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Biology and Physiology of Vines

Kevin C. Vaughn and Andrew J. Bowling
USDA-ARS-SWSRU
P.O. Box 350
Stoneville, MS 38776, USA

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I. INTRODUCTION

Vines have long fascinated botanists. Charles Darwin (1875) dedicated an entire volume to this subject, as he painstakingly documented the movement patterns of these intriguing plants. Curiously, since this rather auspicious scientific beginning, vines have received relatively much less attention from botanists than other plant groups. However, recently there has been a greatly increased interest in this area on the part of plant scientists from many disciplines (Isnard and Silk 2009). In this review, we bring together some historical perspective on the study of vines with more recent physiological and structural investigations on this fascinating group of plants.

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Plants that twine, or use tendrils or holdfasts to climb other plants or objects, have been traditionally classified as vines (Penfound 1966), although a looser classification would include any plant that receives its vertical support from an external object (Gartner 1991). A group of plants sometimes included with vines are trailing plants or scramblers that have lax stems and often possess prickles or other epidermal appendages that allow for the plant to crawl over other plants or ascend above them (Bowling et al. 2008). These lax plants share with the vines the role of "structural parasite," essentially using the upright mass of another plant to support the vine, in lieu of increasing the woodiness of its own tissue to support its mass. Some ground-hugging, prostrate plants that produce long strands, such as *Vinca major*, are also sometimes called vines, even though they lack the ability to climb. In this review we use the term "vine" in its more restrictive sense to mean only those plants that truly ascend other objects, either by twining or with tendrils or holdfasts

Vines are an important component of the flora, with over 9,000 species in just the New World (Gentry 1991). The relative percentage of vine species increases with decreasing latitude. In the tropics, woody vines, known as lianas, occupy a greater percentage of the biome than do vines in temperate climates, partly because the water-conducting anatomy of vines is more suited to a frost-free environment than to more temperate climates (Sperry et al. 1987). Commercially important food-crop vines include grapes, cucurbit species (cucumber, squash, and pumpkin), peas, hops, and sweetpotato. Wild-type soybeans and more ancient cultivars from China are vines, although most of this growth habit has been suppressed in modern cultivars that exhibit shorter and stronger internodes, leading to plants better suited to cultivation and mechanical harvesting practices. Ornamental vines abound, with wisteria, jasmine, morning glory species, sweet peas, English and Irish ivies, and black-eyed Susan vine being some of the more commonly encountered species. The ability of vines to act as structural parasites has made them formidable weeds as well. Morning glories, dodders (*Cuscuta* spp.), and redvine (*Brunnichia ovata*) are pernicious weeds of row crops, and kudzu blankets thousands of hectares of rights-of-way and forests in the southeastern United States. Many weedy vines are tolerant of traditional weed-control methods (Stone et al. 2005). Poison ivy and poison oak (Gartner 1991) are widespread and caused untold numbers of painful skin blistering every year. Two garden plants that have now escaped into the wild, Japanese honeysuckle and Irish ivy, have invaded forest ecosystems. It is likely that the weedy vines will be even more prevalent as a consequence of global carbon dioxide (CO_2) enrichment as vines seem to be more vigorous under enriched CO_2 conditions (Granadas and Korner

2002). Thus, vines touch us both as important food and ornamental plants as well as important agricultural and rights of way pests.

II. EVOLUTION AND TAXONOMIC DISTRIBUTION OF VINES

The vines (or morphological processes that allow a plant to produce either tendrils or vines) must have arisen several times in evolution. For example, the Hartford climbing fern and Japanese climbing fern occur as rare twining examples in the extant pteridophytes that otherwise have few climbing members. However, it is likely that more extensive pteridophyte vines were once in existence, as examples of scrambling, root-climbing, tendril-climbing, and twining pteridophytes have been found in the fossil records (Krings et al. 2003). Thus, the genetic capacity to grow as a vine existed in some of the earliest land plants. Likewise, within the monocots, vines are relatively rare, although the tendril-bearing group of weeds known as greenbriers (*Smilax* spp.) and the twining Gloriosa lily would both be classified as vines. Climbing palms would be more like the scramblers, as they neither twine nor use tendrils, but instead use hooklike appendages born on whiplike rachis leaf extensions (Putz 1990). Because they do not truly twine or coil, they are much less effective at climbing than true vines. Due to the more ephemeral nature of the attachment, they frequently fall from their supports. However, climbing palms are fairly well equipped to climb using a variety of mechanisms (Isnard and Rowe 2008a,b); thus they are an interesting evolutionary parallel with the true vines described elsewhere in this review. In dicots, vines are widespread, although they tend to occur more prominently in some groups than others. The Convolvulaceae and Cucurbitaceae both have large numbers of species with this habit of growth. Fabaceae has many members with these characteristics (e.g., peas), although a number of species in this large group are not vines. Despite the taxonomic diversity of the species involved, each seems to use common mechanisms by it is able to climb.

Gianoli (2004) examined the impact of having the ability to climb on the evolution of a plant group by comparing vines with nonclimbing sister groups. In 38 of the 48 comparisons, the vines group showed greater species diversification than in the nonclimbing sister groups. These data indicate that climbing constitutes a "key innovation" allowing these groups to succeed where the nonclimbing ones did not. With the ability to ascend over would-be competitors, plants that climb would have immediate advantages over their neighbors.

III. CLASSIFICATION OF VINES

Bowling and Vaughn (2009) and Penfound (1966) have classified vines by the methods used to climb. Basically there are three groups: those that use (1) tendrils for climbing, (2) twining stems, and (3) sticky adventitious roots. Some mechanisms of growth are common to all three groups whereas others are unique to a given group.

A. Tendrils

The ability of tendrils to allow vines to climb is truly an anatomical wonder. In vine species with tendrils, these relatively small, almost ephemeral structures can be used to support a vine weighing many times their mass. Tendrils are produced rapidly within the apical meristem of the plant and elongate maximally before coiling (Fig. 1.1). As the stem circumnutates, the tendrils touch potential surfaces about which to climb. When the tendril reaches sufficient maturity, stimulation of the touch response sets in place a series of morphological changes so that the tendril begins to coil around the object. In some cases, specific touch-sensitive cells are noted on the tendril surface (Engelberth et al. 1995), although in other species, no such unique cells are noted. In redvine

Fig. 1.1. Redvine tendrils coiling about a dowel rod. Besides the coiling of the tendril to affix itself to the dowel rod, groups of cells have formed extensions where adhesives are produced to secure the tendril to the support.

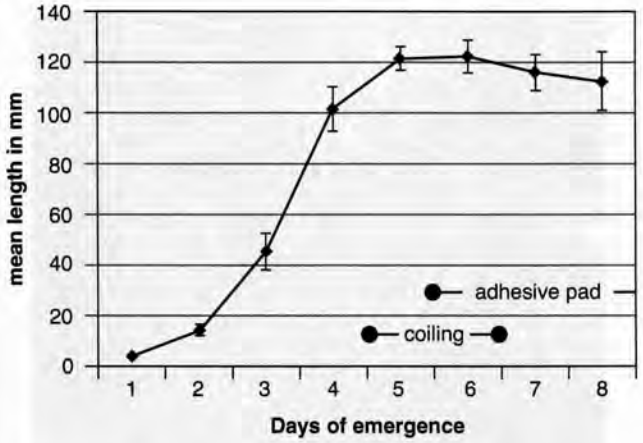

Fig. 1.2. Graph of the development of the redvine tendril. Note that coiling does not occur until the tendril has elongated maximally and that adhesive pad development follows a successful coiling.

(*Brunnichia ovata*), the ability to coil commences as soon as 5 days after initiation of the tendril. In some species, in addition to coiling of the tendril about an object, a group of epidermal cells elongate, form a padlike structure, and secrete an adhesive. (A line diagram of the changes in redvine tendril development is shown in Fig. 1.2.) Shortly after coiling is complete, the tendrils begin a programmed cell death or senescence. Oftentimes these final stages involve the breaking of vacuoles, and a general tanning of the structures occurs due to the free mixing of phenols released from the vacuoles with plastidic polyphenol oxidase. The dried and tanned tendril is highly rigid and relatively impervious to the elements and unpalatable to herbivores.

Tendrils are either highly modified stems or leaves or, in the case of plants such as redvine, formed from both stem and leaves, all possessing the ability to coil. So-called leaf-climbers, such as those vines in the Ranunculaceae, are classified with tendrils as they are anatomically similar to tendrils but produce an expanded lamina that tendrils do not. In grapes, tendrils are actually gibberellin-inhibited inflorescences (Boss and Thomas 2002). In our previous study of tendril diversity (Bowling and Vaughn 2009), we grouped tendrils into three groups: (1) those capable of coiling in any direction, (2) those that coil in one direction only, and (3) those that have adhesive properties. Our investigations of these groups have found both similarities and differences in their internal anatomy.

Redvine is our most well-studied tendril and is capable of coiling in many directions (Meloche et al. 2007; Bowling and Vaughn 2009).

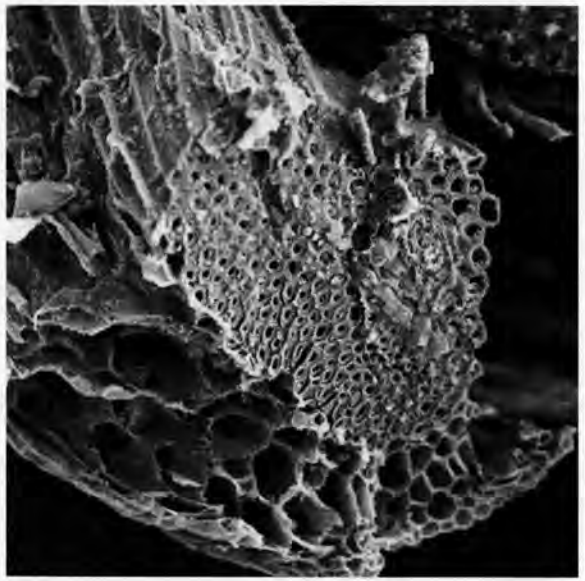

Fig. 1.3. Scanning electron micrograph of a free-hand cross-section from a coiled redvine tendril piece showing a thick layer of fiber cells 3 to 4 cells deep from the epidermis. These are gelatinous (G) fibers.

Redvine tendrils emerge and elongate for about 5 days before coiling is possible (Fig. 1.2). In that time period, the most salient change in tendril anatomy is the formation of a group of fiber cells, as illustrated in the scanning electron micrograph in Fig. 1.3, These cells are easily detected with the LM10 and 11 antibodies that recognize xylans (Fig. 1.4). At day 3, only the xylem elements react, but, by day 4, a second group of cells reacts, and by day 5, these new cells react strongly, forming a cylinder of cells 5 to 6 cell layers deep in the cortical cytoplasm (Figs. 1.3 and 1.4). Thus, the appearance of these fibers paralleled the appearance of the ability of the tendril to coil. Further investigations revealed that these fiber cells had an inner layer with immunolabeling characteristics similar to those in gelatinous (G) fibers of trees (Bowling and Vaughn 2008a). To this point, most reported instances of G fibers were limited to woody specimens, although there have been reports of G fibers in some herbaceous plants (Tomlinson 2008), where they perform similar sorts of movement/change in already existing tissue. The G layer itself is critical in this process, as the rare tendril that fails to coil produces the fibers but no G layers (Meloche et al. 2007).

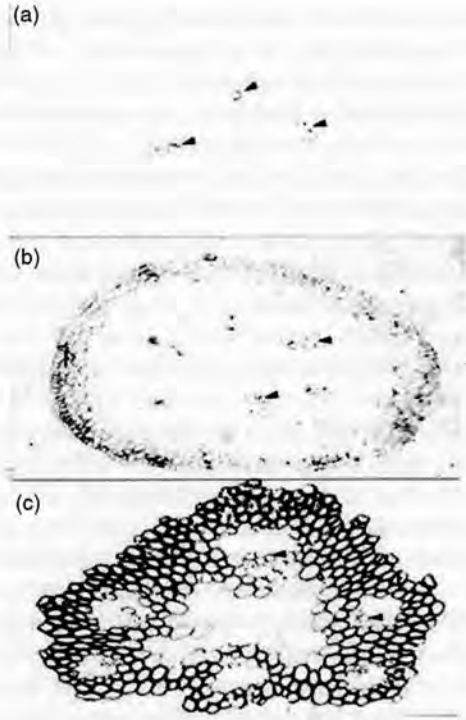

Fig. 1.4. Redvine tendril cross-sections probed with the LM10 antibody that recognizes xylans. At day 3 after emergence, only the xylem elements (arrowheads) react with this antibody. However, at day 4 a new group of fiber cells (f) begins to react, and by day 5 these have increased to form a 4- to 6-cell layer in the cortex of the tendril.

Although the exact mechanism by which G fibers cause the coiling motion is not well understood, our best model of the sorts of interactions that must occur in G fibers (Bowling and Vaughn 2009) is presented here. The G layer of the G fiber contains cellulose enriched in an assortment of mucilaginous polysaccharides such as arabinans, rhamnogalacturonans, and other pectins (Bowling and Vaughn 2008, 2009; Meloche et al. 2007). This is in sharp contrast to the constituents of the secondary wall layers, S1 and S2, of the fiber, which are composed primarily of cellulose, xyloglucans, and xylans (Meloche et al. 2007; Bowling and Vaughn 2008a, 2009). The G layer has the capacity to become highly hydrated, whereas the other layers do not. Upon drying of the G layer, shrinkage of the layer exerts pressure on the S1 and S2 layers. This pressure manifests itself in the net bending of the tissue to accommodate this pressure. Although cortical microtubules can elicit shape changes in

forming cells, G fibers can induce shape changes in cells already formed, especially woody tissue that would be impossible to change otherwise.

Tendrils that coil in just one direction and tendrils with adhesive tips both have G fibers, but the distribution and position differ from those in tendrils that coil in any direction (Meloche et al. 2007; Bowling and Vaughn 2009). In species that coil in one predetermined direction, such as the cucurbits, the G fibers are distributed in a plate along the inner surface of the coil. These were first described by Borzi (1901) as a "Bianconi plate"; later Kaiser et al. (1993) remarked that their occurrence seeming to parallel the occurrence of coiling and that they could be lignified. Bowling and Vaughn (2009) established that they were G fibers but had a more limited distribution than those that coiled freely in all directions.

Tendrils with adhesive tips such as Virginia creeper (Vaughn and Bowling 2008b) and Boston ivy (Endress and Thompson 1976, 1977) attach to a structural host not by coiling about the object but by firmly attaching to a substrate by way of adhesive tips. This strategy allows supports to be climbed that would be difficult using coiled tendrils, such as flat walls. Bowling and Vaughn (2008b) determined that the adhesive at the tip in Virginia creeper occurs as a pad and is a complex mixture of polysaccharides, consisting of debranched rhamnogalacturonan (RG) I, homogalacturonans, arabinogalactans, and callose. Some of the polysaccharides may have been generated by the loss of these components from the primary wall, which also serves to loosen these walls. Such loosening of walls makes the walls more amenable to shape changes so that the tendril tip can conform to the surface to be attached. In addition, individual components of the adhesive seem to play different roles. Callose encased in the mucilagenous pectins has the ability to spread in the presence of moisture, as demonstrated in cell plates (Vaughn et al. 1996). Thus, the pectins and other mucilaginous molecules are spread across the surface of the structure to be attached, filling in the gaps. Arabinans and arabinogalactan proteins (AGPs) appear to be an even more mobile component of the adhesive, filling in spaces between the papillate epidermal cells and even moving into small cracks in the structure that is attached. Coiling of the adhesive tendrils occurs after the adhesive end has established contact with a support. In these tendrils, the G fibers are located in a cylinder, very close to the center of the tendril. This position of the G fibers might set up a smaller radius of coiling and thus allow the coiling to proceed but without causing as much torsion to the tendril (Bowling and Vaughn 2009). Moreover, the tendrils of Virginia creeper often are coiled in one direction for half of the tendril length and in the opposite direction for the remainder. This

coiling reversal phenomenon, similar to what is observed in coiled phone cords, allows the dramatic shortening of a tissue but without as much tension to either ends of the coil. Thus, these adhesive tendrils have a free-coiling mechanism that draws the vine closer to the support, similar to other tendrils. An examination of the related *Parthenocissus stricta* in which there was no adhesive tip but rather the tendrils coiled in all directions indicated that the G fibers distributed much the same as in redvine, between the vascular tissue and the epidermis (K. Vaughn, unpubl.). Although not quite cause and effect, the distribution of the G fibers appears to have a marked effect on the kinds of tendril coiling possible.

Although tendrils with adhesive tips use the adhesive as their primary mechanism for attaching to an object, many other species that use coiled tendrils also produce an adhesive. In the case of redvine, adhesive production occurs after coiling has occurred (Fig. 1.2). Groups of papillate epidermal cells elongate and form a pad, similar to the adhesive tip of the adhesive tendrils. These cells also conform to the shape of the object to which they are attached and secrete an adhesive. Although we have not performed as comprehensive an analyses on the adhesive in the pads, many of the same components found in Virginia creeper tendril adhesive are also found in the adhesive on the pads of homogalacturonans, de-branched RG I, and arabinans (A. Bowling and K. Vaughn, unpublished). Twining stems that we have observed do not produce similar structures involved in mucilage production, with the exception of dodder at sites where haustoria attach to the host (Vaughn 2002). This product is pectinaceous but much simpler in composition and structure than those in the tendrils. Essentially, it is an external version of middle lamellae, enriched in highly deesterified homogalacturonans.

B. Twining Vines

Twining vines are probably the most familiar vines. All members of the Convolvulaceae (including the Cuscutaceae), the largest group of vines, utilize this method for climbing. Twining stems circumnutate rapidly and widely, much more so than nonclimbing plants. A large circumference and rapid circumnutation rate (> 50 Hz) allows them to "hunt" for sites about which to climb. Because of this fact, leaf development is retarded in twining vines compared to nonvines, thereby facilitating movement of the meristem (French 1977; French and Fisher 1977). Once the vine has found suitable mechanical support, two new phases of activity occur. During initial phases, the stem can be removed from the support, will remain supple, and will return to hunting for a new

support. However, if the vine remains in contact with the support for a sufficient length of time, the twining stem becomes fixed in this position, and the vine is unable to easily find a new support if the support is removed. Scanning electron microscopy reveals twisted cell morphology in older twining stems but not in younger ones that straighten as they are cut and placed in fixative (K. Vaughn, unpublished observations). Twining stems appear to elongate close to maximally and then start twining, much as do the tendrils when they are coiling.

The two phases of growth of twining vine stems are also manifested as differences in anatomy. Sher et al. (2001) documented an increase in two types of fiber cells (cells that react positively with the lignin stain phloroglucinol) as the vine begins to twine about a support. Xylary fibers, located near the xylem elements, and a second class of fibers, distributed in the cortex, both increased as the twining stem secured itself to a support. Moreover, the numbers of both types of fibers increased with increasing diameter of the support up to a point, after which the vine could no longer twine about the support. Thus, at least in the case of morning glory, there seemed to be a limit to the size of support that the vine could no longer climb, probably because the vine could not achieve sufficient torsion to do so. Often vines respond to this inability to grow up a large-diameter support by twining about themselves (Fig. 1.5; Bowling and Vaughn 2009). Darwin (1876) also reported several examples of this phenomenon, such as *Solanum dulcrama* being able to twine around

Fig. 1.5. Ivy leaf morning glory plants challenged with two sorts of support. The plant on the left has been challenged with a relatively thin support and easily ascends the structure. The plant on the right is unable to climb the 4.5-cm-diameter dowel rod, and the vine twines about itself.

3-mm supports but not 5- or 6-mm ones. Frictional components also have a role in the ability of a vine to coil about a support, so that roughness of the support and extent and nature of trichomes on the stem surface might have critical roles in climbing success (Silk and Holbrook 2005).

Bowling and Vaughn 2009 probed twining stems with the same series of antibodies as used to probe tendrils. Xylary fibers, xylem elements, and fibers in the cortex all reacted with antibodies to xylan (LM10 and 11), but only the fibers in the cortex were immunolabeled with antibodies to arabinans, RG I, and galactans as were the G fibers in tendrils. These data indicate that in twining vine stems, two fiber types, the G fibers in the cortex and xylary fibers surrounding the xylem elements, appear to be involved in twining. Bowling and Vaughn (2009) interpreted these results that the G fibers would be involved with twining, whereas the xylary fibers would be involved in stiffening the stem. This is a reasonable explanation for the data, as xylary fibers occur in many other plants and do not initiate any twining behavior. However, because both fiber types increase in response to twining, it could be that both are involved in the twining process.

Isnard et al. (2009) added several new potential players to the twining of stems. These authors recognized that a "squeezing force" was required for the climbing stem to clasp supports and found that both the stiffening of the stem and the expansion of stipules at the leaf base were involved in the generation of the squeezing force to stabilize the stem against gravity. It is possible that the xylary fibers found in vines could be involved in this stiffening response whereas the G fibers would be able to cause the actual coiling of the stem as well as generating some of the squeezing force. This would explain why both kinds of fiber cells increase in twining stems.

An *Arabidopsis* mutant with a severe twisting to the stem to the left (anticlockwise; "*lefty*" mutant; Thitamadee et al. 2002) has been likened to the condition of twining stems (Hussey 2002). In this mutant, a change in cortical microtubule organization results in cells that are twisted or leaning. The stem is more spiraled than that of the wild type. However, despite the mutation, the *lefty* mutant of *Arabidopsis* does not twine; it only has a twisted phenotype. Moreover, the phenotype of these cells is not the same as a vine. In both tendrils and twining stems, the stem elongates maximally and the cells are not twisted at this point but rather are aligned in vertical columns. Only when the stem is fixed in the twined position do the cells exhibit a spiraled morphology, but even then the appearance of the cells is different from that in *lefty*. Microtubules are effective agents for determining the shape of primary and secondary cell walls. However, after the walls are already produced, G fibers appear to be principal components that elicit structural change in righting tree

branches, movement of leaves, and contractile roots (Tomlinson 2003; Fisher 2008).

Although a majority of twining vines formed a right-handed (clockwise) coil, some species coil to the left (anticlockwise). In a survey of vines, Edwards et al. (2007) found that a majority of species (92%) coiled to the right only, but for species exhibiting right or left coiling, the incidence of coiling was random. The greatest percentage of vines coiling to the left (33%) were in Eucalypt forests in Australia, perhaps indicating a mild Coriolis effect that favors movement to the right in the Northern Hemisphere and movement to the left in the Southern Hemisphere. However, even in Australia and other points south of the equator, the majority of species coiled to the right. Thus, an overriding mechanism establishes the direction of twining and cannot be changed by external forces, such as direction of the sun or Coriolis effects. If we can interpret from the *Arabidopsis* mutants that microtubules exert a role in the spiraling of the stem, then it might be possible that there are changes in microtubule orientation that might influence handedness of the coiling direction.

C. Adventitious Root Formation

A third class of climbing plants includes those species that use adventitious roots to attach to a support. The most familiar of these is the English ivy (*Hedera helix*). English ivy produces stems that have adventitious roots at each node. When the ivy is growing across a horizontal surface on soil, the adventitious roots penetrate the soil, serving to anchor the vine as well as to provide nutrients. However, when the vine climbs a tree or other support, the roots do not expand as much and produce a close tuft of material, with the mass of roots connected together in an adhesive/mucilage complex that is involved in securing the plant to the support. This adhesive, like the one in the adhesive tendrils, is extremely effective at securing the plant to the support, as anyone who has tried to remove ivies from a house or tree can attest.

Although, to our knowledge, no studies have been conducted on the nature of the ivy adhesive, Groot et al. 2003 investigated that topic in the dwarf climbing fig (*Ficus pumila*) using histochemical techniques. These authors concluded that the adventitious roots excreted a mucilaginous compound, probably pectins and other acidic mucopolysaccharides, based on reactivities to histochemical stains.

Ivy and several vines that utilize this mechanism of vining growth also are dimorphic in their life history. For much of their lives, ivies produce vines that are incapable of producing flowers and fruits. This is the

"juvenile" stage of the plant. Growing the plant on the ground or in pots without support tends to keep the clone in this juvenile state. At some stage, generally as the plant reaches the top of a support, the morphology of the plant changes radically. The stems become sharply thicker and woody, and the plant may then produce flowers and then fruit. This is the adult or shrub stage. Poison ivy and poison oak go through similar morphological changes (Gartner 1991) morphing from vining forms to more shrub- or treelike forms. This inability to produce flowers and fruit in the vine stage of the plant may be due to simple anatomy as vines tend to produce flowers/fruit in leaf axils and branches, but rarely (or never) produce a terminal inflorescence such as in composites, indicating that a different sort of meristem may need to be produced in order for the plant to flower. Because both vine and shrub phases of the life cycle may be maintained as individuals if plants are propagated from a given morph, potentially comparisons could be made of gene expression between the two forms. Gartner (1991) compared shrub and vine morphs of the poison oak plant and found that the shrub versions could ascend to greater heights when unsupported, but the vine phase could only achieve a much more limited height unless supported. The vines never produced the extra, lignified tissue required to achieve an upright habit. When growth of the supported vine was compared to the shrub, the vine phase was much more vigorous in terms of biomass than the shrub form.

Interestingly, most of the English ivies now propagated are derived from a single cultivar called 'Pittsburgh' that has relatively short nodes that root easily. This mutation not only made this a wonderful pot plant but also seems to have reduced the ability of plants descended from 'Pittsburgh' to become "adult" or shrublike and thus rarely produce fruit (K. Vaughn, unpubl. observations). 'Pittsburgh' is highly mutable, and hundreds of ivy cultivars have been registered that trace back to this cultivar, so most of the available commercial clones currently have this same habit. Thus, it is unlikely that use of any of the more modern cultivars of ivy would have any environmental impact, because their spread is solely through the growth of the vine, not by seeds. Moreover, many of these cultivars do not grow well under field or woodland conditions unless under intense cultivation.

IV. HOW IS TOUCH PERCEIVED?

Tendrils are one of the most touch-sensitive of all plant organs, with as little as a 0.25 mg thread drawn across a tendril being able to evoke a coiling (Simons 1992). Darwin (1876) reported a coiling response in the

1- to 5-mg range. Amazingly, the plant is able to discriminate between true touch stimuli and water droplets from rain, so that no coiling happens in the absence of a support (Jaffe and Galston 1968). Stimuli must be applied along the surface of the tendril, and a rough surface is required to initiate the stimulus response (Haberlandt 1904 cited in Engelberth et al. 1995).

The most studied systems in terms of touch response are the tendrils of *Bryonia* by the Weiler group (Kaiser et al. 1993; Engelberth et al. 1995; Engelberth 2003) and of pea (*Pisum sativum*) (Jaffe and Galston 1968). In *Bryonia*, touch perception occurs in epidermal cells with "tactile blebs," ~4 μm outgrowths of the cell raised slightly above the cell surface. In the bleb, the wall makes ingrowths, and the cytoplasm surrounding the ingrowth contains a high concentration of organelles, chiefly mitochondria, Golgi, and smooth endoplasmic reticulum (ER). This area is also enriched in two cytoskeletal elements, microfilaments and microtubules. The blebs are also a site of calcium accumulation (Engelberth et al. 1995). Many other touch-sensitive processes in plants are also under calcium control with calmodulin being one of the proteins downregulated in response to touch (Braam 2003). However, many other vines respond to touch stimulation without the presence of tactile blebs, indicating that other epidermal cells may have this ability to serve as the site of touch stimulation. This may allow greater flexibility in terms of coiling positions than the more preprogrammed touch response noted in *Bryonia*.

The response to touch stimulation can be amazingly quick. *Passiflora gracilis* and *P. sicyoides* coil within 20 to 30 seconds, and *Cyclanthera pedata* coiling may start as early as 30 seconds after touch stimulation (Simons 1992). In redvine, we have shown that the ability to respond to touch stimulation does not occur until G fibers have been produced, indicating their role in the process, but the series of events that causes them to start the coiling process is not well understood (i.e., they might be the motor for the coiling, but what turns on the motor?).

The careful studies of Weiler and colleagues (Weiler et al. 1993, 1994; Engelberth et al. 1995; Engelberth, 2003) have demonstrated the role of jasmonates (Turner et al. 2002) in the process of tendril coiling in *Bryonia*, as the exogenous application of these compounds can themselves induce tendril coiling. Engelberth (2003) produced an elaborate model to describe the interactions that could be involved, including auxin, cortical microtubules, calcium, an oxidative burst, and soluble sugars. The jasmonate pathway does not appear to be a universal inducer of the tendril-coiling process, however, as pea tendrils do not respond to exogenous application of jasmonate (Engelberth et al. 2001). It is possible that indole-3-acetic acid (IAA) and other auxins might have a role in this process.

Although twining stems have been less investigated than tendrils in the touch response, they, too, seem to use jasmonates as part of their touch response (Gianoli and Molina-Montenegro 2005; Atala and Gianoli 2008). Leaf damage and other processes that enhance jasmonate production in the plant also induce twining.

V. LIGHT PERCEPTION AND FINDING A SUPPORT

How does a vine find a support? Certainly, one aspect is random touching of the shoot tip as the vine circumnutates, but are there other mechanisms not involving the random touch? One of the most interesting studies involves *Monstera* (Strong and Ray 1975). Unlike most species that grow toward light, *Monstera* grows toward darkness caused by a tree's (or other support's) shadow. This negative phototropism is called skototropism. However, when the vine reaches the support, the plant changes in morphology to facilitate climbing, and leaf and stem development are altered in anticipation of being able to conduct photosynthesis, indicating that successfully encountering a support triggers a new growth form.

A very interesting and simple study showed how a single species responded to variation in colors of the support (Price and Wilcut 2007). These authors compared the ability of morning glory plants to grow toward poles of different colors and toward maize plants. Interestingly, morning glory made very few vines on black stakes (only 17%), whereas 75% of the plants found green and yellow stakes and made vines. Blue and red stakes were intermediate between these extremes. Maize plants were the most successful supports with a 92% success rate. These data indicate that there may be more than simply sensing shadows made by prospective supporting objects to direct a vine's growth path, as the black poles should have been equally if not more successful supports than the other colors.

The parasitic weed dodder is one of the more interesting vines, as it has no true roots (Sherman et al. 2008), with only tiny leaves and an extremely reduced amount of chlorophyll (Sherman et al. 1999). With only a limited supply of its own resources and little ability to acquire more on its own, quickly locating a suitable host plant is paramount to its survival (Dawson et al. 1994). Recent work by Runyon et al. (2006) has shown that dodder responds to volatile cues from prospective hosts, even discriminating between potentially successful hosts such as impatiens or tomato and a nonsuccessful host such as wheat. One of the volatiles from wheat actually repelled the dodder. Because most grasses would also represent poor choices for a support for any vine (due to lack of strong stems to support the vine), it might be interesting to perform the

same set of experiments with nonparasitic species, especially those in the related Convolvulaceae.

VI. GENETIC APPROACHES

With the advent of molecular biology tools, other questions may be answered that were technically intractable only a few years ago. Some of these go back to simple mutant analysis, such as in the tendril-less mutant of pea (Hofer et al. 2009). In those lines, the leaflets that normally would be tendrils developed expanded lamina as in a normal leaflet. Tendrils are found throughout the Fabae and Cicerae clades of legumes, and these species also had homologues of the *Tl* gene. The authors concluded that tendrils arose as a semidominant mutation in a tendril-less progenitor legume and that tendrils provided a selective advantage to plants possessing this trait. Homologues of *Tl* exist in other species as well, and mutations in these homologies (*LMl1*) also influence lamina expansion (Saddic et al. 2006).

It is likely that reducing lamina expansion is only one factor that must be induced in order to produce tendrils or to convert stems from a normal nontwining habit to a twining one. In common bean, genotypes with both bush-type habit and climbing forms may be found, and initial studies indicated that the inheritance was monogenic for climbing versus bush types (Coyne 1967). However, later authors identified other characteristics and environmental effects on this phenotype (Bliss 1971). To investigate climbing behavior using molecular techniques, Checa and Blair (2008) crossed an aggressive, indeterminate climbing bean with an indeterminate bush bean and developed recombinant inbred lines. By using quantitative trait loci (QTL) technology, they could identify 7 loci for plant height, 9 for climbing ability, 6 for internode length, and 1 for branch number that correlated with ability to vine. Interestingly, most of these loci were in a single linkage group, which may have lead to the concept in initial studies of a relatively simple inheritance for the climbing character, as the linked genes would have inherited nearly as a unit. It will be interesting to identify the genes responsible for each of these characters and to determine if homologues of these genes exist elsewhere, especially in nonclimbing plants.

VII. SUMMARY AND CONCLUSIONS

It is perhaps appropriate in the Darwin Bicentennial Year (2009) that research on one of Darwin's pet projects, the climbing plants, has

aroused renewed interest in this beguiling group of plants (Isnard and Silk 2009). For many years just a handful of workers labored to study vines and tendrils (Jaffe and Galston 1968). We have seen notable progress in a few areas related to vines, although much still needs to be investigated and integrated before a complete picture may be obtained. Indeed, Thomas Andrew Knight's 1812 comments on the lack of experimental work on vines is still somewhat appropriate today: "The motions of the tendrils of plants, and the efforts they apparently make to approach and attach themselves to contiguous objects, have been supposed by many naturalists to originate in some degrees of sensation or perception; and though other naturalists have rejected this hypothesis, few, or no experiments have been made by them to ascertain with what propriety the various motions of tendrils, of different kinds, can be attributed to peculiarity of organization, and the operation of external causes."

Structural studies have established the presence of two potential players in the coiling of tendrils and twining of vines. In the tendrils, G fibers are highly correlated with ability of the tendril to coil (Meloche et al. 2007) and are present in certain locations and distributions that are consistent with the type of coiling behavior (Bowling and Vaughn 2009). In the twining stems, both G fibers and xylary fibers occur; although their distribution and occurrence are not as tightly correlated with the twining as they are with coiling in tendrils, they are found consistently (Bowling and Vaughn 2009). The studies of Isnard et al. (2009) indicate that other anatomical parameters, such as the expansion of stipules at the base of leaves, are involved in generating a "squeezing force" that is required for the vine to stay wrapped to the support. This might also explain the role of the xylary fibers in vines; the presence of these fibers should result in substantial stem stiffening and contribute to the squeezing force. Now that we have some basic understanding of the process of coiling, these systems are well suited for some genetic investigations. For example, G fibers are produced rapidly from day 3 to day 5 in redvine tendrils (Fig. 1.3); comparisons of mRNA (such as subtractive hybridizations) of these stages might allow us to examine the genes that are involved in induction of coiling. For example, we know that xylans are increased dramatically as a result of G fiber production (Fig. 1.3), making this a system to study xylan biosynthesis as well. Mutations that affect the ability of vines to twine and tendrils to coil will be increasingly useful tools in understanding the genetic roots of the ability to be a vine.

Since the pioneering work of Weiler and colleagues (1993) on the roles of hormones in the coiling of tendrils, relatively little work on the physiology of vines has taken place. It is crucial to unraveling the

mechanisms by which tendrils coil and vines twine to understand the cascade of events from the touch stimulation to the actual coiling takes place. The model of Engelberth (1995) is a step toward integrating the data from physiological, biochemical, and structural investigations into a holistic perspective of the coiling process.

A more global perspective is also needed. In the United States, the change to glyphosate-resistant crops has resulted in a shift in the weed species as well, with vines now a much greater percentage of weed problems than before this technology was used in such a widespread manner. The shift in weeds may be exacerbated by the concomitant change in CO_2 enrichment, which also favors vines over nonvines. In the tropics, the enhanced growth of lianas may have even greater impact on an already threatened tropical rain forest. Dealing with these problems will be a major problem for eco-physiologists for the foreseeable future. It is hoped that some of the laboratory studies of vines will give these workers clues regarding approaches that may be taken to solve these daunting problems.

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LITERATURE CITED

Atala, C., and E. Gianoli. 2008. Induced twining in Convolvulaceae climbing plants in response to leaf damage. Botany 86:595–602.

Bliss, F.A. 1971. Inheritance of growth habit and time of flowering in beans *Phaseolus vulgaris* L. _J. Am. Soc. Hort. Sci. 93:715–717.

Borzi, A. 1901. Anatomia dell-appraro sensomotore dei cirri delle cucurbitacee. Atti revev Accad. Lincei, ser. V, Rc.Cl. Sciencia for Materiales Naturales 10:395–400.

Bowling, A.J., and K.C. Vaughn. 2008a. Immunocytochemical characterization of tension wood: Gelatinous fibers contain more than just cellulose. Am. J. Bot. 95:655–663.

Bowling, A.J., and K.C. Vaughn. 2008b. Structural and immunocytochemical characterization of the adhesive tendril of Virginia creeper (*Parthenocissus quinquefolia* [L.] Planch.). Protoplasma 232:153–163.

Bowling, A.J., and K.C. Vaughn. 2009. Gelatinous fibers are widespread in coiling tendrils and twining vines. Am. J. Bot. 96:719–727.

Bowling, A.J., B.H. Maxwell, and K.C. Vaughn. 2008. Unusual trichome structure and composition in mericarps of bedstraw (*Galium aparine* L.). Protoplasma 233: 223–230.

Braam, J. 2004. In touch: Plant responses to mechanical stimuli. New Phytologist 165:373–389.

Checa, O.E., and M.W. Blair. 2008. Mapping QTL for climbing ability and component traits in common bean (*Phaseolus vulgaris* L.). Mol. Breed. 22:201–215.

Coyne, D.P. 1967. Photoperiodism: Inheritance and linkage in *Phaseolus vulgaris*. J. Hered. 58:313–314.

Darwin, C. 1875. The movements and habits of climbing plants. Henry Murray, London.

Dawson, J.H., L.H. Musselman, P. Wolswinkel, and I. Dorr. 1994. Biology and control of *Cuscuta*. Rev. Weed Sci. 6:265–317.

Edwards, W., A.T. Moles, and P. Franks. 2007. The global trend in plant twining direction. Global Ecol. Biogeography 16:795–800.

Endress, A.G., and W.W. Thompson. 1976. Ultrastructural and cytochemical studies on the developing adhesive disc of Boston ivy tendrils. Protoplasma 88:315–331.

Endress, A.G., and W.W. Thompson. 1977. Adhesion of the Boston ivy tendril. Can J. Bot. 55:918–924.

Engelberth, J. 2003. Mechanosensing and signal transduction in tendrils. Adv. Space Res. 32:1611–1619.

Engelberth J., G. Wanner, B. Groth, and E.W. Weiler. 1995. Functional anatomy of the mechanoreceptor cells in tendrils of *Bryonia dioica* Jacq. Planta 196:539–550.

Fisher, J.B. 2008. Anatomy of axis contraction in seedlings from a fire prone habitat. Am. J. Bot. 95:1337–1348.

French, J.C. 1977. Growth relationships of leaves and internodes in viny angiosperms with different modes of attachment. Am. J. Bot. 64:292–304.

French, J.C., and J.B. Fisher. 1977. A comparison of meristems and unequal growth internodes in viny monocotyledons and dicotyledons. Am. J. Bot. 64:24–32.

Gartner, B.L. 1991. Structural stability and architecture of vines vs. shrubs of poison oak, *Toxicodendron diversilobum*. Ecology 72:2005–2015.

Gentry, A.H. 1991. The distribution and evolution of climbing plants. p. 3–49. In: F.E. Putz and H.A. Mooney (eds.), The biology of vines. Cambridge Press, New York.

Gianoli, E. 2004. Evolution of a climbing habit promotes diversification in flowering plants. Proc. Royal Soc. B: Biol. Sci. 271:2011–2015.

Gianoli, E., and M.A. Molina-Montenegro. 2005. Leaf damage induces twining in a climbing plant. New Phytologist 167:385–390.

Granados, J., and C. Korner. 2002. In deep shade, elevated CO_2 increases the vigor of tropical climbing plants. Global Change Biol. 8:1109–1117.

Groot, E.P., E.J. Sweeney, and T.L. Rost. 2003. Development of the adhesive pad on climbing fig (*Ficus pumila*) stems from clusters of adventitious roots. Plant & Soil 248:85–96.

Hofer, J., L. Turner, C. Moreau, M. Ambrose, P. Isaac, S. Butcher, J. Weller, A. Dupin, M. Dalmais, C. LeSignor, A. Bendahmane, and N. Ellis. 2009. Tendril-less regulates tendril formation in pea leaves. Plant Cell 21:420–428.

Hussey, P.J. 2002. Microtubules do the twist. Nature 417:128–129.

Isnard, S., and N.P. Rowe. 2008a. Mechanical role of leaf sheath in rattans. New Phytologist 177:643–652.

Isnard, S., and N.P. Rowe. 2008b. The climbing habit in palms: Biomechanics of the cirrus and flagellum. Am. J. Bot. 95:1538–1547.

Isnard, S., and W.K. Silk. 2009. Moving with climbing plant from Darwin's time into the 21st century. Am. J. Bot. 96:1205–1221.

Isnard, S., A.R. Cobb, N.M. Holbrook, M. Zwieniecki, and J. Dumais. 2009. Tensioning the helix: A mechanism for force generation in twining plants. Proc. Royal Soc. B Biol. Sci. 276:2643–2650.

Jaffe, M.J., and A.W. Galston. 1968. The physiology of tendrils. Annu. Rev. Plant Physiol. 19:417–434.

Kaiser, I., J. Engelberth, B. Groth, and E.W. Weiler. 1993. Touch- and methyl jasmonate–induced lignification in tendrils of *Bryonia dioica* Jacq. Botanica Acta 107:24–29.

Knight, T.A. 1812. On the motion of the tendrils of plants. Read before the Royal Society, May 4, 1812. p. 164–168, In: Anon. A selection from the physiological and horticultural papers published in the Transactions of the Royal and Horticultural Societies by the late Thomas Andrew Knight, Esq., President of the Horticultural Society of London, etc. etc. to which is prefixed a sketch of his life. Published in 1841. (Facsimili edition, ASHS Press, 2001.)

Krings, M., H. Kerp, T.N. Taylor, and E. Taylor. 2003. How Paleozoic vines and lianas got off the ground: On scrambling and climbing carboniferous-early Permian pteridosperms. Bot. Rev. 69:204–224.

Meloche, C.G., J.P. Knox, and K.C. Vaughn. 2007. A cortical band of gelatinous fibers causes the coiling of redvine tendrils: A model based upon cytochemical and immunocytochemical studies. Planta 225:485–498.

Pendfound, W. 1966. The roles of vines in plant communities. Advan. Front. Plant Sci. 17:187–192.

Price, A.J., and J.W. Wilcut. 2007. Response of ivyleaf morning glory (*Ipomoea hederacea*) to neighboring plants and objects. Weed Tech. 21:922–927.

Putz, F.E. 1990. Growth habit and trellis requirements of climbing palms (*Calamus* sp.) in North-eastern Queensland. Aust. J. Bot. 38:603–608.

Runyon, J.B., M.C. Mescher, and C.M. Morales. 2006. Volatile chemical cues guide host location and host selection by parasitic plants. Science 313:1964–1967.

Saddic, L.A., B.R. Huverman, S. Bezhani, Y.H. Su, C.M. Winter, C.S. Kwon, R.P. Collum, and D. Wagner. 2006. The *LEAFY* target LMl1 is a meristem identity regulator and acts together with *LEAFY* to regulate expression of CAULIFLOWER. Development 133:1673–1682.

Sher, J.M., N.M. Holbrook, and W.K. Silk. 2001. Temporal and spatial patterns of twining force and lignification of stems of *Ipomoea purpurea*. Planta 213:192–198.

Sherman, T.D., W.T. Pettigrew, and K.C. Vaughn. 1999. Structural and immunological characterization of the *Cuscuta pentagona* chloroplast. Plant Cell Physiol. 40:592–603.

Sherman, T.D., A.J. Bowling, T.W. Barger, and K.C. Vaughn. 2008. The vestigial root of dodder (*Cuscuta pentagona*) seedlings. Int. J. Plant Sci. 169:998–1012.

Silk, W.K., and N.M. Holbrook. 2005. The importance of frictional interactions in maintaining the stability of the twining habit. Am. J. Bot. 92:1820–1826.

Silk, W.K., and M. Hunnard. 1991. Axial forces and normally distributed loads in twining stems of morning glory. J. Biomechanics 24:599–606.

Simons, P. 1992. The action plant. Blackwell, Oxford, UK.

Sperry, J.S., N.M. Holbrook, M.H. Zimmerman, and M.T. Tyree. 1987. Spring filling of xylem vessels in wild grapevine. Plant Physiol. 83:414–417.

Stone, A.E., T.F. Peeper, and J.P. Kelly. 2005. Efficacy an acceptance of herbicides for field bindweed (*Convolvulus arvensis*) control. Weed Tech. 19:148–153.

Strong, D.R.J., and T.S.J. Ray. 1975. Host tree location behavior of a tropical vine (*Monstrera gigantea*) by skototropism. Science 190:804–806.

Thitamadee, S., K. Tuchihara, and T. Hashimoto. 2002. Microtubule basis for left-handed helical growth in *Arabidopsis*. Nature 417:193–196.

Tomlinson, P.B. 2003. Development of gelatinous (reaction) fibers in stems of *Gnetum gnemon* (Gnetales). Am. J. Bot. 90:965–972.

Turner, J.G., C. Ellis, and A. Devoto. 2002. The jasmonate signal pathway. Plant Cell Suppl. S153–164.

Vaughn, K.C. 2002. Attachment of the parasitic weed dodder to the host. Protoplasma 219:227–237.

Vaughn, K.C., J.C. Hoffman, M.G. Hahn, and L.A. Staehelin. 1996. The herbicide dichbenil disrupts cell plate formation: Immunogold characterization. Protoplasma 194:117–132.

Weiler, E.W. 1993. Octadecanoid-derived signaling molecules involved in touch perception in a higher plant. Botanica Acta 106:2–4.

Weiler, E.W., T. Albrecht, B. Groth, Z.Q. Xia, B. Luxem, H. Lis, L. Andert, and P. Spengler. 1993. Evidence for the involvement in of jasmonates and their octadecanoid precursors in the tendril coiling response of *Bryonia dioica*. Phytochemistry 32:591–600.