Nectar: Properties, Floral Aspects, and Speculations on Origin

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Teaser: Based on the physicochemical properties of phloem and the special water relations of flowers, two possible mechanisms are proposed for the evolutionary origin of nectar.

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Although nectar is crucial for most pollinators, its evolutionary origin has received scant attention. Nectar is derived from the phloem solution. Both have high sugar concentrations (usually 10-30% solutes by fresh mass); the phloem's main solute is sucrose, whereas nectar can also contain considerable amounts of fructose and glucose. The phloem, not the xylem, is the supplier of water to flowers and certain other organs. Therefore, a "leaky phloem" hypothesis for the origin of nectar is presented based on the elevated hydrostatic pressure that can occur within the phloem and the structural weakness of developing phloem tissues. Also, a "sugar excretion" hypothesis is presented considering the solute accumulation resulting from the relatively high transpiration rates of flowers.

Plants invest considerable amounts of carbon and water in reproduction, including the production of nectar by animal-pollinated species. The chemical composition of nectar, which has its source in the phloem solution, has been determined for numerous plant taxa [1,2]. The energetic requirements of the animal species that visit flowers have also been considered in many nectar studies. Indeed, the amount and composition of nectar produced is related to the caloric requirements of many species of pollinators [3–6]. While very specialized plant-pollinator interactions are demonstrably the result of coevolution [7], the question of the evolutionary origin of nectar has received little attention.

Recently, data have become available regarding the carbon and water relations of flowers [8,9,unpublished observations by the authors]. Of particular interest is the relatively high water requirement for flowering and the fact that such water is supplied by the phloem, not by the xylem. Greater understanding of how sugar and water are supplied has arisen from new techniques to measure hydrostatic pressures in the phloem [10] and flow rates of the phloem solution [11]. Here, we propose two complementary mechanisms for the evolutionary origin of nectar based on the water relations of flowers and the physicochemical properties of the phloem. In particular, we present the notion of nectar as the product of a “leaky phloem” and/or a “sugar excreting” mechanism.

Pollination/Nectar production

The evolutionary success of angiosperms can be attributed, at least in part, to an association with animals that facilitates pollination. Early animal pollinators were beetles, as has been determined for extinct plant species and as is the case for basal angiosperms [12,13]. Bees are pollinators of many species, even the predominantly nocturnal flowers of *Hylocereus undatus*, a hemiepiphytic cactus whose flowers are open during only one night and for a few hours of the following day when bee pollination occurs [14]. Some very specialized plant-pollinator interactions have evolved, leading to mutualistic associations in which both the animal and the plant can undergo special adaptations, for example some wasps whose entire lifecycle occurs inside developing fruits of certain *Ficus* species [15], the long bill of hummingbirds who feed from tubular flowers [7], or the floral physiognomy of the insect mimic *Gillesia graminea* (Alliaceae) [16].

The amount of dry mass or energy allocated to nectar production varies considerably, from 3% for *Pontederia cordata* to 20% for alfalfa (*Medicago sativa*) and about 35% for milkweed (*Asclepias syriaca*) [17,18]. The production of nectar often peaks when pollen is most available, as is the case for *Cucurbita pepo* [19] and some *Agave* species [20]. In other instances, nectar secretion is maximal when the stigma is most receptive, as occurs for the columnar cactus *Stenocereus stellatus* [21].

Nectar is secreted through nectaries, which are specialized superficial glands found in a few ferns, a few gymnosperms, and most angiosperms [22,23]. The floral nectaries of angiosperms can be found near the inside base of flowers and usually are vascularized only by phloem [24,25]. Extrafloral nectaries of angiosperms and nectaries of gymnosperms and ferns often lack direct vascular input but they tend to occur near vascular bundles and frequently are associated with developing organs [22–26]. Nectaries have one or multiple layers of a specialized nectar-secreting parenchyma that occurs underneath an epidermis; the epidermis can have modified stomata that lack subsidiary cells and become permanently closed as the nectary matures [23,24] or it can have nectar secreting trichomes [23,27]. Eventually, starch granules in the parenchyma are broken down and nectar is secreted. The amount and activity of invertases determine the relative nectar concentration of sucrose versus its hexose components, fructose and glucose [4,25]. Because the loading of starch into the starch-storing parenchyma consumes energy [28,29], the starch storage and degradation that precede nectar secretion are most likely evolutionarily derived steps that allow better control for the timing of nectar secretion.

Nectar composition

Nectars are relatively concentrated solutions, ranging from about 10% solutes by mass for species that are pollinated by hummingbirds [30], to approximately 20% for nectarivorous passerines [4], and to more than 30% solutes for species that are pollinated by bees [31]. The main solutes are sucrose, fructose, and glucose (Table 1); amino acids comprise about 1% as much mass as the sugars [2,4,32]. For 294 tropical plant species pollinated by vertebrates, sucrose and fructose each average 34% of total soluble sugars and glucose averages 32%, although the sugar concentration of nectar varies substantially (sucrose ranging from 0% to 100% of the total sugars) [1]. The amount of nectar secreted and its composition can even be

Table 1 here

influenced by microenvironmental conditions; for instance, nectar secretion increases with relative humidity for *Epilobium angustifolium*, although it becomes more dilute at higher relative humidities [33].

Water storage and transpiration by flowers

Flower opening signals the maturation of the reproductive structures, enabling access to pollinators. At this time, the various floral structures undergo rapid growth by accumulating considerable amounts of water in the central vacuoles of their cells. For instance, the flowers of the columnar cactus *Stenocereus stellatus* open for only a single night, during which time the male and female reproductive structures, as well as the tepals, acquire turgor and undergo considerable growth [21]. The petals of the neotropical shrub *Turnera ulmifolia* var. *elegans* increase three-fold in length during the 24 hours before flower opening [34]. The stamens of the monocarpic monocots *Agave angustifolia* and *A. subsimplex* reach their final length, averaging 7 cm, during the 2nd day of flowering, and the pistils fully expand approximately 3 days later [20]. Such growth requires a substantial input of water.

An extreme example of the high water costs of flowering is *Agave deserti* [35]. Its reproductive development involves the production of a massive inflorescence that reaches a final height of about 3.5 m at a rate of 10 cm per day. Flowering of *A. deserti* requires approximately 18 kg of water, which is supplied mainly by water stored in the leaves; 4 kg of this are incorporated into the inflorescence structures, while nearly 80% of the water is transpired. For this species, the rate of water loss by transpiration is twice as high for branches with flowers as for branches with buds or with developing fruits [35].

The high water costs of flowering can influence flower morphology, as is case for the alpine skypilot, *Palemonium viscosum*, whose flowers from drier places tend to have smaller corollas than those from more mesic environments, resulting in a lower transpirational water loss in drier areas [36]. Such water costs associated with flowering are of special importance for species from water-limited environments, such as deserts, tropical dry forests, and some alpine ecosystems; interestingly, for many species in such environments, flowering occurs during the dry season [37]. The massive flowers of the cactus pear, *Opuntia ficus-indica*, which can open during the dry spring, transpire 3 g of water per day each, which represents approximately 15% of their mass at the time of anthesis [unpublished observations by the authors]. Reproductive development for *Ferocactus acanthodes*, a barrel cactus from the Sonoran Desert, requires approximately 44 g of water per fruit over 3 months, and nearly 60% of such water is expended during the 7 days of flowering [38]. For this species, petals often have non-functional stomata that remain partially open. In addition, petals of most species have a relatively thin cuticle that is less effective than the thicker cuticle of leaves and stems in preventing a continuous water loss [28,39].

Phloem input to flowers

How does water enter the developing reproductive organs of plants? The xylem is the main water conducting tissue in plants [28,29]. Water flow in this vascular tissue occurs spontaneously, i.e., from regions of higher water potential to regions of lower water potential (Box 1). Whether the supply of water to developing reproductive organs occurs through the xylem can be determined by comparing the water potential of flowers with that of adjacent vegetative organs. Remarkably, the water potential of flowers (and that of developing fruits) is higher than the values measured for the vegetative organs of most species that have been studied, including horticultural species

Box 1
here

such as tomato (*Lycopersicon esculentum*) [40] and cotton (*Gossypium hirsutum*) [41], tropical forest trees [8], and various cacti [42]. Because the flowers are "wetter" than the stem, the supply of water via the xylem is not feasible thermodynamically (Box 1). Moreover, a backflow of water from developing fruits has been shown for *O. ficus-indica* [43] and tomato [40]. Partial blockage of the xylem at the flower-stem junction reduces such backflow for tomato [40] and cotton [41] at later stages of fruit development.

Fig. 1
here

Thus water and photosynthates are supplied to flowers via the phloem (Fig. 1a). The phloem solution is relatively concentrated, containing sucrose as the primary solute (Table 1). The phloem can also transport amino acids as well as organic acids and other solutes [28,29]. Movement of the phloem solution, which is usually from 0.6 to 2.0 m per hour [11,28,29], requires active transport of solutes into the phloem to generate a hydrostatic pressure gradient that in turn results in the flow.

Speculation on the origin of nectar

The interaction of plants with animal pollinators has selected for the production of nectar, but the fact that even nectarivorous insects must also obtain nitrogen from pollen, and nectarivorous vertebrates obtain nitrogen from pollen and insects, hints that nectar might have originally developed independently of any interaction with animals. Furthermore, early pollinators such as beetles were not rewarded with nectar [13], nor are several more recent animal pollinators [16,44]. Thus, nectar is neither necessary nor sufficient as a pollinator reward. We would argue from the properties of the phloem and the phloem solution that two physicochemically feasible mechanisms could have led to the origin of nectar.

"Leaky phloem" hypothesis

Water and photosynthates are supplied to most developing reproductive organs by the phloem, not the xylem. This is also the case for young roots of maize (*Zea mays*) [45] and for young developing stems of *O. ficus-indica* before they become photosynthetically self-sufficient [43]. The net positive hydrostatic pressures in the phloem, which for wheat can exceed 2 MPa (similar to the barometric pressure that a scuba diver would experience at a depth of 200 m!), permits the transport of the phloem solution against large water potential differences [10,28,29]. Cell growth, such as that occurring during flower or stem development, requires the loosening of cell walls and an increase in intracellular hydrostatic pressure [28,29]. Also, the relatively young vascular tissue supplying flowers is less resistant to mechanical stress, becoming progressively more rigid with age [46]. Therefore, high hydrostatic pressures coupled with the mechanical weakness of the expanding cells of developing tissue could result in a "leak" of the phloem solution (Fig. 1b), as occurs for developing stems of various cacti [47] and for phloem "bleeding" of various *Eucalyptus* species [48]. Nectar secretion could thus have originated as a leakage of the phloem solution resulting from the structural weakness of developing tissue exposed to the elevated hydrostatic pressure in the phloem.

"Sugar excretion" hypothesis

The flowers of most plants are substantially less massive than are their fruits [49], presumably saving resources until pollination has occurred and fruit set is guaranteed. Nevertheless, the high rates of water consumption by flowers can result in the accumulation of considerable amounts of carbohydrates, because water is supplied by the phloem, which is concentrated in solutes (Table 1) while the xylem is not [28,29]. For instance, the phloem solution for *O. ficus-indica* is approximately 7% solutes by mass [50], which is relatively dilute, as the phloem solution for other species can exceed 20% solutes [10,29]. Transpiration of 3 g of water per day by *O. ficus-indica* flowers results in a daily solute accumulation of 200 mg per flower [unpublished observations by the authors]. Over the course of flowering that can last 14 days for this species, such solute buildup could substantially reduce the water potential. Nevertheless, the water potential of developing fruits of various species is consistently higher than the values measured for adjacent vegetative organs [40–43]. A decrease in tissue water potential is not observed because the solute residues can be polymerized into mucopolysaccharides, which help maintain the relatively high water potential of flowers [8,51], or are removed from the apoplastic solution and stored as starch granules inside the cells [19,26]. Subsequently, such excess solutes can be excreted in nectar (Fig. 1c). The buildup of starch to be degraded in the tissue of nectaries could have been selected for because it facilitates nectar secretion at sexual maturity for flowers. This is a period of high water consumption during which petals must grow and acquire turgor so that flowers can open, multiple stamens can produce pollen, and stigmas can enlarge as ovules mature. Thus nectar production might have originated as a mechanism to remove the excess solutes supplied by the phloem.

Conclusions and future research

The two hypotheses are complementary and can be relevant at different evolutionary and/or developmental stages. Specifically, the leaky phloem hypothesis (Fig. 1b) can be relevant for early stages of nectar evolution or for non-reproductive organs. The sugar excretion hypothesis can be relevant for later stages of plant evolution, when flowers are already present (Fig. 1c).

Research to test the hypotheses presented should focus on the specific physiological mechanisms of nectar production and their links with flower water relations, particularly with regard to the timing for the maturity of the different floral structures. If nectar is indeed the result of a leaky phloem, then when did the nectaries appear and were they the result of selective pressures by animals? In pea flowers, nectary stomates close as the time for nectar secretion approaches [24]. Does such closure occur to prevent the "loss" of sugars and water? Also, why do nectarless species and nectarless individuals within a population, whose developing tissues are also relatively weak structurally, not produce nectar? With respect to the sugar excretion hypothesis, research should consider the rates of solute accumulation before and after flower opening—or more strictly, before and after pollination—and whether the amount of plant resources destined to "encourage" pollination is comparable to that for seed dispersal. Also, for pollinated flowers, is reabsorbed nectar [19,52] an important source of carbon for fruit development? Whether the water potential is higher for reproductive structures compared with vegetative plant organs should also be investigated for more species.

Underlying the specific questions to be addressed in future research should be the fact that flowering, at the climax of plant sexual reproduction, encompasses the interactions between the gametophytic and the sporophytic generations of plants. Studying such interactions can help explain the distinctive water relations of flowers, the very important role of the phloem for supplying water and carbon to such reproductive organs, and even the origin of nectar.

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Table 1. Representative compositon of nectar [2,23,52,53] and of the phloem solution [29,50,54–56]

Solute	Concentration		Osmotic pressure
	(% of fresh mass)	(mM)	(MPa)
Nectar			
Sucrose	13	300	0.7
Glucose	12	600	1.5
Fructose	10	500	1.2
Phloem			
Sucrose	17	500	1.2
Glucose	1×10^{-2}	0.4	1×10^{-3}
Fructose	1×10^{-2}	0.4	1×10^{-3}

Figure legend

Figure 1. Schematic representation of the proposed mechanisms for the origin of nectar. The phloem, which transports a concentrated solution under high hydrostatic pressures, is the source of water and sucrose for nectar (a) [1,2,4,10,11,23,28,29,52,53]. The “leaky phloem” hypothesis is represented by a leak of phloem solution through a nectary (a pathway of low resistance) due to the high hydrostatic pressure in the phloem (b). The “sugar excretion” hypothesis results from water and sucrose input to flowers via the phloem and a water output via transpiration, with the excess solutes being excreted in the nectar (c).

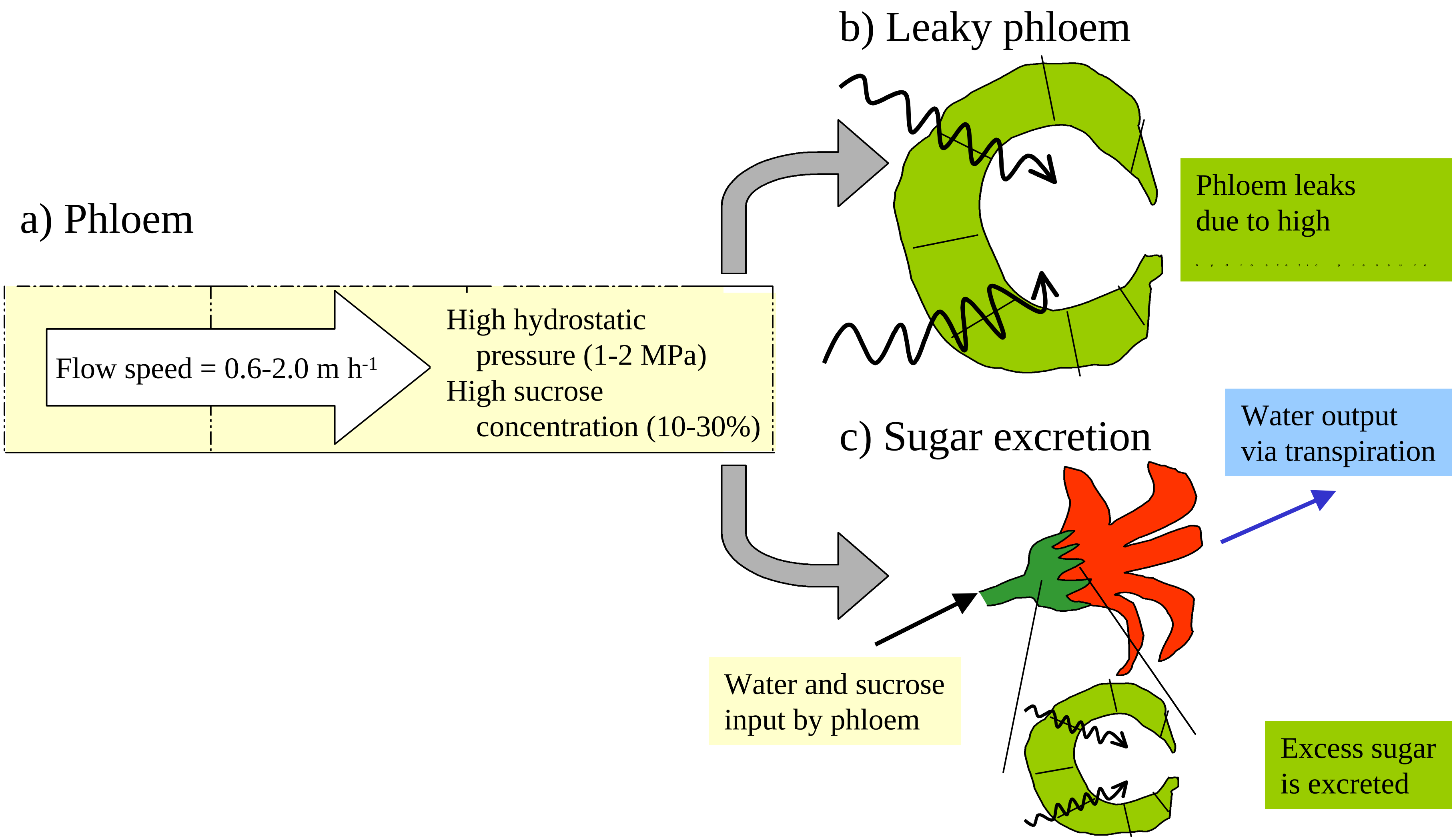
a) Phloem
Flow speed = 0.6-2.0 m h-1
High hydrostatic pressure (1-2 MPa)
High sucrose concentration (10-30%)
b) Leaky phloem
Phloem leaks due to high hydrostatic pressure
c) Sugar excretion
Water output via transpiration
Water and sucrose input by phloem
Excess sugar is excreted

Figure 1

Box text

Box 1. Water pathways and movement [8,28,29]

Plants have two vascular tissues, the xylem and the phloem. The xylem transports the water taken up by the roots upward through the stem to the leaves, where it is transpired (solid lines in Fig. I). The driving force for such a flow is a gradient in the water potential of the xylem solution.

Water potential (Ø, measured in megapascals, or MPa, where 0.1 MPa equals approximately 1 atmosphere) is a widely utilized measure of the free energy per volume of an aqueous solution, represented mathematically as:

$$\text{Ø} = P - \text{Ð} + \text{ñ}gh$$

where P is the hydrostatic pressure; Ð is the osomotic pressure, which for ideal solutions can be approximated by the Van’t Hoff relation, $\text{Ð} = RT\text{Ó}c_j$, where RT is the gas constant times the temperature in Kelvin units and c_j is the concentration of species j; and the gravitational component is the water density (ñ) times the height (h) times the gravitational acceleration (g). For example, Ø can be –0.1 MPa for wet soil, –0.6 MPa in a stem, and about –100 MPa for air at 50% relative humidity (Fig. I). Such differences permit a spontaneous flow of water from higher to lower water potentials from the soil through the xylem to the surrounding air.

As discussed in the text, Ø is greater (less negative) for flowers than for adjacent stems, so water flow into the flowers is not spontaneous (Fig. I)—it goes against an energy gradient for water. In fact, a backflow of water would spontaneously occur from the flower to the stem. Transport of the phloem solution, on the other hand, consumes energy. Photosynthates are actively loaded from the apoplast into the “source” region of the phloem, i.e., near cells in leaves where photosynthesis occurs. The rising solute concentration leads to an increased Ð , which makes Ø very negative. Water is drawn into the phloem by such a negative water potential. The entering water increases *P*, driving flow within the phloem toward the “sink” region where the phloem solution is unloaded, such as in a flower.

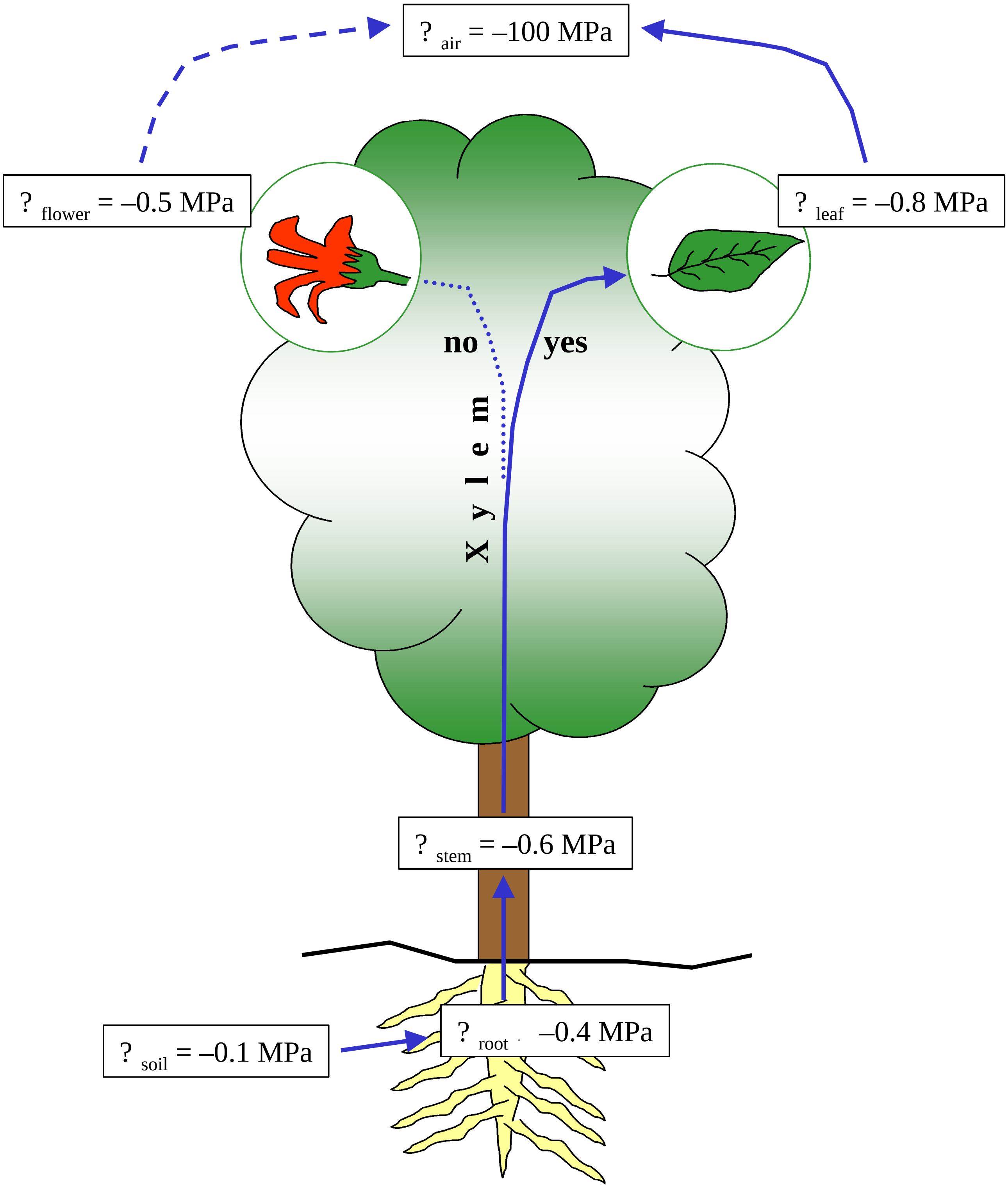

Figure I for Box 1