Strange stem architecture of pachycaulous morning glories

Root Gorelick tells us about the stem architecture in *Ipomoea*, speculating that weird stem architectures may tell us about the evolution of succulence.

Dan Mahr (2012) highlighted the wonderful Mexican succulent trees in the morning glory genus *Ipomoea* in the family Convolvulaceae. Only some members of the genus are included in the Illustrated Handbook of Succulent Plants (Eggli 2002), namely the tuberous rooted southern African species. This list of succulent *Ipomoea* species probably simply reflects the expertise of Ernst van Jaarsveld, who compiled that section of the Handbook. Instead of trying to extend this list of succulent *Ipomoea* species, which I honestly could not do, I will highlight the weird stem architecture of Mexican *Ipomoea* species, focusing on the giant of the genus *Ipomoea arborescens* Sweet.

Most trees of either flowering plants or conifers grow taller via apical meristems and simultaneously grow wider by producing new tissue from a cylindrical vascular cambium. Vascular cambia produce xylem to the inside (centripedal), which transports water. Vascular cambia produce phloem to the outside (centrifugal), which transports the products of photosynthesis. Horticulturists know that when grafting it is important that two stems being joined have some overlap in their vascular cambia so that the scion can continue growing. Many plant stems have a single vascular cambium throughout their entire lives, albeit a cambium that branches when the stem branches. Note use of the adjective ‘vascular’ because there also exist cork cambia, which form a cylinder that only produces tough water-resistant cells, so-called cork cells, that form outer bark.

Pachycaulous species of *Ipomoea*, however, do things a little differently. *I. arborescens* has multiple concentric vascular cambia (Terrazas *et al.* 2011). A cross section of such a plant would look reminiscent of a leek or onion but, unlike leeks or onions, the concentric layers of *Ipomoea arborescens* stems continue growing for years, producing not only fleshy storage tissue (as do leeks and onions), but also concentric layers of wood and inner bark. While unusual, concentric vascular cambia are found in several plant families (Carlquist 2007), including some semi-succulent members of the genus *Cycas* L. (albeit none of the western hemisphere cycads; Norstog and Nicholls 1997), and are often associated with succulent or semi-succulent stems. Liannas are also renowned for successive cambia, such as in *Gnetum scandens* Roxb. (Chamberlain 1935) and *Santaloidella gilletii* G. Schellenb. (Isnard and Silk 2009). Many mesembs, family Aizoaceae, have concentric vascular cambia (Carlquist 2007). See the online Xylem Database (Schweingruber and Landol 2005; http://www.wsl.ch/dendropro/xylemdb/) for beautiful images of stem cross sections, including of concentric vascular cambia in Aizoaceae, such as in *Aptenia cordifolia*. (L. f.) Schwantes. Even stranger, some, but not all, of the concentric vascular cambia of *Ipomoea arborescens* produce xylem to the outside (centrifugal) and phloem to the inside (centripedal) of the cambium, which is known as a ‘reverse cambium’ (Terrazas *et al.* 2011). *I. arborescens* sometimes even produces cambia from pith, which is somewhat unusual. Plus, these vascular cambia that arise in pith only produce phloem.

Vascular cambia produce more than simply xylem and phloem, i.e. wood and inner bark include more than just xylem and phloem cells. Vascular cambia also produce unspecialized thin-walled cells (parenchyma) that form rays between the spokes of xylem cells in wood and between the spokes of phloem cells in inner bark. When splitting wood, these rays are where you place an axe because the thin-walled ray parenchyma cells offer little resistance, at least compared with the thickwalled and heavily-lignified xylem cells that form wood. Ray cells are used in transporting and storing water and products of photosynthesis, as well as other plant metabolites. Thus, a plant with multiple concentric vascular cambia should, all else being equal, produce more storage tissue and be more succulent. Concentric cambia may help in storing water if the vascular cambia produce disproportionally more rays than wood. One of the best common examples of concentric vascular cambia, sometimes known as 'successive cambia', is in beets, *Beta vulgaris*. Cut one open and look at the fleshy concentric rings. In addition to concentric vascular cambia, *Ipomoea arborescens* also produces many short segments of vascular cambium from undifferentiated parenchyma cells in the rays, usually only producing phloem and phloem rays, which are called 'included phloem'. Included phloem is fairly common in semi-succulent plants, e.g. jojoba (*Simmondsia chinensis* C.K. Schneid.). If a stem has multiple concentric vascular cambia, then its evolutionary lineage may possibly have had the freedom to experiment with a subset of these cambia and produce xylem and phloem in the opposite directions, especially if these reverse cambia primarily are used for storage vis-à-vis rays, and not for water or sugar transport vis-à-vis xylem and phloem. There are indeed lots of interesting ways that nature created succulent plants, including adding extra layers of mitotically dividing cambial cells (Robert *et al.* 2011) and maybe even having some reverse cambia, as in the pachycaulous *Ipomoea arborescens*.

The peculiar stem architecture of producing concentric vascular cambia and reverse cambia, however, is not unique to pachycaulous *Ipomoea* species. These are also found in annual vining members of the genus, such as in *I. hederifolia* L. (Lowell & Lucansky 1986; Rajput *et al.* 2008). Liannas are not hugely constrained in having to build orderly wooden scaffolds the way self-supporting upright trees and shrubs are. Thus vines and liannas almost always have peculiar stem anatomy (Isnard & Silk 2009). If I might speculate, succulence may have originated from liannas, which have vastly more variation in stem architecture than do self-standing upright trees and shrubs. Weird stem architectures may tell us about the evolution of succulence.

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