Foliar Sieve Elements: Nexus of the Leaf

William W. Adams III[a,*], Jared J. Stewart[a], Stephanie K. Polutchko[a], Barbara Demmig-Adams[a]

[a] Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, Colorado, USA; william.adams@colorado.edu; jared.stewart@colorado.edu; stephanie.polutchko@colorado.edu; barbara.demmig-adams@colorado.edu

*Corresponding author. Email: william.adams@colorado.edu, phone: +1-303-492-2880

Highlights

- Foliar sieve element features varied with growth environment and among species
- Foliar sieve element features covaried with features of multiple leaf systems
- Foliar sieve element volume correlated with photosynthetic capacity
- Foliar sieve element features correlated with leaf thickness
- Features of sieve elements correlated with those of other vascular cells

Abstract

In this review, a central position of foliar sieve elements in linking leaf structure and function is explored. Results from studies involving plants grown under, and acclimated to, different growth regimes are used to identify significant, linear relationships between features of minor vein sieve elements and those of 1) leaf photosynthetic capacity that drives sugar synthesis, 2) overall leaf structure that serves as the platform for sugar production, 3) phloem components that facilitate the loading of sugars (companion & phloem parenchyma cells), and 4) the tracheary elements that import water to support photosynthesis (and stomatal opening) as well as mass

flow of sugars out of the leaf. Despite comprising only a small fraction of physical space within the leaf, sieve elements represent a hub through which multiple functions of the leaf intersect. As the conduits for export of energy-rich carbohydrates, essential mineral nutrients, and information carriers, sieve elements play a central role in fueling and orchestrating development and function of the plant as well as, by extension, of natural and human communities that depend on plants as producers and partners in the global carbon cycle.

Keywords: foliar vasculature, minor veins, phloem, photosynthesis, sieve elements, tracheary elements

Abbreviations: Companion cell (CC), phloem parenchyma cell (PC), vein density (VD)

1. Introduction

Compared to other leaf cells, sieve elements are diminutive with a small cross-sectional area when viewed perpendicularly to the long axis of a vein (Esau 1977; Adams et al., 2013; Cohu et al., 2013a, 2014; Muller et al., 2014a,b; Stewart et al., 2017a). Sieve elements also comprise the smallest single tissue fraction of foliar veins (Cohu et al., 2013a, 2014; Muller et al., 2014a,b; Stewart et al., 2016, 2019) or the leaf as a whole (Esau, 1977; Muller et al., 2014b). Nevertheless, the sieve element plays an outsize role in the leaf. During leaf emergence and initial expansion, sieve elements of the newly formed primary and secondary, or major, veins are conduits for the import of sugars that provide the fuel and structural building material for leaf construction (Turgeon and Webb, 1973; Schmalstig and Geiger, 1987; Gagnon and Beebe, 1996). As the leaf expands, chloroplasts in foliar mesophyll cells become photosynthetically

competent, stomata become functional, and sugar produced in the leaf exceeds the needs of the leaf. At this point, the leaf undergoes transition from a sink for sugar (wherein consumption exceeds production) to a source of sugar (wherein production exceeds consumption) and, consequently, flow in the sieve elements reverses (Fellows and Geiger, 1974; Turgeon, 1989). In some species, this physiological shift coincides with the maturation of an intricate network of higher-order, or minor, veins that develops from the major veins into the mesophyll tissue during expansion (Turgeon, 2006). Collectively, the cells in these minor veins (as well as major veins in some species; see Turgeon, 2006) support active and regulated processes by which sugars are moved from the sugar-producing mesophyll cells into the sugar-transporting phloem network (Rennie and Turgeon, 2009; Zhang and Turgeon, 2018). The sieve elements within these minor veins are the primary focus of this review. In many instances, we refer specifically to the vascular cells of minor veins in herbaceous annual eudicots, such as sunflower (Fig. 1A; Stewart et al., 2019; see also Wang and Canny, 1985) and *Arabidopsis thaliana* (Fig. 1B; Stewart et al., 2019; see also Haritatos et al., 2000). In other cases, in which minor veins are not invoked, the statements and discussion involve all the foliar vasculature (every order of vein from midrib to the smallest veinlet).

2. Relationship to Photosynthesis

One may expect coordination between photosynthetic activity and leaf components that interact with photosynthesis. Coordination between stomatal opening and photosynthesis maximizes production of photosynthate while limiting water loss (Lawson et al., 2018). Regarding foliar vascular tissues, numerous studies have documented the important role of the water distribution network (via the xylem) that supports the leaf and photosynthesis (for reviews, see Adams et al.,

2018a; Brodribb and Buckley, 2018). In addition to coordination of water flux and photosynthetic activity, the anatomical and ultrastructural infrastructure of the vasculature exhibits acclimatory adjustments in concert with adjustments in maximal photosynthetic capacity (Adams et al., 2013, 2016, 2018a; Cohu et al., 2013b; Stewart et al., 2016, 2017a,b). Whereas relationships were reported between photosynthetic capacity and minor vein tracheary element features, these were less significant than relationships between transpiration rate and water-transport infrastructure (Cohu et al., 2013b; Adams et al., 2016, 2018a, 2018b). On the other hand, relationships between photosynthetic capacity and sieve element numbers and/or volumes were typically highly significant (Cohu et al., 2013b; Muller et al., 2014a; Adams et al., 2016, 2018a; Stewart et al., 2019). In other words, acclimatory changes in the capacity for photosynthesis were typically most aligned with changes in sieve-element infrastructural capacity.

To illustrate some of these relationships, Fig. 2 shows data from several studies of a summer and a winter annual after acclimation to various growth light and temperature regimes. For this comparison with photosynthesis expressed per unit leaf area, sieve element features are scaled to the leaf level either (Fig. 2A) as the product of sieve element number per minor vein × length of vein per leaf area (vein density) or (Fig. 2B) as the product of sieve element cross-sectional area per minor vein × length of vein per leaf area, which approximates sieve element volume per leaf area (Stewart et al., 2019). It had previously been shown that the number of sieve elements per foliar minor vein, which is greater in winter annuals grown under high versus low light intensities or grown under low versus high temperatures, can show significant, linear relationships with photosynthetic capacity when vein density varies very little (Cohu et al., 2013b). For comparisons of species with varying vein density, highly significant relationships

were obtained for sieve element features scaled to the leaf level by multiplication of vein density (Muller et al., 2014a; see also Stewart et al., 2019), as done here (Fig. 2A) for sunflower and *A. thaliana*. The trait of a higher vein density in sunflower leaves compared to leaves of *A. thaliana* (Cohu et al., 2014) is likely important for a summer annual that experiences a greater rate of transpirational water loss per unit leaf area during its growing season compared to a winter annual. Similarly, species growing in more arid environments possessed greater foliar vein density compared to species from more mesic habitats (Dunbar-Co et al., 2009; de Boer et al., 2016), presumably resulting in enhanced distribution of water throughout the leaf (de Boer et al., 2016).

The volume of minor-vein sieve elements per unit leaf area can likely serve as a proxy for the flux capacity for photosynthate export. It is noteworthy that sieve-element volume exhibited a single highly significant positive linear relationship with photosynthetic capacity with overlapping data for sunflower and *A. thaliana* (Fig. 2B), whereas the sieve-element number scaled to the leaf level exhibited two distinct relationships (each significant) with photosynthetic capacity for the two species (Fig. 2A). This divergence between species was associated with a greater number of sieve elements in the minor veins of *A. thaliana* than those of sunflower (Cohu et al., 2013a, 2014; Muller et al., 2014a; Fig. 1). One can conclude that the greater vein density of sunflower did not compensate for the lower number of sieve elements per individual vein, thereby causing sunflower to have lower numbers of sieve elements at the leaf scale. Each individual sieve element is thus also larger in sunflower compared to *A. thaliana* (Fig. 1), which contributes to the single relationship with photosynthetic capacity for sieve element volume per leaf area (Fig. 2B).

For a relationship between photosynthetic capacity and the features of tracheary elements, the situation was reversed in the following way. There was considerable overlap of the data resulting in a single significant positive relationship between the number of tracheary elements scaled to the leaf level (number per minor vein × vein density) and photosynthetic capacity for the two species (Fig. 2C). On the other hand, there were two separate (but each significant) positive relationships for the two species between tracheary element volume per leaf area and photosynthetic capacity (Fig. 2D). This scenario indicates that (i) a lower number of tracheary elements per vein (Fig. 1) and a greater vein density in sunflower compared to *A. thaliana* resulted in the same number of tracheary elements per leaf area and (ii) individual tracheary elements must also be larger in sunflower than in *A. thaliana* (Fig. 1; see also Cohu et al., 2014). To summarize, sieve elements were less numerous at the leaf scale but of larger individual size, while tracheary elements were both similarly numerous (at the leaf scale) and of larger individual size in the summer annual sunflower compared to the winter annual *A. thaliana*. This difference suggests a disproportionally greater emphasis on water transport in summer annuals versus winter annuals by virtue of a combination of tracheary element number at the scale of the individual vein, individual size of these water conduits, and vein density (cf. Cohu et al., 2014).

3. Relationship to Leaf Thickness

We previously documented a significant linear relationship between the thickness of the layers of the leaf's palisade cells and (i) sieve element cross-sectional area per veins as well as (ii) sieve element number at the leaf scale (number per minor vein × vein density) for two summer and two winter annuals (Cohu et al., 2014). These relationships are similarly significant for the

thickness of the entire leaf shown here for sunflower and the winter annuals *A. thaliana* and spinach (Fig. 3), indicating considerable coordination between overall leaf morphology and the conduits for photosynthate export. It is noteworthy that the data points for the summer annual clustered at a lower maximal leaf thickness as well as a lower maximal sieve element number at the leaf scale and a lower maximal sieve element volume per leaf area. Furthermore, the two winter annuals also varied in maximal leaf thickness and sieve element features at the leaf scale. We previously showed that winter annuals, but not summer annuals, increase the number of palisade layers when grown under cool temperature and high light compared to warm temperature and moderate light (Cohu et al., 2014). The particularly thick leaves of spinach could possibly also be associated with this species' membership in the Chenopodioideae (subfamiliy of Amaranthaceae) that includes many halophytes with succulent properties (Piirainen et al., 2017). In any event, it is noteworthy that sieve-element infrastructure closely mirrored these differences in leaf thickness.

4. Relationship Among Minor Vein Vascular Cell Types

Adjustments in sieve-element infrastructure features also closely mirror those of the other vascular cell types (Fig. 4). At the scale of the individual minor vein, there were significant linear relationships between cross-sectional area of sieve elements per minor vein and either (i) cross-sectional area of all other phloem tissue per minor vein (companion and parenchyma cells; Fig. 4A) or (ii) cross-sectional area of tracheary elements per minor vein (Fig. 4B). The correlation coefficients for both relationships further increased when all three metrics were scaled to the leaf level (Fig. 5) by multiplying cross-sectional areas per minor vein × vein density, which results in volumes per leaf area (Stewart et al., 2019). While matching trends

among adjustments in the various vascular cell types may partly be due to developmental constraints, it should be noted that there are also functional ties. All minor-vein vascular tissues make contributions to sugar loading and export through the sieve elements. The phloem parenchyma and companion cells both facilitate the flux of sucrose and active loading (in those species that employ active loading) into the sieve elements (Ayre and Turgeon, 2018). Likewise, in addition to supplying water to the leaf in support of stomatal opening, the tracheary elements supply water to the sieve elements in support of mass flow of sugars out of the leaf for distribution to the rest of the plant (Carvalho et al., 2018; Hesse et al., 2019). This theme is further considered in the following section.

5. Sieve Elements Transport More Than Sugars

Most of the water that passes through the foliar tracheary elements of C_3 and C_4 plants is lost to the atmosphere through transpiration, an inevitable consequence of stomatal opening that is required for adequate diffusion of carbon dioxide into the leaf to support photosynthetic production of sugars. This loss of water also contributes to cooling of leaves and prevention of heat damage under high ambient temperatures and when there is a steep water potential gradient between leaf and atmosphere. Only a negligible fraction of the water that enters a leaf is consumed in metabolism (such as water splitting for photosynthesis, catabolic hydrolysis of molecules, etc.). The major fraction of the remaining water fluxes from tracheary elements to phloem and ultimately into sieve elements as it follows a water potential gradient fueled by the concentration of solutes (sugars) in these sugar conduits (Hölttä et al., 2006; Nikinmaa et al., 2013). Although these fates are mutually exclusive, their consequences are inherently linked since stomatal opening is required for the production of sugars in quantities suitable for export

186 and the export of sugars from leaves is required for continued growth and maintenance of water-
187 acquiring roots. Moreover, sugar export from leaves, expression of associated genes, and
188 allocation to roots can be enhanced under water-limited conditions (e.g., Durand et al., 2016),
189 which suggests the fraction of water allocated to the sieve elements works synergistically, rather
190 than competitively, with the fraction allocated to support stomatal opening. However, to our
191 knowledge, the proportion of water transferred to the phloem versus that lost to the atmosphere
192 has not been quantified, but it is likely that several factors related to plant genotype (evolutionary
193 history), developmental stage, environmental conditions (e.g., water and nutrient availability)
194 during plant development, and prevailing environmental conditions at any given time contribute
195 to determining the relative fate of water delivered to the leaf via the xylem.

196 The function of sieve elements is consistent with the significant positive relationship
197 between cross-sectional areas per vein (Fig. 4B) and volumes per leaf area (Fig. 5B) of tracheary
198 elements and sieve elements. Sugars and associated water influx into sieve elements create
199 positive pressure at the source that, coupled with sugar unloading and water efflux in distant sink
200 tissues (and the resultant lowering of pressure within the phloem), drives mass flow of the sugar-
201 laden sap. This water-circulatory system between xylem and phloem continuously cycles water
202 back and forth between roots and shoots (van Bel, 2003; Hölttä et al., 2006), driven by newly
203 produced photosynthate during the day and sugars remobilized from stored starch at night
204 (Fondy and Geiger, 1982; Schleucher et al., 1998; Weise et al., 2003). Foliar sieve elements are
205 thus active in sugar export 24 h a day, thereby keeping the rest of the plant supplied with energy
206 and building material, regardless of photoperiod length (Mengin et al., 2017; Sharkey, 2017).

207 Since the primary function of the mature leaf is to produce and export energy-rich
208 carbohydrate, coordination should be expected between photosynthetic activity and the phloem

cells that participate in sugar export from the leaf. In addition to sieve elements, these include cells that facilitate loading of photosynthate (all three species examined here are apoplastic loaders) via sucrose efflux channels (SWEET proteins; Chen et al., 2012; Eom et al., 2015; Ayre and Turgeon, 2018), ATPases (that pump protons into the apoplastic space; Offler et al., 2003; Sondergaard et al., 2004; Gaxiola et al., 2007; Falhof et al., 2016; Ayre and Turgeon, 2018), and sucrose-proton symporters (that move sucrose into the companion cells and, in some species, the sieve elements; Srivastava et al., 2008; Rennie and Turgeon, 2009; Slewinski et al., 2013; Duan et al., 2014; Ayre and Turgeon, 2018). The data presented here demonstrate coordination between adjustments in the anatomical bases of photosynthesis and of sugar export during leaf development. Up- and downregulation of photosynthetic function, i.e., light- and CO_2-saturated maximal rate of photosynthesis per leaf area is associated with up- and down-sizing of leaf infrastructure for photosynthesis as can be assessed, e.g., as leaf thickness (Demmig-Adams et al., 2017). It may be possible to incorporate more photosynthetic protein into a single existing chloroplast and more chloroplasts into an existing palisade cell (that could expand in length; Amiard et al., 2005). However, major adjustments in photosynthetic capacity are often associated with infrastructural change during leaf development, such as insertion of additional palisade cell layers (Amiard et al., 2005; Dumlao et al., 2012; Cohu et al., 2014; Adams et al., 2016, 2018a).

A similar principle is apparently at work with respect to leaf vascular infrastructure. It is unclear to what extent existing phloem cells involved in sugar loading may be able to insert additional SWEET proteins, ATPases, or sucrose-proton symporters. However, the data shown here clearly indicate that more and/or larger cells are formed during the development of leaves that feature a greater photosynthetic capacity. This infrastructure expansion may increase the

membrane area available for placement of proteins that facilitate phloem loading as well as plasmodesmatal passages for sugar flux (see discussion in Adams et al., 2013, 2016, 2018a,b; Cohu et al., 2013b). The greater leaf-level volume of sugar-export conduits (sieve elements), and water conduits (tracheary elements) during acclimation to different growth environments presumably favors greater flux volumes. The selective pressure underlying the lowering of photosynthetic capacity (and number of photosynthetic proteins) in growth environments that permit, or require, less photosynthetic activity is understood to be the considerable cost of protein synthesis and turnover (Ishihara et al 2017). The selective pressures that resulted in the accompanying downsizing of sugar- and water-transport infrastructure are less well understood. What is clear is that there is tight coordination in the anatomy of multiple leaf components across species and environments (Adams et al., 2016, 2018a). For the case of photosynthesis, coordination of functional and anatomical aspects is orchestrated via transcriptional control by high-hierarchy gene regulators that respond to environmental cues and, in turn, control hundreds of other regulators (see, e.g., Demmig-Adams et al., 2018). A key example for the transduction of environmental cues are redox-modulated transcription factors (Hüner et al., 2016). Change in the growth environment typically leads to the generation of redox signals in the chloroplast (Demmig-Adams et al., 2014a,b, 2018) that are also relayed to the transcriptional control of nuclear genes (via redox-based chloroplast-nucleus retrograde signaling; Leister, 2019; Unal et al., 2020). It is likely that these same controls also coordinate function and anatomical features of sugar- and water-transport systems with those involved in the photosynthetic production of sugars.

In addition to photosynthate and water, a range of other molecules utilize the sieve elements to move from the leaves to other parts of the plant (van Bel, 2003). Many essential

elements are remobilized from leaves to growing sinks. These mobilized substances include various molecules containing nitrogen (e.g., amino acids, urea, nitrate; van Bel, 1990; Gaufichon et al., 2013; Bohner et al., 2015; Tegeder and Hammes, 2018; Tegeder and Masclaux-Daubresse, 2018; Babst et al., 2019; Ninan et al., 2019; Sample and Babst, 2019), phosphate, sulfate, and potassium (Khan and Choudhuri, 1992; Ning et al., 2013; Jeong et al., 2017), and the mineral micronutrients iron, zinc, copper, sodium, and chloride (Jeschke and Pate, 1995; Römheld and Schaaf, 2004; Shi et al., 2012; Barunawati et al., 2013; Pearce et al., 2014), although the mobilization of the latter seen in herbaceous plants does not appear to occur in evergreen trees during autumn (Shi et al., 2011).

In addition to transporting energy carriers, nutrients, and building blocks, sieve elements transport information carriers used for long-distance signaling (for a recent, comprehensive review, see Koenig and Hoffmann-Benning, 2020). These include at least five classes of phytohormones, multiple lipids, many proteins, and messenger RNAs (some coding for proteins transported in the phloem). These information carriers orchestrate a coordinated response of all plant organs during development and/or in response to changes in environmental conditions (Koenig and Hoffmann-Benning, 2020). Redox signals generated in chloroplasts and mitochondria (Demmig-Adams et al., 2014a,b, 2018) tie developmental and environmentally-induced changes in the leaf's energy metabolism to long-distance signaling by way of, for example, redox modulation of the synthesis, sequestration, and transport of various phytohormones (Foyer and Noctor, 2009; Demmig-Adams et al., 2013; Hüner et al., 2016; Schippers et al., 2016; Srivastava et al., 2017; Tognetti et al., 2017).

Some of these signals originate in the sieve elements of the leaves. For instance, plastids of sieve elements (and those of companion cells) are sites of jasmonic acid synthesis (Hause et

al., 2003), and both jasmonic acid and its precursor 12-oxo-phytodienoic acid (OPDA) are exported from the leaf via the sieve elements (Koenig and Hoffmann-Benning, 2020). Jasmonic acid signaling is an example of how environmental cues from biotic and abiotic stressors (Ali and Baek, 2020; Pérez-Alonso et al., 2021) are transduced to an internal response, such as formation of reactive oxygen species that oxidizes fatty acids of membrane phospholipids to derivates such as OPDA and jasmonic acid (Demmig-Adams et al., 2017), which act as gene regulators. Both OPDA and jasmonic acid can trigger wall/membrane invagination of phloem transfer cells in leaf minor veins (Amiard et al., 2007). In turn, the level of such invaginations was correlated with photosynthetic capacity in several species (Adams et al., 2014, 2016, 2018a).

Changes in calcium (Ca^{2+}) level contribute to the induction of jasmonic acid synthesis as a component of plant defense (Choi et al., 2017; Howe et al., 2018). Toyota et al. (2018) showed that cytosolic calcium levels increased markedly in phloem cells of sink leaves within one or two min after a source leaf was subjected to wounding or herbivory that impacted phloem cells. This finding demonstrates that signaling for induction of jasmonic acid synthesis can be propagated rapidly throughout a plant via the phloem.

6. From Sieve Elements to Larger Scales

Sieve elements not only link multiple functions of the leaf and connect the various organs of the whole plant, but could, by extension, also be seen as a nexus for the terrestrial biosphere and humanity (Adams, 2018). Synthesis and distribution of energy-rich compounds throughout the plant provide the basis for primary production in the major terrestrial biomes (Field et al., 1998) as well as in terrestrial agriculture (Weinzettel et al., 2019). In addition, a large fraction of

carbon is sequestered in plants and soil (Raven and Karley, 2006) as an important component of the global carbon cycle.

Foliar sieve element infrastructure can thus be expected to vary with increases and decreases in primary production in response to contributors to climate change (e.g., rising atmospheric levels of carbon dioxide, elevated temperatures) and their impacts on large-scale phenomena including altered precipitation patterns, rising sea level, forest fires, insect and pathogen outbreaks, etc. and their complex effect on plant productivity. While some of these factors induce increased carbon sequestration by plants (Nemani et al., 2003; Norby et al., 2005; Fu et al., 2018), many result in reduced levels of sequestration and some result in net carbon emission (Cox et al., 2000; Ciais et al., 2005; Olofsson et al., 2011; Rohrs-Richey et al., 2011; Koebsch et al., 2013; Appenzeller, 2015; Björkman and Niemelå, 2015; Han et al., 2015; Hof and Svahlin, 2016; Jones, 2016; Ramsfield et al., 2016; Loehman et al., 2017; Wolton et al., 2017; Wyka et al., 2017; Smart et al., 2020; Enríquez-de-Salamanca, 2020; Witze, 2020; Doyle et al., 2021; Liu et al., 2021; Martinez and Ardón, 2021) that further contributes to the rise in atmospheric carbon dioxide.

Author Contributions

WWA: Conceptualization, Visualization, Funding acquisition, Resources, Supervision, Project administration, Writing – Original Draft. JJS: Investigation, Formal analysis, Visualization, Funding acquisition, Writing – Review & Editing. SKP: Investigation, Formal analysis, Writing – Review & Editing. BD-A: Conceptualization, Visualization, Funding acquisition, Resources, Supervision, Project administration, Writing – Original Draft.

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Conflict of Interest

We declare no conflict of interest.

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References

Adams, W.W. III, 2018. Preface: the importance of leave to life and humanity, in: Adams III, W.W., Terashima, I. (Eds.), The Leaf: A Platform for Performing Photosynthesis. Advances in Photosynthesis and Respiration, Volume 44. Springer International Publishing, Cham, pp. xxvii–xxxiv. https://doi.org/10.1007/978-3-319-93594-2

Adams, W.W. III, Cohu, C.M, Muller, O., Demmig-Adams, B., 2013. Foliar phloem infrastructure in support of photosynthesis. Front. Plant Sci. 4, 194. https://doi.org/10.3389/fpls.2013.00194

Adams, W.W. III, Cohu, C.M., Amiard, V., Demmig-Adams, B., 2014. Associations between phloem-cell wall ingrowths in minor veins and maximal photosynthesis rate. Front. Plant Sci. 5, 24. https://doi.org/10.3389/fpls.2014.00024

Adams, W.W. III, Stewart, J.J., Cohu, C.M., Muller, O., Demmig-Adams, B., 2016. Habitat temperature and precipitation of *Arabidopsis thaliana* ecotypes determine the response of foliar vasculature, photosynthesis, and transpiration to growth temperature. Front. Plant Sci. 7, 1026. https://doi.org/10.3389/fpls.2016.01026

Adams, W.W. III, Stewart, J.J., Polutchko, S.K., Demmig-Adams, B., 2018a. Leaf vasculature and the upper limit of photosynthesis, in: Adams III, W.W., Terashima, I. (Eds.), The Leaf: A Platform for Performing Photosynthesis. Advances in Photosynthesis and Respiration, Volume 44. Springer International Publishing, Cham, pp. 27–54. https://doi.org/10.1007/978-3-319-93594-2_2

354 Adams, W.W. III, Stewart, J.J., Demmig-Adams, B., 2018b, Photosynthetic modulation in
355 response to plant activity and environment, in: Adams III, W.W., Terashima, I. (Eds.), The
356 Leaf: A Platform for Performing Photosynthesis. Advances in Photosynthesis and
357 Respiration, Volume 44. Springer International Publishing, Cham, pp. 493-563.
358 https://doi.org/10.1007/978-3-319-93594-2_18

359 Ali, M.S., Baek, K.-H., 2020. Jasmonic acid signaling pathway in response to abiotic stresses in
360 plants. Intl. J. Mol. Sci. 21, 621. https://doi.org/10.3390/ijms21020621

361 Amiard, V., Mueh, K.E., Demmig-Adams, B., Ebbert, V., Turgeon, R., Adams, W.W. III, 2005.
362 Anatomical and photosynthetic acclimation to the light environment in species with
363 differing mechanisms of phloem loading. Proc. Natl. Acad. Sci. U.S.A. 102, 12968-12973
364 https://doi.org/10.1073/pnas.0503784102

365 Amiard, V., Demmig-Adams, B., Mueh, K.E., Turgeon, R., Combs, A.F., Adams, W.W. III,
366 2007. Role of light and jasmonic acid signaling in regulating foliar phloem cell wall
367 ingrowth development. New Phytol. 173, 722-731. https://doi.org/10.1111/j.1469-
368 8137.2006.01954.x

369 Appenzeller, T., 2015. The new North – stoked by climate change, fire and insects are remaking
370 the planet's vast boreal forest. Science 349, 806-809.
371 https://doi.org/10.1126/science.349.6250.806

372 Ayre, B.G., Turgeon, R., 2018. Export of photosynthates from the leaf, in: Adams III, W.W.,
373 Terashima, I. (Eds.), The Leaf: A Platform for Performing Photosynthesis. Advances in
374 Photosynthesis and Respiration, Volume 44. Springer International Publishing, Cham, pp.
375 27–54. https://doi.org/10.1007/978-3-319-93594-2_3

376 Babst, B.A., Gao, F., Acosta-Gamboa, L.M., Karve, A., Schueller, M.J., Lorence, A., 2019.
377 Three *NPF* genes in *Arabidopsis* are necessary for normal nitrogen cycling under low
378 nitrogen stress. Plant Physiol. Biochem. 143, 1-10.
379 https://doi.org/10.1016/j.plaphy.2019.08.014

380 Barunawati, N., Hettwer Giehl, R.F., Bauer, B., von Wirén, N., 2013. The influence of inorganic
381 nitrogen fertilizer forms on micronutrient retranslocation and accumulation in grains of
382 winter wheat. Front. Plant Sci. 4, 320. https://doi.org/10.3389/fpls.2013.00320

383 Björkman, C., Niemelå, P., 2015. Climate change and insect pests. CABI Publishing,
384 Wallingford

385 Bohner, A., Kojima, S., Hajirezaei, M., Melzer, M., von Wirén, N., 2014. Urea retranslocation
386 from senescing Arabidopsis leaves is promoted by DUR3-mediated urea retrieval from leaf
387 apoplast. Plant J. 81, 377-387. https://doi.org/10.1111/tpj.12740

388 Brodribb, T.J., Buckley, T.N., 2018. Leaf water transport: a core system in the evolution and
389 physiology of photosynthesis, in: Adams III, W.W., Terashima, I. (Eds.), The Leaf: A
390 Platform for Performing Photosynthesis. Springer International Publishing, Advances in
391 Photosynthesis and Respiration, Volume 44. Cham, pp. 27–54. https://doi.org/10.1007/978-
392 3-319-93594-2_4

393 Carvalho, M.R., Losada, J.M., Niklas, K.J., 2018. Phloem networks in leaves. Curr. Opin. Plant
394 Biol. 43, 29-35. https://doi.org/10.1016/j.pbi.2017.12.007

Chen, L.-Q., Qu, X.-Q., Hou, B.-H., Sosso, D., Osorio, S., Fernie, A.R., Frommer, W.B., 2012. Sucrose efflux mediated by SWEET proteins as a key step for phloem transport. Science 335, 207-211. https://doi.org/10.1126/science.1213351

Choi, W.-G., Miller, G., Wallace, I., Harper, J., Mittler, R., Gilroy, S., 2017. Orchestrating rapid long-distance signaling in plants with Ca^{2+}, ROS and electrical signals. Plant J. 90, 698-707. https://doi.org/10.1111/tpj.13492

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, R., De Noblet, N., Friend, A.D., Friedlingstein, P., Grimwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529-533. https://doi.org/10.1038/nature03972

Cohu, C.M., Muller, O., Demmig-Adams, B., Adams, W.W. III, 2013a. Minor loading vein acclimation for three *Arabidopsis thaliana* ecotypes in response to growth under different temperature and light regimes. Front. Plant Sci. 4, 240. https://doi.org/10.3389/fpls.2013.00240

Cohu, C.M., Muller, O., Stewart, J.J., Demmig-Adams, B., Adams, W.W. III, 2013b. Association between minor loading vein architecture and light- and CO_2-saturated rates of photosynthetic oxygen evolution among *Arabidopsis thaliana* ecotypes from different latitudes. Front. Plant Sci. 4, 264. https://doi.org/10.3389/fpls.2013.00264

Cohu, C.M., Muller, O., Adams, W.W. III, Demmig-Adams, B., 2014. Leaf anatomical and photosynthetic acclimation to cool temperature and high light in two winter versus two summer annuals. Physiol. Plant. 152, 164–173. https://doi.org/10.1111/ppl.12154

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184-187. https://doi.org/10.1038/35041539

de Boer, H.J., Drake, P.L., Wendt, E., Price, C.A., Schulze, E.-D., Turner, N.C., Nicolle, D., Veneklaas, E.J., 2016. Apparent overinvestment in leaf venation relaxes leaf morphological constraints on photosynthesis in arid habitats. Plant Physiol. 172, 2286-2299. https://doi.org/10.1104/pp.16.01313

Demmig-Adams, B., Cohu, C.M., Amiard, V., van Zadelhoff, G., Veldink, G.A., Muller, O., Adams, W.W. III, 2013. Emerging trade-offs – impact of photoprotectants (PsbS, xanthophylls, and vitamin E) on oxylipins as regulators of development and defense. New Phytol. 197, 720-729. https://doi.org/10.1111/nph.12100

Demmig-Adams, B., Stewart, J.J., Burch, T.A., Adams, W.W. III, 2014a. Insights from placing photosynthetic light harvesting into context. J. Phys. Chem. Lett. 5, 2880-2889. https://doi.org/10.1021/jz5010768

Demmig-Adams, B., Stewart, J.J., Adams, W.W. III 2014b. Chloroplast photoprotection and the trade-off between abiotic and biotic defense, in: Demmig-Adams, B., Garab, G., Adams, W.W. III, Govindjee (Eds.) Non-Photochemical Quenching and Energy Dissipation in

436 Plants, Algae and Cyanobacteria. Advances in Photosynthesis and Respiration, Volume
437 40. Springer, Dordrecht, pp. 631-643. https://doi.org/10.1007/978-94-017-9032-1_28

438 Demmig-Adams, B., Stewart, J.J., Adams, W.W. III, 2017. Environmental regulation of intrinsic
439 photosynthetic capacity: An integrated view. Curr. Opin. Plant Biol. 37, 34-41.
440 https://doi.org/10.1016/j.pbi.2017.03.008

441 Demmig-Adams, B., Stewart, J.J., Baker, C.R., Adams, W.W. III, 2018. Optimization of
442 photosynthetic productivity in contrasting environments by regulons controlling plant form
443 and function. Intl. J. Mol. Sci. 19, 872. https://doi.org/10.3390/ijms1903872

444 Doyle, J.M., Earley, K.E., Atkinson, R.B., 2021. An analysis of Atlantic white cedar
445 (*Chamaecyparis thyoides* (L.) B.S.P) tree rings as indicators of ghost forest development in
446 a globally threatened ecosystem. Forests 12, 973. https://doi.org/10.3390/f12080973

447 Duan, Z., Homma, A., Kobayashi, M., Nagata, N., Kaneko, Y., Fujiki, Y., Nishida, I., 2014.
448 Photoassimilation, assimilate translocation and plasmodesmal biogenesis in the source
449 leaves of *Arabidopsis thaliana* grown under an increased atmospheric CO_2 concentration.
450 Plant Cell Physiol. 55, 358-369. https://doi.org/10.1093/pcp.pcu004

451 Dumlao, M.R., Darehshouri, A., Cohu, C.M., Muller, O., Mathias, J., Adams, W.W. III,
452 Demmig-Adams, B., 2012. Low temperature acclimation of photosynthetic capacity and
453 leaf morphology in the context of phloem loading type. Photosynth. Res. 113, 181-189
454 https://doi.org/10.1007/s11120-012-9762-5

455 Dunbar-Co, S., Sporck, M.J., Sack, L., 2009. Leaf trait diversification and design in seven rare
456 taxa of the Hawaiian *Plantago* radiation. Intl. J. Plant Sci. 170, 61-75.
457 https://doi.org/10.1086/59311

458 Durand, M., Porcheron, B., Hennion, N., Maurousset, L., Lemoine, R., Pourtau, N., 2016. Water
459 deficit enhances C export to the roots in *Arabidopsis thaliana* plants with contribution of
460 sucrose transporters in both shoot and roots. Plant Physiol. 170, 1460-1479.
461 https://doi.org/10.1104/pp.15.01926

462 Enríquez-de-Salamanca, Á., 2020. Contribution to climate change of forest fires in Spain:
463 emissions and loss of sequestration. J. Sust. Forest. 39, 417-431.
464 https://doi.org/10.1080/10549811.2019.1673779

465 Eom, J.-S., Chen, L.-Q., Sosso, D., Julius, B.T., Lin, I.W., Qu, X.-Q., Braun, D.M., Frommer,
466 W.B., 2015. SWEETs, transporters for intracellular and intercellular sugar translocation.
467 Curr. Opin. Plant Biol. 25, 53-62. https://doi.org/10.1016/j.pbi.2015.04.005

468 Esau, K., 1977. Anatomy of Seed Plants, 2nd Edition. John Wiley and Sons, New York

469 Falhof, J., Pedersen, J.T., Fuglsang, A.T., Palmgren, M., 2016. Plasma membrane H^+-ATPase
470 regulation in the center of plant physiology. Mol. Plant 9, 323-337.
471 https://doi.org/10.1016/j.molp.2015.11.002

472 Fellows, R.J., Geiger, D.R., 1974. Structural and physiological changes in sugar beet leaves
473 during sink to source conversion. Plant Physiol. 54, 877-885.
474 https://doi.org/10.1104/pp.54.6.877

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkoski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. Science 281, 237-240. https://doi.org/10.1126/science.281.5374.237

Fondy, B.R., Geiger, D.R., 1982. Diurnal pattern of translocation and carbohydrate metabolism in source leaves of *Beta vulgaris* L. Plant Physiol. 70, 671-676. https://doi.org/10.1104/pp70.3.671

Foyer, C.H., Noctor, G., 2009. Redox regulation in photosynthetic organisms: signaling, acclimation, and practical implications. Antioxid. Redox Signal. 11, 861-905. https://doi.org/10.1089/ars.2008.2177

Fu, Y.H., Piao, S., Delpierre, N., Hao, F., Hänninen, H., Liu, Y., Sun, W., Janssens, I.A., Campioli, M., 2018. Larger temperature response of autumn leaf senescence than spring leaf-out phenology. Glob. Chang. Bio. 24, 2159-2168. https://doi.org/10.1111/gcb.14021

Gagnon, M.-J., Beebe, D.U., 1996. Establishment of a plastochron index and analysis of the sink-to-source transition in leaves of Moricandia arvensis (L.) DC. (Brassicaceae). Intl. J. Plant Sci. 167, 262-268. https://doi.org/10.1086/297345

Gaufichon, L., Masclaux-Daubresse, C., Tcherkez, G., Reisdorf-Cren, M., Sakakibara, Y., Hase, T., Clément, G., Avice, J.-C., Grandjean, O., Marmagne, A., Boutet-Mercey, S., Azzopardi, M., Soulay, F., Suzuki, A., 2013. *Arabidopsis thaliana ASN2* encoding asparagine synthetase is involved in the control of nitrogen assimilation and export during vegetative growth. Plant Cell Environ. 36, 328-342. https://doi.org/10.1111/j.1365-3040.2012.02576.x

Gaxiola, R.A., Palmgren, M.G., Schumacher, K., 2007. Plant proton pumps. FEBS Lett. 581, 2204-2214. https://doi.org/10.1016/j.febslet.2007.03.050

Han, G., Chu, X., Xing, Q., Li, D., Yu, J., Luo, Y., Wang, G., Mao, P., Rafique, R., 2015. Effects of episodic flooding on the net ecosystem CO_2 exchange of a supratidal wetland in the Yellow River Delta. J. Geophys. Res. Biogeosci. 120, 1506-1520. https://doi.org/10.1002/2015JG002923

Haritatos, E., Medville, R., Turgeon, R., 2000. Minor vein structure and sugar transport in *Arabidopsis thaliana*. Planta 211, 105-111. https://doi.org/10.1007/s004250000268

Hause, B., Hause, G., Kutter, C., Miersch, O., Wasternack, C., 2003. Enzymes of jasmonate biosynthesis occur in tomato sieve elements. Plant Cell Physiol. 44, 643-648. https://doi.org/10.1093/pcp/pcg072

Hesse, B.D., Goisser, M., Hartmann, H., Grams, T.E.E., 2019. Repeated summer drought delays sugar export from the leaf and impairs phloem transport in mature beech. Tree Physiol. 39, 192-200. https://doi.org/10.1093/treephys/tpy122

Hof, A.R., Svahlin, A., 2016. The potential effect of climate change on the geographical distribution of insect pest species in the Swedish boreal forest. Scand. J. For. Res. 31, 29-39. https://doi.org/10.1080/02827581.2015.1052751

Howe, G.A., Major, I.T., Koo, A.J., 2018. Modularity in jasmonate signaling for multistress resilience. Annu. Rev. Plant Biol. 69, 387-415. https://doi.org/10.1146/annurev-arplant-042817-040047

516 Hölttä, T., Vesala, T., Sevanto, S., Perämäki, M., Nikinmaa, E. 2006. Modeling xylem and
517 phloem flows in trees according to cohesion theory and Münch hypothesis. Trees 20, 67-
518 78. https://doi.org/10.1007/s00468-005-0014-6

519 Hüner, N.P.A., Dahal, K., Bode, R., Kurepin, L.V., Ivanov, A.G., 2016. Photosynthetic
520 acclimation, vernalization, crop productivity and 'the grand design of photosynthesis'. J.
521 Plant Physiol. 203, 29-43. https://doi.org/10.1016/j.jplph.2016.04.006

522 Ishihara, H., Moraes, T.A., Pyl, E.-T., Schulze, W.X., Obata, T., Scheffel, A., Fernie, A.R.,
523 Sulpice, R., Stitt, M., 2017. Growth rate correlates negatively with protein turnover in
524 Arabidopsis accessions. Plant J. 91, 416-429. https://doi.org/10.1111/tpj.13576

525 Jeong, K., Baten, A., Waters, D.L.E., Pantoja, O., Julia, C.C., Wissuwa, M., Jeuer, S.,
526 Kretzschmar, T., Rose, T.J., 2017. Phosphorus remobilization from rice flag leaves during
527 grain filling: an RNA-seq study. Plant Biotech. J. 15, 15-26.
528 https://doi.org/10.1111/pbi.12586

529 Jeschke, W.D., Pate, J.S., 1995. Mineral nutrition and transport in xylem and phloem of *Banksia*
530 *prionotes* (Proteaceae), a tree witih dimorphic root morphology. J. Exp. Bot. 46, 895-905.
531 https://doi.org/10.1093/jxb/46.8.895

532 Jones, R.A.C., 2016. Future scenarios for plant virus pathogens as climate change progresses, in:
533 Kielian, M., Maramorosch, K., Mettenleiter, T.C. (Eds.) Advances in Virus Research,
534 Volume 95, Elsevier, San Diego, pp. 87-147. https://doi.org/10.1016/bs.aivir.2016.02.004

535 Khan, R.I., Choudhuri, M.A., 1992. Influence of reproductive organs on plant senescence in rice
536 and wheat. Biol. Plant. 34, 241-251. doi: 10.1007/BF02925876

537 Koebsch, R., Glatzel, S., Hofmann, J., Forbrich, I., Jurasinski, G., 2013. CO_2 exchange of a
538 temperate fen during the conversion from moderately rewetting to flooding. J. Geophys.
539 Res. Biogeosci. 118, 940-950. https://doi.org/10.1002/jgrg.20069

540 Koenig, A.M., Hoffmann-Benning, S., 2020. The interplay of phloem-mobile signals in plant
541 development and stress response. Biosci. Rep. 40, BSR20193329.
542 https://doi.org/10.1042/BSR20193329

543 Leister, D., 2019. Piecing the puzzle together: the central role of reactive oxygen species and
544 redox hubs in chloroplast retrograde signaling. Antiox. Redox Signal.
545 https://doi.org/10.1089/ars.2017.7392

546 Liu, X., He, B., Guo, L., Huang, L., Yuan, W., Chen, X., Hao, X., Xie, X., Zhang, Y., Zhong, Z.,
547 Li, T., Chen, A., 2021. European carbon uptake has not benefited from vegetation greening.
548 Geophys. Res. Lett. 48, e2021GL094870. https://doi.org/10.1029/2021GL094870

549 Loehman, R.A., Keane, R.E., Hollsinger, L.M., Wu, Z., 2017. Interactions of landscape
550 disturbances and climate change dictate ecological pattern and process: spatial modeling of
551 wildfire, insect, and disease dynamics under future climates. Landsc. Ecol. 32, 1447-1459.
552 https://doi.org/10.1007/s10980-016-0414-6

553 Martinez, M., Ardón, M., 2021. Drivers of greenhouse gas emissions from standing dead trees in
554 ghost forests. Biogeochemistry 154, 471-488. https://doi.org/10.1007/s10533-021-00797-5

555 Mengin, V., Pyl, E.-T., Moraes, T.A., Sulpice, R., Encke, B., Stitt, M., 2017. Photosynthate

partitioning to starch in *Arabidopsis thaliana* is insensitive to light intensity but sensitive to photoperiod due to a restriction on growth in the light in short photoperiods. Plant Cell Environ. 40, 2608-2627. https://doi.org/10.1111/pce.13000

Muller, O., Cohu, C.M., Stewart, J.J., Protheroe, J.A., Demmig-Adams, B., Adams, W.W. III, 2014a. Association between photosynthesis and contrasting features of minor veins in leaves of summer annuals loading phloem via symplastic versus apoplastic routes. Physiol. Plant. 152, 174–183. https://doi.org/10.1111/ppl.12155

Muller, O., Stewart, J.J., Cohu, C.M., Polutchko, S.K., Demmig-Adams, B., Adams, W.W. III, 2014b. Leaf architectural, vascular and photosynthetic acclimation to temperature in two biennials. Physiol. Plant. 152, 763–772. https://doi.org/10.1111/ppl.12226

Nemani, R.R.., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B., Running, S.W., 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science, 300, 1560-1563. https://doi.org/10.1126/science.1082750

Nikinmaa, E., Hölttä, T., Hari, P., Kolari, P., Mäkelä, A., Sevanto, S., Vesala, T., 2013. Assimilate transport in phloem sets conditions for leaf gas exchange. Plant Cell Environ. 36, 655–669. https://doi.org/10.1111/pce.12004

Ninan, A.S., Grant, J., Song, J., Jameson, P.E., 2019. Expression of genes related to sugar and amino acid transport and cytokinin metabolism during leaf development and senescence in *Pisum sativum* L. Plants 8, 76. https://doi.org/10.3390/plants8030076

Ning, P., Li, S., Yu, P., Zhang, Y., Li, C., 2013. Post-silking accumulation and partitioning of dry matter, nitrogen, phosphorus and potassium in maize varieties differing in leaf longevity. Field Crops Res. 144, 19-27. https://doi.org/10.1016.j.fcr.2013.01.020

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesdinger, W.H., Oren, R., 2005. Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc. Natl. Acad. Sci. U.S.A. 102, 18052-18056. https://pnas.org/cgi/doi/pnas.0509478102

Offler, C.E., McCurdy, D.W., Patrick, J.W., Talbot, M.J., 2003. Transfer cells: cells specialized for a special purpose. Annu. Rev. Plant Biol. 54, 431-454. https://doi.org/10.1146/annurev.arplant.54.031902.134812

Olofsson, J., Ericson, L., Torp, M., Stark, S., Baxter, R., 2011. Carbon balance of Arctic tundra under increased snow cover mediated by a plant pathogen. Nature Clim. Change 1, 220-223. https://doi.org/10.1038/nclimate1142

Pearce, S., Tabbita, F., Cantu, D., Buffalo, V., Avni, R., Vazquez-Gross, H., Zhao, R., Conley, C.J., Distelfeld, A., Dubcovksy, J., 2014. Regulation of Zn and Fe transporters by the *BPC1*gene during early wheat monocarpic senescence. BMC Plant Biol. 14, 368. https://doi.org/10.1186/s12870-014-0368-2

Pérez-Alonso, M.-M., Sánchez-Parra, B, Ortiz-García, P., Santamaria, M.E., Díaz, I., Pollmann, S., 2021. Jasmonic acid-dependent MYC transcription factors bind to a tandem G-box

motif in the YUCCA8 and YUCCA9 promoters to regulate biotic stress responses. Intl. J. Mol. Sci. 22, 9768. https://doi.org/10.3390/ijms22189768

Piirainen, M., Liebisch, O., Kadereit, G., 2017. Phylogeny, biogeography, systematics and taxonomy of Salicornioideae (Amaranthaceae/Chenopodiaceae) – a cosmopolitan, highly specialized hygrohalophyte lineage dating back to the Oligocene. Taxon 66, 109-132. https://doi.org/10.12705/661.6

Polutchko, S.K., Stewart, J.J., Adams, W.W. III, Demmig-Adams, B., 2021. Photosynthesis and foliar vascular adjustments to growth light intensity in summer annual species with symplastic and apoplastic phloem loading. J. Plant Physiol. 267, 153532. https://doi.org/10.1016/j.jplph.2021.153532

Ramsfield, T.D., Bentz, B.J., Faccoli, M., Jactel, H., Brockerhoff, E.G., 2016. Forest health in a changing world: effects of globalization and climate change on forest insect and pathogen impacts. Forestry 89, 245-252. https://doi.org/10.1093/forestry/cpw018

Raven, J.A., Karley, A.J., 2006. Carbon sequestration: photosynthesis and subsequent processes. Curr. Biol. 16, R165-R167. https://doi.org/10.1016/j.cub.2006.02.041

Rennie, E.A., Turgeon, R., 2009. A comprehensive picture of phloem loading strategies. Proc. Natl. Acad. Sci. U.S.A. 106, 14162-14167. https://doi.org/10.1073/pnas.0902279106

Rohrs-Richey, J.K., Mulder, C.P.H., Winton, L.M., Stanosz, G., 2011. Physiological performance of an Alaskan shrub (*Alnus fruticosa*) in response to disease (*Valsa melanodiscus*) and water stress. New Phytol. 189, 295-307. https://doi.org/10.1111/j.1469-8137.2010.03472.x

Römheld, V., Schaaf, G., 2004. Iron transport in plants: future research in view of a plant nutritionist and a molecular biologist. Soil Sci. Plant Nutr. 50, 1003-1012. https://doi.org/10.1080/00380768.2004.10408567

Sample, R., Babst, B.A., 2019. Timing of nitrogen resorption-related processes during fall senescence in southern oak species. For. Sci. 65, 245-249. https://doi.org/10.1093/forsci/fxy062

Schippers, J.H.M., Foyer, C.H., van Dongen, J.T., 2016. Redox regulation in shoot growth, SAM maintenance and flowering. Curr. Opin. Plan Biol. 29, 121-128. https://doi.org/10.1016/j.pbi.2015.11.009

Schleucher, J., Vanderveer, P.J., Sharkey, T.D., 1998. Export of carbon from chloroplasts at night. Plant Physiol. 118, 1439-1445. https://doi.org/10.1104.pp.118.4.1439

Schmalstig, J.G., Geiger, D.R., 1987. Phloem unloading in developing leaves of sugar beet. II. Termination of phloem unloading. Plant Physiol. 83, 49-52. https://doi.org/10.1104/pp.83.1.49

Sharkey, T.D., 2017. A dichotomy resolved: plant growth can control the rate of starch accumulation. Plant Cell Environ. 40, 2602-2607. https://doi.org/10.1111/pce.13059

Shi, R., Bäßler, R., Zou, C., Römheld, V., 2011. Is iron phloem mobile during senescence in trees? A reinvestigation of Rissmüller's finding of 1874. Plant Physiol. Biochem. 49, 489-493. https://doi.org/10.1016/j.plaphy.2011.03.004

637 Shi, R., Weber, G., Köster, J., Reza-Hajirezaei, M., Zou, C., Zhang, F., von Wirén, N., 2012.
638 Senescence-induced iron mobilization in souce leaves of barley (*Hordeum vulgare*) plants.
639 New Phytol. 195, 372-383. https://doi.org/10.1111/j.1469-8137.2012.04165.x

640 Slewinski, T.L., Zhang, C., Turgeon, R., 2013. Structural and functional heterogeneity in phloem
641 loading and transport. Front. Plant Sci. 4, 244. https://doi.org/10.3389/fpls.2013.00244

642 Smart, L.S., Taillie, P.J., Poulter, B., Vukomanovic, J., Singh, K.K., Swenson, J.J., Mitasova, H.,
643 Smith, J.W., Meentemeyer, R.K., 2020. Aboveground carbon loss associated with the
644 spread of ghost forests as sea levels rise. Environ. Res. Lett. 15, 104028.
645 https://doi.org/10.1088/1748-9326/aba136

646 Sondergaard, T.E., Schulz, A., Palmgren, M.G., 2004. Energization of transport processes in
647 plants. Roles of the plasma membrane H^+-ATPase. Plant Physiol. 136, 2475-2482.
648 https://doi.org/10.1104/pp.104.048231

649 Srivastava, A.C., Ganesan, S., Ismail, I.O., Ayre, B.G., 2008. Functional characterization of the
650 Arabidopsis AtSUC2 sucrose/H^+ symporter by tissue-specific complementation reveals an
651 essential role in phloem loading but not in long-distance transport. Plant Physiol. 148, 200-
652 211. https://doi.org/10.1104.pp.108.124776

653 Srivastava, A., Redij, T., Sharma, B., 2017. Interaction between hormone and redox signaling in
654 plants: divergent pathways and convergent roles, in: Pandey, G.K. (Ed.) Mechanisms of
655 Plant Hormone Signaling under Stress, II, John Wiley & Sons, Inc., Hoboken, NJ, pp. 1-22.
656 https://doi.org/10.1002/9781118889022.ch19

657 Stewart, J.J., Demmig-Adams, B., Cohu, C.M., Wenzl, C.A., Muller, O., Adams W.W. III, 2016.
658 Growth temperature impact on leaf form and function in *Arabidopsis thaliana* ecotypes
659 from northern and southern Europe. Plant Cell Environ. 39, 1549–1558.
660 https://doi.org/10.1111/pce.12720

661 Stewart, J.J., Polutchko, S.K., Adams, W.W. III, Demmig-Adams, B., 2017a. Acclimation of
662 Swedish and Italian ecotypes of *Arabidopsis thaliana* to light intensity. Photosynth. Res.
663 134, 215–229. https://doi.org/10.1007/s11120-017-0436-1

664 Stewart, J.J., Polutchko, S.K., Adams, W.W. III, Cohu, C.M., Wenzl, C.A., Demmig-Adams, B.,
665 2017b. Light, temperature and tocopherol status influence foliar vascular anatomy and leaf
666 function in *Arabidopsis thaliana*. Physiol. Plant. 160, 98–110.
667 https://doi.org/10.1111/ppl.12543

668 Stewart, J.J., Muller, O., Cohu, C.M., Demmig-Adams, B., Adams, W.W. III, 2019.
669 Quantification of leaf phloem anatomical features with microscopy, in: Liesche, J. (Ed.),
670 Phloem: Methods and Protocols. Springer, New York, NY, pp. 55–72.
671 https://doi.org/10.1007/978-1-4939-9562-2_5

672 Tegeder, M., Hammes, U.Z., 2018. The way out and in: phloem loading and unloading of amino
673 acids. Curr. Opin. Plant Biol. 43, 16-21. https://doi.org/10.1016/j.pbi.2017.12.002

674 Tegeder, M., Masclaux-Daubresse, C., 2018. Source and sink mechanisms of nitrogen transport
675 and use. New Phytol. 217, 35-53. https://doi.org/10.1111.nph.14876

Toyota, M., Spencer, D., Sawai-Toyota, S., Jiaqi, W., Zhang, T., Koo, A.J., Howe, G.A., Gilroy, S., 2018. Glutamate triggers long-distance, calcium-based plant defense signaling. Science 361, 1112-1115. https://doi.org/10.1126/science.aat7744

Turgeon, R., 1989. The sink-source transition in leaves. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 119-138. https://doi.org/10.1146/annurev.pp.40.060189.001003

Turgeon, R., 2006. Phloem loading: how leaves gain their independence. BioScience 56, 15-24, https://doi.org/10.1641/0006-3568(2006)056[0015:PLHLGT]2.0.CO;2

Turgeon, R., Webb, J.A., 1973, Leaf development and phloem transport in *Cucurbita pepo*: transition from import to export. Planta 113, 179-191. https://doi.org/10.1007/BF00388202

Unal, D., García-Caparrós, P., Kumar, V., Dietz, K.-J., 2020. Chloroplast-associated molecular patterns as concept for fine-tuned operational retrograde signalling. Phil. Trans. R. Soc. B. 375, 2019.0443. https://doi.org/10.1098/rstb.2019.0443

van Bel, A.J.E., 1990. Xylem-phloem exchange via the rays – the undervalued route of transport. J. Exp. Bot. 41, 631-644. https://doi.org/10.1093/jxb/41.6.631

van Bel, A.J.E., 2003. The phloem, a miracle of ingenuity. Plant Cell Environ. 26, 125-149. https://doi.org/10.1046/j.1365-3040.2003.00963.x

Wang, X.-D., Canny, M.J., 1985. Loading and translocation of assimilate in the fine veins of sunflower leaves. Plant Cell Environ. 8, 669-685. https://doi.org/10.1111/1365-3040.ep11611718

Weinzettel, J., Vackárû, D., Medková, H., 2019. Potential net primary production footprint of agriculture: a global trade analysis. J. Indus. Ecol. 23, 1133-1142. https://doi.org/10.1111/jiec.12850

Weise, S.E., Weber, A.P.M., Sharkey, T.D., 2003. Maltose is the major form of carbon exported from the chloroplast at night. Planta 218, 474-482. https://doi.org/10.1007/s00425-003-1128-y

Witze, A., 2020. The Arctic is burning like never before – and that's bad news for climate change. Nature 585, 336-337. https://doi.org/10.1038/d41586-020-02568-y

Wolton, B.M., Flannigan, M.D., Marshall, G.A., 2017. Potential climate change impacts on fire intensity and key wildfire suppression thresholds in Canada. Environ. Res. Lett. 12, 095003. https://doi.org/10.1088/1748-9326/aa7e6e

Wyka, S.A., Smith, C., Munck, I.A., Rock, B.N., Ziniti, B.L., Broders, K., 2017. Emergence of white pine needle damage in the northeastern United States is associated with changes in pathogen pressure in response to climate change. Glob. Chang. Biol. 23, 394-405. https://doi.org/10.1111/gcb.13359

Zhang, C., Turgeon, R., 2018. Mechanisms of phloem loading. Curr. Opin. Plant Biol. 43, 71-75. https://doi.org/10.1016/j.pbi.2018.01.009

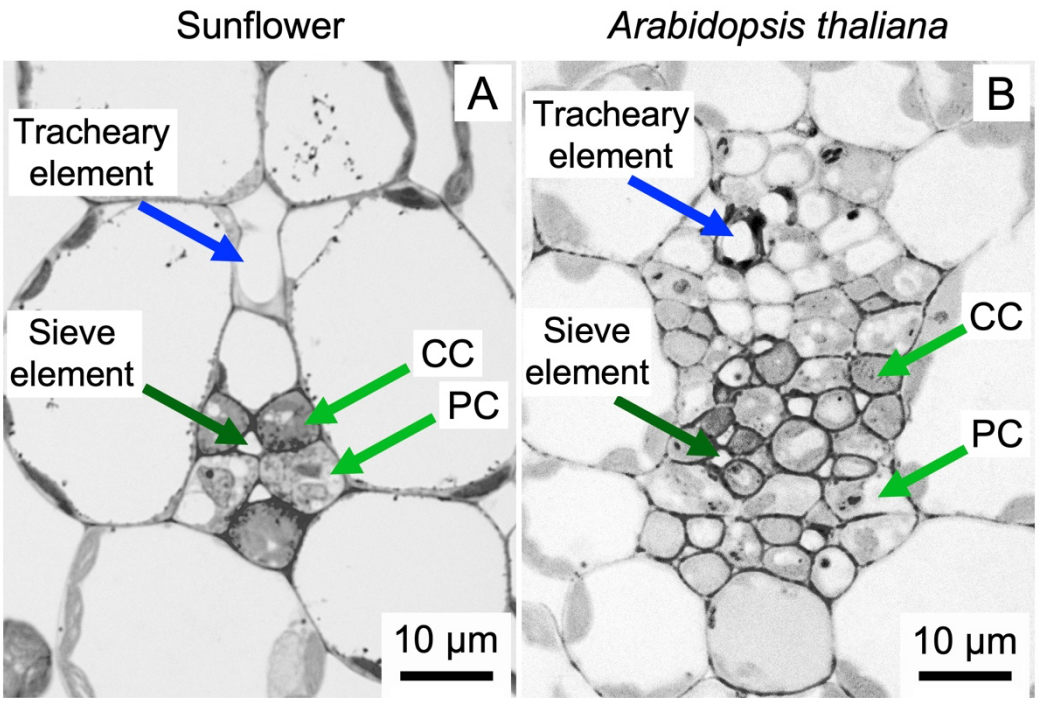
712 **Figure Legends**

713 Fig. 1. Light microscopic images of minor vein cross sections from leaves of (A) sunflower
714 (*Helianthus annuus* L. cv. Soraya) and (B) *Arabidopsis thaliana* (L. Heynh. Columbia-0) that
715 developed under 1000 μmol photons m^{-2} s^{-1} (9-h photoperiod) at leaf temperatures of 25–27°C)
716 (and 20°C during the night). In each image, a blue arrow indicates the location of a tracheary
717 element (one of two in the sunflower vein and one of five in the *A. thaliana* vein), a dark green
718 arrow indicates the location of a sieve element (one of two in the sunflower vein and one of eight
719 in the *A. thaliana* vein), and the light green arrows point to a companion cell (CC) and a phloem
720 parenchyma cell (PC) in each image. For details concerning the preparation and analysis of such
721 cross sections, see Stewart et al. (2019; see also Cohu et al., 2014).
722
723 Fig. 2. Relationship between photosynthetic capacity and (A,C) cell number per minor vein ×
724 minor vein density (VD) and (B,D) cell volume per leaf area of (A,B) sieve elements and (C,D)
725 tracheary elements in leaves of *Arabidopsis thaliana* (green symbols) and/or sunflower
726 (*Helianthus annuus*; orange symbols). The characterized minor veins constituted the third and
727 fourth order in leaves of *A. thaliana* and the sixth and seventh order in leaves of sunflower. Both
728 species were grown under four different growth regimes of 400 or 1000 μmol photons m^{-2} s^{-1} (9-
729 h photoperiod) at leaf temperatures of 25–27°C or 14–16°C (and 20°C or 12.5°C, respectively,
730 during the night). Additionally, *A. thaliana* was grown under 100 or 1000 μmol photons m^{-2} s^{-1}
731 (9-h photoperiod) at a leaf temperature of 20°C (and 12°C at night), and sunflower was grown
732 under 100 and 750 μmol photons m^{-2} s^{-1} (12-h photoperiod) at a leaf temperature of 27–28°C
733 (and 22°C at night). Data from Cohu et al. (2013a,b, 2014), Adams et al. (2016, 2018a), Stewart
734 et al. (2017a,b), and Polutchko et al. (2018, 2021). Lines of fit with shaded 95% confidence

735 intervals for (A,D) *A. thaliana* (green lines and shading) and sunflower (orange lines and
736 shading) separately or (B,C) combined (black lines and gray shading).
737
738 Fig. 3. Relationship between leaf thickness and sieve element (A) cross-sectional area per minor
739 vein and (B) cell number per minor vein × minor vein density (VD) in leaves of *Arabidopsis*
740 *thaliana* (green symbols), sunflower (*Helianthus annuus*; orange symbols), and spinach
741 (*Spinacia oleracea*; dark green symbols). In spinach, the characterized minor veins constituted
742 the fourth and fifth order veins. All species were grown under four different growth regimes of
743 400 or 1000 μmol photons m^{-2} s^{-1} (9-h photoperiod) at leaf temperatures of 25–27°C or 14–16°C
744 (and 20°C or 12.5°C, respectively, during the night). See the legend of Fig. 2 for additional
745 details regarding the minor veins characterized in sunflower and *A. thaliana* as well as additional
746 growth conditions for *A. thaliana*. Data from Cohu et al. (2013a,b, 2014), Adams et al. (2016,
747 2018a), and Stewart et al. (2016, 2017a,b). Lines of fit with 95% confidence intervals (black
748 lines and gray shading).
749
750 Fig. 4. Relationship between the cross-sectional areas per minor vein of (A) companion cells +
751 phloem parenchyma cells (CC + PC) and sieve elements and (B) tracheary elements and sieve
752 elements in leaves of *Arabidopsis thaliana* (green symbols), sunflower (*Helianthus annuus*;
753 orange symbols), and spinach (*Spinacia oleracea*; dark green symbols). See the legends of Figs.
754 2 and 3 for additional details. Data from Cohu et al. (2013a,b, 2014), Adams et al. (2016,
755 2018a), Stewart et al. (2017a,b), and Polutchko et al. (2021). Lines of fit with 95% confidence
756 intervals (black lines and gray shading).
757

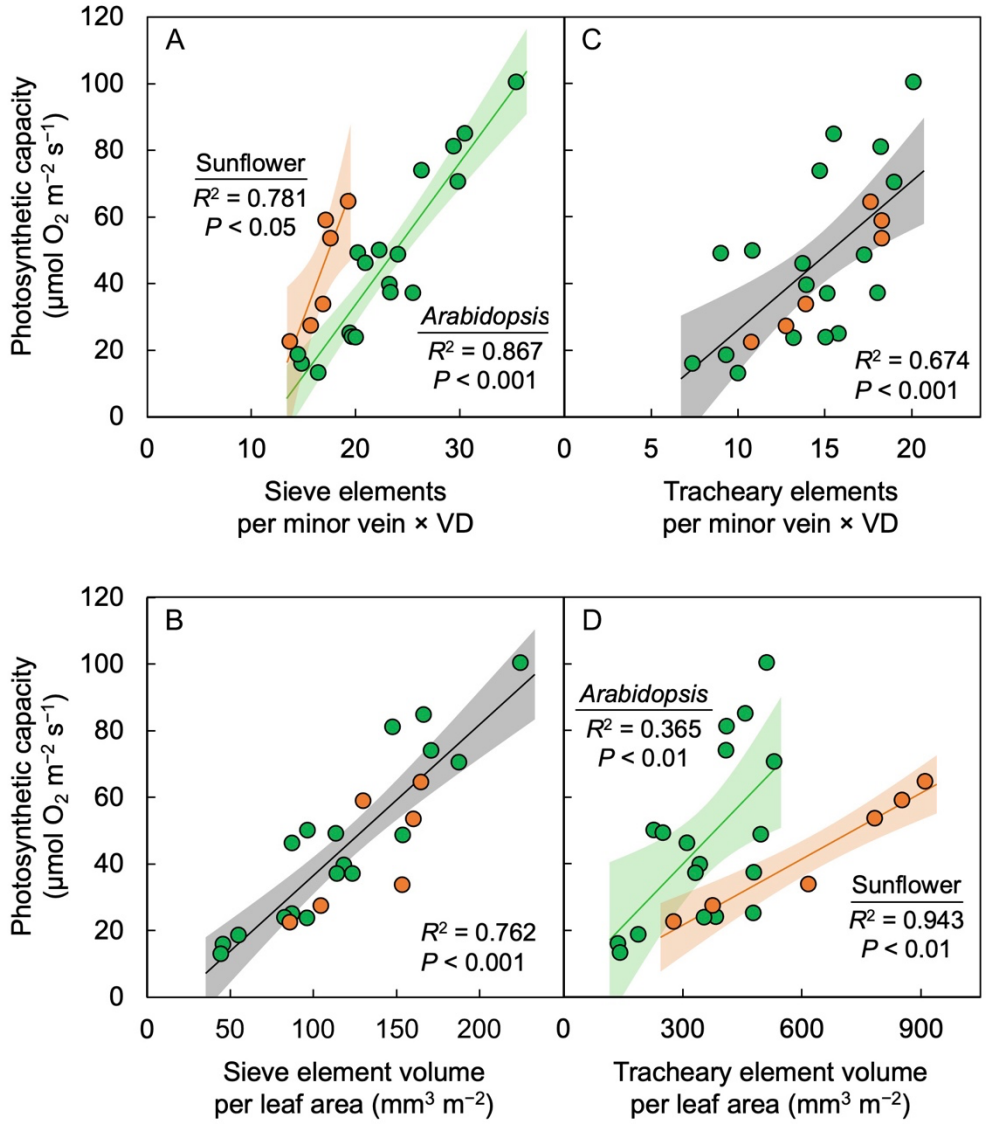
758 Fig. 5. Relationship between the volumes per leaf area of (A) companion cells + phloem
759 parenchyma cells (CC + PC) and sieve elements and (B) tracheary elements and sieve elements
760 in leaves of *Arabidopsis thaliana* (green symbols), sunflower (*Helianthus annuus*; orange
761 symbols), and spinach (*Spinacia oleracea*; dark green symbols). See the legends of Figs. 2 and 3
762 for additional details. Data from Cohu et al. (2013a,b, 2014), Adams et al. (2016, 2018a),
763 Stewart et al. (2017a,b), and Polutchko et al. (2021). Lines of fit with 95% confidence intervals
764 (black lines and gray shading).

765 Fig. 1.


Sunflower
Arabidopsis thaliana
A
Tracheary element
Sieve element
CC
PC
10 µm
B
Tracheary element
Sieve element
CC
PC
10 µm

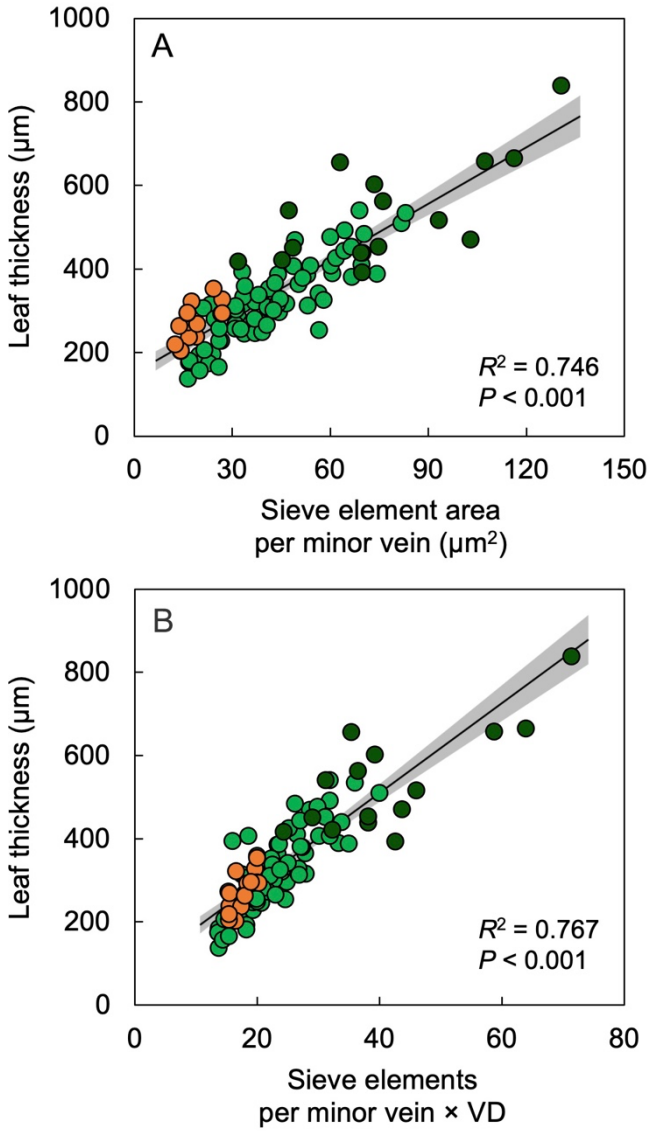
766

767 Fig. 2.


A
C
B
D
Photosynthetic capacity (μmol O2 m−2 s−1)
Sunflower
R2 = 0.781
P < 0.05
Arabidopsis
R2 = 0.867
P < 0.001
R2 = 0.674
P < 0.001
Arabidopsis
R2 = 0.365
P < 0.01
Sunflower
R2 = 0.943
P < 0.01
R2 = 0.762
P < 0.001
Sieve elements per minor vein × VD
Tracheary elements per minor vein × VD
Sieve element volume per leaf area (mm3 m−2)
Tracheary element volume per leaf area (mm3 m−2)

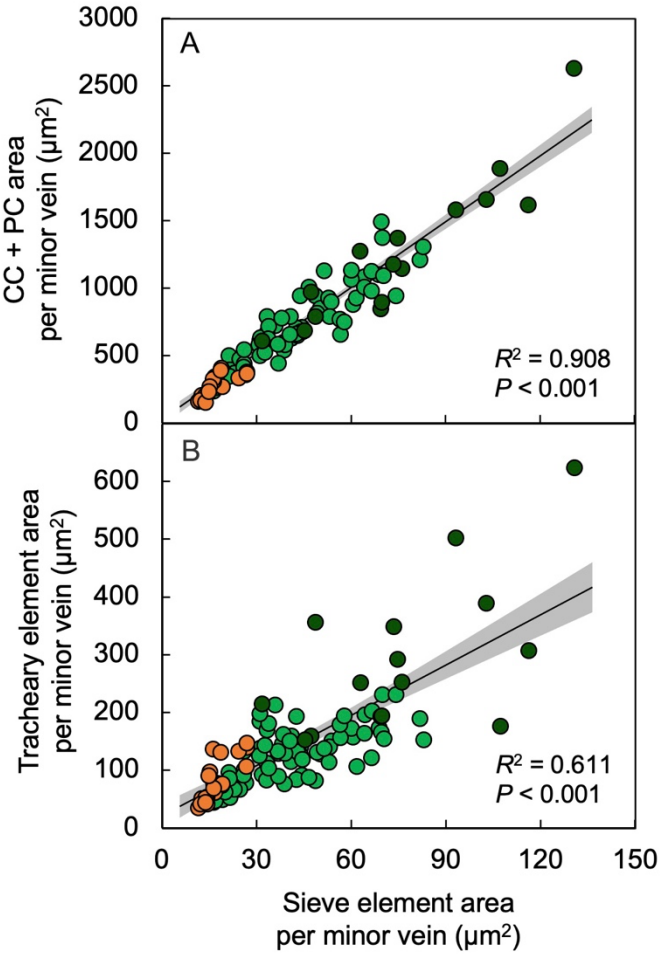
768

769 Fig. 3.


A
Leaf thickness (µm)
1000
800
600
400
200
0
0
30
60
90
120
150
Sieve element area
per minor vein (µm²)
R^2 = 0.746
P < 0.001
B
Leaf thickness (µm)
1000
800
600
400
200
0
0
20
40
60
80
Sieve elements
per minor vein × VD
R^2 = 0.767
P < 0.001

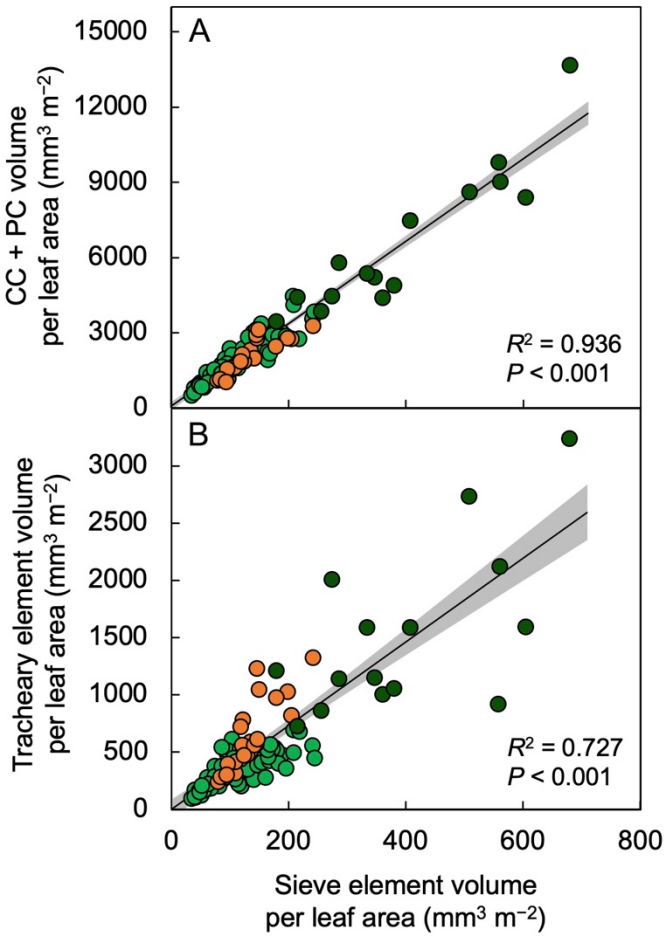
770

771 Fig. 4.


A
B
CC + PC area per minor vein (µm²)
Tracheary element area per minor vein (µm²)
Sieve element area per minor vein (µm²)
R² = 0.908
P < 0.001
R² = 0.611
P < 0.001
0
500
1000
1500
2000
2500
3000
100
200
300
400
600
30
60
90
120
150

772

773 Fig. 5.


A
B
CC + PC volume
per leaf area (mm³ m⁻²)
Tracheary element volume
per leaf area (mm³ m⁻²)
Sieve element volume
per leaf area (mm³ m⁻²)
R² = 0.936
P < 0.001
R² = 0.727
P < 0.001
0
3000
6000
9000
12000
15000
500
1000
1500
2000
2500
200
400
600
800

774