



# Think tank: water relations of Bromeliaceae in their evolutionary context

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Received 31 July 2015; revised 28 February 2016; accepted for publication 1 March 2016

Water relations represent a pivotal nexus in plant biology due to the multiplicity of functions affected by water status. Hydraulic properties of plant parts are therefore likely to be relevant to evolutionary trends in many taxa. Bromeliaceae encompass a wealth of morphological, physiological and ecological variations and the geographical and bioclimatic range of the family is also extensive. The diversification of bromeliad lineages is known to be correlated with the origins of a suite of key innovations, many of which relate directly or indirectly to water relations. However, little information is known regarding the role of change in morphoanatomical and hydraulic traits in the evolutionary origins of the classical ecophysiological functional types in Bromeliaceae or how this role relates to the diversification of specific lineages. In this paper, I present a synthesis of the current knowledge on bromeliad water relations and a qualitative model of the evolution of relevant traits in the context of the functional types. I use this model to introduce a manifesto for a new research programme on the integrative biology and evolution of bromeliad water-use strategies. The need for a wide-ranging survey of morphoanatomical and hydraulic traits across Bromeliaceae is stressed, as this would provide extensive insight into structure–function relationships of relevance to the evolutionary history of bromeliads and, more generally, to the evolutionary physiology of flowering plants. © 2016 The Author. *Botanical Journal of the Linnean Society* published by John Wiley & Sons Ltd on behalf of Linnean Society of London., *Botanical Journal of the Linnean Society*, 2016, 181, 415–440

**ADDITIONAL KEYWORDS:** adaptive radiation – crassulacean acid metabolism – ecophysiology – epiphytism – functional anatomy – succulence.

## INTRODUCTION

When French botanist Antoine de Jussieu in his *Genera plantarum* of 1789 first established the bromeliads as a taxonomic group, he was laying the modest foundations for over two centuries and recording of research on this fascinating family of monocotyledons. Admittedly, de Jussieu did include among his ‘ordine naturale’ such interlopers as *Burmannia* L. (Burmanniaceae), *Xerophyta* Juss. (Velloziaceae) and *Agave* L. (Asparagaceae). He also fell into the popular trap of describing the epiphytic species as ‘parasiticæ’. However, one seemingly minor but important observation recorded in de Jussieu’s brief commentary on bromeliads is the presence of leaves described as ‘vaginantia’ and ‘canaliculata’. This commentary represents one of the earliest references, albeit oblique, to the water-impounding tanks (phytotelmata) characteristic of so many bromeliads.

It would be another hundred years before researchers began exploring in earnest the functional biology of bromeliads, but many of them were then drawn to pay special attention to these tanks and other adaptations in bromeliad water relations, physiology and ecology (Schimper, 1884, 1888; Mez, 1904; Tietze, 1906; Picado, 1913).

Although a few phylogenetic quandaries await resolution, our understanding of the diversity and phylogeny of Bromeliaceae is considerably more advanced than that of de Jussieu. New bromeliad species continue to be discovered (Aguirre-Santoro, Betancur & Holst, 2015; Aguirre-Santoro & Michelangeli, 2015; Büneker *et al.*, 2015; Espejo & López-Ferrari, 2015; Forzza & Leme, 2015; González-Rocha *et al.*, 2015; Leme, 2015; Monteiro & Forzza, 2015; Ramírez *et al.*, 2015; de Sousa & Wanderley, 2015), but with >3300 species already described (Luther, 2012; Govaerts, Luther & Grant, 2013), the discovery of an explanation of the drivers and mechanisms of bromeliad diversification has become one of the overarching aims of

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research into the family. To this end, well resolved, time-calibrated multi-locus molecular phylogenetic trees have been reconstructed, recognizing eight sub-families: (Bromeliaceae, (Lindmaniaceae, (Tillandsiaceae, (Hechtiaceae, (Naviaceae, (Pitcairniaceae, (Bromeliaceae, Puyoideae)))))) (Givnish *et al.*, 2011). Informative analyses have been conducted to assess the impact of putative key innovations on net diversification rates, demonstrating links between the accumulation of species richness in specific lineages and characters such as epiphytism, crassulacean acid metabolism (CAM), impounding tanks, entangling seeds and occurrence in moist, fertile habitats in South American cordilleras (Givnish *et al.*, 2014; Silvestro, Zizka & Schulte, 2014). It is important to note that extreme care should be taken when performing such analyses to use best practice in terms of model calibration and sampling methodology. Quezada & Gianoli (2011) ostensibly recovered CAM as a driver of diversification in Bromeliaceae, but there were two fundamental problems with their analysis rendering this result highly questionable. First, the putative phylogenetic relationships used in this analysis are not consistent with those supported by the most comprehensive molecular phylogenetic analyses. For example, the weight of evidence does not support a sister-group relationship between *Puya* Molina and a clade comprising *Fascicularia* Mez, *Ochagavia* Phil. and *Greigia* Regel (Schulte, Barfuss & Zizka, 2009; Givnish *et al.*, 2011, 2014; Escobedo-Sarti *et al.*, 2013). Second, the character coding fails to capture the complexity of variation in CAM within and between lineages. Both *Puya* and *Tillandsia* L. are coded as CAM genera, whereas both are known to include many C<sub>3</sub> species and in *Puya* there are several intermediates (e.g. Herrera *et al.*, 2010; Quezada, Zotz & Gianoli, 2014). A more rigorous analysis by Silvestro *et al.* (2014) identified CAM as a driver of diversification in Bromeliaceae, but it is too facile to assume this conclusion should apply across the whole family, in which 50% of extant species use C<sub>3</sub> photosynthesis only (Crayn *et al.*, 2015).

A critical dimension of bromeliad biology that has remained absent from these investigations is the suite of underlying traits pertaining to organismal and leaf-level anatomical and hydraulic specialization. These traits undoubtedly make an adaptive contribution to bromeliad survival in mesic and stressful terrestrial and epiphytic habitats ranging from moist montane forest to coastal deserts and from lowland river margins to Andean páramos (Benzing, 2000). Detailed examination of quantitative data on leaf economic, structural and hydraulic traits could provide an enormous insight into the mechanistic basis of ecophysiological diversity in Bromeliaceae. In the context of evolutionary trends in the family, such

data would shed light on the coherence and origins of the ecophysiological syndromes or functional types recognized by Pittendrigh (1948), which are closely connected with water-use strategies. In classifying the bromeliad flora of Trinidad, Pittendrigh identified a series of characteristic functional types: Type I *Soil-Root*; Type II *Tank-Root*; Type III *Tank-Absorbing Trichome*; and Type IV *Atmosphere-Absorbing Trichome*. Benzing (2000) modified Pittendrigh's classification to separate *Tank-Absorbing Trichome* Bromeliaceae and Tillandsiaceae into Types III and IV, respectively, leaving the atmospheric species as Type V. The splitting of Pittendrigh's Type III group along phylogenetic lines should be subjected to further scrutiny. Analysis of larger comparative ecophysiological datasets will indicate whether the phylogenetic distinction is mirrored by a clear divergence in functional type. However, the prevalence of CAM photosynthesis in Type III species and of C<sub>3</sub> photosynthesis in Type IV is expected to have important implications for water relations and therefore Benzing's scheme is provisionally maintained in this work.

These functional types represent an evolutionary progression involving decreasing physiological dependence on the substrate, providing access to epiphytic and lithophytic niche space with reduced interspecific competition (Pittendrigh, 1948; Givnish *et al.*, 1997; Benzing, 2000). Epiphytes account for 56% of all bromeliad species, such that the family ranks second only to Orchidaceae for epiphytic species richness (Zotz, 2013). The atmospheric Type V species, which obtain moisture and nutrients only from direct or occult precipitation, represent the ultimate expression of extreme epiphytism (Schimper, 1888; Benzing, 1978; Benzing & Ott, 1981). Characteristic combinations of innovating traits provide the definition of each functional type and its overall water-use strategy, but Pittendrigh's framework could also be used to explore the evolution of structure and function in finer detail. As different lineages have independently undergone transitions along the functional type series, it is interesting to ask whether convergence in functional type has been achieved through parallel or alternative changes at the anatomical and hydraulic level.

An improved understanding of the controls on water fluxes through bromeliads would also be of broader relevance and utility, as these plants frequently constitute a large fraction of the vascular epiphytic biomass in Neotropical forests and are therefore likely to represent an important component of hydrological and nutrient cycles alongside other vascular and non-vascular epiphytes (Nadkarni, 1984; Veneklaas *et al.*, 1990; Ingram & Nadkarni, 1993; Freiberg & Freiberg, 2000; Höltscher *et al.*,

2004; Köhler *et al.*, 2007; Díaz *et al.*, 2010; Gehrig-Downie *et al.*, 2011). Priority should therefore be given to redoubling efforts to produce fully integrated models of bromeliad water and carbon dynamics to predict responses to climate change and the impacts on ecological function.

Many traits that influence either directly or indirectly the water economy of bromeliads have been identified in the literature, but little attempt has been made to quantify these across large, phylogenetically diverse samples of species. As many bromeliads are equipped with unusual characters that may cause them to deviate significantly from the standard models of soil–plant–atmosphere water fluxes, developing a holistic understanding of their water relations is a peculiar challenge. It is a challenge, however, to which the bromeliad research community must rise if we are to improve our explanations for the unique success of bromeliads in invading so many stressful regions of plant niche space and lessons learned from bromeliad evolutionary physiology may well be also found to extend to other plant groups. This article therefore has two broad aims: to review current knowledge of bromeliad water relations and their integration with other aspects of bromeliad biology; and to use a simple model of the interactions between morphoanatomical, physiological and ecological factors in bromeliad water relations to generate testable hypotheses regarding the evolution of the functional types. In discussing this model I identify fruitful foci for future research with the intention of stimulating renewed efforts in quantifying structural traits of bromeliads and relating these to ecophysiological function in an evolutionary framework.

## A CONSPECTUS OF BROMELIAD WATER RELATIONS

### ROOTS AND STEMS

Perhaps because of the attractive novelty of epiphytism and associated foliar adaptations, relatively little attention has been paid to the structure and function of bromeliad roots. The root to shoot biomass ratio (R:S) varies widely; the Type V atmospheric or nebulophytic *Tillandsia* spp. sometimes lack roots entirely in the mature state, whereas mesomorphic Type I species of *Pitcairnia* L'Her. produce extensive adventitious rooting systems (Lüttge *et al.*, 1986; Benzing, 2000). As reflected in the ecophysiological type series, bromeliad evolution is characterized by a progressive loss of dependence on roots for water absorption in parallel with increased dependence on absorptive trichomes (Pittendrigh, 1948; Benzing, 2000). Type I species are rooted in

the soil and are presumed to obtain the majority of their water from this source, via root vasculature that is fairly typical of monocots, with vessel elements equipped with scalariform end-plates (Tomlinson, 1969). The availability of soil water varies enormously across the different habitats of Type I bromeliads, from the frequently inundated flood plain soils inhabited by hydrophytic *Dyckia distachya* Hassler and *Pitcairnia flammea* Lindl. to the dry, well drained soils associated with many *Puya* spp. (Benzing, 2000; Rocha-Pessoa & Rocha, 2008; Voltolini, Reis & Santos, 2009). There is a dearth of quantitative data regarding variation in the absorptive capacity of roots within and between terrestrial species, whereas it has generally been assumed that the roots of most epiphytic species (Types III–V) make a negligible contribution to plant water balance (Benzing, 2000). However, terrestrial and epiphytic species often develop an intriguing structure around the root surface that has been attributed a role in water and nutrient uptake and storage (Tomlinson, 1969; Pita & Menezes, 2002; Segecin & Scatena, 2004; Proença & Sajo, 2008; da Silva & Scatena, 2011). This structure consists of an outer layer invested with absorptive unicellular root hairs, whereas a suberized and sclerified exodermis limits water loss from reservoirs that may accumulate in a well developed reticulum of air spaces in the inner cortex. Whether the bromeliad exodermal apparatus is able to facilitate the net uptake of water is unclear, but it is conceivably advantageous where canopy soils or bryophyte mats ensure a relatively reliable supply of moisture. Although the histology of this apparatus therefore deviates from that of the velamen radicum that makes a significant contribution to water and nutrient uptake in many members of the other major family of monocotyledonous epiphytes, Orchidaceae (Pridgeon, 1987; Zotz & Winkler, 2013), this could represent an interesting example of convergent evolution. Meanwhile in Type V bromeliads, the cable-like, rot-resistant roots are so heavily sclerified as to preclude any significant absorptive role and they function simply as holdfasts to maintain connection with the phorophyte (Benzing, 1978, 2000; Reinert & Meirelles, 1993). These roots contain vestigial tracheids only, presumably as a result of neoteny and dependence on foliar trichomes rather than roots for water uptake (Benzing, 2000).

The role of specialized roots in Type II species warrants particular note. These species, all belonging to the early-diverging Bromelioideae, display a rudimentary tank-forming habit with multiple low-volume axillary tanks in individual leaf bases, rather than the large central tank of the Type III core Bromelioideae (Pittendrigh, 1948; Benzing, 2000).

These tanks are explored by a mass of foraging, flattened adventitious roots, rendering the plant less dependent on soil roots for water acquisition and nutrition (Pittendrigh, 1948; Lee *et al.*, 1989). An extreme example is provided by *Bromelia humilis* Jacq., which appears to absorb water more or less exclusively through the tank roots and is therefore able to survive effectively as a salt-excluder on the hypersaline substrate of the salinas of coastal Venezuela, with little or no competition from other vascular plants (Lee *et al.*, 1989).

Bromeliad stems are generally reduced in size relative to the foliage, but have the typical monocot structure (Tomlinson, 1969). The picture is complicated only by the often highly extensive leaf traces grouped into collateral bundles and the intracauline roots that may penetrate the stem for some distance before exiting (Tomlinson, 1969; Benzing, 2000). Increased proportional investment in stems is observed in the Andean *Puya* spp., in which stem-succulence is presumed to fulfil a number of functions including water storage to buffer against temperature-limited soil water availability (Benzing, 2000). Experimental work on *Puya* similar to that reported by Goldstein, Meinzer & Monasterio (1984) on the role of capacitance in the Andean giant rosette genus *Espeletia* Mutis ex Humb. & Bonpl. (Asteraceae) would shed further light on these matters. In contrast to the stem-succulent condition in *Puya*, stems of neotenic Type V species such as *Tillandsia usneoides* (L.) L. are sometimes reduced to sclerotic connections between ramets (Benzing, 2000). Many aspects of the biology of bromeliad stems and stolons remain unexplored, such as their possible role as conduits for water, metabolite and signal exchange between ramets and organs (Zotz & Hietz, 2001).

#### SHOOT ARCHITECTURE

The ancestral bromeliad shoot architecture is presumed to be a typical liliaceous rhizomatous rosette (Benzing, 2000). From this, a range of morphologies in different lineages has arisen, each with distinct adaptations relating to water-use strategies (Smith, 1989; Benzing, 2000). Among these, the evolution of the phytotelm or tank form was a major advance that allowed epiphytes access to a more reliably continuous water supply (Schulte *et al.*, 2009; Givnish *et al.*, 2014; Silvestro *et al.*, 2014). Several properties of the tank determine its contribution to whole-plant water relations. The orientation of the rosette will strongly affect the efficiency of precipitation interception. Most tank-forming bromeliads display a striking negative geotropism in the rain-fed mature state (Adams & Martin, 1986c). The efficiency of water

retention is to a great extent determined by the tightness of the overlap between leaf bases. Prototanks in groups such as the early-diverging Bromelioideae are relatively inefficient at retaining large volumes of water because of the low degree of leaf overlap and hence these plants typically continue to depend partly on soil water and are slow-growing stress-tolerators with less ecological flexibility than core Bromelioideae equipped with a central tank (Benzing, 2000; Schulte *et al.*, 2009; Silvestro *et al.*, 2014). The volume of the tank relative to trichome-mediated absorptive capacity and leaf area is of obvious importance in maintaining hydration (Zotz & Thomas, 1999; Schmidt & Zotz, 2001; Zotz & Hietz, 2001). Another factor that must be considered, however, is the tank surface area, as evaporative loss of water from tanks may be significant during periods of intense or extended vapour pressure deficit (Zotz & Thomas, 1999). Some xeromorphic tank species display tubular tanks with a large volume but low exposed surface area, limiting evaporative loss [e.g. *Aechmea nudicaulis* (L.) Griseb.; Benzing, 2000]. The evolutionary patterns brought about by the competing selective pressures imposed by xeric environments for reduced evaporative surface area but increased surface area for the interception of precipitation await quantitative analysis.

Beyond its relation to tank volume and consequent influence over nutritional status and photosynthetic capacity (Zotz, 1997; Zotz, Schmidt & Mikona, 2011), shoot size is of manifold importance for both tank-forming and tank-less species. Many size-related effects operate via the surface area to volume ratio (SA:V), an important determinant of potential transpirational or peristomal water loss and light-quenching efficiency. Reduced size and SA:V have evolved through neoteny in Tillandsioideae, with profound ecophysiological consequences (Benzing & Ott, 1981; Adams & Martin, 1986c; Benzing, 2000). The mechanistic relationships between the anatomy of neotenic species (e.g. a reduced vascular system) and physiology need further investigation.

All bromeliads display a capacity for vegetative reproduction, but the extent to which clonal ramets develop varies between species (Benzing, 2000). Genets of some tillandsioids and *Puya* spp. occur almost exclusively as individual rosettes, whereas many bromelioid epiphytes develop creeping, nest-forming stolons. Meanwhile certain species of *Deuterocohnia* Mez produce cushions of tiny plantlets and the highly reduced Spanish moss (*Tillandsia usneoides*) is famed for its webs of interconnected ramets. The degree of hydraulic conductivity between ramets is unclear. Vascular traces do not provide continuity between ramets of Spanish moss, in which the conduits are anyway extremely reduced (Tomlinson,

1969; Benzing, 2000). However, in other species with less reduced vascular systems, it is possible that inter-ramet connections provide physiological integration, allowing hydrated ramets to 'share' water with more dehydrated ramets, as reported in other clonal species (Alpert & Mooney, 1986; Alpert, 1990; de Kroon *et al.*, 1996; van Kleunen & Stuefer, 1999; Benzing, 2000).

#### LEAF MORPHOLOGY AND STRUCTURE

The leaves of bromeliads vary considerably in size, shape and density (Benzing, 2000). As in other plant lineages, mesic, low-light environments such as forest floor habitats have selected for thin, low-density leaves with a large surface area for water and light interception (Gilmartin, 1983; Valladares, Skillman & Pearcy, 2002). At the opposite end of the scale, highly exposed, upper canopy microhabitats have selected for small, dense leaves with a low SA:V ratio (Benzing, 2000). Rosettes of many narrow rolled or terete leaves with dense trichome layers allow nebulophytic *Tillandsia* spp. to maximize the uptake of transiently available water (Gilmartin, 1983; Martorell & Ezcurra, 2007).

Bromeliad leaves display a number of tissue-level adaptations relevant to water relations. The mesophyll is often traversed by conspicuous axial air lacunae, usually occurring in alternation with vascular bundles (Tomlinson, 1969). The dimensions of these lacunae vary widely, but they are perhaps most impressive in the Type IV epiphytic Tillandsioideae, in which they can account for a large fraction of total mesophyll volume (J. Males, unpubl. data). The role traditionally ascribed to these lacunae is the aeration of tissue submerged below the water-line in tank-forming species (Tomlinson, 1969; Varadarajan, 1986), although this situation does not explain their presence in many lineages lacking central tanks. Indeed, given their frequent occurrence in families across Poales *sensu* APG IV (2016), it seems likely that the propensity for aerenchyma formation is plesiomorphic in Poales and that lacunae have been occasionally co-opted for more specialized functions (e.g. ventilation in aquatic Typhaceae) in specific lineages (Tomlinson, 1969; Jung, Lee & Choi, 2008). Huber & Linder (2012) suggested that the loss of aerenchyma in Restionaceae has enforced a limitation on ecohydrological niche diversity in that family. Beyond the possible importance of lacunae in the aeration of submerged tissues in bromeliad leaves, they may serve as an important conduit for vapour-phase transport of H<sub>2</sub>O. Vapour-phase transport, as contrasted with symplastic, transcellular and apoplastic flux of water in the liquid state, is expected to become quantitatively significant when a

sufficiently steep gradient in temperature or water vapour pressure exists between the internal evaporative sites and the stomatal pore (Sheriff, 1977, 1984; Rockwell, Holbrook & Strock, 2014; Buckley, 2015). Although data are lacking, such gradients are likely to occur frequently among bromeliad species with thick, succulent leaves and deep-set veins. In these species, relatively steep thermal gradients may be established between the epidermis and vascular plane due to thermal capacitance. The most prominent air spaces are observed in species with thin leaves that are more probably in thermal equilibrium with their environment with only shallow internal gradients, whereas the most succulent leaves often have little or no aerenchyma. This reduction in the volume of IAS may assist in limiting the potential for rapid water loss in the vapour phase, although a more detailed physiological and evolutionary analysis would have to be performed to try to ascertain whether increased mesophyll density in bromeliads is causally linked with the potential for steep internal thermal gradients or other factors known to be related to leaf density, such as CAM.

Bromeliad leaves typically express some degree of succulence. This factor is often associated with an adaxial layer of differentiated water storage parenchyma (hydrenchyma), sometimes in conjunction with an additional, thinner abaxial layer (Tomlinson, 1969; Benzing, 2000). The hydrenchyma provides a reservoir of water to buffer against reduced availability in epiphytic, lithophytic, xeric and seasonal environments. The boundary between the hydrenchyma and the photosynthetically active chlorenchyma is variable between taxa, being sometimes smooth and sometimes interdigitating (Tomlinson, 1969). The possible physiological significance of this variation in tissue integration merits further investigation. This form of succulence based on tissue differentiation is associated with drought tolerance rather than drought avoidance because of the ability of the hydrenchyma to release water to the chlorenchyma when the water potential of that tissue decreases during drought (Nowak & Martin, 1997; Benzing, 2000; Martin *et al.*, 2004). Both the ratio of chlorenchyma to hydrenchyma and the leaf volume must also be considered in determining the volume and availability of the reservoir of internally stored water for buffering against fluctuations in transpirational demand and avoiding drought (Ogburn & Edwards, 2012; Griffiths, 2013). A different form of succulence exists in many CAM species, notably among Bromelioideae. Here the voluminous chlorenchyma cells may store large quantities of water with the organic acids associated with CAM. Chlorenchymatous succulence often occurs alongside a reduced investment in hydrenchyma, but there exists a spectrum

involving varying degrees of investment in hydrenchymatous and chlorenchymatous succulent tissues. Further work is required to characterize the functional significance of this variation for water transport. In an evolutionary context, succulence has been credited alongside other xeromorphic traits with facilitating the successful invasion of the South American 'dry diagonal' by terrestrial Pitcairnioideae (Santos-Silva *et al.*, 2013) and is associated with xerophytism, CAM and epiphytism in other bromeliad lineages (Benzing, 2000). The presence of only a single vascular plane in bromeliad leaves might be expected to represent an evolutionary constraint on the degree of succulence that can be maintained (Ogburn & Edwards, 2013). Succulent leaves of some bromeliad species, however, may attain a total thickness of several centimetres. More quantitative anatomical and hydraulic data are needed to ascertain whether this is facilitated by reductions in actual hydraulic path length by the presence of aerenchyma or by the relatively hydraulically isolated position of the adaxial hydrenchyma.

#### LEAF VASCULATURE AND HYDRAULIC CONDUCTANCE

The vasculature of bromeliads is unusual in several respects. Firstly, not unlike some other monocot families (e.g. Araceae, Musaceae and many Orchidaceae), bromeliads possess xylem traces that are dominated by tracheids rather than vessel elements (Tomlinson, 1969; Carlquist, 1975, 2012). Vessel elements are in fact absent from the stems and leaves of most species (Tomlinson, 1969; Carlquist, 1975). Secondly, the xylem elements are highly reduced in diameter, limiting their conducting capacity (Tomlinson, 1969). The vasculature of the leaves of neotenic *Tillandsia* spp. comprises highly reduced phloem and just a few narrow tracheids, an arrangement that probably arose via heterochronic effects (Carlquist, 2009), and which Benzing (2000) argued is compatible with reduced dependence on axial water transport due to the efficiency of trichome-mediated water uptake. The fine details of vascular cell anatomy and the consequences for plant function require further investigation. Thirdly, the xylem is surrounded by an 'endodermoid' layer or parenchymatous sheath of low permeability, restricting exchange of water to and from the xylem (Tomlinson, 1969). With these considerations in mind, we should expect bromeliads to demonstrate relatively low rates of xylem hydraulic conductance and vein leakiness, contributing to low total leaf hydraulic conductance ( $K_{\text{leaf}}$ ). This expectation has been corroborated by reports that axial  $K_{\text{leaf}}$  in *Guzmania lingulata* (L.) Mez is even lower than in many gymnosperms and ferns and much lower than in monocots with less

conservative water use, such as many grasses (Martre, Durand & Cochard, 2000; Maherali *et al.*, 2008; North *et al.*, 2013).

In bromeliads, as in other plants, transcellular fluxes of water are probably facilitated by abundant aquaporins inserted in mesophyll plasma membranes (Smith & Nobel, 1986; Smith, Schulte & Nobel, 1987; Tyerman, Niemietz & Bramley, 2002; Kaldenhoff *et al.*, 2008; Heinen, Ye & Chaumont, 2009). Little work has been done to explore the contribution of aquaporins to bromeliad water relations, although a study by Ohri *et al.* (2007) demonstrated that PIP expression is rapidly induced by rewetting of droughted leaves of atmospheric *Tillandsia ionantha* Planch. This phenomenon may be of outstanding importance for pulse-supplied species (Benzing, 1990). Further exploration of the regulation of aquaporin expression and activity in relation to leaf (re-) hydration across the functional types of bromeliads is required.

Measured leaf xylem tensions in bromeliads are consistently low compared with other plant groups, but comparable with observations for other vascular epiphytes (Smith & Lüttge, 1985; Smith *et al.*, 1986; Martin *et al.*, 2004). Smith *et al.* (1986) reported that two terrestrial species of Bromelioideae in Trinidad displayed sufficiently low xylem tensions during the dry season that they must have been functionally independent of the substrate, using instead water stored in tanks and hydrenchyma to maintain low xylem tension. As these plants had developed soil-penetrating roots, they presumably were able to express a seasonally induced capacity to modify their dependence on soil water uptake. The precise mechanisms for such an effect in the bromeliads have not been established, but could involve the rectifier-like conductivity reported in phylogenetically diverse desert succulents, facilitated by suberization and reduction in root-specific aquaporin activity (Nobel & Sanderson, 1984; López & Nobel, 1991; North & Nobel, 1991, 1992; Nobel & Cui, 1992; Martre, North & Nobel, 2001; North, Martre & Nobel, 2004).

Vulnerability to xylem cavitation is an important limitation on leaf physiological capacity (Tyree & Sperry, 1989) and is closely related to symplast drought tolerance (Vilagrosa *et al.*, 2010). Because of the low xylem tensions and transpiration rates in bromeliads, the threat of cavitation may be low under most conditions. This is compounded by the narrow lumens of the conducting elements of bromeliad xylem, as there is a well established correlation between xylem conduit diameter and hydraulic vulnerability. Bromeliad species capable of hydraulically isolating themselves from their environment during periods of drought might be expected to show particularly limited exposure to routine embolism (Smith

*et al.*, 1986). Species with smaller leaves and higher major vein density may show especially low vulnerability (Scoffoni *et al.*, 2011; Sack *et al.*, 2012), although as discussed above, neotenic species with strong capacity for foliar uptake may be insensitive to xylem embolism anyway. As in many monocot families, bromeliads frequently display high densities of commissural veins linking the parallel axial veins (Tomlinson, 1969). The functional importance of commissural veins is not clear, but may conceivably relate in part to the capacity to bypass embolized xylem conduits and thereby maintain an uninterrupted transpiration stream through the leaf (Sperry, 1986; Sack *et al.*, 2004). According to this logic, high commissural vein density should occur in species adapted to high evaporative demand, but this hypothesis has not been investigated. Horn *et al.* (2009) identified a possible connection between commissural venation architecture and sclerification and leaf strength and longevity in Arecaceae. Given the wide variation in leaf rigidity and its link with shoot and tank architecture in Bromeliaceae, this idea also warrants exploration.

The spatial patterning of leaf veins and their geometry with respect to other anatomical structures is known to relate to many aspects of leaf physiological function throughout the angiosperms (Boyce *et al.*, 2009; Sack & Scoffoni, 2013). Such relationships have not been explored in Bromeliaceae, but whereas they should be expected to approximate those observed in other groups, the detail may differ because of the unique properties of the bromeliads. Interveneal distance (IVD) is a well established predictor of the hydraulic capacity of leaves and is closely linked to photosynthetic capacity and efficiency (Brodrribb, Feild & Jordan, 2007; Brodrribb & Feild, 2010). Empirical and theoretical studies have also shown that the ratio of  $d$  to the vein-epidermis distance (VED) is highly conserved across the angiosperms at a value of approximately 1 for reasons of optimal, homogeneous perfusion of the lamina (Noblin *et al.*, 2008; Zwieniecki & Boyce, 2014). Deviation from  $IVD = VED$  has been described as 'underinvestment' ( $IVD > VED$ ) or 'overinvestment' ( $IVD < VED$ ) in veins (Zwieniecki & Boyce, 2014). Although no published data are available to examine conformity among bromeliads to the typical angiosperm pattern, preliminary measurements suggest that there may be significant deviation in either direction, with important ramifications for bromeliad physiology and evolution (J. Males, unpubl. data). In terms of water relations, underinvestment in veins permits heterogeneity to develop in cell water potential across the lamina, meaning it should be selected against except under shaded conditions at low vapour pressure deficit (VPD; Zwieniecki & Boyce,

2014). The occurrence of underinvestment in bromeliads represents a case of convergent evolution with ferns and other plants of sheltered forest microhabitats. Overinvestment meanwhile involves an apparently wasteful level of expenditure on costly vein structures and should be strongly selected against, under most circumstances. Its occurrence in succulent bromeliads could relate either to a role of the vasculature in the recharge of capacitance in hydrenchyma or to a relaxation of selection for  $IVD = VED$  when trichome-mediated absorption of water represents the dominant inward flux. Further investigation into this subject should yield insights into the strength of theoretical constraints on leaf morphometry and the importance of venation architecture for leaf viability.

#### STOMATA, TRICHOMES AND INDUMENTA

Bromeliad stomata are typically arranged on the abaxial surface in irregular intercostal series (Tomlinson, 1969). Stomatal density varies greatly between species and groups, displaying a weak inverse correlation with trichome density across the ecophysiological Types. Tomlinson (1969) reported average ratios of stomata to trichomes in Pitcairnioideae *s.l.* (Pitcairnioideae plus Brocchinioideae, Hechtioideae, Lindmanioideae, Navioideae and Puyoideae) of 13.6:1, compared with 3.2:1 in Bromelioideae and 1.5:1 in Tillandsioideae. The figure for the atmospheric *Tillandsia* spp. was 0.5:1, and the scattered, inconspicuous stomata of *T. illandsia bryoides* Griseb. ex Baker eluded anatomists until 1989 (Evans & Brown, 1989). These stomatal to trichome density ratios (S:T) reflect evolutionary shifts in water-use strategies, with lower S:T values representing more conservative water use.

Stomata of bromeliads are complex and highly diverse structures, but their functional biology remains understudied. Fundamentally, the behaviour of bromeliad stomata must answer to the same challenge confronting all land plants: CO<sub>2</sub> for photosynthetic assimilation can only be gained from the atmosphere at the expense of lost water vapour (Manzoni *et al.*, 2011). Guard cells of angiosperm stomata lie at the nexus of a host of signalling pathways and integrate this information to adjust pore aperture in such a way as to optimize carbon gain against water loss (Schroeder *et al.*, 2001). Bromeliad guard cells are frequently subtended by a pair of enlarged epidermal or hypodermal subsidiary cells that may almost occlude the substomatal cavity (Tomlinson, 1969). This situation has led some authors to speculate that these cells have taken over part of the function of the guard cells, although as

yet there is little evidence either way (Tomlinson, 1969; Martin & Peters, 1984; Benzing, 2000). Transitions in stomatal complex morphology appear to coincide with key divergences in the bromeliad phylogenetic tree, such as at the bases of core Tillandsioideae and core Bromelioideae, and display convergence in lineages that have invaded similar environmental space (Tomlinson, 1969). Detailed investigation of the functional significance of variation in stomatal complex arrangement in bromeliads is highly desirable.

An early report on gas exchange by the Type V atmospheric *Tillandsia recurvata* (L.) L. was suggestive of the operation of a feed-forward response in stomatal conductance to ambient humidity (Lange & Medina, 1979) and similar observations have been made in *Aechmea nudicaulis* (Griffiths *et al.*, 1986). Various mechanisms for this response have been proposed following reports of its occurrence in many plant groups (Peak & Mott, 2011; Bauer *et al.*, 2013) and it is a phenomenon of potentially profound ecological significance. Direct measurements of the strength of this effect in bromeliads of different functional types have not been reported, but it might be hypothesized that stomata of Type V species, which inhabit the most water-limited, pulse-supplied microhabitats, would be most sensitive to declining humidity in order to conserve captured water (Reyes-García, Mejía-Chang & Griffiths, 2012). Other signals that control stomatal aperture include the phytohormone abscisic acid (ABA), a well characterized elicitor of stomatal closure among seed plants (Munemasa *et al.*, 2015). ABA has been shown to force closure of the pore in *Tillandsia usneoides* (L.) (Martin & Peters, 1984) and appears to accumulate during simulated drought in *Guzmania monostachia* (L.) Rusby ex Mez (Mito & Mercier, 2013).

The absorptive trichomes found in most bromeliad lineages and their valve-like absorptive function have long been a source of fascination for plant scientists (Mez, 1904; Tietze, 1906). The peltate multicellular foliar trichome is a synapomorphy for the family and it has been suggested that the origin of the absorptive function may relate to the association of early-diverging bromeliads (e.g. Brocchinioideae) with oligotrophic habitats on the inselbergs of the Guayana Shield (Medina, 1974; Givnish *et al.*, 1997). Moving from the terrestrial through to the epiphytic and atmospheric bromeliad functional types, trichomes make an increasingly important contribution to total water (and mineral) uptake. A number of secondary characters must be accounted for when considering the contribution of trichomes to plant water balance. These include trichome density and the kinetics of trichome-mediated absorption, which

may be associated with anatomical detail specific to individual lineages (Benzing, 2000).

Trichome density is highly variable across the family, ranging from zero in some *Pitcairnia* spp. to c. 100% cover of the leaf surface in many atmospheric *Tillandsia* spp. (Tomlinson, 1969). Dense trichome cover may help to reduce transpiration and photoinhibition through increased reflectance (Benzing, Seemann & Renfrow, 1978; Pierce *et al.*, 2001; Pierce, 2007), whereas a study by Benz & Martin (2006) suggested that although trichomes did extend the boundary layer at a local scale in 12 *Tillandsia* spp., this effect did not significantly impact on rates of water loss at the scale of the whole leaf or plant. Repeats of these experiments with a more morphologically diverse range of species would be valuable. More certain is that the maximization of water absorption through the presence of a dense array of trichomes is critical to the success of atmospheric bromeliads in pulse-supplied microhabitats (Benzing, 2000). Trichome-mediated water exchange between atmosphere and plants is complex. Martin & Schmitt (1989) identified two separate pools of water in *T. usneoides*: an epidermal pool associated with hydration of the trichome layer at night followed by dehydration after dawn and an internal mesophyll pool being supplied by trichomes but depleted by both stomatal- and trichome-mediated water loss. This effect has subsequently been noted in investigations of gas exchange and oxygen isotope signature in *T. usneoides* (Haslam *et al.*, 2003; Helliker & Griffiths, 2007; Helliker, 2011, 2014) and similar observations have been made in *T. recurvata* (Schmitt, Martin & Lüttge, 1989).

The absorptive capacity of bromeliad trichomes, in terms of water and mineral nutrients, also varies considerably between and within species (Benzing, 1970; Benzing *et al.*, 1976). In Tillandsioideae, trichomes are highly absorptive across the entire leaf surface, whereas in Bromelioideae there is evidence to suggest that trichomes on the leaf sheath, frequently inundated by tank water, are more absorptive than those that occur at lower density on the exposed leaf blade (Benzing, 1970; Benzing *et al.*, 1976). Further work is needed to understand the anatomical and molecular basis of the variation in absorptive capacity demonstrated by different trichome types in different lineages (cf. Sakai & Sanford, 1980; Brighigna *et al.*, 1988; Owen, Benzing & Thomson, 1988; Papini *et al.*, 2010).

The leaves of some bromeliads develop epicuticular layers of hydrophobic waxes and powders. The adaptive function of such indumenta appears to vary between species. In *Catopsis berteroniana* (Schult. & Schult.f.) Mez, loose powders are associated with improving the efficiency of water and prey capture in



tanks co-opted into the role of carnivorous pitfall traps (Gaume *et al.*, 2004). In understory epiphytes of perhumid montane forest, hydrophobic leaf coatings may serve to minimize diffusive limitations to gas exchange (Pierce *et al.*, 2001). It has been demonstrated in species possessing epidermises invested only with hydrophilic trichomes that the establishment of a film of liquid water over the leaf surface may suppress gas exchange and photosynthesis (Mez, 1904; Benzing & Renfrow, 1971; Martin & Siedow, 1981; Benzing, 2000).

#### CELL AND TISSUE WATER RELATIONS

Tissue-level succulence and capacitance is defined at a cellular level by a set of key parameters: cell size, cell shape and cell wall elasticity. Cell size is a critical parameter because it controls the volume of water the cell can hold and the number of membranes water molecules that has to cross when traversing a given distance of symplast and therefore affects the resistance of this pathway. Cell size is additionally linked to nuclear DNA content, which may be subject to selective pressures during the terrestrial-epiphytic transition because of reduced phosphorus availability (Zotz, 2004; Chase *et al.*, 2005; Zotz & Richter, 2006; Leitch *et al.*, 2009; Winkler & Zotz, 2009; Zotz & Asshoff, 2010; Wanek & Zotz, 2011). The hydrenchyma cells of bromeliads are often hexagonal or rectangular in cross-section, this regular shape allowing them to be densely packed, thereby improving tissue-level capacitance and water conservation (Nelson, Sage & Sage, 2005). The elasticity of the walls of a cell, quantified as Young's elastic modulus ( $\epsilon$ ), defines the capacity of the cell to undergo mechanical deformation. Non-photosynthetic hydrenchyma cells typically have highly elastic cell walls (low  $\epsilon$ ) that enable them to undergo reversible shrinkage or deformation, preferentially releasing water to buffer metabolism in photosynthetic chlorenchyma cells during drought (Ekern, 1965; Stiles & Martin, 1996; Nowak & Martin, 1997). There is only one published value of bulk  $\epsilon$  for a bromeliad: 3.3 MPa in *Tillandsia utriculata* L. (Stiles & Martin, 1996). This low value is in accordance with a drought tolerance strategy involving reductions in relative water content, but maintenance of  $\Psi_{\text{leaf}}$ . In contrast, it has long been established that some bromeliads are able to avoid internal drought during periods of desiccating conditions by minimizing water loss to extremely low levels (Sideris & Krauss, 1928, 1955; Benzing & Burt, 1970; Martin & Adams, 1987). This has been associated with conservative stomatal behaviour and impermeable cuticles (Martin, 1994) and may be more common in species with less well developed hydrenchyma.

All published measurements of the osmotic potential of bromeliad cell sap suggest that solute concentrations are low, especially in CAM species and epiphytes (Harris, 1918; Biebl, 1964; Griffiths *et al.*, 1986; Lüttge *et al.*, 1986; Smith *et al.*, 1986; Martin, 1994; Nowak & Martin, 1997; Zotz & Andrade, 1998; Martin *et al.*, 2004). The capacity for osmotic adjustment to drought appears limited (Martin *et al.*, 2004). However, as bulk osmotic potential represents a major determinant of  $\Psi_{\text{TLP}}$  (Bartlett, Scoffoni & Sack, 2012), it should be expected that  $\Psi_{\text{TLP}}$  would be modest in most bromeliads. The most negative values of  $\Psi_{\text{TLP}}$  might be expected to occur in Type I  $C_3$  terrestrial species that: (a) are sufficiently photosynthetically productive to generate a larger osmotic potential; and (b) may have to endure negative endogenous water potential to extract water from soils with low water potential. Less negative values of  $\Psi_{\text{TLP}}$  should be permissible in either terrestrial or epiphytic species with high capacitance even in desiccating conditions because of the ability of capacitance to decouple environmental water supply and transpirational water loss (Benzing, 2000). Capacitance nevertheless correlates inversely with maximal transpiration rate, because internally stored water must often be metered out over extended periods of environmental adversity, whereas low-capacitance mesic species with a ready supply of soil or tank water may transpire freely at reduced hydraulic risk (Benzing, 2000).

#### PHOTOSYNTHETIC PATHWAYS

Approximately 50% of bromeliads use CAM rather than  $C_3$  photosynthesis, following multiple independent origins in the family (Crayn, Winter & Smith, 2004; Crayn *et al.*, 2015). In certain bromeliad lineages, CAM appears to be associated with increased diversification rates, although it does not seem to represent a driver of diversification across the family as a whole (Givnish *et al.*, 2014; Silvestro *et al.*, 2014). CAM has generally been interpreted as an adaptation to environments characterized by high evaporative demand among other stressors, and is therefore intimately associated with plant water relations (Kluge & Ting, 1978; Osmond, 1978; Lüttge, 1987, 2010; Winter & Smith, 1996; Cushman, 2001; Cushman & Borland, 2002; Herrera, 2009). In CAM species, nocturnal opening of stomata allows gas exchange to occur when the leaf-atmosphere vapour pressure deficit is reduced because of lower ambient temperatures, thereby solving the dilemma of 'desiccation or starvation' for a  $C_3$  plant under water-limited conditions (Lüttge, 1997). Obligate CAM bromeliads typically occur in more arid habitats and microhabitats than their  $C_3$  relatives,

including water-limited epiphytic niches (Medina, 1974; Medina *et al.*, 1977; Griffiths & Smith, 1983; Crayn *et al.*, 2004, 2015). Because CAM species require large, highly vacuolate cells for nocturnal acid accumulation, they typically display succulence and densely packed mesophyll (Maxwell, von Caemmerer & Evans, 1997; Nelson *et al.*, 2005; Nelson & Sage, 2008). Strong CAM can also be performed in low-succulence leaves when the proportion of stored citrate to malate increases (Griffiths, 1988; Lüttge, 1988; Benzing, 2000). The physiological and ecological significance of the ratio of accumulated citrate to malate is an exciting topic for further research.

CAM is often highly plastic within species and individuals, with the strength of the expression of each characteristic CAM phase being controlled by recent environmental conditions (Cushman, 2001; Dodd *et al.*, 2002; Haslam *et al.*, 2003; Owen & Griffiths, 2013). Many bromeliads demonstrate two alternative forms of CAM, known as CAM-cycling and -idling (Sipes & Ting, 1985; Griffiths, 1988; Loeschen *et al.*, 1993; Martin, 1994). CAM-cycling, thought to be the least evolutionarily advanced state along the CAM continuum (Silvera *et al.*, 2010), involves nocturnal fixation of respiratory CO<sub>2</sub> behind closed stomata accompanying typical diurnal C<sub>3</sub> fixation. The capacity for CAM-cycling may exist in bromeliad taxa currently considered as C<sub>3</sub> plants because of the difficulty of identifying such capacity in rapid screens of carbon isotope values. CAM-idling, conversely, is an extreme form of CAM in which the stomata remain continuously closed and the only fixation is of respired CO<sub>2</sub> at night. CAM-idling therefore cannot make a net contribution to the carbon balance of a plant. In many cases, CAM-cycling and -idling appear to be reversibly inducible, and drought-inducible CAM has been observed in some species such as the terrestrial *Puya floccosa* (Linden) E.Morren ex Mez (Herrera *et al.*, 2010). In another instance of intraspecific variability in CAM expression, CAM activity has been shown to vary with elevation in *Puya chilensis* Molina (Quezada *et al.*, 2014). There are many examples of CAM bromeliads in perhumid cloud forests, where the classical benefit of CAM in improving WUE is negated by the constantly low VPD. Pierce, Winter & Griffiths (2002) suggested that the benefit of CAM in such environments might lie in the plasticity it affords in photosynthetic responses to variability in leaf wetness, including the capacity to engage in recycling of respiratory CO<sub>2</sub>.

The implications of nocturnal accumulation of malic acid in CAM species for bromeliad water relations remain unclear. Since malate behaves as an ideal osmoticum in a range of CAM plants (Lüttge &

Nobel, 1984; Smith & Lüttge, 1985; Smith *et al.*, 1986), it has been suggested that it might promote improved foliar water uptake, particularly when leaves are wetted with dew (Smith & Lüttge, 1985). In principle, this could be of greatest survival benefit to Type V nebulophytes of coastal deserts in South and Central America, which depend on dew-fall during the dry season (Benzing, 2000). Acid accumulation might alternatively provide an osmotic impetus for the nightly refilling of depleted capacitance, as observed by Smith *et al.* (1987) in *Agave deserti* Engelm. Benzing (2000) speculated that nocturnal hydraulic lift by phreatophytic neighbours might provide water to the root systems of CAM Type I species as they simultaneously generate a CAM-driven water potential gradient to enhance uptake. However, evidence of the biological importance of such effects is at best mixed (Griffiths *et al.*, 1986; Lüttge, 1987, 1988; Martin, 1994; Andrade, 2003), perhaps in part because the absolute values of pre-dawn osmotic potential in CAM bromeliads are still high compared with other plant groups (Smith *et al.*, 1986).

#### PIGMENTATION AND PHYSIOLOGICAL HETEROGENEITY ACROSS LEAF SURFACES

A remarkable property of a number of C<sub>3</sub> tillandsioids and CAM bromelioids is the presence of complex patterns of pigmentation across the leaf surface (Benzing & Friedman, 1981). The most extreme examples are encountered in certain species of *Vriesea* Lindl. (e.g. *V. fenestralis* Linden & André, *V. gigantea* Gaudich.) and consist of a net of chlorophyllous tissue adjacent to axial and commissural vascular bundles interspersed with translucent fenestrae (Benzing & Friedman, 1981). Fenestration may allow the leaf to achieve a large surface area for water and light interception with reduced mineral investment in a manner somewhat analogous to a model proposed for the fenestrae (in this instance physical holes) in leaves of *Monstera* Adans. (Araceae), which also depend on spatiotemporally stochastic sunflecks for carbon gain (Muir, 2013). There have been no dedicated investigations into the metabolic status of tissue in the achlorophyllous fenestrae of bromeliads and its possible role in building organ-level capacitance. Fenestrae are often enclosed by adaxial and abaxial bundle sheath extensions that may allow the water potential in discrete portions of the mesophyll to be drawn down during bursts of high evaporative demand (such as those associated with sunflecks) without propagating this effect throughout the leaf (Buckley, Sack & Gilbert, 2011; Schymanski, Or & Zwieniecki, 2013). The relationships between fenestration or other forms of

heterogeneity in leaf pigmentation, bundle sheath extensions, stomatal distribution, commissural veins and patchiness in gas exchange and metabolic activity could prove a fruitful focus for research.

#### LIFE-CYCLE STAGES

Dependence on water availability is a critical component of the bromeliad regeneration niche (Mondragón *et al.*, 2004; Winkler, Hülber & Hietz, 2005; Bader, Menke & Zotz, 2009; Goode & Allen, 2009; Mantovani & Iglesias, 2010; Montes-Recinas, Márquez-Guzmán & Orozco-Segovia, 2012; Wagner, Bogusch & Zotz, 2013). In some epiphytic species, germination and seedling growth is enhanced by the presence of specialized water-uptake structures (Wester & Zotz, 2011) and a degree of drought tolerance is a key component of the adaptive strategy of epiphytic seedlings (Adams & Martin, 1986a; Bader *et al.*, 2009). Less is known regarding the ecophysiology of seedling establishment in terrestrial species, but many principles from the epiphytic context may apply equally to those terrestrial species associated with water-limited habitats.

The life-history of many bromeliad species is dominated by a transition from a juvenile form to a mature form, which often differ strongly in their morphology and physiology. This was historically regarded as a classic example of heteroblasty, but evidence from large, multi-species datasets suggests that the transition is a slower process better described as ontogenetic drift, with plant size being an important confounding effect (Zotz *et al.*, 2004; Meisner, Winkler & Zotz, 2013). However, it remains true that the water-acquisition strategies of juvenile individuals of these species are generally unlike those of mature individuals. Dew-fed juveniles do not possess an impounding rosette and their narrow or filiform leaves (which minimize SA:V) are more uniformly covered in absorptive trichomes than rain-fed adults, resembling the mature state of neotenic atmospheric species (Adams & Martin, 1986a; Reinert & Meirelles, 1993; Schmidt & Zotz, 2001). Maturation involves the development of the impounding tank, the establishment of opposing gradients of stomatal and trichome density along leaf axes and the broadening of leaf blades. In the case of the C<sub>3</sub> epiphyte *Tillandsia deppeana* Steud., adult individuals are reportedly able to support increased transpiration rates and are less drought-resistant than juveniles (Adams & Martin, 1986b). Some water-conserving physiological adaptations are equally available to both juvenile and adult forms; C<sub>3</sub>-CAM intermediate species are able to express CAM activity throughout their development (Beltrán *et al.*, 2012).

The costs of anthesis in bromeliads has not been quantified in terms of either carbon or water. However, the investment is likely to be at least as physiologically substantial as in comparable plants because of the restricted access to water experienced by many bromeliads and the often exceptionally large size of the inflorescence relative to the vegetative organs (Benzing, 2000). Considerable quantities of water may additionally have to be expended in the construction of specialized reproductive structures and substances such as berries and nectar, which impose an equivalent carbon cost (Ordano & Ornelas, 2005).

Drought-deciduousness as an adaptation to reduce transpirational water loss under dry-season conditions occurs in certain species of *Pitcairnia* and *Brocchinia* J.H.Schult. ex J.A.Schult. & J.H.Schult. and in *Ayensua waipanensis* (Maguire) L.B.Sm. (Benzing, 2000). A related phenomenon observed in many bromeliad species that may be of considerable importance for plant water relations is marcescence, the retention of dead leaves on the living plant. This generally peripheral layer of dead foliage may play a number of protective functions, including thermal insulation and the extension of the boundary layer for gas exchange, thus limiting the rate of transpirational water loss (Smith, 1979; Goldstein & Meinzer, 1983).

#### EXPOSURE AND HABITAT

The degree of exposure to intense sunlight and desiccating winds to which bromeliads are exposed varies widely between habitats and microhabitats. For terrestrial species, the most important influences will usually be latitude, altitude, aspect and the density of any higher forest or scrub canopy. In the case of lithophytic species the impact of aspect may be accentuated by the fact that these tenacious plants may grow on vertical rock faces and it has been suggested that the thermal capacity of the substrate may be an important modulator of transpirational water loss by lithophytes (Szarzynsky, 2000). With epiphytes, the vertical stratification of canopies must also be taken into consideration. Trunk and low-canopy epiphytes are generally exposed only to still, humid air, but moving up through tree-crowns to the uppermost canopy epiphytes will be increasingly exposed to high light and wind (Pittendrigh, 1948). This vertical exposure gradient is steepest in forest occurring on windward slopes and ridge tops and is associated with a characteristic turnover of species that are progressively more tolerant of water limitation (Pittendrigh, 1948; Graham & Andrade, 2004; Cascante-Marín *et al.*, 2006; Reyes-García *et al.*, 2008). Similar turnover between different functional groups occurs along elevational and topographical

transects, interacting with local wind and precipitation patterns (Sugden, 1981). An additional determinant of exposure-related structuring of epiphytic bromeliad distributions is the degree of deciduousness in phorophytes and neighbouring trees. Seasonally dry tropical forest tree communities often contain many deciduous species with canopies that may remain bare following leaf abscission for up to several months (Bullock & Solis-Magallanes, 1990). Epiphytes residing in the crowns of these trees must be capable of acclimating to the dramatically changed conditions during the dry season. *Guzmania monostachia* achieves this in seasonally deciduous forests in Trinidad by inducing CAM and photoprotective mechanisms (Maxwell *et al.*, 1992, 1999; Maxwell, Griffiths & Young, 1994).

#### GENETICS

Little information is known of the genetic determinants of functional traits in bromeliads. Perhaps due to their relatively limited importance for human nutrition and commerce beyond the pineapple [*Ananas comosus* (L.) Merr.], bromeliads have been the subject of few genomic or transcriptomic analyses. However, with a reference genome for pineapple recently published (Ming *et al.*, 2015) and the inclusion of *Brocchinia reducta* Baker in the 1KP project (<http://www.onekp.com>), insights into bromeliad molecular genetics are on the way. Future targeted molecular genetic work might profitably focus on the basis of key traits such as CAM, cell wall elasticity, trichome and stomatal development and function, wetting responses and rosette morphometry.

#### DIVERSIFICATION, ADAPTIVE RADIATION, AND BIOGEOGRAPHY IN BROMELIACEAE

The discourse surrounding the evolutionary history of Bromeliaceae has been dominated by the notion of orogenic and physiographic change in the Neotropics and morphological and physiological key innovations driving invasion of unexplored niche space with subsequent diversification and adaptive radiation (Gentry, 1982; Givnish *et al.*, 2014). Donoghue & Sanderson (2015) introduced the term ‘confluence’ to denote this coming together of exogenous and endogenous factors at a critical point in the history of a biological lineage to promote diversification. Rapid diversification must be distinguished from the phenomenon of radiation, as the crown species richness of a lineage may accrue either quickly or slowly (Givnish, 2015). Furthermore, not all radiations automatically qualify as *adaptive* radiations, as this phrase should be reserved for cases in which there is

real evidence of niche differentiation between crown taxa (Givnish, 2015). In Bromeliaceae, there is, however, extensive evidence of both explosive diversification and true adaptive radiation, a notable example of species-level niche differentiation being the nutritional strategies in *Brocchinia* (Givnish *et al.*, 1997, 2014; Givnish, 2015). Quantitative data and more critical assessment of water-use strategies in other radiations will help determine the degree of ecophysiological niche differentiation and the validity of considering these radiations to be adaptive. It may also assist in establishing whether anatomical constraints on physiology can explain why some lineages, referred to by Donoghue & Sanderson (2015) as ‘depauperons’, have not radiated and remain species-poor.

In cases where restricted geographical ranges of species have already been identified, future research might additionally seek to estimate the contribution of water-use strategies in defining bioclimatic tolerances and distributions of species. This would assist in predicting responses of bromeliads (and consequently the attendant infauna of epiphytic species) to climate change and the impact of these responses on ecosystem functioning and informing conservation efforts for the 71 species listed as Endangered or Critically Endangered (IUCN, 2015).

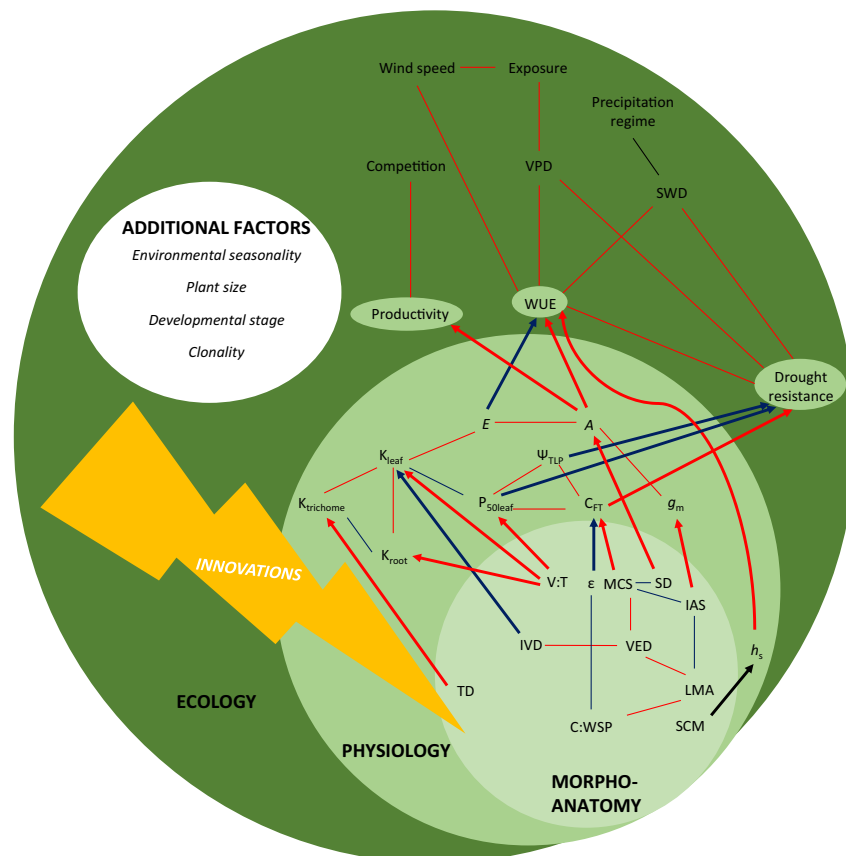
#### TOWARDS A MODEL OF THE EVOLUTION OF BROMELIAD WATER RELATIONS

There are compelling reasons for seeking to develop a comprehensive evolutionary model of bromeliad water relations. First, Bromeliaceae show an extraordinary level of ecophysiological diversity, in connection with unique features such as the absorptive trichome and unusual vascular tissues. Exploring the structural basis of this diversity will not only enhance our knowledge of the bromeliads, but may provide insights into the integration of form and function in vascular plants more generally. Secondly, epiphytic bromeliads are important components of the ecological networks of Neotropical forests due to their provision of phytotelmata and habitat space for faunal, floral and microbial inquilines (e.g. Gonçalves-Souza, Rossa-Feres & Romero, 2010; Płachno & Świątek, 2010; Goffredi, Kantor & Woodside, 2011; Carrias *et al.*, 2014). As an often dominant element of the vascular epiphytic flora, bromeliads are also key components of forest hydrological and nutrient cycles (Nadkarni, 1984; Veneklaas *et al.*, 1990; Ingram & Nadkarni, 1993; Freiberg & Freiberg, 2000; Hölscher *et al.*, 2004; Köhler *et al.*, 2007; Díaz *et al.*, 2010; Gehrig-Downie *et al.*, 2011).

A clearer picture of bromeliad water relations would allow us to appreciate their contribution to forest ecosystems on an increasingly quantitative basis. Thirdly, the epiphytic species are expected to prove particularly vulnerable to climate change because of the strong climatic limitations on the niche spaces of vascular epiphytes (Benzing, 1998; Zotz & Bader, 2009; Zotz *et al.*, 2010). Intense and prolonged drought events are likely to become a more frequent agent of mortality. Mechanistic, biophysical models of physiological tolerances of species based on empirical data may be combined with other factors to predict responses to altered precipitation regimes (Kearney & Porter, 2009; Kearney *et al.*, 2010).

The bromeliad literature does not yet contain sufficient data to allow a quantitative model of the evolution of bromeliad water relations to be elaborated. However, as a stimulus to future work on the development of quantitative models, I present here a sim-

plified, qualitative model. This model suggests how innovations may have been linked to cascades of co-ordinated physiological and morphoanatomical adaptation, contributing to the evolution of the characteristic functional types observed in extant Bromeliaceae. The term 'innovations' is deliberately used here to describe traits or syndromes often proposed elsewhere as 'key innovations' so as to avoid any implications regarding evolutionary diversification rates in this context. Some important factors excluded from consideration in the current model include plant size and environmental seasonality (other examples listed in Figure 1). The model is not intended to incorporate all relevant factors exhaustively, but utilizes a subset judged by the author to be of particular importance. When sufficient data become available for a fully quantitative treatment of this topic, it would be desirable to examine an expanded set of environmental factors and leaf



**Figure 1.** Simplified network of interactions between ecological, physiological and morphoanatomical traits in bromeliad water relations. Expected correlations are indicated by lines between traits within layers and by arrows between traits across different layers. Expected signs of the correlations are colour-coded: red = positive; blue = negative; black = positive or negative. Origins of innovations may directly or indirectly alter the values of these traits and/or cause a rewiring of the network of interactions. Several additional factors that modulate trait values and interactions are identified. Trait abbreviations are listed in Table 1.

traits. All of the hypothetical relationships between the traits in this model are suitable for testing through rapid surveys with broad taxon sampling. These relationships are summarized in Figure 1 and all of the trait abbreviations are defined in Table 1.

The model considers possible evolutionary trends in a core set of morphoanatomical characters involved in leaf water relations and a connected set of physiological traits. Through their integration in productivity, WUE and drought tolerance, these traits interact with important environmental factors such as SWD and VPD. At every level, interactions are modulated by the presence or absence of innovations. Six innovations pertinent to bromeliad water relations are considered here: the absorptive foliar trichome; the tank growth-form; epiphytism; CAM; neoteny; and terrestrial xerophytism. In the first instance, this hierarchical network of traits can be applied to describe the structure-function relationships in the water relations of Type I (soil-root) bromeliads. Specifically, a hypothetical mesophytic  $C_3$  species is a logical starting point because all six innovations are absent in this case. Accepting this Type I species as a baseline, representative species of each remaining functional type may then be considered. In each instance, a characteristic cascade of evolutionary changes in morphoanatomical, physiological and ecological traits associated with the origins or losses of innovations is identified. These hypothetical evolutionary pathways to each of Types II–V *sensu* Benzing (2000) are summarized in Fig. 2.

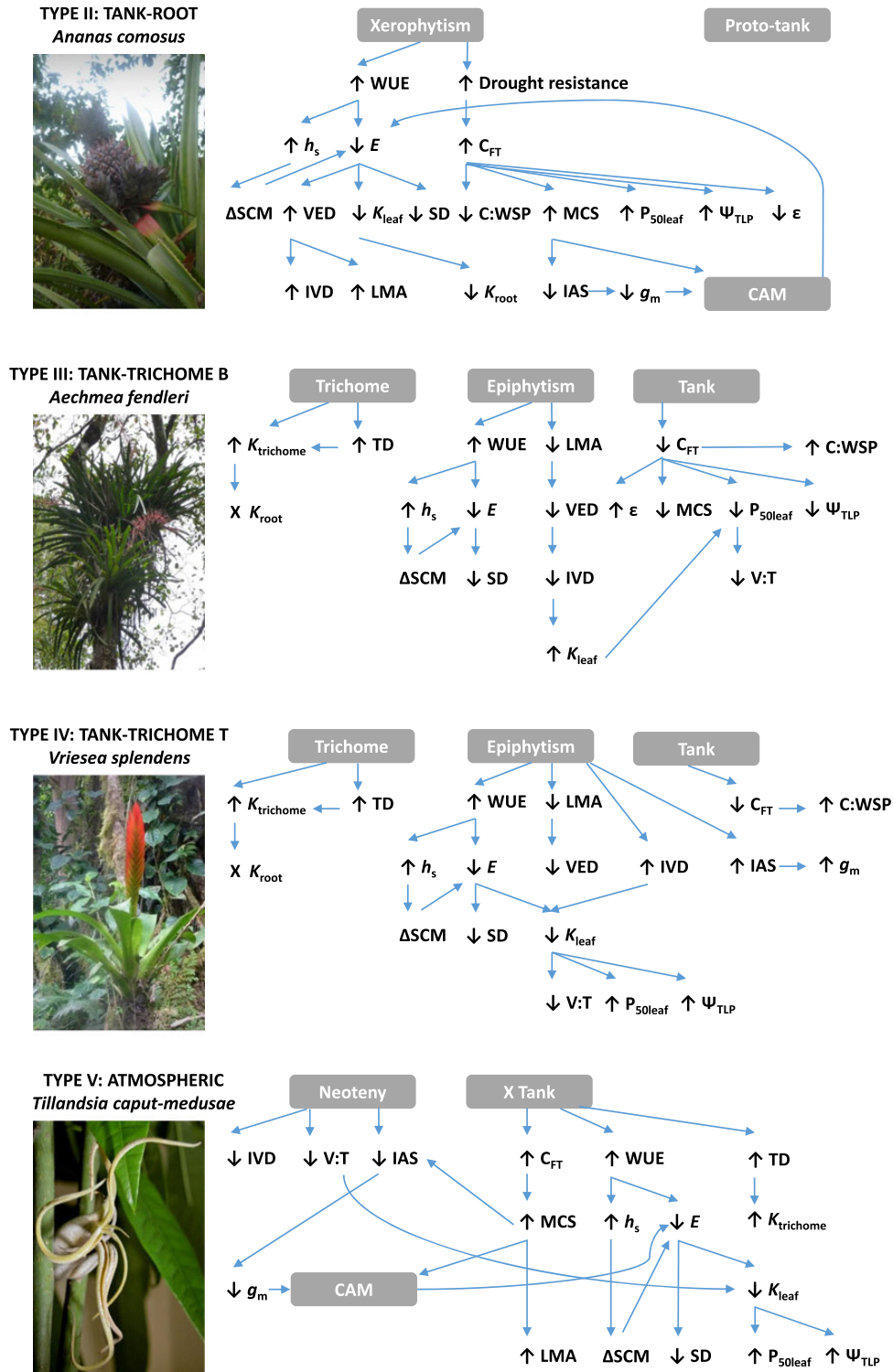
## TYPE II

In the case of the Type II (tank-root) species, all of which are found in the early-diverging Bromelioideae, *Ananas comosus* was selected as a typical example (Fig. 2). This species displays CAM and rudimentary axillary tanks, which both arose during the evolution of Type II species. CAM is unusual among the key innovations considered here, in that it has distinct anatomical prerequisites and therefore cannot be treated as the first step in a cascade of trait changes. Furthermore, Type II proto-tanks may have had relatively limited immediate impact on the evolution of other leaf traits. Instead, xeromorphic adaptation to high SWD and VPD is hypothesized to represent the key initial step on the pathway to the Type II syndrome, with selection for traits conferring enhanced WUE and drought resistance. Increased capacitance at full turgor ( $C_{FT}$ ) would have made an important contribution to drought resistance that enabled Type II species to survive under high VPD and SWD. Improvements in  $C_{FT}$  were probably supported by increased Mesophyll cell size (MCS) and

**Table 1.** Ecological, physiological and morphoanatomical traits used in the cascade model of the effects of key innovations in the evolution of bromeliad ecophysiological types

Ecological traits and environmental factors	
Drought resistance	Integrated drought resistance (drought tolerance and/or drought avoidance)
Productivity	Net photosynthetic productivity
WUE	Water-use efficiency ( $A/E$ )
Competition	Intensity of interspecific competition for resources
Exposure	Degree of exposure to radiation and wind
Precipitation regime	Abundance and seasonal distribution of rainfall
SWD	Soil water deficit
VPD	Leaf-air vapour pressure deficit
Wind speed	Mean wind speed in plant microhabitat
Physiological traits	
$A$	Net $CO_2$ assimilation rate
$C_{FT}$	Capacitance at full turgor
$E$	Transpiration rate
$g_m$	Mesophyll conductance to $CO_2$
$h_s$	Stomatal sensitivity to humidity
$K_{leaf}$	Leaf hydraulic conductance
$K_{root}$	Root hydraulic conductance
$K_{trichome}$	Trichome hydraulic conductance
$P_{50leaf}$	Water potential at 50% loss leaf hydraulic conductance
$\Psi_{TLP}$	Water potential at turgor loss point
Morphoanatomical traits	
C:WSP	Ratio of chlorenchyma thickness to water storage parenchyma thickness
$\epsilon$	Bulk modulus of elasticity
IAS	Internal air space fraction
IVD	Interveinal distance
LMA	Leaf mass per unit area
MCS	Mesophyll cell size
SCM	Stomatal complex morphology
SD	Stomatal density
TD	Trichome density
TVD	Transverse vein density
VED	Vein-epidermis distance
V:T	Ratio of vessel cross-sectional area to tracheid cross-sectional area in leaf xylem

reduced  $\epsilon$  and C:WSP. The last change would have diminished the selective pressure for strongly negative  $\Psi_{TLP}$  and  $P_{50leaf}$  as the presence of a reservoir of water in collapsible WSP buffers the water potential of chlorenchyma cells against fluctuation during drought. The investment in internal capacitance is



**Figure 2.** Expected cascades of trait changes during the evolution of bromeliad Types II–V *sensu* Benzing (2000). Images show a representative species for each functional type (II = *Ananas comosus*; III = *Aechmea fendleri*; IV = *Vriesea splendens*; V = *Tillandsia caput-medusae*). Boxes represent the innovations arising during the evolution of each functional type. The up/down arrows next to traits indicate the expected direction of change in trait value during the evolution of functional type and 'X' denotes the elimination of a trait. Arrows connecting traits show hypothetical causal cascades of adaptive trait changes as described in text. Trait abbreviations are listed in Table 1.

particularly important in Type II species because of the limited ability of the rudimentary axillary tanks to retain water and thereby provide external capacitance.

Higher MCS would also have provided space for nocturnal storage of malic acid in CAM and the low IAS and  $g_m$  associated with high MCS may have provided an additional selective pressure in favour of CAM as a carbon-concentrating mechanism. If diffusion limitation in increasingly densely packed mesophyll of  $C_3$  xerophytes was sufficiently strong, this could have favoured origins of CAM in the same way.

LMA and VED probably increased during xeromorphic adaptation prior to the evolution of CAM and as IVD and VED are generally closely co-ordinated, IVD should have increased with VED. The effect of this would have been an increase in vertical and horizontal hydraulic path lengths and a consequent reduction in the hydraulic capacity of the leaf in line with lower transpirational water loss in xerophytes.  $K_{root}$  probably underwent reduction in proportion with  $K_{leaf}$ . A reduction in leaf xylem V:T could also have been favoured by natural selection in connection with the need for lower leaf hydraulic conductance, especially if this allowed the fraction of the leaf volume occupied by the vasculature to be reduced relative to that occupied by succulent mesophyll or WSP cells.

Other effects of xerophytism probably included lower SD, helping to restrict gas exchange rates. Type II species also display a switch in SCM relative to Type I species, which may conceivably have contributed to enhanced WUE and drought resistance via  $h_s$ . As with all of the epiphytic functional types, the predicted reduction in productivity in Type II CAM xerophytes, associated with more conservative stomatal behaviour and the energetic costs of CAM, may have been compensated for by the reduced burden of interspecific competition in water-limited terrestrial and epiphytic ecospace.

### TYPE III

In Type III species (tank-trichome Bromelioideae), such as *Aechmea fendleri* André ex Mez (Fig. 2), all of the innovations except neoteny are present. CAM was already present in the ancestor of all Type III species and traits associated with leaf-succulence have therefore been a constant fixture in this group. However, a change that did occur during the evolution of Type III species was the origin of rapid trichome-mediated water-uptake, which, in conjunction with the fully-developed tank, virtually eliminated the role of  $K_{root}$ . Meanwhile exploration of water-limited epiphytic niche space involved strong selection for WUE, which may have been obtained partly through the continued operation of CAM and partly

through another change in SCM and  $h_s$ . A reduction in LMA associated with the nutrient limitations associated with epiphytic niches could have been underpinned by decreased VED. A consequent positive effect on  $K_{leaf}$  via the conservation of the VED:IVD ratio would have favoured more negative  $P_{50leaf}$  and decreased V:T. The origin of the extensive external capacitance in the well developed tank is hypothesized to have allowed a reduction in internal capacitance, leading to changes in a set of anatomical and physiological parameters in the reverse direction of those observed during the evolution of the Type II syndrome.

### TYPE IV

Type IV species (tank-trichome Tillandsioideae), including *Vriesea splendens* (Brongn.) Lem. (Fig. 2) are similar to Type III but lack CAM. In the absence of CAM, the tank growth-form and epiphytism selected for increased IAS for improved ventilation of submerged tissues and reduced construction costs, respectively. Similarly, these innovations may have led to increased IVD if wider leaves were more successful at intercepting water and light. Given the thinness of the leaves of Type IV species, this is contingent on the possibility of IVD being decoupled from VED, which is unusual among angiosperms (Zwieniecki & Boyce, 2014). A reduction in V:T may have been important in limiting hydraulic vulnerability to embolism in these species, although a change in SCM probably enhanced  $h_s$ , thereby helping to reduce water loss. The same trichome-facilitated evolution of independence from root-mediated water-uptake occurred in Type IV bromeliads as in Type III bromeliads.

### TYPE V

Finally, Type V species (atmospheric *Tillandsia* spp.), including *Tillandsia caput-medusae* E.Morren (Fig. 2), display absorptive trichomes, epiphytism and CAM but do not form tanks. They are also strongly neotenic and this reduction in the size of the body of the mature plant is associated with tighter mesophyll cell-packing and lower IVD and, perhaps importantly, a reduction of the vasculature. This limits the axial, xylary component of  $K_{leaf}$  and makes the transcellular component (which is under dynamic regulation via aquaporin gene expression) dominant. CAM originated during the evolution of Type V species from Type IV species, probably through a similar pathway to that described for the Type II species above. The combination of epiphytism and the lack of tanks entails a strong selective pressure for drought resistance, especially under the high VPD routinely experienced by pulse-supplied Type V



species. Besides CAM, drought resistance has been achieved through a number of morphoanatomical mechanisms in Type V species, including greatly increased TD and higher  $C_{FT}$  alongside reduced SD, C:WSP and  $\varepsilon$ . The high level of succulence and conservative water-use are hypothesised to be associated with less negative  $P_{50leaf}$  and  $\Psi_{TLP}$ .

#### FUTURE DIRECTIONS

In summary, origins and losses of individual and combined innovations are hypothesized to have

triggered cascades of trait changes at the morphoanatomical and physiological levels during the evolution of the different functional types of bromeliads. The exception is CAM, which has probably repeatedly evolved as a flexible culminating trait in a cascade of adaptations to xeric conditions, rather than precipitating extensive change once it has originated.

The hypothetical trait changes described here should be tested through two major lines of inquiry. The first of these will involve examining relationships between morphoanatomical and physiological

**Table 2.** High-priority topics and questions for a new research programme in bromeliad water relations

Topic	Questions
Root and stem functional diversity	<ul style="list-style-type: none"> <li>• What quantitative contribution do roots make to plant water balance in different ecophysiological Types?</li> <li>• What role do stems play in the physiology of species differing in shoot architecture?</li> </ul>
Stomatal sensitivity to stimuli	<ul style="list-style-type: none"> <li>• How do stomata respond to factors such as humidity, light quality and endogenous drought in different growth forms?</li> <li>• Can responses be related to habitat preferences?</li> </ul>
Significance of stomatal complex diversity	<ul style="list-style-type: none"> <li>• What role do subsidiary and neighbouring cells play in stomatal biology?</li> <li>• How does stomatal complex arrangement relate mechanistically to climate relations and habitat preference?</li> </ul>
Trichome functional diversity	<ul style="list-style-type: none"> <li>• What characters determine variation in trichome absorptive efficiency?</li> </ul>
Vein structure, function and evolution	<ul style="list-style-type: none"> <li>• Can the relationships between xylem conduit and vascular bundle characters and conductance be quantified?</li> <li>• How does venation architecture and detail relate to xylem heterochrony and neoteny?</li> <li>• Does trichome-mediated water uptake make vascular conductance redundant?</li> </ul>
Integration of light, temperature and water relations in spatially heterogeneous environments and spatially heterogeneous leaves	<ul style="list-style-type: none"> <li>• How do environmental factors interact to determine transpirational demand and water dynamics across heterogeneous leaf surfaces?</li> <li>• What role do bundle sheath extensions play in modularisation of the lamina?</li> </ul>
Commissural vein function	<ul style="list-style-type: none"> <li>• Are commissures hydraulically significant in bromeliad leaves?</li> <li>• Does commissure architecture and density relate to leaf strength and function?</li> </ul>
Cell and tissue water relations	<ul style="list-style-type: none"> <li>• How much do cell water relations traits vary across the family?</li> <li>• Are there correlations between these and other physiological traits or with ecological properties?</li> </ul>
Molecular and genetic basis of water relations traits	<ul style="list-style-type: none"> <li>• How are water relations traits and other relevant traits determined at the molecular and genetic level?</li> <li>• What role do aquaporins play in water movement within leaves?</li> </ul>
Life-cycle water budgets	<ul style="list-style-type: none"> <li>• What is the capacity for phenotypic plasticity under different water regimes?</li> <li>• How do water relations vary through bromeliad life-cycles?</li> <li>• How costly are specific developmental processes, e.g. anthesis, clonal propagation?</li> </ul>
Evolution of CAM	<ul style="list-style-type: none"> <li>• Where do bromeliads of intermediate carbon isotope signature fall along the CAM continuum and how does this relate to water availability?</li> <li>• How early did the capacity for CAM-cycling evolve?</li> </ul>
Ancestral state reconstruction, palaeoclimate and palaeovegetation	<ul style="list-style-type: none"> <li>• Can characters of extant species be used to reconstruct ancestral states?</li> <li>• How do these relate to palaeoclimate and palaeovegetation of relevant geographical regions?</li> </ul>

quantitative traits, innovations and environmental factors. By sampling across a wide range of lineages and using a phylogenetically structured approach, this could help shed light on the role of shifts in quantitative traits in supporting the ecophysiological distinctiveness of the functional types. It could also help establish whether there are multiple evolutionary pathways to the same functional type syndrome and explore the diversity within each functional type. Detailed reconstruction of the phylogenetic history of individual lineages, accurate characterization of trait values and ancestral trait reconstruction for each relevant node may help to resolve the historical priority in trait changes.

A second strand of novel research should explore the degree of coordination in the evolution of quantitative morphoanatomical and physiological traits. Bromeliaceae as a family have not been considered in the context of the leaf economics spectrum (LES), which is defined by a system of genetically and environmentally constrained inter-correlated traits (including maximum assimilation rate, respiration rate, leaf mass per unit area, leaf lifespan, leaf nitrogen and phosphorus content) the state of which in a given species is broadly reflective of the ecological strategy of that species (Reich *et al.*, 1999; Wright *et al.*, 2004, 2005; Reich, 2014). Simultaneous quantification of LES traits and other leaf anatomical and hydraulic traits would provide crucial insights into the evolution of structure and function in a single highly diverse family of herbaceous angiosperms and perhaps indicate whether the numerous innovations in bromeliad leaf biology have individually or in consort redefined the accessible regions of trait space. It would also help to address the controversial issue of the extent of coupling (or decoupling) between variation in LES traits and hydraulic traits (cf. Li *et al.*, 2015; Ocheltree, Nippert & Prasad, 2016).

A selection of suggested research priorities aimed at filling gaps in our current understanding of bromeliad water relations is provided in Table 2. With an increasingly clear picture of phylogenetics of Bromeliaceae and access to sophisticated statistical tools for testing hypotheses of evolutionary pattern and process (Givnish *et al.*, 2014; Silvestro *et al.*, 2014), it is an exciting time to be working on the integrative biology of this family, which continues to reward the researcher with ever deeper fascination.

#### ACKNOWLEDGEMENTS

I am indebted to Professors H. Griffiths and J.A.C. Smith for their support and enthusiasm in my forays

into bromeliad biology and to two anonymous reviewers for constructive comments on an earlier version of this manuscript.

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