

WHY VEGETATIVE PROPAGATION OF LEAF CUTTINGS IS POSSIBLE IN SUCCULENT AND SEMI-SUCCULENT PLANTS

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Abstract: Simple leaves are usually conceptualized as terminal organs that cannot develop new roots or shoots. However plants with succulent or semi-succulent leaves in many unrelated families defy this rule. They do so by differentiating leaf parenchyma – which are probably often phloem parenchyma or companion cells, the two of which are often indistinguishable – into new root and shoot apical meristems. Succulent and semi-succulent leaves can survive longer than non-succulent leaves once detached from shoots of their parent plant, possibly enabling them to differentiate and establish a root system before desiccation and/or starvation. Curiously, almost no succulent plants have compound leaves, even though compound leaves are often considered to have properties of both stems and leaves and hence theoretically should have the capability of developing new structures, such as new root and shoot meristems. I discuss some testable predictions arising from these notions and ask whether differences between ability to regrow roots and shoots from detached leaves of monocots versus eudicots is better explained by reticulate versus parallel venation or phylogenetic constraints.

Keywords: phloem parenchyma; companion cell; intercalary meristem; apical meristem; cicatrix, cicatrices; Wiesner test; lignin; phylogenetic constraint; Crassulaceae

LEAVES USUALLY ARE TERMINAL ORGANS

It is impossible to root leaf cuttings from most tree or grass species or even most herbaceous temperate weeds, such as dandelions and hawkweeds. In fact, there do not seem to be any plants with non-succulent leaves of terrestrial plants that are capable of being vegetatively propagated via leaf cuttings, except for maybe via highly technical micro-propagation. By contrast, almost anybody that has grown plants with succulent and semi-succulent leaves, except aloe and some opuntoid cacti, knows that it is often easy – sometimes too easy with some species of *Kalanchoe* Adanson – to vegetatively propagate these plants by leaf cuttings. How is this possible?

The terminal developmental nature of leaves is a possible reason that most plants cannot be easily propagated from leaf cuttings, in stark contrast with shoot and root cuttings. Roots and shoots contain dormant meristems, such as numerous shoot axillary buds at the base of each leaf. For example, areoles in cacti are merely short shoots that can grow new branches or flowers, as well as grow leaves vis-à-vis spines (Buxbaum 1950; Gibson & Nobel 1986). A vascular cambium can be grafted onto another vascular cambium, including natural grafting that occurs frequently with roots (Basnet et al. 1993; Jelenkova et al. 2009; also see discussion and references in Gorelick 2012). Unlike roots and shoots, leaves lack dormant apical meristems. Furthermore, simple leaves lack any secondary growth vis-à-vis lateral meristems, aka cambia.

Leaves are usually conceptualized as terminal organs. While a shoot can grow more shoots, as well as grow leaves, flowers, and roots, a leaf is terminal hence usually cannot grow any additional leaves, shoots, roots, or flowers. Identical arguments apply to leaves being terminal organs in all other vascular plants (gymnosperms, monilophytes, lycophytes), except that flowers are replaced with other forms of reproductive structures. Thus, Agnes Arber (1950) called leaves “partial shoots”. The terminal nature of leaves is especially true with simple leaves. Simple leaves, as well as leaflets on compound leaves, are generally considered the end of the ontogenetic line. Leaves begin their growth from leaf ground tissue and later grow broader leaf blades via marginal blastozones, aka marginal meristems, which are small and ephemeral in simple leaves (Dengler & Tsukaya 2001; Mauseth 2009) (the term ‘blastozone’ unintentionally conveys the very short-lived nature of these zones of mitotic activity). In leaves, “subsequent meristematic activity is intercalary and diffuse” (Beck 2005: 327; citing Donnelly et al. 1999). By contrast, mitotic cell divisions via primary growth in shoots and roots occurs at their distal end, via apical meristems. Growth from leaf intercalary meristems, marginal blastozones, and plate meristems is usually conceptualized as an increase of length and sometimes width of an *already existing leaf*, especially those leaves with indeterminate growth, as we see with growing blades of grasses and even the millennium-old leaves of *Welwitschia mirabilis* Hook.f. (Pear-

son 1929; Evert 2006; van Jaarsveld & Pond 2013) A few plants even have the antithesis of apical meristems in their leaves, namely basal meristems that undergo virtually all mitotic divisions at the proximal end of the leaf, as occurs with the highly lignified leaves of cactus spines (Mauseth 2009).

SUCCULENT LEAVES ARE NOT TERMINAL ORGANS

Many succulent plants, especially in the Crassulaceae, but also in other families, can be grown from leaf cuttings (Kerner & Oliver 1902 [1895]; Hagemann 1932; Yarbrough 1936, citing Schubert 1913). Furthermore, several *Kalanchoe* species in the subgenus *Bryophyllum* Salisb. grow new plantlets along their leaf margins. Cuttings of simple leaves can be successfully propagated from a phylogenetically diverse group of succulent and semi-succulent plants, including eudicots, monocots, basal angiosperms, gymnosperms, and ferns, many of which are listed in Table 1. Kerner & Oliver (1902 [1895]) and Hagemann (1932) provided particularly extensive lists of species that can be propagated from leaf cuttings. My table 1 is largely an update of August Hagemann's (1932) table 1.

Why do only some leaves grow new roots and shoots? There is some literature on this, mostly from the 1930s, mostly on *Kalanchoe* subgenus *Bryophyllum* (Howe 1931; Naylor 1932; Clamp 1934; Johnson 1934; Stoudt 1934, 1938) and the gesneriad *Saintpaulia* (Naylor & Johnson 1937). Here I argue that leaf primary vascular tissues (there is no secondary growth in simple leaves) contain some undifferentiated parenchyma that can later differentiate to form new meristematic regions in fallen or severed leaves or even in unfallen leaves of *Kalanchoe* subgenus *Bryophyllum*. Parenchyma are merely plant cells with thin cell walls (cells with thick cell walls are known as sclerenchyma and those with intermediate width cell walls are known as collenchyma). Undifferentiated parenchyma in leaf vascular tissue is common in stems of succulent plants. Undifferentiated parenchyma is also especially evident in secondary growth of the many xerophytic plant stems with included phloem, i.e. phloem that differentiates from xylem parenchyma rays, as in *Ipomoea arborescens* Sweet (Convolvulaceae), *Simmondsia chilensis* (Link) C.K. Schneid (Simmondsiaceae), and *Bougainvillea spectabilis* Willd. (Nyctaginaceae) (Gorelick 2014). While leaves may be terminal organs, undifferentiated parenchyma in and around leaf vascular tissue is sufficient for growing *de novo* root and shoot apical meristems. The fact that these leaves are succulent probably keeps them alive long enough to grow new apical meristems. "The leaves of *Bryophyllum calicinum* are thick and fleshy, and contain when mature such an abundance of reserve material and water as to render it superfluous that any absorption of nutriment from the environment should take place." (Kerner & Oliver 1902 [1895]: 40). By contrast, non-succulent leaves might perish before incipient apical meristems had sufficient time to develop.

New root and shoot meristems probably develop *de novo* from phloem tissues in the detached leaf. This would provide new apical meristems a way to tap into the vasculature of the detached leaf. Angiosperm primary phloem in leaves is comprised of conducting sieve tube members, companion cells, phloem parenchyma, and phloem fibers. Gymnosperms, monilophytes, and lycophytes have sieve cells in lieu of sieve tube members (Evert 2006). Gymnosperms have albuminous cells (aka Strasburger cells) in lieu of companion cells, whereas monilophytes and lycophytes lack anything like companion cells (Evert 2006). Phloem parenchyma are cells surrounding and supporting conducting phloem, but the term 'phloem parenchyma' is a bit of a misnomer insofar as sieve tube members, sieve cells, companion cells, and albuminous cells are also forms of parenchyma (although some developing primary phloem sieve tube members in some monocots have thicker cell walls, which eventually thin out, so that their mature conducting sieve tube members are once again parenchymous; Evert 2006). Phloem parenchyma may be indistinguishable from or intergrade with companion cells in angiosperms (Esau 1969; Evert 2006). Development of incipient apical meristems from leaves of angiosperm phloem tissue are probably from phloem parenchyma/companion cells because mature sieve tube members lack nuclei and phloem fibers have sufficiently thick cell walls to preclude cell division (Evert 2006).

It is not too surprising that plants can be grown from cuttings of succulent or semi-succulent leaf cuttings because leaves have intercalary (i.e. diffuse) meristematic activity (Donnelly et al. 1999; Beck 2005), from which new root and shoot apical meristems can develop. Leaf intercalary meristems are even known to contain functional conducting xylem and phloem (Evert 2006). While attached to a stem, leaf intercalary meristematic activity produces new leaf tissue. But once no longer attached to stems, there seems to be no reason why intercalary leaf meristems could not produce any other cell types. This may have never been explicitly noted in the literature because many leaves are not succulent, so could not survive long enough after being detached or severed to develop incipient apical meristems.

I also want to briefly discuss two other ideas that do not provide the reason for being able to propagate succulent leaves from leaf cuttings. The first idea is that new plantlets form from a leaf basal meristem. But this cannot be correct because *Bryophyllum* produces plantlets along the leaf margin and also because you can still get new plantlets even if you cut away the petiole or the proximal portion of the detached leaf blade in many other species of succulent plants (Schubert 1913; Raju & Mann 1971). Likewise *Streptocarpus* (Gesneriaceae) leaf cuttings can produce new roots and shoots regardless of whether the leaf was cut parallel or perpendicular to the midvein. Most plants do not have a leaf basal meristem, but instead an intercalary leaf meristem.

	Family	Genera	Succulent or Semi-Succulent	References
Monilophyte	Aspleniaceae	<i>Asplenium</i>	semi	Arthur 1883; Kato 1993; Lu et al. 2011
	Pteridiaceae	<i>Adiantum</i>	semi	Kato 1993; Lu et al. 2011
Gymnosperm	Gnetaceae	<i>Gnetum</i>	semi	van Beusekom 1907; Hagemann 1932
Basal Angiosperm	Nymphaeaceae	<i>Nymphaea</i>	semi	Kerner & Oliver 1902 [1895]; Hagemann 1932
Monocot	Amaryllidaceae	<i>Allium</i>	semi	Kerner & Oliver 1902 [1895]
	Asparagaceae/ Dracaenaceae	<i>Drimia, Eucomis, Hyacinthus, Ornithogalum, Sansevieria, Scilla, Yucca</i>	succulent and semi-succulent	Kerner & Oliver 1902 [1895]; Lutz 1903; Schubert 1913; Hagemann 1932
	Araceae	<i>Amorphophallus, Atherurus</i>	succulent and semi-succulent	Kerner & Oliver 1902 [1895]; Hagemann 1932
	Hypoxidaceae	<i>Curculigo</i>	semi	Kerner & Oliver 1902 [1895]; Hagemann 1932
	Liliaceae	<i>Fritillaria, Gagea, Lilium</i>	semi	Kerner & Oliver 1902 [1895]; Hagemann 1932; Walker (1940)
	Orchidaceae	<i>Malaxis</i>	semi	Henslow 1829; Kerner & Oliver 1902 [1895]
	Xanthorrhoeaceae/ Asphodelaceae	<i>Gasteria, Haworthia</i>	succulent	Haage 1963 [1961]; Pilbeam (1983)
Eudicot	Aizoaceae	many genera; true leaf cuttings, not just leaves on small portions of shoots	succulent and semi-succulent	Jacobsen 1960 [1954]
	Apocynaceae	<i>Hoya</i>	semi	Kerner & Oliver 1902 [1895]
	Begoniaceae	<i>Begonia</i>	semi	Kerner & Oliver 1902 [1895]; Hagemann (1932)
	Brassicaceae	<i>Arabis, Brassica, Cardamine, Nasturtium, Rorippa</i>	semi	Kerner & Oliver 1902 [1895]
	Cephalotaceae	<i>Cephalotus</i>	semi	Slack 1979; Pietropaolo & Pietropaolo 1986
	Crassulaceae	<i>Adromischus, Cotyledon, Crassula, Echeveria, Graptopetalum, Kalanchoe, Sedum</i>	succulent	Schubert 1913; Loeb 1915; Braun 1918; Howe 1931; Naylor 1932; Hagemann 1932; Yarbrough 1932a,b; Clamp 1934; Johnson 1934; Stoudt 1934; Yarbrough 1936; McVeigh 1938; Stoudt 1938; Raju & Mann 1971
	Droseraceae	<i>Dionaea, Drosera</i>	semi	Salisbury 1915; Hagemann 1932; Slack 1979; Pietropaolo & Pietropaolo 1986
	Fabaceae	<i>Clianthus</i>	semi	Kerner & Oliver 1902 [1895]
	Garryaceae	<i>Acuba</i>	semi	Kerner & Oliver 1902 [1895]
	Gesneriaceae	<i>Chirita, Episcia, Saintpaulia, Sinningia, Streptocarpus</i>	semi	Kerner & Oliver 1902 [1895]

The designations ‘succulent’ versus ‘semi-succulent’ are arbitrary, but meant to reflect current usage. Some readers might consider some of these leaves to be non-succulent, i.e. not even semi-succulent. Only some species in each genus can be propagated by leaf cutting; see references for specific species names.

Table 1. Plants that can be propagated from leaf cuttings (probably not an exhaustive list).

	Family	Genera	Succulent or Semi-Succulent	References
Eudicot (cont.)	Lamiaceae	<i>Melissa</i>	semi	Hagemann 1932
	Lentibulariaceae	<i>Pinguicula</i>	semi	Kerner & Oliver 1902 [1895]; Slack 1979; Pietropaolo & Pietropaolo 1986
	Linaceae	<i>Linum</i>	semi	Kerner & Oliver 1902 [1895]
	Papaveraceae	<i>Chelidonium</i>	semi	Kerner & Oliver 1902 [1895]
	Piperaceae	<i>Peperomia</i>	succulent	Mauseth 2009
	Primulaceae	<i>Theophrasta</i>	semi	Kerner & Oliver 1902 [1895]
	Ranunculaceae	<i>Ranunculus</i>	semi	Hagemann 1932
	Rutaceae	<i>Citrus</i>	semi	Kerner & Oliver 1902 [1895]
	Sarraceniaceae	<i>Darlingtonia, Sarracenia</i>	semi	Pietropaolo & Pietropaolo 1986
	Saxifragaceae	<i>Tellima, Tolmiea</i>	semi	Hagemann 1932
	Scrophulariaceae	<i>Torenia</i>	semi	Naylor & Johnson 1937
	Solanaceae	<i>Nicotiana, Solanum</i>	semi	Hagemann 1932

Table 1 (cont.) Plants that can be propagated from leaf cuttings (probably not an exhaustive list).

The second false idea is that the axillary bud forms on the wrong side of the leaf's abscission zone or on both sides of the abscission zone. The former instance might explain the smooth trunks of many Crassulaceae. However, these plants in fact appear to have axillary buds attached to the stem, but are deeply buried and highly dormant. This can be seen by removing the shoot apical meristem, in which case dormant sub-apical meristems will start growing. In the latter case of axillary buds on both sides of the abscission zone, there exists no evidence for a connection between these two hypothetical axillary buds. In fact, there is no evidence for axillary buds ever being on the distal side of the leaf abscission zone, which is the proximal end of the leaf. Furthermore, evidence cited in the previous paragraph of still being able to re-root leaves after the proximal portion of the leaf (e.g. petiole) was discarded implies that new roots and shoots from a leaf cutting are not from an axillary bud.

BRYOPHYLLUM AND OTHER CRASSULACEAE

The subgenus *Bryophyllum* is peculiar insofar as leaves that are still attached to stems contain primordia of new roots and shoots in the notches (crenulations) of the leaf lamina edges (Naylor 1932; Raju & Mann 1971). After some initial growth, but while their parental leaves are still attached to the shoot, growth of these leaf-borne root and shoot primordia are inhibited, probably hormonally, much as apical meristems produce hormones that suppress growth of shoot sub-apical meristems. In some species of *Bryophyllum*, growth of leaf-borne shoot and root

primordia are more inhibited than others. Growth of plantlets on leaf margins of *Kalanchoe daigremontiana* Raym.-Hemet & H. Perrier and *K. tubiflora* Raym.-Hemet are much less inhibited than those of *K. manginii* Raym.-Hemet & H. Perrier and *K. uniflora* Raym.-Hemet. By contrast, shoot primordia have never been documented on leaf margins of any other plants mentioned herein, not even in other members of the Crassulaceae, except in the orchid genus *Malaxis* and two genera of 'walking ferns' (see below for details). Therefore, we should be cautious about generalizing from the extensive research that has been done on *Kalanchoe*.

What do we know about Crassulaceae plants other than *Kalanchoe* that can produce plantlets from detached or severed leaves? A substantial amount is known about propagation from leaf cuttings of *Crassula ovata* E. Mey. ex. Harv. & Sond., *C. multiclava* Lem., *Echeveria elegans* Rose, and *Sedum stablii* Solms (Yarbrough 1936; McVeigh 1938; Raju & Mann 1971; Rost & Paterson 1976). With these species, parts of leaves regenerated almost as readily as did whole leaves, despite no obvious dormant root or shoot apical meristems. Regardless of whether leaves were sliced parallel or perpendicular to what best could be called the mid-vein axis of the leaf, new roots and shoots were always formed on the side of the cut leaf that was originally closest to where the petiole had been attached to the shoot (Rost & Paterson 1976). There is clearly directionality (polarity) in the cut detached leaves, with new apical meristems differentiating on the proximal end of the severed leaf and none on the distal end. There is also directionality (polarity) for regeneration closer

to the original mid-vein than to the outer margins of the leaf (Rost & Paterson 1976), i.e. new apical meristems formed on the centripetal margins of the cut leaf and none on the centrifugal margins. New meristems arise from phloem cells and possibly surrounding parenchyma cells in surviving vascular bundles, such as bundle sheaths, but not from aerenchymous tissues of spongy mesophyll. Thus, cut leaves of *Crassula*, *Echeveria*, and *Sedum* indicate that new meristems arise from phloem parenchyma/companion cells.

It seems that Crassulaceae leaf cuttings undergo the same process of wound healing as do other leaves. They first form pseudocicatrices, which means that tissues around the cut collapse. This causes infolding of the epidermal layers, thereby protecting the cut surface from pathogens and desiccation (Wylie 1927). Next cicatrices form, which are mitotic divisions of mesophyll cells just underneath the pseudocicatrices to form callus tissue (Rost & Paterson 1976). New root and shoot apical meristems arise from parenchyma immediately underneath cicatrices (Rost & Paterson 1976), which is consistent with *de novo* generation of apical meristems from phloem parenchyma/companion cells of detached and/or severed leaves.

MONOCOTS VERSUS EUDICOTS

Typical eudicots have reticulate venation (Coulter 1899; Evert & Eichhorn 2013), so should be less sensitive than monocots to the direction that the leaf is cut, as was seen in *Crassula ovata* (Rost & Paterson 1976). Kerner & Oliver (1902 [1895]) noted that growers of *Begonia* L. make sure that cuts of leaves intersect as many large veins as possible. In terms of ability to regenerate roots and shoots, in principle, the few monocots with reticulate venation should be as insensitive to the direction in which the leaf is cut as typical eudicots. However, the few monocot leaves with reticulate venation – e.g. *Dioscorea* L. (Dioscoreaceae), *Anthurium* Schott (Araceae), and *Smilax* L. (Smilacaceae) – do not seem to have sufficiently succulent leaves to be successfully propagated from leaf cuttings.

Density of veins and venation pattern are important if new meristems originate from phloem tissues, i.e. phloem parenchyma and companion cells, in cut leaves as I asserted above. *Ceteris paribus*, leaves with denser veins should be easier to root from cuttings than leaves with sparser veins. Staining leaves with phloroglucinol (1,3,5-benzenetriol)-HCl, the so-called Wiesner test, allows for simple dissection and quantification of veins and their density in succulent leaves. While the Wiesner test stains for lignin (Pomar et al. 2002) – which is primarily found in xylem and less so in phloem fibers – phloem tissues are invariably associated with xylem in all vascular plants.

Phylogenetic constraint may also explain why it is impossible to propagate *Austrocyllindropuntia subulata* (Muehlpf.) Backeb. from leaf cuttings, a species that has remarkably large and long-lived leaves for

the Cactaceae. That said, I do not know about the density of veins (lignin) in its leaves, a density that might be sufficiently low to also explain the inability of these leaves to grow new root and shoot meristems. Their leaves might also desiccate quickly once detached from shoots, which would also preclude them from growing new root or shoot meristems.

COMPOUND VERSUS SIMPLE LEAVES

Compound leaves seem to possess some stem-like properties, such as the ability to grow additional leaflets and rachises, from their dividing and longer-lived marginal blastozones (Arber 1950; Rutishauser & Sattler 1997; Dengler & Tsukaya 2001; Lacroix et al. 2003; Beck 2005; Eckardt & Baum 2010). Therefore botanists consider compound leaves more complete or 'less partial' than simple leaves.

Even though compound leaves are more stem-like than simple leaves, having properties of both leaves and stems (Arber 1950; Eckardt & Baum 2010), compound leaves seem to be more difficult to root than simple leaves. The reasons for this are poorly understood, but may be that there are very few succulent compound leaves, especially with leaflets (blades) that are succulent. The only plants listed in Table 1 with compound leaves are *Chelidonium* Tourn. ex. L. (Papaveraceae), *Clianthis* Sol. ex Lindl. (Fabaceae), *Atherurus* Blume (Araceae), and *Amorphophallus* Blume ex Decne (Araceae), all but the last of which are only marginally semi-succulent. While leaf blades and leaflet blades of compound leaves are usually not very succulent, petioles of compound leaves can be quite succulent, as in the voodoo lily *Amorphophallus*, all species of which seem to all be able to be propagated from petiole cuttings (Hagemann 1932; Avent 2007). The much greater success with rooting *Amorphophallus* petiole cuttings than leaf blade cuttings (Avent 2007), indicates that the important factor in successfully rooting leaf cuttings is having sufficient food and water storage in succulent (parenchymous) tissues. Furthermore I can only think of one plant with truly succulent compound leaf blades in the Crassulaceae, Aizoaceae, Piperaceae, Xanthorrhoeaceae/Asphodelaceae, or Asparagaceae/Dracaenaceae, namely *Kalanchoe pinnata* (Lam.) Pers., which has pinnately compound leaves, but only on older growth (Jacobsen 1960 [1954]). If compound leaves are more stem-like primarily because of copiously dividing marginal blastozones (marginal meristems), then this might explain the rarity of rooting detached compound leaves insofar as each individual divided marginal blastozone may be relatively short-lived.

CONCLUDING REMARKS

Oddly, other than Raju & Mann (1971) and Rost & Paterson (1976), nobody has been investigating how detached succulent leaves can grow new roots and shoots since the 1930s.

It should come as no surprise that meristems can arise from leaf parenchyma given that apical meri-

stems and lateral meristems (cambium) arise from almost any type of parenchyma in roots and shoots. In roots and shoots with secondary growth, not only is there lots of included phloem in xylem rays, but also new cambium – both vascular and cork cambium – arising from parenchyma in cortex and epidermis (e.g. Isnard & Silk 2009; Pace et al. 2009; Spicer & Groover 2010). New cambium can even arise from phloem parenchyma cells in inner bark such as in the non-succulent desert plant *Ephedra* L. (Alosi & Alfieri 1972), as well as probably in the other two extant genera of Gnetales, *Gnetum* L. and *Welwitschia* Rchb., which have successive (i.e. concentric) vascular cambium (Chamberlain 1935). Probably not coincidentally, semi-succulent new plants of *Gnetum gnemon* L. can be grown from leaf cuttings (Hagemann 1932, citing van Beusekom 1907). Similarly, new root and shoot apical meristems should be able to grow *de novo* from diffuse leaf intercalary meristems, especially those leaf intercalary meristems that contain phloem parenchyma and companion cells.

Cells with thicker cell walls, i.e. collenchyma and sclerenchyma, seem to lack the ability to divide mitotically and therefore lack the ability to grow new meristems. Thus, it is difficult to root leaves of plants with highly collenchymous or sclerenchymous lignified leaves, such as in *Yucca* L. (Asparagaceae) and *Zamia* L. (Zamiaceae), even if their leaves store large amounts of water. However, Lutz (1903) claimed that *Yucca gloriosa* L. can be grown from leaf cuttings, a claim that I have not seen elsewhere. Leaves best grow new root and shoot meristems when they have lots of parenchyma, store lots of water, and have low surface-to-volume ratios. Detached and/or severed leaves need parenchyma for both apical meristem regeneration and for water storage until they can grow new roots.

Nucleated parenchyma cells (in general) and phloem parenchyma/companion cells (in particular) have the remarkable ability to develop into meristems. Development of new roots and shoots is suppressed, probably hormonally suppressed, in leaves that are still attached to stems. The only instances where new plantlets are grown from margins of leaves that are still attached to shoots are many species of subgenus *Bryophyllum*, the walking ferns *Asplenium rhizophyllum* L. (= *Camptosorus rhizophyllum* (L.) Link), *A. ruprechtii* Sa. Kurata in Nameg. (= *C. sibiricum* Rupr.), and *Adiantum caudatum* L., all of which have leathery leaves for ferns, and the orchids *Malaxis monophyllos* (L.) Sw. and *M. paludosa* (L.) Sw. For the many other plants that can be propagated via leaf cuttings, once leaves are detached or severed and, if the leaf has stored sufficient water to survive, new root and shoot apical meristems can usually develop and grow new large roots and shoots. This ability to grow new meristems probably depends on there being a high enough density of phloem tissue in the detached leaf. If these *de novo* apical meristems on leaves develop from or adjacent to functional phloem in succulent leaves, then the new plantlets can tap into fairly substantial amounts of photosynthesized

sugars to possibly grow new plant tissues.

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