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COMMENTARY

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Inside out: Measuring the effect of wood anatomy on the efflux and assimilation of xylem-transported CO_2

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Carbon dioxide concentrations (including aqueous CO_2, carbonic acid, bicarbonate and carbonate) in woody tissues can be up to 750 times higher than atmospheric CO_2 concentrations, ranging from <1% to >26% versus atmospheric ~0.04% (Figure 1) (Teskey et al., 2008). CO_2 formed through respiration is generally assumed to diffuse to the atmosphere from tissues adjacent to where it is produced. This CO_2 build-up in the stem is due to the diffusional barriers in woody and bark tissues. CO_2 in the stem has three fates: (a) it can be re-fixed for photosynthesis; (b) it can be used for anaplerotic reactions; or (c) it can exit the plant either adjacent to where it was produced (radial diffusion) or in an area remote from its point of origin (xylem-transported CO_2). Not accounting for assimilation of xylem-transported CO_2 may result in underestimating total plant photosynthesis. Alternatively, overlooking the transport of CO_2 away from its point of origin complicates the estimation of respiration in stems, branches or even leaves. For example, CO_2 efflux from the stem may not solely represent stem respiration, but it may represent CO_2 generated through respiration in areas remote from the point of efflux (Stutz et al., 2017). Additionally, wood anatomy and branching architecture likely influence how much and how far xylem-transported CO_2 travels (Figure 2). Few studies have combined measurements of both the efflux of xylem-transported CO_2 from trees together and the assimilation of xylem-transported CO_2. Excitingly in this issue of *Plant, Cell & Environment*, Salomón et al. (2021) demonstrate the importance of xylem-transported CO_2 in plants with different wood anatomies by comparing the amount of xylem-transported CO_2 used for photosynthesis to the amount effluxed.

1 | XYLEM-TRANSPORTED CO_2 IS USED FOR PHOTOSYNTHESIS

When Bloemen, McGuire, Aubrey, Teskey, and Steppe (2013a) fed $^{13}CO_2$ to *Populus deltoides* saplings, they showed that less than 20% of the supplied CO_2 was used for photosynthesis by analysing tissue samples with isotope-ratio mass spectrometry (IRMS). Stem and branch photosynthesis accounted for most of this fixed CO_2, while a small amount was fixed through leaf assimilation. The remaining CO_2 was assumed to efflux from the stem, branches and leaves of the plant, although the proportion and rate of efflux from these locations were unknown. Isotopic laser absorption spectroscopy can measure the rate and location of xylem-transported CO_2 efflux (Salomón, De Roo, Bodé, Boeckx, & Steppe, 2019; Shimono, Kondo, & Evans, 2018; Stutz et al., 2017; Tarvainen et al., 2020). This method revealed that a substantial amount of xylem-transported CO_2 effluxed from branches and stems of angiosperm trees (Mincke, Courtyn, Vanhove, Vandenberghe, & Steppe, 2020; Salomón et al., 2019). However, Tarvainen et al. (2020) showed in mature *Pinus sylvestris*, a conifer with tracheid anatomy, that there is a little vertical movement of xylem-transported CO_2, implying that wood anatomy may impact where and how much xylem-transported CO_2 is used for photosynthesis.

2 | COMBINING TECHNIQUES REVEAL HOW XYLEM-TRANSPORTED CO_2 IS USED WITHIN SAPLINGS

Salomón et al. (2021) nicely combined the methods of isotopic laser absorption spectroscopy and IRMS to measure both the efflux and assimilation of xylem-transported CO_2 from saplings with three different wood anatomies. The authors found after feeding $^{13}CO_2$ to saplings with distinct wood anatomies that (a) most of the xylem-transported CO_2 effluxed to the atmosphere, and (b) wood anatomy influenced how much of this CO_2 was used for photosynthesis (Figure 2b). In all species tested, the efflux of xylem-transported CO_2

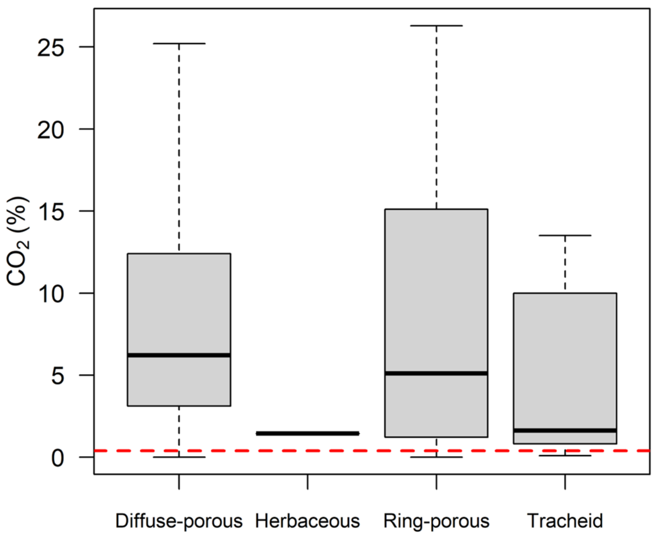

FIGURE 1 Concentrations of CO_2 in stems across different wood anatomies. Boxplot represents the [CO_2] of tracheid, diffuse- and ring-porous species and a single herbaceous species. The red dashed line represents the [CO_2] in the atmosphere. Concentrations of CO_2 in the stem are higher in all species when compared with atmospheric [CO_2]. Data from Teskey, Saveyn, Steppe, and McGuire (2008), Etzold, Zweifel, Ruehr, Eugster, and Buchmann (2013), Stutz, Anderson, Zulick, and Hanson (2017), Tarvainen et al. (2020), and Salomón, De Roo, Bodé, Boeckx, and Steppe (2021)

from the stem was high, and very little reached the canopy. Only a small amount was assimilated, predominantly in the woody and bark tissues of the stem. However, the amount assimilated differed across the species tested, with oak and maple fixing 20% and less than 1% of the xylem-transported CO_2, respectively.

Do these findings indicate the impact of xylem-transported CO_2 for photosynthesis is minor and can be ignored? Quite the contrary, both high stem CO_2 concentrations and the efflux of CO_2 from stems have consequences for estimating gross photosynthesis and plant respiration. For instance, if the efflux of xylem-transported CO_2 in the light is high, then it will appear that the rate of gross photosynthesis is lower than if there was no efflux of xylem-transported CO_2. Additionally, determining the efflux of darkened branches without considering stem assimilation will lead to an overestimation of the efflux of xylem-transported CO_2 in the light. Furthermore, it is difficult to differentiate between locally respired CO_2 and non-labelled xylem-transported CO_2, which might have travelled far from its point of origin. Any photosynthetic tissue can use xylem-transported CO_2 for photosynthesis. When cut branches are supplied with labelled xylem-transported CO_2, much of the label is fixed by woody tissue, although some xylem-transported CO_2 is used for leaf photosynthesis (Bloemen, McGuire, Aubrey, Teskey, & Steppe, 2013b; McGuire, Marshall, & Teskey, 2009). Since only a small portion of xylem-transported CO_2 reaches the leaves, it is unlikely that xylem-transported CO_2 has a substantial impact on models of leaf photosynthesis (Hanson & Gunderson, 2009). In the dark, xylem-transported CO_2 effluxes from leaves (Stutz et al., 2017), while in the light, it is used for leaf photosynthesis (Stutz & Hanson, 2019). Yet, experiments with cut leaves showed that xylem-transported CO_2 contributed little to leaf photosynthesis (Stutz & Hanson, 2019). When stomata are closed, such as during drought stress, leaf photosynthesis and sap flow are reduced, thereby in such conditions xylem-transported CO_2 might be more important for photosynthesis (De Roo, Salomón, & Steppe, 2020). Stem and branch photosynthesis is important for repairing xylem embolisms and maintaining hydraulic conductivity (Cernusak & Cheesman, 2015; De Roo et al., 2020, b; Liu et al., 2019), and xylem-transported CO_2 provides the substrate for this process.

3 | HOW DO WOOD ANATOMY AND TREE ARCHITECTURE AFFECT THE FATE OF XYLEM-TRANSPORTED CO_2?

Wood anatomy and tree structure influence the flux of CO_2 out of the stem and thus the build-up of CO_2 in the stem. In maple, with diffuse-porous anatomy and high radial diffusivity, 97% of the xylem-transported CO_2 effluxed from the stem. In cedar, which has tracheid anatomy and low radial diffusivity in addition to low cell density, the build-up of CO_2 in the stem is greatly limited (Figure 2). Yet, in cedar, over half of the labelled xylem-transported CO_2 was unaccounted for. This discrepancy might be related to the diffusion of xylem-transported CO_2 from the branches. Branches have reduced diffusional limitations, thereby increasing their potential to allow xylem-transported CO_2 to efflux (Figure 2a). Additionally, young branches have thinner bark, which allows light to penetrate deeper into photosynthetic tissues, likely increasing the amount of xylem-transported CO_2 used for photosynthesis. Tracheid species, including cedar, show lower radial diffusivity that in turn allows the label to travel further, though no measurements of radial diffusivity from the branches were carried out. Measurements using gas-tight bags over the branches did not indicate significant amounts of xylem-transported CO_2 either effluxing from terminal shoots or assimilated in leaves (Salomón et al., 2021). Additionally, the resolution of the IRMS method might limit the detection of all xylem-transported CO_2 and further explain the unaccounted amount of it. The greater the branching and the longer the distance that labelled xylem-transported CO_2 has to travel, the less likely it becomes to detect it at tissues remote from its origin. Collectively, these limitations might explain the unaccounted xylem-transported CO_2 in cedar. A solution to, at least partially, overcome the problem of unaccounted for xylem-transported CO_2 might be to expand the period over which measurements were carried out to provide enough time for the signal to reach the canopy.

4 | FUTURE DIRECTIONS

By combining isotopic laser absorption spectroscopy and mass spectrometry, Salomón et al. (2021) show that in saplings much of the xylem-transported CO_2 effluxed from the stem and that wood

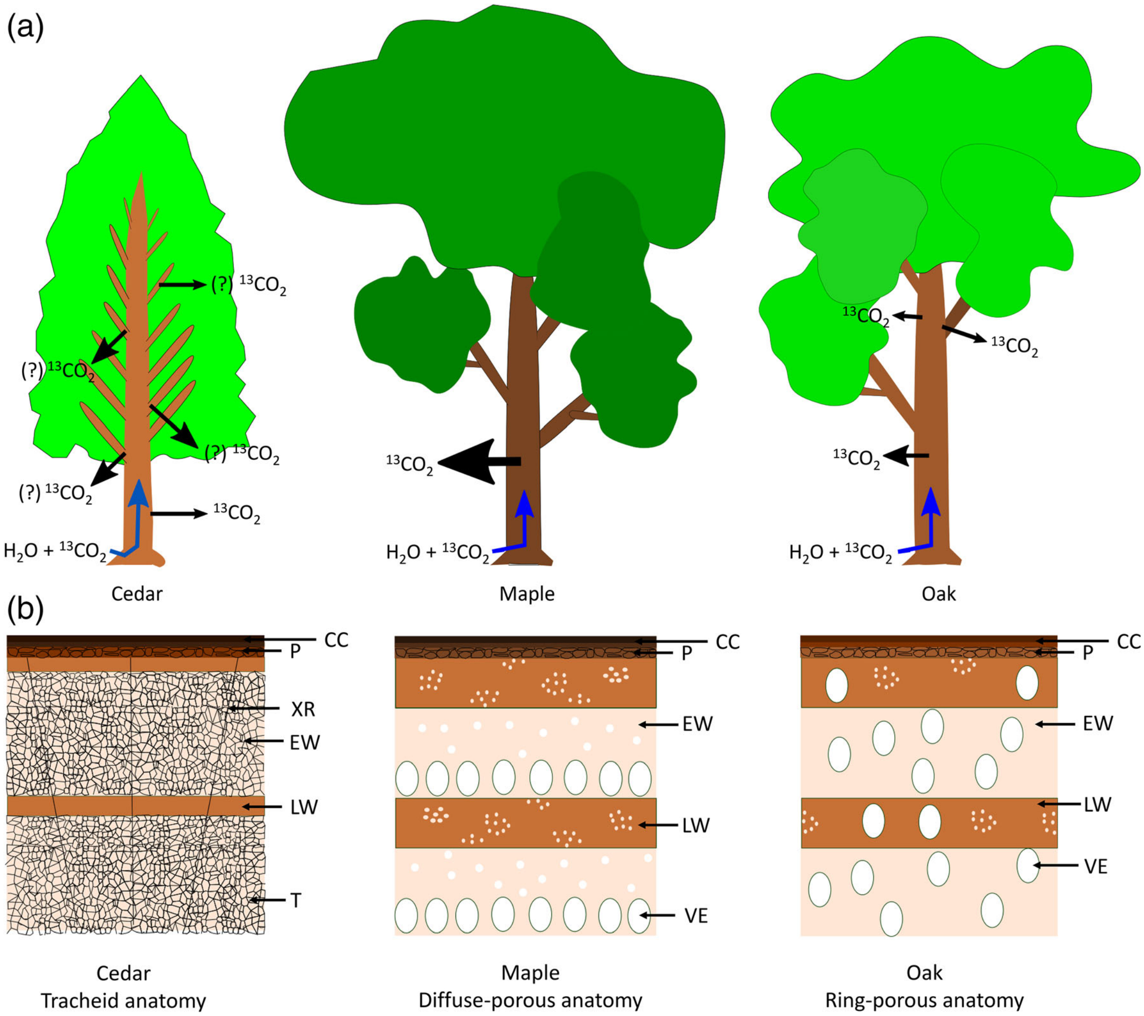

FIGURE 2 Tree structure and wood anatomy influence the movement of xylem-transported CO_2 through trees. Trees were allowed to take up water with dissolved $^{13}CO_2$ (blue arrows), (a) Black arrows indicate the efflux points of xylem-transported CO_2 from the tree or points where xylem-transported CO_2 is hypothesized to efflux (question marks). The number of branches is hypothesized to influence how labelled CO_2 effluxes out of the tree. (b) Wood anatomy of tracheid, diffuse-porous and ring-porous species. Differences in wood anatomy impact the efflux of labelled CO_2 out of the tree stem. CC, cork cambium; EW, earlywood; LW, latewood; P, phloem; T, tracheid; VE, vessel element; XR, xylem ray [Colour figure can be viewed at wileyonlinelibrary.com]

anatomy played a significant role in this efflux. Xylem-transported CO_2 added to the base of saplings either effluxed or was fixed in the stem through photosynthesis or anaplerotic reactions, while only a small amount made it to the canopy. This finding enhances our understanding of how carbon moves through plants, although further studies are still needed to determine the distance that xylem-transported CO_2 can travel before being effluxed or assimilated. Determining this distance and the factors that contribute to it is important for modeling future plant productivity and climate conditions, as it is possible that only CO_2 respired in the upper portions of the stem reaches the canopy. Until such a detailed understanding is obtained, existing models should continue to be experimentally validated. For instance, despite CO_2 continually being added to the stem through respiration, Hölttä and Kolari (2009) predicted that the concentration of CO_2 in the stem decreases with tree height. Their model should be validated by measuring the CO_2 concentration at both the base and terminal branches of the same individual. One final intriguing question is how the utilization of xylem-transported CO_2 changes in response to environmental conditions. Because its assimilation does not incur the same water loss as from atmospheric carbon dioxide, xylem-transported CO_2 would seem to be potentially more important during episodes of drought and heat stress. Detailed knowledge of the flux of this CO_2 will become more important as climate change gradually increases the frequency and severity of drought and extreme heat.

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CONFLICT OF INTEREST

The authors have no declared conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in Figure 1 are openly available in previously published peer-reviewed journal articles found in the Reference section. These manuscripts include Teskey et al. (2008), Etzold et al. (2013), Stutz et al. (2017), Tarvainen et al. (2020), and Salomón et al. (2021).

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REFERENCES

Bloemen, J., McGuire, M. A., Aubrey, D. P., Teskey, R. O., & Steppe, K. (2013a). Transport of root-respired CO_2 via the transpiration stream affects aboveground carbon assimilation and CO_2 efflux in trees. *New Phytologist*, *197*, 555–565.

Bloemen, J., McGuire, M. A., Aubrey, D. P., Teskey, R. O., & Steppe, K. (2013b). Root xylem CO_2 flux: An important but unaccounted-for component of root respiration. *Trees*, *30*, 343–352.

Cernusak, L. A., & Cheesman, A. W. (2015). The benefits of recycling: How photosynthetic bark can increase drought tolerance. *New Phytologist*, *208*, 995–997.

De Roo, L., Salomón, R. L., Oleksyn, J., & Steppe, K. (2020). Woody tissue photosynthesis delays drought stress in *Populus tremula* trees and maintains starch reserves in branch xylem tissues. *New Phytologist*, *228*, 70–81.

De Roo, L., Salomón, R. L., & Steppe, K. (2020). Woody tissue photosynthesis reduces stem CO_2 efflux by half and remains unaffected by drought stress in young *Populus tremula* trees. *Plant, Cell & Environment*, *43*, 981–991.

Etzold, S., Zweifel, R., Ruehr, N. K., Eugster, W., & Buchmann, N. (2013). Long-term stem CO_2 concentration measurements in Norway spruce in relation to biotic and abiotic factors. *New Phytologist*, *197*, 1173–1184.

Hanson, P. J., & Gunderson, C. A. (2009). Root carbon flux: Measurements versus mechanisms. *New Phytologist*, *184*, 4–6.

Hölttä, T., & Kolari, P. (2009). Interpretation of stem CO_2 efflux measurements. *Tree Physiology*, *29*, 1447–1456.

Liu, J., Gu, L., Yu, Y., Huang, P., Wu, Z., Zhang, Q., … Sun, Z. (2019). Corticular photosynthesis drives bark water uptake to refill embolized vessels in dehydrated branches of *Salix matsudana*. *Plant, Cell & Environment*, *42*, 2584–2596.

McGuire, M. A., Marshall, J. D., & Teskey, R. O. (2009). Assimilation of xylem-transported ^{13}C-labelled CO_2 in leaves and branches of sycamore (*Platarius occidentais* L.). *Journal of Experimental Botany*, *60*, 3809–3817.

Mincke, J., Courtyn, J., Vanhove, C., Vandenberghe, S., & Steppe, K. (2020). Studying in vivo dynamics of xylem-transported $^{11}CO_2$ using positron emission tomography. *Tree Physiology*, *40*, 1058–1070.

Salomón, R. L., De Roo, L., Bodé, S., Boeckx, P., & Steppe, K. (2019). Isotope ratio laser spectroscopy to disentangle xylem-transported from locally respired CO_2 in stem CO_2 efflux. *Tree Physiology*, *39*, 819–830.

Salomón, R. L., De Roo, L., Bodé, S., Boeckx, P., & Steppe, K. (2021). Efflux and assimilation of xylem-transported CO_2 in stems and leaves of tree species with different wood anatomy. *Plant Cell Environ*, *44*, 3494–3508. https://doi.org/10.1111/pce.14062

Shimono, H., Kondo, M., & Evans, J. R. (2018). Internal transport of CO_2 from the root-zone to plant shoot is pH dependent. *Physiologia Plantarum*, *165*, 451–463.

Stutz, S. S., Anderson, J., Zulick, R., & Hanson, D. T. (2017). Inside out: Efflux of carbon dioxide from leaves represents more than leaf metabolism. *Journal of Experimental Botany*, *68*, 2849–2857.

Stutz, S. S., & Hanson, D. T. (2019). Contribution and consequences of xylem-transported CO_2 for C_3 plants. *New Phytologist*, *223*, 1230–1240.

Tarvainen, L., Wallin, G., Linder, S., Nasholm, T., Oren, R., Lofvenius, M. O., … Marshall, J. D. (2020). Limited vertical CO_2 transport in stems of mature boreal *Pinus sylvestris* trees. *Tree Physiology*, *41*, 63–75.

Teskey, R. O., Saveyn, A., Steppe, K., & McGuire, M. A. (2008). Origin, fate and significance of CO_2 in tree stems. *New Phytologist*, *177*, 17–32.

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