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# Observations on Splash Seed Dispersal Among Neotropical Gesneriaceae

Jonathan Ertelt

Vanderbilt University Dept. of Biological Sciences, Box 351634, Station B. Nashville, TN 37235, USA.

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

were more fully open when wet, thus supporting the hypothesis of Brodie (1951). Exploring splash cup seed dispersal within the Melastomataceae, Pizo and Morellato (2002) documented specialization in the whole infructescence that facilitates splash seed dispersal. In species they studied, the arrangement of fruit is such that the upper fruits do not obstruct water from hitting lower fruits thereby allowing all to be effectively dispersed via falling water. Seed shape and size has been more recently acknowledged to vary substantially in splash seed dispersed plants, though the seed are almost exclusively small to minute (Nakanishi 2002, Weber & Skog 2007) and weigh less than seed in non-splash dispersed plants but still weigh more than wind-dispersed plants (Nakanishi 2002).

Pijl (1982) characterized a similar ''spring board'' like mechanism and considered that such features represented yet another water-facilitated mode of seed dispersal related to but differing from splash dispersal. Nakanishi (2002) detailed this and several other more developed specializations for water-mediated dispersal in the form of various valves and springboard structures. Pizo and Morellato (2002) characterized an even more specialized form, a ''squirting'' mechanism in *Bertolonia* Raddi (Melastomataceae). In this species seeds are ejected from the corners of the three-cornered fruits via drops of water hitting a persistent ovary apex, the mechanism aptly named ''bertolonoid'' despite being found in other species (Pizo & Morellato 2002). Further complex specializations with this morphology have been described and examined within other plant groups including Aizoaceae (Parolin 2006).

### Environment

Environments where splash-dispersed plants are found vary greatly but most include a high degree of probable exposure to rain and/or splashing water. Several of the plants Sevile (1953) studied grow in the splash zones of waterfalls or below moist cliffs where water can collect and fall. Forest understories are also common environments for splash seed dispersal where again rain can collect and fall, this time from the overhead canopy. Observations in temperate environments suggest this type of dispersal morphology is found among some small herbaceous plants that occur in relatively open areas where occasional direct rainfall can facilitate dispersal (Nakanishi 2002). A study involving tropical species has indicated that the dense vegetation of the tropical rain forest is often common habitat for splash-dispersed species (Pizo & Morellato 2002). Weber (2004) refers to constantly wet rain forest as characteristic habitat, while cloud forest with dense moss mats and relatively low plant diversity are also implicated for some groups including Gesneriaceae (see details below).

## Splash cup Seed Dispersal in Gesneriaceae

Based on our expanded understanding of characters, mechanisms and environmental factors that all facilitate splash seed dispersal in flowering plants, I have undertaken a review of Neotropical Gesneriaceae to identify potentially splash seed dispersed species in the family. The review process included first-hand experience with some species, examination of historical and current literature, and communications with various experts in Gesneriaceae taxonomy and morphology.

I have identified 24 genera and a minimum of 189 species exhibiting some form of splash seed dispersal morphology (Table 1). Twenty of the 24 identified genera are thought to be exclusively splash seed dispersed, having this morphology expressed in all species in each of these genera. The four remaining genera (*Gesneria* L., *Kohleria* Regal, *Seemannia* Regal, and *Sinningia* Nees) each have one or more species exhibiting splash seed dispersal but are not exclusively so and thus some species exhibit alternative modes of dispersal.

I tentatively assign the 24 genera exhibiting splash seed dispersal to five tribes (Table 1) based on Wiehler (1983) and Weber and Skog (2007). While tribal-level taxonomy is changing somewhat based on recent molecular-based phylogenetic studies (see Weber et al. 2013 and Möller & Clark, 2013), it appears none-the-less that splash seed dispersal has evolved numerous times across disparate genera in Gesneriaceae. To facilitate further study of this remarkable phenomenon, I detail both the morphology and ecological conditions that are diagnostic for this mechanism in Gesnericeae and provide particular examples of novel features in some genera and species. Additionally, I include the first-ever formal description of modified calyces acting as splash seed dispersal mechanism in Gesneriaceae and hypothesize how these structures function.

### Morphology in Gesneriaceae

In broadest terms, splash cup seed dispersal morphology within the Gesneriaceae involves only one type of fruit, the capsule. However, the known variations demonstrate how diverse this fruit type can actually be and how a variety of ovary positions, modes of dehiscence and associated morphology can result in splash dispersal mechanisms.

**Fruit and seed variation.** This diversity includes 1) fleshy capsules that dehisce dorsally splitting

TABLE 1. Genera of Neotropical Gesneriaceae exhibiting splash cup seed dispersal morphology. For each genus the tribe is indicated, followed by the number of splash cup species and the total number of species. Several tribal designations are followed by question marks, indicating some placement difficulties; the tribes indicated are not a perfect fit but are the closest fit with the current parameters. Under the fruit type four base types are recognized: (D) fleshy capsule dehiscing dorsally splitting hypanthium to the base; (L) fleshy or dry capsule dehiscing loculicidally; (B) bivalved dry or fleshy capsule; (C) capsule. Modifications to base fruit types are mentioned. The presence of a persistent calyx is indicated with (+) after the fruit type.

| Genus/Tribe/Species | Fruit type | Environment |
|---|---|---|
| *Chautemsia* (Gloxinieae) 1:1 | D | Decid. forest, wet/dripping limestone outcrops |
| *Chrysothemis* (Episcieae) 7:7 | B+ | moist forest, wet rocks, mossy rocks & ground |
| *Cremersia* (Episcieae?) 1:1 | B+ loculicidally to 180° | primary rain forest, granite outcrops |
| *Cremosperma* (Beslerieae) 25:25 | C+ membranous, dehisce irregular | wet humus/moss on slopes, rocks, mossy trees |
| *Cremospermopsis* (Beslerieae?) 2:2 | C+ dehisce irreg. & disintegrates | humid shady forest, close to streams |
| *Diastema* (Gloxinieae) 20+:20+ | B+ dehisces both sides, 1 to base | wet forest, damp rocks, often near streams |
| *Gasteranthus* (Beslerieae) 36:36 | B+ 2 or 4 valved, compressed | shaded humid ravines, often near water, streams |
| *Gesneria* (Gesnerioideae) 5:46 | B | shaded rocks & wet cliffs |
| *Gloxinella* (Gloxinieae) 1:1 | D | shaded damp forest, often near water, mossy rocks |
| *Gloxinia* (Gloxinieae) 3:3 | L dehisces but not hypanthium | shaded damp forest, river banks, mossy rocks |
| *Gloxiniopsis* (Gloxinieae) 1:1 | D | shaded damp forest, often near water, mossy rocks |
| *Heppiella* (Gloxinieae) 4:4 | L+ | damp mossy rocks, tree base facultative epiphyte |
| *Kohleria* (Gloxinieae) 7:17 | B+ dehisces 1 slit, apex to base | exposed areas within rain forest, understory herbs |
| *Lampadaria* (Episcieae?) 1:1 | L+ opens fully, somewhat fleshy | wet rocks in forest |
| *Lembocarpus* (Episcieae?) 1:1 | L+ opens 180° | montane rain forest on granite outcrops |
| *Monopyle* (Gloxinieae) 17:17 | D+ opens starting from the center | wet & shady places in forest |
| *Napeanthus* (Napeantheae) 23:23 | B+ capsule opens, disintegrates | shady damp areas, mossy rocks, stream banks |
| *Niphaea* (Gloxinieae) 3–5:3–5 | C+ stiff hairs on inner wall by slits | damp shady places, rocks, earth banks |
| *Nomopyle* (Gloxinieae) 2:2 | D | humid forest understory, moist humus, mossy rocks |
| *Pearcea* (Gloxinieae) 18:18 | B/L+ reflexing interior walls | forest understory |
| *Phinaea* (Gloxinieae) 2–3:2–3 | B+ fleshy/dry, opens to 180° | humid forest understory |
| *Rhoogeton* (Episcieae?) 4:4 | L+ bivalved, opens to 180° | forest understory along streams |
| *Seemannia* (Gloxinieae) 1?:4? | D mystery sp, not typical | on earth banks, rocks in forest |
| *Sinningia* (Gesnerioideae) 4:65+ | B+ 2 forms, 1 like *Diastema* | forest plants in shade among rocks |

the hypanthium to the base (''D'' in TABLE 1, FIGURES 1A,B; 2D), 2) fleshy or dry capsules that dehisce loculicidally (''L'' in TABLE 1), 3) bivalved dry or fleshy capsules (''B'' in TABLE 1, FIGURES 1C; 2B,C) and 4) morphologically ''typical'' capsules that include other features that facilitate splash seed dispersal (see below).

Within this diversity of the fruit types for splash dispersal, the exposed seeds may be dry and separate or may be contained within a glutinous matrix that either dries or possibly is diluted and dissolved by the subsequent introduction of water. There are also seed shape differences (Kvist 1991; Kvist & Skog 1992, 1996) and at least a third of the understory genera of Gesneriaceae have either papillate projections (Skog & Kvist 2000, 2002) or protruding funicles of varying lengths (Feuillet & Skog 2002, Kvist & Skog 1988, Weber & Skog 2007). Their role in splash dispersal correlation with this mechanism of dispersal is not currently known.

**Fruit position.** The fruits are either held above the foliage on an erect pedicel (FIGURE 2C), or on a long pedicel angled more horizontal and outstretched above or beyond the foliage (FIGURE 2B,D). In all cases, the fruit is parallel to the ground and opening apically to the canopy or sky above. This orientation is noted repeatedly throughout the taxonomic literature in many genera of Gesneriaceae (Kvist & Skog 1988, 1996; Skog 1976; Skog & Kvist 2000; Boggan et al. 2008; De Araujo et al. 2010). A more recently described genus, *Lampadaria* Feuillet & L.E. Skog, is actually named for this form of fruit presentation, the genus name coming from the Latin word for torchbearer ''referring to the long peduncle holding the compact inflorescence above the foliage'' (Feuillet & Skog 2002: 344). Clark and Skog (2009) make note of movement of the pedicels to a more erect position in a species of *Pearcea* Regal as well as two in *Gasteranthus* Benth. species and suggest that it might contribute to either pollination or seed dispersal. This movement has been noted as well in *Gloxinella* (H.E. Moore) Roalson & Boggan (D. Martens, pers. comm.) as well as in species in *Diastema* Benth.

**Associated morphology.** An additional character, not previously linked to splash cup seed dispersal

morphology. For each genus the
umber of species. Several tribal
ies; the tribes indicated are not a
four base types are recognized:
leshy or dry capsule dehiscing
base fruit types are mentioned.

| Environment |
|---|
| wet/dripping limestone outcrops |
| vet rocks, mossy rocks & ground |
| forest, granite outcrops |
| ss on slopes, rocks, mossy trees |
| forest, close to streams |
| mp rocks, often near streams |
| ravines, often near water, streams |
| & wet cliffs |
| forest, often near water, mossy |
| forest, river banks, mossy rocks |
| forest, often near water, mossy |
| cks, tree base facultative epiphyte |
| within rain forest, understory |
| forest |
| forest on granite outcrops |
| places in forest |
| reas, mossy rocks, stream banks |
| laces, rocks, earth banks |
| understory, moist humus, mossy |
| ory |
| understory |
| ory along streams |
| s, rocks in forest |
| n shade among rocks |

oliage (FIGURE 2B,D). In all
el to the ground and opening
or sky above. This orienta-
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era of Gesneriaceae (Kvist &
g 1976; Skog & Kvist 2000;
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ore) Roalson & Boggan (D.
) as well as in species in

**gy.** An additional character,
to splash cup seed dispersal




FIGURE 1. Images of various types of splash-dispersed seed fruit in Gesneriaceae. **A.** *Chautemsia calcicola*, a fleshy capsule dehiscing dorsally from hypanthium to base (photo by K. Cichocki). **B.** *Monopyle* sp., a fleshy capsule which starts to dehisce from the center (photo by K. Cichocki). **C.** *Phinaea pulchella* fruit is a bivalved capsule, opening to 180° (photo by K. Cichocki). **D.** *Sinningia speciosa* includes a bivalved capsule that opens 180° and dries, leaving the seeds on the large cup-like calyx (photo by K. Cichoki).

morphology is the presence of a persistent calyx. This feature is present in 17 of the 24 genera hypothesized to exhibit splash seed dispersal documented in this study (TABLE 1). The enlarged and sometimes fused sepals of the calyx are thought to aid in forming a cup in these species and various degrees of fruit separation, decay or loss, also occur in many of those identified (FIGURES 1D; 2A,C).

It is noted within the most recent monograph of the genus *Gasteranthus* (Skog & Kvist 2000) that with some species the sepals are often larger in fruit. The fruit is typically a compressed semi-fleshy capsule opening with two or four valves. The fruit or fruits that are held erect are either positioned on top of or are contained partly within the calyx, depending on the ovary position (FIGURE 2C). For those fruits formed from a semi-inferior or inferior ovary, the calyx is persistent and the fruit upon dehiscence typically splits the calyx and surrounding tissue, the hypanthium. It is with the superior ovary position that the persistent calyx becomes more significant, often forming more of the splash cup rather than the walls of the fruit (FIGURES 1D, 2A).

*Cremospermopsis* L.E.Skog & L.P.Kvist has a dry capsule that dehisces irregularly and then the thin-walled top and sides of the opened fruit disintegrate (Skog & Kvist 2002) leaving the seeds held within the persistent calyx to be splashed out by water. Similarly, the capsule produced in *Napeanthus* is noted to not persist after it opens (Weber & Skog 2007) and might also function similarly. In several species of *Sinningia*, including *Sinningia macrophylla* (Nees & Mart.) Benth. & Hook. ex Fritsch in Engl. & Prantl., the upright capsule dehisces on both sides but does not open completely. The seeds spill out from the sides into the cup formed by the calyx lobes where they can be splash dispersed (FIGURES 1D, 2A).

Yet another example of calyces possibly facilitating splash dispersal is found in *Chrysothemis* Decaisne. Here, the calyx actually has fused lobes that are known to collect water. However, it has been suggested that this feature is meant to inhibit

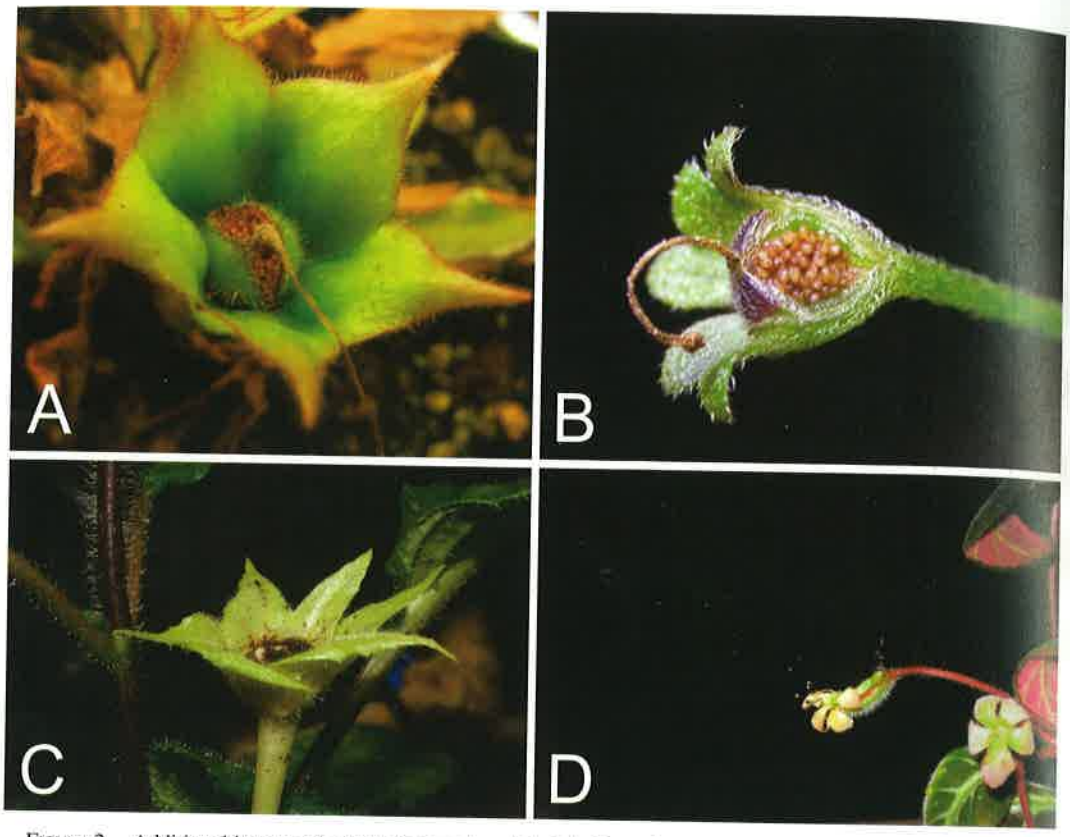


FIGURE 2. Additional images of splash-dispersed seed fruit in Gesneriaceae. **A.** *Sinningia macrophylla* utilizes the large cup-like persistent calyx as a seed holder once the bivalved capsule opens and dries (photo by A. LaVergne). **B.** *Diastema latiflorum* seeds held in the cup-like capsule (photo by D. Martens). **C.** *Gasteranthus villosus* utilizes the large and persistent calyx to hold and possibly help direct the seeds as the water splashes (photo by J. Ertelt). **D.** *Gloxinella lindeniana* fruits held out on a horizontal pedicel which probably helps catapult the seeds with the ballistics of water (photo by D. Martens).

herbivory of immature fruit (Carlson & Harms 2007). Regardless, ants are considered to be the seed dispersers in this genus due to the presence of lipid-rich enlarged funicles (Weber 2004). I could find no literature reference to numerous *Chrysothemis* plants surrounding either terrestrial or epiphytic ant nests due to discarded seeds as can be seen with the epiphytic ant garden genus *Codonanthe* (Mart.) Hanst, another genus with species known to be ant-dispersed due to either a seed covering aril or a fleshy funicle (Skog 1979). In some species though, shorter funicles appear to coincide among the species in *Chrysothemis* with fused calyces, suggesting a reduction in form associated with one form of dispersal in favor of morphology for splash dispersal.

## Environment for Splash Seed Dispersal in Gesneriaceae

As is the case in other plant groups, environment appears to be correlated with this type of morphological adaptation in Gesneriaceae but very little is conclusively known. Parolin (2006) suggested that the energy from rain in the rain forest might well cause seed to splash from 1–3m, with the result that the germinating seed and growing plants would not compete with the mother plant for available resources, but would likely land and grow in favorable conditions. Over time as more plants become established and a population forms there's an increased likelihood of attracting pollinators. In fact Parolin predicted that "A closer analysis of dispersal mechanisms of the highly diverse tropical flora presumably will present a high number of species adapted specifically to ballistic dispersal by rain" (2006: 514). Splash-dispersed species of Gesneriaceae are found principally in humid understory forest, often involving streams, wet or moss-covered rocks or where moss mats routinely cover the ground. All the genera listed (TABLE 1), in addition to having fruit types in keeping with this morphology, have

*ingia macrophylla* utilizes the
es (photo by A. LaVergne). **B.**
*teranthus villosus* utilizes the
ashes (photo by J. Ertelt). **D.**
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ely cover the ground. All
ε 1), in addition to having
ith this morphology, have



species that occupy this rain forest understory environment. No species examined to date that exhibit splash seed dispersal have been identified from environments other than those described here.

Splash seed dispersal species might not only be correlated with wet understory environments, but are possibly more successful in these habitats as a result of this novel seed dispersal mechanism. Kvist (1991) commented on the occurrence of *Pearcea*, known to exhibit splash seed dispersal, in these environments where vascular plant diversity is exceedingly low. Such environments are also typical for other genera of gesneriads exhibiting splash seed dispersal including *Napeanthus* Gardn., *Monopyle* Moritz ex Benth., *Diastema*, *Gasteranthus*. Kvist (1991) speculated that the Gesneriaceae might well be the most represented flowering plant family for this particular habitat. It has been suggested as well that the understory genera are more advanced (Kvist 1991, Kvist & Skog 1996), though the understanding of this fruiting morphology being a switch from wind to animal dispersal may now be replaced with an increased understanding of water ballistics and splash cup morphology. It is possible that splash seed dispersal facilitates or even increases the chances that seeds are deposited in more available microenvironments thereby increasing the chance of survival here. While entirely speculation at this point, this hypothesis warrants further investigation.

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