



BROMELIACEAE: A BRIEF PROFILE AND SOME TOPICS THAT WARRANT FURTHER INQUIRY

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PREFACE

Seldom do professionals and laypersons exchange in writing technical information even though doing so could benefit all participants. It's a missed opportunity when family Bromeliaceae is the subject, and the would-be consumers are botanists, commercial growers, and hobbyists. For these individuals, one of the greatest of the impediments is a dichotomized literature with technical data and jargon-rich narratives served up for the first audience and for the second a more casual less exacting mix. It's this special issue of *Selbyana* that represents my effort to help narrow this gap—to author a publication useful for individuals with different levels of preparation and different reasons for wanting to know more about where the bromeliads came from and how they operate today. It's my hope that every reader whatever their incentive will find its contents useful and perhaps even inspiring enough to prompt further inquiry into the evolution and performance of this fascinating group of plants.

The information presented in the introduction to Bromeliaceae and the following ten topical essays occasionally is redundant and the cross-referencing extensive compared to the number of citations that require consulting the primary scientific literature. It's a tactic designed to make as self-contained and explanatory as reasonable what some individuals might consider a rather daunting body of information. As compensation, anyone wishing to explore many of the covered subjects in more detail can consult the bibliography. A glossary tailored for the non-specialist further ties the contents of this volume of *Selbyana* into a higher order whole by including examples drawn from Bromeliaceae. Where reliance on a rarified term cannot be avoided it's usually defined at first use. Several of the essays could serve as a basis for a workshop or mini course. The artwork, except for some of the photographs, is original with the author.

Most of the facts contained in the following essays first appeared in dozens of what already is a substantial and growing collections of publications that comprise the scientific literature devoted to bromeliad biology. Given that a narrative's impact can be diminished by too many citations I've cited only enough such reports to illustrate the kinds of questions being addressed and methods employed by today's plant scientists. Treatments that deal with photosynthesis, mineral nutrition and water relations prevail because these are the aspects of botanical structure and function that most decidedly place Bromeliaceae ahead of most of the other angiosperm families as ecologically mega-diverse and the home of some of the plant kingdom's most impressive practitioners of unusual, sometimes even novel, lifestyles. Excluded because they don't figure prominently in the presentations are publications concerned primarily with horticulture and taxonomy. Those reference that are included are accompanied by summaries of their contents.

Below are examples of the kinds of questions raised in this special issue of *Selbyana* most of which relate to subjects treated in the final six of the ten essays.

1. How close are the most highly derived of the atmospheric bromeliads to the limits of botanical specialization? Are their eco-survival bandwidths accordingly narrow?
2. How vulnerable are the bromeliads to global change, particularly to climate change and to over fertilization

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by rising concentrations of atmospheric CO₂? What about the effects of twice the amount of naturally occurring reactive nitrogen?

3. Is the physical miniaturization exhibited by the most diminutive of the atmospheric bromeliads part of an adaptation to twig epiphytism?
4. Is there functional significance to the banding and other foliar ornamentations that occur so widely among the tank-bearing members of subfamilies Bromelioideae and Tillandsioideae and if so, what is it?
5. How do the microflora (= microbiome) that resides in a bromeliad's phytelma (= tank) assist its nutrition and promote its welfare in general? What substances are exchanged, and is a capacity to utilize organic nitrogen a special trait exclusive to tank-mediated nutrition? In what ways do the tank bromeliads render their phytelmata hospitable to beneficial fauna as well as useful microbes?
6. Has epiphytism guided bromeliad speciation and if so how?
7. What triggered the crown radiation of Bromeliaceae beginning about 20 million years ago?
8. What conditions (selective pressures) favored refinement of the bromeliad trichome? How does this minute epidermal appendage play such a pivotal role for many bromeliads under so many different circumstances?
9. Why has the phytelma shoot been such a powerful driver of success for Bromeliaceae when presence of a similar device in other families (e.g., Asteliaceae) has not?
10. How would the woodland ecosystems that host abundant bromeliads respond if these plants were reduced in number and taxonomic diversity or eliminated by global change? How would system wide processes like nutrient cycling and retention and photosynthesis be affected?

Keywords: Bromeliaceae, water relations, mineral nutrition, plant immobility, genomics, adaptation, plant body, epiphytism, atmospheric, environmental response, climate change

Photographs and illustrations by David Benzing unless otherwise noted.

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ESSAY AA: INTRODUCTION

More than two thousand years ago a curious Greek philosopher exclaimed “*horror vacui*” upon observing how air behaves when subjected to different pressures. What Aristotle discovered on that occasion remains with us today embodied in the familiar axiom “Nature abhors a vacuum”. Had this ancient scholar been privy to the contents of this special issue of *Selbyana* he could have added that life as well is a space filler—in this case a filler of inhabitable space—and even better that life creates more of the same. Such a revelation would have been eminently defensible given that of all of the hundreds of families of flowering plants few matches Bromeliaceae as a doer of both deeds. To appreciate why this is so we need only examine its members many of which qualify as ecological engineers—as plants that inordinately influence the structure and dynamics of the ecosystems of which they constitute exceptionally influential parts (Benzing 2000).

Better than half of the bromeliads obtain what they need to grow and reproduce in peculiar ways and from unconventional sources. In addition, they do so under conditions that often exceed in harshness and deprivation those experienced by most land-dwelling flora. Moreover, it’s not just the epiphytes and lithophytes that account for the family’s extraordinary success as creators of habitable space, but also many of its soil-rooted terrestrials. It’s what evolution has wrought for the most specialized of the bromeliads relative to their capacity for stress-defiance and ability to colonize space largely devoid of other vascular flora that receives top billing in the following ten Essays. Featured as well is the unequalled recruitment of life-sustaining assistance from mutualistic biota that range from microbes to mammals.

The following ten narratives are crafted to serve two not entirely distinct audiences. The first consists of serious hobbyists and professional growers and the second of botanists and practitioners of related academic disciplines. Individuals who fit the first description should consider the following brief profile of Bromeliaceae preparation for the subsequent more detailed presentations all of which require some knowledge of basic botany. A more elaborate than usual glossary is provided to assist these less seasoned readers. Essays A-D being the most straightforward of the lot will prove particularly useful for the non-specialist, whereas the better prepared consumers upon reading E-J may discover new and productive ways of thinking about subjects with which they already are quite familiar.

Vital statistics, origins, and phylogeny

Bromeliaceae probably achieved its status as a distinct family, which means when it became recognizable by today’s taxonomic criteria, sometime early during its crown radiation meaning somewhere around 20 million years ago (**Figure 1AA**). The daughter lineages produced as this event unfolded owe their existence to a stem lineage whose own beginning dates back to yet an earlier ex-

pansion. The family’s evolution to become what we see today—close to 3600 species assigned to more than 75 genera distributed unequally among eight subfamilies—occurred as Planet Earth was undergoing a prolonged period of cooling that 2.6 million years ago gave way to the Pleistocene Epoch with its abruptly alternating glacial and warmer climates that fostered additional speciation within what by that time were the family’s current subfamilies, down to and including many if not most extant (= living) genera. Additional promoters of diversification beginning in the Pliocene Epoch were mountain building (= orogeny) and repeated marine transgressions and retreats caused by fluctuating sea levels. The increasingly recognized important role played by hybridization, past and present, in bromeliad evolution is aired in **Essay E**.

Proto-Bromeliaceae wasn’t alone in its response to the Pliocene-Pleistocene, geologic/climatic dynamic, but it certainly ranked among the most profoundly affected of the impacted flora. Particularly favorable for its robust crown expansion were the repeated oceanic intrusions that submerged from several directions much of South America’s extensive low-lying interior. The break ups (vicariance; see **Essay E**) of what had been wide ranging populations and the subsequent divergence to new species status of many of the fragments remains evident today in the high incidence of endemism among the bromeliad communities of the north and central Andes, the Brazilian Shield/Atlantic Forest region and the Guayana Highlands of northern South America. An area farther north that includes much of Mexico, parts of the Caribbean, and Central America turned out to be yet another site of exuberant diversification in this instance involving components of early subfamily Tillandsioideae other than those whose descendants would end up centered within what today is the Atlantic Forest biome and neighboring drier landscapes.

According to what’s known about angiosperm phylogeny the stem lineage fated to become Bromeliaceae evolved slowly at first (exhibited status) within nascent order Typhales. Still uncertain is what triggered its eventual quickened pace. Was the impetus the acquisition of what now are one or both of the family’s signature attributes they being the leafy tank and the absorbing trichome? More likely what favored the vigorous speciation and adoption of the unusual life strategies (e.g., atmospheric epiphytism) featured among several of its younger lineages (e.g., core Tillandsioideae) was a coincidental coming together of these two plus additional more common place traits a number of which are identified below and more fully described in **Essays A, B, F, H**.

The brocchinioid lineage being relic within and sister to the rest of its family provides a suggestive look-back at why Bromeliaceae became exceptionally diverse in terms of its vegetative structure and function and ecology (**Figure 1AA**). Most revealing among its survivors (20 species all assigned to *Brocchinia*) is a suite of unusual enablement’s several of which occur as more refined adaptations among the members of one or more of the fami-

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Bromeliaceae plastid DNA phylogeny

bars indicate ± 1 s. d. of node age

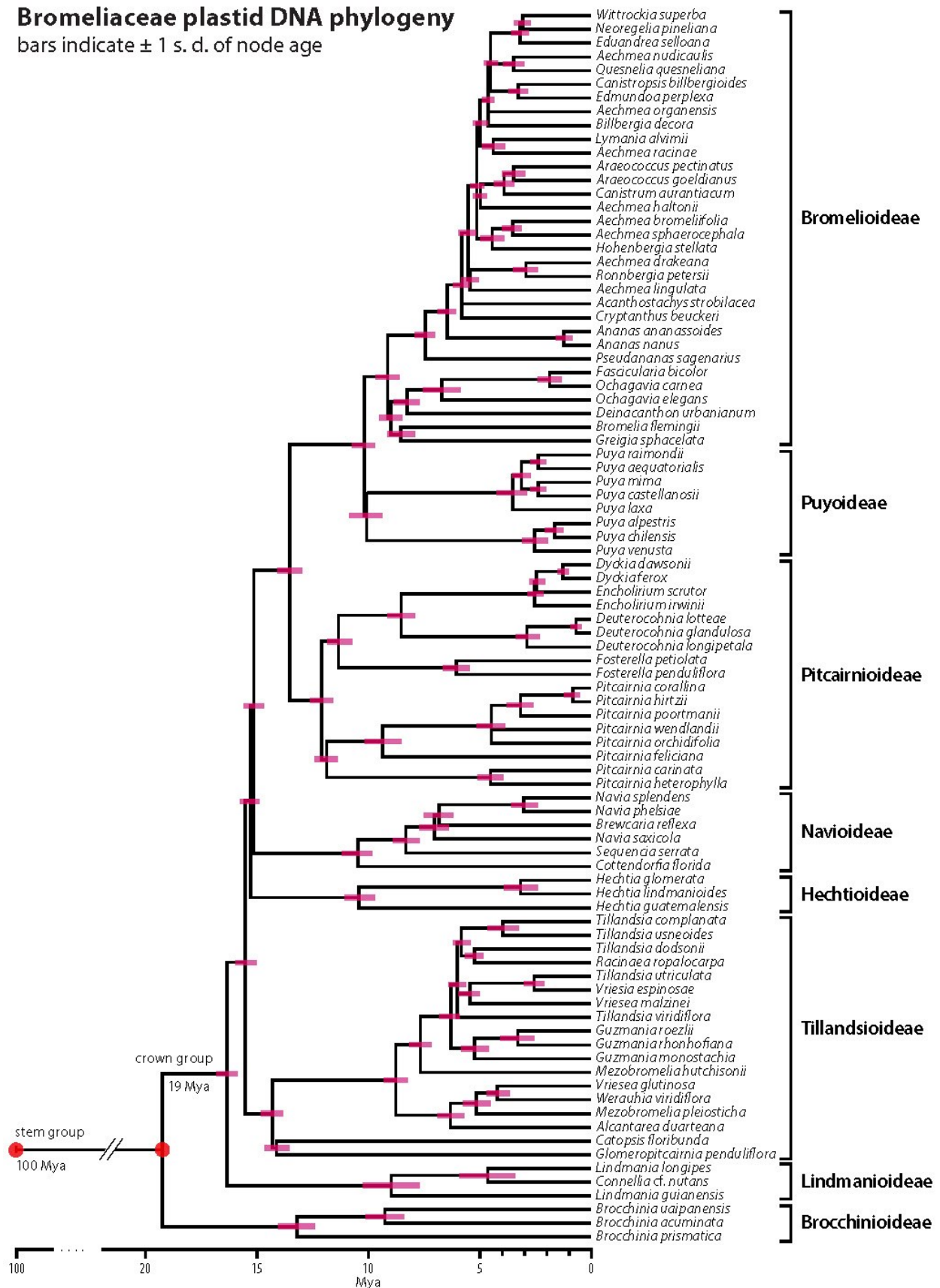


Figure 1AA: A DNA-based phylogeny of Bromeliaceae that reveals the relationships among representative genera and the eight subfamilies.

ly's more recently emerged lineages. Particularly provocative are carnivory, feeding by ants, mineral nutrients derived from litter and animal waste, absorbing foliar trichomes, phytotelms, and much diminished dependence on roots. The outstanding question boils down to this: is the hyper-diverse sometimes novel ecology manifested by today's Bromeliaceae attributable to life history influencing traits already expressed when the family embarked on its crown radiation?

To be a bromeliad usually means being a slow growing perennial herb (= no woody tissues present) that requires no less than 2–3 years for initial flowering. Repeated flowering (= polycarpy) comes close constituting a second family norm where each ramet (= secondary shoot) following the seedling shoot needs at least a full year to mature plus several more to ripen its single crop of fruit and export to daughter ramets unexpended nutrients (Figures 2AA, 4AA). The family's few monocarps (= plants that flower but once) require a decade or more to marshal the resources necessary to fuel that single life-ending reproductive effort with some *Puya* spp. rivaling for longevity the century plants of family Agavaceae.

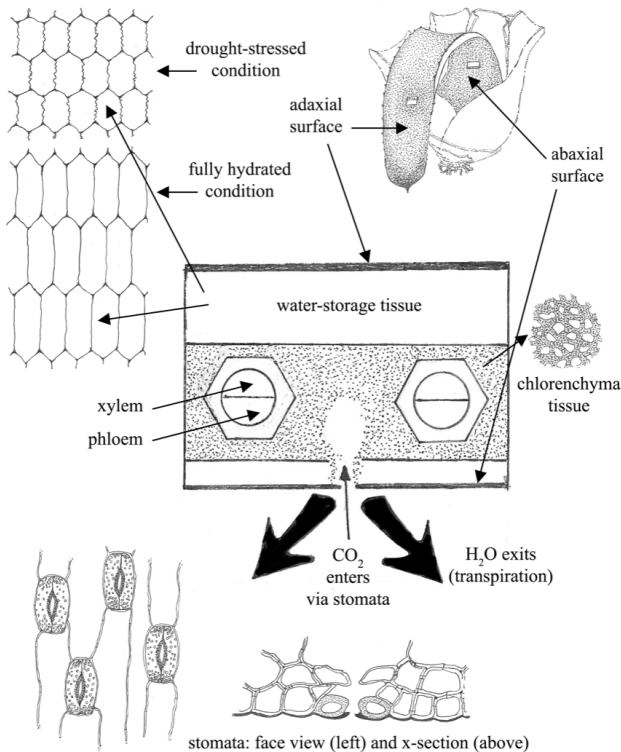


Figure 2AA: The leaf anatomy of a tank-bearing bromeliad illustrating gas exchange through stomata. The different sized arrows indicate that the transpiration ratio (the amount of H₂O expended relative to the quantity of CO₂ fixed during photosynthesis) being so large presents the most serious liability for plants that live on land (Essay A). Note that in addition to the moisture stored in an open leafy tank (phytotelm) the leaves contain water storage tissue that contracts during drought as it releases its contents to keep adjacent photosyn-

Bromeliaceae also demonstrates much mosaic evolution. While the group's propensity to exploit resource-deficient hence stressful habitats often is aided by a major reorganization and refinement of the vegetative body, its flowers, fruits, and seeds remain relatively faithful to ancestral conditions (Figures 1C, 2–3D).

The family's DNA-determined phylogeny further reveals that homoplasy (= convergent and parallel evolution and the loss and gain of body parts) explains the taxonomically separated multiple occurrences of much of the peculiar morphology and physiology that defines its modern condition (Figures 1–5AA). For example, the phytotelm-bearing (= tank equipped) shoot has arisen separately in subfamilies Bromelioideae, Brocchinioideae, and Tillandsioideae and foliar trichomes capable of supplementing to fully replacing absorbing roots occur in Brocchinioideae and Tillandsioideae and to a lesser degree in Bromelioideae (Figure 3AA). CAM-type photosynthesis has evolved much more frequently sometimes followed by its diminishment presumably as the effected lineage experienced shifted growing conditions. Today, many closely related species differ on this basis with one or more conducting CAM and the balance the more basic C₃-type mechanism (Essay A). Additional homosplastic traits include carnivory, drought-deciduousness, and myrmecotrophy (= plant feeding by ants), epiphytism, and much having to do with sexual reproduction most notably floral peculiarities harmonized to encourage visitations by bats, birds, and representatives of numerous categories of insects (Figure 3D).

Vegetative morphology

It can be difficult to identify the oldest of the multiple body plans that the members of a broadly diversified clade (= a group comprised of all of the species derived from a common ancestor i.e., a stem lineage) often display, but fortunately Bromeliaceae doesn't pose this challenge. Whereas the earliest monocots possessed primitive dicot among their monocot features the stem group responsible for the family's crown radiation probably did not. More likely, its members already exhibited the familiar strap-shaped, parallel veined foliage with sheathing bases and a fibrous root system (Figures 2, 4AA). The stem's vasculature, rather than forming a continuous ring as for most of the modern dicots probably occurred as it still does among the extant monocots as a series of scattered discrete bundles each of which consists of water conducting xylem and food transporting phloem tissue (Figures 2AA, 4AA).

The short-stemmed non-impounding shoot exemplified by predominantly terrestrial and lithophytic genera (e.g., *Fosterella*, *Pitcairnia*) almost certainly most closely resembles the family's prototypic body plan. If so, the pattern of growth described under the previous heading hasn't changed much over considerable geologic time, which is to say that most of the living bromeliads remain modular with each subunit (ramet) consisting of a compact shoot that ends its growth by producing a terminal

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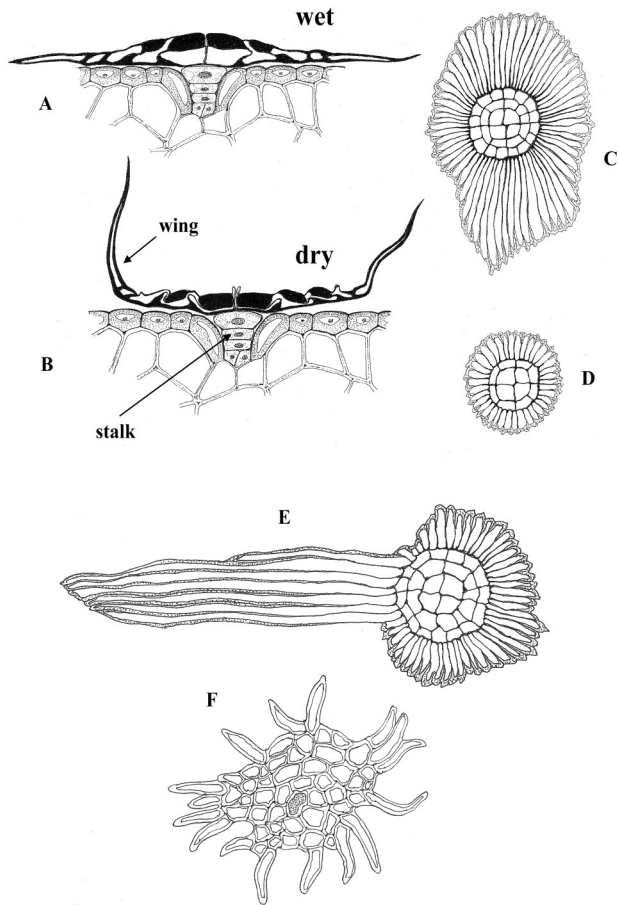


Figure 3AA (also see **Figure 4F**): The foliar trichome. **A, B** illustrate the type born by many atmospheric bromeliads sectioned to show how the wing of its cap flexes up and down as the more centrally located of its cells swell and shrink as the leaf surface to which it is attached alternately is moistened and dries. In effect, sculpted lower cell walls opposed by equally rigid complimentary shaped upper walls joined together by flexible radial walls allow the thick central portion of the cap to rise and fall thereby controlling what can enter but not exit the leaf interior along the chain of living cells that comprise the trichome stalk. The cap depicted in **B** is only partially collapsed to better illustrate its action. The caps atop the trichomes born by three tillandsioid species (**C** = *Tillandsia ioantha*, **D** = *Catopsis nutans*, **E** = *T. tectorum*) are included to illustrate how this structure varies across the subfamily plus a fourth (**F**) to show the less concentrically organized structure of the caps that characterize most other Bromeliaceae.

inflorescence plus one or more axillary buds destined to become the next in a series of ramets produced by a kind of branching labeled sympodial (**Figure 4AA**). Leaves that are most often born in a tight spiral elongate from basal meristems, which makes the individual appendage oldest at its tip and youngest just above its point of departure from the supporting adventitiously rooted stem (**Figure 7F**).

The body type just described is exceptionally versatile as demonstrated by its support of numerous lifestyles. The version faithful to the phytotelm design grants access to enough moisture and nutrients from a variety of sources to enable its owner to abandon soil for anchorage on substrates that need provide nothing more than mechanical support, a host (= a phorophyte) for instance (for the epiphytes), or an expanse of solid rock (for the lithophytes). Here and there the basic modular arrangement has given way to its unitary alternative as a means in a few instances to achieve tree-like proportions. It's here as well that thick rigid walled cells derived from an apical meristem, as for the palms, have proven equal to the dicot's wood for strengthening the robust stems and heavy crowns of the sentinel-like *Puya* spp. and *Brocchinia micrantha* (**Figure 4AA**). It's also worth noting that a handful of small-bodied species produce axillary inflorescences (e.g., *Tillandsia complanata*).

Four traits stand out among the many that underlie bromeliad success as epiphytes, lithophytes, and terrestrials native to arid and/or nutrient-deficient habitats. The

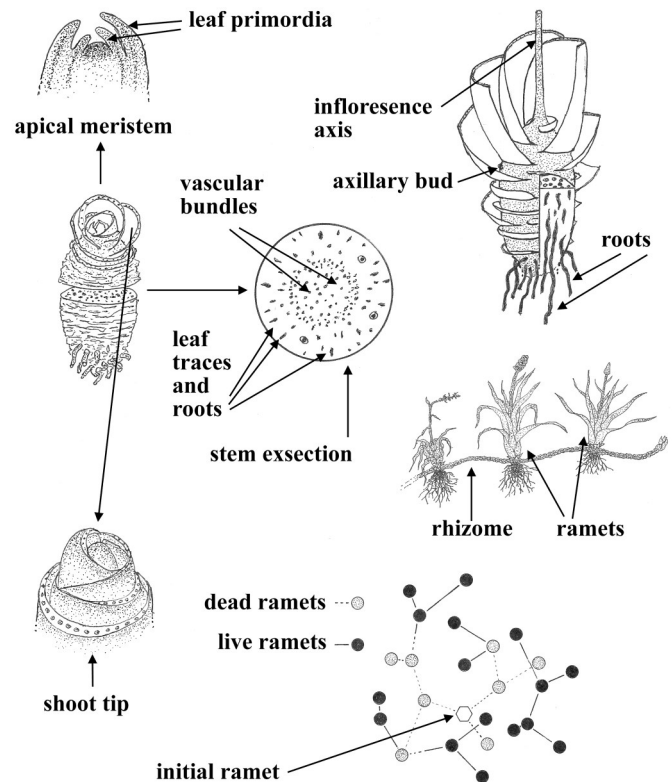


Figure 4AA: The shoot and root morphology of a tank-bearing bromeliad. Note how the roots exit the stem well below their points of origin and that they occur interspersed among the stem vascular bundles that comprise the stele from which they originate. The apical meristem of the shoot is shown intact and sectioned.

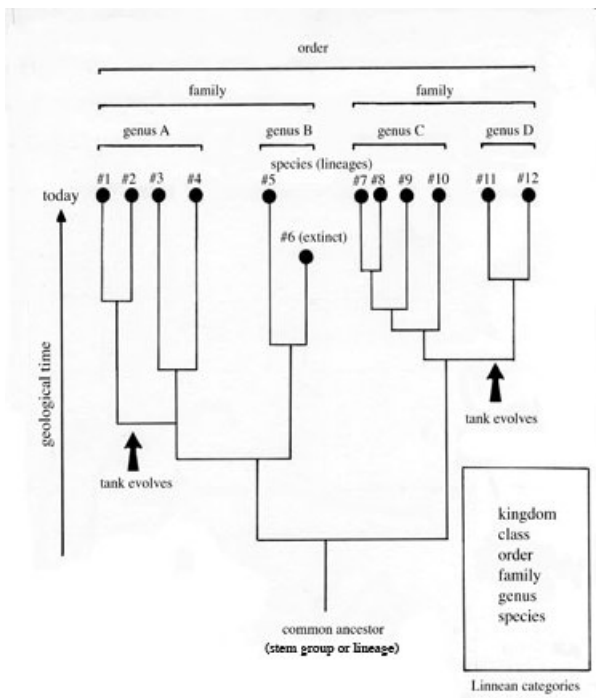


Figure 5AA: A hypothetical phylogeny crafted to illustrate the genetic juxtapositions among 11 extant and one extinct lineage, how the Linnean taxonomic categories nest in hierarchical order beginning with species through order and an example of parallel evolution (homoplasy) that resulted in a dual emergence of the leafy tank (phytotelm). Consult the text for additional detail.

first three being a greatly diminished root system, a tank-equipped (phytotelm) shoot and the absorbing trichome involve botanical structure and function (**Figures 2AA–4AA, 7F**). Number four being water-conserving CAM-type photosynthesis governs carbon/energy balance and water relations, so its treatment belongs under the forthcoming heading eco-physiology (**Essay A**). Because CAM occurs widely among the higher plants the much more limited presence of the phytotelm-type shoot and even more so the absorbing trichome, warrant higher priority in our analyses. As for enabling trait number one, hundreds of non-bromeliads scattered through more than a dozen families share similarly diminished root systems, but almost all as aquatics (e.g., *Ceratophyllum*), so for them this condition arose under the guidance of natural selection operating within a wholly different environmental context (**Essays F, H**).

Essays F and H describe how the atmospheric-type body plan (e.g., *Tillandsia usneoides*) grants ecological opportunity denied the possessors of its antecedent tank-centered architecture. Even so, rhizome structure, leaf shape, size, and color in various combinations allow the latter species access to multiple sources of nutrients and numerous kinds of living space (**Figures 5–7F**). Short rhizomes, for example, mandate tight packing (e.g., most phytotelm-bearing members of subfamily Tillandsioideae), whereas connections measured in tens of centimeters

result in loose networks of widely separated ramets (e.g., *Neoregelia* spp.) and for the robust terrestrials as exemplified by *Bromelia karatas* means to produce impenetrable thickets of heavily armed foliage. Which axillary buds positioned along the stem develop into next generation offshoots can influence whole plant form and function. The closer to the base of the terminal inflorescence the more crowded the resulting daughter ramets and the more debris can accumulate close to roots and foliage equipped with absorptive trichomes (**Figure 7F**).

Essay B explores the suitability of the phytotelm type shoot in its various iterations to host the biota required to mineralize intercepted litter, to process captured prey and to nurture living providers of nutrients such as frogs. **Essay F** considers how this leafy contraption benefits its owners at the chemical level. Considering their enablement of the family’s importance all these phenomena call for deeper inquiry. What, for instance, is the functional significance of the tank shoot’s often elaborately ornamented foliage (**Figure 4B**)? Might these displays help recruit beneficial tank dwellers, or as residents help secure their safety or both? And what about microbes? How closely does what transpires in the vertebrate gut with its dynamic microbiome parallel happenings in the leafy cavities maintained by so many bromeliads? To what extent have specific combinations of shoot size, shape, color, and physiology evolved to accommodate shade versus undiminished sunlight, to retain water in an open reservoir through extended dry spells or to intercept and extract nutrients from impounded solids?

Having identified benefits, what’s negative about possessing a tank—the adverse tradeoffs? How does its presence restrict ecological opportunity? For one, anchorage on twigs and similarly weak perches is denied all but the most diminutive of the tank-bearer the urn-shaped *Catopsis* spp. being good examples. And life deep within an evergreen canopy can imperil a plant that depends on foliage densely congested on short stems (**Figure 2I**). Constrained capacity to energize photosynthesis must be an especially serious challenge for the *Billbergia* spp. and others equipped with self-shading steeply tubular ramets. Conversely, deposits of light-blocking litter can create the same problem for species equipped with flatter shoots. **Essays F and H** describe what’s known about how the atmospheric bromeliads left tank-related constraints behind as they adopted means to colonize more resource-deficient living spaces (**Figure 1H**).

Evolution beyond the tank-bearing ramet stage didn’t require abandonment of all that had come before as modularity, sympodial branching, and determinant growth culminating in a terminal inflorescence continue to describe the hundreds of atmospheric-type bromeliads. It did relax what had been constraints on leaf form and phyllotaxis (= the arrangement of leaves on stems) as root function diminished and the foliar trichome took over as the chief device for obtaining moisture and nutrients. This anatomical repositioning and combining of disparate

functions highlight two important phenomena: the remarkable plasticity of the monocot version of the vascular plant body and the role this flexibility has played in the emergence of a lifestyle that's unique among the flowering plants. Variations on the atmospheric theme are discussed in **Essay H**.

How the atmospheric bromeliads became what we see today demonstrates one of evolution's fundamental characteristics this being that heritable change occurs largely by reshuffling existing traits and/or by bringing about their repurposing or modification. True novelty is the exception, but when it occurs its consequence can be dramatic including tolerance for previously lethal growing conditions and pursuit of new ways that a plant can make its living. Bromeliaceae exemplifies both. From the tank-dependent came the atmospheric-type lifestyle, which in turn made possible colonization of habitats that require of their resident's extraordinary stress-tolerance and special means to access moisture and nutrients (**Figure 4G**). This progression could occur only because certain pre-existing attributes were amenable to reworking coincident with the arrival of key revolutionary traits that complimented or replaced more conventional ones. Such was the case when the absorbing trichome in its most functionally refined state co-opted the role formerly played by the leafy phytotelm just as the latter eliminated need for absorbing roots and access to soil.

Only a handful of bromeliads lack their family's signature umbrella-shaped foliar trichome. It's a novel device whose functions are atypically diverse as epidermal appendages go, and these functions co-occur in different combinations depending on the species (**Figures 3AA, 4F**). Where most conventionally structured as in subfamily Pitcairnioideae it appears to provide only what most foliage needs where exposed to the atmosphere that being predominantly mechanical means to slow transpiration, discourage enemies and shield against photo-injury. But for the phytotelm-bearing bromeliads, and even more for the atmospheric types, what accrues beyond or in addition to the usual is ecologically transformative.

Nutrition, photosynthesis, and water relations

It would be odd if the peculiar ecology and physical form that describe so much of Bromeliaceae weren't accompanied by similarly unconventional ways of making a living, most interestingly, by how nutrients and water are acquired and used. Not surprising, this logic fails to apply for the most fundamental of plant life's processes such as cellular respiration and protein synthesis, but it does for a spate of higher-level performances that require integrated action by specific cells, tissues, and organs. It's the ways that these body parts interact and complement one another that allows different species to succeed under different growing conditions, particularly those related to climate. This is why carbon/energy balance (photosynthesis), water relations and mineral nutrition warrant the label eco-physiology rather than general or basic physiology. What

follows are brief introductions to these three operations all of which receive fuller consideration in **Essays A, B**.

Only one of the major mechanisms that the higher plants employ to evade the devastating effects of drought doesn't occur among the bromeliads. Missing is the resurrection strategy whereby a subject's water content is tied to the wetness of its immediate surroundings, which assures that this value fluctuates rapidly and to extremes in concert with that of the source (**Essay A**). A couple of rock-dwelling *Pitcairnia* spp. reportedly survive deep desiccation, but it takes a prolonged dry spell to reach such profound deficits (up to 95%) meaning that the affected subject cannot be considered poikilohydrous like the "resurrection" type ferns and mosses. Drought deciduousness, although uncommon in the family, can be well developed (e.g., *Pitcairnia heterophylla*). Drought-endurance serves much more of Bromeliaceae whereas true aquatics are few (e.g., the rheophytic pitcairnias). Finally, substantial portions of the memberships of Tillandsioideae and Pitcarinioideae, some Bromelioideae and a scattered species in other subfamilies qualify as mesophytes meaning that although short of being wetland natives they exhibit no obvious preparedness to resist, avoid or tolerate more than modest dry downs.

Essay A explains how photosynthesis and water use are inextricably linked, and why the two being interlocked constitutes globally—for agriculture and in the wild—the most powerful of nature's constraints on plant growth and reproduction. It also describes xeromorphology (= anatomy adapted for plant retention of absorbed moisture) and the physiological and phenological (= seasonal schedule) quirks that allow flora to avoid or tolerate hyper-arid conditions. Life cycles brief enough to complete within a single rainy season, and seasonal deciduousness for the perennial allow species so endowed opportunity to counter predictable (seasonal) dry weather, but the bromeliads, most of which are evergreen and never short-lived, must have more or less continuous access to moisture, be drought deciduous or sequester excess moisture (be succulent or tank-equipped) and use it with extraordinary efficiency.

No data indicate that the bromeliads require any unusual mineral elements, but at least a few species have proven capable of sequestering non-nutritive substances that include several of the so-called technological metals (e.g., chromium, copper) and certain gasses (e.g., SO₂, mercury vapor; **Essay B**). Because of these propensities several *Tillandsia* spp. have been used to monitor air quality at sites across tropical and subtropical North and South America. A sampled colony of *Tillandsia paucifolia* growing on mangroves along Florida's south gulf coast contained as much sodium as some of the true halophytes (= genetically determined salt-tolerant plants), and experimental subjects representing the same species exhibited luxury consumption taking up phosphorus far beyond short term needs. Conversely, assays of other species suggest that key elements, particularly nitrogen and phosphorus, can occur in bromeliad foliage at concentra-

tions well below those considered adequate for most crops.

Much is already known about how the bromeliad trichome, and phytotelm-equipped shoot replace root systems, but inquiry into the ways that third parties assist mineral nutrition have lagged by comparison. In effect, trichome-bearing foliage renders the leafy tank somewhat akin to a botanical stomach with its resident detritivores (= invertebrates that consume dead plant material) and communities of microbes acting in lieu of digestive enzymes to release from intercepted biomass nutrients for plant use. Especially promising on this score is the ongoing effort by a group of Brazilian scientists to understand tank leaf function at the molecular level. **Essays B and F** describe preliminary results plus how certain tank-inhabiting microbes fix gaseous nitrogen (N₂) into botanically usable (= reactive) forms (**Figure 7F**).

It remains to be determined whether the fungi that live within or on the foliage of at least some bromeliads contribute nutritionally to their hosts in ways analogous to what the mycorrhizal types provide for soil-rooted flora. And it's not just the tank-dwelling microbes and fauna at issue here, but as well the diverse air breathers that occupy the spaces among the older dry leaf bases of the large phytotelm-equipped individual. Ants are enticed to feed the ant-house species (**Figures 1, 5B**) while a smaller subset of behaviorally more plant-dependent species literally farm another group of bromeliads (e.g., *Aechmea mertensii*) in a way that includes the sowings of seeds during the building of covered aerial runways and nests. Finally, carnivorous *Brocchinia reducta* consumes primarily ants while epiphytic *Catopsis berteroniana* (**Figure 6B**) is adapted to harvest airborne prey (**Essay C**).

Reproduction

Numerous pollination syndromes, gender expressions and breeding systems mix and move genes for the angiosperms. For the bromeliads its wind alone of the major conveyors of pollen that's missing whereas ornithophily (= pollination by birds) is overrepresented, especially among the tillandsioids (= members of subfamily Tillandsioideae), and chiropterophily (= pollination by bats) has evolved in at least four of the eight subfamilies (**Figure 1AA**). Diverse kinds of insects participate as well the flowers visited emitting fragrances that range from floral to cadaverous with the forager's reward mostly consisting of pollen and/or nectar. Many of the most diminutive members of subfamily Tillandsioideae produce seeds unassisted (**Essay H**). For many bromelioids (= members of subfamily Bromelioideae) and tillandsioids fruit set depends less on alluring petals and sepals than on brightly colored bracts and foliage (**Figures 3D, 4B**).

The typical bromeliad flower is described as perfect meaning bisexual, but dioecism (= male and female flowers born on separate individuals) has emerged repeatedly

and sometimes early enough during the history of a genus to affect its entire membership (e.g., *Hechtia*), but more commonly later with the result being two or more gender expressions. *Catopsis nutans* includes bisexual and dioecious populations and *Aechmea mariae-reginae* is trioecious, its three genders (= floral morphs) being male (= staminate), female (= pistillate) and hermaphroditic (= perfect flowered). Monoecism, the arrangement whereby the individual plant produces female and male flowers or combined perfect and unisexual types, has emerged in *Cryptanthus*. Both self-compatibility (= fruit set possible with self-pollen) and self-incompatibility are common, the incidence of the former probably being more frequent than the latter. Close relatives that more often differ by mating system than gender expression indicate that of the two options it's the former that's the more amenable to evolutionary change.

Most herbaceous perennials flower repeatedly so the low incidence of monocarpy among the bromeliads fits a global pattern. The family's far more common modular body design is especially well-suited to promote not only serial sexual but vegetative propagation (**Figure 4AA**). Sever the rhizomes that connect adjacent ramets, a natural eventuality for long-lived *Bromelia* spp. among others, and what results are populations of physiologically autonomous daughters that constitute clones (= genets). Keep in mind that vegetative and reproduction by seed yield different benefits, and for the former it's the preservation of tested genotypes. While the number of offspring tends to be modest the robustness of the individual progeny compared to that of an embryo inside a seed assures that among the advantages of asexuality is the holding of previously occupied territory. Gene flow and recombination and the colonization of new and re-colonization of formerly occupied sites are the primary sexually-obtained benefits that if absent would preclude adaptation and speciation (**Essays C, D**).

The occasional bromeliad reaps in combination some the benefits of sexual and asexual reproduction by ripening what appear to be seeds that contain clusters of parental cells (pseudo-embryos) instead of true embryos that by definition result from unions between sperm and eggs (**Figure 2D**). *Tillandsia intermedia* along with several more similarly epiphytic relatives engage in a practice that crudely parallels the above by generating fair sized plantlets on inflorescences whether or not capsules had developed there first. However, being aerial by habit the chances of post-dispersal success seem likely to be poor. The grass-like offshoots that develop around the bases of the young ramets of quite a few of the soft leaved tillandsioids (e.g., *Guzmania lingulata* var. *minor*) usually fail to be replaced later by one or more robust daughters located closer to the inflorescence. Axillary bud(s) destined to produce ramets usually remain dormant until the parent shoot ceases production of foliage in favor of a growth-terminating inflorescence (**Figure 4AA**).

The bromeliad fruit is either a capsule (dry walled, multi-seeded and dehiscent) or a berry (fleshy walled, indehiscent and multi-seeded). What's contained inside the former comes in three versions: naked, equipped with a small wing, or tuft of hairs or a more dispersal-enabling umbrella-shaped coma constructed of thin extensions of the seed coat (**Essay C; Figure 1C**). The more intriguing among the fruit-seed combinations are those that match identifiable groups of dispersers. The two most revealing among what may be many additional more subtle target-specific arrangements engage birds or bats. Both enclose seeds hard-coated enough to pass intact through a vertebrate gut. Qualities that distinguish members of the first category include small size (<2.0 cm), mostly white or blue and no perceptible odor. The second bat-favored product is larger, dull except for a coat of silvery trichomes and rotten smelling at ripeness. A third much smaller assemblage of berry-producers employ seeds possibly equipped with a diffusely organized minute edible appendages (= aril) that suggests tandem dispersal, first by a bird or mammal and then, following retrieval from feces, by arboreal nest-gardening ants.

Speaking of reproduction it's worth keeping in mind that it takes no more than an organism's presence for it to influence much of what transpires nearby and often well beyond. No individual can avoid all sorts of engagements because creatures whatever their identity or lifestyle depend for what they need on their surroundings—surroundings that include climate, resources, and beneficial and antagonistic agents. Being immobile it's especially important that a plant tune its performance, and some much more than others, to match its life-affecting circumstances some of which are biotic and others abiotic herbivores and soil type being respectively two familiar examples (**Essays C, I**). Think back to your high school biology textbook and recall how many lines were needed just to illustrate the interconnectedness of the participants in an ecosystem's food web.

Reproduction hands down ranks among the most illustrative of the stages of a plant's life cycle to illustrate the necessity of community-wide coordination because sexual success so often requires animal assistance and must occur when conditions favor seed set and development and then dispersal. Consider just pollination, a phenomenon that involves coordination with and competition for individual floral foragers and ultimately the maintenance of the populations of those same animals. Several co-occurring Costa Rican bromeliads, acting in concert with neighboring flora, flower on staggered schedules reportedly to sustain populations of shared pollen vectors. Cues available to mediate such arrangements range from the celestial to the onset and conclusion of wet and dry seasons. A consistent flowering schedule signals many a bromeliad's capacity to perceive day length (e.g., cultivated *Tillandsia xerographica* during September/October in northern Ohio; **Essay I**). On the other hand, the precipitous drops in temperature that cause certain tropical or-

chids to flower (e.g., *Sobralia* spp.) have yet to be reported for a bromeliad.

Ecology and importance in ecosystems

This brief profile opened with Bromeliaceae portrayed as modest in size yet exceptionally diverse by vegetative form, function and ecology with much of its membership adept at pursuing challenging lifestyles while anchored on substrates hostile to more conventionally adapted flora. Although adequate as a brief introduction it ignores the family's performance deficiencies several of which markedly constrain its ecological breath and geographic extent. This being said, the message of the coming Essays emphasizes the impressive—how so many of its members operate exceptionally well often dominating habitats and even qualifying as keystone elements in communities located high up in forest canopies, situated on sheer rock faces and rooted in arid soils. At the same time know that it is underrepresented if present at all in many widely occurring kinds of neotropical habitats.

It's definitely the absorbing trichome and leafy tank that allow so many species to deviate from their family's ancestral reliance on soil to live as epiphytes, users of inselbergs as exemplified by Brazil's Sugarloaf Mountain and as denizens of the barren rocky field habitats scattered across the geologically ancient Guayanan and Brazilian Shields. Terrestrials assigned to *Aechmea*, *Bromelia* and similarly vigorous clone-forming members of additional genera play key roles as colonizers/stabilizers in many coastal strand and dune formations across the Caribbean region south to Brazil's Restingas. *Tillandsia landbeckii* forms near monocultures in parts of Peru's hyper-arid Atacama Desert sustained exclusively, except during El Niño years, by coastal fogs. Elsewhere, especially deep inside dense evergreen forests and in wetlands, any bromeliads present seldom amount to more than minor players. Only the occasional *Puya* spp. and a few additional family members tolerate deep frost, clearly the most telling of the climatic constraints on family success.

Bromeliaceae wouldn't be nearly as appealing as a source of subjects for scientific inquiry if its members were wholly terrestrial because no other family barring Orchidaceae along with the ferns demonstrates as well how nonparasitic plants utilize other flora as substrates. Again thanks to the presence of phytotelms and absorbing trichomes for all but the ant-nest garden specialists and a few others, nothing restricts the aerial bromeliad's anchorage to some narrowly proscribed substrate. Where pluvial conditions prevail the arboreal species, along with abundant lichens and bryophytes, can burden canopies with metric tons of biomass per hectare. At the opposite extreme, hot dry woodlands from Mexico to Bolivia support extensive communities of grey tillandsias along with some equally xerophytic ferns. Spanish moss alone can exceed by volume of photosynthetic tissue that main-

tained by its oak and cypress hosts along the Gulf and south Atlantic coasts of the United States.

The atmospheric and *Tillandsia usneoides*, by shading and breaking branches can seriously debilitate a host, and *T. recurvata* hastens the demise of portions of the crowns of *Prosopis glandulosa* with its girdling wiry roots. Bromeliads equipped with tanks offer compensation by delivering positive services across densely colonized woodland ecosystems. Large individuals become biodiversity hot spots (**Essays B, F**), and along with the provision of high quality habitat comes another contribution in the form of up to thousands of liters/hectare of impounded water able to cool and humidify canopy air. Significant as well are the mantles of suspended humic soil created with the assistance of decomposers that feed on bromeliad litter and the contents of tanks. Absent these varied inputs faunal inventories would be shorter and include fewer of the invertebrates that create such bridge-works and in turn use them to travel between canopy and forest floor further blurring the physical separation of these adjacent living spaces. Much awaits discovery regarding the epiphytic bromeliads and not only about how they and their associated biota interact, but how they affect an ecosystem's mineral cycling, aggregate photosynthesis, and more.

Except for the most ornamental *Cryptanthus* spp. and *Orthophytum* spp. and a scattering of members of several additional genera, the terrestrial bromeliads take a horticultural back seat to the epiphytes and lithophytes hundreds of which are currently in cultivation. Part of the problem, for lack of a better descriptor, is ordinariness. Except for the presence of spines the bulk of the hechtias, dyckias and such, while vegetative, aren't particularly distinct from dry-land natives that represent *Agave*, *Aloe* and certain members of several additional morphologically comparable monocot genera. Worse yet only the most discerning of observers is apt to recognize in nature that a non-flowering *Cottendorfia* along with the other grass impersonators, or a *Greigia* whatever its growth stage, are even bromeliads! Compare this lack of distinction with the myriad shapes, textures and striking colors displayed

by so many of the tank-formers and atmospheric (e.g., **Figures 4B, 3D**).

The future of Bromeliaceae in commerce and nature

Weak barriers to gene exchange between species have long permitted breeders to combine through conventional hybridization many of the bromeliad's most desirable traits. *Ananas*, the most genetically engineered of the genera being the exception, much of the credit for what's been manipulated so far is owed amateurs. Manufactured hybrids abound a fair number of which involve parents assigned to different genera, but so far none to separate subfamilies. Given the rapid development of ever more refined technologies (e.g., CRISPR-type editing tools) bromeliad improvement will soon embrace new and exciting approaches. One that's sure to come line will involve genome modification beyond the usual additions and subtractions of individual genes, for example, up regulating those parts of genomes responsible for mediating the synthesis of desired pigments. Until then, cultivated stock will remain dominated by selected wild types and hybrids made the old-fashioned way.

What lies ahead for Bromeliaceae in nature? Most vulnerable to extinction will continue to be populations with the narrowest distributions the most threatened of which occupy only a single Guayanan tepui (e.g., many *Navia* spp.), a Brazilian inselberg (e.g., *Tillandsia neglecta*) or an isolated forest remnant. At the same time, it's hard to imagine Spanish moss ever experiencing anything much beyond local extirpations. Habitat loss and over-collecting currently head the list as most pervasive of the many threats, but climate change and the fertilizing effects of anthropogenic CO₂ and reactive nitrogen could well end up exacting even higher tolls if humans continue to vaporize fossil fuels at current to even greater rates (**Essay J**). In the final analysis, it's the family's epiphytes that stand the best chance of becoming leading botanical indicators of global change, but which ones if any will count among the earliest responders remains to be seen.

ESSAY A. WATER RELATIONS

It's obvious that it takes more than water to fabricate a plant's body, but what else is needed and how is it obtained and from where? Usually, the dozen plus essential so-called mineral nutrients (e.g., calcium, nitrogen and phosphorus) along with moisture enter the higher (= vascular) plant through its roots. Its aerial portion—the shoot—is dedicated instead to capturing the solar energy needed to convert CO₂ absorbed from the atmosphere plus water from the ground into the simple sugar glucose with molecular oxygen (O₂) as the companion product. As such, the green plants operate as autotrophs (= self-feeders) because unlike the heterotrophs (e.g., animals and fungi) their nutritional opposites, they literally build themselves from the just identified elemental substances instead of consuming ready made biomass.

More than half of Bromeliaceae secure water and mineral nutrients through organs other than roots and often from sources other than soil. The family's epiphytes and lithophytes (= plants that grow upon other plants and rocks respectively) draw from a variety of alternatives, but once again it's the quantity of available moisture and a plant's capacity to obtain and use it efficiently that determine success. Moreover, it's difficult to rely on appearance alone to discern the vital services provided by some of the most unconventional of a highly specialized bromeliad's attributes, the presence of dense layers of elaborate trichomes cloaking the so-called atmospheric-type species being a prime example. It's the peculiarity of these traits that bears witness to the evolutionary twists and turns that produced the novel lifestyles practiced by the most adaptively extreme of the bromeliads.

How plants that spend their lives on land keep themselves adequately hydrated involves two steps the first being the absorption of water from an external source and the second its judicious use of that resource in the pursuit of photosynthesis. Neither act occurs obstacle-free. What's listed below constitutes a series of facts provided as preparation for the following description of water management as it is performed by the bromeliads.

1. The moisture present in a plant's body represents only a minute fraction of what it had absorbed prior to the making of that measurement.
2. This reality pertains because little plant-consumed water becomes a constituent of the organic molecules (e.g., cellulose) that make up botanical-type biomass, i.e., a plant's body.
3. The absorbed moisture that doesn't end up used to produce a plant's body escapes as vapor back into the atmosphere and mostly through stomata that also allow CO₂ to enter to fuel photosynthesis (**Figure 2AA**).
4. Moisture expended in this manner equals transpiration and the price that a plant must pay to live on land.

5. Expending so much hard-won moisture to conduct photosynthesis is unavoidable because the diffusion gradients that cause CO₂ and water vapor to diffuse in and out respectively of a leaf favor water loss (**Figure 2AA**). Carbon dioxide moves less massively because its concentration in air is quite low (~0.03% by volume). By contrast, the air inside a leaf is routinely saturated with water vapor (relative humidity = 100%; water vapor deficit = 0), while the moisture deficit in air tends to be much higher.
6. Bromeliads cannot extract water from humid air not even the atmospheric types despite their possession of abundant absorbing trichomes. Moist air does slow transpiration and the more so the smaller its water vapor deficit.
7. Entries #4 and 5 explain why the cost in expended water of capturing CO₂ for photosynthesis is so steep and accordingly, why anything that reduces the transpiration ratio (= units of water expended per unit of dry matter produced) elevates a plant's water use efficiency thus reducing its demand, which ultimately heightens its drought tolerance.

The antecedents of Bromeliaceae were terrestrial (= soil rooted), and they likely exhibited form and function including the conduct of water relations (i.e., water management) much like what continues among many of its members that remain soil-dependent today. In other words, the family's ancestors much like a substantial portion of its modern species, were served by conventionally apportioned and developed and fully performing shoot and root systems.

During the past 15–20 million years, and especially through the most recent 2.6 millions of this number (= the Pleistocene Epoch), growing conditions across much of tropical America underwent substantial climate change. Adding to this widespread chaos was vigorous mountain building in what now is the area occupied by the northern Andean cordillera. Similar plant-altering disturbance prevailed within what today falls within the national boundaries of countries that include Brazil, Bolivia and Peru. Elements of a then younger Bromeliaceae responded with bursts of evolution and speciation some of which allowed certain of the family's lineages to enter old but formerly impenetrable and newly emergent habitats.

By what means did the elements just cited of pre-modern Bromeliaceae faced with rapidly changing circumstances including elevating topography deviate from what back then already were time tested genotypes and phenotypes, and why did only some of the family's lineages adopt life styles that hadn't existed before and then proceed to spawn hundreds of species? What we see today indicates that the lineages that met this challenge most successfully included the precursors of clades (= all of the species derived from a single ancestral lineage) identified by taxonomists as *Aechmea*, *Cryptanthus* and *Neoregelia*, the first and third genera broadly defined,

along with numerous additional taxa and core Tillandsioideae. Lineages that experienced less spectacular radiations or those characterized by more speciation than adaptive divergence include what today are exemplified by genera such as *Navia* and *Puya*.

One trait that contributed inordinately to the family's extraordinary ecological diversification is plain to see: architectural plasticity that arguably exceeds the norm set by the angiosperms overall. What had to exist beginning at least 15–20 million years ago was a genetic program—that portion of the genome that governs an organism's ontogeny (= development)—able to massively transform for certain of the family's early elements the basic monocot-type body plan (**Essay F**). It was this potential guided by Darwinian (= natural) selection that explains the emergence of leafy catchments (= phytotelms) and the functional refinements of the epidermal trichome to states that allowed shoots to replace roots for all of their usual services short of mechanical anchorage. All of this revolutionary change occurred while flowers, fruits and seeds remained comparably static.

Much adaptive fine-tuning followed replacement of the root system's traditional foraging role by a greatly elaborated shoot system. Today, semi-arid habitats and dry microsites in wetter locations through tropical America host tank-equipped family members (e.g., many *Billbergia* or *Aechmea* spp.) that feature narrow, steep sided phytotelmata (= a phytotelm with its contents) configured to retard evaporation and avoid sun scald (**Figure 3B**). Species that produce shallower, broader tanks (e.g., many *Vriesea* and *Neoregelia* spp.) inhabit humid woodlands that subject their aerial and terrestrial bromeliads to heavy rains of nutrient-containing litter and filtered sunlight that's most effectively intercepted by horizontally oriented thinner foliage. Still other species employ shoots adapted to secure mineral nutrients from captured prey and so on (e.g., **Figure 1B**).

Whether perfected beforehand or while absorptive duties were shifting from roots to impounding shoots, an up grading of the foliar trichome yielded the organ that's made possible the life form—the atmospheric type—that depending on the species remains unmatched in the family for stress-tolerance and architectural streamlining (**Essay H; Figure 2F**). The resulting capacity to operate minus a more typically developed root system frees up material resources for reallocation elsewhere, a condition that's most pronounced among the densely trichome-covered grey *Tillandsia* spp. (again the atmospheric bromeliads) some of which, if bearing needle-like foliage (e.g., *T. tectorum*), can survive largely on dew or cloud water. Today the bromeliad trichome occurs in many shapes and densities on foliage and varies from water repellent to hydrophilic, but to what benefit and for which species and under what conditions mostly awaits deeper inquiry (**Essay H; Figure 3AA**).

The vegetative body that served the antecedents of today's Bromeliaceae clearly had to undergo major reor-

ganization to deliver the most impressive of the family's modern eco-performances and lifestyles, but what goes on within? What about water management and photosynthesis? It's axiomatic that structure and function go hand in hand, that the two represent opposite sides of the same coin. Most assuredly, more than anatomical modifications and relocated functions decide how the least traditionally configured of the bromeliads reconcile their requirement for moisture with its availability under so many, often demanding circumstances. Once again, we return to carbon-energy gain—to photosynthesis—the most fundamental and water-expensive of the tasks that the land-based plant must accomplish sustainably. So how does the acquisition of carbon and energy in the form of glucose vary to match so many different growing conditions?

The toughest of the challenges that a dry-growing plant (= xerophyte) faces boils down to its need to achieve a sustainable transpiration ratio, and the drier the environment the smaller this number must be. Compliance requires an array of traits that dictate how glucose is produced and when during the day-night cycle and sometimes also at what time of year (**Figure 1A**). As usual, nature is rife with exceptions, some of which are bromeliads. High water use efficiency is not the leading determinant of plant survival where profligate expenditures pose no problem, for instance for wetland flora. Most ill prepared for drought for this reason among the bromeliads are the *Pitcairnia* spp. that inhabit swift moving streams (the rheophytes) and a scattering of marsh-dwelling relatives (e.g., *Greigia* spp.). However, accomplishing acceptable rates of growth and reproduction within the limits imposed by a less than optimal water supply remains crucial for the vast majority of higher plants including all but a few bromeliads.

As already noted, photosynthesis is the process whereby plants use solar energy, CO₂ and water to manufacture glucose after which the carbon, hydrogen and oxygen atoms that make up this simple sugar plus some of the absorbed mineral nutrients end up chemically combined as plant-type biomass. It's the light required to accomplish this outcome that poses a problem because it's during the day when temperatures peak and relative humidity bottoms out that the atmosphere is best prepared to desiccate wet objects. Yet the transpiration ratios achieved by the bromeliads can be as low as 50 to more than 1000 to one. This greater than 20-fold range would be puzzling were it not for the fact that more than half of the family's members can fix CO₂ in total darkness via a second biochemical pathway into a second product that's not glucose. More precisely, the high performing species conduct CAM-type as opposed to the more primitive, single pathway-based C₃-type photosynthesis. CAM (= Crassulacean acid metabolism) is merely an augmented version of the more fundamental C₃ mechanism (**Figure 2A**).

Plants that perform C₃-type photosynthesis grow where moisture is plentiful at least during the growing season, and among the bromeliads this category includes

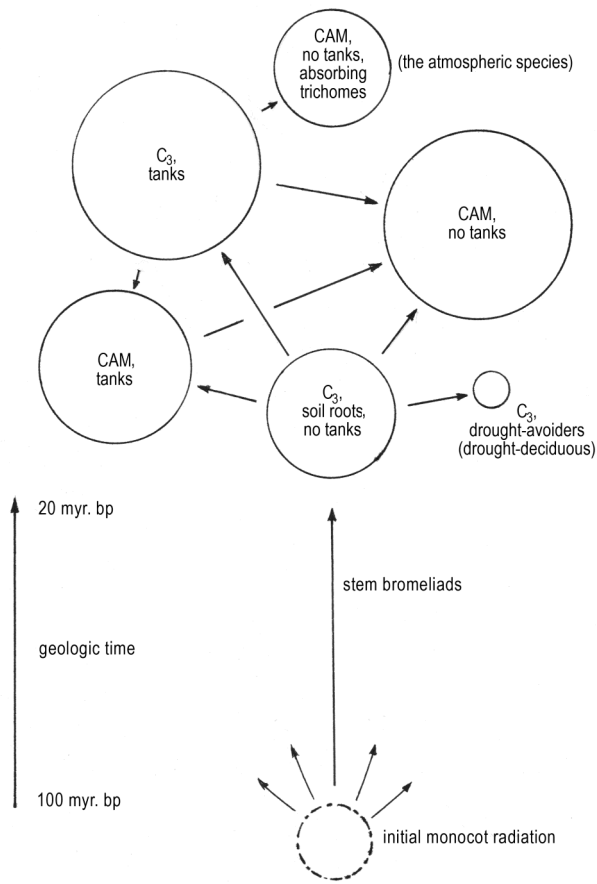


Figure 1A. How the membership of Bromeliaceae distributes among a series of categories that describe how water is obtained and used. Circle sizes approximate the portions of the family’s species that qualify for each designation and the arrows the evolutionary pathways followed as certain lineages evolved from one condition to another. Included are some of the traits that define the categories. A significant number of species manifest trait complexes that place them between categories.

the thin leafed, soil-rooted types that dominate genera such as *Cryptanthus*, *Fosterella* and *Pitcairnia*. Soft bodied, tank bearing members of subfamily Tillandsioideae that comprise *Catopsis*, *Guzmania* and most of *Vriesea* also rely on this biochemically less circuitous of the two food-making pathways. We already know that daytime is the least propitious interval during the diurnal (= 24 hr.) cycle to acquire CO₂ when the cost is denominated in units of expended (transpired) moisture. Accordingly, the C₃-type bromeliads experience relatively poor water use efficiencies as witnessed by transpiration ratios that fall near the upper end of the range cited above. It’s hard to imagine a stronger impetus for evolving a way to abandon this more ancient of these two ways of capturing CO₂. Why it remains so common is explained below.

Figure 3A illustrates the diurnal patterns traced by CO₂ and water vapor as these two gasses diffuse through stomata in and out respectively of the foliage of C₃-type and CAM-performing bromeliads. Note that transpiration

for the first subject begins to accelerate at dawn only to fall back to near zero around dusk while the course followed by CO₂ is the reverse mirroring daytime access to the solar energy required for the green cells within leaves to convert it directly into glucose (**Figure 2AA**). Some dark respired CO₂ continues to diffuse out through the night, but by day it, along with the CO₂ acquired from the atmosphere, ends up consumed by photosynthesis. Although the apertures (= stoma) of the stomata of C₃-type plants remain closed through the night minor leakage occurs allowing some additional water to be lost but far less than occurs by day.

The shapes of our C₃-type specimen’s gas exchange curves compared to those of a practitioner of CAM (**Figure 3A**) confirm that reversing the interval during which CO₂ is acquired from the atmosphere will improve (reduce) a transpiration ratio, i.e., increase water use efficiency (**Figure 3A**). The CAM-performing plant achieves this advantage by fixing CO₂ obtained from the atmosphere after the sun goes down. And this time the product, which is malic acid rather than glucose, must contain less chemical energy, i.e., must be energetically cheaper to make. Fortunately for the CAM-equipped individual, the CO₂ that gets fixed into this simple organic acid, a feat that obliges that it expend some of its energy reserves primarily that embodied in stored starch, can be regenerated later via a chemical breakdown process known as decarboxylation (**Figure 2A**). Because decarboxylation is light-induced it cannot take place before sunrise after which the retrieved CO₂ now trapped inside the leaf can be re-fixed, this time into glucose some of

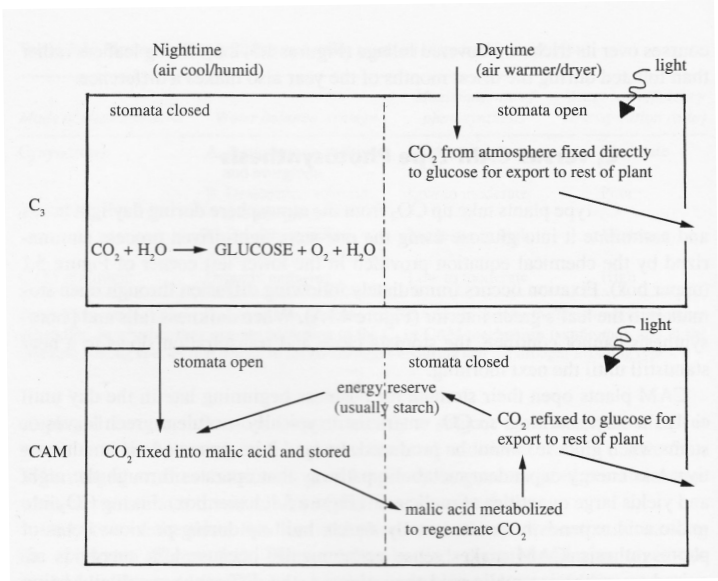


Figure 2A. The biochemistry of C₃ and CAM-type photosynthesis. Note that the CAM-performing bromeliad must expend some of its carbohydrate reserves (mostly starch) nightly to dark-fix CO₂ into malic acid. In essence, CAM amounts to a CO₂ capturing and concentrating mechanism that among additional unidentified benefits increases water use efficiency.

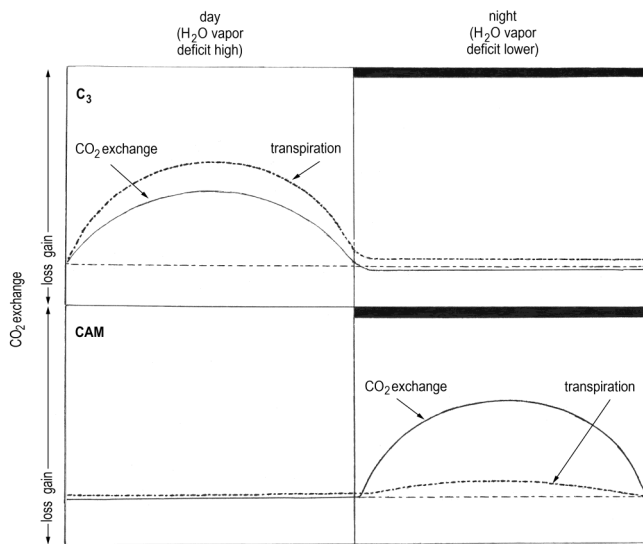


Figure 3A. Contrasting patterns of CO₂ and water vapor exchange during a 24-hour day-night (diurnal) cycle by C₃ and CAM-type bromeliads. The upper panel shows how the C₃-type subject expends a substantial amount of water over the course of a day as it gains carbon, while at night transpiration falls to near zero and some dark-respired CO₂ leaks through closed stomata. Most of the water expended by the CAM-equipped subject pictured in the lower panel occurs after dark when its stomata have opened to allow CO₂ to diffuse inward prior to its fixation into malic acid.

which is allocated for growth with enough held back to energize once more by drawing on stored reserves the synthesis of the next night's quota of malic acid.

The CAM-equipped bromeliads include within their relatively thick foliage abundant hydrenchyma tissue whose collapsible colorless cells store moisture far in excess of their owner's short term needs (**Figure 2AA**). During droughts what amounts to a hydric backup migrates as needed to keep adjacent more desiccation-sensitive photosynthetic tissue sufficiently supplied with moisture thereby prolonging the production of glucose beyond what otherwise would be possible. It's this relatively delicate green layer that sequesters and then decarboxylates the malic acid synthesized the previous night. In essence, it is this highly active tissue having daytime access behind closed stomata to a rich supply of CO₂ generated by the disassembling a reservoir of dark-fixed malic acid that allows the CAM-type bromeliad to conduct photosynthesis with minimal transpiration, but not as it turns out without also incurring a significant performance tradeoff.

A CAM-equipped bromeliad's ability to store malic acid is modest and accordingly so is its capacity to generate enough glucose to match the rate of growth achievable by a C₃-type competitor assuming that both subjects are experiencing optimum growing conditions. A typical grey *Tillandsia* demonstrates this built-in constraint by requir-

ing multiple years to progress from seed to first flowering, quite a long time compared, for example, to a typical *Pitcairnia* sp. Things could be worse however: slow growth mandated by CAM-type photosynthesis and associated anatomical traits that limit light and CO₂ capture would constitute a serious liability were its practitioner's welfare more dependent on competitive prowess than capacity to tolerate drought.

Figure 1A shows how the bromeliads distribute among categories based on how moisture is obtained, retained and ultimately expended. Drought-avoiding, a label articulated more precisely as drought-deciduous, describes family members that dodge injurious desiccation by eliminating transpiration hence photosynthesis while it's least sustainable until humid weather returns. The few bromeliads that employ this strategy (e.g., *Pitcairnia heterophylla*) do so by shedding their desiccation-vulnerable C₃-type performing foliage before dry weather can inflict a lethal water deficit. It's a tactic that requires the ability to anticipate seasonal change as described in **Essay I**, coupled with foliage productive enough to meet a plant's needs for an entire year during a wet season that may extend less than half as long.

The drought-enduring bromeliads, unlike the drought-avoiding kind, conduct net photosynthesis through all but the most prolonged bouts of rain-deficient weather. When dehydration does exceed a certain threshold the most proficient practitioners lapse into a kind of quiescence as standard CAM-type photosynthesis gives way to a related non-growth-sustaining mode of CO₂ fixation known as CAM-idling. Glucose production continues, but at a rate adequate only to recycle respired CO₂ within what now are leaves continuously buttoned up until precipitation returns to eliminate a moisture deficit and allow stomata to resume their pre-stress regulation of gas exchange. CAM-idling is what it sounds like, a way to keep not an engine barely running to save fuel until more power is needed, but a mechanism that keeps a plant physiologically prepared to return to business as usual when enough water again becomes available to support net photosynthesis.

Figure 1A points out that a majority of the bromeliads are either drought-enduring CAM-equipped xerophytes or mesophytes, meaning in this second instance relatively profligate water users (C₃-types). The latter category likely includes the family's recent ancestors as well as many of the extant (= living) species deemed most primitive according to the DNA-based phylogeny presented in **Figure 1AA**. Even so, C₃-type photosynthesis turns out to be sustainable in many moderately arid habitats where enough precipitation occurs to keep a leafy reservoir (= tank) at least partially filled through enough months of the year. Complicating this picture still further, quite a few species fall between the categories arrayed in **Figure 1A**. *Guzmania monostachia*, for example, switches between C₃ and CAM-type photosynthesis depending on the severity of the experienced water deficit (**Essay F**).

Ongoing investigations of *Guzmania monostachia* indicate that several aspects of its leaf anatomy contribute in previously unrecognized ways to its inordinate capacity to adjust to the steep fluctuations in light intensity and humidity that characterize hyper-seasonal tropical climates. Some of the traits responsible for this exceptional performance reside in the mesophyll, the tissue located between the parallel veins that run the length of a leaf's blade. They act by heightening a subject's capacity to rehydrate rapidly and maintain intact (prevent cavitation) the columns of water that flow through the xylem's conduits (= vessels) that occupy about half of each vein (**Figures 2AA, 7F; Males 2017; Males and Griffiths 2017; North et al. 2015, 2019**). It also appears that moisture flows outside as well as within vessels.

Miniaturization may explain why at least one diminutive bromeliad transports water in a way that's distinct from what most of the higher plants do being more like that performed of necessity by certain mosses owing to their lack of xylem vascular systems. Covered instead with hydrophilic epidermal trichomes and cup shaped leaf-like enations water readily flows by capillarity across all surfaces hydrating the entire gametophyte—the structurally more elaborate stage of the two-staged bryophyte life cycle (**Essay D**). In similar fashion, point-applied moisture spreads across densely trichome-covered *Tillandsia usneoides* shoots and much faster than were it moving within stems and foliage (**Herppich et al. 2018**). Could it be that the xylem tissue that serves one of the most anatomically reduced atmospheric bromeliads consists largely or entirely of vestigial vessels (**Essay H; Figure 2H**)?

Attributes that include how densely trichomes invest foliage and their characteristics, mode of carbon gain, degree of succulence and a couple of less visible traits

that concern water relations don't always indicate where a particular bromeliad lives or its life history strategy. Both the epiphytes and lithophytes include C₃ and CAM-equipped members of Tillandsioideae, and much of subfamily Bromelioideae practice some degree of CAM irrespective of substrate. Variety along these same lines applies for the phytotelm-equipped shoot. Circuitous evolutionary histories marked by shifting circumstances, particularly climate experienced, must account to some extent for these inconsistencies. Absent more definitive information, the best criterion for estimating a bromeliad's requirement for moisture is its gross anatomy, specifically, how xeromorphic (= adapted to store and retain excess moisture) is its foliage.

Too little space has been devoted to this first essay to cover all that's worth knowing about how the bromeliads conduct photosynthesis and obtain and use water. Little or no mention was made of several phenomena such as the fact that too much moisture kills subjects that feature dense investments of foliar trichomes (**Essay H; Figure 4F**). The same applies even more for the intricacies of carbon gain. To what degree, for example, are certain of the family's C₃-type species given their mesophytic nature, prepared by how their stomata perform to prioritize water conservation overgrowth? What about the CAM-conducting species? Finally, there's an especially glaring gap when it comes to the most compelling issue of all: how are the wild-growing bromeliads responding to global change? All we can do at this point is wait and see (**Essay J**). In the meantime, rest assured that mastery of the information presented in this narrative better prepares its consumers to grow bromeliads successfully as well as tackle the remainder of this special issue of *Selbyana*.

ESSAY B. BROMELIAD NUTRITION

Many years ago, while I was teaching an introductory biology course that included a fair dose of botany, one of my students expressed a negative sentiment loud enough for virtually everyone nearby to hear. “Plants yuck” he almost shouted probably prompted by what struck him as yet another wasted 50 minutes. I wondered then and occasionally still do how an undergraduate bent on earning a liberal arts degree could so thoughtlessly disparage the energizer of our planet’s bio-support system. More to the point, how could anyone be less than awed by the twin realities that it’s photosynthesis that ultimately sustains *Homo sapiens* and that plants produce more chemicals useful to humans than all of Earth’s other creatures combined? Most amazing of all both feats are accomplished using nothing more than sunlight, CO₂, water and a handful of so-called mineral nutrients (**Essay A**)!

Plants are autotrophs (= self-feeders) in the sense that they literally manufacture their own bodies using only the sun’s electromagnetic emissions, CO₂ and water plus the modest subset of chemical elements alluded to above. The nutritionally less competent heterotrophs—the animals, fungi, and a large majority of the microbes—do the reverse. Rather than producing cells, tissues and organs from scratch they break down (= mineralize) pre-existing biomass and use the products that are the same as those that the autotrophs use to make their bodies. It’s the repeated building and tearing down accomplished by these opposing modes of nutrition that keeps in circulation for repeated reuse nitrogen and phosphorus and the other dozen or so mineral nutrients. In the final analysis, what’s going on here boils down to a series of sun-driven cycles one for each of the substances essential for life.

The fact that biomass contains chemical elements beyond the carbon, hydrogen and oxygen atoms present in CO₂ and water confirms that autotrophy as practiced by plants involves more than photosynthesis. Nitrogen, for example, is a routine constituent of protein and DNA contains phosphorus as well. The light-harvesting capacity of a chlorophyll molecule requires the presence of a chemically bound magnesium atom and so on. These additional elements end up in biomass because plants not only fix CO₂ into the simple sugar glucose using sun-delivered energy, but they also accumulate and build into their bodies the afore mentioned essential mineral nutrients. Mineral nutrition, as this dimension of autotrophy is known, involves some of the most under appreciation of botanical adaptations. It’s the unusual twists and turns that this process follows as it occurs among the bromeliads that this second Essay is all about.

The bipartite body possessed by most of the land dwelling flora has long been thoroughly tested having been in service for more than 400 million years (**Essay F**; **Figure 1F**). It consists of a root system dedicated to the securement of moisture and mineral nutrients, usually

from the ground, and an aerial portion—the shoot system—tasked with capturing CO₂ and sunlight as its contribution to autotrophy. About half of the bromeliads remain wedded to this historic, anatomically enforced division of labor so for their kind it’s business as usual regarding the source of the mineral nutrients and how they are secured. Major departures from this ancient arrangement characterize the rest of Bromeliaceae, and for these species deviations from the conventional determine from where nutrients come from and whether other organisms assist in their acquisition and processing.

Possession of a water-filled cavity, or what to a biologist is a phytotelm, explains how much of the membership of our featured family has succeeded in colonizing so many kinds of soil-free habitats (**Figure 2AA**). Even so many facts about the leafy bromeliad tank await discovery, for example, where geographically, how long ago and in response to what evolutionary incentives did this multi-purposed device make its debut (**Essay G**). Was its presence a precondition for accommodating challenging substrates (e.g., the face of a rocky cliff), or did it evolve after the family’s penetration of living spaces particularly well suited to exploit its adaptive potential (e.g., the forest canopy)? Were the habitats where bromeliads reign supreme today relatively vacant prior to colonization by the family’s most specialized members, a category that includes those equipped with phytotelms?

DNA reveals that multiple independent emergences explain why multiple bromeliad lineages employ the same cistern-like device to collect phytomass (= plant biomass), particularly litter (= plant debris), and nurture the symbiotic organisms needed to liberate some of its nutrient content for use by the hosting plant (**Figures 5AA, 6F**). This singularly moist chamber with its permeable walls is analogous to a botanical stomach, but to operate in lieu of roots embedded in soil under so many different circumstances requires the variety illustrated in **Figure 1B**. Today, well over one thousand species rely on phytotelmata (= a phytotelm plus its contents) as a primary source of mineral nutrients and water. Much of the architectural nuance and foliar ornamentation displayed in **Figures 2B–6B** probably represent finely tuned adaptations.

At this point it’s not possible to say whether the tank shoot was adopted to improve water relations or extract nutrients from impounded debris or both, but subsequent modifications involving leaf color, texture, shape and size expanded its utility. A lax, flat rosette comprised of broad leaves, for example, is well suited to harvest shade light, whereas greater exposure and drier air call for something more funnel-shaped that while better equipped to reduce evaporation from an exposed reservoir the price paid is a less effective device for intercepting falling foliage (**Figures 1B, 3B**). Body waste from frogs that spend daytime hours hunkered down in tall slender bromeliad shoots may help lessen this tradeoff’s impact. Further inquiry also might reveal whether the ornamentations that

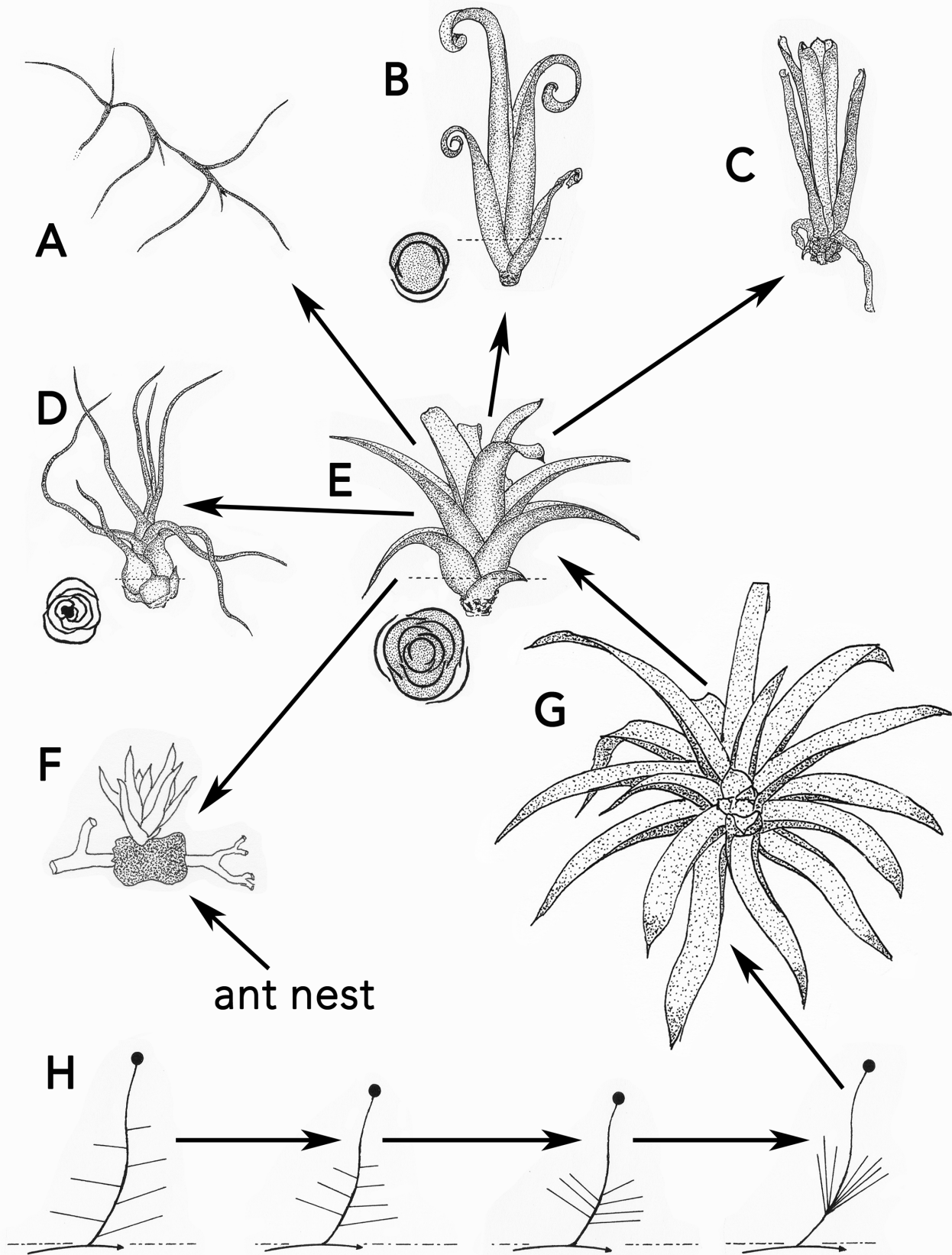


Figure 1B: The evolution of the tank-equipped bromeliad shoot. **A.** *Tillandsia usneoides*, the ultimate streamlined product among the progressively stripped-down atmospheric species. **B.** Tank shoot architecture suitable for operation in arid, sun drenched microsites along with a cross section showing the deep central tank. **C.** Carnivorous *Brocchinia reducta*. **D.** Ant-house *Tillandsia bulbosa* sectioned to show the enclosed leaf base chambers. **E.** The generalized tank along with a cross section revealing multiple, shallow leaf base chambers. **F.** An ant-garden bromeliad rooted in a carton nest. **G.** Proto-tank architecture. **H.** The origin of the tank shoot.

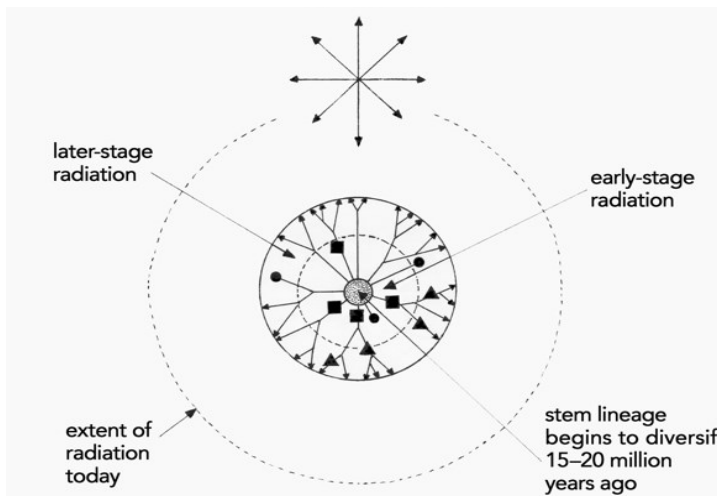


Figure 2B: A hypothetical depiction of how Bromeliaceae, beginning 15-20 million years ago, experienced a proliferation of lineages and where and when during this event the tank shoot emerged (squares = early emergences; triangles = somewhat later emergences). Three of the early lineages (circles) had short lives while eight others survived to produce daughter lineages. Taken separately the four early and four somewhat delayed tank origins exemplify parallel evolution (a type of homoplasy in the parlance of the taxonomist; **Figure 5AA**), but the four early origins better identify the stem (= ancestral) group as predisposed to evolve tanks. Also, the earlier the tank-equipped shoot emerged the more extensive its occurrence would be across the family's current membership (not shown).

mark the foliage of so many of the phytotelm-equipped species help recruit beneficial tank-dwellers or conceal their presence from predators thereafter (**Figure 4B**).

Additional inputs enter the bromeliad phytotelm as nitrogen fixed from the atmosphere by resident microbes, particularly cyanobacteria, in excretions from those mentioned plant-using vertebrates, and not just frogs, and from invertebrates that run the gamut behavior-wise from the occasional tank visitor to those that live and breed nowhere else (**Essay F**). The more sporadic of the arrivals include nutrient-rich items such as the failed eggs of frogs and what's left unconsumed by carnivorous critters such as centipedes and spiders. In what chemical forms and in which combinations nutrients arrive depend as well on site-specific circumstances. Myriad variables, for instance, whether a particular subject is anchored below, within or at the top of a tree and how favored by the local tank users make differences.

It's the bromeliads that feed on animals that come closest to being botanical heterotrophs. Just three species, two assigned to genus *Brocchinia* and a third to *Catopsis*, earn Bromeliaceae its place among the handful of families that make up the inventory of carnivorous angiosperms (**Figures 1B, 6B, 4G**). Realization that a plant can consume animals rather than the other way around goes back more than two centuries, but more recently have *Catopsis berteroniana* and the two brocchinias been recognized as practitioners of this oddly mixed nutrition no doubt be-

cause none of the trio is as conspicuously prey-use adapted as the bladderworts, pitcher plants, and sundews and especially the Venus' flytrap the most spectacular of all of the photosynthetic predators. Even so, *Brocchinia reducta* is worth highlighting if only because it alone among the meat-eating bromeliads emits from its tank-shoot a floral-like fragrance that's especially alluring to ants the most abundant of the kinds of prey that share its habitats.

All three carnivorous Bromeliaceae stand apart from their fully autotrophic relatives by featuring unusually yellow tank-forming foliage bearing well developed powdery cuticles (**Figure 6B**). Not only do these deposits announce a peculiar kind of nutrition they support its operation in two ways. As a waxy lubricant, they prevent hapless animals from ascending the steep sides of tanks much like the stiff backward oriented hairs foil the victims of certain pitcher plants. Struggling prey eventually drown soon to be consumed by a host of invertebrate scavengers and microbes. Unlike the individual pitcher type leaf the entire phytotelm functions as a deadfall trap although the precipitation that collects inside lacks the plant-produced enzymes that the members of certain other families (e.g., Nepenthaceae) depend upon to mineralize their catch.

Catopsis berteroniana alone receives the second manner of assistance this time owing to the optical properties of its cuticle. Sunlight, particularly its ultraviolet component, by reflecting off the same slippery white surfaces that deny victims sound footing reduces the shoot's visibility thereby increasing the likelihood that an insect passing within range will collide with an object that it cannot see, tumble into its tank only to tire while attempting to escape eventually drowning and ending up reduced to its elemental components by an array of scavenging heterotrophs—organisms that being aquatic escape the depredations of their botanical host. Visual deception is a particularly convenient tactic for *C. berteroniana*. Requiring high exposure to drive enough photosynthesis, it tends to grow silhouetted against open sky where flying insects, many of which instinctively navigate toward skylight to avoid obstructions, are prone to bash into propitiously obscured *Catopsis* shoots.

The two brocchinias and *Catopsis berteroniana* share a third trait that's got nothing to do with slippery light reflecting cuticles, and it suggests why their peculiar mode of nutrition came about. It's nutritional insufficiency. Being an epiphyte that requires high exposure plausibly explains why *C. berteroniana* has switched from being vegetarian to omnivorous. Ancient soils long depleted of much of their stores of phosphorus, potassium and several additional key mineral nutrients may have favored the same outcome for the Guayana Highland endemics *Brocchinia hectioides* and *B. reducta*. Members of three additional families of prey-consuming plants occur alongside the brocchinias bolstering the argument that carnivory grants significant botanical benefit where conventionally sourced nutrients are scarce. *Catopsis berteroni-*



Figure 3B: A tank shoot configured for service in arid sunny microsites illustrated by *Aechmea bracteata*, with *Tillandsia fasciculata* in the background. Photograph by Ella Baron.

ana comes off as somewhat more primitively equipped than its two terrestrial relatives to rely on meat diet perhaps because being an epiphyte, even a high light demanding type, provides at least some access to litter.

Neotropical ants, being abundant and diverse by where and how they nest and behave, it's not surprising that numerous arboreal types interact to mutual advantage with a fair number of bromeliads. These so-called myrmecotrophic (= ant-fed) family members manipulate their zoological benefactors in two ways, one of which results in ant-garden and the other ant-house mediated plant nutrition (**Figures 1B, 5B**). The species that make up category one root exclusively in carton, a manufactured composite that certain arboreal ants use to build their aerial nests and covered runways. Dispersal from old to developing gardens depends on pheromone-laced seeds that worker ants obligingly employ as construction material that upon germination begin reinforcing with roots whatever has been built. This first arrangement becomes even more powerfully mutualistic when the more aggressive of the ants deter intruders including reckless biologists. To the participating bromeliad's detriment, among the protected biota are pastured ant food-providing aphids and scale insects.

A much larger assemblage of ants, along with a bevy of arthropods that includes cockroaches, earwigs, and termites, favor the dead and moribund foliage that surrounds the more centrally located, younger water-holding leaves of the litter-impounding bromeliads. Species that offer the best of the more enclosed cavities available for nest establishment include *Brocchinia acuminata* and *Aechmea brassicioides*. *Tillandsia caput-medusae*—a signature ant-house type—rewards its six legged, occupants with what amount to series of internalized swollen leaf axils, each liberally lined with trichomes capable of absorbing nutrients provided experimentally as if delivered by ants (**Figure 5B**). To have ant-house providers in three sub-families within Bromeliaceae further supports the existence of a family-wide propensity to adopt unconventional modes of mineral nutrition.

Being an atmospheric-type bromeliad, an even more specialized condition, is to be able to subsist entirely on nutrients delivered in precipitation, aerosols, and airborne particulates. *Tillandsia recurvata* satisfies this criterion in spades where it thrives on telephone wires suspended beneath unobstructed sky. To perform so well on such meager fare is attributable to three traits: capacity to scavenge minerals from hyper-dilute solutions, growth down-



Figure 4B. *Vriesea splendens* displaying ornamented foliage.



Figure 5B. Ant-house *Tillandsia caput-medusae* complete with ants.

regulated to lower nutritional demand and a body configured to deliver extraordinary nutrient-use economy attributable mostly to a substantially reduced root system (**Essays F, H**). Sluggish growth is all but universal among perennials adapted to impoverished habitats, but not the other two attributes. Moreover, it's the atmospheric bromeliads that demonstrate so persuasively how foliage bearing multi-functioning epidermal trichomes can shape a land plant's ecology and how it makes its living.

Subfamily Tillandsioideae demonstrates how, by way of a Darwinian mechanism known as neoteny, tank-mediated gave rise to atmospheric type nutrition—easily the family's most bizarre response to stringent growing conditions. Thin broad leaves bearing widely scattered trichomes, a capacious tank, a moderately developed root system and relatively robust growth were the order of the day when this evolutionary progression began. What ensued required a genetically based developmental program amenable to natural selection such that certain juvenile characteristics possessed by ancestors could be retained in the adult stages of descendants (**Essay F**). Traits that emerged during this process include the dramatically reduced root system, thicker foliage densely covered with trichomes and no tank. Invisible, but no less requisite for atmospheric-type performance, was the replacement of C₃ by CAM-type photosynthesis (**but see Essay H**).

It's likely that the material economy gained by downsizing the root system comes at a cost, but if so then what is it? Leafy tanks and absorbing trichomes secure most or all of the nutrients and water needed by the phytelium-producing and the atmospheric type bromeliads

respectively, but does what remains of a diminished root system still benefit its owner in unrecognized ways? Fully developed this organ system performs vital tasks in addition to anchorage and absorption, the synthesis of hormones and the harboring of useful fungi being two examples. So how do the most specialized of the atmospheric (e.g., Spanish moss) compensate for near complete abandonment of half of the original land plant body? Have all of the responsibilities usually met by roots become those of the shoot or have one or more been eliminated (**Essay F**)?

Turning to a related subject, Bromeliaceae along with numerous other flowering plant families follows a botanical theme although it's not among the most pronounced. More exemplary are the grasses (Poaceae) most of which share the same body plan, flower and fruit type, and nearly all depend on wind for pollination. What's more, most of the communities dominated by such plants are short statured and only modestly biodiverse. Most members of the cabbage family (Brassicaceae) lack nutrition-enhancing mycorrhizas and are short-lived herbs that bear four-parted, insect pollinated flowers that yield an equally invariant capsular fruit filled with small naked seeds. Virtually all the species that comprise Fagaceae—the beeches, chestnuts and oaks—are heavy seeded, dense-wooded long-lived trees and shrubs most of which are wind pollinated and harbor a distinct type of mycorrhiza. While it's true that the bromeliads over-occur where drought and nutritional stresses are pronounced, they meet both challenges in ways as varied as their body plans, lifestyle, and source of mineral nutrients.

What accounts for a family's botanical theme in the first place? DNA is yielding ever more complete phylogenetic trees for the higher plants including Bromeliaceae, and pursuing this initiative further is eminently desirable. No one committed to botanical science is going to question the value of knowing the evolutionary relationships among species, genera and so on. But there are many additional different kinds of discovery possible from such efforts and what's already known is helping to uncover the nature and origins of the traits that underlie family themes. With luck future inquiry and creative techniques will reveal how pervasive among the lineages that led to modern Bromeliaceae was the tendency to evolve leafy tanks and nutrient and water absorbing trichomes. And don't forget about timing: were such potentials realized before, during or after the family began its on-going mega-radiation, and what was it that set this spectacular expansion in motion (**Figure 2B**)?

What we need now are redoubled efforts to discover how the bromeliad's exceptional ecological, structural and functional diversity came about and why here instead of in other monocot families. Why have tanks and trichomes so powerfully shaped so many aspects of bromeliad ecology when the same hasn't happened for taxa with similarly equipped members such as Asteliaceae and

Figure 6B. Carnivorous *Catopsis berteroniana*. Photograph by Bruce Holst.



BENZING: ESSAY B. BROMELIAD NUTRITION

Commelinaceae? In neither instance are these traits associated with as much speciation or as many life history strategies. Only a handful of the included species possess both devices, and few grow as epiphytes or lithophytes. These meager statistics pale compared to the number of bromeliads that either bear tanks, or as atmospheric, evolved from ancestors that did. Perhaps too little time

has passed, or natural selection hasn't been strong enough to foster similar outcomes elsewhere. Clearly, it's going to take ecologists, geneticists and physiologists as well as taxonomists working in concert to reconstruct a truly comprehensive evolutionary history of Bromeliaceae. But let's face it, isn't this systematic botany's ultimate goal?

**ESSAY C. HOW BROMELIADS
COPE WITH IMMOBILITY**

As children and perhaps even for decades thereafter many of us watched a popular TV show that featured a frog famous for his incessant complaining about being green. While a talking amphibian can disparage cost-free its color for a plant to do the same would be nothing short of ridiculous. But what if the trait at issue had been mobility rather than pigmentation? Having roots rather than legs means no way to hide or choose one's neighbors and certainly no opportunity to achieve Kermit's celebrity. And what about needing the help of strangers to reproduce? Finally, think about how reliance on photosynthesis and soil rather than bugs for nutrition mandates spending a lifetime in the same place fated to endure foul weather and assault by any pathogen or predator that happens to come your way.

Bromeliads, despite their immobility, still manage to exert considerable influence over who mates with whom

and to a lesser extent where their offspring grow up. What grants this control are fragrances, food rewards and timing along with flower and fruit shape, size and color. It's a dizzyingly complicated business in which closely related populations often utilize different agents (e.g., hummingbirds pollinate much of subgenus *Tillandsia* versus bats, hummingbirds and insects for the watch spring billbergias; **Figure 3Dabc**). Clearly, the traits that make up the pollination and to a lesser extent, the seed dispersal syndromes are numerous and varied and the organs involved (e.g., petals versus sepals) have evolved at different rates as Bromeliaceae underwent its spectacular adaptive radiation (**Table 2D**). Interestingly, not one family member is wind pollinated although seed dispersal is another matter (**Figure 1C**).

Bromeliads also employ a variety of mating systems and gender expressions to influence how the genes contained in sperm combine with those in eggs (**Figure 2D**). Except when the subject is a sterile hybrid, self-incompatibility likely explains why hand-pollinated flow-

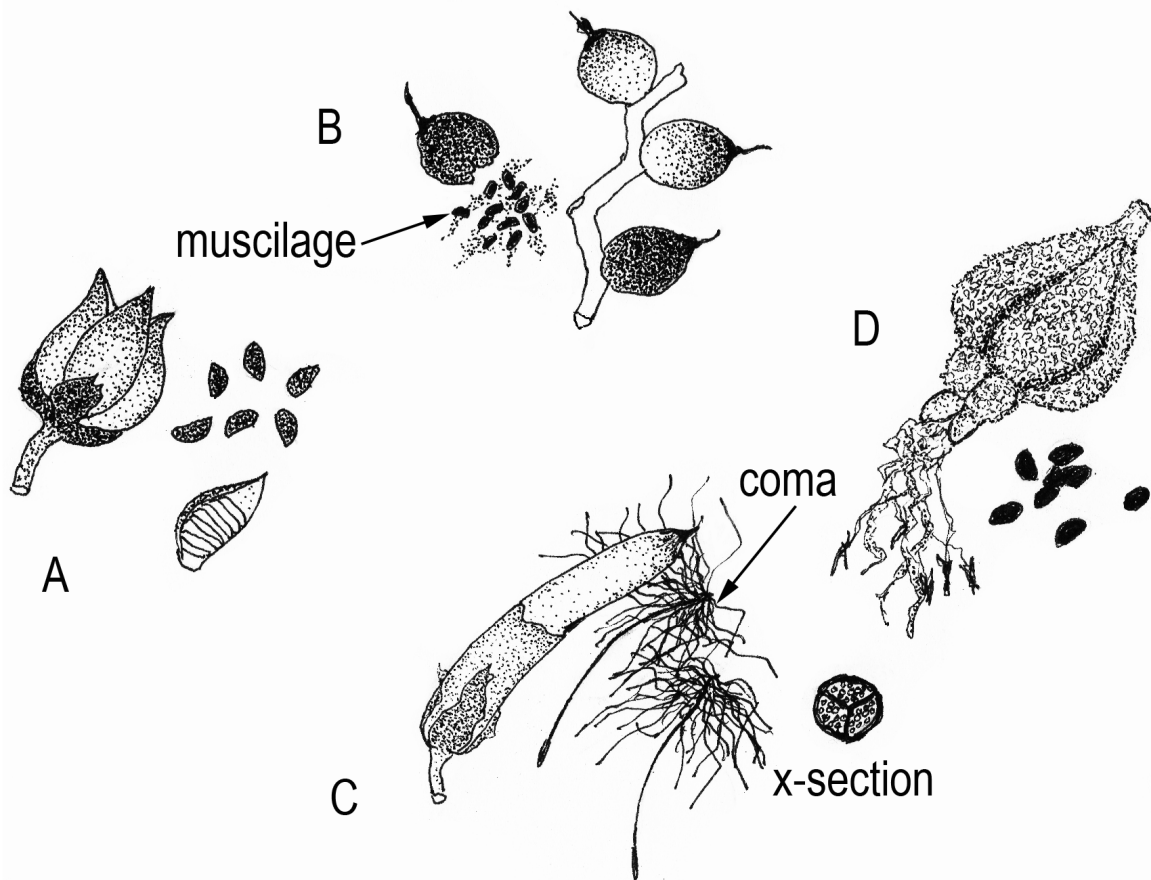


Figure 1C: Fruits and seeds of four bromeliads. **A.** Dehiscent capsule of *Dyckia* sp., a pitcairnioid, showing dry seeds that lack well developed appendages. **B.** Berries and extruded seeds of *Aechmea* sp. **C.** Wind-dispersed seeds and whole and x-sectioned capsules of *Guzmania monostachia*, a tillandsioid. **D.** Berry and seeds of *Billbergia* sp. None are drawn to scale.

ers fail to set fruit, a condition that all too often applies for the most popular of cultivated stock (e.g., *Aechmea fasciata*). Less common are the autogamous species, the most extreme versions (e.g., *Aechmea bracteata*) of which set unassisted just about every potential fruit following displays of numerous small non-showy blossoms. Dioecism (= separate male and female plants) also mandates outcrossing (= allogamy) throughout *Hechtia* and for scattered members of additional genera including *Catopsis* where geographically distinct dioecious and bisexual populations can occur within the same species (e.g., *C. nutans*). Consult the introduction and **Essay D; Figure 2D** for a fuller description of how the bromeliads exchange and recombine genes.

Bromeliaceae is endowed with a fairly extensive array of fruit and seed types, and member species employ a mixture of animate and inanimate agents to disperse young. The family's most primitive lineages (e.g., *Brocchinia*) produce capsules (= dry walled, many seeded, dehisce when mature) whose contents are at best only modestly suited for long distance travel being naked or bearing no more than rudimentary wings or tufts of hairs (**Figure 1C**). Members of capsule-producing subfamily Tillandsioideae (= the tillandsioids) do better, their minute wind-delivered seeds being equipped with an elaborate buoyancy-enhancing coma (**Figure 1C**). It's within subfamily Bromelioideae (= the bromelioids) that fruits and seeds deviate most from the family's capsular prototype and because animals provide carriage, this is where parents enjoy the greatest navigational control.

The berries (= fleshy walled, many seeded, indehiscent) of Bromeliaceae come in multiple colors, shapes, and sizes with perceptible odors being uncommon. The attracted frugivores (= fruit eating animals) receive for their service rewards that take the form of carbohydrates rather than lipids or protein. Bright pigments, modest size and the absence of fragrance identify birds as the targeted carriers for hundreds of species (**Figure 1C**). Fruits that contain easily extruded mucilage-covered seeds are especially effective for the epiphytes as they encourage bill wiping against rough bark. Passage through a disperser's gut is another mechanism, one that requires seeds that bear hard coats. Berries ripened by some of the bat-serviced bromeliads are much larger, less colorful and at maturity notably odiferous (**Figure 1C**). Those of *Billbergia robert-readii*, among others in this largely South American genus, are clothed in dense layers of light reflecting trichomes that probably help guide nighttime foragers.

A half dozen or so of the aerial bromelioids (e.g., *Aechmea mertensii*) notable for their unerring association with an ant-produced composite called carton, manage the required narrowly targeted dispersal via a complicated mutualism with the six-legged manufacturers of this soil-substitute. Several species of tree dwelling ants play their part by collecting the seeds of these finicky epiphytes, seeds that by releasing pheromone-like chemicals if not

the actual agents themselves induce the required ant performance. It's a response that assures that the seeds in question end up as ant-cultivated flora whose root systems return the favor by reinforcing otherwise more fragile nests and covered runways. Tandem dispersal is yet another ant-assisted strategy. Frugivores act first by consuming berries without swallowing all of the seeds some of which end up bill-wiped on bark, while others appear later in feces but in both cases with some still adhering flesh. Ants do their part by collecting and moving seeds undamaged by either action.

It shouldn't come as a surprise that a subset of bromeliads has adopted sure-fire ways to access ant carton because as rooting media go it ranks among the highest in quality of those available in the canopies of wet, low elevation neotropical forests. Other animals provide similar although less defined substrates as exemplified by the *Billbergia* spp. that favor knotholes some rendered more nutrient-rich owing to their daytime use as refuges for fruit bats. An historical landmark that isn't as easily assessed is what prompted the family's divergence some 15–20 million years ago from its presumed prototypical capsule type fruit, an arrangement that continues to serve with various modifications the memberships of seven of the eight bromeliad subfamilies (**Figure 1C**). And why as well has wind carriage reached its most refined state in Tillandsioideae one of the three most species-rich subfamilies? Likewise, what explains the transition to berries in Bromelioideae? Did these different modes of dispersal emerge in response to different selective pressures, i.e., growing conditions, or simply by chance?

How does animal versus wind-mediated seed dispersal compare on a cost versus benefit basis? Does anything else differentiate the practitioners of these strategies beyond the strategies themselves that might favor investments in the respective devices plus whatever more is necessary to operate in a particular mode? Bromeliads differentiated by reproductive strategy including fruit type frequently co-occur, root on the same kinds of substrates and perform similarly a variety of life's essential operations. A large majority of the bromelioids and tillandsioids conduct CAM-type photosynthesis or depend on leafy tanks (phytotelma) for nutrients and moisture leaving roots devoted primarily if not exclusively to mechanical securement. Could it be that seed dispersal by animals versus wind for this family costs about the same and simply represents another example of how for plants there's more than one way to accomplish the same outcome?

No population can persist once it no longer places at an acceptable rate enough offspring in enough safe sites, a safe site being a physical space that provides whatever is necessary to nurture the earliest most vulnerable of a plant's life cycle stages. For an epiphyte, a safe site may consist of a knothole, or a patch of lichen situated on an otherwise naked branch or for an arid-land terrestrial a square centimeter or two of shaded soil beneath a nurse

shrub. Liquid precipitation that lingers just a few hours longer or a temperature that's only a few degrees below what prevails a short distance away can spell the difference between seed and seedling success versus failure. Growing conditions will matter less as the colonist becomes more robust. As life progresses still further safe sites for other organisms may materialize as exemplified by the tank bromeliads that in their role as powerful eco-engineers become assembly points for what in due course become exceptionally bio-diverse micro-ecosystems (**Essay F; Figure 7F**).

Safe sites are user-defined, and a version that meets the needs of one species may do the same for one or more others with which its niche requirements overlap. Interspecific (= between members of different species) competition can be keen, and the availability of a specific kind of safe site can limit the sizes of populations as much as inadequate supplies of moisture or some key nutrient. Durability in addition to the usual chemical and physical properties further differentiate safe sites. A patch of bark, a crack in the face of a rocky cliff and a swatch of bare soil can emerge and disappear too quickly to serve any but the most short-cycled of flora. In effect, safe sites amount to moving targets. Spatial distribution is a third variable as depicted by the three patterns illustrated in **Figure 2C**. To qualify as a resource for a given species a safe site must accommodate certain of that population's

attributes of which seed longevity, germination requirements and mobility are among the most important.

If the relationship between safe site and dispersal mode remains a little hazy the following comparison should help clear things up. It also describes how for some plants time replaces physical mobility as a critical dimension of the process itself. Short-cycled annuals, those that competitively depress the yields of invaded row crops such as maize produce abundant, small long-lived naked seeds essential enabling traits for short cycled weeds (**Table II**). For a population of this description to persist where substrates are disturbed infrequently the longevity of its seeds and their requirement for germination will exceed in importance transportability. Such species as they must launch far more progeny through time than physical distance. Plants that require more time as perennials in turn require more stable living spaces. Their safe sites, often being widely scattered, makes for their kind long distance dispersal the more life sustaining of the two options. The bromeliads more closely adhere to the second than the first of these two dynamics.

Dispersal in time not only mandates that many of the seeds produced be buried they also must lie dormant a condition that enters them into what's known as a seed bank until cued by some disturbance-based stimulus to germinate as much as decades later (**Essay I**). That trigger—usually exposure—signals that the overburden is again disrupted and that access to the abundant sunlight that short cycled plants require is restored. No seed banks are known for the epiphytic or lithophytic bromeliads or would such an arrangement benefit them or any other perennials that grow on similarly impenetrable substrates. Why light induces the seeds of certain Bromeliaceae, some being epiphytes, to germinate is puzzling. Returning to dispersal through space, the seed rain illustrated by A in **Figure 3C** depicts a workable pattern when the vector is turbulent air and for B when a flock of birds and digestion-resistant seeds serve instead. Take a minute or two to decide which of the three distributions of safe sites illustrated in **Figure 2C** best match the dispersal mode of an unwanted kitchen garden alien, an epiphyte and a nurse plant-dependent perennial native to arid landscapes.

Too little is known to report how a particular mode of seed dispersal influences a specific bromeliad's capacity to maintain its populations. Habitat loss and over collection by humans are growing problems for investigators, and poor accessibility precludes study of much of what remains pristine. This is not to say that what's in plain sight doesn't signal possibilities for productive inquiry. *Tillandsia paucifolia*, for instance, a wind-dispersed epiphyte that ranges from northern South America into southern Florida at a site at the latter region fails to place most of its germinated seeds more than a few meters beyond the maternal parent. Is what seems to be a wasteful performance sustainable because the many fewer seeds wafted farther afield potentially to younger hosts are better equipped than the less mobile individual

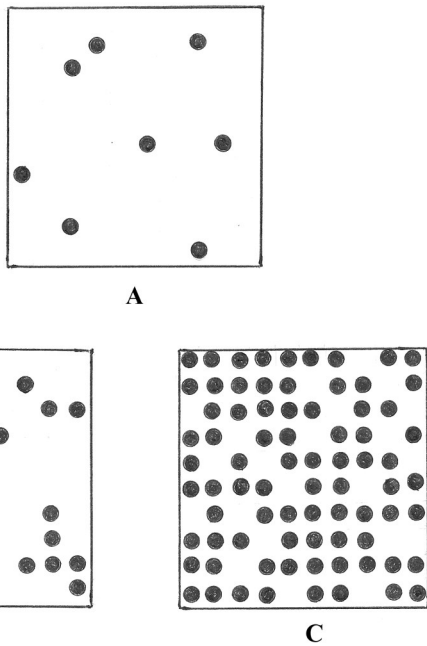


Figure 2C: Three grids illustrating the same number of distributions of safe sites. A. Scattered as expected for a savanna dwelling epiphyte, B. Somewhat more aggregated as expected for a dry growing terrestrial that requires a nurse plant, C. Dense and relatively uniform as expected for a short cycled herb adapted to persist on frequently disturbed soils.

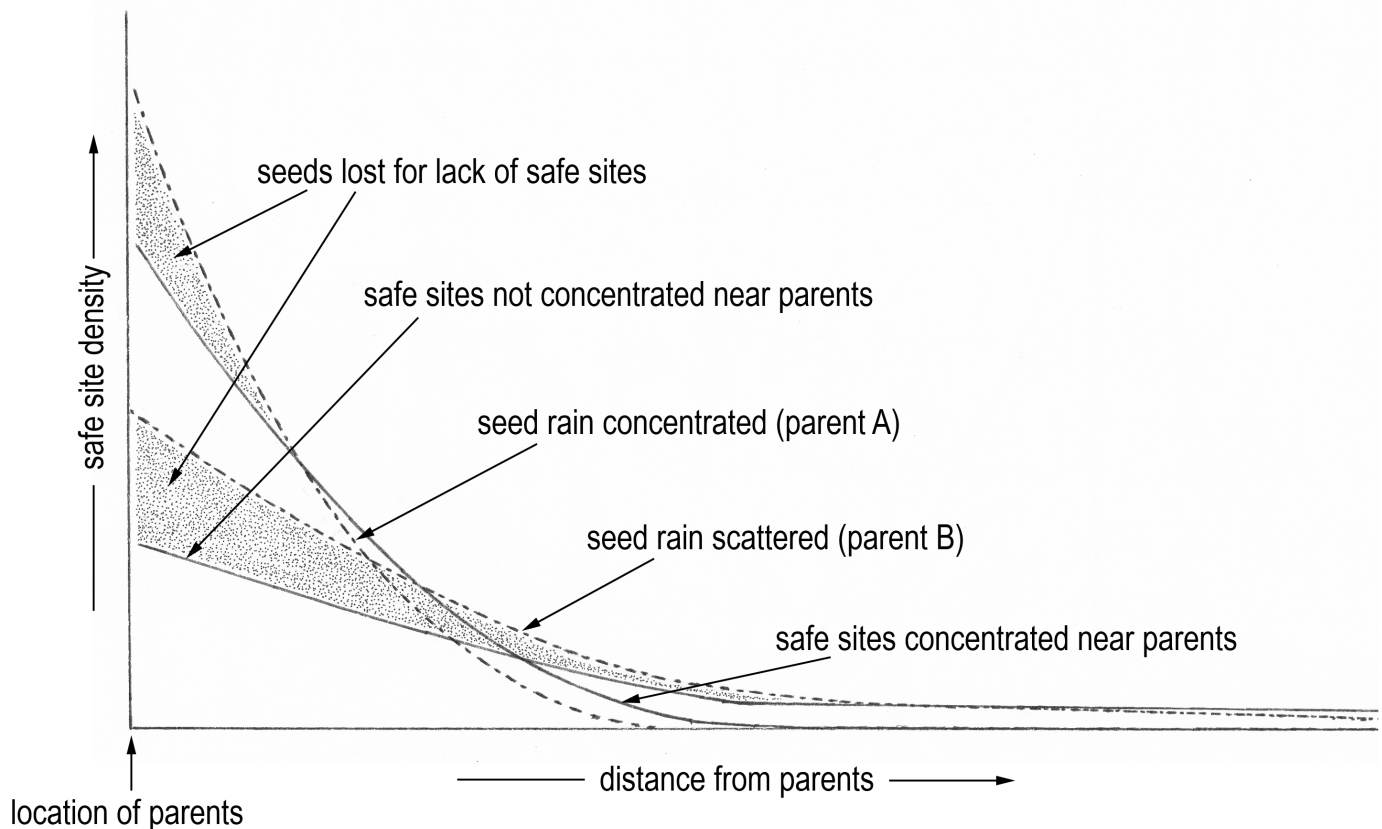


Figure 3C: The vertical axis of this graph indicates the number of safe sites per unit area, whereas the horizontal axis the distance from two parents, both of which have shed the same number of seeds. Dotted line A indicates the shape of the seed rain produced by animal-dispersed parent A and dotted line B the pattern generated by wind-dispersed parent B. The areas under the two solid lines that indicate the distributions of safe sites are roughly equal and therefore so is the number of secured safe sites. Results: Parent A will waste fewer seeds when safe sites are clumped and the same pertains for parent B when its sites are more scattered. Parent A is less effective in recruiting remote safe sites than Parent B and vice versa. These two patterns represent opposite ends of a spectrum, and most of the determined patterns fall somewhere in between.

to sustain a population? If so, what might those special qualities be?

When it comes to Tillandsioideae, there's no reason to presume that because wind provides the motive force for its entire membership that the aerial performance of the group's seeds doesn't vary (**Figure 2C**). Much desired are inquiries aimed at identifying traits that affect seed mobility and sedimentation using controlled wind speeds and heights at release. Seed weight, and various dimensions of the elaborate coma such as the ratio of the length of the stem of the umbrella to the diameter of the expanded top and its wettability all warrant consideration. Adhesiveness could be another decisive factor, and it too is imminently testable. Those hairs responsible for the splayed coma top range from smooth to jointed and twisted. And don't forget about *Catopsis* spp. whose seeds bear a kinky coma at both ends. A study by Chaves-Sáhagún et al. (2019) that compared seed anatomy, ger-

mination and mobility represents a good start. Their six *Tillandsia* subjects differed on all three counts except for terminal velocity in still air, which was slow consistent with unusually high capacity for wind dispersal.

Individuals curious about the mechanics of bromeliad seed dispersal are well advised to prioritize subfamily Bromelioideae. Reproduction for these species requires accommodating the dietary needs, sensory capabilities and mobility's of diverse fauna. Moreover, the berries and seeds involved, being more diverse in many respects compared to the capsular fruit and its contents, promise that many worthwhile discoveries lie ahead (**Essay G**). It's even possible that some of Kermit's relatives despite being green or any of the other colors that grace the frogs of Tropical America number among the dispersers of Bromeliaceae!

ESSAY D. GENES, GENOMES, AND GENE POOLS AND WHY AND HOW BROMELIADS ENGAGE IN SEX

Sometimes you encounter it in print, but more often it's spoken that Darwinian evolution operates by trial and error when correctly put it operates the other way around. Error must precede trial in the sense that mutations, what constitute molecularly based copy errors, are inherent to the DNA replication process and fortunately so because otherwise nature couldn't winnow lesser from better adapted organisms (genotypes). Absent natural selection, life in its millions of versions (species) simply couldn't keep up with environments that endlessly change. It's these chemical errors filtered by natural selection that permit biological species, and the lineages of which they are parts to avoid extinction. Moreover, testing the viability of such errors is only one part—an essential part to be sure—of how the members of a species manage a pool of shared genes (**Figures 1D, 1E; Essay E**). Sex, another component of this fitness-promoting mechanism as it serves the bromeliads, is the subject of the following narrative.

Keep in mind as you read this fourth Essay that a biological lineage is an unbroken series of self-perpetuating populations whose members draw from a pool of genes in a way similar to how books get checked out of a library (**Figure 1E**). And the similarity doesn't end here. Just as a library collections manager regularly

discards outdated volumes to make room for upgrades the management of a gene pool by its users requires that its contents be regularly subjected to natural selection. This being the case, it's reasonable to consider the biological species and the lineage of which it is a part, a collection of genes that undergoes testing every time its borrowers sire offspring (**Figure 1D**). Bottom line: it's informative to view the individuals that comprise a species short term custodians of genes drawn from a common pool, and that by doing so grant nature its opportunity to favor for continuance or reject as deleterious individual genes according to their effects on Darwinian fitness.

The more powerfully a trait influences the sexual performance of its bearers the more it determines the organization and composition of the gene pool shared by those individuals. A floral fragrance or a food reward that attracts a certain kind of pollinator will have much to say about how the genes in pollen (= male contribution) are combined with those in eggs (= female contribution). Traits that aren't so intimately involved in sexual performance may contribute as well but less directly, for instance, by determining for a perennial how many years are required to progress from seed to first flowering or at what stage in the life cycle mortality peaks. Ultimately, it's gene pool composition, dynamics and organization that determine the life history strategy of a species—decides how and where it occurs, which in turn mirrors how that gene pool must be managed by its users (**Essay H**). **Table 1I** identifies some of the traits that determine

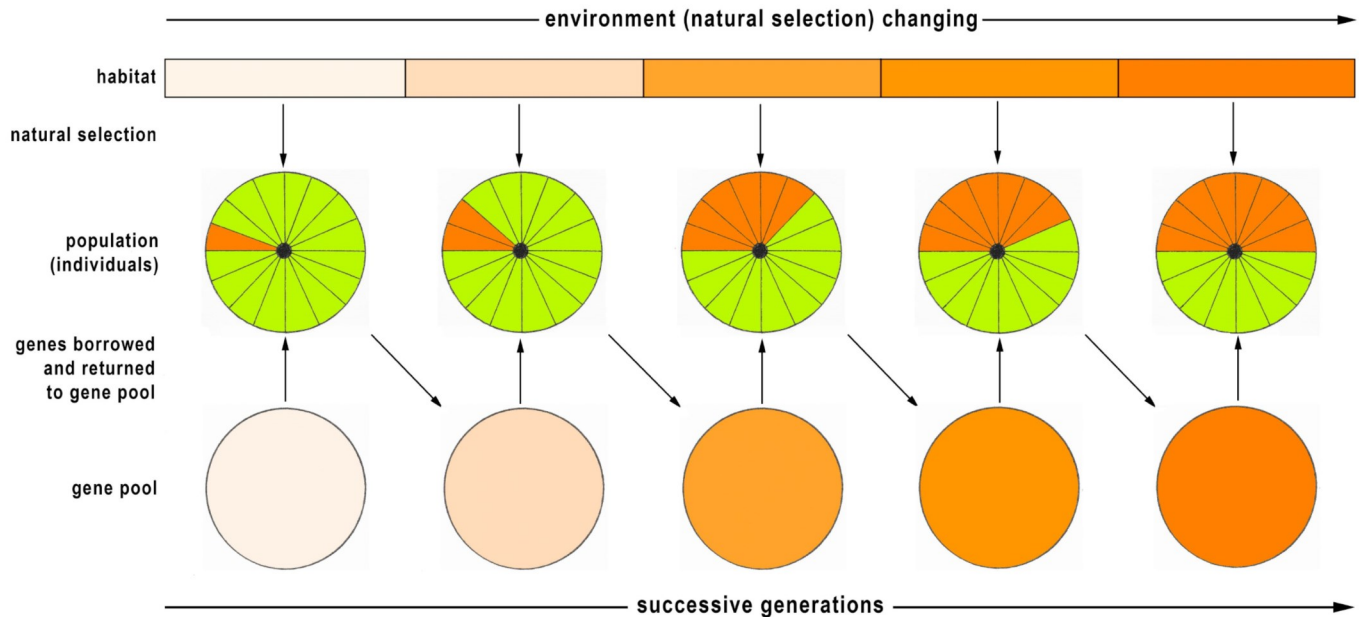


Figure 1D: A diagram illustrating how a lineage equals a progression of self replacing populations served by a longer lived pool of genes, genes that every generation get tested by natural selection for their value as contributors to the fitness of their temporary custodians. Genes are periodically added and subtracted and some of the retained are modified as part of the evolutionary process. Note from the graded shades of orange that the five generations and their shared pool of genes are changing as the parent lineage evolves as necessary to keep up with an ever-shifting environment.

Table 1D: Examples of traits that determine life history strategy and as such vary among species versus those that occur in all green plants.

Life history determining traits	Ubiquitous housekeeping traits
Fecundity (= # seeds/lifetime)	Chlorophyll present
Floral syndrome (e.g., moth)	Protein synthesis occurs
Fruit type/dispersal agent (e.g., berry/bird)	Oxidative respiration occurs
Growth rate (e.g., slow)	Phloem tissue present
Competitive ability (e.g., moderate)	Apical meristems present
Germination requirement (e.g., light)	Stomata present
Height at maturity (e.g., 1-2 ft.)	Sexual reproduction occurs
Shade/sun tolerance (e.g., shade tolerant)	Undergoes alternation of 1N/2N generations
Drought tolerance (e.g., moderate)	Flowers produced
Years to sexual maturity (e.g., 5+)	Fruits produced

two plant life history strategies and **Table 1D** a number of additional traits that do not.

How is what’s just been described accomplished? Eukaryotic, as opposed to prokaryotic organisms (Archaea and the true bacteria), as exemplified by the bromeliad illustrated in **Figure 2D**, engage in a life cycle that consists of two stages (phases). The nuclei within the cells that make up the individual during its so-called haplophase or 1N stage contain an unmatched set of chromosomes whereas during its 2N or diplophase stage these same gene-bearing structures occur in matched (= homologous) pairs. The haplophase of the higher plant, what also is known as its gametophyte, produces sperm and eggs (= gametes) that by fusing initiate the 2N sporophyte stage. The sporophyte for its part gives rise to separately gendered gametophytes by way of haploid spores that represent the products of reductive (= meiotic) rather than mitotic (= non-reductive) divisions of special diploid mother cells. Juxtaposed, the 1N and 2N phases equal the botanical alternation of generations—a circular arrangement that for the reasons described above reduces a population of inter-fertile plants fundamentally to a pool of repeatedly tested, i.e., naturally selected genes.

Recognizing the sporophyte stage of a bromeliad is easy, but not its haplophase (**Figure 2D**). The latter is more challenging because the female gametophyte spends its brief existence nourished by and embedded within the parent sporophyte, specifically within one of its ovules. Its male counterpart does the same while developing within the anther of a stamen to become a pollen grain, whose sole purpose is to produce and deliver sperm to a target as described below. In effect, virtually the entire haplophase, both female and male components, occurs literally surrounded by diploid (sporophyte) tissue. **Figure 2D** further shows that the bromeliads, being flowering plants, exhibit an alteration of generations centered on the seed habit, a condition that constitutes a major improvement for exchanging genes and dispersing progeny that emerged some 300 million years ago. The geologically older ferns, horse tails and lycophytes (= the clubmosses) lack seeds still producing free-living mostly bisexual gametophytes from air-dispersed haploid spores, a relic condition that evolved to serve the aquatic antecedents of the higher plants (**Essay F**).

So how does a bromeliad perform sex—make the transition from diplophase to haplophase? Note in **Figure 2D** that male gametophytes develop by the thousands inside four-chamber structures called anthers one of which is located at the tip of a stamen, six of which make up the male portion of a bromeliad flower (**Figure 3D**). Female gametophytes in far smaller numbers start out inside those previously mentioned ovules—one per ovule—located within pistils, the female counterpart of the stamen only one of which is present per flower. The conveyance of pollen from anther to pistil constitutes pollination and the subsequent fusion of sperm and egg fertilization. Sperm reach eggs via pollen tubes that emerge one per pollen grain to grow through the pistil beginning at its terminally situated stigma down through its style to its swollen, basally located three-chambered ovary and from there into the ovules (**Figure 2D**). Fertilized ovules, each now containing an embryonic sporophyte, have by this action become seeds within fruits, either capsules or berries depending on the species (**Essay C**).

Now we’re prepared to appreciate how the alternation of generations (life cycle) as it plays out among the angiosperms makes plant-directed gene pool management a reality. Most Bromeliaceae bear perfect (= hermaphroditic) flowers genetically determined to be either self-compatible or self-incompatible, which means that sperm can or cannot fertilize eggs produced by the same individual—that if operating according to the second arrangement (= breeding system) that every seed, actually the embryo (a young sporophyte) inside, has two parents one being maternal and the other paternal (**Figure 2D**). Species that belong to genera such as *Hechtia* are obligate out-crossers as well but by virtue of being dioecious, the individual plant bearing exclusively male (= staminate) or female (= pistillate) flowers. A third much smaller group of bromeliads employ monoecious systems where every

member of a population produces staminate and pistillate or staminate plus perfect flowers (e.g., *Cryptanthus*).

The occasional self-compatible hermaphrodite sets seeds unassisted by a third party and consequently is described as spontaneously allogamous (i.e., an automatic out-crosser). Two much larger blended subsets of species make up the balance of the self-compatible category. One extreme approaches exclusive outcrossing and the other selfing with the majority falling somewhere between. Members positioned at the former end of the spectrum employ a variety of strategies to avoid selfing. Some mature their sexual appendages asynchronously, pollen being shed and same flower stigmas receptive at different times of the day or on consecutive days (e.g., numerous tillandsias). Others produce flowers configured to encourage visitors to deposit in-coming pollen before picking up fresh loads for delivery elsewhere. An individual’s breeding system does not predict other aspects of its reproductive process perhaps the most consistent of the exceptions being the associations between self-compatibility and monocarpy (e.g., *Tillandsia utriculata*), but the way pollen is exchanged and seeds are dispersed doesn’t say much about a species’ life history strategy or its ecology. If additional patterns exist, and it seems that they should they must be subtle.

Table 2D lists most of the pollination syndromes employed by Bromeliaceae along with their defining characteristics. The ornithophilous (= hummingbird-dependent) type is the most frequently occurring of the lot having repeatedly evolved and often subsequently lost during adaptive radiations particularly among the epiphytes native to high elevation habitats. (Shifts have also left formerly bird-dependent species better served by bats.) The most consistent of its floral markers are an absence of odor and red bracts contrasted by elongate, colorful petals rolled into a stiff tube from which the six stamens and a single style topped by a tripartite stigma protrude (**Table 2D**; **Figures 2D, 3D**). Nectar is abundant and sugar-rich (different sugars for species served by different pollinators) as required by the high caloric de-

mands of its visitors. Chiropterophilous (= bat) flowers are large and bell-shaped (e.g., *Werauhia* spp.), or if small, numerous and densely clustered with the former usually equipped with flared white or pale pastel petals. Hexose rich nectar and/or pollen are plentiful, and the emissions of any floral odors are most pronounced at night (**Figure 3D**). The spontaneously self-pollinating blossoms of autogamous *Tillandsia recurvata* secrete no nectar, release no fragrance and possess no brightly pigmented appendages. Overall small size further enhances the material economy achieved by this exceptionally prolific bromeliad. Insect-serviced flowers vary most of all and by color, odor, shape, size and reward consistent with the diverse needs, sensory capacities and behaviors of visitors that include bees, flies and moths.

As of this writing too little is known to more than speculate about how a specific kind of pollinator influences gene pool composition, structure and dynamics. It’s been said that wide-ranging trap liners (e.g., some but not all hummingbirds) and bats together service more of the bromeliad species than all of the other agents combined. Also opined is the notion that the family’s high incidence of self-compatibility compensates for flowers that owing to their targeting of specialized pollinators if self pollen would too often fail to set fruit. Seed compared to pollen dispersal has received even less study as noted in **Essay C**. All that’s currently known being considered, it’s fair to say that many interesting questions about sex and related bromeliad biology remain little explored. For instance, which aspects of this or that kind of pollinator most powerfully select for specific floral traits? Is it food preference, the animal’s visual or olfactory acuity or the shape or size of its body? How important is competition with neighbors, and which of the floral syndromes once lost are more or less difficult to restore?

Having identified the diverse traits that grant the flowering plants capacity to persuade third parties to help manage the gene pools upon which they depend what about the longevity, i.e., permanence, of these attributes and the combinations in which they operate? Characteris-

Table 2D: The traits that characterize the most common floral syndromes occurring among the bromeliads.

Agent	Fragrance	Color	Reward	Gender	Anthesis
Bird (Hummingbird)	None	Bright	Nectar	Bisexual	Diurnal
Bat	Non-floral	Bright-night reflective	Nectar and/or pollen	Bisexual	Nocturnal
Bee/wasp	Floral	Pastels	Various	Various	Diurnal
Autogamous	None	None	None	Bisexual	—
Moth	Floral	Bright-night reflective	Nectar	Bisexual	Dusk/night

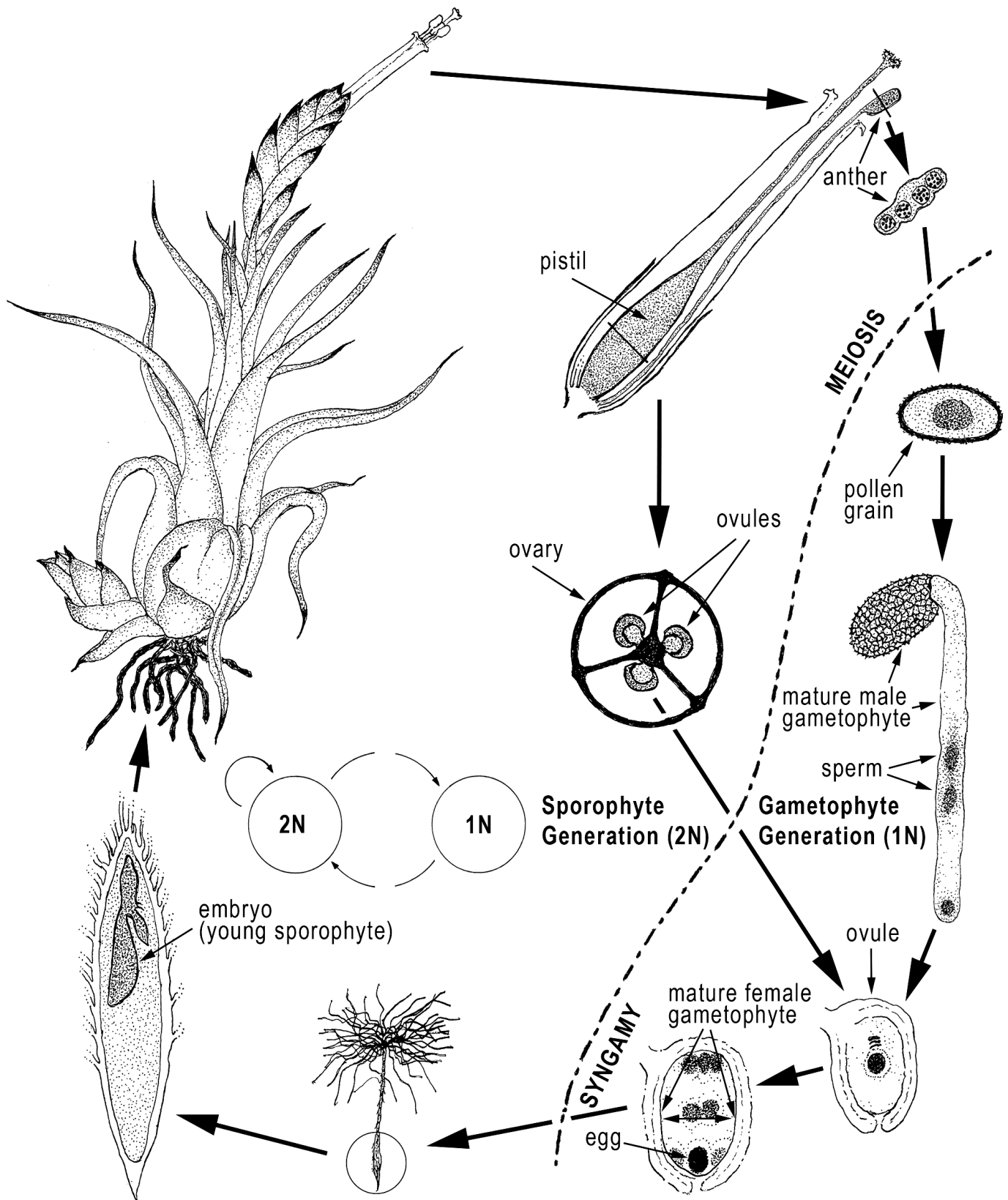


Figure 2D: The life cycle (alternation of generations) of hummingbird-pollinated wind-dispersed *Tillandsia paucifolia*. The circular arrow that begins and ends with the diplophase indicates asexual reproduction. See the text for additional detail. None of the structures are drawn to scale.



Figure 3D: The inflorescences of three *Billbergia* spp. that illustrate the same number of floral syndromes. **A.** *Billbergia stenopetala*; hummingbird pollinated. **B.** *B. horrida*; insect pollinated. **C.** *B. robert-readii*; bat pollinated. Note how the color and size of the inflorescence bracts and petals most conspicuously differentiate the three species. *Billbergia stenopetala* flowers are odorless while those of the other two emit fragrances, that of *B. horrida* being pleasant and of *B. robert-readii* more like rotten fruit. The dense cover of light reflecting trichomes displayed by *B. robert-readii* probably helps orient its night-flying pollinators.

tics such as breeding system, pollination syndrome and seed mobility being under genetic control are subject to natural selection (evolution). The power of many a trait to affect a gene pool's disposition also depends on certain of its bearer's additional attributes plus all sorts of externalities such as climate and geographic occurrence none of which remain static through the lifetimes of lineages. Perhaps because so many tradeoffs and antagonisms occur among plant traits their failure to occur in consistent combinations even when supporting the same life history strategies shouldn't be surprising.

Several thought provoking questions are worth mentioning as part of this treatment of the relationship that exist between how bromeliads reproduce and the genetic architectures of their populations. Is there a biological explanation for why certain aspects of geographic distribution, life style and sexual mechanics also occur in so many different combinations (**Essay G and above**)? What explains the existence of so many kinds of breeding systems, gender expressions and ways of promoting out-crossing and self-fertilization? How much functional redundancy occurs within this realm. Why are certain wide-ranging species (e.g., *Tillandsia utriculata*) monocarpic at some locations and at others polycarpic (= iteroparous meaning flowering repeatedly via sequentially produced ramets) (**Figure 4AA**). Might this picture be this complicated in part because of the inherently high versatility of the flower? Finally, how responsible are phylogenetic constraints for this puzzling variety?

Accidents of history may explain why the members of some separated parts of geographically fragmented species exchange genes by different means. Florida's miniscule colony of *Catopsis nutans* bears perfect flowers while farther south through much of the rest of its extensive Mesoamerican range it's dioecious. Could the Florida condition be attributable to a single wind-delivered hermaphrodite recruited from a source population that back then and possibly still today was less than comprised wholly of unisexual individuals? More commonly it's the mating system rather than gender expression that varies as exemplified by *Guzmania monostachia*, which is autogamous in Florida and allogamous at least at some locations farther south. *Tillandsia caput-medusae* self-fruits in parts of southern Mexico, but not at all at least at some its Costa Rican sites. Brightly pigmented versus duller floral bracts appear to accompany self-incompatibility in both instances.

Fruits and their contents offer additional perhaps exceptional opportunity to manage gene pools as the embryo within a seed being diploid incorporates twice as many genes as the haploid pollen grain (**Figure 2D**). Consult **Essay C** to learn more about targeted dispersal, for example, how the arboreal ant-nest users, all of which belong to subfamily Bromelioideae, employ seeds that emit pheromone-like chemicals and in some cases perhaps bear rudimentary edible appendages (= aril) to colo-

nize developing from established carton nests. Conversely, bat-ingested seeds end up deposited across a variety of kinds of daytime roosting sites and those delivered by birds scatter even more widely. Wind, being completely mindless, accounts for the most randomly configured seed shadows of all (**Figure 3C**).

Figuring out how a bromeliad manages its shared gene pool is a daunting challenge, much more than determining the histories of the mediating devices and mechanisms. Fragrance chemistry, the presence of osmophores (= fragrance glands) and nectaries (= nectar secreting glands), petal color and the timing of anthesis (= flower opening) among other floral attributes differ widely within many clusters of closely related species indicating quick response to guiding selection. Traits that prevail with little exception across genera and subfamilies indicate deeper genetic entrenchment, examples of which include ovary position (superior versus inferior) and fruit type (capsule versus berry). Even more firmly embedded in the gene pool and reflective of extended evolutionary history is the three-parted symmetry to which almost all bromeliad flowers conform (**Figure 2D**).

What's been presented above depicts the botanical species as a pool of shared repeatedly borrowed and tested genes, which is fair enough but how about viewing the individual gene as autonomous and striving to survive as proposed by the English biologist and popular author **Stephen J. Dawkins (2016)**? Does his attribution provide insight on why the higher plants including the bromeliads conduct sex in so many different ways? More to the point, does it make sense to accept his idea that genes compete

to express themselves on pain of elimination from the gene pool should they fail? According to Dawkins it all boils down to a drive for immortality using temporary custodians to demonstrate, via repeated testing, why a given gene warrants preservation. Few biologists these days grant to the gene Dawkin's reputed self-determination let alone his implied willfulness. Perhaps his thesis will prove totally dismissible, but none-the-less it's thought provoking to attribute to the gene qualities that exceed what's needed to code an organism's phenotype.

This forth Essay describes how unlike mutations over which neither the effected individual or its parent species has control gene pools management is a different story. For the angiosperms—a group that includes family Bromeliaceae—it's the reproductive apparatus and the flower in particular owing to its many variations that influences most directly gene pool composition, organization and dynamics. Life history traits that involve other parts of the plant body and concern other aspects of botanical performance contribute less to nothing at all. To persist through time a lineage must maintain its gene pool such that its users/testers remain as fit as those that came before. Ultimately, it's a gene pool's capacity to respond positively to natural selection that permits its continuance in a world fraught with instability. Sexual reproduction, genomes and gene pools are central players in this balancing act between life and death. Viewing genes as semi-autonomous players, and even selfish ones, helps make some sense of this complicated dimension of evolutionary biology. The following **Essay (E)** further elevates this discussion by examining genes and plant populations from a different vantage point.

ESSAY E. THE BIOLOGICAL SPECIES: ORIGIN, ADAPTATION, AND GENETICS

The biological species owes its existence to Darwinian evolution, whereas the cultivar (or cultigen) is a human invention. The former amounts to a Mendelian population, which is to say that its members are inter-fertile, i.e., can interbreed, and are more closely related one to another than to the individuals that make up other species. The members of species share additional attributes including similar but not identical genotypes and phenotypes, the latter amounting to the outward manifestation of the former (**Essays D, H**). As this essay unfolds remember that to persist a species must continuously adapt (= evolve), a feat that a cultivar being manufactured rather than forged by natural processes cannot.

Notions about what constitutes a kind of organism, and how different kinds relate to each other have shifted markedly over time in concert with changing interpretations of the material world. For instance, the bizarrely mosaic creatures that so richly populate Greek mythology accord with the conviction widely held during classical times and for quite a while since that life is imminently transmutable to the extent in fact that even lifeless objects can become animate. Such belief survived until finally put to rest by skeptics such as the Italian physician Francesco Redi (1626–1697) who debunked spontaneous generation that by then had already become a stubborn echo of the archaic acceptance of extreme biological fluidity. Some of the most obdurate of scholarly minds were finally persuaded otherwise when Redi and his contemporaries demonstrated, for example, that fly maggots don't spring anew from rotting meat, or that despite their shared superficial resemblance ripening heads of wheat never become crop-destroying caterpillars.

The pendulum swung in the opposite direction when what's known as the typological (= invariant) species concept replaced the hyper-flexible Greek version of kind. Carl Linnaeus (1707–1778), the widely heralded father of modern plant and animal taxonomy, counted among the many more Western thinkers who during the eighteenth century considered all forms of life the work of a deity, or more precisely, that all living things are an Abrahamic God's Special Creations. Species according to this definition are rigidly fixed—essentially immutable. The occasional anomalous individual, owing to its failure to conform to its imputed Divine Archetype, was dismissed forthwith as nothing more than a mistake, something not unlike a mechanical copy error. And then came Charles Darwin's (1809–1882) landmark *The Origin of Species* in 1859 followed several decades later by rediscovery of Gregory Mendel's (1822–1884) similarly provocative breeding experiments with garden peas.

Too little was known about genetics or inheritance to formulate the modern species concept prior to the rediscovery of Mendel's work and some subsequent findings of others. What this accumulating information made pos-

sible included formulation of what's known today as the evolutionary or Mendelian synthesis, a construct that casts the species (the Mendelian population) as a self-perpetuating, self-correcting (evolving) pool of genes (**Essay D; Figure 1D**). In effect, the species defined this way is at its core a collection of highly organized interacting genes that represents only the most recent iteration in a self-perpetuating self-correcting pool of genes that in its historical entirety equals a lineage (**Figures 1D, 1E part A**). No two individuals drawing from the same pool are identical as stated above, a reality that every seasoned bromeliad grower knows from experience. Species whose members differ more among themselves than usual are described as polymorphic but remember that some degree of intra-specific (= within species) variation is universal, and as we shall see it can be beneficial. Consult **Essay D** for more about gene pools and their management.

Modern plant taxonomists appear stubbornly committed to the typological species concept when, as required by the International Code of Botanical Nomenclature, they designate type specimens. It's but one of several conventions mandated for describing and naming species previously unknown to science. Use of the type (= short form) does hark back to the Doctrine of Special Creation, but in its modern application it simply serves to confirm and record the existence of the species that it represents. A specimen so designated, accompanied by a Latin or English description (diagnosis) of its gross physical characteristics, its date and site of collection, notes on its ecology and the collector's identity speaks for its kind although neither it or any other single individual given the universality of polymorphism can live up to this goal. Types are maintained in botanical museums called herbaria, the largest of which house millions of dried, pressed plants mounted on stiff paper. **Figure 2E** illustrates the holotype for the Ecuadorian native *Pitcairnia dodsonii* so named to recognize its discoverer.

It was Charles Darwin who following decades of astute observation documented in his 1859 publication proposed that older lineages beget younger lineages (**Figures 5AA, 2B**). What he so convincingly described is speciation a process that operates by several means to achieve the same result: daughter species (**Figure 1E part B**). Divergent-type speciation occurs when a single parent lineage—what amounts to a self-perpetuating pool of genes—breaks up such that its members, the individual custodians of these genes, become two gene pools (Mendelian populations) rendered genetically isolated one from the other by one of the mechanisms identified below. Summarizing, what begins with the fragmentation of a single gene pool over time and because of those fragments experiencing different regimens of guiding natural selection and a phenomenon known as genetic drift eventually diverge enough genetically and phenotypically to qualify as daughter species. Speciation of the reticulate type requires two lineages similar enough genetically to hybridize in the manner illustrated graphically in **Figure 1E part D**.

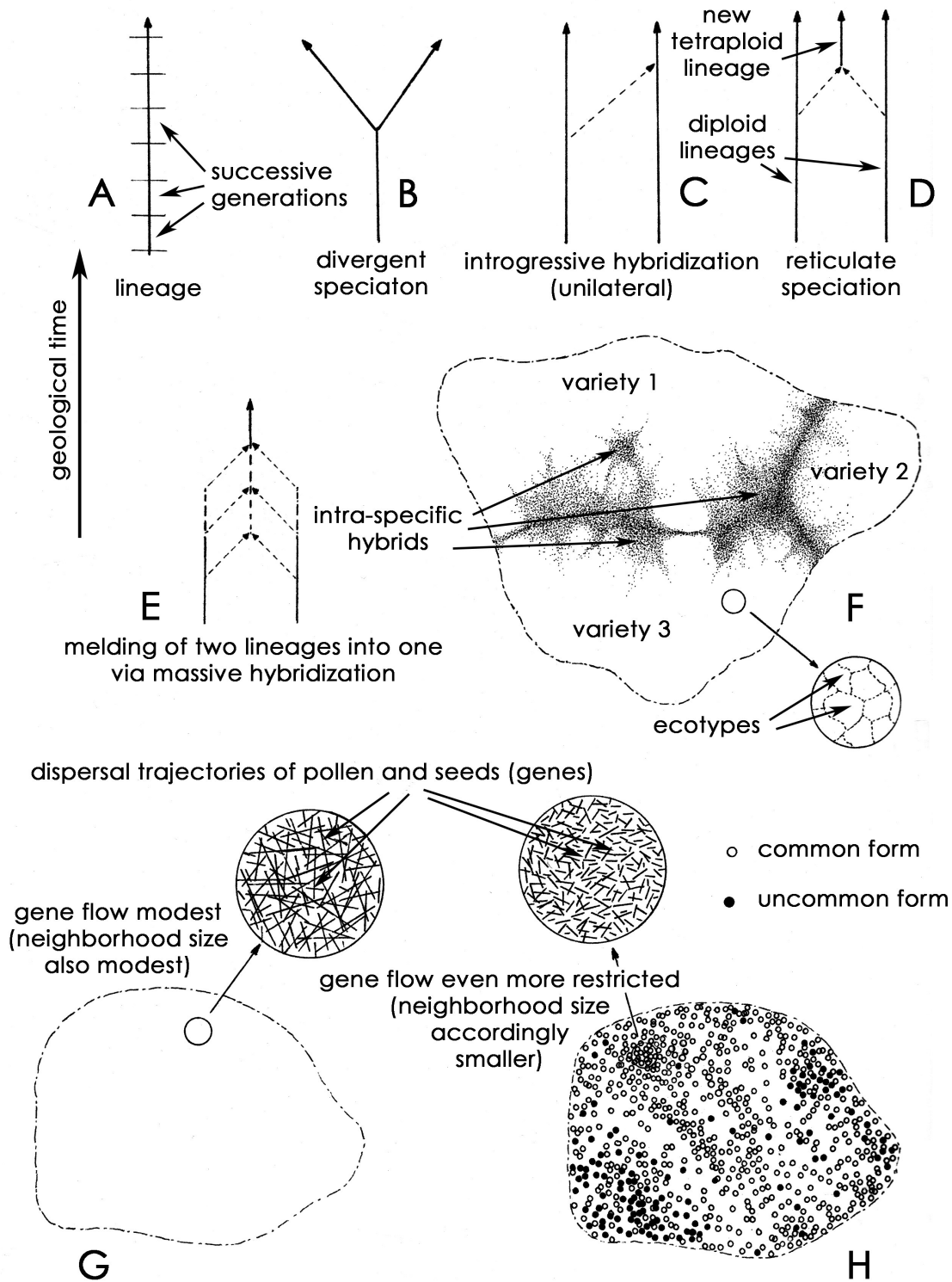


Figure 1E: **A.** a lineage showing its seven most recent generations; **B.** divergent speciation whereby a single parent lineage gives rise to two daughter lineages; **C.** introgressive hybridization that can result in selective gene transfer from one lineage to another (unilateral in this case) across an incompletely developed (leaky) reproductive barrier; **D.** reticulate speciation involving polyploidy where hybrids between two diploid lineages produce a third tetraploid lineage; **E.** the melding of two previously distinct lineages (gene pools) as a consequence of gene pool-swamping by hybridization; **F.** the geographic distribution of a polymorphic species that consists of three varieties and multiple ecotypes; **G.** the geographic distribution of a species illustrating the influence of gene flow on effective population size; **H.** the geographic distribution of a species with more restricted gene flow (less mobile pollen and/or seeds) and smaller neighborhood size than illustrated in G. Also shown in H are the geographic distributions of two forms within a single species.

Closely related lineages, being products of recent speciation events, remain for a time inter-fertile and while this condition persists can exchange genes unilaterally or bilaterally via hybridization possibly followed by backcrossing (Figure 1E part C). Certain circumstances can allow what amount to modestly divergent gene pools and gene pool fragments to merge to again become one as illustrated in Figure 1E part E. Interspecific (= between species) hybrids aren't common in nature, however, owing to internal (= physiological), or environmentally imposed barriers to fruitful unions one type or another of which was required to allow the emergence of daughter species as described in the previous paragraph. Frequent external barriers to gene exchange between sexually compatible gene pools and gene pool fragments include geographic separation (= non-overlapping ranges), dependence on different kinds of specializing pollinators and the absence of the growing conditions (often physically disturbed substrates) that hybrids often require. So, it's to be expected that the incidence of hybridization and its results will be highest where the growing conditions that participating parents require are themselves homogenized, or put more precisely, scrambled by some natural event (e.g., hurricane) or human agency.

That interspecific hybridization tends to end badly shouldn't be surprising because mixing genes from sources (gene pools) adapted to different growing conditions should diminish the product's fitness. But when backcrossing is involved and gene exchange is only partial and confined to beneficial genes, i.e., when gene flow is selective and positive, it can lift the augmented lineage's fortunes (Figure 1E part C). Archaic *Homo sapiens* engaged in enough introgressive-type hybridization to explain why if a person's ethnicity is European, it's likely that up to two percent of his or her genome is a gift that keeps on giving having come some 40,000 years ago from our extinct sister species *Homo neanderthalensis*. Genes borrowed from this closely related pool have been winnowed during those 40 millennia since by natural selection and what remains codes for traits such as skin and hair color plus certain aspects of immune function that had they been purged as well might have left us even more vulnerable to certain diseases that remain problematic today.

Recognition is growing that horizontal gene transfer effected through hybridization while uncommon nevertheless has been a major driver of biological evolution among both plants and animals. Recent assessments of fossil DNA for instance tell us that in addition to possessing genes donated by our extinct closest relative our gene pool further includes genes infused from at least a half dozen additional lineages included in what once was a far larger genus *Homo*. So it's fair to view our species as constituting a genetic amalgam, a synthesis of genes many of which were tested at different times by other populations experiencing different circumstances and Darwinian selection before they came to us. Signs suggest us that a similar process could be underway within Bro-

meliceae. The most likely participants are clusters of closely related lineages marked by frequent co-occurrences (e.g., certain clades within *Tillandsia*).

Polyploidization—the multiplication of complete sets of chromosomes is a second way that daughter lineages arise as illustrated in Figure 1E part D. It happens in more than one way, but most often when members of a pair of at least partially inter-fertile diploid lineages that generate the occasional unreduced (2N) sperm or eggs mate via these same anomalous gametes (Essay D; Figure 2D). The resulting tetraploid (4N) hybrids if self-fertile will sire 4N progeny thereafter by what now has become unerring production of 2N gametes. Possession of a duplicated compliment of chromosomes, one that consists of a diploid set from each parent lineage, precludes successful backcrossing because the resulting triploid (3N) offspring most often are sterile. You can see why speciation by this second route is described as reticulate (= net-like) rather than divergent (= open branching). Polyploidy has played a decisive role in bromeliad history a minor example being the doubling that yielded the 4N



Figure 2E: The holotype of *Pitcairnia dodsonii* deposited at the herbarium of the Marie Selby Botanical Gardens (SEL).

pineapple that in the hands of plant geneticists has been further improved (domesticated) to become one of the most valuable of commercial fruits.

Returning to a subject previously mentioned only in passing, how does polymorphism influence Darwinian fitness? For one, it's integral to a dynamic that involves gene pools, population structure and geography, and for number three specifically the uniformity or lack thereof of the growing conditions to which the members of wide-ranging species must adjust. Why it's needed is captured in the following statement: the greater the range occupied by a Mendelian population and the more varied the growing conditions to which its members must adapt the more polymorphic that species will (must) be. So how does a species operating as a collection of genes with its members—the custodians of its genes—as individuals being constrained by narrow eco-tolerances and specific requirements as described in detail below still manage to occupy space that features mosaic-like growing conditions? How for instance does a widely distributed terrestrial bromeliad adjust to spatial discontinuities in soil fertility, pH and drainage? It's polymorphism that in this example represents the kind of evolutionary fine-tuning that provides a good share of the needed flexibility (**Essays D, H**).

Guzmania monostachia demonstrates through its display of pale versus deep carmine floral bracts at different locations across its Mesoamerican/northern South American range how polymorphism tends to be more pronounced among widely distributed versus more insular (= geographically confined) species. The individuals with the weaker of the two floral signals come from south Florida where virtually every flower yields a capsule apparently whether visited by a pollinator. Cost effective use of resources is a strong contributor to Darwinian fitness, so absent the need for outside assistance to set fruit in Florida why not down-regulate anthocyanin synthesis and commit what's saved for some continuing need(s)? Intra-specific (within species) variation also includes more complex performance such as synchronizing flowering and seed dispersal with local duration and arrival and departure dates of wet and dry seasons and when certain pollinators fly. Polymorphism doesn't always enhance fitness of course. How else to explain why Spanish moss varies several fold by the robustness of the individual ramet across its record setting north/south distribution?

Figure 1E parts F and H illustrate how the genes within a gene pool (a species) are arrayed across a hypothetical geographic range that features non-uniform growing conditions. Recall from what **Essay D** reports about pollination, breeding systems and seed dispersal that genes move somewhat independently, and where located at any time is determined by where their temporary custodians are growing. The gene pool displayed in **Figure 1E** occupies space that consists of three sub regions each of which is characterized by distinct circumstances to which resident flora must adapt. The individuals depicted in **Fig-**

ure 1E accordingly owe their accommodations (= adaptations) to local conditions—to traits acquired in response to three site-specific regimens of guiding natural selection. Should the members of our divergent trio of subpopulations become distinct enough to meet certain criteria they would warrant recognition as the same number of varieties, a taxonomic rank that approximates the zoologist's subspecies. Note how bands of inter-varietal hybrids separate our three subpopulations evidence that the underlying gene pool still amounts to just one robustly polymorphic species.

Figure 1E part F further illustrates an intra-specific category known as the ecotype many more of which compared to the taxonomic variety can fit into a given geographic area. Ecotypes represent the outward expressions of a kind of gene pool differentiation that's too minor to warrant assigning to its segregate's Latin names. The traits involved tend to be quantitative meaning governed by quantitative trait loci, which means that they influence performance such as drought and shade-tolerance by degree rather than all or nothing (= not binary). Moreover, they frequently amount to less pronounced versions of the same attributes that distinguish varieties and even higher taxa. Compared to the formal variety, the ecotype represents a response to growth-influencing conditions that may shift imperceptively (to us) and often across short distances. To date, little has been published about ecotypes among the bromeliads, but surely, they exist.

Like the intra-specific rank variety, the taxonomic form receives a Latin designation even though it's based on fewer and often just one conspicuous trait such as leaf shape or petal color. Forms within species range from two to many, and their representative are scattered rather than geographically segregated as applies for the variety and ecotype, but again it's the underlying gene pool that's responsible for spatial distribution (**Figure 1E part H**). For example, a bromeliad that qualifies as the white version, meaning no anthocyanins present, of what for its species is typically a lavender flower may be nothing more than an individual that harbors two copies—is homozygous recessive—for a defective allele (= version) of a gene that mediates a step in the biochemical pathway that's responsible for the synthesis of a particular pigment. The spatial distribution of these color variants is determined by the locations of the custodians that bear the functional (i.e., dominant) versus the nonfunctional (i.e., recessive) alleles of the gene that controls whether petals are chemically disposed to reflect primarily lavender or all the wavelengths that comprise visible (white) light.

Before moving beyond the subject of relationships among gene pool structure and management, polymorphism and adaption it's worth a quick look at intra-specific (within a species) gene flow to illustrate how evolution operates at the level of and within a Mendelian population. If the genes exchanged when conspecifics (= members of the same species) mate move substantial distances, then the areal extent of the land occupied by ge-

netically similar individuals within the larger species-wide distribution will exceed that of a second species whose pollen and seeds are less mobile. How many individuals occupy these respective zones along with their size vary but the amount of genetic sub-structuring that results can influence capacity for fine grained adaptation and by extension ability to accommodate local growing conditions (**Figure 1E part H**). *Tillandsia usneoides* meets the first condition, and its close relative *T. recurvata* the second the difference between the two being attributable largely to the divergence of their breeding strategies. Predictably, Spanish moss, being insect-pollinated and self-incompatible, is locally the less genetically diverse than routinely autogamous ball moss.

What about taxonomic nomenclature? When a species is said to be described, which is another way of saying when it's known to science, it's been assigned a scientific binomial the first half of which identifies its genus just as a surname states a person's family affiliation. The second name, its specific epithet, equals its given name. Varieties receive trinomials, the third part of the name being preceded by the abbreviation var. (e.g., *Tillandsia fasciculata* var. *densispica*). Being a form makes a name still longer (e.g., *T. fasciculata* var. *densispica* forma *alba*), although three labels suffice when no varieties are recognized. *Tillandsia fasciculata* is represented by three varieties in Florida, only one of which includes a white flowered form, and its representatives are interspersed geographically among its more abundant lavender-petaled counterparts. All three varieties occasionally grow comingled, which probably reflects the disturbed (homogenized) state of so much of what remains of south Florida's original woodland habitat.

Summarizing briefly, plant species arise in multiple ways and the polymorphism that they typically exhibit to some degree to some extent represents Darwinian adjustment to growing conditions that differ within all but the

most confined of geographic ranges. Contamination of a gene pool (species) by alien genes because of hybridization with another species can destabilize the recipient's pool although the result is beneficial if the exchange is appropriately selective (= filtered; **Figure 1E, F, G, H**). Horizontal (= across as opposed to within populations) gene swapping effected in this manner increasingly is being recognized as a major driver of plant evolution, but whether this phenomenon has played as important a role among the bromeliads as it has, for example, for the red and white oaks, two clades within genus *Quercus* and for us, remains to be seen. Characteristics cited in the formal description of a type specimen (the holo-type), including those conspicuous enough to distinguish varieties and forms and the species itself, may contribute little to nothing to biological fitness. Holo-types often are not typical representatives of the populations whose existence they document.

A few comments about cultigens are in order before closing. While a species, having been molded by the Darwinian process is natural the most commercially exploited of the cultivated bromeliads fall short of this criterion, but mostly not by much. Plant domestication is a more transformative process, and its products vary accordingly bearing in the most extreme cases little resemblance to wild-type antecedents (e.g., maize). Except perhaps for the pineapple, no Bromeliaceae show evidence of the rigorous genetic manipulation required to engineer qualities equivalent to those that allow 7.5 billion humans to be sustained by the grain staples and to lesser degrees a diverse collection of fruits, root crops, and vegetables. As for the bromeliads, it's perfectly reasonable to label an exceptionally showy specimen of *Tillandsia cyanea* a representative of a species, compared to the corn plant that has experienced so much genetic manipulation that it couldn't survive for more than a generation or two were it to find itself untended back in its ancestral Central American home.

**ESSAY F. THE VASCULAR PLANT BODY:
HOW ABANDONMENT OF VERSION 1.0
SUPERCHARGED BROMELIAD EVOLUTION**

About 425 million years ago evolution brought forth a new kind of plant that contrary to all of the previous versions could tolerate air's capacity to desiccate wet objects. Among the attributes that made this performance possible was a body that until then had been little differentiated structurally or functionally but now consisted of two distinct portions one fashioned to operate above, that being the shoot system and the other, the root system, below ground (**Figure 1F**). It was this bipartite architecture, along with a vascular system for distributing water and the products of photosynthesis among various tissues and organs that allowed a botanical invasion of Earth's terrestrial from its aquatic realm. And it didn't take long thereafter for what had been barren uplands to host a vascular flora that today consists of some 400,000 species about 3600 of which are bromeliads.

Odd as it may seem, a small subset of today's higher plants have abandoned the two-parted body plan, and stranger still they grow where moisture is either superabundant or challengingly scarce. While it's not important to know which of these two environmental extremes most often accompanies the state of being rootless or nearly so why the non conformers jettisoned a trait central to the botanical colonization of land is worth our consideration. That such a profound transformation was even doable bears witness to the imminently malleable nature of the vascular plant body. And of the species best positioned to

demonstrate this reality, few exceed the most ecologically unconventional members of family Bromeliaceae. It's this structural fluidity, specifically, the emphasis on shoots at the expense of roots that provides grist for this sixth essay. But before proceeding to how and why this momentous event occurred it is important to realize that a certain benefit accrues when a shoot assumes functions ordinarily performed by roots.

First off, how is it that possession of a bipartite body was crucial for the successful invasion of land yet some of the participating lineages have readopted the less differentiated earlier version of that same divided body (**Figure 1F**)?

A pair of questions provide guidance. Number one is which of the two architectures is the better suited to carry out operations in two disparate kinds of space—the first being the atmosphere and the second a discrete volume of soil—instead of just one as for the nonvascular antecedents of the vascular plants? Question number two is how can different functions following their refinements for performance on land in different organ systems be physically relocated into one, that one being the shoot? Keep in mind when addressing the second more vexing question that photosynthesis and the acquisition of water and mineral nutrients as conducted out of water differ enough mechanistically to raise problems if located at the same anatomical address. Illustrations are a good way to explore this conundrum so we will employ for this purpose a contrasting pair of vascular plants—an atmospheric bromeliad and a submerged aquatic—but not before completing a short exercise.

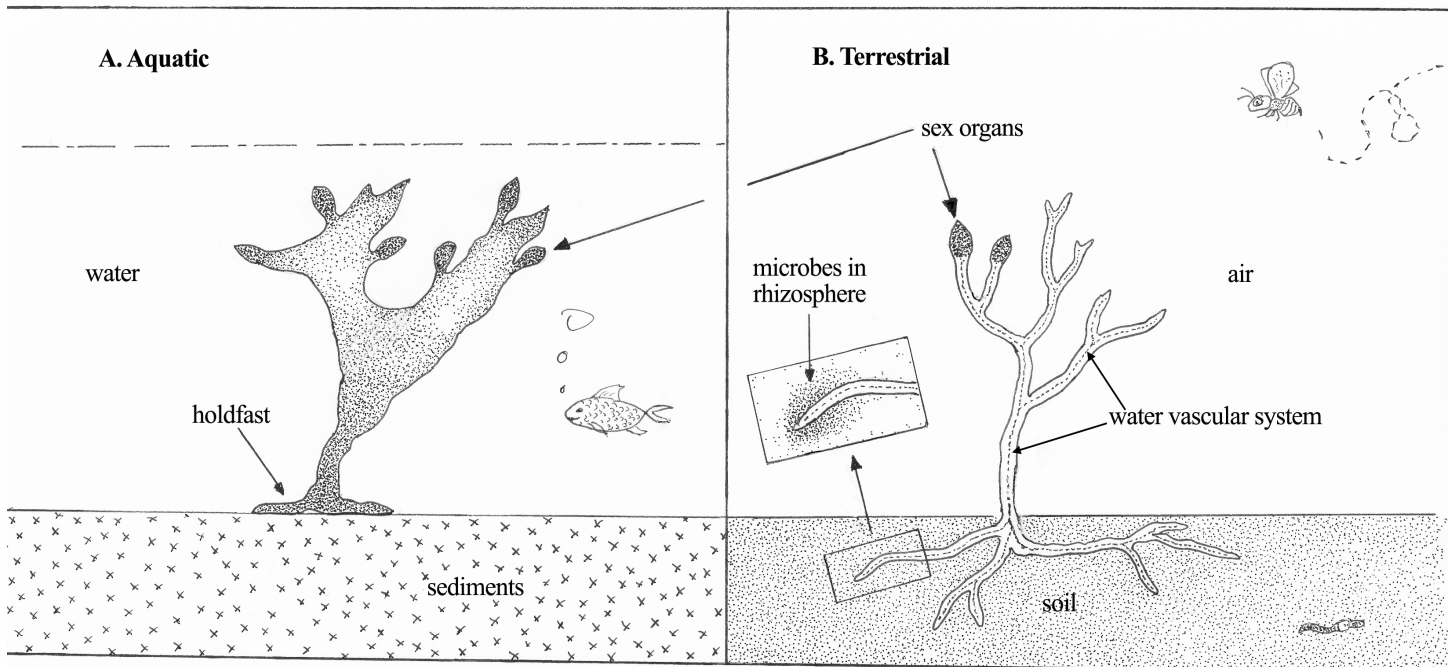


Figure 1F: Depictions of the aquatic predecessor of the vascular plants and its desiccation-defying, land-colonizing immediate descendant. Note the relatively undifferentiated body of **A** as opposed to the distinctly bipartite organization of **B** and its possession of a water transport system (= xylem). Also shown is how certain free-living soil-dwelling microbes densely populate the so-called rhizosphere where they and roots exchange useful substances.

Imagine that you've been asked to design a dry-growing plant able to subsist on solar energy, CO₂ from the atmosphere and mineral nutrients and water obtained during fleeting contacts with hyper-dilute solutions and aerosols. Your invention also must favor sexual reproduction to the extent that it allocates for this purpose resources usually committed to body parts tasked with other responsibilities. Choosing CAM-type photosynthesis and enough collapsible leaf tissue (= hydrenchyma) to store lots of water (succulence) to meet the drought-related requirement would be a no brainer because both traits accomplish exactly this for thousands of xerophytic species distributed across dozens of flowering plant (= angiosperm) families (**Figures 2AA, 2A**). But equipping your creation with capacity to absorb moisture and nutrients under such dire conditions would call for something extraordinary. In the final analysis, the most distinctive of your hypothetical plant's attributes would be a cover (= indumentum) of specialized trichomes like those illustrated in **Figure 3AA** plus a body appointed to deliver exceptional resource use efficiency. It would in fact be the embodiment of something that already exists, namely an atmospheric-type bromeliad.

The stereotypical atmospheric bromeliad (assuming one exists) is well suited to be the first of our two illustrations because its roots are much diminished structurally and dedicated primarily to exclusively to mechanical support. It's a condition that required shifting responsibility for acquiring moisture and mineral nutrients to the shoot a part of most vascular plants that's already tasked with performing photosynthesis. In other words, what had been a long standing spatial separation of two complicated processes has disappeared among the grey tillandsioids (= members of subfamily Tillandsioideae) leaving both to operate from the same location—again in the shoot that part of the vascular plant body fundamentally designed to house only the second of these two operations. So why did this consolidation occur, and what are its consequences ecologically and otherwise? Was the Darwinian incentive to evolve in this direction to improve on the status quo or forge something new, perhaps entry into what had been hostile territory or the adoption of a novel life history strategy? Finally, attributes that challenge the limits of what botanical evolution can deliver must exist, and what's analyzed below may qualify as such.

Given the near catalytic role that the bipartite body played during the botanical invasion of dry land, why don't all of the modern vascular species possess more or less equally apportioned shoot and root systems? What is it that accounts for the archaic condition of the retrograde types? Could it be the nature of the living space—specifically its physical uniformity? Is it reasonable to posit that the more uniform it is the more its residents can depart from what form-wise remains in place for all but a small minority of the higher plants? Especially noteworthy as cited above for fostering such reversals are hydric sites and in marked contrast habitats characterized by scarce plant-accessible moisture and nutrients. Aquatic

Elodea canadensis, example subject number two, also is nearly root-free and its shoots contain much diminished water vascular systems. Our atmospheric bromeliad, given its decidedly arid circumstances provides an interesting parallel because by anchoring on impenetrable substrates by strictly mechanical roots it might as well be suspended in air much as *E. canadensis* grows almost entirely surrounded by water.

Recall that it was moisture in super abundance or in growth-retarding supply that guided or allowed a modest subset of taxonomically diverse vascular plant lineages to return to the body plan that had sustained their aquatic pre-vascular ancestors, but why did this happen and by what means was it accomplished? Natural selection had to be involved in its usual fashion by purging less fit individuals as the lineages in question adjusted (adapted) to wet or dry-trending growing conditions (**Essays D, E**). Moreover, each stage of this progression had to impart fitness in the Darwinian sense. In other words, the lineages on their way to the modern rootless condition as a consequence of that trajectory could not incur seriously reduced reproductive power, i.e., fecundity. Arguably, the most plausible incentive for this reproductively sustainable transition was economic, but whether or not improved resource use efficiency provided the impetus it automatically arrived as roots faded in favor of a shoot system rendered multipurposed by novel structural and functional elaboration.

Unfettered by drought, our *Elodea* specimen—illustrative subject number two contrary to the atmospheric bromeliad—could grow fast enough to reproduce sexually within months post germination, or it could as it does, delay or minimize seed production taking advantage instead of its unlimited access to moisture to overwhelm weaker growing neighbors. The atmospheric bromeliad being sluggish by comparison due to the suppressive effect of aridity on photosynthesis, requires years not months to reach first flowering so status as a competitor is relatively weak (**Essays A, H**). Apparently, it's the availability of key resources, particularly moisture, that account for why our two lineages pursue divergent life history strategies, one as a robust competitor and the other a plodding, stress-tolerating perennial. What they share that plausibly explains their parallel rootless condition is physically uniform living space, which in one case is far more conducive to photosynthesis than the other.

Our contrasting examples identify a crucial energy-based botanical fact of life, that it's the centrality of carbon/energy gain that unimpeded by drought, or by scarcity of any other required resource, makes possible sufficiently vigorous growth to fuel performances such as the massive build ups of biomass that clog drainage ditches and canals much to the consternation of their human users. What would *Elodea* being advantaged by capacity for such aggressive behavior gain by maintaining roots and xylem tissue, or by producing more seeds in such resource-rich environments when doing so might

compromise competitiveness? The life style practiced by *Elodea* clearly emphasizes vigor rather than precocious or abundant sexual reproduction. A wholly different pattern prevails for our subject number two where drought suppresses carbon gain, slows growth and extends juvenility. The result in demographic terms is pre-reproductive mortality heightened enough to assure that the individual progeny has little chance of replacing itself. Consult **Figure 2F** for a graphic depiction of this comparison based on seven life history traits.

Now take a minute to imagine being our exemplary atmospheric bromeliad perched within the canopy of some semiarid Mexican woodland. Your botanical sojourn would likely end prematurely as a result of one of several kinds of incidents and one in particular. Your chance of surviving long enough to accomplish your Darwinian imperative—that of replacing yourself—would be pretty dismal given the lengthy interval that you would need to survive to achieve sexual maturity compared to the durability of the twig or patch of bark upon which your life as an obligate epiphyte would depend. Now think about how powerfully this reality plus the depressive effects of arid climate on seed production and pre-reproductive survival would select for enhanced material use economy. How evolution has solved this problem for the atmospheric bromeliads demonstrates how botanical adaption can involve major transformation. In this case, that transformation required the physical combining of what formerly were spatially separated operations the result of which was major ecological innovation followed by abundant speciation.

Rarely does any plant grow unencumbered by a growth-limiting supply of some indispensable resource be it sunlight, moisture or a key mineral nutrient. Scarcity sufficient to depress vigor is one of nature's foremost impediments to botanical success. Deserts impose deep drought and for the native of the lower reaches of a dense evergreen forest the stiffest challenge is shade and so on. So adopting more cost-effective ways to gain and/or use one or more scarce resources should rank among the most powerful of the Darwinian incentives to which plants respond. In short, it wouldn't make economic sense for an atmospheric bromeliad facing a drought-imposed suppression of photosynthesis and diminished pre-reproductive survival to retain a typical bipartite-type body when all that its root system provides is mechanical securement. Why not redirect some of what's required to produce and maintain a more typical root system to reproduction? Why invest in a part of the body that's become more expensive than justified by its truncated service? It's this rationale combined with the environmentally uniform living space issue that seems to explain why the hundreds of grey *Tillandsia* spp. possess one of the two most noteworthy of their defining characteristics: few short-lived roots or none at all.

It's unfortunate to have no recourse other than speculation to explain why the atmospheric bromeliads rank

among the small minority of vascular plants that lack bipartite architecture. Fortunately, no such constraint applies when the subject turns to how certain processes that once were physically separated and evolved to operate under different circumstances now perform acceptably despite being structurally superposed. So how is it that CO₂ can be acquired across a boundary that's additionally tasked with acquiring mineral nutrients and regulating water balance? How does the foliar surface of an atmospheric bromeliad allow multiple, inherently antagonistic processes to co-occur free of intolerable complications? Is it possible that this arrangement indeed does impose an as yet unrecognized but tolerable degree of impairment? Whatever the answer, note in **Figure 3F** that a scanning electron micrograph of a tiny patch of *Tillandsia ionantha* leaf surface reveals two kinds of conduits. First are the stomata that mediate gas exchange and the second the epidermal appendages (trichomes) that allow moisture

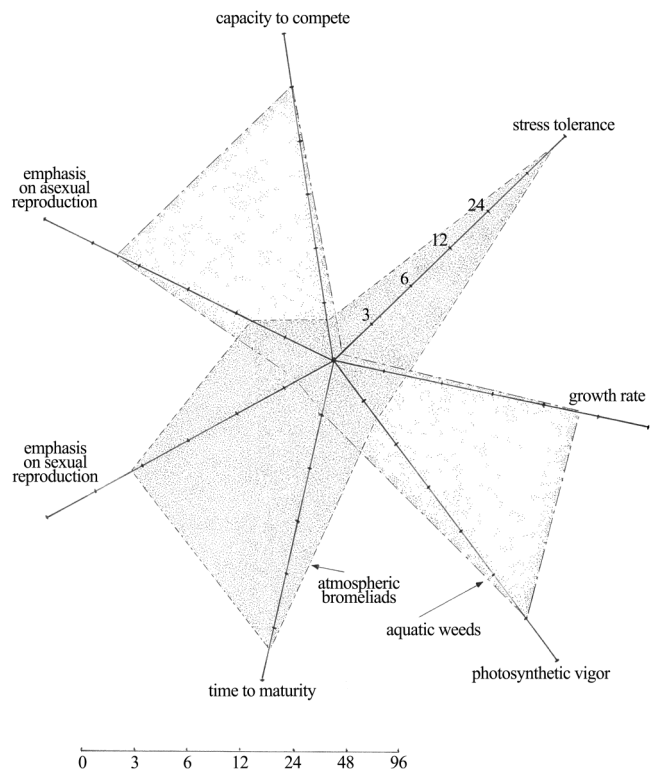


Figure 2F: Seven traits that vary in ways that distinguish the life history strategy of a submerged aquatic herb such as *Elodea* sp. from that of an atmospheric bromeliad. This graphic shows how two habitats one characterized by abundant moisture and the other by pronounced droughtiness can drive evolution toward the same simplified body plan. Note that the units used to indicate the magnitudes of these quantitative traits aren't provided. Viewed in terms of resource use versus environmental supply this model visualizes how seven life history traits acting in concert deliver two life style responses one to unlimited and the other to minimal access to water and how they affect capacity to grow and conduct photosynthesis.

and nutrients to enter the shoot and retard their escape along the same route (**Figures 3AA, 4F**).

The capacity of the bromeliad trichome to assume the absorptive tasks ordinarily assigned to roots varies from non-existent to absolute depending on the species. Moreover, reliance on trichomes doesn't come cost-free because of how the dead cells that comprise the caps of the most specialized version of this remarkable device behave when wet versus dry. While dry, the wing of the cap flexes upward away from the epidermis proper granting the now exposed stomata unimpeded access to open air (**Figures 3AA, 3F, 4F**). Upon remoistening, however, the cap cells re-engage causing the wing to return to its horizontal position, which causes the formation of a film of moisture that slows to a crawl the movements of CO₂ and O₂ in and out of the leaf interior.

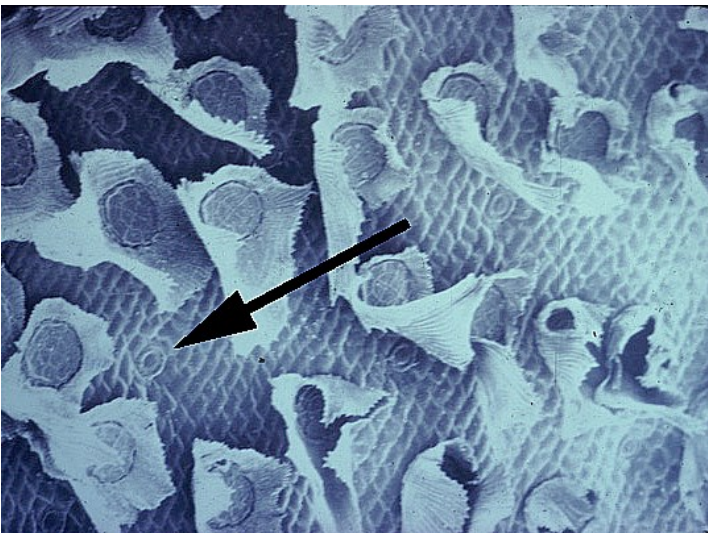


Figure 3F: A scanning electron micrograph revealing the structural detail of the surface of a leaf of *Tillandsia ionantha*. Note the expanded wing plus the four central cells and the ring cells that collectively comprise the caps of this bromeliad's absorbing trichomes. Several stomata are also shown. See also **Figure 3AA**.

Should the subject be experiencing a water deficit, or if it needs more of a particular mineral nutrient(s), both will enter the uppermost stalk cell, which is living, and course downward. But moistened too long the affected subject suffocates, and irrigated too little it desiccates beyond recovery. If it's counter intuitive that such a thin layer of moisture can be so life affecting remember that the rate at which most gasses diffuse through water is many fold slower than through air.

Now you know why the atmospheric bromeliads perform so poorly when subjected to more than brief wettings separated by longer bouts of breezy dryness. For lack of a better descriptor what we're dealing with here are plants rendered pulse-adapted by virtue of their novel attributes. All is well as long as shoots remain surface dry most of the time and growth doesn't outpace the supply of some critical nutrient. All of this comes down to the fact

that a dense layer of umbrella shaped trichomes individually equipped with a versatile cap and attached by a fast track absorbing stalk is essential. It seems that multiple factors, some widely occurring like CAM-type photosynthesis and others exclusive to this group (e.g., absorbing trichomes, few or no wiry short-lived roots) explain why the most specialized members of Bromeliaceae thrive seemingly on the edge of botanical capacity. While this arrangement works well within narrowly defined circumstances, it renders lethal the very conditions that flora adapted to more hospitable sites require. In short, atmospheric Tillandsioideae may have gotten itself via over specialization into an adaptive cul-de-sac, or put more bluntly, into what amounts to an evolutionary dead end.

Members of a second group of bromeliads that by count exceeds 2000 species rather than a fully developed root system rely on a leafy phytotelm, a device that while not exclusive to any one family has no equal elsewhere as a resource for other biota. Moreover, none of the additional plants so equipped occur in densities sufficient to suspend above ground thousands of liters of water per hectare to create what amount to extensive suspended wetlands. Cooling and humidifying woodland air are additional ecosystem-wide services. Authors of many stripes have asserted further that the tank-forming bromeliads create aerial equivalents of real soil rendering their kind providers of quarters for diverse invertebrates more commonly encountered on the forest floor. It's a greater stretch to imply that the leaves that line a phytotelm's cavity don't just replace, but actually operate like ordinary roots. While efforts to identify the diverse users of the phytotelm-bearers have been underway for more than 150 years only recently has what the hosting plant reaps in return begun to receive its due attention (**Essay B**).

Compared to their more architecturally abbreviated atmospheric-type relatives, the phytotelm-type bromeliads continue to sport fairly extensive root systems a necessity for bearing the weight of an often substantial shoot(s) along with its accumulated contents. The propensity for a sizable fraction of the tank species to anchor on relatively hospitable substrates—moss and debris-covered bark or rock rather than naked bark for example—perhaps explains why their roots remain able to generate root hairs, something often reported by growers. Freedom from reliance on roots as the organs primarily responsible for acquiring moisture and nutrients increases as the subject progresses from its juvenile stage to being large enough to support a leafy reservoir. Once achieved, this advanced state of affairs renders the shoot responsible both for its traditional duties and for acquiring most if not all of the individual's needed moisture and nutrients as for the atmospheric.

Considering the myriad lifestyles that possession of a phytotelma fashioned from foliage makes possible why don't more families match the bromeliad's tank-supported success? It's strange that nothing close to the same outcome exists elsewhere among the monocot taxa that share similar form. After all, how much evolutionary

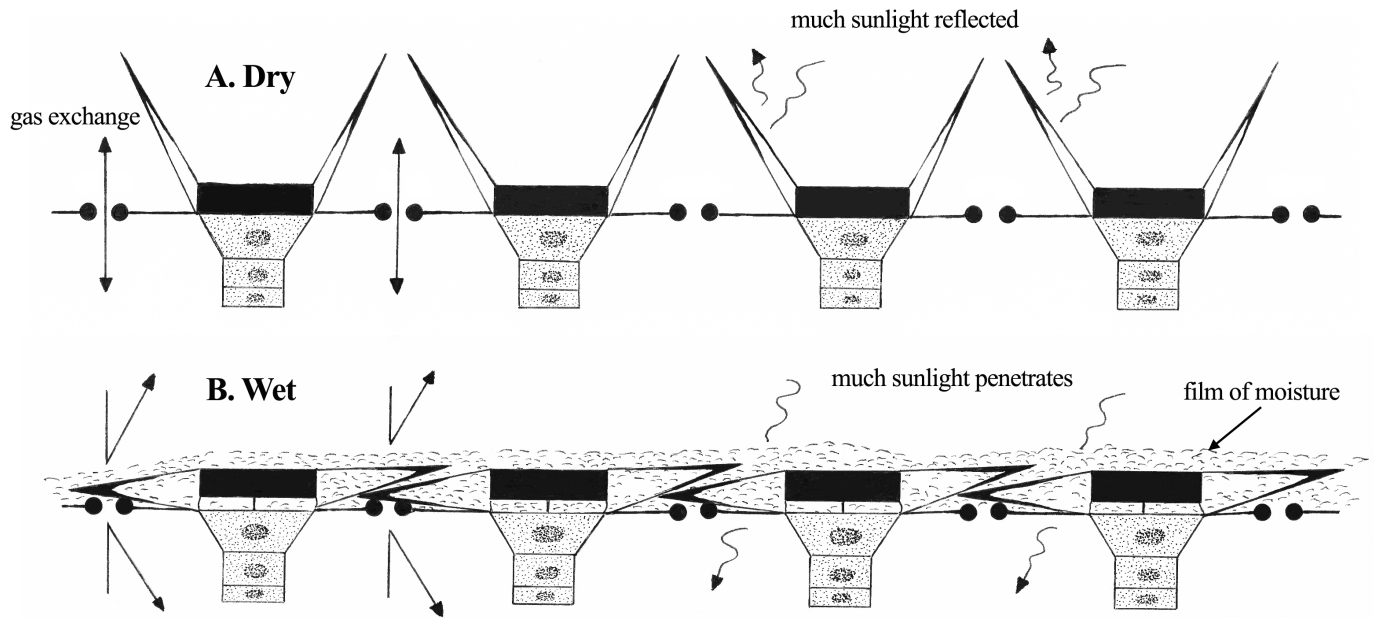


Figure 4F: The atmospheric type trichome and its influence on gas exchange and the absorption versus reflection of incident sunlight. Image **A** depicts how the wings of the trichomes covering a stretch of dry leaf surface by standing upright reflect much sunlight and don't impede gas exchange and **B** these same caps flattened while engorged with moisture greatly reducing gas exchange and by being translucent allow more sunlight to reach the leaf interior. Reflecting so much light while dry the trichome cap also reduces heat gain thereby compensating in part for a CAM plant's modest capacity to benefit from the evaporative cooling that attends transpiration.

opportunity separates a shoot that bears congested, strap shaped leaves produced by basal meristems from another that does the same but with more tightly overlapped foliage capable of impounding useful substances (**Figures 5F–7F**)? Could it be that the bromeliad trichome was uniquely disposed to evolve capacity for absorption sufficient to replace that of roots? And or was this potential uniquely realized in Bromeliaceae in response to conditions that prevail in the interior of its tank shoot with the refinements of trichomes described above for atmospheric-level performance coming on line later? If the answer is affirmative, then perhaps it was the existence of a widely occurring monocot body plan that in only one instance (lineage) just happened to co-occur with a peculiar kind of epidermal appendage that explains how one family has achieved such prominence as a home for epiphytes and lithophytes as well as their diverse microbial and animal symbionts.

Botanists have long been aware that mycorrhizal fungi (= root-inhabiting species that swap useful substances with their hosts) enhance an infected plant's capacity to scavenge phosphorus and certain other mineral nutrients from impoverished soils, and that legumes obtain nitrogen from root-inhabiting bacteria. More recently it's become recognized that free-living microbes, particularly those that inhabit the rhizosphere—the soil immediately adjacent roots—assist plant nutrition as well (**Figure 1F**). Given these precedents, is it far fetched to suspect that the micro-biota that resides in a leafy tank are functionally equivalent to the heralded human gut micro-

biome? It's already been demonstrated that at least some bromeliads harbor tank-dwelling nitrogen fixers (e.g., cyanobacteria), and that fungi of yet to be determined nutritional significance live on the surfaces of and within the foliage of certain atmospheric *Tillandsia* spp. More thoroughly documented compared to that alluded to above is the occurrence among the leaf base chambers of the tank-equipped bromeliads of many of the same macro-invertebrates that help reduce litter to humus on the forest floor (**Figures 6–7F**).

Research currently underway is revealing how the non-nitrogen fixers among sampled tank-dwelling microflora contribute to their host's nutrition as a consequence of their own way of living under often narrowly defined conditions. The saprophytes, the ultimate mineralizers of impounded litter, segregate according to stringent requirements and tolerances (**Essay B**). Particularly useful for these kinds of inquiries are DNA probes tailored to identify subgroups within the archaeal and eubacterial communities some of which require oxygen-poor micro-sites (= the anaerobes) while others (= the aerobes) the exact opposite (**Figure 7F**). Of the photo-autotrophs present some conduct the kind of photosynthesis that generates molecular oxygen (O_2) in addition to glucose as do the higher plants and others the non-oxygen (= anoxygenic) yielding, more primitive microbial way of harnessing the sun's energy to manufacture food. Despite being so small some of these mini-ecosystems harbor many and possibly the entire array of procaryotes responsible for the chemi-

cal conversions through which nitrogen and sulfur cycle on global scales.

The presence of anaerobes so close to others that demand free oxygen confirms that steep chemical-physical gradients develop within bromeliad phytotelmata loaded with wet organic matter (**Figures 6–7F**). Carbonic acid, an indicator of the amount of dissolved CO₂ present, fluctuates tending to rise at night as the bromeliad and its residents dark-respire only to fall back the following morning as the photo-synthesizers resume their normal solar-driven daytime activity. Many a coastal mudflat and wetland soil host similar microbial communities, although not all of their characteristics accord with what's known about what resides within and goes on inside the tanks of the few bromeliads surveyed so far. But, on one point we can be sure: the phytotelma-bearing species have had ample time to forge with their microbial occupants mutualistic arrangements that involve tapping the flows of nutrients and energy that elsewhere tie whole populations of such organisms into self-sustaining ecosystems. It's also worth finding out whether tank-equipped Bromeliaceae enhance such assistance by secreting or leaking into their tanks metabolites such as conventional roots liberate into soil (**Figure 1F**).

Plenty of non-bromeliads confirm that absorbing trichomes, intercepted organic matter and truncated bodies aren't the only tickets to success where the most stress-tolerant epiphytes and lithophytes grow. Consider just the orchids thousands of which fare as well as their bromeliad neighbors in some of the harshest living spaces occupied by vascular flora. Not only are the participating orchids traditionally apportioned, their aerial roots usually conduct photosynthesis without compromising their utility as foragers of mineral nutrients and moisture. Likewise, a number of co-occurring, equally stress-tolerating ferns (e.g. the Resurrection Fern, *Pleopeltis polypodioides*) remain bipartite although trichomes often densely invest rhizomes and foliage. Plausible explanations for why different lineages have become adapted in different ways to the same circumstances exist, but reviewing them here is beyond our purpose.

Figures 1B and 5F illustrate how by virtue of its many refinements the bromeliad phytotelm grants its bearers access to nutrients located in sources far beyond just shoot-impounded debris. Readers wishing to delve deeper into this subject should consult **Essay B** because what follows concerns how, assisted by the occupants of their phytotelmata, the tank-equipped types obtain what spent phytomass (= plant biomass) contains that makes its capture cost-effective. Just ahead is how the contents of a leafy tank compare with true soil, how it becomes soil-like and to what extent tank-forming foliage has been evolutionarily reengineered to add to its traditional services what roots ordinarily do. Specifically, how are the lower and upper parts of such appendages modified to operate under markedly divergent conditions? Keep in mind throughout that in the final analysis our subjects are

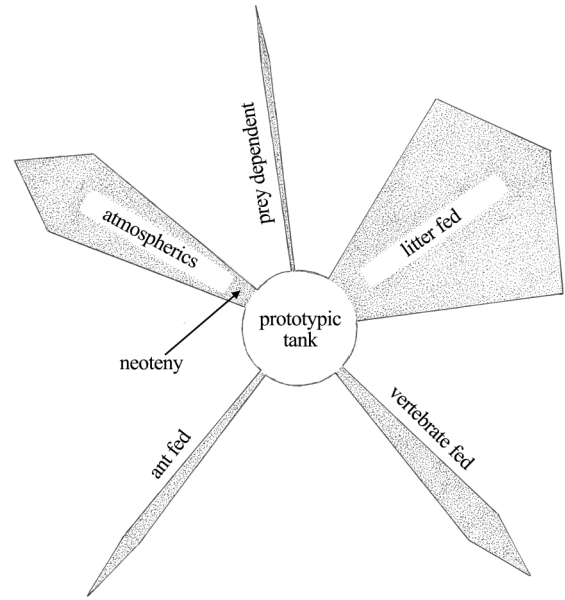


Figure 5F: How the prototypic tank shoot evolved to provide access to multiple unconventional sources of nutrients and how its disappearance as a consequence of neoteny yielded the body that supports the atmospheric type life style. Arrow thickness approximates the numbers of participating species.

dependent on miniature ecosystems populated by residents—plant benefiting and otherwise—that range from microbes to higher vertebrates. **Figure 6F** illustrates the shoot of a *Guzmania monostachia* specimen cut away to reveal its humus-filled leaf base chambers, and **Figure 7F** a labeled version of the same thing.

The solids captured in the phytotelm of a forest-dwelling bromeliad, while less by volume than the amount of terrestrial soil exploited by many a similar sized, more conventionally organized plant it's obviously a viable alternative. This is so even though half or more of the nitrogen and phosphorus that woody perennials commit to their foliage has been retrieved for reuse prior to shedding. Whatever the precise numbers, our concern here is what's left behind—probably as much as 1.0% by dry weight for nitrogen and approximately one fifteenth this concentration for phosphorus—because it's this residual that's available for third party benefit. The question remaining is whether the tank biota involved grant the hosting bromeliad its opportunity to garner enough of what's left behind to make the support of its microbial assistants worthwhile. Is the fact that several phytotelm equipped bromeliads have proven able to absorb urea, certain amino acids and several additional low molecular weight nitrogen-containing organic molecules evidence of capacity adopted to compete with microbial helpers (**Figure 7F; Aguetoni et al. 2009; Matiz et al. 2017, 2019; Takahashi & Mercier 2011; Pereira et al. 2018**)?



Figure 6F: A sectioned shoot of *Guzmania monostachia* exposing the humus contained in the inflated axils of its tank-forming leaves.

How does a tank-forming leaf differ from the more ordinary monocot kind? Given that the former type possesses a sheath-like expanded base able to operate under water or embedded in moist humus while the blade is surrounded by air, wouldn't it be odd if little of functional importance also differed across its linear extent? **Figure 7F** reveals some internal differentiation. Like most monocot leaves parallel veins alternating with air-filled channels traverse the entire organ, but in this case the diameters of the latter as well as their interspacing broaden upon reaching the sheath. Presumably, the flaring of these conduits quickens the flow of oxygen-enriched air coming from the blade to a region that possessing no stomata or green tissue. Leaf thickness decreases somewhat as well, and the neat rows of stomata located between the veins peter out in the same direction. When it comes to trichomes the picture is somewhat ambiguous. Those that contact the shoot's impounded contents versus above tend to be more densely distributed, and they feature broader caps. Whether being situated below is accompanied by superior absorptive capacity hasn't been tested, but it seems likely.

How are the tasks performed at different sites across a phytotelm-type leaf coordinated? Studies of how plants behave overall suggest that cross talk among different tissues and organs is ubiquitous. If so, then to what degree does what satisfies this need for a tank bromeliad parallel what happens when the root system of a more conventionally structured plant informs via xylem-delivered hormones the shoot about the amount of moisture remaining in the supporting soil? We can assume that whatever works for the tank producers is part of a coordinated network of sensing and responding devices crafted by Darwinian evolution to reduce a subject's chance of experiencing lethal desiccation (**Essay I**). No matter how similar the basic process higher level details probably deviate

from the ordinary as is likely necessary to accommodate the peculiar architecture and distribution of functions that characterize the tank-forming leaf. Future investigators may discover, for example, that compared to say a corn plant that operates as a physiologically integrated whole, the individual leaf performs more autonomously as the phytotelm of which it is a part alternately fills and empties.

An investigator preparing to conduct an experiment must gather enough subjects to produce statistically acceptable results and this isn't always practical or even possible. In the latter case, the solution requires settling for a proxy as has been done to study human inheritance by manipulating other organisms ranging from fruit flies to garden peas (**Essay E**). A remedy of this sort applies for efforts to study the performance of the phytotelm-type bromeliads—a sizable and diverse group—where the best candidate we've got as of this writing is *Guzmania monostachia*. This wide-ranging tank-former earned its status as representative of its kind by default largely because it was chosen as the subject for early explorations of epiphyte eco-physiology. And again, by chance rather than choice it turns out to be an outlier owing to its extraordinary ability to regulate water use and avoiding photo-injury, a capacity enabled in part by its preparedness to switch between two carbon fixation pathways, namely C_3 and CAM-type photosynthesis (**Essay A**). For better or worse, *G. monostachia* is the source for much of what's about to be described.

Once again, what should we make of the fact that the tank-type leaf operates under two widely disparate conditions, one dark and wet and relatively oxygen-free and the other dry and better illuminated and ventilated. What happens at these environmentally distinct locations and in the area between, and how are their disparate services coordinated to serve the whole? Communication as cited above is crucial and photosynthesis illustrates why. Drawing CO_2 from the atmosphere levies a cost in water transpired, and if a subject's hydric reserve were exhausted while food making continued disaster would result (**Essay A**). Fortunately, *Guzmania monostachia*'s fine-tuning to fluctuating climate makes it an accomplished practitioner of a tactic that calls for multidimensional regulatory oversight. It turns out, for instance, that nitrogen nutrition constitutes an additional voice regarding how water is used to fix CO_2 , proof positive that no less than for you and me this plant's survival depends on a complicated network of highly integrated processes not all of which appear outwardly as interconnected as they truly are.

Consult **Essay A** to refresh your memory about how thousands of dry growing plants that range from bromeliads to cacti employ CAM-type photosynthesis to use water more economically while manufacturing glucose than would be possible via the more primitive C_3 pathway. While CAM-mediated CO_2 fixation is less productive of biomass compared to its more water-use-intensive alternative, the former delivers the added benefit of promoting immunity to photo-injury, a threat that

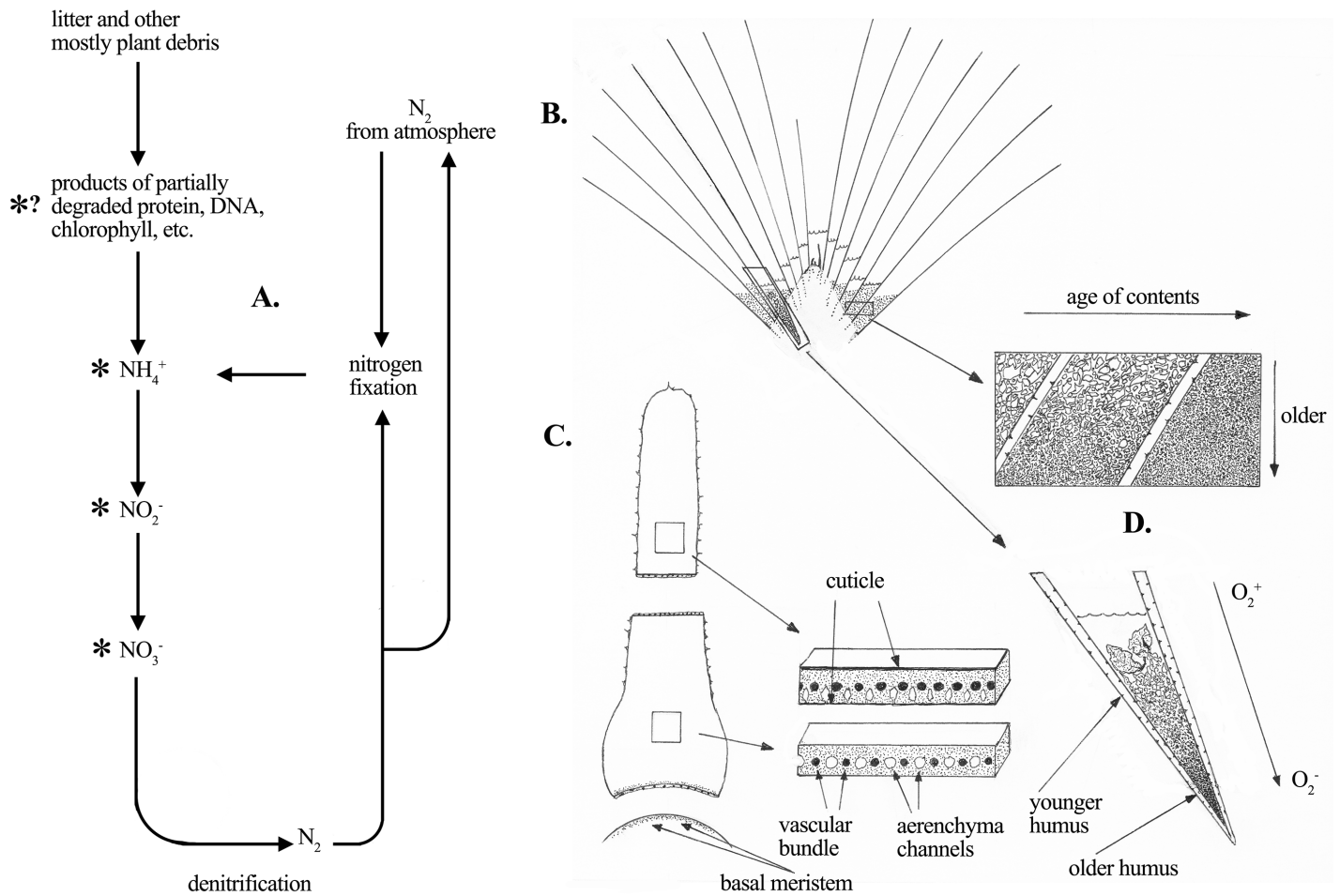


Figure 7F: The fate of tank-intercepted litter and the nitrogen contained therein. **A.** The chemical forms of nitrogen present in the phytotelmata of a litter-dependent bromeliad only some of which are plant nutrients (indicated by asterisks). That fraction converted to molecular nitrogen (N_2) being a gas, escapes into the atmosphere. Not shown are additional losses that result from tank flushing by precipitation and as constituents of the bodies of departing fauna. In effect, the same stages through which nitrogen cycles globally may occur in miniature within some bromeliad phytotelmata. **B.** A tank shoot sectioned to show the locations and relative ages of its impounded biomass. **C.** A leaf of *Aechmea bracteata* illustrating the internal anatomy of its blade and base and the location of the basal meristem from which leaves arise. **D.** A portion of a phytotelma showing how intercepted debris is steadily reduced to ever smaller particles by detritivores, and how microorganisms create the oxygen-free environment that allows the anaerobes among them to help finish the task of reducing (mineralizing) litter to its elemental constituents.

mounts as foliage experiences heightening drought-induced stress. Being able to switch between these two biosynthetic pathways prepares *Guzmania monostachia* to tolerate fluctuating wet and dry weather while anchored on shrubs and trees that exacerbate its hydric challenge by seasonally shedding and replacing their foliage. But how does our subject know when to shift gears and how is this accomplished? Only recently have some of the pieces begun falling together. **Essay I** describes how plants sense water deficits, and now we know from *G. monostachia* that the signal that induces CAM in at least one bromeliad is strongest while the affected individual is nitrogen-starved, and its major source of supply, however meager, is chemically reduced meaning present predominantly as NH_4^+ rather than as NO_3^- (**Figure 7F**).

For anyone seeking an unambiguous example of how a bromeliad's physiology is coordinated via chemical communication, once again *Guzmania monostachia* comes to mind. Plants, as demonstrated by this intermediate C_3 -CAM-type species, use hormones along with various signaling molecules to up and down regulate in timely fashion vital tissue and organ-specific activities. We've already seen that *G. monostachia* does this for shifting conditions that involve light and humidity that if not followed by appropriate responses would exact a high toll as noted for water use versus photosynthesis. At least three substances come into play when our model tank bromeliad experiences drought severe enough to force its stomata to close, a condition that causes the radiant energy that continues to stream down from an unrelenting sun to build up enough to injure the photosynthetic

apparatus of what by that time has become seriously challenged. The workings of this trio of chemicals are best known for abscisic acid (ABA) a hormone that affects plant growth and metabolism in multiple ways that include the regulation of seed germination and bud dormancy in addition to water use. Number two is peroxide (H_2O_2), a powerful oxidant with number three being nitric oxide (NO), an agent that regulates numerous cellular events crucial to the wellbeing of plants and animals (**Mioto and Mercier 2013**).

Fortunately for the investigator bent on studying drought-tolerance there's a clever way to speed up in the laboratory what weather imposes slowly in nature. Simply immerse the experimental plant, or whichever of its organs or tissues are targeted, in water containing ethylene glycol, the same agent employed to depress the freezing point of the fluid used to cool your car's engine. This technique was applied to *Guzmania monostachia* and one week later harvested foliage, now partially dehydrated by the osmotic power of a 30% glycol solution, had become both chemically and functionally transformed.

Concentrations of ABA, that inducer of CAM-type photosynthesis, had risen throughout the treated organs. Levels of peroxide and nitric oxide had gone up as well, but the former only in the bases of treated leaves and for the latter primarily in the blades. Abscisic acid had further reduced the subject's vulnerability to drought and photo-injury by cueing the synthesis of an array of antioxidants whose functions among others include neutralizing corrosive free radicals produced as described above when

closed stomata deny the CO_2 supply needed to conduct sufficient photosynthesis to consume enough absorbed solar radiation to stave off plant damage. What we have here is a signal cascade and induced cellular responses all set into motion by a plant's alerted stress detectors (**Essay I**).

The time having arrived to wind things up, our brief review begins with the litter-impounding bromeliads. These are the most numerous among the types of phytotelm-equipped species, and they rank highest as ecological subsets demonstrate alternatives to vegetable matter as nutrient sources (**Figures 1, 5–6B**). Several of these outliers exhibit low (*Catopsis berteroniana*) or moderate (*Brocchinia reducta*) grade expressions of carnivory and still others reliance on nutrients received nondestructively from tank-dwelling mutualists that range from nitrogen-fixing cyanobacteria to frogs and salamanders. Remember also that phytotelm-dominated architecture preceded even more derived arrangements that include what's exemplified by ant-house *Tillandsia caput-medusae* and even more impressively by the neotenic, most structurally abbreviated, trichome-reliant atmospherics (**Essay H; Figures 5B, 5F**). Everything considered, there's a simple way to test the most profound of the lessons embedded in this essay. Posed as a question, it goes like this: how much of the ecological, functional and structural variety attributed to Bromeliaceae in this essay would exist had the family's ancestry not included lineages able to abandon the bipartite vascular plant body?

ESSAY G. THE EPIPHYTIC BROMELIADS: ORIGINS, ADAPTATIONS, AND BIODIVERSITY

Epiphytism is a botanical lifestyle that applies when one plant, an epiphyte, grows non-parasitically upon another plant known as its phorophyte. Close to 10% of the angiosperms (flowering plants) meet this criterion and they hail from more than 80 families. However, only a handful—Bromeliaceae being one—account for most of the roughly 31,000 conforming species, and it's this family again, exceeded only by Orchidaceae, that most broadly exploits the living space that accommodates plants of this description. The structural and functional variety that underpins this success is evident even in comparisons of many pairs of closely related populations. Leaf thickness, texture and reflectivity, to cite one example, reveal that *Tillandsia xerographica* needs substantially more light and less moisture than shade-tolerant drought-sensitive *T. leiboldiana*. Another dimension of eco-diversity known as ecological habit, a distinction that includes a subject's reliance on a specific kind of substrate, isn't so easily discerned. Appearance alone tends not to reveal whether a particular species roots consistently in the ground, on rocks or in the crowns of trees. This seventh essay examines bromeliad epiphytism, specifically, its origin, operation and significance in ecosystems.

The surest way to appreciate the difficulties inherent to life as an epiphyte would be to assume the place of one of its practitioners (**Figure 2D**). Challenge accepted your lesson would begin with dispersal as a seed to a suitable patch of bark that should it be missed—a high probability—your adventure would end almost before it began. Following a successful launch and landing, survival over the following weeks to months would hinge on the staying power of a couple of adhesive hairs or a bit of sticky mucilage (**Figure 1C**). Then, after becoming more firmly anchored by holdfast roots, years would be required to marshal the resources, often from thinly provisioned sources—think mineral nutrients dissolved in precipitation—needed to mature and reproduce. Timing would be crucial because replacing yourself would have to occur prior to an event, most likely a dislodgment, that would assure a swift death on the ground. On the other hand, options for sustaining yourself up to this point would have been numerous because none of the devices and mechanisms employed to make a botanical living defines the epiphytes as a group. Should the subject you replace be a bromeliad it wouldn't matter whether it depended on a leafy tank, or on roots or on a cloak of root-substituting trichomes, or if it conducted C₃ or CAM-type photosynthesis (**Essay A**).

Before moving on, it's important to put to rest two misconceptions about epiphytes. The first is the notion that being no more than modest-sized encouraged the terrestrial ancestors of the epiphytes “to move” up into the forest canopy to access brighter sunlight. The second concerns gravity in the sense that to be what amounts to a

botanical arborealist requires no more than a means to defy what for the obligate epiphyte constitutes a deadly force. Claim number one imputes willfulness where none can exist, and number two oversimplifies reality. In fact, the mix and number of traits that support flora that spend lives anchored above ground is extensive, but which traits and in what combinations serve a particular species depends on its taxonomic affiliation and the circumstances to which it is adapted. The lengthy list of the means for obtaining and using resources by the species so equipped explain why canopy-based flora can account for more than half of the botanical inventory characteristic of the most bio-diverse of tropical forests. Being broadly based taxonomically further assures that much of what the vascular epiphytes add to an ecosystem is delivered in numerous forms in multiple ways.

Now that it's clear that epiphytism is facilitated by diverse traits in multiple combinations how do such arrangements compare with those that serve the natives of other kinds of habitats? How close do they match what sustains the residents of a forest understory or a desert community? If only partially overlapped which are the shared traits and do they provide similar service? Keep in mind that life stage and timing belong in this mix as the benefits provided by this or that trait may be expressed only during germination or while a subject is experiencing severe drought. Returning to the issue of growth habit, what distinguishes the epiphytes from their closest relatives that colonize rocks or that root only in the ground? And what about mortality? Why, following a fall from its host does the obligate epiphyte almost always die? Does this inevitability tell us that utilizing another plant for mechanical support is a marginally sustainable eco-strategy? What about facultative epiphytism, and how much do growing conditions in a woodland's canopy versus below differ across the many kinds of forested ecosystems that harbor arboreal flora?

The presence of at least a few epiphytes in most of the sizable taxa above the rank of family indicates that epiphytism has emerged repeatedly and apparently with considerable evolutionary ease. But to what extent are these historic events comparable. Which traits came together first and in what order and in response to what Darwinian incentives? Why, although epiphytism occurs so broadly, do so few families account for most of its practitioners? Beyond what's required to counter gravity to what else do the most epiphyte-rich angiosperm families such as Araceae, Gesneriaceae, Piperaceae and Orchidaceae in addition to Bromeliaceae owe their over representation above ground? Many of the adaptations (e.g., succulence, CAM-type photosynthesis) that sustain epiphytes and lithophytes likely do much the same, i.e., provide similar service, for tens of thousands of soil-rooted terrestrials. Indeed, many of the species that endure the conditions that prevail at one or the other end of the climatic gradient featured in **Figure 1G** are facultative types, which is to say that for them life is doable on and above ground.

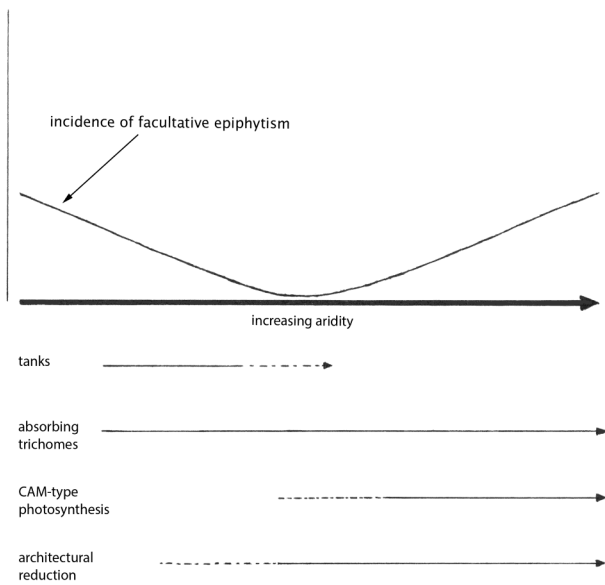


Figure 1G: How humidity relates to certain aspects of the structure, function and ecology of the epiphytic bromeliads. Facultative as opposed to obligate epiphytism is most common at the wet and dry ends of this gradient of climates. Under what conditions the four most enabling of the attributes possessed by these species assist survival are illustrated as well. The solid parts of arrows indicate where contributions to fitness are highest and where dotted their influence is less. See text for additional details.

It should come as no surprise to read that attributes such as large seeds and bulky bodies aren't conducive to epiphytism. Think about the conifers along with numerous species-rich woody, predominantly tropical flowering plant families such as Annonaceae, Lauraceae and Mimosaceae none of which includes more than a few epiphytes. A more workable, but still significant impediment is sluggish growth particularly where multiple years pass on the way to sexual maturity. Conversely, lightweight seeds (or spores), substantial drought-tolerance, a cheaply constructed (= herbaceous) body and animal-mediated pollination are positive traits although none beyond the fourth appears essential for life free of root access to the ground. Wind pollination, a widely exploited syndrome among the terrestrials—think grasses and oaks—appears ill-suited for epiphytes probably owing to the hyper-dispersed structure of so many of their populations and the high cost of producing the required abundant pollen.

For a trait to be an adaptation it must help elevate Darwinian fitness, i.e., it must heighten its possessor's chance of passing its genes on to future generations. Context is all-important because whatever the aspect of structure, function or timing at issue, its presence needs to promote benefit where its owners naturally grow. In other words, it's the nature of the subject's circumstances, what it has to contend with, that make the difference. No organism will perform equally well or even survive under conditions other than those to which its kind have been

shaped by natural selection, and the more specialized in this respect the narrower its eco-tolerances as illustrated graphically in **Figure 2G** and presented more comprehensively in **Essay H**. What's more, functional tradeoff is the consistent attendant of biological specialization as demonstrated by the dense covers of absorptive trichomes that invest the shoots of the atmospheric bromeliads, species that lifestyle-wise represent the least conventional members of a family well known for its uncommon qualities. Where opportunity to rehydrate is infrequent and fleeting these minute devices deliver life-sustaining service. Wetted too often or for too long their bearers suffocate having at that point become over irrigated (**Figures 2F, 4F**).

Only the uncommon hyper-wet woodland provides its aerial flora enough moisture to conduct photosynthesis at mostly their maximum attainable rates, conditions being far less accommodating where most of the epiphytic bromeliads grow. Moving to the right along the climatic gradient plotted in **Figure 3G** reveals by two diverging arrows how plant-available moisture falls faster for canopy-anchored flora than that rooted below. Whereas supplies remain sufficient for deeply rooted terrestrials as dry seasons lengthen this isn't the case for the bark-dwelling lichens and mosses and their accumulated remains that make up the suspended soil-like media upon which the more drought-vulnerable of the vascular epiphytes depend for moisture during dry weather. Possession of a tank compensates, but only to a point after which this device becomes a liability (**Figure 3G**). It's this difference in

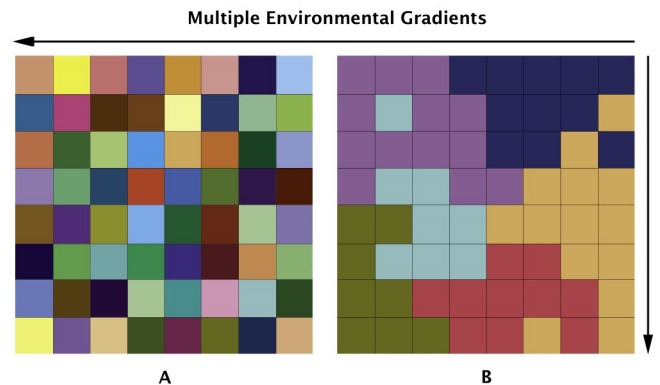


Figure 2G: The relationships between structural and functional specialization and ecological breadth. Both grids incorporate 64 spatial niches (= living spaces each of which is characterized by a unique combination of growing conditions) aligned along multiple environmental gradients such as annual rainfall, length of a dry season and type of substrate. Each color indicates a different lineage (species). Grid A illustrates how an ancestral lineage that generates ecologically specialized daughter lineages has filled a heterogeneous living space compared to another less able to deliver the same level of performance. Daughter lineages in the second case being less specialized (having broader eco-bandwidths) will be fewer in number and occupy multiple, ecologically similar (adjacent) niches.

access that explains why such a large portion of the higher plant species present in a humid tropical forest can be arboreal while the membership of this same category accounts for no more than a few percent where tree crowns offer near desert like conditions much of the year. Not only has the proportion of epiphytes undergone the steeper of the two declines so has the number of families to which they belong.

A second dynamic adds to the trend just described (**Figure 3G**). This time it's the relationship between a critical stage in the plant life cycle and the durability of aerial versus terrestrial substrates (anchorage). Variable number one in what is a passive but precarious association for epiphytes is the average length of time required by the members of a population—again of an epiphyte—to progress from germination to reproductive maturity, the all-important metric introduced above. The second is the lifetime of the elevated perches that our subjects require. The first variable is climate-sensitive because photosynthesis, being water-expensive, is slowed by drought and this in turn increases the time that a plant needs to

reach sexual maturity. In the final analysis, the longer a substrate remains serviceable the greater its capacity to mechanically support a perennial whose juvenile stage is prolonged by drought. Why the traits that grant drought-tolerance for the higher plants slow growth and maturation is explained in **Essay A**.

Why of the numerous lineages that have made the transition from ground to aerial life have so few gone on to launch exuberant radiations where aridity severely constrains photosynthesis? Could it be that evolution hasn't more often assembled the trait networks necessary for existence at the dry end of the gradient depicted in **Figure 3G**? Does this suggestion make sense considering how most of the attributes that serve the most stress-tolerant of the epiphytes do the same for numerous terrestrial xerophytes (= dry growing plants; **Essay A**; **Figure 2AA**)? Might we be witnessing a consequence born primarily of ecological disturbance—disturbance in this instance being the short lives of acceptable substrates (e.g., bark)? Keep in mind that ecological disturbance is one of those many plant-defined variables. The rate of turnover of a substrate

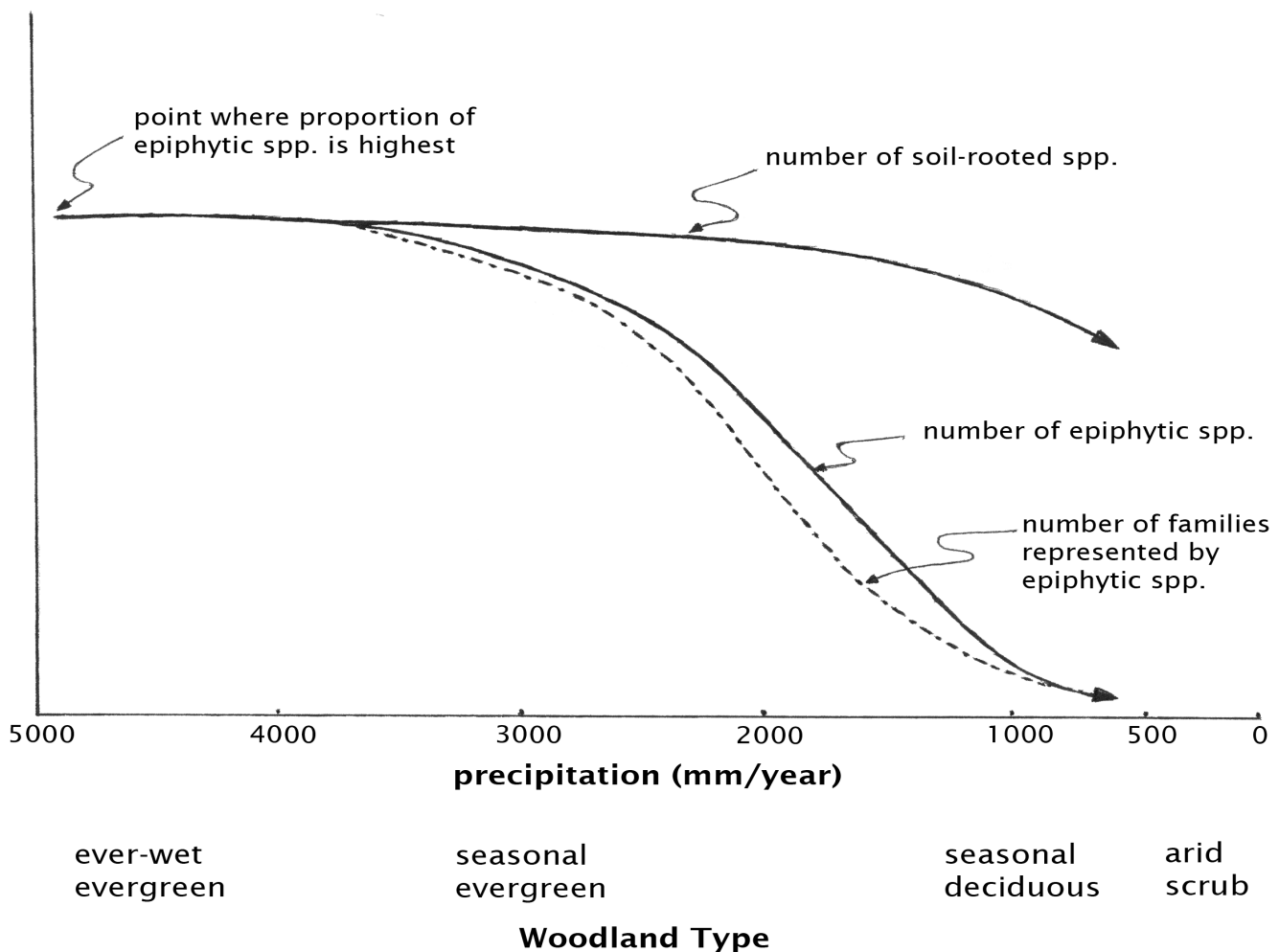


Figure 3G: How moisture supply influences the occurrence and taxonomic diversity of epiphytic versus soil-rooted flora.

that constitutes intolerable disturbance for a slow growing subject won't be so for its more vigorous counterparts all else being equal. It's possible that how fast aerial substrates come and go combined with the growth-suppressing effects of drought have excluded all but the memberships of a modest collection of exceptionally resource-capture-use efficient, stress-tolerant species that hail from just a few families of ferns and flowering plants among the most prominent of the latter being Bromeliaceae.

Hyper-wet conditions certainly favor epiphytism, but additional promoters exist as well, another being access to arboreal ants amenable to enticement to deliver plant-usable nutrients and/or to serve as body guards against roving herbivores (e.g., genus *Myrmecodia* spp. of family Rubiaceae and *Tillandsia caput-medusae*; **Figures 1, 5B**). Now add to this growing list the benefits that accrue from having no need to produce anatomical (e.g., spines) or chemical deterrents against the many vegetarians that don't climb trees. Still another advantage reaches its zenith at the dry end of our humidity continuum. The conditions that an arid woodland ecosystem presents to its resident epiphytes include living spaces that although stress-inducing can be in another respect quite forgiving if the resident is small-bodied and properly shaped. To be almost surrounded by air and light perched on a twig makes quite advantageous a kind of anatomical streamlining illustrated by the much-diminished root system of an atmospheric bromeliad (**Essays F, H**). It's possible that the attending gain in resource use economy is contributing markedly to the stress-tolerance that an epiphyte having no access to soil requires to colonize some of the starkest of habitats penetrated by vascular flora (**Essays F, H**).

Having established that epiphytism is an eco-strategy enabled by numerous traits and combinations of traits (trait complexes) it's time to examine how various Bromeliaceae participate. It's best to begin by reviewing where among the family's eight subfamilies its arboreal and lithophytic members occur, and then see what this says about origins and evolutionary incentives (**Figures 1AA, 4G**). Next, we'll move on to how roughly half of the family, that half being the 50% that lacks access to earth soil as non-parasites, has opted for novel alternatives. Individuals wishing to know more about these departures from terrestrial life can consult **Essays A, B and F**. Lastly, how these unusual ways of making a botanical living came about and how do they relate one to another is topic number three. A pair of equally compelling phenomena barely mentioned in this essay but worth treatments of their own are how some of the adaptations that underpin bromeliad epiphytism benefit other organisms and/or grant the plants that possess them substantial roles as players in ecosystem-wide processes such the building and cycling of nutrient capital.

It's unrealistic to expect to discover how often terrestrial spawned epiphytic lineages during the roughly 20 million years since Bromeliaceae set off on its on-going

crown expansion (**Essay H; Figures 1AA, 2B**). But of one fact we can be certain: of these many historic events two would exceed the rest by influence on the family's current size and ecological diversity. Judging by its pervasiveness among their memberships, epiphytism emerged early during the expansions of subfamilies Bromelioideae and Tillandsioideae. Subfamily Pitcairnioideae, although similarly species-rich, remains predominantly terrestrial drought-deciduous *Pitcairnia heterophylla* being one of its few exceptions. Brocchinioideae, the phylogenetically oldest of the eight subfamilies, contains around 20 species in its single genus only a small minority of which are arboreal and none consistently so. Despite being the most ancient of the surviving bromeliad genera—a true family relic—*Brocchinia*'s foray into the aerial world isn't just anemic it's probably among the most recent (**Figure 4G**). The memberships of the remaining four subfamilies (Hechtioideae, Lindmanioideae, Navioideae and Puyoideae) are products of radiations that occurred within relatively narrow terrestrial themes (**Figure 1AA**).

Neoregelia and *Vriesea* broadly defined (*sensu lato*) plus a handful of related genera include numerous examples of relatively recent, or better put, secondary origins of bromeliad epiphytism. But be advised that some published accounts of growth habit lack ignore significant nuance. Facultative versus obligate epiphytes occur in all these genera and many others in subfamilies Bromelioideae and Tillandsioideae. Closely related populations, some terrestrial and others about as exclusively aerial, abound as well. For this much variety to prevail suggests that during the family's expansion many of its lineages repeatedly crossed what were and likely remain ecologically ill-defined boundaries between lives spent anchored on bark versus rooted in or on soil. Ever-wet conditions are particularly conducive to this kind of fluidity and no small number of the atmospheric exhibit similarly mixed performances toward the arid end of the climate continuum illustrated in **Figure 3G**. Evidentially, it's where growing conditions within and below a forest's canopy differ most—specifically, across the middle of our humidity gradient—that populations occur whose members thrive exclusively as either epiphytes or terrestrials.

The facultative epiphyte *Brocchinia tatei* easily passes as a phytotelm-equipped member of subfamily Tillandsioideae, and strictly terrestrial *B. micrantha* is by far the largest of the family's cistern producers. Grown in full sun, *B. acuminata* being only an occasional canopy user, if not an accidental epiphyte, produces shoots comprised of overlapping leaves whose inflated bases provide dry nesting sites for colonies of plant-feeding ants. Smaller, slenderer tank-forming *B. reducta* is a particularly deviant terrestrial member of its genus that substitutes small animals, primarily ants, for its presumably non-carnivorous ancestor's reliance on intercepted litter if tank-equipped, or if not just soil (**Figure 4G**). A much-reduced root system provides anchorage, but likely not much else. Its elaborate foliar trichomes (for a bromeliad) have proven

A second hypothesis describes how epiphytism arose within a stock that later would become modern Bromelioideae, a subfamily that includes many exclusively terrestrial genera (e.g., *Cryptanthus*, *Greigia*, *Fascicularia*), several of which contain wetland natives and *Dyckia*, *Encholirium* and *Orthophytum* that exemplify the dry land growers. Perhaps most important as a key adaptation and a feature that deviates markedly from what prevails in *Brocchinia* is the drought-tolerance exhibited (e.g., via CAM-type photosynthesis) by a majority of the bromelioid epiphytes and lithophytes. Particularly provocative are the tank-bearing members that often sprawl horizontally suspended up to tens of centimeters above their typically rocky substrates. Cultivate a representative of this group and within a few years your efforts will yield a tangle of tank shoots cantilevered by elongated rhizomes equipped with aerial roots (**Figure 4AA**). Although technically terrestrial, but no longer dependent on soil, such a plant should fare about as well anchored on a woody host or on rocks. The epiphytes, ignoring the few extreme pendent species, although tending to be more compact than closely related terrestrials otherwise exhibit similar architecture.

The network of inter connected tank-equipped shoots and the knob-like remains of those already expired illustrated in **Figure 4AA** trace the wanderings of a rhizomatous clone-forming *Neoregelia* sp. that had spent more than a decade advancing across a patch of open sandy soil. The youngest cohort was elevated up to 40 cm above grade with the space beneath filled with spent foliage supplemented by what appeared to be the decaying remains of spent phytotelmata. As such, it can be viewed as figuratively if not literally poised at the threshold of epiphytism. All that would be required to leave the ground for life in the forest canopy would be a simple ramp up of the counter-gravitational growth responsible for what already is the partial departure from soil exhibited by the specimen just described. In effect, this transition would have been accomplished by way of secondary hemiepiphytism. Whatever the incentive for the proposed ascension into the canopy possession of a tank at the time would have constituted additional preparation for life emancipated from terrestrialism. When it comes to why evolve a tank it's back to Brocchinioideae: was the Darwinian impetus enhanced access to moisture, to nutrients or to both? And what about light?

Figure 4G shows how bromeliad epiphytism has progressed through four evolutionary grades to reach a high level of specialization attended possibly by similarly elevated vulnerability to extirpation. Presumably at greatest risk being the most narrowly adapted to challenging growing conditions are the atmospheric types except for *Tillandsia usneoides* along with its equally weedy relatives (**Essay H**). To reach this point required a multipurposing of the foliar trichome and a major structural and functional reconfiguration of the entire vegetative body (**Essays F, H**). Such a gross transformation wouldn't have been possible had the lineages involved been

encumbered by phylogenetic constraints powerful enough to block either of these alterations. Had the antecedents been woody to cite an obvious example, certainly grade four and likely also grades two and three would not have been possible. Being equipped instead with a less expensive more malleable monocot-type body permitted access via a tank-based intermediate grade three to atmospheric-type grade four and delivery of what ranks among the most exceptional of the ecological performances delivered by land-dwelling vascular plants (**Figures 5F, 4G**).

What about redundancy? Has the family accomplished any of its most noteworthy evolutionary breakthroughs more than once? The answer is a definite yes, and among the most outstanding of the conspicuous examples is epiphytism a condition already noted as occurring in subfamilies Bromelioideae, Brocchinioideae, Pitcairnioideae and Tillandsioideae (**Figure 5AA**). And what's more, aerial life predicated on a leafy tank almost certainly emerged in at least two geographic regions one being the wet savannas of the Guayana Highlands and for early Bromelioideae somewhere within the area occupied today by what remains of Brazil's Atlantic Forest where a version of lithophytism, as suggested above, set the stage for life spent non-parasitically in the crowns of woody hosts. Epiphytism within Pitcairnioideae, given its scattered uncommon occurrence both geographically and within the few contributing genera, precludes assessment that's anywhere near what is possible for Brocchinioideae and Bromelioideae.

Three attributes most substantially set the atmospheric-type bromeliads apart from the rest of their subfamily. Trait numbers one and two are the near complete to total absence of tanks and roots and number three the presence of a dense mantle of root-substituting foliar trichomes. Succulent foliage rather than an open reservoir (tank) meets the requirement for a moisture reserve with one of the exceptions being *Tillandsia gardneri* with its broad but thin foliage. Further enhancing the capacity of these species to defy the constraints imposed by drought and impoverished substrates is the enhanced resource-use economy achieved at the expense of a fuller developed root system (**Essay F**). And for the likes of Spanish moss having the most truncated shoots (ramets) of all—just three leaves apiece—cost is lower still. So equipped, it's the ability of these bromeliads to successfully capture and deploy scarce pulse-delivered resources, both moisture and key ions, that elevates the atmospheric to a level above the rest of the family's epiphytes and lithophytes. None of this specialization comes cost-free of course. Given that as tolerance for stress mounts growth and maturation slow, and with the latter comes heightened vulnerability to pre-reproductive death at the hands of failing substrates in addition to the usual candidates (**Essay A**).

The atmospheric bromeliads vary on all three grade four criteria and probably for life-determining, species-specific reasons (**Essay H**). It's hard to imagine that the myriad body plans, surface textures and trichome charac-

teristics that make these plants so alluring to hobbyists have nothing to say about ecology and life history strategy (**Figure 2H**). It's obvious that numerous slender leaves sporting dense covers of trichomes topped by elevated elongated caps (e.g., *Tillandsia tectorum*, *T. plumosa*) signal reliance on occult water, precisely what prevails much of the year in the relatively rain-free, but frequently cloud and mist shrouded habitats occupied by these two species (**Figure 3AA**). Astute growers understand that the bromeliads that fit this description languish or die outright under conditions favored by their heat- and drought-hardier relatives such as Mexican *T. concolor* and certain populations of *T. paucifolia* (foliage stiff and thick, trichome caps flat, symmetrical and tightly overlapping). Many of the lithophytes (e.g., *Tillandsia araujei* and *T. albida*) produce leafier, longer stemmed ramets equipped with scattered and sparsely branched roots than typical for the epiphytes and so on (**Figure 2H**). How a Darwinian mechanism known as neoteny promoted what the atmospheric bromeliads as a group have become is presented in **Essay F**.

Some of the most intriguing of the unanswered questions about the epiphytic bromeliads and the atmospheric types in particular concern performance as populations on challenging substrates. Do the surfaces used by these plants for anchorage ever become saturated? How, even where seed rains are dense, can so much of what appear to be media suitable for colonization remain vacant? Perhaps more to the point, what factors render a particular microsite acceptable, and how much do the spatial niches of multiple co-occurring populations overlap? What allows a dozen or so grey *Tillandsia* spp. to share the same thinly foliated canopy of a scrubland forest? Ecological equivalence wouldn't matter if the combined reproductive effort of such a community is too meagre or mortality too high to permit competition, intra- or inter-specific, to determine its structure. Does physical disturbance ever make a difference? How about ecological succession and influences imposed by neighboring non-bromeliads?

Lots of questions have been aired in this essay some partially addressed and others only stated. One of the former type concerns the evolutionary grades of bromeliad epiphytism illustrated in **Figure 4G**. Are just four sufficient to recognize all the major steps that led to the most advanced manifestation of this lifestyle? Number three, the category erected for the phytotelma-assisted types, is strongly homoplastic its defining attribute, the leafy tank, having evolved repeatedly once in *Brocchinia* and again in Bromelioideae and Tillandsioideae. The atmospheric by contrast constitute only part of the third of these three taxa yet there may be more variety here than meets the eye (**Figure 4G**). Could it be that more functional diversity than currently recognized segregates these closely related species into two or more distinct entities each worth a stage in itself? Again, what about stage three? Finally, is there enough difference between more and less specialized and extinction-vulnerable bromeliads to justify using this important criterion as basis for another scheme?

The casual reader may find much of what's presented in this seventh narrative rather esoteric, but not likely the grower curious about why so many of their charges combine extraordinary stress tolerance with high vulnerability, and that they bring to bear such unconventional means to obtain and use resources. Unfortunately, much worth knowing remains undiscovered, for example, why do some of our subjects require more narrowly defined substrates than others. So, what are the take home lessons? For one, it's confirmation that cultural practice that mimics what goes on in nature leads to improved shapes and colors and more successful propagation. At the same time, it's fair to add that much of what remains undiscovered about bromeliad ecology and evolution will be primarily of interest to scientists. Someday perhaps we'll even get to know the details of what underlies obligate epiphytism and which traits and at what stage(s) in the life cycle ecological habit is established. In the meantime, rest assured that for a bromeliad to grow on a cliff face or on a woody host requires plenty more than a means to defy gravity.

ESSAY H. THE ATMOSPHERIC BROMELIADS: WHAT WE DO AND DON'T KNOW ABOUT THEM

Bromeliaceae isn't especially rich in species, but it's outstanding for displaying exceptional botanical structure, function and lifestyle. What justifies this accolade wouldn't exist was it not for the profound plasticity of the monocot version of the vascular plant body (**Introduction; Essay F; Figure 2AA**). What follows is a critique of the consequences of this endowment as manifested by the biologically and architecturally least conventional family members—by what are known colloquially as the grey tillandsias, the air plants, the atmospheric bromeliads or simply the atmospheric. Four questions will guide this exercise: how do these species differ from their closest relatives, how and why did they come to be what we see today, how much do they vary among themselves and finally, being so specialized how might they fair as the threat posed by global change continues its on going intensification?

Why feature the grey tillandsias in this eighth of ten essays instead of something like *Aechmea* of subfamily Bromelioideae or *Pitcairnia* of subfamily Pitcairnioideae? Better yet why not *Brocchinia*? Its barely 20 plus species make it a far more manageable candidate for the kind of analysis intended here, and when it comes to mineral nutrition its members exceed in functional variety all of the hundreds of atmospheric combined. To my thinking *Brocchinia* is the lesser choice for three reasons. First, as sister lineage to the rest of Bromeliaceae, it's already received more than its share of scientific inquiry. Second, the atmospheric mightily exceed the rest of the family's membership for overall botanical novelty, and they definitely lead when the criterion shifts to horticultural appeal. Rare is the cultivated *Brocchinia* while no self respecting hobbyists would dare fail to include at least a couple of air-plant-type tillandsias in their living collection. Lastly, it's well worth inquiring about whether embracing a life style that deviates from botanical norms as much as that of the atmospheric imperials survival in what indisputably is a deteriorating global bio-support system.

Before launching our effort it's worth calling attention to several facts. First, Bromeliaceae is the largest of the flowering plant families that's almost entirely confined to the New World proof positive of its place among the geologically most recently arrived of the clades of angiosperms granted equivalent taxonomic rank (**introduction**). DNA further indicates that Tillandsioideae, the home of the atmospheric, warrants recognition as one of the most recently diversified of the family's eight subfamilies. Even so, the tillandsioid-type reproductive apparatus—fruit and flower—remains more monocot-conventional rendering the atmospheric first rate demonstrators of mosaic evolution (**Essay C**). Unsettled is whether these hundreds of densely trichome-equipped species are monophyletic within Tillandsioideae—in oth-

er words are derived from a single lineage—or if they constitute an evolutionary grade their defining features having evolved in parallel from multiple ancestors in this case closely related antecedents.

The traits that set the atmospheric apart from their closest relatives reside in parts of the body that perform vegetative, or better put, routine maintenance functions. And as noted above, the sex organs remain much as before probably because they already were adequate to serve the atmospheric-type life style. It does appear that reduced size, one of several trends that pervade the group, has influenced reproductive mode. Like the rest of Bromeliaceae pollinators and mating systems vary among the grey tillandsias except that below an ill-defined boundary the more diminutive the individual ramet, the more likely the species at issue is sexually self-compatible (**Essay D**). To rank among the most structurally diminished of all means that fruit-set is apt to be spontaneous to boot—no outside assistance needed. But as usual there are exceptions. *Tillandsia usneoides* with its moth-pollinated, self-incompatible but tiny flowers demonstrates that even for the most streamlined of subjects pronounced reduction isn't a consistent arbiter of breeding mode.

What most conspicuously differentiates the atmospheric from the rest of their subfamily is how during development they allocate biomass such that the result is an abbreviated body clothed with multi-functioned trichomes. Most eye-catching is the often bizarrely shaped individual shoot (ramet) combined with a much-diminished root system. It's a combination that's recapitulated in a series of related extant species consistent with stepwise derivation from ancestors equipped with the same tank-dominated body plan that in moister sites continues to support a substantial portion of modern Tillandsioideae (**Essay F; Figure 1B**). We'll explore this legacy, particularly the constraint imposed by possession of a leafy tank (phytotelm) in more detail below. We'll also learn that abandoning one body plan for another during the colonization of previously inaccessible kinds of eco-space obliged exchanging one functional tradeoff for another the second of which conceivably heightens its bearer's vulnerability to extirpation.

What can we learn about the atmospheric by comparing their lives with those of the non-bromeliads that also operate minus all but few roots or none at all? Where do these species grow and how do they operate? Numerous submerged aquatics qualify along with the mistletoes with their host-invading haustoria. A third group encompasses the chlorophyll-free orchids (e.g., *Gastrodia*) that except for their inflorescences remain below ground parasitizing fungi that serve as proxies for roots. In all three instances, as for the atmospheric, resource use economy rose as roots faded and other organs or microbes took over what had been their absorptive functions. But the challenge (burden?) that accompanies rootlessness isn't experienced evenly across this disparate group being greatest for Bromeliaceae. No medium equal to water for

the aquatics, soil for the mostly subterranean orchids or host tissue for the mistletoes insulates the grey tillandsias against desiccation. Bottom line: the atmospheric have few and maybe no peers when it comes to operating with a markedly minimalist body while almost completely exposed to the atmosphere's power to desiccate unprotected organisms.

In addition to the absence of a phytotelm and a conventionally developed root system it's the multi-functioned foliar trichome that most decisively distinguishes the atmospheric from the rest of their subfamily and even more from the rest of the family (**Essay F**). For that matter, nothing possessed by any of the other angiosperms matches this minute organ's singular ability to at once assist its owners trap beneficial air borne particulates, regulate light reception, reduce heating and promote the rapid uptake and retention of moisture and the capture of mineral nutrients during fleeting contacts with hyperdilute sources such as precipitation (**Figures 2F, 3AA**). None of the root-free non-bromeliads cited above possess a foliar epidermis able to perform as many potentially antagonistic operations. Given the many attending constraints, it's difficult to imagine a more daunting challenge for maintaining adequate hydration and mineral nutrition than what the atmospheric bromeliads face as aptly labeled air plants. Once again we face the questions where did the atmospheric come from and how, in what ways do they vary one from another and how do the group's key traits influence performance under different growing conditions?

Addressing question number one, it's tempting to propose that aridity and the relatively short lives of substrates are what account for heightened resource use efficiency being the Darwinian incentive for a coupled deemphasis of the root system and functional refinement of the foliar indumentum (= trichome cover). Drought played its part by diminishing the ancestor's capacity for photosynthesis and by extension depressed its fecundity an outcome that added to the challenge imposed by relatively short lived aerial substrates. The more time that an epiphyte needs to reach sexual maturity the more likely its perch and its user will fail before that occupant can disperse seeds i.e., replace itself. Returning to economics, the fates of the resources freed up by curbing allocations to roots and down sizing shoots, is pivotal to this hypothesis. In effect, it demands that they be redirected to make more or hardier progeny to compensate for drought-heightened pre-reproductive mortality, i.e., the death of juveniles. More is said about this hypothesis below.

The bromeliad trichome, an indispensable supporter of the atmospheric-type life style, ranks among the plant kingdom's most functionally sophisticated epidermal appendage although what it does compared to a flower is mundane albeit no less crucial for survival. So it's odd that we remain ignorant of so much of its anatomical variety, manner of operation, and ecological significance. How, for instance, does a dense indumentum of trichomes

assist one atmospheric *Tillandsia* grow where temperatures run high and dry seasons long, while a different version supports a second species that experiences cooler air and moisture in more plentiful supply? Why do the atmospheric differ regarding how readily their leaf surfaces when wetted, dissipate films of moisture that if too persistent turn lethal (**Essay G**)? Why does the trichome cap range from oval to asymmetric and rigid to flexible and its attitude from horizontal to vertical relative to the underlying epidermal surface (**Figure 3AA**)? Do these variations parallel particular life history strategies or growing conditions? Do certain qualities of leaves (e.g., their shapes and juxtapositions) or ramets (e.g., lax versus compact) vary in concert with any peculiarities of the foliar epidermis?

Imagine how precarious life must be for a member of *Tillandsia tectorum* that as a high Andean native must subsist largely on mist-sized droplets combed from cool turbulent air. Might this be the requirement that explains why its body, factoring in its liberal endowment of trichomes topped with attenuated caps, possesses a surface to volume ratio that far exceeds that of most of its relatives? And what would happen if its supply of moisture were to increase appreciably or its delivery vehicle to shift to some less favorable form (e.g., drops versus aerosols)? At what point would a moisture-saturated layer of trichomes block stomata (gas exchange) long enough to suffocate what at that point would be an over-irrigated bromeliad (**Figure 4F**)? What about the effects of a climate that's shifted in the opposite direction, that's changed enough to challenge by virtue of the same surface to volume metric our hypothetical subject's ability to avoid lethal desiccation? How do the two tolerances compare (**Essay J**)? How broad is the operating range between?

Know what certain attributes can tell us and it's possible to discern a bromeliad's requirements for growth (e.g., shade vs. sun, dry vs. wet). The experienced grower can at a glance determine whether a particular atmospheric will respond favorably or otherwise to the intense heat and humidity that prevail in Florida during summer and year round in Singapore. Generally speaking, subjected to tropical wet lowland conditions the poorest performers are those cited above that feature shoots comprised of numerous filiform leaves covered with abundant trichomes bearing elongated caps whose tips extend well above the epidermal surface. Might such predictions be made even reliable by including traits overlooked so far because they aren't as easily assessed? Might the wettability of a leaf's surface or the time required to dry say as much about the growing requirements of a particular specimen than the visible features of its indumentum? And don't forget that no combination of attributes can sustain a plant's optimal growth except under the conditions that naturally selected for those traits (**Essay J** and below).

The atmospheric native to hot dry habitats probably don't experience or respond to drought the same way. One type exemplified by *Tillandsia concolor* features a compact shoot carpeted by a dense layer of trichomes topped by circular to oval caps tightly appressed against the underlying surface. Such highly reflective trichomes backed by a robust epidermis, which in turn overlies colorless water storage tissue shield the even more deeply embedded and vulnerable chlorenchyma (= photosynthetic tissue; **Figures 2AA, 1H**).

Tillandsia recurvata, an exemplifier of a second condition, exhibits foliage whose interiors consists mostly of densely packed green cells that perform triple duty by in

addition to performing photosynthesis and storing moisture also sequester nightly the malic acid produced by CAM-mediated CO₂ fixation (**Figure 3A**). An unexpectedly delicate epidermis bearing trichomes with elevated asymmetric, mobile caps further accords with water relations unlike those of their more robust neighbors. Perhaps members of type two rely on dew to restore substantial daytime losses while the individuals that comprise category one are built to retain more moisture more tenaciously because their main supply being precipitation is a less reliable source (**Cháves-Sáhagún et al. 2019**).

Tillandsia bulbosa demonstrates how trichomes born by the same individual can differ by structure and behav-

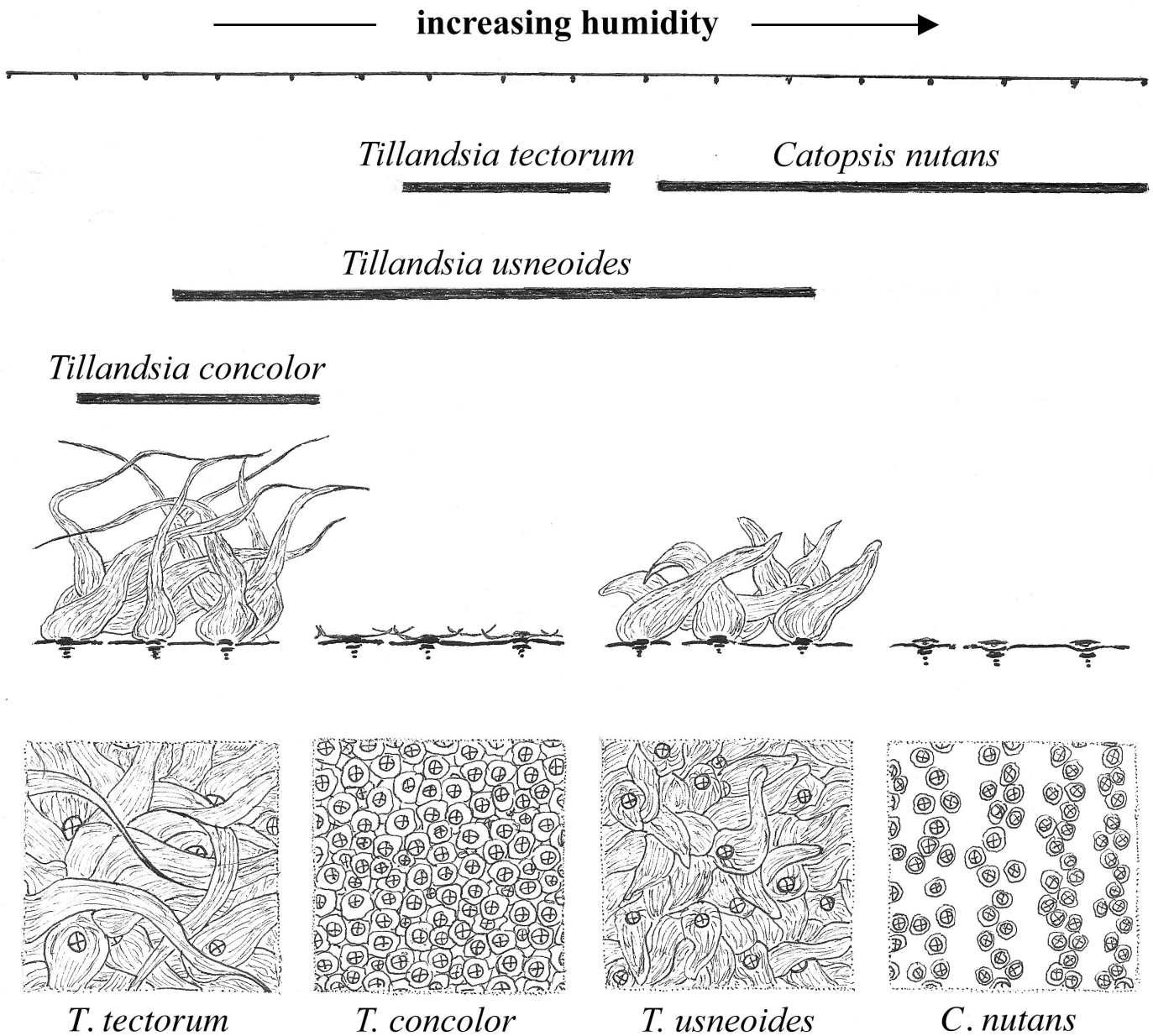


Figure 1H. The ranges of humidity tolerated by four types of tillandsioid bromeliads along with the structure and densities of the trichomes that comprise their accompanying foliar indumenta. Tank-equipped *Catopsis nutans* alone is not an atmospheric type.

ior and also probably by function depending on where on the shoot they occur (**Figure 1B**). If present on the upper surfaces of the in-rolled leaf blades they bear caps equipped with raised flexible wings whereas for those inserted on the opposing side of the same organs the same structures remain flat and transparent while wet and dry. Water drops don't spread whereas if deposited on the flared leaf bases they do quickly rendering visible the chlorophyll present in the underlying mesophyll. The rate at which moisture applied in this manner flowed across the surfaces of a series of leaves harvested from additional species varied, but not knowing the climates experienced in nature by owners diminished the value of these results. Conducted on subjects known to subsist on specific forms of moisture, e.g., mist (= occult precipitation), dew or large droplets, would make data obtained this way more useful. The same applies for determinations of how quickly wetted foliage dries in stagnant versus moving air, again using weight changes to quantify results.

Recovery post desiccation is the ultimate test of a plant's ability to survive drought, and high performance is essential for the grey tillandsias that by life style and type of substrate experience near complete exposure to air. And like surface drying it too is easily quantified. All that's needed is a balance capable of milligram-range determinations, a transparent chamber that can be just about any ordinary glass container, a chemical desiccant and a light source cool enough to avoid overheating an incubation chamber's contents. The question to address is equally straightforward: how much of a dry-down can a subject experience short of death, and how much time is required to reach that point of no return? One experiment revealed that ramets of *Tillandsia ionantha* could rehydrate and restore pretreatment capacity to conduct photosynthesis within days following desiccation that had exceeded 50% and required more than a month to develop. Nothing reported so far indicates that any of the atmospheric performers as dramatically as the resurrection-type mosses and ferns that fully recover on both counts within hours following one to a few days loss that can occur fast enough to exceed 95% (**Essay A**).

Returning once again to origins and evolution, the emergence of the atmospheric-type bromeliads required abandonment of the phytotelm-equipped shoot, a complex adaptation that to this day continues to serve same subfamily lineages in sites suitably moist (**Figure 1H**). While such an arrangement promotes fitness where conditions allow a shoot comprised of tightly overlapping leaves with inflated bases inserted in a tight spiral around a truncated stem, represents an option-restricting architecture where moisture is less abundant (**Figure 2AA**). It appears that abandonment of the phytotelm-type shoot by lineages equipped with multifunctional trichomes set off an adaptive radiation that generated numerous body plans all free of the liability that attends storing moisture in an open-air reservoir (**Figure 2H**). Think about the result—about how the members of species-rich mesophytic genera such as *Guzmania* and *Vriesea* differ only modestly by shoot ar-

chitecture one from another relative to what exists in *Tillandsia* broadly defined. Now turn to shoot size (e.g., *T. bryoides* versus *T. xerographica*) and caulescence. Finally, consider this: how small a shoot can become and maintain an operable tank and how large before many otherwise suitable anchorages aren't strong enough to bear its weight?

Species that produce caulescent (= long stemmed) shoots bearing scattered sparsely branched roots—not a commonly encountered arrangement among the atmospheric (e.g., *Tillandsia araujei*, *T. ionantha* var. *van hyningi*)—grow on durable supports too often to dismiss the association as merely coincidental. If it's cause and effect then what is it that explains this pattern? Could it be that producing fewer less determinant shoots than typical for the epiphytes reflects a relaxed need to recruit anchorages at the same rate when rocky outcrops serve as substrates instead of trees? Is the acaulescent (= short stemmed) epiphyte better prepared by its more condensed (faster maturing?) shoot to maintain its numbers given the more ephemeral nature of the second of these two kinds of mechanical support? Remember what was pointed out earlier, that for an anchorage to provide what's needed by a particular plant its life span must exceed the interval required by that plant to mature and have a chance to replace itself on a younger perch (**Essay G**).

Why would a lineage long served by a phytotelm-equipped shoot leave behind this time-tested arrangement in favor of a novel alternative? The **introduction (AA)** provides the easy answer it being “nature abhors a vacuum”. A more substantial explanation identifies the Darwinian incentive for abandoning what remains operational for hundreds of extant relatives as opportunity to enter less plant welcoming living space. The transformation from tank-assisted to atmospheric-type life style was assisted by neoteny, a genetically based mechanism that alters development (= ontogeny) such that certain traits manifested during the juvenile stage of an ancestor become part of the adult stage of its descendants. It's reasonable to assume that an exposed reservoir can not meet plant demand under substantially more arid conditions, but what would be its replacement and how would it come about? Did the trichome acquire its capacity to replace roots during the seedling stage of the putative ancestor or while lining the phytotelm of the adult? Regardless of which portrayal applies the atmospheric throughout life—both by structure and function—resemble the seedling stage of the modern tank-equipped tillandsioids except for the sexual precocity acquired through the neotenic process.

Figures 4F, 1H illustrate how departing from the phytotelm-type body was accompanied by a repurposing of the foliar trichome, an event that in some respects caused tolerance for humidity to narrow. Landmarks along the way can be seen in the ways that trichomes distribute across the surfaces of leaves and their varying states of refinement. Note the widely dispersed, modestly

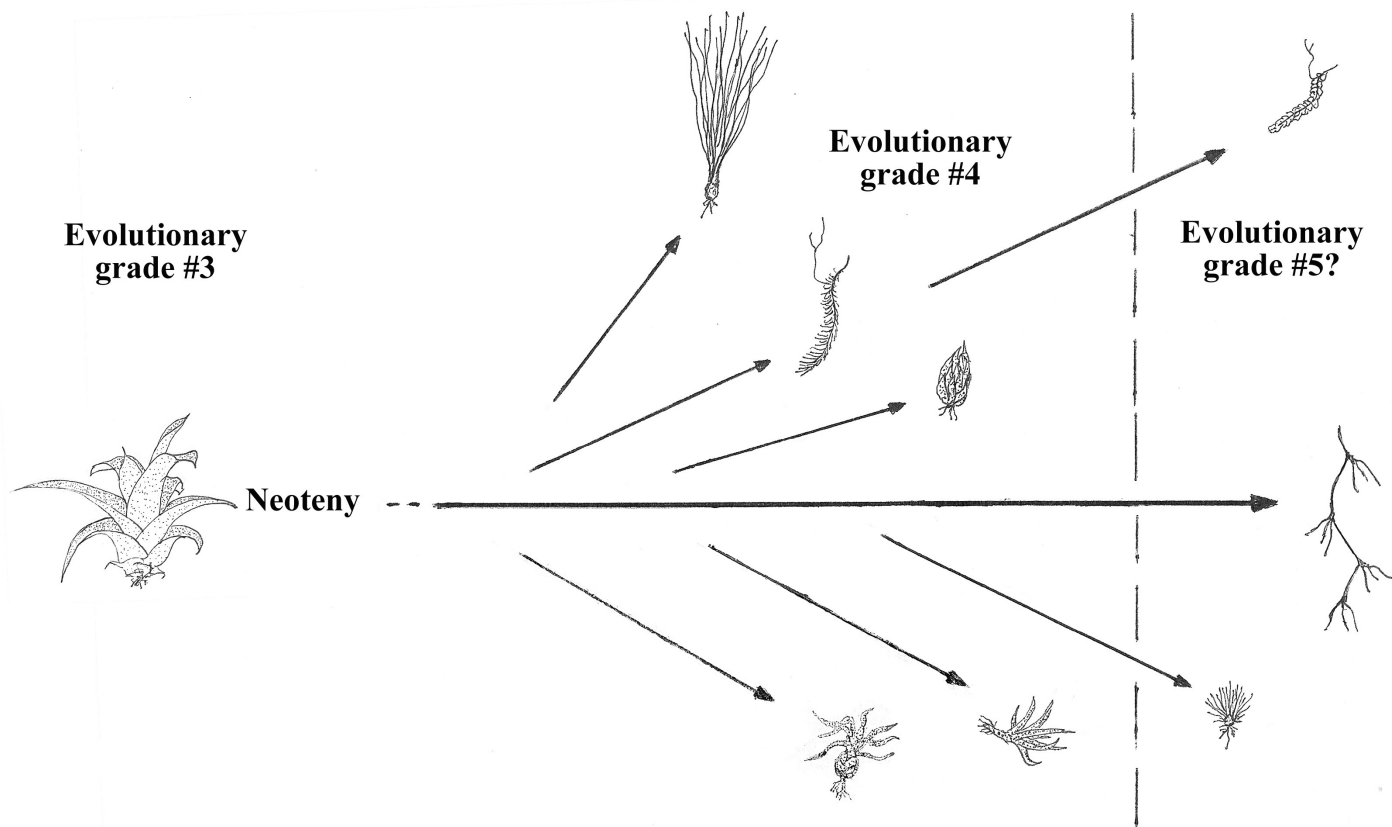


Figure 2H. Body types possessed by the atmospheric bromeliads. Evolutionary grade four and possibly an unrecognized grade five (see Figure 4G) are represented as neotenic descendants from grade three level ancestors.

capped trichomes displayed by tank-dependent *Catopsis nutans* (Figures 3AA, 2G). The three grey tillandsias possess more densely distributed trichomes topped by asymmetric shaped caps. Consistent with the proposed hypothesis, they occupy narrower positions along the humidity gradient. What this picture illustrates boils down to performance and tradeoff: the greater the subject's reliance trichomes in place of roots and tanks the narrower its capacity to tolerate more than narrowly defined ranges of humidity. Yet the trichome still allows and perhaps promotes much flexibility for its users taken as a group. Recall that *Tillandsia concolor* endures punishing heat and prolonged seasonal drought in Mexican dry forests, whereas *T. tectorum* occupies cool Andean sites moistened frequently by cloud water (Figure 3H). *Tillandsia usneoides*' performance, evidentially being less constrained, accords with its record geographic range and occurrence in diverse kinds of habitats.

Now it's time to take a closer look at botanical End Time, specifically, what is it about a population that determines its vulnerability to extirpation, and where the atmospheric fit into this picture. Consider this phenomenon as it is influenced by traits, specifically how possession one type of trait versus another affects vulnerability. Photosynthesis ranks among the least problematic of traits as witnessed by its almost ubiquitous occurrence through the plant kingdom and thus its operational viability under myriad growing conditions.

Conversely, possession of a dense investment of bromeliad-type trichomes, while no less life sustaining for its possessors serves only a single group of related species and at a cost of narrowed eco-tolerance, which compounds the already precarious live style that comes with being an epiphyte or lithophyte (Essay G). Proceeding from the above, might the grey tillandsias be pushing the boundaries of what's doable for the higher plants? Have they adapted themselves into a kind of Darwinian cull-de-sac? Is it reasonable to suspect that at least some more than most others lack the flexibility required to counter challenges that include climate change and the more direct effects of the on-going buildups of CO₂ and additional heat-trapping gases (Essay J)?

Polymorphism, a phenomenon that expands eco-bandwidth (= eco-flexibility) hence resilience, describes a genetically based condition whereby no two members of an interbreeding (Mendelian) population possess the same genotype so no identical phenotypes exist either (Essays D, E). To appreciate how this kind of intra-specific (= within a species) variety serves a species think back to our hypothetical *Tillandsia tectorum* that experienced increasingly wet and then drier conditions. Its survival as a population facing the first of these two challenges would depend on the allelic status of the genes that determine tolerance for humidity. If the appropriate genes (specifically their alleles) are present the individuals so endowed will reap a survival advantage such that their



Figure 3H. *Tillandsia concolor*, left, in cultivation at Marie Selby Botanical Gardens (photograph by Wade Collier, and *Tillandsia tectorum* from Ecuador in situ (photograph courtesy of Selby Gardens).

kind will eventually come to dominate the survivors. Adaptation at the population level will be achieved when all of the members of our imagined lineage possess the genetically based means to tolerate what earlier would have ended the lineage (**Figure 1E**)

Were the atmospheric bromeliads stripped their defining traits would they be less vulnerable to global change? The answer being probably yes calls for a deeper than usual examination of life's inherent flexibility, which in fact is at once broad and narrow. Most of us were taught in some long forgotten high school biology class that life in its nearly countless forms has made virtually every kind of physical space that Planet Earth offers into space occupied by organisms. Viewed this way life indeed is imminently flexible. But seldom mentioned is a second reality that such an impressive performance depends on proper packaging. The take home lesson comes down to this: life is not a single all encompassing phenomenon because such an arrangement flat-out wouldn't work. Of necessity, it's partitioned into discrete, genetically mostly isolated subunits called species, or when viewed as lineages, as series of self-perpetuating populations. Structured otherwise it couldn't respond to Darwinian selection as required by growing conditions that everywhere continuously change (**Essay D**).

Life's limited flexibility is demonstrated by the fact that each of the millions of species inhabiting earth today requires a narrowly proscribed niche one that represents only a tiny fraction of those available globally. The glacier-inhabiting microbes that occupy that stark living space thrive undaunted by frigid temperatures while members of a second group succeed living in near boiling water. Neither population can tolerate the conditions that favor the other. A similar much tighter pattern among plants applies for soil pH, the availability of moisture and sunlight and much more. In effect, one species' required conditions will inhibit or flat-out kill others. Reality is this: to do something well, say tolerate severe drought, comes at the cost of increased vulnerability to excess

moisture. Although every species is unique in what it needs and tolerates there is a range and species at the most flexible end are the generalists the specialists being their opposites. Precedents indicate that given our planet's rapidly deteriorating capacity to support life that the future looks brighter for the creatures that fit the first more comfortably than the second of these two descriptions.

It would be unwise at this juncture for anyone no matter how credentialed to presume to know botanical life's vulnerability to global change's multiple threats including when it is packaged in the form of the grey tillandsias. Judging by its extensive geographic distribution and high local abundance *Tillandsia usneoides* and similarly opportunistic (= weedy) *T. recurvata* probably enjoy the greatest of the group's eco-flexibility while the most insular (= characterized by narrow geographic ranges) species, particularly the high altitude-growers, by operating at the opposite extreme are more vulnerable. Additional non-climatic factors further elevate some of the second group's likelihood of extinction, a good example being the geographic constraints imposed by uneven topography. The smaller and more spatially confined a population the greater its chances of elimination by a random event. In addition to passive agents like fire and severe storms there are plenty of pathogens and predators including *Homo sapiens* whose threats range from altered climates to land use conversions (**Essay J**).

Where should inquiry proceed from here? One promising avenue would involve extending to the grey tillandsias recent investigations of the foliage of a variety of herbs including several tank bromeliads (**North et al. 2017; Males and Griffiths 2017; Males 2017**). These efforts already have revealed that certain aspects of leaf anatomy influence water relations in previously unrecognized ways. Eco-performance in nature should be targeted as well. While it's true that the grey tillandsias possess much in common they probably differ in interesting ways

BENZING: ESSAY H. THE ATMOSPHERIC BROMELIADS

some of which might turn out to be unexpectedly profound. For example, do all of the atmospheric perform CAM-type photosynthesis, and when over-exposed to sunlight do they dissipate excess excitation energy by the same mechanisms (**Essay A**)? If CAM is shared across the atmospheric why do they conserve, store and transport water in so many different ways? Why presume that all are drought-enduring xerophytes when in fact

many may qualify as something else? And don't forget that we've barely begun to plum the secrets of the bromeliad trichome. In the final analysis, pursuit of the subjects covered in this essay could tell us much about how close evolution has brought some of the atmospheric bromeliads to the line that separates what's botanically sustainable and what is not.

ESSAY I. HOW BROMELIADS PERCEIVE AND RESPOND TO THEIR SURROUNDINGS

Imagine trudging across a tropical savanna under a cloudless sky lugging a backpack that's feeling heavier by the minute. Being a member of *Homo sapiens* would be your salvation because opportunity for relief would be as close by as the nearest patch of shade. But what about the obliging tree as it would be facing the same threat less easily avoided? Unable to think, or move, or call 911, how does a plant deal with stifling heat beneath the same blazing sun? And what does it do when challenge arrives in the form of a swarm of hungry insects or a virulent pathogen? What about severe drought? Much is known about how we humans gage and adjust to our circumstances, but what about flora?

All organisms on pain of death must monitor their surroundings, and for a plant this means perceiving and reacting often simultaneously to signals arriving from multiple sources. It's a daunting task because relevant information arrives in diverse forms, for instance, as the blue versus red portions of the sun's radiation. Human beings, again to cite the most familiar example, employ cue receptors that speak the same language, and for us it's eyes and ears for images and sounds. Finally, what a signal elicits depends on what the recipient needs this time illustrated by a pair of photoperiodic bromeliads growing side by side. Short days will induce the winter-flowering individual dependent on some winter-active pollinator to do just that while its companion, being genetically programmed to respond to the longer days of July, will remain vegetative consistent with its one or more aspects of life history strategy (= ways of living). What these two differing performances demonstrate is how plants use nature's signals to coordinate their activities in fluctuating environments.

To be able to perform as described above confirms that plants possess something akin to a nervous system tailored by evolution to serve life forms that lack willfulness and mobility. This ninth essay describes such an apparatus drawing upon what's currently known about how flora generally, and the bromeliads in particular, regulate their activities through deployment of a perceptron, a still poorly understood device functionally equivalent to what we humans use to negotiate our dynamic world (**Figure 1I**). While it won't be possible to come away knowing a botanical perceptron's material nature readers will better understand how plants monitor, process and respond to what goes on in the world in which they live. But first we need to review what's meant by biodiversity, phenotype, trait and trait complex after which it will be time to move on to how plants pursue life history strategies guided by conditions and events to which they must respond but have no control.

It's the angiosperms that reign supreme accounting for more than 95% of all the species that comprise the higher or vascular plants. However, being no more than a

head count, this statistic says nothing about the group's true biodiversity, about how much roughly 375,000 kinds of plants differ relative to where and how they grow, what they need to grow and how they remain on friendly terms with their surroundings. All of this pertains because an adaptive radiation is more than a proliferation of lineages (species). More significant biologically is the attendant forging of new traits and the refinement and repurposing of old ones that together enable new ways of living sometimes in formerly inaccessible habitats (**Essays D, H**). **Table 1I** demonstrates this principle by listing key components of two trait complexes that support two distinct lifestyles and assigns their practitioners to separate slots in a taxonomy based on eco-performance rather than phylogenetic relationship.

The term biodiversity, like the acronym DNA has been bandied about long enough to have become just another often inappropriately employed entry in the public lexicon. Today, few of its users appreciate its relevance when it comes to its meaning expressed in terms of traits and trait complexes rather than whole organisms (numbers thereof). So, what is a trait? For our purpose it's any aspect of an organism that's a phenotypic or outward expression of its genotype (or genome). As **Table 1I** points out many a trait is an integral part of a life history strategy but distinguishing attributes that qualify from those that isn't always easy. Does a peculiar shape of a leaf, or its color or how flowers are born on an inflorescence all of which in taxonomic keys differentiate bromeliad species, contribute to the operation of their possessors? Sometimes inapparently yes considering that it's the synergisms and complementarities that attend the combining of traits that can allow even the seeming unlikely candidate help enable a life history strategy.

Traits tend to be nested (hierarchical). They differ by phylogenetic age and how deeply genetically entrenched. Ancient traits, such as reproduction through deployment of flowers, a condition that emerged about 140 million years ago, occur more broadly in the taxonomic sense than their modifications (= nested secondary traits), exemplified in this case by the pollination syndromes illustrated in **Figure 3D**. Traits differ further depending on whether induced or routinely manifested, i.e., whether facultative or constitutive (**Table 2I**). The latter, an example being succulent foliage covered by dense layers of trichomes, help hundreds of bromeliads tolerate chronic stressors such as drought (**Introduction; Essay A**). Easily overlooked because they aren't always expressed are the induced types that despite being conditional are just as important as the constitutive kind. An individual's preparedness to synthesize a toxic chemical upon attack by a pathogen is just as important for the understory-dwelling bromeliad as its fixed capacity to tolerate shade.

Traits that in species-specific combinations dictate specific life history strategies in turn match specific sets of growing conditions. And their component parts—the individual traits—operate together essentially performing

Theorized Botanical Perceptron

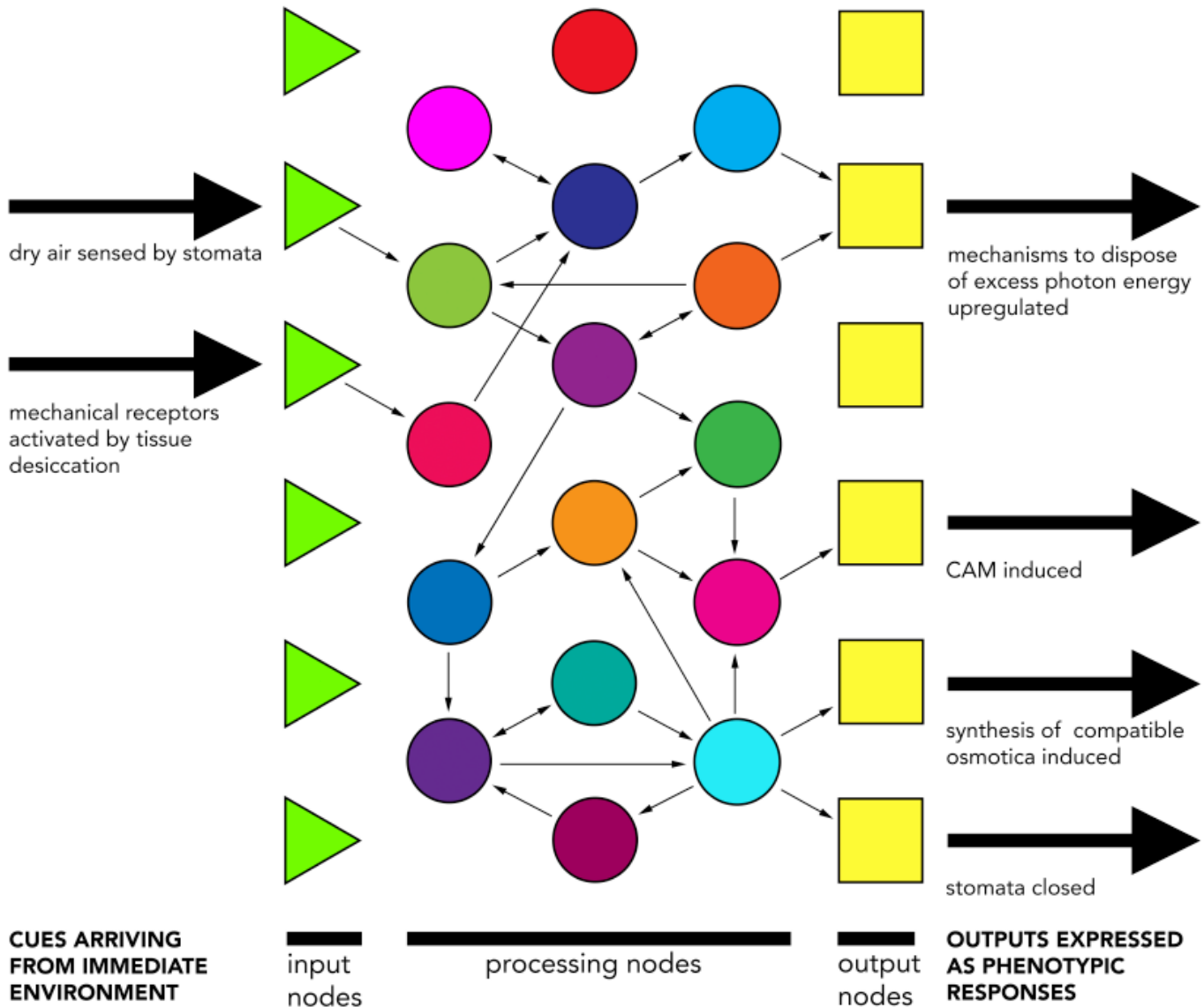


Figure II: The three principal parts of a perceptron: the first being a layer of nodes that perceive cues and a second that delivers the elicited responses. Multilayered number three lies between numbers one and two, and it functions to evaluate and prioritize signals before they effect chemical, structural or behavioral dimensions (traits) of the recipient. Sensory pigments, mechanoreceptors, molecular recognition systems and so on serve as input nodes. Signals move among the processing nodes like electrical polarities traverse a neural network.

as functionally concerted wholes. No *Tillandsia* possesses succulent foliage and a dense indumentum unless it also conducts CAM-type photosynthesis (but see **Essay H**). Likewise, humid dark sites call for phenotypes that feature smaller, less reflective trichomes scattered across wider, thinner C₃-type foliage (**Essay A; Figure 1H**). A leafy tank is never part of the first trait complex any more than a strongly light reflecting epidermis is compatible with the second. All in all, it's useful to consider a botanical phenotype as an evolved, cue-orchestrated network of coordinated traits that determines how and under what circumstances its owner can grow. Having covered the

relevant terms and concepts, it's time for how flora use cues to stay abreast of their ever-changing surroundings.

It's long been known that sunlight drives photosynthesis, but not so much that energy from the same source benefits plants in ways beyond food making, or that too much can cause irreversible injury. It's because of this second reality that nature has come up with an array of fixed and inducible traits to reduce the incidence of photo-damage (**Essay A**). Permanent covers of light-scattering trichomes and epidermal cells that on demand synthesize and sequester red to purple anthocyanin pigments constitute the first line of defense. Should this shield prove in-

ESSAY I. HOW BROMELIADS PERCEIVE AND RESPOND TO THEIR SURROUNDINGS

Table 1I: Two sets of traits the members of each of which constitute portions of a trait complex that enables a particular life history strategy. Species engaged in similar life history strategies often are not closely related owing to the high incidence of convergent evolution (homoplasy) among the angiosperms.

Life history strategy of an annual	Life history strategy of a stress-tolerant perennial
The supporting substrate (terrestrial soil) is frequently disturbed and at least moderately fertile, well-watered and exposed to intense sunlight. No bromeliads employ this strategy.	The supporting substrate is stable, its fertility various and its access to moisture seasonally depressed. Exposure to sunlight is high. Many epiphytic and terrestrial bromeliads meet these cri-
Life cycle short, as brief as a few months	Multiyear life cycle
Body cheaply constructed (herbaceous rather than woody)	Body construction expensive (woody or much sclerenchyma present)
Growth rapid	Growth slow
Seeds small, long lived and germination light-dependent	Seed characteristics various
Breeding system self-compatible	Breeding system various, often sexually self-incompatible
Shade-intolerant	Shade-intolerant
Maximum photosynthetic rate high	Maximum photosynthetic rate modest to low
Water use efficiency poor	Water use efficiency high
Physical stature and size at maturity modest	Physical stature and size at maturity various
Defensive chemistry poorly developed	Defensive chemistry often well developed

adequate a substantial dose of carotenoid pigments along with photosensitive chemicals within the more deeply located green tissues stand ready to quench excessive excitation energy (**Figure 2AA**). Foliage oriented to minimize exposure to direct beam sunlight and CAM-type photosynthesis (CAM-idling) protect as well (**Essay A**).

Sunlight varies in intensity, spectral composition and duration depending on calendar date, location and weather so plants can use it to direct as well as power growth to match need with local conditions. Utilized in the first mode it cues inducible traits as part of a complicated still incompletely understood system of pervasive regulatory control. Being comprised of multiple wavelengths (= colors) only narrow bands of which can activate a particular sensing pigment goes a long way in explaining how a celestial body some 94 million miles distant from Earth can mediate dozens of disparate morphogenetic (= developmental) botanical events. Contrary to the cue-perceiving pigments the two chlorophylls (= chlorophyll a and b) absorb across the visible spectrum, although unevenly, as necessary to harvest the much greater amount of solar energy required to synthesize glucose from CO₂ and water (**Essay A**).

Now check out the pair of *Tillandsia utriculata* specimens imaged in **Figure 2I**. Individual A grew bathed in unfiltered sunlight near the top of the crown of its densely foliated host while plant B, likely one of its siblings, experienced shade lower within the same canopy. Note that the former's shoot is the more compact, stiff leafed with a purple color and upright assuring superior capacity to impound litter and moisture. Its companion features more lax green foliage, and while less able to impound as much

material among its overlapping leaf bases, it's the superior harvester of diffuse (= shade) light. Had a third individual been present and anchored around mid-canopy it would have possessed a phenotype roughly intermediate between those exhibited by specimens A and B. As this pair of bromeliads shows, many of the fixed versus inducible traits are best considered extremes along a continuum made possible by the plant's so-called phenotypic plasticity, a type of structural and functional malleability that's only somewhat distinct from the evolutionary (permanent) kind described in **Essay H**.

Table 2I: Plant traits. Those listed in the left-hand column exemplify the inducible (facultative) category and on the right the more fixed (constitutive) type.

Synthesis of feeding deterrents	Herbaceous or woody body
Closure of stomata in response to drought	Fruit type
Modification of the photosynthetic apparatus to most effectively utilize shade compared to stronger sunlight	Duration of the life cycle (annual vs. perennial)
Drought-induced switching between C ₃ and CAM-type photosynthesis	Trichome form and function
Adoption of sun versus shade morphology	Pollination syndrome



Figure 2I: Two individuals illustrating the sun (A, left) and shade (B, right) phenotypes of *Tillandsia utriculata* achieved because of experiencing different exposures to sunlight in different parts of the crown of a single evergreen tree in Sarasota, Florida. Consult the text for a fuller explanation.

Subject A differs further from B by how the light harvesting (= the light reactions) versus the CO₂ fixing (= dark reactions) parts of the photosynthetic apparatus are constructed. The sun's rays being undiminished above compared to filtered (weakened and spectrally altered) within the host crown has induced the shade-grown individual to commit proportionally more of its resources to assemble a light gathering device that's best suited to harvest scarce photons while its more fully exposed counterpart having access to abundant sunlight has favored an augmented capacity to fix CO₂ (**Essay A**). Remember that CO₂ was equally available to both contenders while the opposite applied for sunlight. As for drought-tolerance, the shade-grown individual, because it experiences less evaporative demand owing to its cooler more humid microsite doesn't need as much tank capacity as specimen A, and its drooping foliage is better oriented to intercept the scattered photons that comprise shade light.

Figure 2I also demonstrates what's called acclimatization, a kind of phenotypic plasticity that represents adjustment to different growing conditions. Our pair of featured specimens is doing exactly this and going one step further by proving that even two subjects born of the

same maternal parent perceive variations in multiple cues—light, humidity and temperature in this case—and that they respond appropriately. Had our two bromeliads been subjected to each other's growing conditions their phenotypes would have been the reverse. So, it appears that although *Tillandsia utriculata* owes its basic character to a moderately dry-growing history, it remains flexible enough, both anatomically and physiologically, to maintain its fitness when challenged by a trio of climatic variables each of which announces its measure to the perceiving plant in one of three different languages.

Most of the cues to which plants respond consist of solar radiation, humidity, gravity, intervening organisms and temperature. For light to induce a seed to germinate, a young leaf to expand or a bromeliad to flower requires the presence of an appropriate pigment(s), and for all three of these so-called morphogenetic phenomena, it's a series of red/infrared light absorbing phytochrome molecules. While in one of two light-absorbing molecular configurations these protein-based receptors trigger signal cascades that drive the corresponding responses. In the alternate form they become physiologically silent. Which of the two prevails often depends on the red/infrared ratio of the

solar radiation to which the target is exposed. Our two *Tillandsia utriculata* specimens developed differently in part because unfiltered sunlight compared to what passes through foliage contains proportionally more red than infrared radiation. The blue component, by energizing a second array of pigments, regulates a second series of events that include phototropism (= growth toward a light source) and the dawn opening of stomata.

Drought being nature's most frequent suppressor of photosynthesis makes the availability of moisture the predominant global arbiter of growth and ultimately of botanical success. Like over-exposure to sunlight flora avoid lethal desiccation in multiple ways (**Essay A**). A robust epidermis bearing a thick cuticle and a dense layer of trichomes to further retard evaporation helps hundreds of dry-growing bromeliads meet this challenge (**Figures 2AA, 2F, 1H**). At the same time the high cost of such elaborate anatomy imposes an expensive tradeoff compounded by an opportunity cost in the form of the greater amount of glucose that could have been synthesized had more productive C₃-type but less water use efficient foliage been present to take over during the rainy season (**Essay A**). Equipped to do this, a subject could take greater advantage of the rainy season's wetness to grow faster without sacrificing capacity to continue carbon gain albeit at a lower more water use efficient rate during the drier months. So far, evolution hasn't produced a bromeliad capable of this kind of versatility.

Pigments being unsuited to perform what's required forces plants to perceive drought by alternate means one of which has a mechanical component. As a subject denied sufficient irrigation dries the contents of its living cells that when fully hydrated press firmly against the enclosing cellulosic walls shrink (= lose turgor pressure) setting off yet another signal cascade. The result includes stomata that close and the synthesis of low molecular weight compatible solutes (e.g., certain simple sugars and amino acids) that contribute by staving off subcellular injury. Some bromeliads (e.g., *Guzmania monostachia*), when challenged switch from C₃ to CAM-type photosynthesis, a tactic that heightens the economy with which what remains of a dwindling supply of moisture is used to maintain photosynthesis although again at a reduced rate (**Essays A, F**).

Many plants, particularly perennials native to hyper-seasonal landscapes, rely on shifting temperature and precipitation and probably more often on photoperiod to coordinate activities such as growth spurts and reproduction with favorable weather, or to avoid climate-related threat by lapsing into states of physiological quiescence or full-blown dormancy. Heat's suitability for its role in such action derives in part from its rate-setting influence on the synthesis and degradation of growth promoters and inhibitors the performances of which regulate key metabolic processes. **Essay A** describes how the timings of growth and dormancy of different organs prepare *Pitcairnia heterophylla* to survive dry seasons. Its tropical rather than

temperate zone distribution suggests that it is photoperiod that sets guides its phenology (=seasonal schedule of life cycle events).

Don't believe that because plants lack animal type immune systems that they can't defend themselves against pathogens, and the same applies, although by different means, for much larger assailants. Here again the botanical version of a zoological precedent is multifaceted and based on fixed and inducible traits. The former includes an extensive array of tannins, alkaloids, essential oils, and much more that exemplify the secondary or specialized metabolites that plants produce to defend their most nutrient-rich hence expensive (caloric and nitrogen/phosphorus-rich) tissues (e.g., seeds, leaves). Augmenting these digestion inhibitors, feeding deterrents, and flat-out toxins are physical barriers such as spines, stiff hairs and robust epidermal layers. More subtle impediments include tough vascular bundles, and other scarified (= thick, hard walled) tissues that in addition to defying chewing and piercing mouth parts increase the resistance of evergreen foliage and other long-lived organs to normal wear and tear (**Figure 2AA**).

It's not known how fully the bromeliads are engaged in the proverbial arms race that's been raging for hundreds of millions of years between the higher plants and their myriad adversaries. Presumably, like the angiosperms generally, they too are genetically prepared to bring to bear chemical defenses often faster than an assailant can evolve means to tolerate if not outright destroy (detoxify) them. However, there's a cheaper alternative, and at least some family members appear to be its beneficiaries, especially those native to exceptionally resource-deficient habitats. Tissue assays indicate that the bodies of several *Brocchinia* and *Tillandsia* species contain remarkably low concentrations of key nutrient elements, especially nitrogen and phosphorus, that substantially diminish their value as food for herbivores. The presence of much indigestible fiber may reduce food value even further.

Returning to pathogens, flora protect themselves from infections in multiple ways one of which is immune system-like in the sense that it involves the chemical recognition of effector by receptor molecules. An invader, let's say a fungus, reveals its presence to a potential host by virtue of one or more substances (= effectors) built into its surface, possibly the polymer chitin or one of its components that like cellulose for plants is a structural constituent of the fungal cell wall. Once alerted, the target can synthesize one or more toxins and should the assailant be an animal a feeding deterrent. Or host cells near the intruder can undergo genetically programmed cell death (= apoptosis) walling off what thereafter will be no more than an innocuous tissue inclusion. One of the most spectacular of the induced defenses against invertebrates involves the release of jasmonic acid, a hormone that's so attractive to certain predatory insects that its vapor re-

cruits for the endangered plant bodyguards ready and able to devour its antagonists.

It's increasingly common these days to learn that yet another alien aphid, beetle or whatever is elevating some native tree's vulnerability to a second threat such as drought, a phenomenon that reveals that a plant's ability to counter nature's insults is not boundless. So, what's going on here? Could it be that something finite, perhaps an energy reserve(s), limits resilience? If true, then how does a distressed subject determine the most propitious use of that exhaustible resource? How, when faced with drought while residing in a deciduous forest that's about to leaf out would a bromeliad know not to allocate something in short supply to heighten its ability to more effectively utilize shade light while its stomata, forced to remain closed to conserve what moisture is left are going to prevent photosynthesis anyway? In other words, how does a plant threatened from two or more directions at the same time prioritize to avoid wasting critical assets on less than its most pressing problem? Recent advances in artificial intelligence and machine learning raise some intriguing possibilities.

Figure 11 offers up a stylized depiction of what earlier was identified as a perceptron. Its best-known biological analogue is the mammalian nervous system, but our interest concerns the type that serves the higher plants. Any perceptron worth the name improves with experience as in machine learning, and nature has duly complied by producing multiple iterations individually tailored to support the same number of plant life history strategies. What's proposed here presumes that computer-driven algorithms designed to deliver artificial intelligence have botanical as well as zoological equivalents. The underlying predicate is quite simple, that drawing on what's known about systems designed for unrelated applications can tell us how plants, despite their sedentary lifestyle and compared to animals their low-grade differentiation into cells, tissues and organs nevertheless hold their own in dynamic environments.

In its most abbreviated form, a perceptron consists of three layers of nodes one tasked with receiving inputs—information about significant goings on in the environment—and a second for delivering the cue-elicited outputs with the third layer sandwiched between to operate as the data processor (**Figure 11**). As indicated above, stimuli of value to plants include day length and insect attack with the induction of flowering and the release of jasmonic acid vapor being among the possible outputs. Inputs, following their translation from cue to electrochemical language, are shuttled among the nodes that comprise layer number three until ready for expression as aspects (traits) of the subject's phenotype tailored to satisfy corresponding needs. Genes participate by governing

what must be produced the product being as simple as a feeding deterrent to the reprogramming of an entire shoot so that it flowers rather than adding more foliage.

There's no other way to put it: residing in every bromeliad there's got to be something functionally equivalent to a perceptron. And like our computer-based model it's a device that self corrects—that acclimatizes and evolves to accommodate respectively the short and long-term changes that all habitats experience and to which their residents must adjust (= adapt). In this case, instead of tweaking an algorithm as a user must do to improve the output of a computer program it's natural selection that keeps a botanical perceptron's performance in tune, but only within limits. As impressive as the latter's capacity to learn (evolve) may be it cannot always make the grade. Should climate or something else that adversely impacts plant welfare change too rapidly, or the necessary adjustment is mechanistically impossible, or it's stymied by a phylogenetic constraint then the affected lineage will fail (**Essays H and J**).

Most of the cues and receptors that plants use to coordinate their performance with environmental conditions are identified and reasonably well understood, but this cannot be said for how information once perceived by a non-photosynthetic pigment, for example, is translated into a life-sustaining response. The same applies for drought and assaults by pathogens and predators. Unfortunately, it's a deficit that's likely to improve only incrementally because as we now know the outputs at issue of which there are many range from relatively straight forward—the opening and closing of a stoma, for example, to bewilderingly complex such as how an inductive photoperiod prompts that bromeliad shoot to switch to producing reproductive instead of vegetative organs.

So what's the value of knowing how plants gage and respond to their circumstances? For one, it increases incentive to pay your bromeliads their well-deserved respect. Because let's face it, they aren't just sitting on a greenhouse bench or affixed to a piece of bark oblivious to their surroundings. Like us, they're continuously monitoring their dynamic worlds and responding accordingly, but by ways that we've only begun to fathom that make possible their immobile lifestyle (**Essay C**). Remember that unlike humans, plants cannot satisfy their needs and avoid threats by cake walking from one propitious site to another. Rather, they must rely on a perceptron-like device coupled to an elaborate trait complex that combined dictate how cues are read, and appropriate responses made. If the sophistication by which plants exploit their living spaces were the measure of intelligence, then the workings of a bromeliad's perceptron would define its botanical IQ as far superior to its human counterpart.

ESSAY J. BROMELIADS IN THE CROSSHAIRS OF GLOBAL CHANGE

Vanishing sea ice, starving polar bears and retreating glaciers leave no room to doubt that Earth is experiencing epic change, and that it's human activity that's causing the Arctic to heat up faster than almost anywhere else on the planet. Knowing full well what's under way far to our north what should we anticipate for the plants and animals that hail from lower latitudes? Will continued burning of fossil fuels and the release of additional carbon from other geo-sequestered sources (e.g., limestone) prove even more disruptive for tropical biota? Does being adapted for equable rather than harsh growing conditions condemn such species to an even grimmer future? Whatever is in store, it won't be uniform in its impacts not even among the bromeliads.

Were the threat to tropical flora nothing more than a degree or two of additional warmth we wouldn't have nearly as much to worry about, but unfortunately the problem has additional dimensions, and therefore "global" modifies "change" in the title of this tenth and final essay. Global change subsumes climate change, global warming, habitat loss and a plethora of additional, less publicized phenomena, all of which directly or otherwise and by as many different means are diminishing Earth's capacity to support our species and countless others. Consider fossil fuels the combustion of which releases into the atmosphere not only carbon as CO₂ but additional problematic emissions. Among the less publicized offenders are sulfur in the form of SO₂, the main precursor of acid rain and reactive nitrogen meaning nitrogen in molecular combinations that like CO₂ can nourish plants in ways that alter ecosystems (**Essay B; Figure 7F**).

To appreciate why the ecosystems that harbor bromeliads as well as the bromeliads themselves are poised to or are already responding to Earth's changing environments, consider how a humid tropical forest accommodates densely packed populations of plants and animals many relegated by narrowly defined needs and tolerances to narrowly proscribed niches (**Essay I**). It's here that Bromeliaceae can be both overrepresented and exceptionally influential. And it's here as well that its members vary most by performance some co-opting more than their share of resources while others as demonstrated by the tank-formers create more of the same. Competition, predation and mutualistic symbiosis tie the diverse components of such assemblages into hierarchies and networks, with food webs most often cited to exemplify this inter connectedness. Ever-wet tropical woodlands are true systems—unusually complex ecosystems and their occupants by engaging in often intimate interaction impart to the whole its characteristic structure, stability and resilience.

How climate change will alter the face of tropical American botany depends on how much rising temperatures shift where rain falls, how much falls and at what time during the year. Changes of this nature warrant our

attention because it's the availability of moisture more than temperature *per se*—except at high elevations—that most powerfully influences photosynthesis, the primary determinant of growth and reproduction and thereby botanical success (**Essay I**). Plant life on land is least climatically challenged where warm moist conditions prevail year-round as described above for the hyper-humid tropical forest. But seasonality—regularly alternating wet and arid periods—is more the rule at low latitudes, and where dry seasons are long the local bromeliads must be drought-deciduous or evergreen and if the latter equipped to perform water-conserving CAM-type photosynthesis (**Essay A; Figures 2, 3A**). As we shall see, any departure from the status quo, whether climatic or otherwise if it outpaces a lineage's capacity to adapt (evolve), heightens its vulnerability to extirpation.

Climate change is but one of our planet's many naturally occurring oscillations, and because it usually moves slowly by geologic standards most affected fauna and flora manage either to adapt in place or migrate to less impacted regions. The rare massive as opposed to routine base line rate of extinction requires something catastrophic like the meteor impact that 66 million years ago wiped out the dinosaurs except for a few lineages of primitive birds, or it could be one of Earth's rare episodes of colossal volcanism like the one 240 million years ago that ended the Permian Epoch by causing enough global warming and ocean acidification to extinguish 95% of the then existing biota. Today, extinctions are spiking once again, but this time we are the cause as our population surges and its support demands more energy and earth's finite material resources. So how are the bromeliads apt to fare in the decades ahead, and which ones are least or most likely to endure and why?

The bromeliads that depart farthest from the basic monocot body plan owe their deviant architectures to natural selection that by guiding change in novel directions wrought two positive outcomes: access to resources from other than soil and enhanced resource use economy (**Essays A, B, F**). Many of the stages leading up to the most extreme of these departures and their functional and ecological consequences are displayed by extant species (**Figure 5F**). **Figure 2G** shows how the tank-shoot fails where moisture is too scarce to sustain such a drought-vulnerable design (**Essay H**). The most punishing of arid sites host the CAM-equipped, thick leaved (= succulent) types that rather than depending on an exposed reservoir husband their reserves within hypodermal tissues that supply moisture as needed to keep adjacent more desiccation-sensitive green tissues adequately hydrated (**Figures 1A, 2AA**). Among the most finely tuned to humidity of the family's members are the so-called atmospheric types, a group that includes some of the drought-hardest species many of which also rank among the most vulnerable to over watering (**Essay H; Figure 4F**).

It won't require more than modest shifts in the amounts of precipitation delivered or in its scheduling to

exact a significant toll where flora and climate exist in delicate balance as described below for many a tropical montane cloud forest. Chronic alteration of monthly inputs by only a few centimeters or adding or subtracting a couple of weeks from a wet season could weaken or even end the more tenuous of those crucial connections among the organisms that inhabit the bio-diverse woodlands described above. For plants, scheduling is a particularly sensitive point of vulnerability as there are good, indifferent and unworkable times for performing vital activities such as flowering and seed dispersal. Finally, a population needn't be the immediate target to experience the consequences of an adverse event should it occur somewhere up or down stream in a complex ecosystem's vast network of densely packed interacting players.

Drought-deciduous *Pitcairnia heterophylla*, a long-lived perennial that annually progresses through a sequence of growth stages illustrates bromeliad vulnerability to climate change. At around the rainy season's reliably scheduled end it jettisons its entire array of C₃-type leaves having during the preceding wet months accumulated enough photosynthate (= products of photosynthesis) to support dry season flowering and fruiting along with the initiation of one or more renewal ramets (**Figure 4AA**). Although the resources required to fuel these multiple developments are substantial sufficient reserves remain so that when rain returns those young ramets can flush their single set of leaves preparatory to repeating the previous year's whole plant performance. Quite likely, *P. heterophylla* employs photoperiod rather than weather, a less consistent environmental signal, to time these water-expensive activities to match a fluctuating moisture supply (**Essay A**). So, here's the relevant question: could this bromeliad avoid drought and conduct enough photosyn-

thesis were the prevailing wet season to contract by more than a week or two?

What about topography? The floras that clothes the flanks of tropical mountains are stratified resulting in series of vertically stacked climate-defined life zones that in responding to global warming already are migrating upward (**Figure 1J**). Cloudbanks are pivotal players especially at the higher locations because they provide much of the plant-usable moisture most notably for any epiphytes present. As these delivery systems ascend and sometimes dissipate, what formerly were plant communities attuned to stable narrowly circumscribed microclimates experience more intense insolation and dryer air. Further exacerbating this trend is the conversion of subjacent forest to cropland a development that assures that rising air now less humid cannot promote former amounts of cloud formation at any elevation. Add in the photo-destructive effects of exposure to unfiltered sunlight and it doesn't take long to eliminate what had been thriving floras of which C₃-type bromeliads often constitute prominent parts. Prospects for outrunning a veritable climatic steamroller aren't encouraging and especially where the highest peaks are too low to be long-term providers of the cool humid conditions that cloud forest including its component epiphytes requires.

Climate change being attributable in large part to the elevation in Earth's atmosphere of a major heat trapping gas places CO₂ front and center in this discussion. But it's this same gas operating in a second mode that warrants our concern as well. This additional action is revealed by conducting an experiment that involves incubating a variety of kinds of plants in growth chambers filled with normal air to which additional CO₂ has been added. Some of our botanical guinea pigs, mostly the C₃-types, would

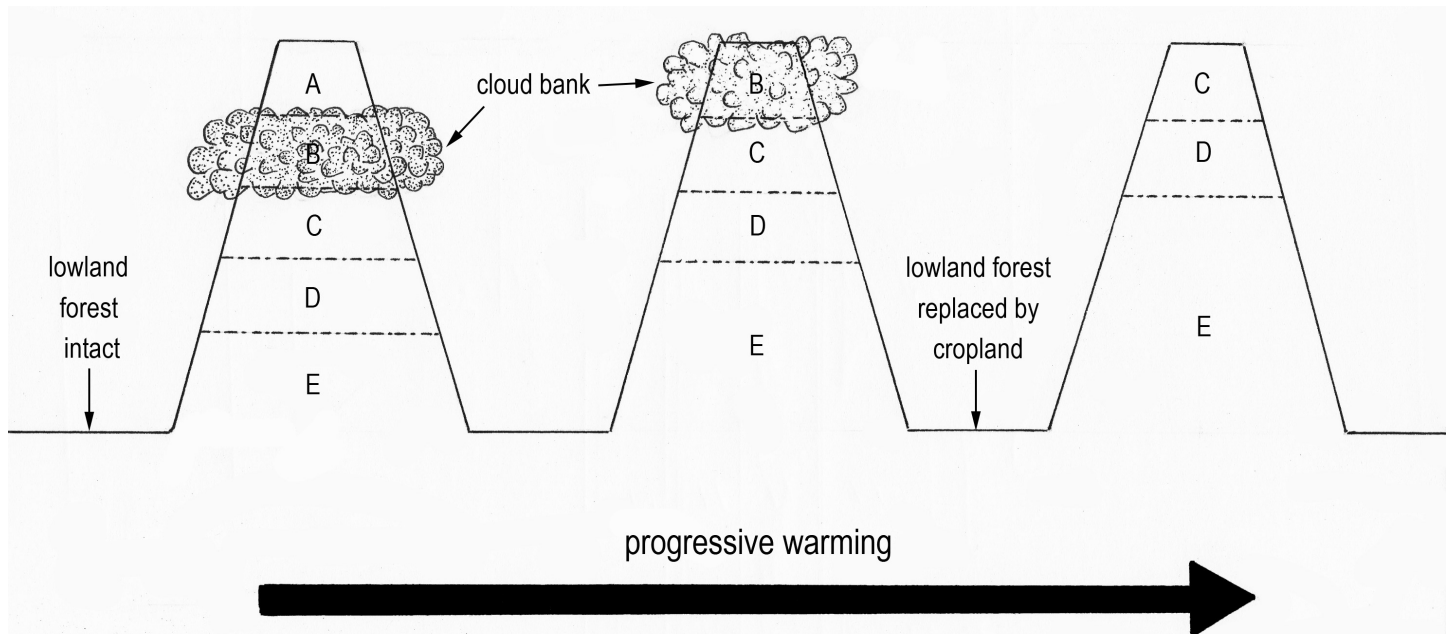


Figure 1J: A schematic illustrating how global warming is driving vertically stacked life zones up the flanks of many tropical mountains. Particularly life-altering is the accompanying ascensions and dissipations of the cloudbanks responsible for maintaining the high humidity and filtered sunlight that much montane flora requires. Land conversion is exacerbating this progression.

respond by growing faster while at the same time expending less moisture. In other words, these subjects would begin using water more efficiently than before. If our experiment went on for months, requirements for nitrogen might fall as well because less of the machinery (e.g., catalytic proteins) needed to fix CO₂ would be needed to produce the same amount of photosynthetic product (Essay A). A relaxed call for nitrogen-rich molecules in turn means less nutritious forage for herbivores (Figure 2J).

Beetles alone account for at least 30,000 of the millions of kinds of plant-consuming invertebrates, and because the diets of insects tend to be narrow host switching is not a widely available option. And pairings between herbivore and host usually being specific assures that a large majority are delicately balanced as well. If we presume that what's going on in Nature is paralleled by what transpired in our CO₂ enrichment experiment then some fraction of the plant-dependent arthropods of our world may already be experiencing nutritional stress, perhaps enough in some cases to allow what formerly had been higher quality C₃-type food plants to be stronger performers in botanical competitions. Should a population so released from its natural control possess what else is necessary it could become one of an ecosystem's major play-

ers, i.e., a keystone species (= plays a crucial role in ecosystem functioning). The result would be a system-altering cascade set into motion simply because one of its botanical components responded aggressively to supplemental CO₂ either by growing faster or by using moisture and nitrogen more efficiently (Figure 2J).

The Appendix (and associated Figure) explain in greater detail how an augmented (or rising) supply of CO₂ can affect a plant's demand for moisture and nitrogen and the efficiency with which the latter two resources are used for growth. Briefly put, the story reads as follows: land-dwelling flora avoid expending moisture unnecessarily by adjusting the apertures (= stoma) of their stomata just enough to fully supply (= saturate) with CO₂ what's known as a plant's IPC (= immediate photosynthetic capacity; Essay A; Figure 2AA). IPC varies short and long-term rising and falling according to conditions that fluctuate within and around the individual photosynthetic organ. A nitrogen deficiency, for example, depresses IPC until restored days to months following the addition of fertilizer whereas the suppressive effect of shade caused by a passing cloud lasts but minutes before carbon fixation bounces back to its former higher rate. In essence, whether driven by conditions in or outside a leaf, fluctuations in IPC are closely tracked by shifts in stomata aper-

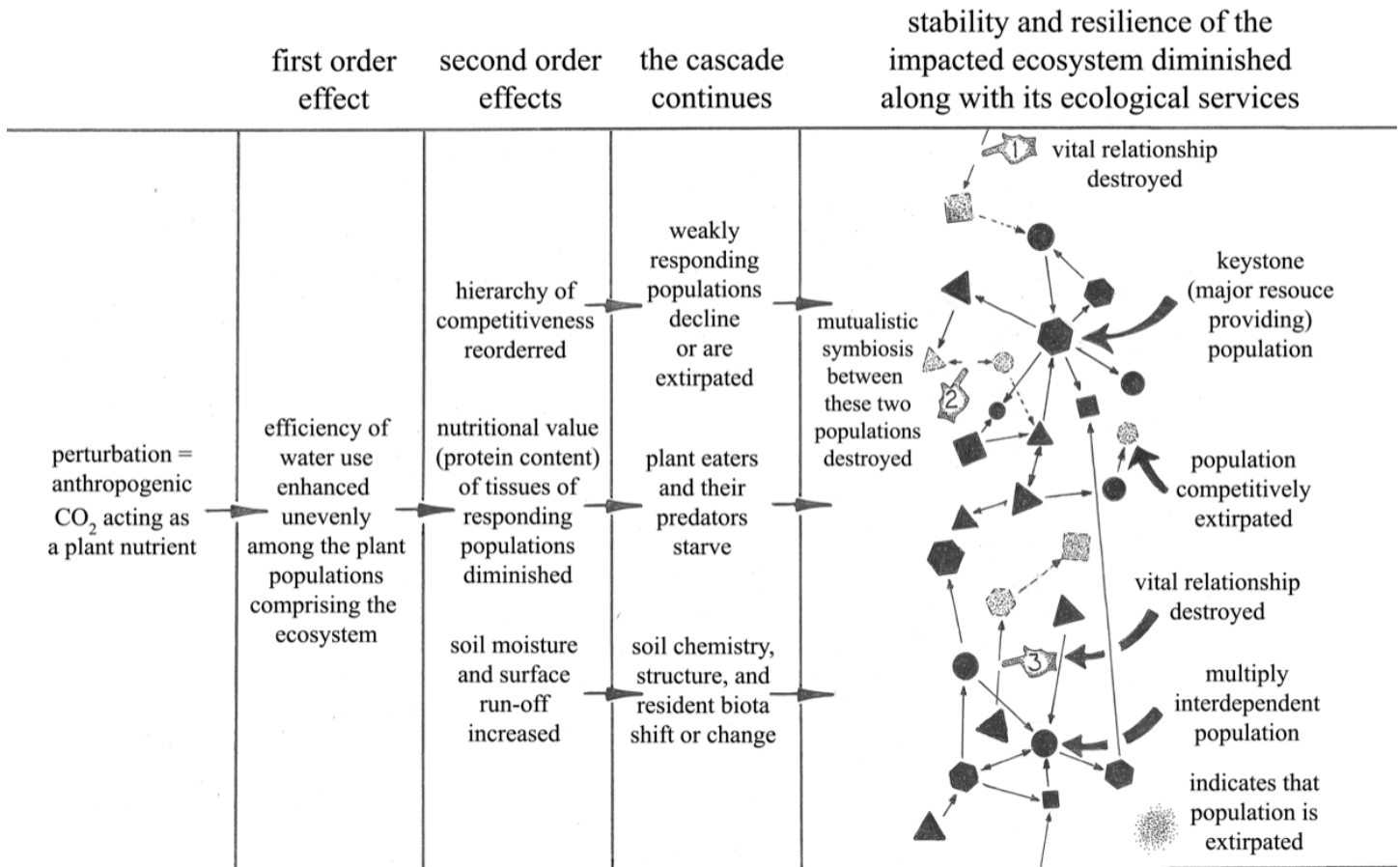


Figure 2J: A schematic illustrating how the current buildup of CO₂ in Earth's atmosphere could by enhancing the growth rate and/or water use efficiency of one or more resident populations of plants could trigger a cascade of events capable of altering the structure and dynamics of an entire hosting ecosystem.

ture (= leaf surface permeability) assuring tight coordination between CO₂ fixation and transpiration.

The tight coupling of IPC and water and nitrogen use illustrates botanical optimization a principle of great adaptive significance. Illusions to economy and efficiency are used repeatedly in this and the preceding nine essays because the deployment of resources cost effectively, particularly when supplies are thin, is a powerful driver of plant evolution. But don't confuse these two concepts with optimization. Economy and resource use efficiency are context-free in that they deal with absolutes—they simply describe how much of something is expended to produce a certain amount of something else (**Essays F, H**). Context has no relevance whereas for optimization it does. To optimize is to achieve the best outcome possible under a specific set of circumstances. In the grand scheme of life, it's optimization that's the true arbiter of bio-success, and efficiency to the extent that it contributes to fitness is its handmaiden. Plant form and function are better described as optimized by natural selection than rendered more economical or efficient.

Returning to an aspect of global change, the combustion of fossil fuels is mobilizing worldwide about as much reactive nitrogen, the kind usable by organisms, as originates from natural sources. At some heavily industrialized European sites this supplementation is pernicious adding to problems already caused by CO₂ enrichment. Such an abrupt onset of a major over-abundance of not one but two key plant nutrients, CO₂ being the other, wouldn't threaten the integrity of species and ecosystems nearly as much were most flora not adapted to subsist on relatively sparse supplies of both substances. Remember that a scarcity of nitrogen (or phosphorus) rivals that of moisture as the most frequently growth limiting of the material resources that plants require. To so heavily augment natural supplies cannot help but promote floristic change some of which is underway already.

Recall that species equal populations each confined by its needs and tolerances to specific kinds of habitats and ecosystems (and specific spatial inches within; **Essays D, H**). Attributes that support a particular species' life history strategy and thereby dictate its ecology include those that govern how moisture and nutrients are obtained and used. So how do populations respond when resource(s) whose scarcity had historically constrained growth abruptly appear in evolutionary time as available in more plentiful supply? Populations that fall at the low end of the range of vigor exhibited among the higher plants tend to owe their relatively tepid response to genetics having adopted slow growth to help reduce demand for some resource that for their lineage had long been ex-

perienced in short supply. Opposite these obligatory slow-pokes are the conditional species that can perform better. Flood an ecosystem with a nutrient whose supply previously had limited growth potential for much of its resident flora and the former type at best will respond no more than modestly. Conversely, the population whose vigor had been held in check by suboptimal supply will perform better perhaps even robustly enough to turn the tables on one or more of its formerly superior but somewhat less resource-responsive competitors.

What else adverse might emerge within neotropical ecosystems as Earth's biosphere becomes warmer and more abundantly supplied with nutrients and when some of the most plant growth-influencing aspects of precipitation shift? We've already considered situations that alter plant-predator relationships and botanical competitions and the accompanying potential for ecosystem-wide consequences. What other chain reactions might materialize and to what effect? For example, will *Aechmea nudicaulis* and *Vriesea neoglutinosa* and the several additional tank-forming bromeliads that occur abundantly in the Restinga formations of coastal Brazil respond in ways that enhance or diminish their contributions to land building and dune stabilization? And what about the epiphytes? Do they interact enough for us to anticipate alterations in the composition and structure of their communities as the availabilities of CO₂ and nutritive nitrogen continue to rise? Are the most ecologically extreme of the bromeliads—the atmospheric—going to be the first in their family to suffer the ill effects of global change (**Essay H**)?

Today it's possible to only speculate about where, by what measure, and how soon we'll know the entirety of the consequences of humanity's insults of our planet's life support system. As for plants, they simply differ too much relative to their vulnerability to injury and extinction. No one, regardless of authority or credentials should venture more than qualified statements about how additional warmth, chemically altered precipitation or elevated atmospheric CO₂ are going to impact this or that species, community or ecosystem. And don't expect more definitive answers any time soon. Being mostly slow growers' additional decades may have to pass before even the most expert among us can differentiate the bromeliad populations in decline from those that so far remain impervious to the worst that global change has delivered so far. At this point who can say. Bromeliaceae already may have accumulated a substantial extinction debt, which means that numerous of its populations despite appearing viable today already are experiencing irreversible decline toward nonexistence.

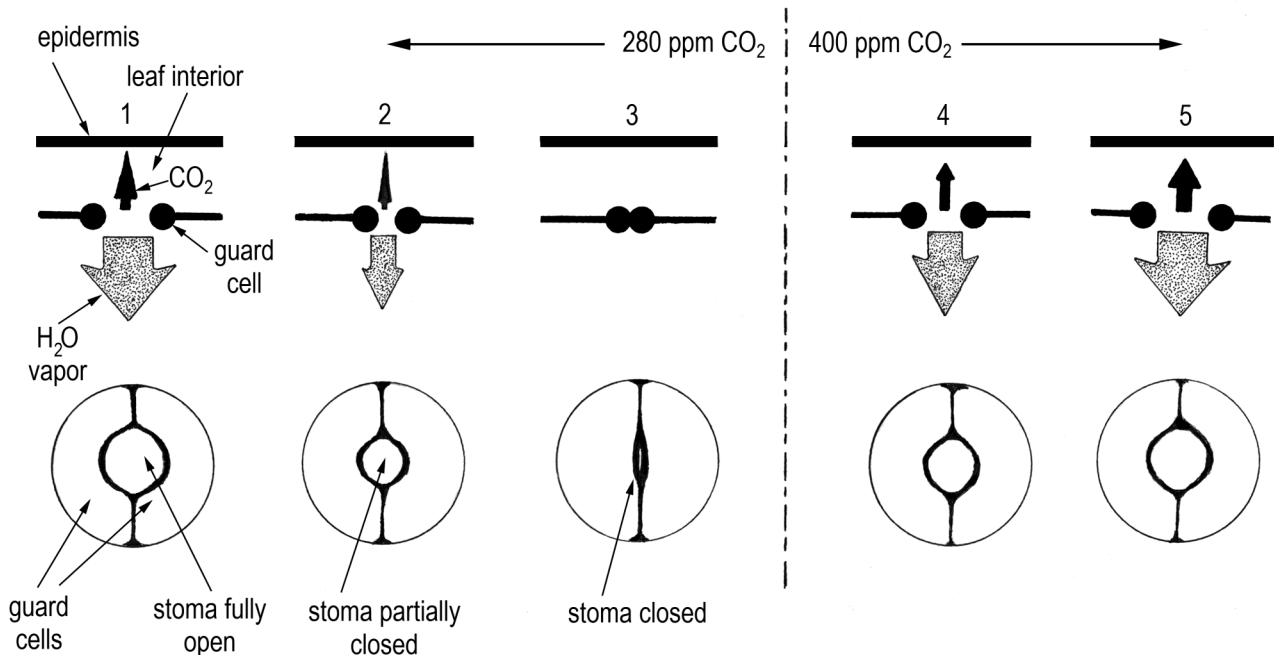
APPENDIX

The following narrative explains how the land plants by virtue of possessing sensitive highly regulated stomata avoid using more water than necessary to fully engage their fluctuating immediate photosynthetic capacity (IPC). IPC is a measure of how rapidly CO₂ can be fixed by a leaf or other green organ at a given instant not according to its potential but under the changing conditions that prevail inside and around that organ. Explained by the following five demonstrations is how mounting supplies of CO₂ and nutritive nitrogen are influencing botanical water and nitrogen use efficiency and productivity (photosynthesis).

Demonstration #1 in the **Figure below** shows CO₂ diffusing into the interior of a leaf from an atmosphere that contains this gas at the preindustrial concentration of about 280 ppm at a stomata-regulated rate just adequate to fully utilize the organ's IPC to convert CO₂ into glucose. None of the other conditions required to conduct photosynthesis are submaximal—are limiting photosynthesis below full potential. Demonstration #2 shows how light intensity having been diminished by a passing cloud reduces the same organ's IPC causing it to adjust the apertures of its stomata to again allow only enough CO₂ to enter to fully supply (saturate) what now is its conditionally reduced IPC. Because stomata also regulate transpiration the ratio of CO₂ assimilated to water lost remains relatively unchanged from what it was when

all conditions were maximally favorable, i.e., when more light was available to energize photosynthesis. In other words, water use efficiency (= transpiration ratio) didn't change a great deal despite the tandem reductions of IPC and sugar production. Still later, drought stress (illustration #3) has eliminated IPC, which in turn caused the stomata to close preventing what otherwise would be water expended unaccompanied by net photosynthesis.

The crucial difference between demonstrations #1-3 and #4 and #5 is a CO₂ supply elevated from 280 to today's ~415 ppm. Consequently, the stomata of #4 have compensated by narrowing their stoma because enough CO₂ can enter from what has become an enriched supply to saturate an IPC undiminished by shade or drought. In this forth arrangement the transpiration ratio has fallen elevating water use efficiency. IPC in the final demonstration (#5) is now elevated 25% having benefited from precipitation enriched in reactive nitrogen. As such, its stomata haven't narrowed as much as those for #4 because more CO₂ is needed to fully utilize an IPC boosted by supplemental nitrogen. Of the five leaves #5, because it's drawing CO₂ from an enriched source and it possesses 25% more IPC than the leaves experiencing conditions #1-4, theoretically can make sugar fastest and use H₂O most economically, i.e., achieve the highest water use efficiency and rate of photosynthesis. Informed by the above information, which of the five leaves featured in this demonstration would be most beneficial as food for a foraging herbivore?



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GLOSSARY

- Abscisic acid (ABA):** a plant hormone that regulates many processes including the induction of CAM-type photosynthesis and the enforcement of bud and seed dormancy.
- Abscission zone:** a thin band of separation or abscission tissue located near the base of the leaves of certain *Pitcairnia* spp. and a few other bromeliads that avoid desiccation during dry seasons by shedding their foliage, i.e., the anatomical basis for drought-deciduousness.
- Acclimatization:** (see phenotypic plasticity): an adjustment in structure and or function that an organism undergoes in response to changed circumstances (**Figure 2I**).
- Accidental epiphyte:** a species whose members only occasionally grow on a woody host.
- Adaptation:** a trait that by its presence increases an organism's biological fitness under specific circumstances (e.g., succulence for a drought-enduring bromeliad).
- Adaptive radiation:** an evolutionary phenomenon characterized by proliferation and divergence of multiple lineages from a single ancestral (stem) lineage (e.g., the crown radiation of Bromeliaceae).
- Adventitious:** arising more or less randomly as illustrated by roots that emerge along the rhizomes and leafy stems of many bromeliads (**Figure 4AA**).
- Allele:** a version or form of a multi-allelic gene. Some alleles are dominant or incompletely dominant over other recessive versions of the same gene.
- Alternation of generations:** the life cycle of the higher plant in which the individual passes through a haplophase (1N) and then a diplophase (2N) stage known respectively as the gametophyte and sporophyte stages or generations (**Figure 2D**).
- Allogamy:** sexual reproduction that involves the union of sperm and eggs produced by two rather than a single bisexual individual. The parents may not be members of the same clone.
- Anaerobe:** an organism that lives in oxygen-free environments, the opposite of aerobe.
- Angiosperm:** a flowering plant (a member of division Magnoliophyta).
- Ant garden:** the flora that certain arboreal ants plant and tend on their carton nests. The relationship is complicated, mutually beneficial and obligatory for many of the participating flora including several of the bromeliads
- Ant-house:** a label that applies to a number of bromeliads and other species that host ant nests within their bodies (e.g., *Tillandsia caput-medusae*; **Figure 5B**)
- Anthesis:** the act of flowering.
- Anthocyanins:** the water-soluble pigments that impart blue to purple to red color to petals, fruits and more.
- Apical dominance:** a phenomenon whereby the apical meristems of shoots inhibit lateral branching by producing hormones that enforce dormancy on axillary buds.
- Apical meristem:** the mass of embryonic (stem) cells located at the tips of roots and stems that cause their growth in length.
- Aerenchyma:** a tissue in which the empty spaces located between adjacent plant cells are much enlarged to promote air movement (e.g., the channels located between adjacent vascular bundles in the leaves of many bromeliads (**Figure 2AA**).
- Archaea:** a group of ancient bacteria distinct from the true bacteria (eubacteria).
- Aril:** a small edible appendage attached to many ant-dispersed seeds.
- Asexual reproduction:** the production of offspring by means that do not involve unions of eggs and sperm. The resulting progeny are genetically identical to the single parent, i.e., they constitute a clone.
- Atmospheric bromeliad:** (see also grey tillandsias): a member of subfamily Tillandsioideae that appears grey owing to the presence of dense layers of light-reflecting trichomes on its foliage and the absence of a tank, also known shorthand as an atmospheric.
- Autogamy:** (see self-compatibility): reproduction that involves unions of eggs and sperm produced by the same bisexual individual.
- Autotrophy:** describes an organism that manufactures all of its own food usually via photosynthesis.
- Axillary bud:** a bud located in the axil of a leaf (**Figure 2AA**).
- Backcross:** a term that describes what occurs when first generation progeny (F₁) of an interspecific hybrid cross with one of the two parents of the original hybrid.
- Basal meristem:** a band of meristematic (stem) cells located at the base of a monocot leaf responsible for producing most of its length (**Figure 7F**).
- Berry:** a type of fruit characterized by fleshy walls and multiple seeds. Members of subfamily Bromelioideae produce berry-type fruits (**Figure 1C**).
- Body plan:** the basic form of the body of an organism.
- Bract:** an anatomically modified leaf that serves a primary purpose other than photosynthesis (e.g., protection, attraction of pollinators; **Figure 3D**).
- Bromelioid:** an adjective that refers to members of subfamily Bromelioideae.
- C₃-type photosynthesis:** a mechanism that uses solar energy and water to fix CO₂ into the simple sugar glucose so-called because one of the intermediate products of this synthesis contains three carbon atoms (**Figure 2A**).
- CAM-type photosynthesis:** a mechanism that allows a plant to capture at night the CO₂ destined to end up as sugar via the light-driven C₃-type mechanism during the following day (**Figure 3A**). The product of the initial dark fixation is malic acid.
- Capsule:** a type of fruit, dry at maturity that splits open (dehiscent), many seeded, the most common type of fruit among the bromeliads (**Figure 1C**).
- Carbon fixation:** the process whereby CO₂ is catalyzed to produce glucose or an organic acid (e.g., malic acid during CAM).
- Carton:** a composite material that certain species of arboreal ants manufacture to build their nests and covered runways.
- Carotenoid:** a member of a class of yellow to orange chemical compounds that perform a variety of cellular functions including assisting the green plants harvest solar radiation and avoid photo-injury when over-exposed to sunlight.
- Caulescent:** an adjective that refers to the stem. Roots that arise in stems are considered caulescent in origin (**Figure 4AA**).
- Chlorenchyma:** a tissue equipped with chloroplasts (**Figure 2AA**).

- Clade:** all the species derived from a common ancestor. Clades are nested in the sense that a family is a clade comprised of one or more genera each of which is a lesser clade (**Figure 3AA**).
- Cladogenesis:** = speciation.
- Climate change:** one aspect of global change, used here to describe a phenomenon largely driven by human activities that alter the chemistry and heat trapping capacity of Earth's atmosphere, hence its climate.
- Clone:** all of the asexually produced progeny that arise from a union of a single sperm and egg. Members of a clone share the same genotype.
- Coma:** a tuft of hairs that extend from the seeds of some bromeliads that assist their dispersal by air (**Figure 1C**).
- Conspecific:** belonging to the same species as in two members of the same species.
- Constitutive:** permanently expressed as applied to traits such as succulence as opposed to facultative-type (induced) traits.
- Convergent evolution:** the independent evolution of the same trait in two or more lineages in which the genetic basis for that trait(s) differs (see parallel evolution and homoplasy).
- Cost/benefit:** the ratio of benefit gained per unit of input invested to achieve that gain. It is used, to assess the efficiency with which plants acquire, allocate and use resources such as water for growth and reproduction.
- Crown radiation:** (see adaptive radiation): the evolutionary expansion beginning with a stem lineage that generates many daughter lineages all of which comprise a taxon such as a family (**Figure 1AA**).
- Cultivar (cultigen):** opposite of wild type, a domesticated plant.
- Cuticle:** the layer of waxy material that covers the epidermis of plant organs (**Figure 7A**).
- Decarboxylation:** the chemical recovery of a CO₂ molecule from a molecule of an organic acid such as malic acid during the CAM process (**Figure 2A**).
- Deciduous** (see abscission zone): an adjective that describes organs, usually leaves, that plants shed following their separation by a distinct abscission zone.
- Determinant growth:** growth genetically programmed to be limited in extent exemplified by the bromeliad ramet that typically produces a certain number of leaves and then a single terminal inflorescence. Vines illustrate indeterminate growth.
- Detritivore:** an invertebrate animal that feeds on dead organic material (detritus). The tank bromeliads depend on this kind of organism to help them recover mineral nutrients contained in intercepted biomass.
- Developmental program:** that part of a genome that directs and regulates an individual's development (ontogeny) and ultimately determines its body plan and much more.
- Dicot:** a member of Dicotyledonae one of the two taxonomic classes that comprise division Magnoliophyta.
- Diocism** (see monoecism): a term that describes a condition whereby a species consists of two kinds of individuals one of which produces only male (staminate) flowers and the other only female (pistillate) flowers.
- Diplophase** (see haplophase, alternation of generations): the 2N (diploid) or sporophyte stage of the higher plant life cycle.
- Disturbance:** a term used by ecologists to describe the results of environmental events such as fire or plowing that disrupts a biological community.
- Drought-avoidance** (see abscission): a life history strategy whereby a plant avoids injury or death by shedding certain organs, usually foliage, that if retained during drought would result in serious desiccation.
- Drought-endurance** (see drought-avoider): a life history strategy whereby a plant withstands drought short of having to discontinue photosynthesis like the drought-avoider.
- Ecological engineer** (see keystone species): a plant whose presence in an ecosystem improves conditions in that ecosystem for other biota, e.g., the tank-forming bromeliads.
- Eco-physiology:** those aspects of physiological performance amenable to fine-tuning to match local growing conditions as opposed to the more consistent aspects of metabolism (e.g., which type of photosynthesis is conducted (C₃ vs. CAM) versus the how proteins is synthesized).
- Environmental cue:** a signal that originates in the environment that when perceived by an organism allows it to coordinate its activities with its ever changing circumstances (e.g., photoperiod).
- Epidermis:** the outermost tissue of an organism that usually consists of a single layer of cells. It may be quite elaborate consisting in part of trichomes as well as stomata (**Figure 2F**).
- Epiphyte:** a plant that grows upon another plant.
- Eucaryotic** (see procaryotic): an adjective that describes organisms whose cells contain a discrete nucleus and other membrane bound organelles, includes all organisms (the eucaryotes) except for Archaea, eubacteria and the cyanobacteria.
- Evolutionary grade:** a state or level of evolutionary advancement. The seed bearing plants represent one evolutionary grade and the spore bearing types (the pteridophytes) another more primitive one. Similarly, the tank-bearing and atmospheric bromeliads represent separate evolutionary grades the former being less advanced (derived) than the latter (**Figure 4G**).
- Excitation energy:** energy derived from sunlight that if accumulated faster than an overexposed leaf can consume it by using it to fix CO₂, or dissipate it in some other way, will experience photo-injury.
- Extant:** to be living not extinct.
- Facultative epiphyte:** a species whose members grow on and above ground although not necessarily at the same locations.
- Fecundity:** reproductive output or potential to produce progeny.
- Fitness** (see natural selection): a Darwinian concept/measure of an organism's capacity to reproduce under a certain set of circumstances and thus pass its genes on to the next generation.
- Form:** a formal intraspecific taxonomic category (**Figure 1E**)
- Fruit:** the product of a pollinated flower that occurs in many versions but always consists of one or more seeds and often associated organs.
- Functional tradeoff:** an unavoidable reduction or loss of one or more benefits (e.g., functions, capacities) because of possessing another trait (e.g., water unavoidably expended to gain CO₂ during photosynthesis).

- Gamete:** sex cell: sperm and eggs.
- Gender expression:** the functional sex of a plant.
- Generalist** (see survival bandwidth): a term that describes organisms characterized by broad tolerances for growing conditions that accordingly can occupy relatively broad geographic distributions and/or range into diverse kinds of habitats—the opposite of specialist.
- Genetic drift:** a non-Darwinian process whereby evolution occurs as a random process in a random direction rather than as a response to natural selection that heightens biological adaptation.
- Genome:** all the genes possessed by an individual organism.
- Genotype:** the nature of the genes possessed by an individual organism.
- Gene pool:** all the genes possessed by all the individuals that comprise a species or any other sexually reproducing population.
- Glabrous:** lacking hairs (trichomes), naked.
- Global change:** a term applied to the multiple changes caused by human activity that threaten the global bio-support system.
- Glucose:** the simple sugar produced by photosynthesis.
- Guayana Shield:** one of the two most ancient of the exposed geological formations of South America—home of the phylogenetically oldest of the surviving bromeliads, *Brocchinia*.
- Habit:** a nebulous term that describes a plant’s physical proportions (e.g., tree versus herb), manner of growth (e.g., annual versus perennial) and the type of required substrate and living space (e.g., epiphyte vs. terrestrial plant).
- Haplophase:** (see gametophyte, diplophase, alternation of generations).
- Hemi-epiphyte:** a plant that spends only part of its life as an epiphyte.
- Hermaphrodite:** a condition that describes an individual that produces sperm and eggs, is bisexual.
- Heterotrophy:** the nutritional opposite of autotrophy. Heterotrophic organisms subsist on organic substances ultimately produced by autotrophs (e.g., all fungi and animals).
- Higher plant:** (see vascular plant).
- Homoplasy:** a term that describes situations in which the same trait has evolved independently in two or more lineages. It may not indicate relationship. Such redundancy results from parallel or convergent evolution or the independent loss or gain of the same trait (**Figure 5AA**).
- Humic:** rich in organic matter (humus).
- Hydraulic capacitance:** tissue water storage capacity.
- Hydrenchyma:** a tissue devoted to primarily to water storage (**Figure 2AA**).
- Hydrophyte:** an aquatic plant.
- Hypodermis** (see hydrenchyma): a usually colorless water storage tissue located immediately beneath an epidermis.
- Immediate photosynthetic capacity (IPC):** the ability of a plant or one of its organs to conduct photosynthesis at a particular instant. IPC changes in accordance with the availability at that instant of the most rate limiting of the resources (e.g., supply of solar energy and CO₂) needed to conduct this process as well as the physiological state of the plant itself.
- Indumentum:** a cover of something on a plant surface—a layer of trichomes in the case of Bromeliaceae (**Figure 2F**).
- Inflorescence:** that part of the shoot dedicated primarily to the production of flowers and their products.
- Inselberg:** a low mountain or granitic prominence that rises abruptly above more or less flat topography.
- Intercauline:** an adjective that refers to roots that originate within stems and pass down that organ before emerging—a widely occurring feature among the bromeliads (**Figure 4AA**).
- Keystone species** (see ecological engineer): a species that has inordinate influence in an ecosystem by providing some important product or service for certain co-occurring biota.
- Life history profile** (see life history strategy): a compellation of all the adaptations, life cycle characteristics as so on that determine how a particular plant or its species makes its living, interacts with its environment and much more.
- Life history strategy:** how a plant makes its living (e.g., as a tank versus trichome-dependent bromeliad).
- Lifestyle:** same as life history strategy.
- Lineage:** a sexually inter-fertile population (species) as it continues generation upon successive generation through geologic time.
- Lithophyte:** a plant that regularly grows on rock.
- Litter:** plant debris particularly abscised foliage.
- Luxury consumption:** the accumulation of a nutrient far beyond an organism’s immediate needs.
- Macronutrient:** one of the six mineral nutrients that plants require in amounts far greater than those for the micronutrients (e.g., nitrogen, phosphorus, potassium).
- Malic acid:** a four carbon organic acid that’s the product of the fixation of CO₂ during the first (dark) step of CAM-type photosynthesis—also a widely occurring fruit acid (**Figure 2AA**).
- Mating systems:** the diverse genetically mediated mechanisms that influence gene flow within interbreeding populations. (e.g., dioecism, pollen whether self-compatible or incompatible).
- Meiosis:** the division of a diploid mother cell to produce four haploid sex cells (sperms and eggs), a reduction division as opposed to mitosis, where the daughter cells possess the same ploidy level as the mother cell.
- Meristem:** a tissue comprised of meristematic (stem) cells that divide to yield what become mature cells and tissues. What a meristem produces depends on its location (apical versus basal (**Figures 4AA, 7F**)).
- Mesomorphic:** an adjective that’s describes a plant that is anatomically adapted to live where drought is normally not life threatening.
- Mesophyll:** a tissue comprised of relatively unspecialized parenchyma cells that comprise the bulk of the interiors of many organs such as leaves (**Figure 1A**).
- Microbiome:** a community of microorganisms that lives within or on the body of a higher organism for example in the human gut and the tank of a bromeliad.

- Micronutrients** (see macronutrients): mineral nutrients that plants require in smaller amounts than the macronutrients (e.g., zinc, copper, boron).
- Mineral nutrition:** the utilization by plants of the macro- and micronutrients as opposed to fixed carbon obtained via photosynthesis.
- Mineralization:** the final stage in the reduction of biomass to its elemental constituents, accomplished by the microbial decomposers.
- Modular growth:** growth that results in a succession of redundant semi-autonomous subunits, or ramets in the case of most of the bromeliads (**Figure 4AA**).
- Monocarp:** flowering but once at the end of a life cycle—the opposite of polycarp (e.g., *Tillandsia dasylirofolia*).
- Monocot:** a member of Monocotyledonae one of the two taxonomic classes that comprise division Magnoliophyta.
- Monoecism** (see breeding system): a condition that describes plants that produce two kinds of flowers: bisexual and unisexual usually male (e.g., certain species of *Cryptanthus*).
- Mosaic evolution:** a condition that describes an organism that possesses traits some of which are highly derived and others that have changed less over the same interval.
- Mutualism:** a type of symbiosis where both parties benefit from their relationship (e.g., ant nest-garden ants and their cultivated plants).
- Mycorrhiza:** a physical combination of a root and one or more of a variety of fungi that help the botanical partner acquire nutrients such as phosphorus in exchange for nutrients that the fungus needs from the host plant.
- Myrmecophyte** (see myrmecotroph): a plant that participates in mutualistic symbiosis with ants (**Figure 5B**).
- Myrmecotrophy:** fed by ants (e.g., *Tillandsia caput-medusa*; **Figure 5B**).
- Natural (Darwinian) selection:** a process whereby agents of environmental origin selectively eliminate the least fit members of a population leading over time to changes (evolution) in a population's gene pool structure and composition.
- Neoteny:** the evolutionary mechanism that operates by modifying the developmental program (ontogeny) of the individual such that traits formerly expressed early in the life cycle persist into the adult stage.
- Niche:** a concept that refers to the role that an individual or a population plays in a habitat or ecosystem.
- Niche space:** a concept that refers to the virtual space that an individual or population occupies by virtue of its capacity to accommodate all of the conditions that define or prevail in that space.
- Nitric oxide (NO):** a signaling molecule that plays important regulatory roles in plants and animal physiology.
- Obligate epiphyte:** a species whose members always grow on woody hosts.
- Ovule:** an unfertilized seed (**Figure 2D**).
- Parallel evolution** (see convergent evolution and homoplasy): the separate acquisition of a trait by two or more lineages because they share a recent ancestor, they share genetically based propensities to evolve the same traits when subjected to the same selective pressures.
- Perfect flower:** a flower that includes both functional male and female organs.
- Perceptron:** a hypothetical apparatus that allows organisms to perceive their circumstances and respond accordingly (**Figure 1I**).
- Phenology:** an organism's seasonal calendar for conducting its seasonal activities (e.g., bud break, flowering).
- Phenotypic variation or plasticity** (see acclimatization): variation in the phenotypic expression of a genotype that reflects its capacity to adjust to its owner's immediate circumstances (e.g., sun and shade forms of *Tillandsia utriculata*; (**Figure 2I**).
- Phloem:** the food conducting tissue of a vascular plant (**Figure 2AA**).
- Photo-injury:** damage to the light harvesting apparatus of a green plant by over exposure to sunlight.
- Phototroph:** an organism that makes its own food using solar energy (e.g., green plants).
- Photoperiodism:** an organism's use of day length to time season-sensitive activities such as flowering.
- Phylogenetic constraint:** a condition that prevents a lineage from adopting a particular trait or evolving in a particular direction because of its genetic legacy i.e., the evolution of high competitiveness by a lineage already will adapted to tolerate severe drought.
- Phylogeny:** the evolutionary history (genealogy) of a group of related organisms (**Figure 1AA**).
- Phytotelm:** a naturally occurring cavity in a plant capable of holding water, an example being the leafy tank from which the phytotelm-or tank-equipped bromeliads draw moisture and nutrients (**Figure 7F**).
- Phytotelmata:** (see phytotelm): a phytotelm with its contents that include aquatic organisms (**Figure 7F**).
- Phytochrome:** a red-far red absorbing plant pigment that mediates numerous growth responses.
- Pistillate flower:** a flower that contains functional female sex organs only.
- Pitcairnioid:** an adjective that describes members of subfamily Pitcairnioideae.
- Plant economics:** a concept that recognizes that as plants grow and reproduce, they adhere to certain principles of economics that promote efficiency in the acquisition and use of resources such as nitrogen, water and the products of photosynthesis to promote fitness.
- Poikilohydry:** a condition whereby the water content of an organism fluctuates dramatically according to the humidity of its environment. Such plants also are described as desiccation-tolerant or resurrection types.
- Pollination syndrome:** a suite of mostly floral traits employed by plants to disperse pollen by targeting specific kinds of vectors including birds, bats, insects and wind (**see table 2D; Figure 3D**).
- Polycarp** (see monocarp): a condition that describes perennials that flower repeatedly as is the case for a large majority of the bromeliads (**Figure 2AA**).
- Polyploid** (see tetraploid): an adjective that describes a plant comprised of cells that harbor more than a diploid set of chromosomes.

- Polymorphism:** a condition displayed by populations whose members differ one from another by genotype and phenotype.
- Population:** a group of interbreeding individuals. Species are populations many of which are comprised of formally recognized intraspecific populations (e.g., varieties).
- Ramet:** a single shoot or module produced by sympodial branching (e.g., most bromeliads; **Figure 4AA**).
- Reactive nitrogen:** nitrogen within molecules that plants can use as nutrients (e.g., NH_4^+ , NO_3^-).
- Restinga:** a low statured, broad-leafed coastal strand type community within the Atlantic Forest biome that ranges along much of the southeastern coast of Brazil and at many locations features dense populations of tank-forming bromeliads.
- Rheophyte:** a wetland plant that inhabits flowing water at least part of the year (e.g., some *Pitcairnia* spp.).
- Rhizome:** a usually horizontally oriented stem that bears scale-like foliage and connects the successive ramets of modular bodies plants (e.g., most bromeliads; **Figure 4AA**).
- Rhizosphere:** the area immediately adjacent to a root, frequently heavily populated by microbes, some of which interact positively with that root (**Figure 1F**).
- Sclerenchyma:** a type of tissue comprised of thick walled sclerenchyma cells that often protects softer tissues or provides mechanical support as exemplified by the wiry texture of the roots of the epiphytic bromeliads.
- Seed:** an ovule following fertilization of the egg that it contained (**Figure 2D**).
- Seed dispersal syndrome:** a suite of traits that a plant employs to encourage a specific agent (e.g., wind, bird) to disperse its sexually produced offspring.
- Self-compatibility** (see mating system, autogamy): the genetically based condition that allows a bisexual plant to produce seeds with its own pollen.
- Self-incompatibility** (see mating system, allogamy): the genetically based condition that prevents a bisexual plant from producing seeds with its own pollen.
- Sexual reproduction:** the production of offspring that result from unions between sperm and eggs.
- Shoot:** the usually aerial portion of a vascular plant, the part that consists of stems, leaves and sexual organs as opposed to the usually subterranean root system.
- Spatial niche:** a living space characterized by a specific combination of growing conditions.
- Specialist:** used here to describe a species broadly tolerant of growing conditions, i.e., has a broad survival bandwidth—the opposite of an ecological generalist.
- Speciation** (see cladogenesis): the act of a parent lineage (species) giving rise to one or more daughter lineages (**Figure 1E**).
- Subspecies:** (see variety; **Figure 1E**)
- Stem group or lineage:** a lineage that give rise to a crown radiation (**Figures 3A, 1E**).
- Staminate:** an adjective that describes a male flower.
- Stomata:** the epidermal apparatus that includes a pore, stoma or aperture that by opening and closing regulates gas exchange between the plant interior and the surrounding atmosphere (**Figures 1A, 2F**).
- Stress:** the physiological condition experienced by an organism when seriously deprived of some vital resource or challenged by another kind of life-threat.
- Succulence** (see hydrenchyma): a term that describes the possession of large amounts of water storage tissue most often in foliage (the leaf succulent) or stems (the stem succulent).
- Survival bandwidth** (see specialist and generalist): the measure of an organism's eco-tolerance that determines the conditions under it can survive in nature.
- Sympodial branching:** a type of dichotomous branching that results in one determinant and one indeterminate branch. Among the bromeliads, it's the axillary bud that forms the vigorous branch while the other terminates its development by producing a terminal inflorescence.
- Taxon (taxa = plural):** a group of plants recognized as comprising a formal taxonomic category such as a species, family or order.
- Tank** (see phytotelm).
- Tetraploid** (see polyploidy): a plant comprised of cells each of which contains four sets of chromosomes.
- Tillandsioid:** a member of subfamily Tillandsioideae.
- Transpiration:** the loss of water by a plant as vapor mostly through its stomata (**Figure 1A**).
- Transpiration ratio** (see water use efficiency).
- Trichome:** an epidermal appendage that most plants possess in some form to perform one or more of a variety of functions that include the absorption of moisture and mineral nutrients for the most specialized of the bromeliads (**Figures 2-3F**).
- Triocism** (see gender expression): a condition whereby a population consists of three morphs or genders, namely individuals that produce only staminate or pistillate or perfect flowers.
- Variety:** a formal intraspecific taxonomic category (**Figure 1E**).
- Vascular bundle:** a strand of phloem and xylem tissue that supplies plant organs such as leaves and the stems (**Figure 1A**).
- Vascular cambium:** the meristem responsible for producing the xylem and phloem that expands the girth of the stems and roots of woody plants.
- Vascular plant** (see higher plant): a plant that possesses xylem and phloem conducting tissues.
- Vicariance:** the geographic separation of populations or parts of populations, a driving force in the speciation process.
- Water-use efficiency** (see transpiration ratio): the ratio of moisture expended via transpiration to dry matter produced by photosynthesis during the same interval.
- Wild type:** an organism that has not been domesticated or in any other way altered genetically, the opposite of cultivar.
- Xeromorphic:** an adjective that describes a plant anatomically equipped to withstand drought.
- Xerophyte:** a plant adapted to survive drought (e.g., many bromeliads).
- Xylem:** water conducting tissue or wood if produced by a vascular cambium (**Figures 1A, 2AA**).



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