

Trade-offs tip toward litter trapping: Insights from a little-known Panamanian cloud-forest treelet

1 | INTRODUCTION

Each plant's development unfolds along many trade-off axes. One common trade-off is engendered by the differential allocation of tissues to harvest essential resources from the surrounding environment. Generally, photosynthetic leaves capture light energy and carbon dioxide, whereas roots take up water and mineral nutrients. Since these specialized functions are usually performed in separate realms – above- and belowground, respectively – plants must differentially invest in the construction of above- versus belowground organs to meet their resource requirements (e.g., Mokany et al., 2006). Furthermore, plants tend to develop leaf and root morphology and placement to make efficient resource harvests (e.g., Valladares et al., 2002). Accordingly, design trade-offs also shape plants' adaptive architectures. In light of these broad trade-offs, *Quadrella antonensis* (Woodson) Iltis & Cornejo (Capparaceae), a shrub or small tree restricted to the understory of a few montane cloud forests in Panama, presents a paradox: why does it appear to be so clearly adapted to capture and retain fine debris in “trash baskets” (see Figure 1) when this necessarily reduces light absorption and photosynthesis?

The most distinctive features of *Q. antonensis* are those that inspired its common names (*basurera*, trash-basket plant) – clusters of large leaves tightly spiraled along stem and branch tips. These leaf-cluster baskets collect fine litter that falls from overtopping vegetation. It is impossible for the leaves of the plant to be arranged in a way that maximizes light and litter capture simultaneously. An alteration in the leaf arrangement to avoid self-shading or shading by captured litter would render the arrangement relatively ineffective at litter capture. To cluster, overlap, or otherwise arrange leaves to effectively capture litter unavoidably reduces light capture efficiency in an already shady forest understory.

Why would natural selection favor a plant architecture that partially obscures its necessary photosynthetic surfaces? In other words, is there a counterbalancing advantage to litter trapping that overcomes the obvious carbon-balance costs? Here, we begin to address this question using *Q. antonensis*.

2 | ECOLOGY OF LITTER TRAPPING IN *QUADRELLA ANTONENSIS*

Neither Paul H. Allen, who collected the holotype (Allen collection #2948; Missouri Botanical Garden barcode MO-107310) in 1942, nor Robert E. Woodson, Jr., who briefly described the species with the basionym *Capparis antonensis* (Woodson et al., 1948), discussed the plant's distinctive litter-trapping habit. In a taxonomic treatment of a non-litter-trapping congener, Iltis (1981) mentioned the “ecologically remarkable ‘detritophilous’” *C. antonensis* and Dressler (1985) pondered its “humilectic” (humus collecting) nature in some detail. Iltis and Cornejo (2010) subsequently revised the taxonomy to *Q. antonensis*. Dressler, Iltis, and Cornejo assumed that litter trapping was advantageous, presumably for nutrient acquisition. In support of this assumption, Dressler (1985) noted that the plant produces copious adventitious roots from its branches into the trash baskets and that these roots clearly help retain litter and its resulting humus, both within the baskets themselves and along a portion of the stem or branch below each basket where the oldest leaves have dehisced and fallen away.

In our study population in the Altos de Campana National Park, Republic of Panama and based on our unpublished estimates from sporadic censuses over a 5-year period, we found that each well-developed leaf-cluster basket contains about 20 living leaves, each basket produces about two new leaves per year, and individual leaves can survive more than 5 years. In addition, the primary or ground root system is poorly developed (Dressler, 1985), except in small saplings, whereas the aboveground adventitious roots (which are present on plants as small as those having only four fully expanded leaves) have both root hairs and arbuscular mycorrhizal associates.

At our study site, Sánchez de Stapf (2001) demonstrated through two manipulative field experiments that litter trapping is indeed advantageous. For her first experiment, she selected 40 plants, each with two to six baskets, and on each plant she chose two similar baskets on separate branches as a pair. For her second experiment, she selected 80 small plants, each with a single apical basket, and paired the plants by proximity. For each pair of baskets in each experiment, she randomly chose one basket as a control. During the course of



FIGURE 1 The Panamanian trash-basket plant, *Quadrella antonensis*. (a) A small individual with a single apical leaf-cluster basket; (b) a medium-sized individual with several leaf-cluster baskets; and (c) a close-up view of adventitious roots. Photographs (a–b) by K. E. Harms; (c) by J. W. Dalling

a year, she removed litter monthly from the treatment baskets and compared new leaf production per basket with their paired control baskets. Litter removal statistically significantly reduced new leaf production per basket: for the first experiment from an average of 2.3 ± 0.7 (SD) new leaves in control baskets to 1.8 ± 1.1 in litter-removal baskets (paired t test, $p = .003$) and for the second experiment from 3.3 ± 2.3 to 2.8 ± 2.1 (paired t test, $p = .04$). Therefore, *Q. antonensis* plants appear both to invest in acquiring resources from their litter baskets through adventitious root production, and benefit from litter through increased productivity. Similar investments and benefits are likely to occur to varying degrees in other litter trapping shrubs and trees, but the presumed benefits have not been investigated in detail.

3 | A BRIEF SURVEY OF LITTER TRAPPING

In a recent comprehensive review of “filter feeders of the plant kingdom,” Zona & Christenhusz (2015) defined litter trappers as “plants that, by virtue of growth habit and morphology, trap or channel falling debris... and use the nutrients derived from this detritus for their own growth.” They noted that defining this trait is challenging, as litter trapping may be incidental, or in the case of some bromeliads, aroids, and ferns, trapping primarily functions for the impoundment of water. While litter capture is common and widespread among epiphytes, the trait also occurs in at least 30 families and over 90 genera of non-epiphytic terrestrial plants. Among trees and shrubs, litter trapping is associated with “*Schopfbaum*” or “branched *Schopfbaum*” (as in *Q. antonensis*) architecture, consisting of rosettes or crowns of leaves borne on a single stem or at the ends of sparse branches (Zona & Christenhusz 2015). *Schopfbaum* trees and shrubs account for more than 40 genera of litter trappers, and have evolved independently multiple times within a few species-rich genera (e.g., *Psychotria*; Lachenaud & Jongkind, 2013).

A further distinction – applied here to woody terrestrial litter trappers – recognizes litter baskets created by rosettes of leaves with short petioles, as in *Q. antonensis*, versus those in which the litter falls between the leaves and is funneled by long petioles to the base of the trunk or stem (Zona & Christenhusz, 2015). The long petiolate form occurs in several species of palms and tree ferns. Because long petioles trap litter beneath the canopy of leaves, litter capture in these plants is less likely to affect light capture than in short petiolate forms where leaf surfaces help trap litter.

The production of adventitious roots inside the accumulated litter – a trait more convincingly indicative of an adaptive nutrient-uptake function – is much less frequently found than litter trapping itself (Zona & Christenhusz, 2015). An example of an additional woody terrestrial, litter-trapping species with adventitious roots is *Q. dressleri*, named by Cornejo and Iltis (2010) to commemorate Robert Dressler’s seminal work on Panamanian terrestrial litter trappers. Like *Q. antonensis*, this unbranched *Schopfbaum* treelet is restricted to forest understory sites on a few mountain tops in central Panama (east of and allopatric to *Q. antonensis*’ geographic range). In a survey of litter trappers in the Golfo Dulce region of Costa Rica, Weissenhoffer et al. (2008) found 24 terrestrial litter-trapping species, including eight species of palms (six with adventitious roots in the accumulated humus) and eight species of treelets (two with adventitious roots in the accumulated humus); they noted that in the region – owing to their abundance – terrestrial litter trappers “obviously play a significant ecological role.” Similarly, Kenfack et al. (2007) reported that throughout the 50-ha Korup Forest Dynamics Plot in Cameroon “the understory is dominated by an odd group of litter-trapping treelets,” including species with adventitious roots (D. W. Thomas, pers. comm.). In the case of the coffee relative *Coffea magnistipula* in West Africa, leaf blades funnel debris into cup-like stipules and adventitious roots grow into the resulting humus (Stoffelen et al., 1997). In any case, adaptive advantages to terrestrial litter trapping, or specific functions such as nutrient uptake by adventitious roots, mostly have been assumed rather than demonstrated or tested.

4 | BENEFITS OF LITTER TRAPPING: A CALL FOR MORE RESEARCH INTO ITS ADAPTIVE SIGNIFICANCE

Our observations and reports about other litter trappers suggest the following mutually compatible potential advantages to litter trapping across taxa. Plants may extract resources directly from intercepted boluses of litter and humus (via roots or other absorptive surfaces) – to increase overall nutrient uptake; to avoid competition with other organisms foraging in the soil (e.g., by providing priority access to nutrients such as potassium that are readily leached out of organic matter); or to obtain better stoichiometric ratios of elements from decomposition of fine litter than would be obtained from decomposition sources on the ground (e.g., coarse woody debris, which generally has higher C:N and C:P ratios than fine litter). Alternatively or in concert, nutrients released from intercepted litter may be directed via stemflow toward aboveground roots, or other absorptive surfaces (e.g., Weissenhoffer et al., 2008, suggest cataphylls and leaf bases in litter-trapping *Clavija costaricana*), or into the soil in which the plants are rooted in the ground (Raich, 1983). Although most published speculation about and research into the benefits to litter trapping focus on the plants' nutrient economies (Benzing, 1990; Ng, 1980; Zona & Christenhusz, 2015), there are several other potential benefits.

Via litter trapping, plants might manipulate or otherwise interact favorably with organisms from the broader community, possibly even shaping species-interaction webs to their advantage. Insects, fungi, microbes, and other organisms live in their aboveground “private compost heaps” (Dressler, 1985) and could provide myriad benefits. For example, protective ants could live in the litter, specialized decomposers could live in the humus, or the milieu could attract carnivores that dissuade or remove would-be herbivores. In an intriguing example, Ngai and Srivastava (2006) found that a predatory tank-dwelling damselfly increased nutrient cycling in an epiphytic, litter-, and water-trapping tank bromeliad. Reduced rates of leaf herbivory, owing to decreased apparency or physical accessibility, could result from a combination of litter accumulation and humus formation on live leaves. Aboveground deployment of fine roots could reduce overall rates of root herbivory. Thermoregulation is also a possibility, perhaps especially for species found in cold climatic zones (similar to the thermoregulatory advantages afforded to Andean *Espeletia schultzei* by retention of its own dead leaves; Smith, 1979). In any case, very little work has been done to determine the potential for these types of possible benefits to litter trapping for most terrestrial litter trappers.

5 | CONSERVATION CONCERNS

Demographic processes are slow in *Q. antonensis*. Plants grow slowly and have very low reproductive output. During what appeared to be a typical reproductive year at our Altos de Campana study site (based

on our casual observations over several years), Sánchez de Stapf (2001) carefully assessed each of 112 reproductively-sized individuals each month. All of these plants were >1.4-m tall, which is larger than the smallest individual we have observed with flowers or fruits at the site. Only 30 of these individuals produced flowers or fruits, and among those only 10 fruits (none containing more than 14 seeds) reached maturity – 3 on a single plant (Sánchez de Stapf, 2001). They appear to be plants living on an economic knife-edge – in shaded sites where there is enough light to maintain a positive carbon balance, but where nutrients are in sufficiently short supply that litter trapping provides a net benefit. As researchers continue to study litter trappers in the field, these life-history traits of slow growth and infrequent reproduction may prove to be common among them, in which case those with small overall population sizes are likely to be especially sensitive to anthropogenic disturbances and threatened with extinction.

Like many terrestrial litter trappers, *Q. antonensis* is globally rare. It is only known from a few highland locations in central Panama, most of which have tenuous prospects for long-term population viability. For example, our study population in Altos de Campana National Park is embedded within and clearly influenced by an anthropogenically disturbed landscape (Terborgh, 1999).

6 | CONCLUDING REMARKS

As the list of terrestrial litter-trapping plants grows, we predict that most will tend to be found where temperatures allow broad, long-lived evergreen leaves, since deciduous leaves or needles are likely less well-suited to capture and retention of fine litter. We also predict that plants with adventitious roots in aboveground humus will tend to occur where there is sufficient moisture throughout the year to maintain aboveground humus formation and water – with attendant mineral – uptake (Dressler, 1985). Finally, poor soil-borne nutrient status (or possibly water-logged soil) is likely to be a key condition tipping the balance toward litter trapping plus adventitious root formation. Even though we do not have nutrient data for soils at our study site, characteristics of the site suggest very poor nutrient status, including abundant *Podocarpus* trees, which are generally reliable indicators of low nutrient soils (Palma et al., 2020; Punyasena et al., 2011).

Although we can speculate on the conditions that selectively favor litter trapping, relatively little is known about the relative costs and benefits of litter trapping across environmental conditions. In addition, there has been no formal phylogenetic or evolutionary assessment of ancestral conditions preceding litter trapping. It is plausible that efficient and effective litter trapping could evolve from incidental litter capture combined with phenotypically plastic production of adventitious roots (Herwitz, 1991; Nadkarni, 1994). Similarly, we do not know how often – once adopted and adaptively elaborated – litter trapping is evolutionarily lost.

Comparisons may be drawn between litter-trapping plants and carnivorous and certain myrmecophilous plants in which morphology is adapted for nutrient acquisition from prey and ants, respectively (Thorogood & Bauer, 2020, discuss similar trade-offs between photosynthetic potential and nutrient acquisition in carnivorous plants). The largely detritivorous pitcher plant, *Nepenthes ampullaria* – from an otherwise almost entirely carnivorous genus – illustrates the functional similarity of carnivorous and litter-trapping habits (Moran et al., 2003). Via a cost-benefit model, Givnish et al. (1984) proposed environmental conditions in which carnivory and myrmecophily would be favored; they predicted that carnivory should be restricted to sunny, moist sites with low nutrient availability. By contrast they suggested that myrmecophily can occur in shaded habitats where additional benefits beyond mineral nutrient acquisition are possible, such as defense by ants. Like myrmecophily, litter trapping may offer selective advantages to occupying shaded sites. For example, in shady environments, the construction cost of litter traps could be repaid over the long lifetimes of the slow-growing component leaves, in contrast with the traps of carnivorous plants in sunny environments, that appear to require more frequent replacement to enable the plants to continue to capture prey. In any case, litter-trappers would not be expected to occur in open, sunny sites, because whence would the litter come?

As researchers continue to bring litter-trapping plants out of obscurity, we need concerted efforts to determine the cost-benefit balance for these species and the selective consequences that tip the balance toward litter trapping. Litter-removal and addition experiments across environmental gradients could be used to estimate the cost, benefit, and net-benefit curves envisioned by Givnish et al. (1984); stable isotope studies could be used to trace nitrogen uptake and use.

Just as the tick-tock pendulum in a grandfather clock cannot simultaneously tick to the right and tock to the left, developmental trade-offs render plants incapable of possessing all possible tools of the plant trade, *i.e.*, none can perform all possible functions with maximal efficiency. Accordingly, the natural world is replete with surprising, often obscure, adaptations like those found among the litter trappers.

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AUTHOR CONTRIBUTIONS

All authors contributed toward the fieldwork, statistical analyses, writing, and editing of the manuscript.

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