APPENDIX 1. Continued.

Taxon	Accepted name
Pentaraphia celsioides (Griseb.) M.Gómez	**Gesneria celsioides**
Pentaraphia corrugata (Griseb.) M.Gómez	**Gesneria libanensis**
Pentaraphia craniolaria (Sw.) Decne.	**Gesneria fruticosa**
Pentaraphia cubensis Decne.	**Gesneria cubensis**
Pentaraphia depressa (Griseb.) M.Gómez	**Gesneria shaferi**
Pentaraphia duchartreoides C.Wright	**Gesneria duchartreoides**
Pentaraphia ferruginea C.Wright	**Gesneria ferruginea**
Pentaraphia floribunda (Lem.) Benth. & Hook.f. ex Carriere	**Gesneria libanensis**
Pentaraphia glandulosa Griseb.	**Gesneria glandulosa**
Pentaraphia gloxinioides (Griseb.) M.Gómez	**Gesneria gloxinioides**
Pentaraphia humilis (L.) Hanst.	**Gesneria humilis**
Pentaraphia incurva Griseb.	**Gesneria binghamii**
Pentaraphia libanensis (Linden ex C.Morren) Hanst.	**Gesneria libanensis**
Pentaraphia reticulata (Griseb.) M.Gómez	**Gesneria reticulata**
Pentaraphia salicifolia Griseb.	**Gesneria salicifolia**
Pentaraphia triflora Griseb.	**Gesneria wrightii**
Pentaraphia verrucosa Decne.	**Gesneria cubensis**
Pentaraphia viridiflora (Decne.) Hanst.	**Gesneria viridiflora**
Pheidonocarpa corymbosa (Sw.) L.E.Skog subsp. **cubensis (C.V.Morton) L.E.Skog**	
Pheidonocarpa cubensis (C.V.Morton) Borhidi	**Pheidonocarpa corymbosa** subsp. **cubensis**
Phinaea pulchella (Griseb.) C.V.Morton var. pulchella	
Rhytidophyllum acunae C.V.Morton	**Rhytidophyllum acunae**
Rhytidophyllum coccineum Urb.	
Rhytidophyllum crenulatum DC.	
Rhytidophyllum earlei (Urb. & Britton) C.V.Morton	
Rhytidophyllum exsertum Griseb.	
Rhytidophyllum exsertum Griseb. subsp. *villosulum* (Urb.) Borhidi	**Rhytidophyllum exsertum**
Rhytidophyllum exsertum Griseb. subsp. *wrightianum* (Griseb.) Borhidi	**Rhytidophyllum exsertum**
Rhytidophyllum floribundum Lem.	**Gesneria libanensis**
Rhytidophyllum intermedium Urb. & Ekman	**Rhytidophyllum minus**
Rhytidophyllum lomense (Urb.) C.V.Morton	
Rhytidophyllum minus Urb.	
Rhytidophyllum mogoticola Borhidi & O.Muñiz	**Rhytidophyllum exsertum**
Rhytidophyllum petiolare Griseb.	**Rhytidophyllum rupincola**
Rhytidophyllum rhodocalyx Urb.	
Rhytidophyllum rupincola (Urb.) C.V.Morton	
Rhytidophyllum tomentosum (L.) Mart. var. *nudum* Urb. f. *villosulum* Urb.	**Rhytidophyllum exsertum**
Rhytidophyllum tomentosum (L.) Mart. var. *nudum* Urb. f. *viscidum* Urb.	**Rhytidophyllum exsertum**
Rhytidophyllum villosulum (Urb.) C.V.Morton	**Rhytidophyllum exsertum**
Rhytidophyllum wrightianum Griseb.	**Rhytidophyllum exsertum**
Rhytidophyllum wrightii Griseb. ex C.Wright	**Rhytidophyllum exsertum**
Tussacia sanguinea (Pers.) Heynh.	**Columnea sanguinea**
Vireya sanguinolenta Raf.	**Columnea sanguinea**

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Notes and Observations on Root-Shoot Reproduction of Clonal Populations of Herbaceous Streamside Gesneriaceae

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Abstract. Meristematic activity is well documented within the Gesneriaceae. The anatomical development of secondary shoots from sub-surface roots resulting in clonal populations evidenced in other angiosperm groups has not been described. Anatomical studies as well as horticultural and habitat observations demonstrate the existence of this growth mechanism in two New World genera; *Drymonia*, in Episcieae, and *Gasteranthus* in Beslerieae. A species from a third genus and another tribe, *Gesneria*, in Gesnerieae has been observed to exhibit the same type of secondary growth. The species examined are clearly different in several key characters, but all are streamside growers in humid rain forest. The anatomical similarities of this growth habit are discussed along with possible reasons for this type of growth and the significance of the habitat.

Key words: *Gasteranthus*, *Drymonia*, ecological niche, adaptive development, ramets

Introduction

Within the Scrophulariales (now considered part of Lamiales) "some of the individual families are ecologically specialized" (Cronquist 1968). Though this is not from Cronquist's more recent treatment on the classification of flowering plants, and it is referring to specialized families rather than genera and species, the idea of ecological specialization can be applied as well to many genera and species within the large family Gesneriaceae. In the plants under examination here, the majority of one genus and a select few species within the second genus occupy the same rain forest understory streamside ecological niche and would appear to be specialized to their particular habitat.

Interest in the presence of root-shoot vegetative reproduction originated with the observation of new shoot growth from what appeared to be horizontal surface roots growing adventitiously from mature plants of *Drymonia turrialvae* Hanst. These plants were being grown in a large habitat simulation. Subsequently a similar growth habit was observed in plants of *Gasteranthus corallinus* (Fritsch) Wiehl. growing in a smaller habitat simulation. Since these initial observations were made, root-shoot growth has been noted in other species of *Gasteranthus*, both in cultivation and in the field. This type of growth has not previously been described within the Gesneriaceae. Wiehler (1983) noted the retention of "a residue of meristematic activity" but discussed it only in terms of leaves, shoots, nodes and inflorescences. He discussed three types of asexual reproduction, including new vegetative growth in stems and at nodes; new plants forming from meristematic tissue in leaf and leaf petiole material; and the production of propagules instead of flowers as a result of challenging conditions (Wiehler 1983: 68–69). The first of the three is closest to what is described here; however, as this is root tissue and not stem tissue and as a result does not typically have nodes, none of the asexual reproduction types described deal with secondary shoot development from roots.

Several stem modifications are commonly found within the Gesneriaceae, including stolons, rhizomes and scaly rhizomes, aerial propagules, and tubers. Scaly rhizomes, aerial propagules and tubers occur predominantly in species which experience a distinct dry season or in a few cases that grow as epiphytes. The plants being examined here typically occupy a rain forest understory habitat with relatively consistent high humidity, low to medium light and almost constant moisture of a tropical forest streamside niche. They can be found growing across wet rocks or with roots in moss, leaf litter or humus on the stream bank or on the slope above.

This exploration is to address whether or not the observed growth is in fact secondary shoot growth coming from roots, and if this is the case, to explore this concept as an adaptation to an ecological niche.

Materials and Methods

Plant samples from both *Drymonia turrialvae* and *Gasteranthus corallinus* that appeared to be roots with shoots as described above were collected from plants in cultivation. Several sections were collected from each species. Microscopic observations were made of external surfaces and cross sections. Further observations were made of other species in the field and in a greenhouse setting with plants in cultivation.

Observations

The tissue giving rise to the new shoots in both species is root tissue. Support for this comes from the absence of nodes or buds on the exterior surface, the absence of pith within the vascular tissue, and the radial growth pattern of the vascular tissue that lacks distinct vascular bundles. By contrast the stems of both species exhibit standard characteristics of stem tissue including the presence of nodes and axillary buds on the exterior surface as well as leaf scars; the presence of pith throughout the central region; and a distinct ring of vascular tissue typical of dicot stem tissue.

Further supporting evidence was found by examining cross sections of stolons from species of *Alsobia* and *Episcia*, genera in the Gesneriaceae that normally produce stolons. The stoloniferous growth habit is perhaps the closest to that being examined here, although the stolons typically travel above the ground and have obvious regularly occurring nodes and shoots. The stolon cross sections taken at several different stages of development within both genera consistently exhibit a distinct vascular cylinder with pith in the central region typical of stem tissue (not shown). A comparison of root and shoot cross sections demonstrating these anatomical differences is shown in FIGURE 3 and described in the legend for that figure.

FIGURE 1 illustrates the radiating vascular tissue in the cross section of a *Drymonia turrialvae* root (A), along with two lengths of root of the same species showing the emerging secondary shoots (B). The upper root section in FIGURE 1B has two buds clearly visible as well as evidence of a suberin-like substance on the epidermis of a substantially thick 1.5mm diameter root. In contrast, the lower root section in FIGURE 1B, with one adventitious bud, is otherwise quite smooth, the section measuring not quite 0.5mm in diameter. The cross section in 1A is taken from the upper root.

A similar though less developed central region of vascular tissue surrounded by more succulent epidermal cells in the cross section of a root of *Gasteranthus corallinus* can be seen in FIGURE 2A. In the second picture, FIGURE 2B, is a slightly more developed root-shoot arrangement of the same species, with the otherwise undifferentiated adventitious root showing one shoot initiating from it. The shoot, growing down and forward in FIGURE 2B has already started to develop its own secondary roots, and the first two leaves of this shoot are evident.

FIGURE 3 illustrates the root-shoot arrangement spatially and in terms of vascular tissue differences with another section of *Drymonia turrialvae*. The radial vascular tissue of the root (A) is clearly contrasted with the cylinder of vascular tissue surrounding a central core of pith seen in the two stem sections (B and C). This figure is further detailed through the labels provided in the legend.

DISCUSSION

The two species examined here are New World genera; *Drymonia* in the tribe Episcieae and *Gasteranthus* in Beslerieae. A third genus, *Gesneria*, in Gesnerieae, has also been noted to have root-shoot growth in cultivation (E. Varley, pers. comm.). Many species of *Gesneria* inhabit streamside splash-zone areas on islands in the Caribbean, so the addition of this third genus may lend further credence to the view that this particular vegetative reproductive growth is an ecological adaptation within the Gesneriaceae.

This particular habitat does appear to encourage root-shoot vegetative reproduction. Since the initial microscopic studies demonstrated that this is shoot growth from surface and subsurface roots, the same type of growth has been noted for six other species of *Gasteranthus*. While most of these have been seen in cultivation, a large plant of *Gasteranthus imbricans* (J.D. Smith) Wiehl. was found to have numerous shoots emerging from roots which were growing across wet rocks in a small stream outside BriBri, Costa Rica (pers. obs). It may be inferred that as the majority of the species in this genus grow in similar habitat, the same type of vegetative reproductive growth will be noted in others as well. The same cannot be said for the genus *Drymonia*.

The majority of species in *Drymonia* are epiphytic shrubs or lianas. This root-shoot reproduction has not been observed so far in any of the epiphytic species, although it has been looked for in more than a dozen species in cultivation. ''*Drymonia turrialvae* often inhabits dark, damp openings near waterfalls or streams occupying a site where the plants are in the spray from the falls or stream as water runs over the rocks'' (Skog 1979: 914). This species is one of perhaps six or so species in this genus to grow and thrive in this type of understory streamside habitat. The fact that this type of vegetative reproduction has not been recorded previously and is noted thus far only with this species in *Drymonia*, noted once with a species of *Gesneria* that grows in similar conditions as well as with several species of *Gasteranthus* certainly suggests that this may be an ecological adaptation.

Janzen (1975) wrote briefly regarding this same form of asexual reproduction in the tropics, focusing especially on forest vines and on the woody plants of the deciduous forest. Choosing to refer to the process more accurately as a form of asexual multiplication, he offered several possible reasons why this type of ''crown expansion'' is so abundant in the tropics. Although his focus was towards woody plants a few of his observations bear consideration towards this application in Gesneriaceae.

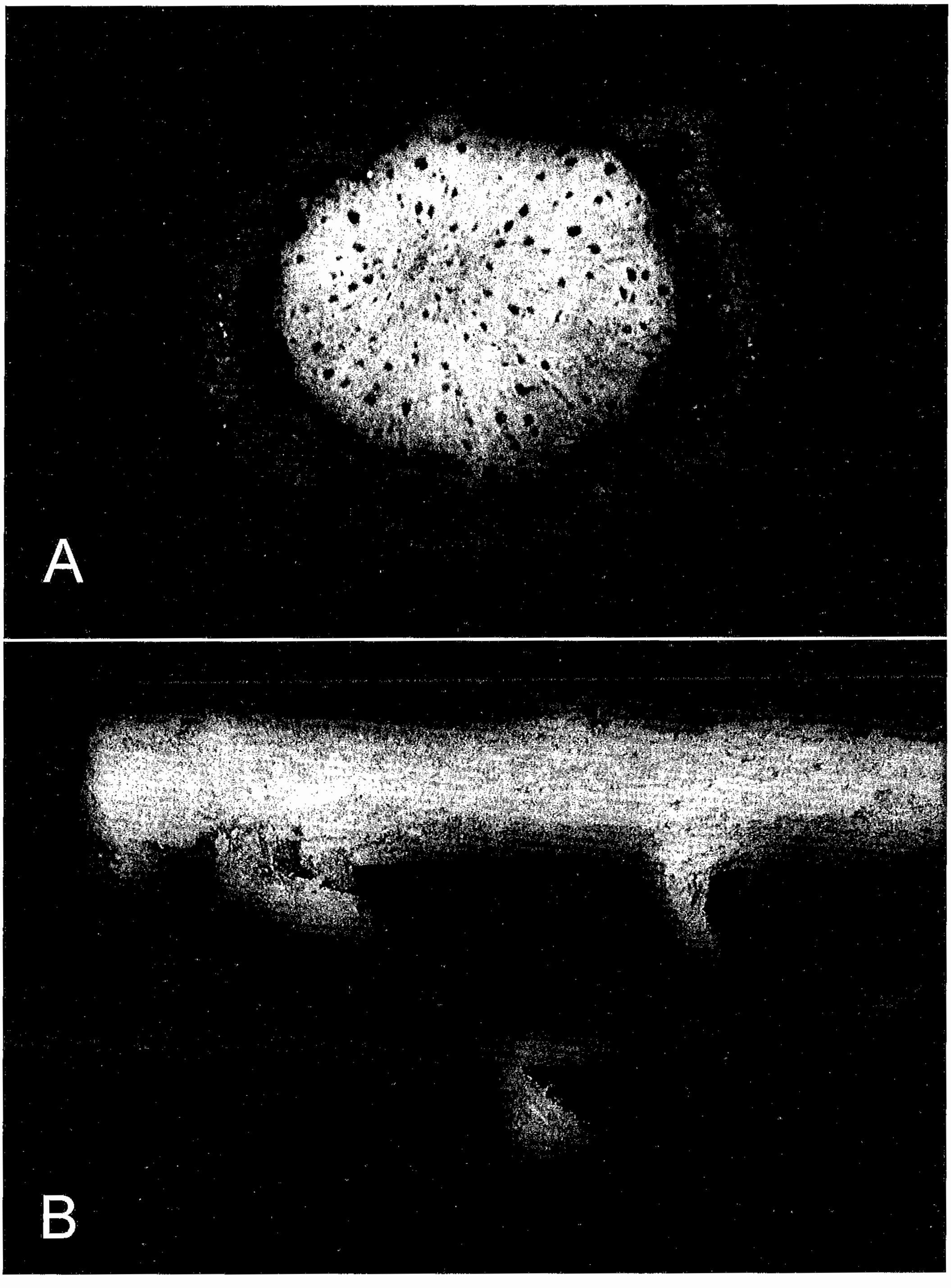

FIGURE 1. *Drymonia turrialvae* root sections and cross section showing secondary shoot initiation and the characteristic radial pattern of vascular tissue. Cross section is from the upper root section, both with diameter of 1.54mm. Smaller root section with one shoot initiating has diameter of 0.455mm.

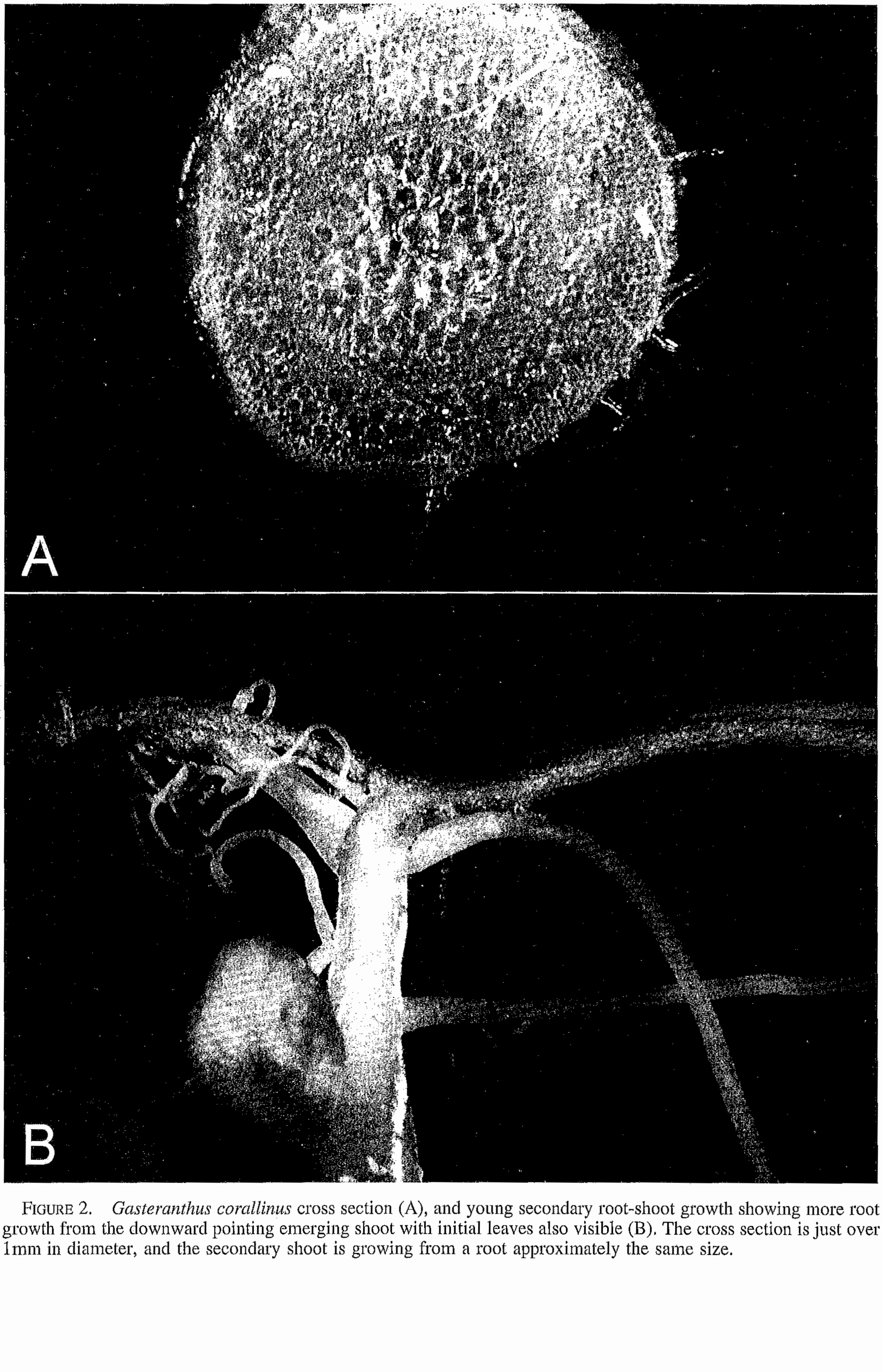

FIGURE 2. *Gasteranthus corallinus* cross section (A), and young secondary root-shoot growth showing more root growth from the downward pointing emerging shoot with initial leaves also visible (B). The cross section is just over 1mm in diameter, and the secondary shoot is growing from a root approximately the same size.

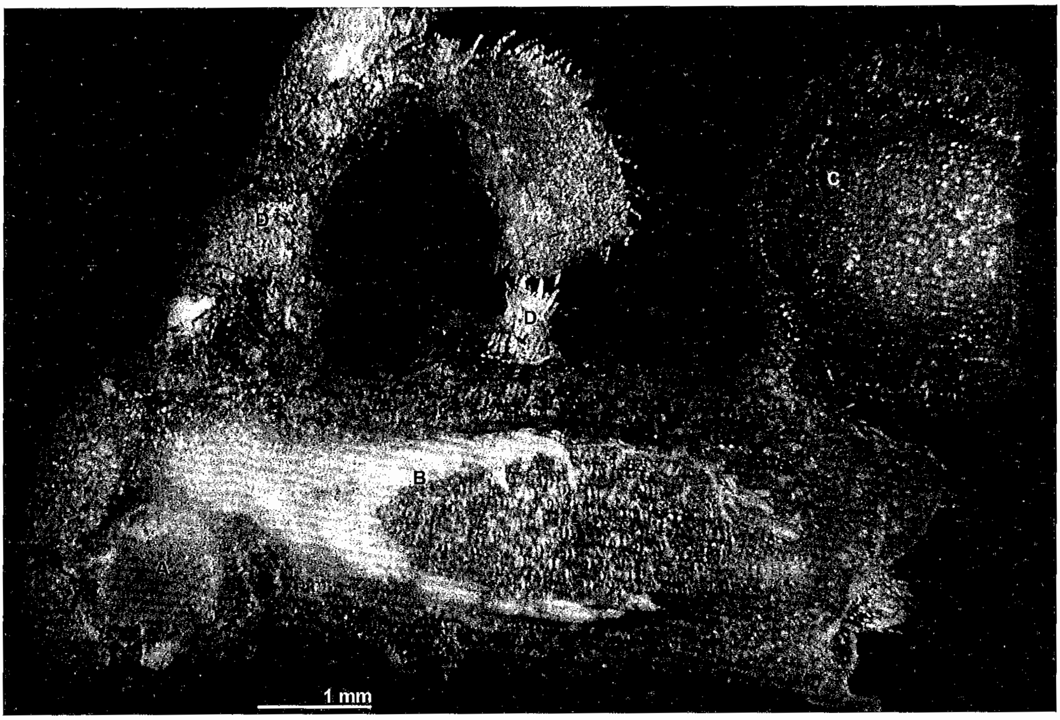

FIGURE 3. *Drymonia turrialvae*. **A.** Cross section through root. **B.** Diagonal section through shoot showing vascular tissue in ring with pith inside. **C.** Cross section through the same stem, showing the same arrangement of vascular tissue and central pith. **D.** Two secondary shoots emerging from the initial shoot growth from the root, demonstrating the abundance of meristematic tissue.

It was pointed out that the shoots growing from the roots of an established plant have the resources of the mature plant available to them, resources much greater than those contained within a seed, as well as suggesting that there is a much greater race against time inherent in a seed or seedling's chance for establishment and survival (Janzen 1975). These points are applicable to the herbaceous plants discussed here. However, some difficulty arises with the genus *Drymonia*, as it seems that the same points could also apply to the epiphytic and liana members of this genus. The root-shoot production has not been noted in any of these species examined so far. Thus, within this family at least, the root-shoot form of asexual multiplication would seem to favor adaptation to the typically streamside understory habitat.

In this particular ecological niche, the microenvironments where *Drymonia turrialvae* and numerous *Gasteranthus* spp. commonly occur, new sucker shoots may take advantage of more than just the resources of the established plant. Virtually all the common cultural requirements are being supplied on a constant basis: mild temperatures, some air circulation always with high humidity, moderate light levels, and especially for those plants in the splash-zone or immediate streamside area, abundant moisture to the roots and likely a constant wash of low concentration nutrients delivered through the moving water. The benefit of a well-anchored plant is of particular significance in this habitat niche. In areas where seeds and seedlings could easily get washed away, the adventitious shoots can by contrast establish and grow to maturity in a habitat well suited for their continued survival.

Janzen (1975) also noted the advantage of gaining crown size in ''habitats where seedling establishment is extremely difficult.'' Greater mature plant size means potentially more seeds to be dispersed. Since the root-shoots are still part of the original plant, what is seen as an entire streamside community or population of the same species might actually be just one or a few plants with what appear to be many others that are in fact all connected by these surface and sub-surface roots.

The advantage of a larger population of mature plants becomes even stronger for increased seed production when the plants involved demonstrate a trap-line pollination strategy. Though field observations of pollinators are still relatively few, Dressler (1968) noted pollination of *Drymonia turrialvae* by scent collecting *Eulaema nigrifacies* males. Wiehler (1975) in his re-establishment of the genus *Gasteranthus* observed that the known species of *Gasteranthus* can be divided into two obvious groups, one with typical ornithocephalus flowers and the other with flowers of the type visited by Euglossine bees. *Gasteranthus corallinus* has bright orange, pouched, hypocyrta-shaped corollas, a typical hummingbird flower. Thus the two species most closely examined here as well as the others discussed all do exhibit a trap-line pollination strategy and would benefit from a larger population of mature plants flowering over a more extended time and more regular visits from specific trap-line pollinators, likely resulting in increased fruit production as a result.

The understanding of how this adaptive feature has developed is still not certain, nor is it certain what initially triggers the root-shoot production in a given plant. In several of the species mentioned it has been noted that stress to the established plant through pruning or an unusual, even brief drying out period, could be an initiating factor (E. Varley, pers. comm.). Wiehler (1983) notes adverse conditions as a possible factor in prompting some of the other types of vegetative reproduction described. However stress has not always appeared to be the case with these plants starting to produce root-shoots in cultivation.

There are clearly additional research possibilities with this root-shoot asexual reproduction, particularly involving what initializes this type of growth as well as how widespread it may be. After recently presenting this material the possibility of it having been noted in two Old World genera from similar habitats was raised. Now that this type of growth has been demonstrated, more examples may be brought forward. It is significant that this root-shoot form of vegetative reproduction can be added to the list of those represented in the Gesneriaceae.

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Observations on Splash Seed Dispersal Among Neotropical Gesneriaceae

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Abstract. The concept of a splash cup morphological structure that utilizes the force of dripping water or rain to facilitate dispersal was first documented among several fungi and non-vascular plant genera during the 1940s and 1950s. It is now recognized that there are fruits that employ splashing activity for seed dispersal in at least 15 angiosperm families. Within the Gesneriaceae this type of fruiting structure has been commented on in several Old World genera and for a few New World genera but has never been comprehensively treated. In this paper, I document for the first time this fruiting structure as potentially present in representatives from 24 genera and a minimum of 189 species across five tribes of the Neotropical Gesneriaceae. Additional notes detailing morphology and environmental conditions characteristic of splash seed dispersal in Gesneriaceae are included. The persistent calyx found in some species of gesneriads is hypothesized to assist in this splash seed dispersal morphology.

Key words: follicular fruits, fleshy capsules, rain-dispersed seeds, kinetic dispersal, hydrochory

Introduction

Splash cup morphological structures in fungi and plants, where rain or falling water mechanically disperse spores, seeds or propagules, have been recognized for some time. As far back as the early 1940s splash cup mechanisms in fungi and plants were being described (Brodie 1951). In most examples among fungi and bryophytes, a minimal amount of structural specialization is apparent to facilitate water dispersal of gametes. However, true splash-cup dispersal exists in some groups. For example, the bird's nest fungi family (Nidulariaceae) develops a rather specialized cup-shaped form containing fruiting bodies (peridioles) that are ejected from the "nests" via falling water (Miller & Miller 1988). Similarly, the liverwort genus *Marchantia* L. (Marchantiaceae) produces elaborate structures on the top of the thallus known as gemmae cups, employed in splash dispersal of asexual gemmae (Equihua 1987).

Among the flowering plants, splash cup dispersal strategy is most commonly associated with seed dispersal rather than gametes and has been documented in no fewer than 15 families of angiosperms (Savile 1953, Pijl 1982, Nakanishi 2002, Pizo & Morellato 2002, Parolin 2006). In the Gesneriaceae, several studies and reviews (e.g., Burtt 1970, 1976; Weber & Skog 2007, Chautems et al. 2010, De Araujo et al. 2010) have mentioned splash dispersal in the family. No study to date has detailed the combination of features that characterizes this type of seed dispersal in the family. The purpose of this paper is to define splash dispersal fruits in terms of morphological traits and environmental conditions, detail the occurrence of splash seed dispersal in Gesneriaceae, and to document the over 20 genera of Neotropical Gesneriaceae hypothesized to exhibit this mode of seed dispersal.

Defining Splash Seed Dispersal in Flowering Plants

Morphology

The defining features of splash cup seed dispersal have broadened since first described. Early on, Brodie (1951) was quite specific in defining structures, indicating that fruit or associated organs were funnel or vase-shaped with the sides at a 60–70 degree angle from the base. He described these fruit walls as structurally sound but with enough flexibility such that the force of the water would not break them down, and with an anchoring structure or stem that prevented the cups from tipping. Brodie also indicated that the main opening faced away from the body of the plant or fungus, and noted that flowering plant capsules in particular were likely to be more open when they were wet. Seeds were also thought to be exclusively small and rather uniform among splash seed dispersed plants (Brodie 1951). Sevile (1953) added to this list of characters and described a flaring lip present in splash cup fruits he examined. Sevile also noted that there was movement of the flowering stem, determined to be a phototropic response (Sevile 1953), to orient the fruit. The stems were observed to orient vertically so that when the fruit opened it was open to the sky.

In more recent studies, the scope and arrangement of structures associated with splash seed dispersal have been broadened to include a variety of features and forms. Nakanishi (2002) detailed capsules that are cup- or boat-shaped, often with a vertical pedicel, and observed that many fruits