Not that long ago, the CO2 efflux from a plant organ was attributed to metabolic reactions and activity only in that same organ. For tree stems, however, we know that CO2 transported in the xylem and originating from other plant compartments compromises stem respiration measurements. Now, Stutz et al. (2017) have shown that leaf CO2 efflux, in addition, does not solely represent leaf metabolic processes but is affected by xylem-borne CO2.

Knowledge of the processes of carbon (C) allocation and cycling in plants and ecosystems is important for understanding the terrestrial C cycle as a whole and changes as a result of anthropogenic impacts. The potential of ecosystems to sequester C from the atmosphere reflects the balance between C assimilation and the complex set of respiration processes (Trumbore et al., 2013). Even though respiration is likely to be the most important determinant of the C balance in terrestrial ecosystems (Valentini et al., 2000), understanding of the mechanistic background is far from complete. On the one hand, respiration is affected by direct environmental cues that regulate respiratory metabolism (Atkin et al., 2005). However, on the other hand, substrate supply for respiration, which is indirectly coupled to environmental drivers (e.g. via their effects on photosynthesis), controls respiratory CO2 fluxes (Högberg and Read, 2006). Besides photosynthesis, phloem transport and the partitioning of assimilates among different C pools affect substrate availability for respiration. We need greater acknowledgement that our view of the controls of respiration fluxes is incomplete (e.g. Hagedorn et al., 2016) and that the ‘system plant’ might be more complex than previously thought.

CO2 efflux from a given plant organ is not necessarily an indicator of its respiratory activity

Only recently, a major new challenge became obvious: CO2 efflux is not only affected by the catabolic metabolism of a given organ, but also by the respiration rate of plant compartments coupled via the transpiration stream to that organ. Thus, the CO2 exchange of stems, for example, is influenced by downstream CO2 production in the roots and the transpiration stream, adding within-plant spatial interconnectivities (Teskey et al., 2008).

While it was previously usually assumed that CO2 produced in roots and stems escaped these organs more or less directly into the surrounding atmosphere, there is now strong evidence for trees that at least part of this CO2 remains inside the plant, gets dissolved in the xylem sap, and is then transported acropetally (Teskey and McGuire, 2002; McGuire and Teskey, 2004; Teskey et al., 2008). Whilst parts of this xylem-transported CO2 escape from stems and branches into the atmosphere, up to almost 20% can be re-assimilated, with the highest contribution made by woody branches (Bloemen et al., 2013).

Using a 13C-labelling approach, Stutz et al. (2017) have now shown that CO2 originating from the xylem also contributes to leaf CO2 efflux, and they were also able to quantify the contribution of xylem-originating CO2 to this flux (Box 1). Moreover, they determined the retention of CO2 in the leaf as a result of anaplerotic processes in the dark. While there are now a number of papers reporting analyses of the effect of xylem transport of CO2 on stem or branch efflux (e.g. Bowman et al., 2005; Gansert and Burgdorf, 2005; Teskey and McGuire, 2005; Maier and Clinton, 2006), there is a lack of information on its contribution to ‘leaf respiration’. There is one observation by Stringer and Kimmerer (1993) showing that over 99% of xylem-transported CO2 is fixed in the light, whereas 80% of the transpired label escaped the leaves in the dark. For a whole tree, based on a mass balance approach, Bloemen et al. (2013) calculated that about 90% of the xylem CO2 left the tree via the stem and branches before reaching the leaves.

Stutz et al. (2017) related leaf efflux of xylem CO2 (13C-labelled) to ‘real’ leaf respiration (non-labelled) and showed that flux can approach 50% of the latter depending on transpiration rate and xylem CO2 concentrations. By taking the effects of light-enhanced dark respiration into account – an
Box 1. CO₂ fluxes in plant stems and leaves

Up to 50% of root-respired CO₂ is transferred via the xylem stream aboveground (Bloemen et al., 2013) and reaches the stem sapwood (in woody plants). Part of this CO₂ escapes from the stem to the atmosphere, whilst part is assimilated via Rubisco in the photosynthetically active bark and via phosphoenolpyruvate carboxylase. Moreover, (net) uptake of atmospheric CO₂ might occur in green stems. Living tissues in bark (e.g. phloem parenchymatic and companion cells) and wood (e.g. ray parenchyma) as well as the stem cambium produce CO₂ via respiration that might partially escape to the atmosphere, be partially re-fixed, but also dissolve in the xylem sap and thus contribute to xylem CO₂. Depending on the ratio between the CO₂ transport rate from the roots, stem efflux, stem assimilation and contribution of stem respiration to xylem CO₂ transport, the xylem CO₂ concentration might increase or decrease along the plant axis, but there is no information on acropetal xylem CO₂ gradients available in the literature. The phloem might also transport CO₂ but similarly no published data are available. In the leaves the efflux of leaf-respired CO₂ plus the xylem-derived CO₂ contribute to the total efflux. Stutz et al. (2017) showed that the efflux of xylem CO₂ can approach 50% of the leaf respiration flux, but due to the difficulties of obtaining realistic twig-tip xylem concentrations and our lack of comprehensive data on night-time transpiration, generalizations might be difficult. Part of the xylem CO₂ is fixed in the leaves in the night for anaplerotic reactions. Estimations of day-time respiration fluxes are notoriously difficult. During the day, leaf respiration rates might decrease due to substantial changes in leaf metabolism (Tcherkez et al., 2009), but the contribution of xylem CO₂ efflux might increase as transpiration rates are higher. If considerable amounts of xylem CO₂ are fixed via photosynthesis, leaf-level photosynthetic measurements with classical gas-exchange measurement devices might underestimate leaf photosynthetic capacities. Note that the size of arrows does not indicate any quantitative differences in fluxes.
CO2 approaching the leaf will be assimilated. Thus, we are
xylem flow rates (Teskey et al., 2015) reported that
most of the xylem CO2 reaches the atmosphere via
trunks and stems. If the assumption of Bloemen
et al. (2013) that most of the xylem CO2 reaches the atmosphere via
trunks and stems is correct, the CO2 concentrations reaching the leaves might be lower than the ones taken into account by Stutz et al. (2017), and thus they might overestimate the effective night-time flux. During the day, transpiration will be higher, but xylem CO2 concentrations vary inversely with xylem flow rates (Teskey et al., 2008) and at least part of the CO2 approaching the leaf will be assimilated. Thus, we are far from being able to quantify the contribution of CO2 produced in roots and stems but released by the leaves. More research is needed to quantify xylem CO2 concentrations along the plant axis and changing with time, as are direct measurements of the efflux of xylem-borne CO2 via the leaf over diel timecourses.

Leaf respiration in the light – old issues, new problems

During the light period, not only anaplerotic CO2 fixation, but also photosynthetic assimilation of xylem CO2, is likely to occur. Moreover, leaf respiration in the light is notoriously difficult to study. Only recently, Farquhar and Busch (2017) postulated that the Kok effect and the Laik approach, which are usually applied, are error-prone and not straightforwardly applicable to estimate day respiration. Even though from a biochemical point of view it is well-known that the TCA cycle is not closed down in the light, and changes in the commitment of major biochemical pathways in the light and during light-to-dark transitions point to a reduction of CO2 release from glycolysis and the TCA cycle (Tcherkez et al., 2009; Werner et al., 2011), Farquhar and Busch (2017) suggest that it is currently best to assume that dark respiration in the light equals the respiration rate in the dark at the same temperature. If we now take into account that various amounts of xylem CO2 – depending on the variation of transpiration rate and of CO2 production, release and re-fixation in heterotrophic tissues – contribute to day-time CO2 efflux from the leaf, the situation gets even more complicated. Not only the complex and still poorly understood changes in leaf metabolism in the light, but also xylem-mediated teleconnections, will affect the measured CO2 fluxes. Moreover, net CO2 exchange measurement at the leaf level – an indispensable tool for plant physiology and ecology – will be incorrect if considerable amounts of the xylem CO2 are fixed, leading to underestimations of the real CO2-fixing capacity of a leaf.

New challenges for understanding respiration – spatial and temporal influences on respiration

There is growing evidence that the CO2 efflux from above-ground tissues is affected by CO2 production from distant tissues connected via the xylem, and thus does not solely represent the local metabolism but rather the integrated plant activity weighted by the transpiration rate and the – still not sufficiently understood – assimilation in, and CO2 efflux from, different plant organs. And as if this situation were not complex enough in spatial terms, recent research indicates that temporal interconnections also affect leaf and canopy respiratory CO2 fluxes. Gessler et al. (2017) showed that in addition to the current environmental drivers affecting respiration, the antecedent conditions as mediated by the circadian clock were involved. This circadian control is assumed to act as an adaptive memory to adjust plant metabolism based on environmental conditions from previous days and thus adds a temporal component to respiration and its control. All these recent findings indicate that at least parts of our understanding of plant respiration have been too simplistic, but at least we do now have the tools in hand to fully account for spatial and temporal controls.
The amino acid glutamate (Glu) acts as a fast excitatory neurotransmitter in mammals. Its importance in plant signalling was recognized with the discovery of channel proteins similar to mammalian Glu receptors, as well as distinct changes in root-system architecture in response to very small amounts of soil Glu. Based on natural genetic variation within Arabidopsis, Walch-Liu et al. (2017) have now identified a major locus underpinning this root response, as well as several loci controlling it through gene by environment interactions with nitrate and temperature. It is a significant step towards unraveling crosstalk between signalling pathways that enable plants to adjust their growth and development to multiple environmental stimuli.

In order to survive as a sessile organism in a given environment a plant needs to adjust its growth and development to environmental factors such as light and temperature and the availability of water and mineral nutrients. They therefore possess a sensory system of receptors and downstream...