **PhD** Co-Supervisor

Subject: Modelling the impact of elevated CO₂, N fertilisation, drought and climate warming on wood anatomy and tree-ring wood density signals in adult trees: comparing empirical and process-based approaches

Mlle Tania Fort (2016-present), INRA-ISPA, **PhD** Co-Supervisor

Subject: Plant-microbiota interactions: influence of microclimate on leaf microbiota and feedback effects on leaf physiology and phenology

Mr Regis Burlett (2017-present), INRA-BIOGECO & INRA-ISPA, **PhD** Co-Supervisor

Subject: Investigating the causes of drought-induced mortality in trees

Gimeno, T., Royles, Ogée, J., Wohl, S., Jones, S., Sauze, J., West, J., **Burlett, R. & Wingate, L.** (2017) *New Phyt.*

Wingate, L., Ogée, J. Burlett, R., Bosc, A., Devaux, M., Grace, J., Loustau, D. & Gessler, A. (2010). *New Phyt.*

Wingate, L., Ogée, J. Burlett, R., & Bosc, A. (2010). *Global Change Biology.*

Mr Damien Herfurth (2010), University of Bordeaux, **MSc** Co-Supervisor

Subject: Modelling carbon and oxygen isotope signals in Pine trees

Ms Perrine Philippe (2010), University Henri-Poincaré, **MSc** Supervisor

Subject: Application of the use of digital photography to determine vegetation phenology

Ms Tamara Markovic (2011), University of Belgrade, **MSc** Supervisor

Subject: Investigating the inter-annual variability of cellulose carbon isotope composition in trees.

Ms Sarah Wilkinson (2011), University of Bangor, **MSc** Supervisor

Subject: Modelling the inter-annual variability in wood density and tracheid anatomy.

Wilkinson, S., Ogée, J., Domec, J-C., Rayment, M.B. & **Wingate, L.** (2015) *Tree Physiology.*

Ms Heather Plumpton (2013-2014), University of Cambridge, **MSc** Supervisor

Subject: Investigating the effects of elevated CO₂ and N fertilisation on the inter-annual variability of cellulose on wood density and carbon and oxygen isotope signals in trees.

Voelker, S. L.,**Plumpton, H.J.,.... & Wingate, L.**, (2015) *Global Change Biology.*

Ms Regina Hirl (2014), Technical University of Munich, **MSc** Co-Supervisor

Subject: Modelling the impact of climate on the oxygen isotope composition of grassland water pools and cellulose signals

Ms Juliette Maire (2015) University of Lorraine, **MSc** Supervisor

Subject: Investigating the link between digital camera colour signals and leaf pigments.

Ms Noelia Saavedra (2015), Rey Juan Carlos University, Madrid, **MSc** Co-Supervisor

Subject: Investigating the impact of drought on nocturnal stomatal conductance

Ms Retno Novvitasari Hery Daryono (2017) University of Bordeaux, **MSc** Supervisor

Subject: Measuring earthworm carbonic anhydrase activity using COS and CO¹⁸O.

Ms Elise Likiliki (2017) University of Bordeaux, **MSc** Co-Supervisor

Subject: Investigating the phenology of COS emissions from bryophytes..

Mr Ludovic Lacombe (2018) University of Bordeaux, **MSc** Supervisor

Subject: Fluxes of COS from *Alliaria petiolata*.

UNDERGRADUATE STUDENTS

Mr Tom Flatman (2013), University of Stirling, Scotland **BSc**. Thesis Supervisor

Subject: Effects of elevated CO₂ on tracheid anatomy in Loblolly pine trees

Mr Callum Tyler (2015), Queensland University of Technology, Australia **BSc**. Internship Supervisor

Subject: Implementation of a web-interface to visualise real-time imagery from a European Phenology Camera Network

Mr Thomas Sajus (2016), University of Bordeaux, **BSc**. Internship Supervisor

Subject: Development of a fully automated manifold and user-interface for the rapid measurement of the stable isotope composition of CO₂.

APPENDIX III : FUNDING MY RESEARCH

RESEARCH PROJECTS CO-ORDINATED

Co-ordinator of an ANR-Bordeaux Idex Postdoctoral Fellowship

«ISOEMB The ISOtopic signature of drought-induced EMBolism: from the leaf to the tree stem»
with Dr Paula Martin-Gomez
[2018] (€127,530)

Co-ordinator of a Marie Sklodowska-Curie Actions Intra-European Fellowship Award

«COBADIM - Characterising Congo Basin drought resilience: an integrative modelling approach»
with Dr Koen Hufkens
[2018] (€173,076)

Co-ordinator of a Fulbright/Aquitaine Regional Council Foreign Scholarship Award

«DITECC – Dual Isotopes in Tree Ecophysiological Responses to Climate Change»
with Dr Jason West (Texas A & M University)
[2015]

Co-ordinator of a Marie Sklodowska-Curie Actions Intra-European Fellowship Award

«USIFlux Unveiling Stomata 24/7: Using StIable Isotopes and COS to quantify diurnal and nocturnal carbon and water vegetation-atmosphere Fluxes under future climate scenarios»
with Dr Teresa Gimeno
[2015] (€173,076)

Co-ordinator of an ANR-Bordeaux Idex Postdoctoral Fellowship

«USIFlux Unveiling Stomata 24/7: Using StIable Isotopes and COS to quantify diurnal and nocturnal carbon and water vegetation-atmosphere Fluxes under future climate scenarios»
with Dr Teresa Gimeno
[2014] (€127,530)

Co-ordinator of a European Research Council Starting Grant

«SOLCA Carbonic Anhydrase: where the global CO₂, COS and H₂O cycles meet»
[2013] (€1,701,882)

Co-ordinator of an INRA Department EFPA Projet Innovant

«Modelling the impact of a long term (16-yr) elevated CO₂ and N fertilisation experiment

on wood anatomy and tree ring cellulose $\delta^{13}\text{C}$ signals in adult trees»
[2013] (€8,000)

Co-ordinator of a Becas Chile Phd Fellowship

« Investigating the link between phenology and ecosystem function of temperate tree species using colour signals »

with Dr Andrés Plaza-Aguilar

[2011-2016](€160,000)

Co-ordinator of an INRA/ANR Phd Fellowship

« Investigating the relationship of carbonic anhydrase activity in soils to environmental drivers using a multi-tracer approach »

with Dr Joana Sauze

[2013-2016](€98,000)

Co-ordinator of an INRA Department EFPA and EA Equipment Moyenne Grant

«Laser spectrometer for the fast measurement of stable isotope ratios ($^{18}\text{O}/^{16}\text{O}$, $^{17}\text{O}/^{16}\text{O}$ and D/H) in water vapour and liquid water »

[2012] (€35,000)

Co-ordinator of a Jim Gray Seed Grant from Microsoft Research

«Develop web-based tools for the study of phenology using a digital camera network»

[2010] (\$49,000)

Co-ordinator of a Natural Environment Research Council Advanced Fellowship Award

«Linking the atmosphere and terrestrial biosphere carbon and water cycles using oxygen isotopes»

[2009] (£635,765)

Co-ordinator of a Marie Curie Intra-European Fellowship Award

«Linking the atmosphere and terrestrial biosphere carbon and water cycles using oxygen isotopes»

[2009] (€173,000)

Co-ordinator of an INRA Department EFPA Projets Innovants Award

«Towards a better understanding of the oxygen isotopic signature of CO_2 released by vegetated soils »

[2008] (€8000)

IMPLICATION IN RESEARCH PROJECTS

CNRS-ISOTOP_AAP 2018

co-ordinated by Dr Pierre Cartigny IPGP, Paris

« Analyse des trois rapports isotopiques du soufre, du carbone et de l'oxygène de COS et détermination des fractionnements isotopiques associés à son incorporation par les plantes.»

Contribution: Named co-investigator and co-author
[2018](€25,487)

Labex Cote Project

co-ordinated by Dr Corinne Vacher INRA BIOGECO

«MicroMic Forecasting changes in microclimate and microbial diversity within tree canopies under climate change scenarios»

Contribution: Named investigator and co-author
[2017-2019](€181,599)

EU COST ACTION CA15226

co-ordinated by Prof Roberto Tognetti , Italy

« CLIMO Climate Smart Forestry in Mountain Regions »

Contribution: Working Group III Co-ordinator
[2016-2019]

Université of Bordeaux PhD Bourse

co-ordinated by Dr Corinne Vacher INRA BIOGECO

« Plant-microbiota interactions: influence of microclimate on leaf microbiota and feedback effects on leaf physiology and phenology »

Contribution: Co-supervisor and co-author
[2016-2019](€98,000)

Projet Region Aquitaine

co-ordinated by Dr Corinne Vacher INRA BIOGECO

«ATHÉNÉ ATtenuation des effets du cHangement climatique sur la biodiversité et les services ecosystemiques des forets d'AquitaiNÉ»

Contribution: Named investigator and co-author
[2016-2019](€300,604)

Project ANR Blanc

co-ordinated by Dr Jérôme Ogée INRA ISPA

«ORCA **O**n the **R**egulation of **C**arbonic anhydrase **A**ctivity and the COS and CO¹⁸O fluxes in terrestrial plants»
[2013-2017](€645,775)

High Council for Scientific and Technological Co-operation between France-Israel Grant
co-ordinated by Dr Jérôme Ogée INRA ISPA
«An integrated analysis of water use in Mediterranean Pine Forests»
[2009](€65,000).

UK-Japan 2008 Collaborative Project Grant
Co-ordinated by Prof. John Grace Univ. of Edin.
«Joining expertise of UK and Japan to install new cameras to observe impacts of climate warming»
[2009](1,500,000 Japanese Yen)

Project ANR Blanc
co-ordinated by Dr Jérôme Ogée INRA ISPA
«MIST Modelling Isotope Signals in Tree Rings»
[2007-2010](€328,028)

NERC Large Equipment Bid
Co-ordinated by Professor John Grace Univ of Edin.
«Tunable Diode Laser Spectrometer to study Ecosystem Gas Exchange»
[2004](£100,000)

APPENDIX IV : COLLABORATIONS

PAST AND PRESENT COLLABORATORS

- Jan 2016- present** **Université de Laval** | **Quebec, Canada**
Collaboration with Dr Alexis Achim
Investigating the impact of elevated CO₂ and N fertilisation on inter and intra-annual wood density signals in trees
- April 2017- present** **INRA Genosol** | **Dijon, France**
Collaboration with Dr Samuel Mondy
Investigating the metagenomic and metatranscriptomic response of European soils to N fertilisation.
- April 2016- present** **INRA BFP** | **Bordeaux, France**
Collaboration with Drs Frederic Delmas & Frederic Gevaudrant
Measuring the pH response of COS uptake by a range of different classes of Carbonic anhydrase.
- April 2016- present** **INRA Biogeco** | **Bordeaux, France**
Collaboration with Dr Corinne Vacher
Measuring and modelling the influence of microclimate on phyllosphere community structure.
- July 2015- present** **Texas A&M** | **Texas, USA**
Collaboration with Dr Jason West
Investigating the role of mesophyll conductance in the leaf-atmosphere exchange of COS and CO¹⁸O of different plants.
- Sept 2015- present** **Carnegie Institute of Science** | **Stanford, USA**
Collaboration with Drs Mary Whelan & Joe Berry
Modelling the soil-atmosphere exchange of COS and CO¹⁸O across different ecosystems.
- Sept 2015- present** **The University of Arizona** | **Arizona, USA**
Collaboration with Dr Laura Meredith and Rick Wehr
Measuring and modelling the variability of soil carbonic anhydrase activity across ecosystems and the link to soil microbial communities.
- Feb 2015- present** **University of Harvard** | **Massachusetts, USA**
Collaboration with Drs Roisin Commane and Rick Wehr
Modelling the ecosystem-atmosphere exchange of COS, ¹³CO₂ and CO¹⁸O at a deciduous broadleaf forest.
- Jan 2013- present** **Technical University of Munich** | **Munich, Germany**

Collaboration with Prof. Hans Schynder and Regina Hirl

Modelling the oxygen isotope composition of grassland water pools and sward cellulose using MuSICA.

Jan 2014- 2017 University of Basel | Basel, Switzerland

Collaboration with Prof. Ansgar Kahmen & Dr Daniel Nelson

Linking temporal variations in leaf water pools to wax stable isotope biomarkers.

Jan 2012- 2018 INRA Agroecology, University of Dijon | Dijon, France

Collaboration with Dr Pierre-Alain Maron

Linking microbial biodiversity and carbonic anhydrase activity across biomes.

Jan 2010- 2016 University of Cambridge | Cambridge, UK

Collaboration with Prof. Howard Griffiths and Dr Jessica Royles

Reconstructing primary productivity in Antarctica over the past 3000 yrs using $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals in peat moss banks.

Jan 2011- 2015 Max Planck Institute for Biogeochemistry | Jena, Germany

Collaboration with Dr Mirco Migliavacca

Developing algorithms for extracting phenological parameters from digital images.

Jan 2011- 2015 Environmental Protection Agency of Aosta Valley, ARPA | Torgnon, Italy

Collaboration with Drs Edoardo Cremonese, Marta Galvagno and Gianluca Filippa

Developing algorithms for extracting phenological parameters from digital images.

Jan 2009- 2015 University of Edinburgh | Edinburgh, UK

Collaboration with Prof. John Grace, Prof Maurizio Mencuccini, Dr Caroline Nichol, Dr Toshie Mizunuma

Linking canopy phenology to net ecosystem exchange in temperate forests

Jan 2010- 2012 University of Chicoutimi | Quebec, Canada

Collaboration with Dr Sergio Rossi and Dr Annie Deslauriers

Reconstructing past growing season $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals at Northern tree line sites.

Jan 2010- 2012 University of Helsinki | Helsinki, Finland

Collaboration with Dr Pertti Hari, Dr Eero Nikinimaa, Dr Eloni Sonninen, Dr Timo Vesala, Dr Emmi Hiltunen

Reconstructing past growing season $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals at Northern tree line sites.

Jan 2010- 2012 University of Pierre & Marie-Curie | Paris, France

Collaboration with Dr Camille Risi

Validating water isotope signals in ecosystem water pools using the isotope-enabled ORCHIDEE land surface model.

- May 2010- 2012 University of Tokyo** | Tokyo, Japan
Collaboration with Dr Kei Yoshimura
 Reconstructing past growing season $\delta^{18}\text{O}$ signals in cellulose using the isotope-enabled global circulation model, IsoGSM
- May 2010- 2012 Technische Universität Dresden** | Dresden, Germany
Collaboration with Professor Barbara Köstner and Dr Thomas Grünwald
 Linking growing season length to tree-ring cellulose deposition and phenology
- Jan 2009- 2011 Leibniz-Zentrum für Agrarlandschaftsforschung** | Berlin, Germany
Collaboration with Dr Arthur Gessler
 Investigating post-photosynthetic isotope fractionation processes in a Maritime pine ecosystem.
- Jan 2009- 2013 University of Tsukuba** | Tsukuba, Japan
Collaboration with Dr Kenlo N. Nasahara – UK-Japan Collaborative Project Grant
 Linking canopy phenology and net ecosystem exchange to remotely sensed indices using webcams in the UK and Asia.
- Mar 2008- present University of Harvard** | Massachusetts, USA
Collaboration with Dr Andrew Richardson
 Linking canopy phenology and net ecosystem exchange across FLUXNET sites using an international webcam network.
- Mar 2008- present Helmholtz Institute** | Leipzig, Germany
Collaboration with Dr Matthias Cuntz
 Modelling the impact of leaf and soil isotopic gas exchange on the $\delta^{18}\text{O}$ of atmospheric CO_2 at the global scale.
- Mar 2008- present LEMP, CEA-CNRS** | Cadarache, France
Collaboration with Dr Bernard Genty – Marie Curie Intra-European Fellowship (LATIS)
 Developing laboratory and field techniques to estimate the carbonic anhydrase activity of soils.
- Oct 2007- 2011 BIOEMCO, Université Pierre et Marie Curie** | Thiverval-Grignon, France
Collaboration with Dr Thierry Bariac, Dr Ulli Seibt and Dr Kadmiel Maseyk – ANR Project MIST
 Investigating the temporal variability in $\text{H}_2^{18}\text{O}^{16}\text{O}$ and $\text{C}^{18}\text{O}^{16}\text{O}$ signals exchanged between a pine ecosystem and the atmosphere.
- Dec 2006- present BIOGECO, INRA** | Pierroton, France
Collaboration with Dr Didier Bert
 Reconstructing past growing season $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ tree ring signals at European, Israeli and North American flux sites.
- Jun 2004- 2008 Université Paris-Sud Orsay** | Orsay, France

Collaboration with Professor Jaleh Ghashghaie and Dr Camille Bathellier
Investigating post-photosynthetic carbon isotope fractionation processes in a Mediterranean ecosystem.

Jun 2004- 2007 Stanford University **| San Francisco, USA**
Collaboration with Professor Joe Berry and Dr Ulli Seibt
Investigating the $\delta^{18}\text{O}$ signals of soil and leaf CO_2 exchange

Jun 2004- present Weizmann Institute of Science **| Rehovot, Israel**
Collaboration with Professor Dan Yakir, Dr Eyal Rotenberg and Yakir Preisley
An integrated analysis of water use in Mediterranean Pine forests.

Jun 2003- present Universidade Técnica de Lisboa **| Lisbon, Portugal**
Collaboration with Professor Joao Santos Pereira, Dr Raquel Lobo de Vale and Mr Pedro Almeida
Investigating the temporal variability in $\text{H}_2^{18}\text{O}^{16}\text{O}$ and $^{13}\text{C}^{18}\text{O}^{16}\text{O}$ signals exchanged between Mediterranean soils and the atmosphere.

APPENDIX V : COMMUNICATIONS

ORAL CONFERENCE AND SEMINAR PRESENTATIONS

- [1] Barbeta, A., Jones, S., Clavé, L., Fréjaville, B., Wingate, L. & Ogée, J. Ecohydrological study of a refugial *Fagus sylvatica* population using stable isotopes Geophysical Research Abstracts, Vol. 20, EGU2018-18983, Vienna, France, 9-13th April 2018
- [2] Kaisermann, A., Ogée, J., Sauze, J., Wohl, S., Jones, S., Whelan, M., Meredith, L., Launois, T. & Wingate, L. Disentangling the rates of carbonyl sulphide (COS) production and consumption and their dependency with soil properties across biomes and land use types. Geophysical Research Abstracts, Vol. 20, EGU2018-13199, Vienna, France, 9-13th April 2018
- [3] Gimeno, T. E., Saavedra-Berlanga, N., Ogée, J., Medlyn, B.E. & Wingate, L. Testing for non-stomatal limitations to optimisation behaviour under drought on contrasting plant functional types. Geophysical Research Abstracts, Vol. 20, EGU2018-7659, Vienna, France, 9-13th April 2018
- [4] Wingate, L. Promoting frontier Earth system research and female role models using dedicated geoscience symposiums. Geophysical Research Abstracts, Vol. 20, EGU2018-5132, Vienna, France, 9-13th April 2018 (INVITED)
- [5] Wingate, L., Using a multi-functional enzyme-based approach to constrain the magnitude of the terrestrial biosphere CO₂ sink. CREAM, Barcelona, Spain, 14th March 2018 (INVITED)
- [6] Wingate, L., Using novel approaches to estimate the strength of the terrestrial biosphere CO₂ sink. From the deep past to the Anthropocene: coupling Earth system function to climatic change. Talence, France, 8-9th March 2018 (INVITED)
- [7] Wingate, L., The SOLCA ERC project: a personal reflection on perseverance. ERC information and networking event. Talence, France, 7th March 2018 (INVITED)
- [8] Wingate, L., Ogée, J., Launois, T., Sauze, J., Jones, S., Kaisermann, A., Wohl, S., Meredith, L. & Cuntz, M. Linking variations in soil-atmosphere COS exchange to soil community structure. INRA, Nancy, France, 23rd Nov 2017
- [9] Wingate, L., Ogée, J., Launois, T., Sauze, J., Jones, S., Kaisermann, A., Wohl, S., Meredith, L. & Cuntz, M. The impact of microbial carbonic anhydrase activity on atmospheric concentrations of CO¹⁸O and COS at large scales. The 10th International Carbon Dioxide Conference, Interlaken, Switzerland, 24th August 2017
- [10] West, J., Ogée, J., Burlett, R., Gimeno, T., Genty, B., Jones, S., Wohl, S., Bosc, A., Cochet, Y., Domec, J.C. & Wingate, L. Partitioning internal diffusion resistances and CO₂ isotope exchange in leaves. *Proceedings of the annual meeting of the Ecological Society of America (ESA)*, Portland, Oregon, 6th-11th Aug 2017.
- [11] Wingate, L., Preisler, Y., Bert, D., Rotenberg, E., Yakir, D., Maseyk, K. & Ogée, J. Modelling drought-induced dieback of Aleppo pine at the arid timberline. Swiss Federal Institute for Forest, Snow and Landscape Research, WSL Seminar Series, Zurich, Switzerland, 28th -29nd June 2017 (INVITED)
- [12] Likiliki, E., Gimeno, T., Ogée, J. & Wingate, L. Acclimation and seasonal coupling of photosynthesis, respiration and carbonyl sulfide exchange in bryophytes. XXI Simposio de botánica criptogámica, Aranjuez, 20th-24th June, 2017.
- [13] Gimeno, T., Ogée, J. & Wingate, L. Estimating the contribution of bryophytes to the atmospheric COS budget. Geophysical Research Abstracts, Vol. 19, EGU2017-13117, Vienna, Austria, 26th April 2017.

- [14] **Wingate, L & Gimeno, T.** Using novel approaches to estimate the CO₂ sink strength of the terrestrial biosphere. Fédération de recherche biologie intégrative et écologie, Bordeaux, France, 17th Feb 2017 (**INVITED**)
- [15] **Gimeno, T.,** Ogée, J., Royles, J., Gibon, Y., **West, J., Burlett, R., Jones, S., Sauze, J., Wohl, S.,** Bernard, C., Genty, B. & **Wingate, L.** Bryophyte gas exchange dynamics reveal a significant COS sink in the dark and source in the light. XIV Medecos & XIII AEET Spanish Ecology Meeting, Sevilla, Spain, 2nd, Feb 2017
- [16] **Wingate, L.** Developing multi-tracer bridges to tackle Earth system puzzles. Earth System Science Symposium. University of Zurich 30th, Jan 2017 (**INVITED**)
- [17] Knauer, J., De Kauwe, M.G., Lin, Y.S., Duursma, R., Williams, C.A., Arneeth, A., Clement, R., Isaac, P.R., Linderson, M-L., Limousin, J-M., Meir, P., Martin-St. Paul, N.K., **Wingate, L.** & Medlyn, B. Discrepancies between leaf and ecosystem measures of water use efficiency. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 12th-16th Dec. 2016
- [18] **West, J.,** Ogée, J., **Burlett, R., Gimeno, T.,** Genty, B., **Jones, S., Wohl, S.,** Bosc, A., **Cochet, Y., Domec, J.C. & Wingate, L.** Towards improved quantification of internal diffusion resistances and CO₂ isotope exchange in leaves. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 12th-16th Dec 2016
- [19] **Jones, S., Sauze, J.,** Ogée, J., **Wohl, S.,** Bosc, A. & **Wingate, L.** An approach to non-destructively measure soil carbonic anhydrase activity and soil water δ¹⁸O. British Ecological Society, Liverpool, UK 12th-15th Dec 2016
- [20] **Wingate, L.** L'impact de l'anhydrase carbonique sur les concentrations atmosphériques globales de CO¹⁸O et COS. Après-midi scientifique de la Société française des isotopes. Muséum national d'histoire naturelle, Paris France 7th Dec 2016 (**INVITED**)
- [21] **Wingate, L.** Using novel approaches to estimate the strength of the terrestrial biosphere CO₂ sink. Université of Laval, Quebec Canada 17th Nov 2016 (**INVITED**)
- [22] **Wingate, L.,** The impact of carbonic anhydrase on the atmospheric concentrations of CO¹⁸O and COS at large scales. Global Change Seminar Series, University of Edinburgh, Edinburgh, UK 26th Oct 2016 (**INVITED**)
- [23] **Gimeno, T., Wingate, L.** Bryophyte gas-exchange dynamics along varying hydration status reveal significant COS emission in the light. The Biosphere-Atmosphere Exchange and Global Budget of Carbonyl Sulfide Workshop, Hyytiala, Finland 5-9th September 2016.
- [24] Meredith, L., Singer, E., Boye, K., Whelan, M., von Sperber, C., Pang, E., **Wingate, L.** Ogée, J., Berry, J. & Welander, P. Microbial, physical and chemical drivers of COS and ¹⁸O-CO₂ exchange in soils. 16th International Symposium on Microbial Ecology, Montreal, 21-26th Aug 2016
- [25] **Wingate, L.** Developing multi-tracer theory to constrain critical zone processes in land surface models. Soil Resources Symposium, ETH, Zurich, Switzerland 7th July 2016 (**INVITED**).
- [26] **Hirl, R.,** Ogée, J., **Wingate, L. & Schnyder, H.** Stable oxygen and carbon isotope signals in cellulose of temperate humid grassland vegetation: an integrative examination using the MuSICA model. Plant Biology Europe EPSO Congress, Prague, Czech Republic, 26th -30th June 2016.
- [27] **Launois, T.,** Peylin, P., Belviso, S., Bopp, L., Ogée, J., **Wingate, L. & Cuntz, M.** A mechanistic description of the global COS cycle consistent with atmospheric measurements and its potential to evaluate gross primary production of vegetation models. Geophysical Research Abstracts, Vol. 18, EGU2016-14926, Vienna, Austria, 17th -22nd April 2016.
- [28] **West, J.,** Ogée, J., **Burlett, R., Gimeno, T.,** Genty, B., **Jones, S., Wohl, S.,** Bosc, A. & **Wingate, L.** A new approach to quantifying internal diffusion resistances and CO₂ isotope exchange in leaves. Geophysical Research Abstracts, Vol. 18, EGU2016-16367, Vienna, Austria, 17th -22nd April 2016.

- [29] Ogée, J., Wehr, R., Commane, R., [Launois, T.](#), Meredith, L., Munger, B., Nelson, D., Saleska, S., Zahniser, M. Wofsy, S. & **Wingate, L.** Developing multi-tracer approaches to constrain the parameterisation of leaf and soil CO₂ and H₂O exchange in land surface models. Geophysical Research Abstracts, Vol. 18, EGU2016-16764, Vienna, Austria, 17th -22nd April 2016.
- [30] **Wingate, L.**, Preisler, Y., Bert, D., Rotenberg, E., Yakir, D., Maseyk, K. & Ogée, J. Modelling drought-induced dieback of Aleppo pine at the arid timberline. Geophysical Research Abstracts, Vol. 18, EGU2016-13207, Vienna, Austria, 17th -22nd April 2016.
- [31] **Wingate, L.** Developing multi-tracer theory to constrain soil processes in land surface models. Soil processes and climate models. Inaugural workshop for the International Soil Modelling Consortium, Austin, Texas, USA 29th March-1st April 2016 (**INVITED**).
- [32] Ogée, J., [Sauze, J.](#), Kesselmeier, J., Genty, B., Whelan, M., Van Diest, H., Launois, T. & **Wingate, L.** A new mechanistic framework to predict OCS fluxes from soils. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 14th-18th Dec. 2015.
- [33] **Wingate, L.**, Wehr, R., Commane, R., Ogée, J. [Sauze, J.](#), [Jones, S.](#), [Launois, T.](#), [Wohl, S.](#), Whelan, M., Meredith, L., Genty, B., [Gimeno, T.](#), Kesselmeier, J., Bosc, A., Cuntz, M., Munger, B., Nelson, D., Saleska, S., Wofsy, S. & Zahniser, M. The impact of Carbonic Anhydrase on the partitioning of leaf and soil CO¹⁸O and COS gas exchange across scales. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 14th-18th Dec. 2015 (**INVITED**).
- [34] [Jones, S.](#), [Sauze, J.](#), Ogée, J., [Wohl, S.](#) & **Wingate, L.** Simultaneous and non-destructive measurement of soil surface water d¹⁸O and carbonic anhydrase activity. Thermo Scientific IRMS Users Meeting, Nantes, Bordeaux, France, 26th-27th Nov. 2015 (**INVITED**).
- [35] **Wingate, L.** Investigating the impact of Carbonic Anhydrase on the atmospheric concentrations of CO¹⁸O and COS across scales. 8^{ème} journée thématique de l'Observatoire Aquitain des Sciences de l'Univers, Bordeaux, France, 19th November 2015 (**INVITED**).
- [36] **Wingate, L.** and the European ICOS phenology camera network. Opportunities to investigate the functional phenology of ecosystems using a European Phenology Camera Network. French ICOS Infrastructure Inauguration, Pierroton, France, 24th Sept 2015 (**INVITED**).
- [37] **Wingate, L.**, Preisler, Y., Bert, D., Rotenberg, E., Yakir, D., Lepoittevin, C., Maseyk, K. & Ogée, J. Investigating drought-induced dieback of Aleppo pine at the arid timberline. Xyleme International Meeting, Bordeaux, France, 7th-9th September, 2015.
- [38] [Gentsch, L.](#), Ogée, J., **Wingate, L.**, Sturm, P., Siegwolf, R., Werner, R.A., Buchmann, N. & Knohl, A. Linking carbon isotope signatures of night-time leaf-respiratory and daytime assimilatory CO₂ fluxes observed with laser spectrometry under field conditions. Geophysical Research Abstracts, Vol. 17, EGU2015-1021, Vienna, Austria, 13th -17th April 2015.
- [39] [Hirl, R.](#), Schnyder, H., Auerswald, K., Vetter, S., Ostler, U., Schleip, I., **Wingate, L.** & Ogée, J. Seasonal and inter-annual dynamics in the stable oxygen isotope compositions of water pools in a temperate humid grassland ecosystem: results from MIBA sampling and MuSICA modelling. Geophysical Research Abstracts, Vol. 17, EGU2015-9312, Vienna, Austria, 13th -17th April 2015.
- [40] Achim, A., [Plumpton, H.](#), Auty, D., Ogée, J., McCarthy, H., Bert, D., Domec, J.-C., Oren, R. & **Wingate, L.** Can rising CO₂ concentrations in the atmosphere mitigate the impact of drought years on tree growth? Geophysical Research Abstracts, Vol. 17, EGU2015-12638, Vienna, Austria, 13th -17th April 2015.
- [41] [Sauze, J.](#), Ogée, J., [Launois, T.](#), Kesselmeier, J., Van Diest, H. & **Wingate, L.** A new mechanistic framework to predict OCS fluxes in soils. Geophysical Research Abstracts, Vol. 17, EGU2015-5209, Vienna, Austria, 13th -17th April 2015.

- [42] Ogée, J., **Wingate, L.**, Bosc, A. & Burrell, R. &. Seasonal variations in soil carbonic anhydrase activity in a pine forest ecosystem as inferred from soil CO¹⁸O flux measurements. Geophysical Research Abstracts, Vol. 17, EGU2015-5342, Vienna, Austria, 13th -17th April 2015.
- [43] **Wingate, L.** and the European Phenology Camera Network. Opportunities to investigate the functional phenology of ecosystems using a European Phenology Camera Network. Geophysical Research Abstracts, Vol. 17, EGU2015-4701, Vienna, Austria, 13th -17th April 2015.
- [44] **Wingate, L.** and the European Phenology Camera Network. Opportunities to investigate the functional phenology of ecosystems using a European Phenology Camera Network. Dept. of Organismic Ecology and Biology, University of Harvard, Massachusetts, Boston, Feb 2015.
- [45] **Wingate, L.** Impact of microbial carbonic anhydrase on the atmospheric concentrations of CO¹⁸O and COS at large scales. Plants and Climate Seminar Series, Dept. Earth and Planetary Sciences, University of Harvard, Massachusetts, Boston, Feb 2015 (**INVITED**)
- [46] **Plaza-Aguilar, A.**, Ogée, J., Morison, J., Wilkinson, M., **Mizunuma, T.**, Eaton, E., Griffiths, H., Grace, J. & **Wingate, L.** Comparing seasonal differences in the phenology and physiology of Oak and Ash trees using RGB signals. Joint meeting of the British Ecological Society and Société Française d'Ecologie, Grand Palais, Lille, France 9th-12th December 2014
- [47] **Wingate, L.** Impact of microbial carbonic anhydrase on the atmospheric concentrations of CO¹⁸O and COS at large scales. Joint meeting of the British Ecological Society's Plants, Soils, Ecosystems and Plant Environmental Physiology special interest groups: Carbon cycling: from plants to ecosystems, University of Manchester 16th-17th October 2014 (**INVITED**)
- [48] **Wingate, L.** Impact of ecosystems on the atmospheric concentrations of CO¹⁸O and COS at different scales. LabEX CÔTE International Summer School "Transfer and interactions between ecosystems", Bordeaux 16th-20th June 2014 (**INVITED**).
- [49] Royles, J., Amesbury, M., Ogée, J., **Wingate, L.**, Convey, P., Hodgson, D., Griffiths, H., Leng, M., Charman, D. Stable isotopes and Antarctic moss banks: plants and soil microbes respond to recent warming on the Antarctic Peninsula., EGU General Assembly, Geophysical Research Abstracts, Vol. 16, EGU2014_5256, Vienna, Austria, 30th April, 2014
- [50] Migliavacca, M., Cremonese, E., **Wingate, L.**, Galvagno, M., Filippa, G., Ogée, J., **Mizunuma, T.**, Richardson, A. & Sonnentag, O. NEON Phenocam Workshop, Boulder, Colorado, USA 8th -11th October 2013
- [51] **Wingate, L.** & Ogée, J., Seasonal contribution of soil CO₂ invasion to the total CO¹⁸O flux from a pine forest ecosystem, AGU Chapman Conference: Soil mediated drivers of coupled biogeochemical and hydrological processes across scales 2013, Biosphere 2, Arizona, USA 21st -24th October 2013 (**INVITED**).
- [52] Ogée, J. & **Wingate, L.** Global estimates of land photosynthesis inferred from the global budget of δ¹⁸O in atmospheric CO₂: the crucial role of soil micro-organisms , AGU Chapman Conference: Soil mediated drivers of coupled biogeochemical and hydrological processes across scales 2013, Biosphere 2, Arizona, USA 21st -24th October 2013 (**INVITED**).
- [53] **Wingate, L.** & Ogée, J. Investigating high-resolution stable isotope signals of annual tree rings across a moisture gradient with the MuSICA model. COST-SIBAE Meeting: Challenges in the applications of stable isotopes across disciplines and scales, Wroclaw, Poland, 14th-19th May 2013 (**INVITED**).
- [54] Ogée, J. & **Wingate, L.** A process-based interpretation of the stable C and O isotope signals in the soil-plant-atmosphere continuum using the ecosystem model MuSICA. COST-SIBAE Meeting: Challenges in the applications of stable isotopes across disciplines and scales, Wroclaw, Poland, 14th-19th May 2013 (**INVITED**).

- [55] **Gentsch, L.**, Sturm, P., **Wingate, L.**, Ogée, J., Siegwolf, R., Hammerle, A., Plüss, P., Baur, T., Barthel, M., Buchmann, N. & Knohl, A. COST-SIBAE Meeting: Challenges in the applications of stable isotopes across disciplines and scales, Wroclaw, Poland, 14th-19th May 2013
- [56] **Gentsch, L.**, Sturm, P., Hammerle, A., Siegwolf, R., **Wingate, L.**, Ogée, J., Barthel, M., Plüss, P., Baur, T., Buchmann, N. & Knohl, A. Field measurements of photosynthetic ¹³C discrimination of *Fagus sylvatica* branches using laser spectrometry. JESIUM conference, Leipzig, Germany, 2nd -7th September 2012
- [57] Griffiths, H., Meyer, M., Royles, J., Horwath, A., Ogée, J., **Wingate, L.** & Villarreal, J-C. Crossing the boundaries: Photosynthetic limitations and water use in association with bryophyte morphological progression and phylogeny. Society of Experimental Biology Symposium, Salzburg, Austria, 28th June - 2nd July 2012.
- [58] **Wingate, L.** & Ogée, J. Interpreting the stable isotope composition of tree-ring cellulose. European Science Foundation Workshop, The significance of xylem hydraulic plasticity for reconstructing past environments, Kippel, Switzerland, 15th-17th May 2012. (**INVITED**).
- [59] Ogée, J. & **Wingate, L.** How complex do process-based models need to be to interpret high-resolution tree-ring stable isotope variations? Tree Rings in Archaeology, Climatology and Ecology conference, Potsdam, Germany, 9th-12th May 2012. (**INVITED**).
- [60] Ogée, J., **Wingate, L.** et al., Modelling Isotope Signals in Tree rings. ANR Colloque Changements Environnementaux, Bordeaux, France, 21st-22nd May 2012
- [61] Gessler, A., **Wingate, L.**, Ogée, J., Offermann, C., Kodama, N. The link between assimilation and belowground processes - stable isotopes as tools to assess carbon transfer. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 5th-9th Dec. 2011
- [62] Blonquist, J.M., **Wingate, L.**, Ogée, J. & Bowling, D. Constraining canopy transpiration and gross primary productivity with measurements of photosynthetic ¹³C discrimination. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 5th-9th Dec. 2011
- [63] Griffiths, H., Royles, J., Horwath, A., Hodell, D., Convey, P., Hodgson, D., **Wingate, L.** & Ogée, J. Bryophytes as climatic indicators: moss and liverwort photosynthetic limitations and carbon isotope signals in organic material and peat deposits. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 5th-9th Dec. 2011
- [64] **Wingate, L.** and the European FLUXNET webcam network. Keeping an eye on the European carbon balance. PhenoAlp Conference 2011, Torgnon, Italy 12th -14th Oct 2011 (**INVITED**).
- [65] Ogée, J. **Wingate, L.** Studium Conferences, Hydrogen isotopes as environmental recorders, Orléans, France, 15th – 16th Sept, 2011.
- [66] **Wingate, L.** and the European FLUXNET webcam network. On Detecting Phenology with Digital Cameras, Hyperspectral Remote Sensing and Eddy Covariance Measurements across Europe, FLUXNET Specnet Open Conference 2011, Berkeley, California, USA 7th -9th June 2011 (**INVITED**).
- [67] **Wingate, L.** Linking water and carbon cycles with the $\delta^{18}\text{O}$ of CO₂ fluxes. University of Antwerp, Antwerp, Belgium 2011 (**INVITED**).
- [68] **Wingate, L.** Linking water and carbon cycles with the $\delta^{18}\text{O}$ of CO₂ fluxes. Helmholtz Centre Potsdam, GFZ German Research Centre for Geosciences, Potsdam, Germany 2011 (**INVITED**).
- [69] **Wingate, L.** Principles of isotopic fractionation during photosynthesis and water cycling. University of Gothenburg, Gothenburg, Sweden 2011 (**INVITED**).
- [70] **Wingate, L.**, Ogée, J., Burlett, R., Bosc, A. Tunable diode laser spectroscopy techniques for ecosystem CO₂ isotopologue exchange studies. Short Course on Laser-based Isotope Ratio Analyzers: From the User Perspective SC2/IG16, EGU 2011, Vienna, Austria, 3rd -8th April 2011 (**INVITED**).

- [71] **Wingate, L.**, Ogée, J., Burlett, R., Bosc, A. Seasonal leaf and soil water isotope dynamics obtained from the $\delta^{18}\text{O}$ signals of CO_2 fluxes. EGU General Assembly, Geophysical Research Abstracts, Vol. 13, EGU2011_9334-2, Vienna, Austria, 3rd -8th April 2011.
- [72] Ogée, J., **Wingate, L.**, Bert, D., Stievenard, M., Jouanguy, J., Lambrot, C., Pierre, M. & Feron, A. Long-term plant response to drought revealed by tree ring stable isotope analysis. EGU General Assembly, Geophysical Research Abstracts, Vol. 13, EGU2011_6238-2, Vienna, Austria, 3rd -8th April 2011.
- [73] **Wingate, L.**, Ogée, J., Burlett, R., Bosc, A. Tunable diode laser spectroscopy techniques for ecosystem CO_2 isotopologue exchange studies. BASIN Meeting, San Francisco, California, USA, 12th Dec. 2010 (**INVITED**).
- [74] **Wingate, L.**, Ogée, J., Burlett, R., Bosc, A., Devaux, M., Loustau, D., Grace, J. & Gessler, A. Photosynthetic carbon isotope discrimination and its relationship to the carbon isotope signals of stem, soil and ecosystem respiration. American Geophysical Union (AGU) Fall Meeting, San Francisco, California, USA, 13th-17th Dec. 2010 (**INVITED**).
- [75] Barbour, M., **Wingate, L.** & Ogée, J. New stable isotopic techniques to investigate links between terrestrial carbon and water cycles. Canopy processes in a changing climate, IUFRO Canopy Processes Working Group Conference, Victoria and Tasmania, Australia, 7-15th Oct, 2010
- [76] **Wingate, L.**, and the FLUXNET webcam network. New approaches to monitor phenological change across flux sites. UK-Japan Workshop on Climate Change and Phenology, British Embassy, Tokyo, Japan 25th-27th August, 2010 (**INVITED**).
- [77] **Wingate, L.** Using a multi-tracer approach to constrain the contribution of CO_2 gross fluxes at large scales. University of Leeds, UK, 2010 (**INVITED**).
- [78] **Wingate, L.** Understanding the recent 'divergence' between tree-ring temperature proxies and temperature observations. University of Cambridge, Cambridge, UK, 2011.
- [79] **Wingate, L.**, Ogée, J., Burlett, R. & Bosc, A. Seasonal leaf and soil water isotope dynamics obtained from the $\delta^{18}\text{O}$ signals of CO_2 fluxes. WAVACS Workshop on the water isotopologues in the atmosphere. Université Pierre & Marie Curie, Paris, France, 27th – 30th April, 2010.
- [80] **Wingate, L.** Using stable isotopes to determine the contribution of respiration to ecosystem carbon fluxes in forests. 24th New Phytologist Symposium: Plant respiration and climate change: scaling from mitochondria to the globe, Oxford, UK 11th-14th April, 2010 (**INVITED**).
- [81] Ogée, J., **Wingate, L.**, Jouanguy, J. A multi-layer transport model of soil water isotopologues in the root zone: applications for the simulation of $^{18}\text{O}/^{16}\text{O}$ signals from soil CO_2 efflux and wood cellulose. *European Science Foundation Workshop, Stable Isotopes and Biogeochemical Cycles in Terrestrial Ecosystems*, Ascona, Switzerland, 21st-26th Mar, 2010.
- [82] **Wingate, L.**, Ogée, J., Maseyk, K., Burlett, R., Seibt, U., Bosc, A., Richard, P. & Bariac, T. Measuring and modelling the evaporative enrichment of water pools in Maritime pine trees over daily and seasonal time-frames. Annual Colleeque Xyleme-Eau-Croissance, Bordeaux, France, 23rd – 25th November, 2009.
- [83] Ogée, J., and **Wingate, L.** Le transport de l'eau dans les plantes vu sous l'angle de la géochimie isotopique. Annual Colleeque Xyleme-Eau-Croissance, Bordeaux, France, 23rd – 25th November, 2009.
- [84] **Wingate, L.**, Ogée, J., Burlett, R., Bosc, A., Devaux, M., Grace, J. & Loustau, D. Continuous measurement of $^{13}\text{CO}^{18}\text{O}$ fractionation during evapotranspiration, photosynthesis and respiration. Joint research symposium between France (INRA) – Japan (JSPS) on the use of stable carbon isotopes to understand the carbon cycle in forests, Kyoto, Japan, 2nd November 2009 (**INVITED**).
- [85] Ogée, J., **Wingate, L.**, Jouanguy, J., Bert, D., Lambrot, C., Devaux, M., Stievenard, M., Pierre, M., Loustau, D. & Berbigier, P. Can intra-annual stable isotope signals in tree-ring cellulose be used to extend Fluxnet

- data-model analysis to larger temporal and spatial scales? 8th Asiaflux Workshop, Sapporo, Japan 27th-29th October, 2009.
- [86] **Wingate, L.**, Richardson, A., Mizunuma, T., Nasahara, K.N., Saigusa, N., Muraoka, Y., Nagai, S., Jacobs, N., Sanchez-Azofeifa, G.A., Wilkinson, M., Morison, J., Köstner, B., Grünwald, T., Braswell, R., Grace, J. and the FLUXNET webcam network. Keeping an eye on the carbon balance. 8th Asiaflux Workshop, Sapporo, Japan 27th-29th October, 2009 (**INVITED**).
- [87] **Wingate, L. & Ogée, J.**, Modelling the oxygen isotope signals of H₂O and CO₂ between forested soils and the atmosphere. European Science Foundation Cost Action ES806, WG2 Workshop, Stable isotopes in biosphere-atmosphere-earth system research (SIBAE) Innsbruck, Austria, 23rd-25th Sept, 2009 (**INVITED**).
- [88] **Wingate, L.**, Burlett, R., Bosc, A., Grace, J., Loustau, D. and Ogée, J. Does a strong seasonal disequilibrium exist between the oxygen isotope signals of leaf and soil CO₂ exchange? Second mini symposium on the use of stable isotopes in tree physiology and forest ecology, Nancy, France, 3rd July 2009.
- [89] Ogée, J., **Wingate, L.**, Jouanguy, J., Bert, D., Lambrot, C., Devaux, M., Stievenard, M., Pierre, M., Loustau, D. & Berbigier, P. Can intra-annual stable isotope signals in tree-ring cellulose be used to extend Fluxnet data-model analysis to larger temporal and spatial scales? EGU General Assembly, Geophysical Research Abstracts, Vol. 11, EGU2009-2444, Vienna, Austria, 19th-24th April, 2009.
- [90] Ogée, J., Barbour, M.M., **Wingate, L.**, Bert, D., Bosc, A., Stievenard, M., Lambrot, C., Pierre, M., Bariac, T. & Dewar, R.C. A simple, single-substrate model to interpret intra-annual stable isotope signals in tree-ring cellulose. EGU General Assembly, Geophysical Research Abstracts, Vol. 11, EGU2009-2213, Vienna, Austria, 19th-24th April, 2009.
- [91] **Wingate, L.**, *Ogée, J., Cuntz, M., Genty, B., Reiter, I., Seibt, U., Peylin, P., Yakir, D., Miller, J., Burlett, R., Maseyk, K., Mencuccini, M., Pendall, E., Shim, J.H., Barbour, M.M., Hunt, J., Mortazavi, B., & Grace, J. The influence of soil carbonic anhydrase on the partitioning of gross CO₂ fluxes using the oxygen isotopes of CO₂ and water. EGU General Assembly, Geophysical Research Abstracts, Vol. 11, EGU2009-2424, Vienna, Austria, 19th-24th April, 2009.
- [92] **Wingate, L.**, Richardson, A., Weltzin, J.F., Nasahara, K.N. & Grace, J. and the FLUXNET Webcam Team. Keeping an eye on the carbon balance: linking canopy development and net ecosystem exchange using an international webcam network. European Geophysical Union (EGU) General Assembly, Geophysical Research Abstracts, Vol. 11, EGU2009-4489, Vienna, Austria, 19th-24th April, 2009 (**INVITED**).
- [93] **Wingate, L.**, Ogée, J., Seibt, U. and Cuntz, M. Do soil micro-organisms influence the oxygen isotope composition of atmospheric CO₂? JESIUM: 2nd European Stable Isotope Users Meeting, Giens, France, 31st August-5th Sept. 2008.
- [94] Ogée, J., **Wingate, L.**, Burlett, R., Bosc, A., Devaux, M., Loustau, D., Sartore, M. and Grace, J. Understanding seasonal oxygen isotope signals of photosynthesis and respiration at the ecosystem scale using a chamber TDL system. JESIUM: 2nd European Stable Isotope Users Meeting, Giens, France, 31st August-5th Sept. 2008.
- [95] **Wingate, L.**, Understanding the oxygen isotope signals of CO₂ exchanged between forests and the atmosphere. INRA EPHYSE, Bordeaux, France, 2008
- [96] **Wingate, L.**, Burlett, R., Bosc, A., Cross, A., Devaux, M., Grace, J., Loustau, D., Seibt, U. and Ogée, J. Measuring carbon and oxygen isotope signals of photosynthesis and respiration: first field results from a chamber system coupled to tunable diode laser spectrometers. American Geophysical Union (AGU) Fall Meeting, Abstract No. B11E-03: Investigation of Carbon and Water Cycle Processes using Isotopes: New Techniques, Data, and Analyses, San Francisco, California, USA, 10th-14th Dec. 2007 (**INVITED**).

- [97] Ogée, J., Barbour, M.M., Dewar, R.C., **Wingate, L.**, Bert, D., Bosc, A., Lambrot, C., Stievenard, M., Bariac, T., Berbigier, P. and Loustau, D. A single-substrate model to interpret high-resolution intra-annual stable isotope signals in tree ring cellulose. AGU Fall Meeting, Abstract No. B11E-02: Investigation of Carbon and Water Cycle Processes using Isotopes: New Techniques, Data, and Analyses, San Fransisco, California, USA, 10th-14th Dec. 2007.
- [98] Burlett, R., Bosc, A., Wingate, L., Ogée, J., Devaux, M. and Loustau, D. Etude des échanges isotopiques (¹³C et ¹⁸O) du CO₂ au sein d'un écosystème forestier. *9th Journées d'Ecologie Fonctionnelle*, 19th-22nd Mar 2007.
- [99] Luyssaert, S., Janssens, I.A., Matteucci, G., **Wingate, L.**, Beer, C., Ciais, P *et al.* Relationships between GPP, NPP, NEP, Ra and Rh in forest ecosystems. *Open Science Conference on The Greenhouse Gas Cycle in the Northern Hemisphere*, Sissi-Lassithi, Crete, 14th-18th Nov 2007.
- [100] Seibt, U., **Wingate, L.** and Berry, J. The "Flood of the Century" as isotopic fingerprint in canopy δ¹⁸O signatures. AGU, Fall Meeting, San Francisco, USA, Dec 2006.
- [101] Burlett R., Ogée J., Bosc A., **Wingate L.**, Loustau D. Mesure rapide (10Hz) des isotopomères du CO₂ atmosphérique par diode laser modulable (TDL). *9th J2M Journées de la Mesure et de la Métrologie*, Balaruc-les-Bains, France 9th-12th Oct 2006, 8 p.
- [102] **Wingate, L.** An isotopic excursion through atmospheric and metabolic signals from conifer forests following a seasonal rhythm. Global Change Seminar Series, School of GeoSciences, University of Edinburgh, UK, 2006
- [103] **Wingate, L.** An isotopic excursion through atmospheric and metabolic signals from conifer forests following a seasonal rhythm. John Innes Centre, Norwich, UK, 2006
- [104] **Wingate, L.**, Grace, J., Kutsch, W. and Kutsch, C. The phenology of carbon allocation in forests: monitoring its variability at different scales. Phenological change, causes and consequences. Association of Applied Biologists, Royal Botanic Gardens of Edinburgh, Edinburgh, UK, 20th Oct 2006 (**INVITED**).
- [105] Seibt, U., **Wingate, L.** and Berry, J. Improving predictions of the δ¹⁸O of evaporating site leaf water: The Craig-Gordon-Dongmann approach. *IAEA International Workshop on Isotope Effects in Evaporation*, Pisa, Italy, May 2006.
- [106] Mencuccini, M., **Wingate, L.**, Maseyk, K., Seibt, U., Massheder, J., Almeida, P., Ghashghaie, J., Yakir, D. and Pereira, J.S. Tracing soil gas exchange dynamics after rain pulse events through high-resolution time-series of the δ¹⁸O of soil CO₂ efflux at a Mediterranean site. *The vulnerability of Mediterranean terrestrial ecosystems to climate change*, Rome, Italy, March 2006.
- [107] **Wingate, L.**, Seibt, U. and Ogée, J. An isotopic excursion through atmospheric and metabolic signals from conifer forests following a seasonal rhythm. *SIBAE-BASIN Stable Isotope Meeting: Isotopes as tracers as ecological change*, Tomar, Portugal, 13th-15th Mar 2006 (**INVITED**).
- [108] Hemming, D., Griffiths, H., Loader, N., Marca, A., Robertson, I., **Wingate, L.** and Yakir, D. Looking forward to the future of large-scale isotope networks in ecological change research. *SIBAE-BASIN Stable Isotope Meeting: Isotopes as tracers as ecological change*, Tomar, Portugal, 13th-15th Mar 2006 (**INVITED**).
- [109] Seibt, U., **Wingate, L.**, Hemming, D., Lloyd, J. and Berry, J. Observations and modelling of oxygen isotopic signatures of the CO₂ efflux from a forest soil. AGU, 86 (52) Fall Meeting Suppl., Abstract No. B22B-04, San Francisco, USA, Dec 2005.
- [110] Seibt, U., **Wingate, L.**, Hemming, D., Lloyd, J. and Berry, J. Nocturnal stomatal conductance and the δ¹⁸O signature of foliage gas exchange and canopy air: Field observations in two forest ecosystems. *Proceedings of the annual meeting of the Ecological Society of America (ESA)*, Montreal, Canada, Sept 2005 (**INVITED**).

- [111] **Wingate, L.** Measuring the isotopic composition of respired CO₂ using chamber methods. University of Utah, Salt Lake City, USA, 2005
- [112] Seibt, U., **Wingate, L.**, Hemming, D., and Berry, J. Field observations of oxygen isotopes from two forest ecosystems – linking the water and carbon cycles at the ecosystem scale. EOS Transactions. AGU, 85 (47) Fall Meeting Suppl., Abstract No. H54C-06, San Francisco, USA, Sept 2004.
- [113] Seibt, U., **Wingate, L.** and Lloyd, J. The leaf is where they meet: measuring ¹³C and ¹⁸O discrimination during photosynthetic gas exchange. *Abstracts of the SIBAE-BASIN Stable Isotope Meeting: Flux partitioning using stable isotopes*, Interlaken, Switzerland, April 2004 (**INVITED**).
- [114] **Wingate, L.** Measuring the isotopic composition of respired CO₂ using chamber methods. University of York, York, UK, 2004 (**INVITED**).
- [115] **Wingate, L.** Measuring component and ecosystem discrimination against ¹³CO₂ using chamber methods. Instituto Superior de Agronomia, Lisbon, Portugal, 2004
- [116] Seibt, U., **Wingate, L.** and Lloyd, J. The role of canopy processes in the isotopic composition of CO₂ and O₂. *Proceedings of the 6th International Carbon Dioxide Conference*, Sendai, Japan, 2001.

POSTER PRESENTATIONS

- [117] **Kaisermann, A.**, Ogée, J., **Sauze, J.**, **Wohl, S.**, **Jones, S.**, **Gutierrez, A.** & **Wingate, L.** Disentangling the rates of carbonyl sulphide production and consumption and their drivers in soils. ISME17, Leipzig, Germany, 12-17th August 2018
- [118] Ogée, J., Genty, B. & **Wingate, L.** Revisiting the role of carbonic anhydrase activity on the CO¹⁸O discrimination during photosynthesis. 1st European Congress on Photosynthesis Research, Uppsala, Sweden, 25th-28th June 2018
- [119] **Wingate, L.**, **Launois, T.**, Cuntz, M., Meredith, L., **Sauze, J.**, **Jones, S.**, **Wohl, S.**, **Kaisermann, A.**, & Ogée, J., A novel CO¹⁸O dataset and modelling framework to constrain estimates of photosynthesis at the global scale. Geophysical Research Abstracts, Vol. 20, EGU2018-6098, Vienna, France, 9-13th April 2018
- [120] **Wingate, L.** Promoting frontier Earth system research and female role models using dedicated geoscience symposiums. Geophysical Research Abstracts, Vol. 20, EGU2018-5132, Vienna, France, 9-13th April 2018.
- [121] **Kaisermann, A.**, **Jones, S.**, **Wingate, L.** Title From the deep past to the Anthropocene: coupling Earth system function to climatic change. Talence, France, 8-9th March 2018.
- [122] **Jones, S.**, **Kaisermann, A.**, Ogée, J., **Wohl, S.**, **Gutierrez, A.** & **Wingate, L.** Oxygen isotope composition of soil-atmosphere carbon dioxide exchange and carbonic anhydrase activity. From the deep past to the Anthropocene: coupling Earth system function to climatic change. Talence, France, 8-9th March 2018.
- [123] **Gimeno, T. E.**, **Saavedra-Berlanga, N.**, Ogée, J., Medlyn, B.E. & **Wingate, L.** Testing for non-stomatal limitations to optimisation behaviour under drought on contrasting plant functional types. From the deep past to the Anthropocene: coupling Earth system function to climatic change. Talence, France, 8-9th March 2018.
- [124] **Cochet, Y.**, Domec, J.C., Achim, A., Ogée, J., **Wingate, L.** Quantifier les impacts d'une concentration élevée en CO₂ atmosphérique et d'une fertilisation azotée sur la densité du bois chez *Pinus taeda*. 85e Congrès de l'ACFAS, Paris France 17th-21st April, 2017.
- [125] Auty, D., Achim, A., Domec, J.C., Ogée, J., & **Wingate, L.** Effects of elevated CO₂ and N-fertilisation on wood density and growth in Loblolly pine trees. SAF 2017 National Convention, Albuquerque, New Mexico, 15th-19th Nov, 2017.

- [126] Ogée, J., Genty, B. & **Wingate, L.** Revisiting the role of carbonic anhydrase activity on the CO¹⁸O discrimination during leaf photosynthesis. Gordon Research Conference, CO₂ Assimilation in plants from genome to biome. Barga, Italy 1st-5th May 2017.
- [127] **Kaisermann, A.**, Ogée, J., **Wohl, S.** & **Wingate, L.** Plant species influence soil carbonyl sulfide fluxes. British Ecological Society, Liverpool, UK 12th-15th Dec 2016.
- [128] **Gimeno, T.**, Royles, J., Ogée, J., **Jones, S.**, **Burlett, R.**, West, J., **Sauze, J.**, **Wohl, S.**, Genty, B., Griffiths, H., & **Wingate, L.** Bryophyte gas-exchange dynamics along varying hydration status reveal significant COS emission in the light. 17th International Congress on Photosynthesis Research, Maastricht, Netherlands, 7th -12th Aug 2016.
- [129] **Launois, T.**, Ogée, J., Commane, R., Wehr, R., Meredith, L., Munger, B., Nelson, D., Saleska, S., Wofsy, S., Zahniser, M. & **Wingate, L.** Developing multi-tracer approaches to constrain the parameterisation of leaf and soil CO₂ and H₂O exchange in land surface models. Geophysical Research Abstracts, Vol. 18, EGU2016-993-2, Vienna, Austria, 17th -22nd April 2016.
- [130] **Gimeno, T.**, Royles, J., Ogée, J., **Jones, S.**, **Burlett, R.**, West, J., **Sauze, J.**, **Wohl, S.**, Genty, B., Griffiths, H., & **Wingate, L.** Investigating the impact of light and water status on the exchange of COS, ¹³CO₂, CO¹⁸O and H₂¹⁸O from bryophytes. Geophysical Research Abstracts, Vol. 18, EGU2016-12692, Vienna, Austria, 17th -22nd April 2016.
- [131] **Jones, S.**, **Sauze, J.**, Ogée, J., **Wohl, S.**, Bosc, A. & **Wingate, L.** Non-destructive measurement of carbonic anhydrase activity and the oxygen isotope composition of soil water. Geophysical Research Abstracts, Vol. 18, EGU2016-787, Vienna, Austria, 17th -22nd April 2016.
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Tracing photosynthetic isotope discrimination from leaves to soil

The fate of carbon (C) following photosynthetic assimilation is, quite rightly, currently the subject of intense research. The principal reason for this interest is that the rate of C turnover in ecosystems feeds back into the global C cycle, where anthropogenic emissions increase CO₂ concentrations by an estimated 10 Gt every year (IPCC, 2007). While this constant addition of CO₂ is currently compensated in part by the biosphere acting as a net sink for the globe, there is an urgent need to understand how different ecosystems will respond under changed environmental conditions. Predicting the rates of C turnover in ecosystems requires a good understand-

ing of C assimilation, allocation and respiration in plants and soil, in order to inform process modelling. However, despite abundant research into respiration, we still lack a fundamental understanding of the way in which C moves through the plant–soil–atmosphere continuum. In this issue of *New Phytologist*, Wingate *et al.* (2010b, pp. 576–589) make use of the natural fluctuation in the isotopic composition of assimilated C in order to trace its fate to a number of respiratory fluxes. The approach is both elegant and novel: by continuously measuring the photosynthetic discrimination between the stable isotopes ¹²C and ¹³C, they obtained a continuous ‘signal’ for the newly assimilated C. This discrimination showed fluctuations from diurnal to seasonal temporal scales, and Wingate *et al.* (2010b) were able to follow the temporal trends observed during assimilation (which were verified using isotope-specific C assimilation modelling) into respiration fluxes from tree stems and the soil. While previous studies have demonstrated the transmission of the photosynthetic isotope signal within the plant on the basis of intermittent measurements, this study breaks new ground by monitoring C isotope fluxes of assimilation and respiration continuously and over an extended period. This unique data set therefore allows a thorough analysis of the temporal correlation between the isotopic ‘signal’ from assimilation and respiration terms. The time lags observed, from leaf to stem and soil, are broadly similar to those observed using alternative methods (Ekblad & Höglberg, 2001; Höglberg *et al.*, 2008; Subke *et al.*, 2009; Mencuccini & Höglberg, 2010). However, rather than simply confirming these results, the authors were able to identify variations in these time lags likely to be linked to phenological phases when there is tight coupling between the supply of fresh photosynthates and respiratory activity in the soil (whether this occurs inside the roots or is carried out by heterotrophic organisms receiving plant C through exudations). Rather than simply showing that C allocation differs during different periods in the growing season (Höglberg *et al.*, 2010), Wingate *et al.* (2010b) can identify the exact timing of when a synchronicity between assimilation and belowground respiration occurs and when it does not occur. This suggests that it may not be possible simplistically to use natural abundance ¹³CO₂ measurements for short-term partitioning of soil autotrophic and heterotrophic respiratory fluxes in forest ecosystems, especially during periods in which autotrophic respiration is weakly linked to photosynthesis. At the same time, a gradual shift in photosynthetic discrimination over the length of the growing season was detectable in the soil CO₂ efflux signal, and there is considerable potential in using multi-year measurements to derive long-term flux partitioning between autotrophic and heterotrophic sources. Also, such isotope data may improve our ability to model and constrain both contemporary and historic global C transfers, making more widespread measurements of isotope specific C fluxes in ecosystems throughout the world a realistic and exciting prospect.

We now await similar, comparative studies on different vegetation types (e.g. C₃ and C₄) and biomes.

'The technical obstacles to this are colossal, but then the same would have been said about fast ¹³C measurements in the past.'

Methodologically, this study marks a new step in the use of fast-response isotope spectrometers. Previous work has explored the potential of using tuneable diode laser absorption spectrometers (TDLASs) in ecological research (Bowling *et al.*, 2003; Griffis *et al.*, 2005), and clearly demonstrated that there are novel areas in which it can be applied. Other studies have provided new insights into the isotope exchange of ecosystems (Griffis *et al.*, 2008), or leaf-level isotope effects (Barbour *et al.*, 2007; Bickford *et al.*, 2009), but, arguably, Wingate and co-workers (2010b) utilize this analyser to its full capacity by simultaneously sampling from different ecosystem components at high frequency and over the major part of the growing season. This kind of highly resolved isotope flux data from different ecosystem components would have been unthinkable even 5 yr ago, when the application of TDLASs in ecology was in its infancy. To put this in perspective, it would have taken *c.* 180 yr to obtain the same number of analyses by means of conventional isotope ratio mass spectrometry (IRMS) and off-line sampling. Indeed, the wealth of data generated during this study means that much of the information contained in this data set still remains to be explored. For example, there is a strong possibility that the short-term shifts observed in photosynthetic discrimination can provide new insights into environmental controls and biochemical switches in plant metabolism, and can help to elucidate the balance between stomatal and biochemical regulation of photosynthesis inputs during periods of plant stress. Along with the $\delta^{13}\text{C}$ of respired CO₂, the TDLAS system also supplies information on the $\delta^{18}\text{O}$ of respired CO₂, which provides independent insights into, and constraints on, gross CO₂ flux partitioning at the ecosystem and global scales and provides an additional tracer of plant, soil and ecosystem water cycling (Wingate *et al.*, 2009, 2010a). We look forward to future publications originating from this set of data.

Considering how far this technology has developed in recent years, we also anticipate the next generation of analysers, with no doubt even better accuracy and more frequent time resolution. Even at an order of magnitude below the present

frequency of ¹³CO₂ analyses, high-frequency analyses of natural abundance ¹⁴C, or the isotopomers of CH₄ and N₂O, would open new avenues for the exploration of ecosystem C (and nitrogen (N)) dynamics and enable the development of multiple isotope models in plant–soil systems. The technical obstacles to this are colossal, but then the same would have been said about fast ¹³C measurements in the past.

In addition to these technological accomplishments, the setting up and maintenance of a multiplexed chamber system with an integrated calibration facility for the TDLAS is far from trivial, and the work presented in this paper results from the combination of considerable skills in mechanical and electronic engineering, programming and data evaluation. Before laser absorption systems capable of discriminating between stable C isotopes in air were available, the transporting of traditional IRMS systems into the field was the only option for real-time monitoring of isotopic abundance. This has been successful in only a few cases (Schnyder *et al.*, 2004; Subke *et al.*, 2009), and, despite IRMS delivering data of higher accuracy than data obtained by laser absorption, these data are often compromised by the difficulties inherent in taking a mass spectrometer from the comfort of a laboratory, and the necessity of having to operate using small gas volumes with little or no preconditioning. TDLAS systems offer a more field-applicable option for such measurements, and while technical advances in recent years have simplified such high-frequency measurements, the implementation of this method, as in the Wingate *et al.* (2010b) paper, is no mean feat. With other fast-response cavity-ring-down-based isotope analysers becoming available, we are likely to see more applications of real-time monitoring of isotope fluxes. As the maintenance requirements of such systems are reduced, through greater sophistication in signal processing, there is the real possibility that, in existing CO₂ flux monitoring systems (chamber-based as well as atmospheric flux systems) within the FLUXNET network, the fast-response CO₂ analyser will be complemented or replaced by an isotope version, adding a new dimension to the existing monitoring data bases.

Wingate *et al.* (2010b) also clearly show the limitations of using photosynthetic discrimination as a marker to trace the fate of assimilates in plant–soil systems. Unlike the situation for photosynthesis, where isotopic discrimination caused by enzyme-specific affinities and physical diffusion parameters are well described and readily modelled, a real lack in our understanding of the isotopic effects that occur during respiration is exposed. While 'respiration' is generally treated as a uniform process at the plant organ scale by ecophysicologists, it is well known that, at the mitochondrial scale, there is a suite of processes that result in CO₂ release (Barbour & Hanson, 2009). As the glucose molecule has a systematic isotopic bias within its intramolecular distribution of C atoms (Wingate, 2008), and different respiratory pathways 'attack' specific parts of the C backbone of the

molecule, the isotopic signature of respired CO₂ is also modified by the respiratory pathway. This isotopic fluctuation therefore confounds the interpretation of the time signal provided by short-term photosynthetic discrimination. The possibility of re-fixation of root respired CO₂ which dissolves in xylem water and is transported aboveground (Aubrey & Teskey, 2009) represents a further potential source of confounding isotopic mixing. At present, isotope-enabled plant C models cannot resolve these effects, but it is likely that a combination of experiments, monitoring and modelling will eventually allow a better understanding of the way in which C is processed at the mitochondrial scale. This would require an integrated approach for our understanding of respiration from the mitochondrial to ecosystem (or even global) scale. The significance of this task has clearly been recognized, with a recent symposium organized by the New Phytologist Trust bringing together researchers working on respiration across all scales (Atkin *et al.*, 2010). With advances in our understanding of respiratory fluxes in all respective areas, a 'system approach' (*sensu* Barbour & Hanson, 2009) to modelling respiration becomes feasible, and holds considerable promise to allow a meaningful partitioning of C pathways in ecosystems. This 'systems approach' extends to the entire plant–soil continuum across terrestrial ecosystems, as it becomes increasingly clear that the processes occurring within plants and within the soil are interdependent and have to be studied together.

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Key words: carbon turnover, isotope exchange of ecosystems, photosynthetic discrimination, plant–soil–atmosphere continuum, respiratory fluxes.