Concerted anatomical change associated with CAM in the Bromeliaceae

Journal:	<i>Functional Plant Biology</i>
Manuscript ID	FP17071.R2
Manuscript Type:	Research paper
Date Submitted by the Author:	04-Jan-2018
Complete List of Authors:	Males, Jamie; University of Cambridge, Plant Sciences
Keyword:	CAM plants, Epiphytes, Bromeliaceae

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Concerted anatomical change associated with CAM in the Bromeliaceae

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Running title: CAM anatomy in bromeliads

Summary

CAM is a flexible photosynthetic mode which confers robust environmental resilience. This investigation tackles the scarcity of data linking the evolution of anatomy and CAM function, showing that in a highly diverse plant family, co-option and augmentation of existing succulence was integral to multiple origins of CAM. Not only do the results clarify the evolution of CAM, they could also help define the baseline level of cell- and tissue-succulence required in efforts to bioengineer CAM into food and biomass crops.

Abstract

Crassulacean acid metabolism (CAM) is a celebrated example of convergent evolution in plant ecophysiology. However, many unanswered questions surround the relationships between CAM, anatomy, and morphology during evolutionary transitions in photosynthetic pathway. An excellent group in which to explore these issues is the Bromeliaceae, a diverse monocot family from the Neotropics in which CAM has evolved multiple times. Progress in the resolution of phylogenetic relationships among the bromeliads is opening new and exciting opportunities to investigate how evolutionary changes in leaf structure has tracked, or perhaps preceded, photosynthetic innovation. This paper presents an analysis of variation in leaf anatomical parameters across 163 C₃ and CAM bromeliad species, demonstrating a clear divergence in fundamental aspects of leaf structure in association with photosynthetic pathway. Most strikingly, the mean volume of chlorenchyma cells of CAM species is 22 times higher than that of C₃ species. In two bromeliad subfamilies (Pitcairnioideae and Tillandsioideae), independent transitions from C₃ to CAM are ~~clearly~~ associated with

Males

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CAM anatomy in bromeliads

30 increased cell-succulence, while evolutionary trends in tissue thickness and leaf air space
31 content differ between CAM origins. Overall, leaf anatomy is clearly strongly coupled with
32 photosynthetic pathway in the Bromeliaceae, where independent origins of CAM have
33 involved significant anatomical restructuring.

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35 Keywords

36 Functional anatomy; succulence; vascular epiphytes; xerophytism

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55 Introduction

56 Crassulacean acid metabolism (CAM) is a major adaptive syndrome that has evolved
57 convergently in numerous angiosperm lineages (Winter and Smith 1996). CAM is an
58 augmented photosynthetic pathway based on temporal segregation of C₄ and C₃ metabolism
59 (Osmond 1978), leading to enhanced water-use efficiency (WUE) and performance under
60 arid climates (Keeley and Rundel 2003). CAM also raises the internal CO₂ concentration to
61 extremely high levels (Cockburn *et al.* 1979), which may help to reduce photorespiratory
62 fluxes in stressful environments (Lüttge 2002).

63 The relationship between CAM and specialised succulent leaf anatomy is well-established
64 (Gibson 1982). The operation of CAM is contingent upon large mesophyll cells with large
65 vacuoles for malate storage. This cell-succulence often scales up to tissue-level or
66 morphological succulence, and indeed most plants recognised as being of ‘succulent’ *Gestalt*
67 (*sensu* Ogburn and Edwards 2010) are CAM plants (Nyffeler *et al.* 2008). There is great
68 interest in the nature of the structure-function relationships since they are fundamental to
69 efforts to engineer CAM into C₃ food and fibre crops for sustainable, climate-resilient
70 production (Borland *et al.* 2011, 2014). However, many aspects of these relationships remain
71 obscure. For instance, despite the acknowledged link between CAM and leaf anatomy, and
72 perhaps because CAM activity represents a quantitative spectrum rather than a binary trait
73 (Silvera *et al.* 2010a), there is surprisingly little clarity surrounding the question of whether
74 succulence tends to evolve before, after, or contemporaneously with CAM (Edwards and
75 Ogburn 2012; Hancock and Edwards 2014; Males, 2017).

76 One approach to addressing the question of priority in the evolution of succulence and CAM
77 would be to examine in detail the evolutionary history of a radiation of plants containing C₃
78 and CAM elements. Few examples of such studies exist, but they include a recent
79 investigation of the timing of the origins of succulent leaf anatomy and CAM in the
80 Agavoideae (Asparagaceae) undertaken by Heyduk *et al.* (2016). By combining a high-
81 resolution phylogenetic analysis of the clade with a survey of carbon isotope ratio ($\delta^{13}\text{C}$)
82 values, these authors were able to reconstruct the evolution of CAM in the Agavoideae, and
83 compared this with phylogenetic trends in quantitative anatomical parameters, including leaf
84 thickness, average mesophyll cell area, internal air space fraction, and the number of vascular
85 planes in the leaf. It was concluded that a succulent, ‘CAM-like’ leaf anatomy had evolved
86 before significant CAM activity originated in this lineage. Whether such conclusions are of

87 general applicability is uncertain, and it is therefore desirable that similar, comparable studies
88 be carried out in other groups.

89 An excellent candidate for further investigation of the association of divergences in leaf
90 anatomy with variation in CAM capability is the Neotropical bromeliad family
91 (Bromeliaceae). The bromeliads, which number some 3,500 species (Butcher and Gouda
92 2016), display a range of photosynthetic types, including C₃, strong CAM, inducible CAM
93 (C₃-CAM), and C₃ with weak CAM-cycling (Medina 1974; Martin 1994; Pierce *et al.* 2002a;
94 Crayn *et al.* 2015). Across the whole family, CAM is an important contributor to adaptive
95 ecophysiological diversity (Griffiths and Smith 1983; Smith *et al.* 1986; Pierce *et al.* 2002b;
96 Crayn *et al.* 2015), and in some lineages CAM, epiphytism and the tank growth-form have
97 acted as key innovations, spurring elevated rates of net species diversification (Givnish *et al.*
98 2014; Silvestro *et al.* 2014). CAM has evolved on multiple independent occasions throughout
99 the family, providing natural replication for hypothesis testing (Crayn *et al.* 2004, 2015; Fig.
100 1). Relatively well-defined independent origins of CAM have been placed in the genus
101 *Tillandsia* (Tillandsioideae), at the base of *Hechtia* (Hechtioideae), and at the base of the
102 Xeric Clade (*Deuterocohnia*-*Dyckia*-*Encholirium*) in the Pitcairnioideae. By contrast,
103 phylogenetic uncertainty means that it is not yet clear whether CAM arose in the common
104 ancestor of the Bromelioideae and Puyoideae, or if the pathway has evolved convergently in
105 these two subfamilies, perhaps multiple times in each (Crayn *et al.* 2015).

106 [FIGURE 1]

107 This general picture of the distribution of CAM in the Bromeliaceae has recently been
108 supported by the results of an extensive survey of $\delta^{13}\text{C}$ values for 1893 species performed by
109 Crayn *et al.* (2015). Their data confirmed the previously-reported bimodal distribution of
110 $\delta^{13}\text{C}$ values in the Bromeliaceae (Medina *et al.* 1977; Griffiths and Smith 1983; Pierce *et al.*
111 2002a). This bimodality is a recurrent feature of CAM evolution, and is often interpreted as
112 meaning that C₃-CAM intermediate phenotypes are either evolutionarily unstable or of lower
113 fitness relative to full C₃ or strong CAM phenotypes (Winter and Holtum 2002; Silvera *et al.*
114 2005, 2010a,b; Crayn *et al.* 2015). However, a number of bromeliad species do show $\delta^{13}\text{C}$
115 values that fall in the intermediate zone (ca. -23.0 to -19.0‰, referred to as the Winter-
116 Holtum Zone, WHZ). WHZ $\delta^{13}\text{C}$ values could result either from strong diffusional
117 constraints in C₃ species (e.g. through stomatal limitation or pronounced succulence), or
118 hard-to-diagnose C₃-CAM intermediacy ('cryptic CAM'; Crayn *et al.* 2015). The proportion

of WHZ species falling into either of these categories is at present unknown. It is also important to note that $\delta^{13}\text{C}$ values for species which engage in only short bursts of CAM activity will be C_3 -like.

I hypothesised that multiple independent origins of CAM in the bromeliads involved concerted leaf anatomical specialisation, including increased chlorenchyma cell size and denser cell packing. To test this hypothesis, I combined original anatomical data with reassessment of published anatomical resources for comparison with variation in photosynthetic pathway across 163 representative bromeliad species. The results cast light on the integrative biology of the bromeliads, but also provide timely insights on the general principles of structural-functional interactions in CAM plants, with potential applications in ongoing bioengineering programmes.

Methods

Anatomical traits

To investigate the evolution of anatomical specialisation in association with CAM in the bromeliads, a set of key parameters that could be characterised for a wide range of C_3 and CAM species was identified. These included chlorenchyma cell diameter, leaf thickness, thicknesses of chlorenchyma and hydrenchyma tissues, internal air space fraction, and the cross-sectional area of the longitudinal air channels that often occur between vascular bundles in bromeliad leaves (Tomlinson 1969). Photosynthetic pathway was assigned on the basis of the $\delta^{13}\text{C}$ values reported by Crayn *et al.* (2015).

Because of the limited availability of living material for many important lineages, a combinatorial approach was taken which involved bringing together evidence from new anatomical measurements and reanalysis of published images of leaf cross-sections. New measurements were made on leaves of 44 species, which were complemented by measurements made on published cross-sectional images for an additional 119 species. In the case of new measurements, transverse sections were hand-cut from the proximo-distal centre of the leaf-blade and mounted on a light microscope. Microphotographs were captured, and ImageJ (NIH, Bethesda, MD, USA) was used to measure the mean diameter of chlorenchyma cells, total leaf thickness, chlorenchyma and hydrenchyma thicknesses in the centro-lateral centre of the leaf, and the mean area of air channels. For some analyses (as indicated in the

text), air channel area was normalised by leaf thickness to yield a measure of relative air channel area. Anatomical measurements were performed on at least six replicate leaves drawn from one or more plants, and cell-level measurements were made on at least twenty cells of each type per leaf section. Plants were selected from the living collections of Cambridge University Botanic Garden (CUBG), RBG Edinburgh (RBGE), RBG Kew (RBGK) and Marie Selby Botanical Gardens (MSBG). The complete species list with garden origins is provided in Supplementary Table S1.

Reanalysis of published cross-sectional images was carried out by searching the literature for transverse leaf cross-sections from representative species. Only images with sufficient resolution and reliable scale bars were used. These images were imported to ImageJ, and the same set of anatomical parameters were then measured. While this method meant that each species was generally characterised on the basis of only a single replicate, it allowed for extensive taxonomic coverage and generated compelling results for further investigation with more intensive sampling and replication. Full details of image sources are given alongside the species list in Supplementary Table S1.

For 42 species, infiltration-derived values of internal air space fraction reported in Males and Griffiths (2017a) were available for comparison with anatomical data. Briefly, infiltration was performed using leaf slices under vacuum with an isotonic mannitol solution (appropriate concentration determined according to ambient temperature and leaf water potential as measured with a pressure chamber- PMS Instruments, Albany, OR, USA). Bulk tissue porosity was determined on the basis of the change in sample mass.

Comparisons across CAM origins in Pitcairnioideae and Tillandsioideae

Comparisons were made between C₃ and CAM species across the complete species set ($n = 163$), as well as across evolutionary transitions in photosynthetic pathway in the Tillandsioideae and Pitcairnioideae subfamilies. The phylogenetic frameworks for comparisons within these subfamilies were based on recently-published molecular phylogenetic analyses (Wagner *et al.* 2013; Krapp *et al.* 2014; Saraiva *et al.* 2015; Barfuss *et al.* 2016; Schütz *et al.* 2016; Pinangé *et al.* 2017). Notably, Schütz *et al.* (2016) performed analyses using sequences from 91 species including 87 Pitcairnioideae. They identified a deep split between two main lineages in the C₃ genus *Pitcairnia*, which formed a polytomy with the remainder of the subfamily, while the C₃ genus *Fosterella* was recovered as

monophyletic and sister to all species in the exclusively CAM Xeric Clade (Fig. 2). Although existing taxonomic concepts within the Xeric Clade were not supported, with both *Deuterocohnia* and *Encholirium* appearing to be paraphyletic, the proposed single origin of CAM at the base of the Xeric Clade is not challenged by this topology (Crayn *et al.* 2015).

[FIGURE 2]

Meanwhile, a recently-published phylogeny and taxonomic reclassification of the Tillandsioideae based on a multi-locus molecular and morphological analysis provides a clearer framework for examining the evolution of CAM and leaf anatomy in this speciose and ecologically important subfamily (Barfuss *et al.* 2016). Fig. 3 shows the backbone phylogeny for Tillandsioideae according to the results presented by Barfuss *et al.* (2016). In the Crayn *et al.* (2015) carbon isotope dataset, values of $\delta^{13}\text{C}$ greater than -23.0‰ occurred in two *Alcantarea* species, seven *Guzmania* species, three *Mezobromelia* species, 11 *Racinaea* species, and 19 *Vriesea* species, hinting at the possibility of widespread low-level ~~weak~~ CAM in the subfamily.

[FIGURE 3]

Maps of approximate anatomical trait evolution in these two subfamilies were created using cladograms and the R package phytools (Revell 2012). These maps do not incorporate information on evolutionary distance and are intended as heuristic illustrations of general trends.

Statistical analysis

All statistical analysis was performed in R (R Development Core Team 2008). Data were checked for departure for normality, and log-transformed prior to linear regression modelling where indicated in the text. Paired *t*-tests were used to compare mean trait values between functional groups.

Results

Anatomical traits

211 [TABLE 1]

212 [FIGURE 4]

213 The complete anatomical dataset for all species is available in Supplementary Data Table S2,
 214 and is summarised in Table 1. Across all species ($n = 163$) there were statistically significant
 215 positive correlations between log-transformed chlorenchyma cell diameter and chlorenchyma
 216 thickness ($r^2 = 0.37$, $p < 0.001$; Fig. 4A), and between cell diameter and leaf thickness ($r^2 =$
 217 0.26 , $p < 0.001$; Fig. 4B). C_3 and CAM species segregated clearly in this bivariate
 218 morphospace, with CAM species showing significantly thicker leaves ($F = 16.30$, $p < 0.001$)
 219 and higher cell diameters ($F = 64.57$, $p < 0.001$). Cell diameter was the stronger effect of the
 220 two, reflecting the importance of cell-succulence for the efficient operation of the CAM
 221 cycle. The ratio of chlorenchyma to hydrenchyma thickness differed significantly ($F = 9.64$, p
 222 < 0.001), and this was driven by significantly higher chlorenchyma thickness in CAM species
 223 ($F = 30.87$, $p < 0.001$), and not by variation in hydrenchyma thickness ($F = 0.82$, $p = 0.441$).
 224 Across all species, chlorenchyma thickness was positively correlated with leaf thickness ($r^2 =$
 225 0.73 , $p < 0.001$; Fig. 4C), and this relationship was slightly stronger in CAM species ($n = 89$,
 226 $r^2 = 0.70$, $p < 0.001$) than in C_3 species ($n = 71$, $r^2 = 0.59$, $p < 0.001$). Hydrenchyma thickness
 227 was more weakly positively correlated with leaf thickness across the full species set ($r^2 =$
 228 0.45 , $p < 0.001$; Fig. 4D), but this relationship was considerably stronger in C_3 species ($r^2 =$
 229 0.83 , $p < 0.001$) than in CAM species ($r^2 = 0.41$, $p < 0.001$). It therefore appears that
 230 interspecific variation in leaf thickness is more strongly driven by variation in hydrenchyma
 231 thickness in C_3 bromeliads and by variation in chlorenchyma thickness in CAM bromeliads.

232 For the 42 species for which data on internal air space fraction were available, there was a
 233 negative relationship between this anatomical parameter and chlorenchyma cell diameter (r^2
 234 $= 0.42$, $p < 0.001$; Fig. 4E), showing that more pronounced cell-succulence tends to restrict
 235 air space volume. CAM species therefore showed significantly lower internal air space
 236 fraction ($F = 17.47$, $p < 0.001$). For a set of 154 species, measurements of mean air channel
 237 area were made. When air channel area was normalised by leaf thickness, there was no
 238 significant correlation with cell diameter, but CAM species showed significantly lower values
 239 than C_3 species ($F = 8.53$, $p < 0.001$; Fig. 4F). This implies that for a given leaf thickness,
 240 CAM species will tend to have significantly smaller air channels than C_3 species.

241 [FIGURE 5]

PCA performed on log-transformed data for chlorenchyma cell diameter, leaf thickness, chlorenchyma thickness, and air channel area highlighted trait divergences between C_3 and CAM lineages within subfamilies (Fig. 5). Hydrenchyma thickness was not included as it had already been shown not to differ significantly between C_3 and CAM species. The first two principal components explained 60.46% and 25.33% of the total variance respectively. Loadings for each of the four traits were closely aligned with these axes. Absolute air channel area aligned with PC1, while chlorenchyma cell diameter, leaf thickness and chlorenchyma thickness all aligned with PC2. This suggests that while there may be evolutionary developmental coordination between cell sizes and tissue dimensions, absolute air channel area can vary independently. Systematic differences in proportional leaf air content between C_3 and CAM species may therefore often be driven by differences in leaf thickness rather than air channel area. In the Pitcairnioideae and Tillandsioideae, comparable evolutionary trajectories could be identified across the PC1-PC2 morphospace in association with the transition from C_3 to CAM, involving either no major change in absolute air channel area (which is nevertheless equivalent to a reduction in relative air channel area when the increase in leaf thickness is considered) or the loss of air channels.

Comparisons across CAM origins in Pitcairnioideae and Tillandsioideae

Within the Pitcairnioideae ($n = 19$), there was a positive correlation between leaf thickness and mean chlorenchyma cell diameter ($r^2 = 67.78$, $p < 0.001$), with CAM species showing significantly higher cell diameter ($F = 62.99$, $p < 0.001$), chlorenchyma thickness ($F = 19.84$, $p < 0.001$), and leaf thickness ($F = 18.14$, $p < 0.001$). Mean cell diameter was 2.7 times higher in CAM species than in C_3 species. Although the effect was considerably weaker, CAM species also displayed significantly lower relative air channel area ($n = 18$, $F = 6.65$, $p = 0.020$). The phylogenetic distribution of trait values suggested that a change in chlorenchyma cell size at the base of the Xeric Clade was closely associated with the origin of CAM in the Pitcairnioideae (Fig. 6A). There was a reasonably clear distinction in leaf thickness between the Xeric Clade and earlier-diverging lineages, although the *Fosterella cotocajensis*-*F. chiquitana* pairing showed values comparable with many Xeric Clade species, and the miniaturised *Deuterocohnia scapigera* displayed a much lower value than other Xeric Clade species (Fig. 6B). Chlorenchyma thickness was clearly higher in the Xeric Clade than in the C_3 grade, with the exception again being the diminutive *D. scapigera* (Fig.

6C). Relative air channel area was comparatively high in *C₃ Pitcairnia* species and was highest in *F. chiquitana*. However, the two other *Fosterella* species showed considerably lower values, which also occurred throughout the CAM Xeric Clade (Fig. 6D). Overall, it appears that the origin of CAM at the base of the Xeric Clade Pitcairnioideae was associated with a contemporaneous increase in chlorenchyma cell size and chlorenchyma and leaf thicknesses, which may have been preceded by a reduction in relative air channel area prior to the divergence of *Fosterella*.

[FIGURE 6]

In the Tillandsioideae ($n = 85$) there was also a positive correlation between leaf thickness and cell diameter ($r^2 = 29.25$, $p < 0.001$), and CAM species again showed significantly higher cell diameter ($F = 185.90$, $p < 0.001$), chlorenchyma thickness ($F = 16.43$, $p < 0.001$), and leaf thickness ($F = 15.60$, $p < 0.001$). Mean cell diameter was 4.2 times higher in CAM species than in *C₃* species. There were also sufficient data available to demonstrate a significant negative correlation between internal air space fraction and chlorenchyma cell diameter ($n = 25$, $r^2 = 66.67$, $p < 0.001$), with CAM species showing lower air space fraction ($F = 51.10$, $p < 0.001$). Similarly, CAM Tillandsioideae showed significantly lower relative air channel area ($n = 85$, $F = 20.28$, $p < 0.001$). The association of the transition from *C₃* to CAM in *Tillandsia* with change in leaf anatomical trait values is clearly illustrated in Fig. 6. The contrast between the *C₃* and CAM lineages is particularly strong for chlorenchyma cell diameter (Fig. 7A). For leaf thickness, the highest values were primarily clustered in the CAM *Tillandsia* lineages, but there was a second cluster of relatively high values in the genus *Alcantarea*, many of which attain very large rosette sizes and are known as the ‘giant bromeliads’ (Fig. 7B). Similarly, the highest values of chlorenchyma thickness occurred in CAM *Tillandsia* lineages, except for several CAM species in subgenus *Tillandsia*, and a core clade within *Alcantarea* (Fig. 7C). Relative air channel area was reduced at the base of *Tillandsia* and showed further declines in more derived CAM *Tillandsia* lineages (Fig. 7D). Overall, the transition(s) from *C₃* to CAM in *Tillandsia* appear to have involved a pronounced increase in chlorenchyma cell size and reduction in relative air channel area, whereas increased chlorenchyma and leaf thicknesses may have been important in specific lineages but do not show a clear-cut relationship with CAM across the subfamily as a whole. It was notable that the *C₃* species *T. complanata*, which is nested among CAM lineages,

showed trait values more similar to other non-*Tillandsia* C₃ species than to CAM *Tillandsia* species. This suggests that reversion to C₃ within *Tillandsia* lineages may have ~~required~~ been associated with a reversal of the anatomical changes associated with the initial origin of CAM.

[FIGURE 7]

Discussion

Structure-function relationships lie at the heart of CAM biology, linking cell and tissue anatomy with the physiological activity of the CAM cycle. However, we still have a relatively limited understanding of the extent to which the evolution of CAM in numerous lineages of vascular plants has been contingent upon pre-existing anatomical intermediacy or on *de novo* anatomical innovation (Edwards and Ogburn 2012; Hancock and Edwards 2014). Of the many groups in which this issue might be explored, the Bromeliaceae, in which CAM has evolved independently several times and occurs in strong, weak and intermediate forms, offer one of the best opportunities and is recognised as an emerging model system in plant evolutionary ecology (Palma-Silva *et al.* 2016). The preliminary analysis of leaf anatomy and its relationship to photosynthetic pathways presented here, despite the limitations imposed by the availability of plant material, identifies clear relationships between leaf anatomy and CAM capability among the bromeliads. It therefore represents an important first step towards a more complete picture of the structural basis of CAM across the increasingly well-resolved phylogenetic lineages of the Bromeliaceae.

Chlorenchyma cell-succulence

Of fundamental importance to the efficient operation of CAM is the presence of large, highly vacuolate cells for organic acid accumulation during the dark period (Gibson 1982). The bromeliads are no exception, as the data presented here demonstrate. The mean cell diameter for CAM species was 2.8 times higher than the equivalent value for C₃ species, which corresponds to an approximately 22-fold higher volume for roughly spherical cells, which are characteristic of the chlorenchyma of many bromeliad species. This result is consistent with findings from other plant groups, such as those of Borland *et al.* (1998), who showed that the degree of cell-succulence is correlated with the degree of CAM expression in the Neotropical

tree genus *Clusia* (Clusiaceae). In the Portulacineae, multiple lineages show concomitant shifts towards higher cell- and tissue-level succulence and increased CAM activity (e.g. Guralnick and Jackson 2001), and there is similar evidence for groups such as *Senecio* (Asteraceae; Fioretto and Alfani 1988). Likewise, transitions from C_3 to CAM activity in inducible CAM species (e.g. *Peperomia* spp.) often involve an increase in chlorenchyma succulence (Holthe *et al.* 1992). It is important to note that in some exceptional CAM lineages (e.g. *Cissus*, Vitaceae), cell size and tissue thicknesses remain comparatively low (Virzo de Santo *et al.* 1983). This may relate to the drought-deciduousness of such species (Olivares *et al.* 1984).

Cell-succulence may confer additional physiological benefits not directly related to CAM, including the enhancement of hydraulic capacitance without potentially costly investment in non-photosynthetic hydrenchyma. This could partly explain the prevalence of chlorenchyma cell-succulence over hydrenchyma-based water storage in CAM epiphytes inhabiting resource-limited microhabitats, such as the Core Bromelioideae (Benzing 2000; Males 2016). CAM may also be involved in water remobilisation in the chlorenchyma, since malate fluctuations in CAM have occasionally been ascribed putative roles in such processes (Lüttge and Ball 1977; Lüttge and Nobel 1984; Smith *et al.* 1987). This idea could be fruitfully revisited in light of improved modelling approaches and molecular methods.

The developmental and molecular genetic basis of variation in cell size in the bromeliads is currently unknown, but could relate to endoreduplication or vacuolar factors (Mishiba and Mii 2000; Barow 2006; Braun and Winkelmann 2016). Further insights could be sought through genomic and transcriptomic techniques, using the recently-published pineapple (*Ananas comosus* (L.) Merr.) genome as a springboard (Ming *et al.* 2016).

Leaf and tissue thicknesses

The correlations identified here suggest that the presence of larger chlorenchyma cells in CAM bromeliads is an important driver of higher chlorenchyma thickness, which in turn drives higher leaf thickness than is observed in C_3 species. In all-cell succulents, the increased diffusional constraints in thicker leaves may impose greater commitment to CAM, as for instance in the Crassulaceae (Teeri *et al.* 1981). Unexplained variance in the relationships between cell sizes and tissue thicknesses in the bromeliads can be attributed to other anatomical factors known to vary between species, such as the number of cell layers in

the chlorenchyma and the extent of spongy-palisade differentiation (Benzing 2000). By contrast, variation in leaf thickness in C₃ bromeliads appeared to be driven primarily by variation in hydrenchyma thickness. The relationship between variation in hydrenchyma thickness and CAM activity has long been a point of debate. In other plant groups, variation in hydrenchyma anatomy is decoupled from variation in chlorenchyma mesophyll conductance to CO₂, which may be an important determinant of a plant's commitment to CAM (Ripley *et al.* 2013). Meanwhile in atmospheric *Tillandsia* bromeliads, Loeschen *et al.* (1993) demonstrated that respiration in the hydrenchyma tissue is probably not a quantitatively important source of CO₂ for CAM-cycling, and it is known that relative investment in hydrenchyma often shows a high degree of phenotypic plasticity associated with microhabitat acclimation (Males 2016). Further clarification of the adaptive significance of phenotypic plasticity in bromeliad leaf anatomy is highly desirable.

Internal air spaces

The association of CAM in the bromeliads with the reduction of leaf air spaces (quantified either as volumetric internal air space fraction or cross-sectional area of air channels normalised by leaf thickness) is consistent with evidence from other plant groups (Smith and Heuer 1981; Nelson *et al.* 2005; Nelson and Sage 2008). In a study that included 18 phylogenetically-diverse CAM species, Nelson *et al.* (2005) showed that these species showed significantly lower values of internal air space fraction than C₃ and C₄ species. They found that there was only a weak correlation between internal air space fraction and cell size, suggesting that air space reduction in CAM species is not necessarily just a by-product of cell-succulence, but instead might have been selected for to reduce the leakiness of CAM (Nelson and Sage 2008). While this will tend to improve the efficiency of CAM, it simultaneously increases the resistance to CO₂ diffusion from stoma to chloroplast, thereby reducing the efficiency of C₃ photosynthesis (Maxwell *et al.* 1997). Since CO₂ supply is rarely limiting for dark fixation by PEPC (Borland *et al.* 1998), an anatomically-mediated trade-off between C₃ and CAM efficiency may be set up, with a threshold internal air space fraction below which selection will tend to favour tighter cell-packing and further reductions in air spaces to enhance CAM efficiency (Nelson and Sage 2008). How far this hypothesis might go towards explaining the bimodal distribution of $\delta^{13}\text{C}$ values in the bromeliads and other taxa with CAM elements awaits comprehensive assessment.

Sage and Khoshnavesh (2016) recently proposed that the presence of air channels in leaves could provide reservoirs for the accumulation behind closed stomata of respiratory CO₂ which could be refixed by the C₃ pathway to maintain a near-neutral carbon balance. This ‘passive carbon-concentrating mechanism’ (pCCM) paradigm, for which there is some evidence in closely-related Typhaceae (Constable and Longstreth 1994), could theoretically undergo evolutionary modification to use C₄ metabolism, and might therefore be of special relevance to the evolution of CAM in the Bromeliaceae, where CAM-cycling has been widely reported (e.g. Martin and Adams 1987; Griffiths 1988; Fetene and Lüttge 1991; Loeschen *et al.* 1993), and may represent a form of cryptic CAM in species that do not display nocturnal atmospheric CO₂ uptake. Furthermore, bromeliad stomata are highly sensitive to micro-environmental perturbation, leading to extended periods of minimal stomatal conductance during which the ability to utilise respiratory CO₂ could be advantageous (Lange and Medina 1979; Lüttge *et al.* 1986; Males and Griffiths 2017b). Testing of the pCCM model in the bromeliad context should be a priority for future ecophysiological research into these plants. An additional (and not mutually exclusive) hypothesis is that aerenchyma (or other large internal air spaces) may help increase mesophyll conductance to CO₂ during C₃ photosynthesis in bromeliad leaves, similar to the situation in *Oryza* (Xiong *et al.* 2017).

Anatomical character changes associated with origins of strong CAM in the Pitcairnioideae and Tillandsioideae

The structure-function relationships described above were examined more closely in the phylogenetic context of two independent origins of CAM in the Bromeliaceae: at the base of the Xeric Clade in the Pitcairnioideae, and at the base of *Tillandsia* in the Tillandsioideae. The Pitcairnioideae ~~subfamily~~ offers the clearest picture of anatomical specialisation associated with the evolution of CAM. In the C₃ genera *Pitcairnia* and *Fosterella*, which form a grade that is sister to CAM Xeric Clade, leaves are usually relatively mesomorphic. The data presented here show that the origin of CAM at the base of the Xeric Clade was associated with a concerted reorganisation of leaf structure, including a 2.7-fold increase in chlorenchyma cell diameter (corresponding to a near 20-fold increase in volume), an equivalent trebling of chlorenchyma thickness, and a 2.2-fold increase in leaf thickness. While Xeric Clade species did tend to show reduced relative air channel area compared with

433 C_3 species, the occurrence of low relative air channel area in 2/3 *Fosterella* species suggests
434 that this change may have occurred before the divergence of *Fosterella*. Thus in the case of
435 the Pitcairnioideae, the leaf architecture inherited by the ancestor of the Xeric Clade may
436 already have been somewhat favourable to the evolution of CAM, but this potentiality had to
437 be compounded by substantial *de novo* increases in cell-succulence and tissue dimensions for
438 the efficient operation of strong CAM. Since the morphology and anatomy of Xeric Clade
439 Pitcairnioideae is broadly comparable to that of species in the CAM genus *Hechtia* (Males
440 and Griffiths, unpublished), it is plausible that similar leaf anatomical character shifts relative
441 to the C_3 ancestral stock occurred during the evolution of CAM in *Hechtia*.

442 In the Tillandsioideae, all species of non-*Tillandsia* genera are C_3 tank-epiphytes, many of
443 which are relatively mesomorphic and restricted to humid microhabitats. Comparison of the
444 results of the latest and most comprehensive phylogenetic analysis of the Tillandsioideae
445 (Barfuss *et al.* 2016) with available information on photosynthetic pathways (Crayn *et al.*
446 2015) suggests that there was probably one origin of CAM at the base of *Tillandsia*, followed
447 by repeated reversions to C_3 in subgenera *Tillandsia*, *Pseudovriesea* and *Viridantha*, and in
448 the *T. australis* and *T. biflora* complexes. If *T. complanata* is representative of other C_3
449 revertants, then much of anatomical change associated with the initial transition from C_3 to
450 CAM must have repeatedly been reversed, suggesting a high degree of evolutionary lability
451 in foliar anatomy within *Tillandsia*. A secondary gain of CAM function may have occurred in
452 subgenus *Pseudovriesea*, but more detailed physiological information will be required to
453 elucidate the trajectory of photosynthetic evolution in this group. While the anatomical data
454 presented here should be interpreted with some caution since the density of taxonomic
455 sampling is relatively low, they suggest that the origin of CAM at the base of *Tillandsia*
456 involved a dramatic increase in chlorenchyma cell diameter (4.2-fold, corresponding to a 73-
457 fold increase in volume), alongside a reduction in relative air channel area. The possible
458 relationships between anatomical changes and developmental neoteny warrant further
459 investigation (Benzing 2000). As has been remarked by other authors, cell-succulence need
460 not necessarily scale up to morphological succulence (Ogburn and Edwards 2010), and the
461 diminutive growth-forms of some of the xeromorphic CAM *Tillandsia* species, which often
462 occupy highly exposed epiphytic, epilithic and arenicolous microhabitats, provide good
463 examples of this. While chlorenchyma and leaf thicknesses were relatively high in some
464 CAM *Tillandsia* species, this was not universal. Variation in these properties could relate to

differences in other aspects of the ecophysiology of these species, such as moisture harvesting or light relations (Martorell and Ezcurra 2007; Reyes-García *et al.* 2012).

The origins of CAM in the Pitcairnioideae and Tillandsioideae can both be said to have involved a substantial increase in cell-succulence, but the relative importance of increased tissue and leaf thicknesses and reduced air space volume appears to have differed in either case. This highlights how, depending on the phylogenetic background, the evolution of CAM can incorporate the co-option of different existing leaf traits with anatomical innovation. This is somewhat consistent with the results of the study of Heyduk *et al.* (2016) on the evolution of succulent leaf anatomy and CAM in the Agavoideae (Asparagaceae), but perhaps suggests a role for more substantive anatomical change in origins of CAM in the bromeliads. More broadly, these results are consistent with a longstanding and growing corpus of evidence linking increased succulence with increased CAM capacity.

Anatomical correlates of facultative and weak CAM in the Bromeliaceae

While the foregoing discussion has focussed on the anatomical features associated with constitutive strong CAM, this is not the only form of CAM that occurs in the Bromeliaceae. While there is limited evidence for CAM-like metabolite fluctuations in species of C_3 genera in other subfamilies, such as *Fosterella schidosperma* (Pitcairnioideae; Christopher and Holtum 1998), environmentally-inducible facultative CAM and CAM-cycling (evidenced by significant nocturnal organic acid fluctuations in the absence of detectable nocturnal net CO_2 uptake) have been identified primarily in two groups: the non-*Tillandsia* Tillandsioideae and *Puya* (Puyoideae). In the case of the Tillandsioideae, the operation of drought- and high-light-inducible facultative CAM in the C_3 -CAM epiphyte *Guzmania monostachia* has been the subject of extensive physiological investigation (McWilliams 1970; Medina 1974; Medina *et al.* 1977; Maxwell *et al.* 1992, 1994, 1995, 1999). The phylogenetic analysis of Barfuss *et al.* (2016) places *G. monostachia* in a clade (Clade G1) with *G. nicaraguensis*, *G. melinonis*, *G. angustifolia*, *G. fusispica*, and *G. sanguinea* that is sister to the rest of the genus (Clade G2). Although the branch leading to *G. monostachia* is rather long, raising the possibility that CAM capability has arisen in this species during a relatively long period of genetic isolation, more intensive assays for CAM-like physiology in other species of Clades G1 should be undertaken. Additional species in Clade G2 should also be assayed for CAM under different environmental conditions and at different developmental stages, since Beltrán

et al. (2013) demonstrated that drought-stressed juvenile plants of *G. lingulata* are able to perform low-level CAM-cycling, with the effect of reducing respiratory carbon loss. More recently, Carvalho *et al.* (2017) have demonstrated the importance of CAM for the prevention of oxidative stress in juvenile plants of *G. monostachia*, underpinned by the more succulent mesophyll of juveniles relative to mature plants. Increased within-leaf morphoanatomical heterogeneity in mature leaves of this species is meanwhile associated with complex spatial patterns of CAM activity and inducibility (Freschi *et al.* 2010; Rodrigues *et al.* 2016).

Examining the links between leaf anatomy and facultative CAM in *Chusia* (Clusiaceae), Zambrano *et al.* (2014) found that facultative CAM species could be distinguished from C₃ species by their large palisade mesophyll cells. When *G. monostachia* is compared with other *Guzmania* species in the dataset presented here, no such differential in cell size is apparent, and the only anatomical trait showing possible evidence of specialisation in association with the species' unique physiological capability is relative air channel area. However, this comparison is based on measurements made on well-watered plants in the C₃ mode. Previous work has demonstrated that acclimation by *G. monostachia* to seasonal exposure in deciduous tropical forests involves anatomical reorganisation including a halving of internal air space fraction and an increase in leaf thickness and cell-succulence (Maxwell 1992). Instead of the fixed anatomical adaptation that occurs in constitutive CAM species, this facultative CAM species therefore utilises enhanced acclimatory capability to provide the appropriate anatomical setting for CAM as that pathway is induced. Physiological phenomena such as the translocation of water from hydrenchyma in leaf bases to CAM-performing apical leaf regions further increase the flexibility of *G. monostachia* in fluctuating environments (Freschi *et al.* 2010).

Two Tillandsioideae species shown by Pierce *et al.* (2002a) to accumulate significant quantities of organic acid overnight and therefore perhaps using weak CAM were identified by these authors as '*Vriesea barclayana*' and '*V. ospinae*'. The former species is now recognised as *Tillandsia barclayana* in the subgenus *Pseudovriesea* (Grant 1993; Barfuss *et al.* 2016). Similarly, '*V. cereicola*', for which CAM-like $\delta^{13}\text{C}$ values were recorded in the table published by Martin (1994), has now been reclassified as *T. cereicola* in subgenus *Pseudovriesea* (Grant 1993; Horres *et al.* 2000; Barfuss *et al.* 2016), and the same is true for '*V. hitchcockiana*', now accepted as *T. hitchcockiana* in subgenus *Pseudovriesea* (Grant 1993). Meanwhile '*V. ospinae*' was transferred by Barfuss *et al.* (2016) to the new genus *Goudaea* as *G. ospinae*. *Goudaea* is placed in Cypuropsidinae (Vrieseae), as sister to a clade

comprising the new genera *Zizkaea* and *Josemania*, and a complex that includes *Mezobromelia* and a fourth new genus, *Cipuroopsis*. Another species in a genus placed by Barfuss *et al.* (2016) in the Cipuropsidinae for which significant nocturnal acid accumulation has been reported is *Werauhia sanguinolenta* (Pierce *et al.* 2002a). The improved phylogenetic resolution provided by recent analyses therefore suggests that while CAM-like organic acid fluctuations are largely confined in the Tillandsioideae to *Tillandsia* species, they do occur in at least three other groups in the Core Tillandsioideae: the genera *Werauhia* and *Goudaea* in the Cipuropsidinae (Vrieseae) and the genus *Guzmania* in the non-core Tillandsieae (Tillandsieae). This broad phylogenetic footprint of weak CAM raises the question of whether it has arisen independently in each of these lineages, or is present but unrecognised across the Core Tillandsioideae and perhaps beyond. Low-level organic acid fluctuations certainly occur in other C₃ bromeliads, including non-core Tillandsioideae (Medina 1974; Pierce *et al.* 2002a). This question can only be answered through more taxonomically extensive and methodologically intensive physiological screening, guided by the latest phylogenetic framework.

A second group of bromeliads that is of great interest for exploring complex patterns in CAM evolution is the genus *Puya* (Puyoideae). This terrestrial genus includes approximately 225 species (Butcher and Gouda 2016), which are distributed across the Andes and central Chile, and many of which show $\delta^{13}\text{C}$ values consistent with CAM or C₃-CAM physiology (Crayn *et al.* 2004, 2015). Herrera *et al.* (2010) demonstrated the ability of *P. floccosa* to induce increased weak CAM activity in response to drought, while Quezada *et al.* (2014) showed that the proportional contribution of CAM to carbon balance in populations of *P. chilensis* varied in line with latitude and climate. Phylogenetic analyses of *Puya* suggest that there are two major CAM lineages within the genus (Jabaily and Sytsma 2010, 2013), although it is unclear whether cryptic CAM capability was inherited from a shared common ancestor with the Bromelioideae or CAM arose *de novo* on multiple occasions within *Puya*. In this connection, a key target for improving our understanding of CAM evolution in the Bromeliaceae will be the definitive resolution of the phylogenetic relationships among the early-diverging genera of the Bromelioideae subfamily. While the vast majority of Bromelioideae are CAM plants (Crayn *et al.* 2015), C₃ photosynthesis is known to occur in *Fascicularia*, *Greigia* and *Ochagavia*, which are sometimes placed with the CAM genus *Deinacanthon* as the earliest-diverging clade in the subfamily (Silvestro *et al.* 2014). However, other trees have placed the CAM genus *Bromelia* in that position (Schulte *et al.*

2009), or have grouped *Bromelia* with the C₃ genera (Givnish *et al.* 2011, 2014), or have been unable to resolve the topology (Horres *et al.* 2007; Escobedo-Sarti *et al.* 2013; Evans *et al.* 2015). Resolving relationships in this problematic phylogenetic grade will shed light on photosynthetic evolution in the Bromelioideae, and in *Puya* by extension. Once this has been achieved, investigation of the coordination in the evolution of quantitative leaf anatomical traits and photosynthetic diversity in *Puya* should be performed. *Puya* leaves are generally rather succulent and contain reduced air spaces (Males and Griffiths 2017a), but there is currently a lack of comparable anatomical data for most species.

It has been suggested that selection for weak CAM could occur independently of selection for strong CAM in some scenarios (Silvera *et al.* 2005; Herrera 2009; Silvera *et al.* 2010a; Winter and Holtum 2014; Winter *et al.* 2015), which could explain the apparent compatibility of weak and strong CAM with contrasting leaf architectures in the Bromeliaceae. Whereas weak CAM can apparently occur, at least at low levels, in species with relatively voluminous internal air spaces and modest cell sizes, strong CAM is clearly associated with reduced air spaces and larger cells. However, since there is the possibility that the evolution of strong CAM in *Tillandsia* may have proceeded from an ancestral Core Tillandsioideae stock with weak CAM capability, any statement on the role of leaf anatomy in defining distinctive adaptive peaks for weak and strong CAM would at present be premature.

The relationships between leaf anatomy, CAM efficiency, and dependency on CAM for carbon gain are mediated by a network of trade-offs between diffusional constraints, capacity for respiratory CO₂ capture, total capacity for vacuolar acid accumulation, and tissue leakiness to CO₂ during decarboxylation. Future work on the evolution of CAM in the bromeliads and other plant groups should seek to characterise anatomical thresholds in terms of the minimal level of succulence associated with the transition to the ability to perform flexible low-level CAM and the maximal level of succulence associated with the shift to being 'committed' to strong CAM for routine carbon uptake.

Conclusions

The evolution of CAM in the Bromeliaceae is a complex story, involving multiple independent gains and losses of this flexible physiological syndrome. The relationship between CAM and leaf anatomy in the bromeliads generally follows patterns identified in analyses of more phylogenetically disparate CAM lineages. Increased chlorenchyma cell size

and chlorenchyma thickness and reduced internal air spaces are strongly associated with CAM, although the relative importance of changes in each of these traits for the evolution of efficient CAM physiology varies among different cases of C₃-to-CAM transitions. The relationship between leaf anatomy and weak CAM is currently less well-defined, and integrated research on the ecophysiology, molecular physiology and anatomy of relevant lineages is needed to provide clarification in this area. Particular attention should be given to the possibility of passive CO₂ concentration as an intermediate phenotype linking functional leaf anatomy with photosynthetic innovation.

Acknowledgements

JM received funding from Natural Environment Research Council award 1359020, and received a Bromeliad Society International Harry Luther Scholarship to perform research at MSBG. The assistance of Bruce Holst (MSBG), Marcelo Sellaro (RBG Kew), and Pete Brownless (RBG Edinburgh) in sourcing plant material is gratefully acknowledged.

Conflict of interest statement

The author declares no conflicts of interest.

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Figure 1. Phylogenetic distribution of CAM across major lineages of the Bromeliaceae (not all genera shown). Phylogeny based on Givnish *et al.* (2014) and Silvestro *et al.* (2014); photosynthetic pathway assignment based on Crayn *et al.* (2015). Closed stars indicate instances of Winter-Holtum Zone $\delta^{13}\text{C}$ values in predominantly C_3 genera; open stars indicate instances of C_3 -like $\delta^{13}\text{C}$ values in predominantly CAM genera.

Figure 2. Phylogeny of Pitcairnioideae reported by Schütz *et al.* (2016). Photosynthetic pathway assignment based on Crayn *et al.* (2015). Light grey lines = C₃ lineages; black lines = CAM lineages. Black stars = WHZ $\delta^{13}\text{C}$ values in C₃ lineages.

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890 Figure 3. Phylogeny of Tillandsioideae reported by Barfuss *et al.* (2016), using new taxonomic designations
 891 proposed therein. Photosynthetic pathway assignment based on Crayn *et al.* (2015). Light grey lines = C₃
 892 lineages; dark grey lines = C₃-CAM lineages; black lines = CAM lineages. Black stars = WHZ δ¹³C values in C₃
 893 lineages; white stars = C₃-like δ¹³C values in CAM lineages.

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Figure 4. Relationships between log-transformed values of leaf anatomical parameters in C_3 , C_3 -CAM and CAM bromeliads: (A) chlorenchyma cell diameter vs. chlorenchyma thickness ($n = 163$); (B) chlorenchyma cell diameter vs. leaf thickness ($n = 163$); (C) leaf thickness vs. chlorenchyma thickness ($n = 163$); (D) leaf thickness vs. hydrenchmya thickness ($n = 163$); (E) chlorenchyma cell diameter vs. internal air space fraction ($n = 42$); (F) chlorenchyma cell diameter vs. air channel area normalised by leaf thickness ($n = 154$). Solid lines show linear regressions for statistically significant correlations; in (C) and (D) solid lines show regressions for C_3 species and dashed lines show regressions for CAM species.

Figure 5. Biplot of PC1-PC2 morphospace resulting from principal components analysis of anatomical data for 153 bromeliad species. Trait loadings: AC = absolute air channel area; Ch = chlorenchyma thickness; d = chlorenchyma cell diameter; LT = leaf thickness. Convex hulls are displayed covering species loadings grouped by subfamily and photosynthetic pathway. Red and green arrows indicate approximate evolutionary trajectories across the PC1-PC2 morphospace associated with the C_3 to CAM transition in the Pitcairnioideae and Tillandsioideae respectively.

Figure 6. Phylogenetic distribution of leaf anatomical trait values for selected Pitcairnioideae. (A) Chlorenchyma cell diameter (μm); (B) leaf thickness (μm); (C) chlorenchyma thickness (μm); (D) aerenchyma area (μm^2) normalised by leaf thickness. Phylogenetic relationships based on Wagner *et al.* (2013), Krapp *et al.* (2014), Schütz *et al.* (2016), and Pinangé *et al.* (2017). Black stars indicate CAM species; black edges indicate absence of data for terminal taxa.

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Figure 7. Phylogenetic distribution of leaf anatomical trait values for selected Tillandsioideae. (A) Chlorenchyma cell diameter (μm); (B) leaf thickness (μm); (C) chlorenchyma thickness (μm); (D) aerenchyma area (μm²) normalised by leaf thickness. Phylogenetic relationships based on Barfuss *et al.* (2016). Black stars indicate CAM species; black edges indicate absence of data for terminal taxa.

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	<i>d</i> (μm)	LT (μm)	H (μm)	C (μm)	C: H	IAS (%)	A (μm)
C ₃ Bromelioideae (<i>n</i> = 5)	34.46 ± 4.64	1865.23 ± 160.09	1178.70 ± 147.54	686.53 ± 25.59	0.62 ± 0.09	5.00 ± 0.00	7153.5 0 ± 7153.50
CAM Bromelioideae (<i>n</i> = 49)	38.31 ± 1.50	1295.22 ± 115.53	399.05 ± 66.34	896.17 ± 79.42	4.47 ± 0.72	6.72 ± 0.20	44097.46 ± 8945.25
C ₃ Pitcairnioideae (<i>n</i> = 9)	11.76 ± 0.66	751.64 ± 103.41	553.27 ± 109.92	198.37 ± 15.72	0.46 ± 0.08	15.81 ± 0.16	12730.56 ± 4568.82
CAM Pitcairnioideae (<i>n</i> = 10)	31.51 ± 3.33	1680.08 ± 282.17	1096.40 ± 214.41	583.68 ± 80.62	0.57 ± 0.08	5.57 ± 0.45	8974.44 ± 1615.95
C ₃ Puyoideae (<i>n</i> = 2)	20.02 ± 0.55	1298.30 ± 97.27	855.08 ± 44.12	443.22 ± 53.15	0.52 ± 0.04	6.02 ± 1.86	0.00 ± 0.00
C ₃ -CAM Puyoideae (<i>n</i> = 1)	18.81	1414.52	924.88	489.64	0.53	5.84	0.00
CAM Puyoideae (<i>n</i> = 1)	18.31	1371.22	912.32	458.90	0.50	4.55	0.00
C ₃ Tillandsioideae (<i>n</i> = 55)	14.87 ± 0.53	553.71 ± 33.47	298.50 ± 18.34	255.21 ± 20.78	0.90 ± 0.06	13.02 ± 0.39	30047 ± 3665.31
C ₃ -CAM Tillandsioideae (<i>n</i> = 1)	17.01	494.12	262.50	231.62	0.88	18.02	11992
CAM Tillandsioideae (<i>n</i> = 29)	62.16 ± 4.87	1144.13 ± 123.67	460.66 ± 64.78	683.47 ± 95.99	1.21 ± 0.11	5.90 ± 0.19	7883.29 ± 2604.14

934

935 Table 1. Summary of mean trait values (± SE).

Table S1. Source of plant material or cross-sectional images for all bromeliad species used in this investigation.

Genus	Species	Reference/Collection
<i>Acanthostachys</i>	<i>strobilacea</i>	Proença and Sajo 2007
<i>Aechmea</i>	<i>alba</i>	Faria et al. 2012
<i>Aechmea</i>	<i>bromeliifolia</i> var <i>albobracteata</i>	Faria et al. 2012
<i>Aechmea</i>	<i>bromeliifolia</i> var <i>bromeliifolia</i>	Faria et al. 2012
<i>Aechmea</i>	<i>capixabae</i>	Aoyama and Sajo 2003
<i>Aechmea</i>	<i>carvalhoi</i>	Faria et al. 2012
<i>Aechmea</i>	<i>castanea</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>conifera</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>corymbosa</i>	Aoyama and Sajo 2003
<i>Aechmea</i>	<i>digitata</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>fasciata</i>	CUBG
<i>Aechmea</i>	<i>glandulosa</i>	Aoyama and Sajo 2003
<i>Aechmea</i>	<i>hostilis</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>lamarchei</i>	Faria et al. 2012
<i>Aechmea</i>	<i>leucolepis</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>maasii</i>	Faria et al. 2012
<i>Aechmea</i>	<i>perforata</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>racinae</i>	Aoyama and Sajo 2003

<i>Aechmea</i>	<i>rodriguesiana</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>rubens</i>	Horres et al. 2007
<i>Aechmea</i>	<i>saxicola</i>	Sousa et al. 2005
<i>Aechmea</i>	<i>triangularis</i>	Faria et al. 2012
<i>Aechmea</i>	<i>victoriana</i> var <i>discolor</i>	Aoyama and Sajo 2003
<i>Aechmea</i>	<i>warasii</i>	Aoyama and Sajo 2003
<i>Aechmea</i>	<i>weberbaueri</i>	Horres et al. 2007
<i>Aechmea</i>	<i>weilbachii</i>	Aoyama and Sajo 2003
<i>Alcantarea</i>	<i>burle-marxii</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>duarteana</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>extensa</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>farneyi</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>geniculata</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>glaziouana</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>nahoumii</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>nigripetala</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>patriae</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>roberto-kautskyi</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>trepida</i>	Versieux et al. 2010
<i>Alcantarea</i>	<i>vinicolor</i>	Versieux et al. 2010
<i>Ananas</i>	<i>comosus</i>	RBGK
<i>Araeococcus</i>	<i>micranthus</i>	Aoyama and Sajo 2003

<i>Araeococcus</i>	<i>parviflorus</i>	Aoyama and Sajo 2003
<i>Billbergia</i>	<i>distachia</i>	Proença and Sajo 2007
<i>Billbergia</i>	<i>euphemiae</i>	Pereira et al. 2011
<i>Billbergia</i>	<i>porteana</i>	Proença and Sajo 2007
<i>Bromelia</i>	<i>antiacantha</i>	Pereira et al. 2011
<i>Bromelia</i>	<i>arenaria</i>	Monteiro et al. 2011
<i>Bromelia</i>	<i>balansae</i>	Proença and Sajo 2007
<i>Bromelia</i>	<i>binotii</i>	Monteiro et al. 2011
<i>Bromelia</i>	<i>goyazensis</i>	Monteiro et al. 2011
<i>Bromelia</i>	<i>humilis</i>	CUBG
<i>Bromelia</i>	<i>morreniana</i>	Monteiro et al. 2011
<i>Bromelia</i>	<i>reversacantha</i>	Monteiro et al. 2011
<i>Bromelia</i>	<i>scarlatina</i>	Monteiro et al. 2011
<i>Catopsis</i>	<i>berteroniana</i>	Palací et al. 2004
<i>Catopsis</i>	<i>floribunda</i>	Palací et al. 2004
<i>Catopsis</i>	<i>juncifolia</i>	Palací et al. 2004
<i>Catopsis</i>	<i>morreniana</i>	Palací et al. 2004
<i>Catopsis</i>	<i>nitida</i>	Palací et al. 2004
<i>Catopsis</i>	<i>paniculata</i>	Palací et al. 2004
<i>Catopsis</i>	<i>sessiliflora</i>	Palací et al. 2004
<i>Cryptanthus</i>	<i>acaulis</i>	CUBG
<i>Cryptanthus</i>	<i>bivittatus</i>	CUBG

<i>Deuterocohnia</i>	<i>brevifolia</i>	CUBG
<i>Deuterocohnia</i>	<i>lorentziana</i>	CUBG
<i>Deuterocohnia</i>	<i>meziana</i>	RBGE
<i>Deuterocohnia</i>	<i>scapigera</i>	Santos-Silva et al. 2013
<i>Dyckia</i>	<i>bracteata</i>	Santos-Silva et al. 2013
<i>Dyckia</i>	<i>choristaminea</i>	RBGE
<i>Dyckia</i>	<i>rariflora</i>	RBGE
<i>Dyckia</i>	<i>remotiflora</i>	CUBG
<i>Dyckia</i>	<i>tuberosa</i>	Proença and Sajo 2007
<i>Encholirium</i>	<i>pedicellatum</i>	Forzza 2005
<i>Fascicularia</i>	<i>bicolor</i>	CUBG
<i>Fosterella</i>	<i>albicans</i>	Horres et al. 2007
<i>Fosterella</i>	<i>chiquitana</i>	Rex et al. 2007
<i>Fosterella</i>	<i>cotacajensis</i>	Rex et al. 2007
<i>Guzmania</i>	<i>claviformis</i>	Medeiros 2015
<i>Guzmania</i>	<i>lingulata</i>	CUBG
<i>Guzmania</i>	<i>monostachia</i>	CUBG
<i>Guzmania</i>	<i>paniculata</i>	Medeiros 2015
<i>Guzmania</i>	<i>retusa</i>	Medeiros 2015
<i>Guzmania</i>	<i>sanguinea</i>	Medeiros 2015
<i>Guzmania</i>	<i>ventricosa</i>	Casañas Suárez and Jáuregui 2011
<i>Guzmania</i>	<i>wittmackii</i>	RBGE

<i>Lutheria</i>	<i>glutinosa</i>	CUBG
<i>Lutheria</i>	<i>splendens</i>	CUBG
<i>Lymania</i>	<i>corallina</i>	Aoyama and Sajo 2003
<i>Lymania</i>	<i>globosa</i>	Aoyama and Sajo 2003
<i>Mezobromelia</i>	<i>capituligera</i>	Medeiros 2015
<i>Mezobromelia</i>	<i>pleiosticha</i>	Gomes-da-Silva et al. 2012
<i>Ochagavia</i>	<i>carnea</i>	CUBG
<i>Ochagavia</i>	<i>elegans</i>	CUBG
<i>Ochagavia</i>	<i>litoralis</i>	RBGE
<i>Pitcairnia</i>	<i>cristalinensis</i>	Santos-Silva et al. 2013
<i>Pitcairnia</i>	<i>encholirioides</i>	Santos-Silva et al. 2013
<i>Pitcairnia</i>	<i>imbricata</i>	CUBG
<i>Pitcairnia</i>	<i>integrifolia</i>	CUBG
<i>Pitcairnia</i>	<i>paniculata</i>	MSBG
<i>Pitcairnia</i>	<i>xanthocalyx</i>	CUBG
<i>Puya</i>	<i>alpestris</i>	CUBG
<i>Puya</i>	<i>chilensis</i>	CUBG
<i>Puya</i>	<i>mirabilis</i>	CUBG
<i>Puya</i>	<i>venusta</i>	CUBG
<i>Quesnelia</i>	<i>arvensis</i>	Mantovani et al. 2012
<i>Quesnelia</i>	<i>edmundoi</i>	Mantovani et al. 2012
<i>Quesnelia</i>	<i>seideliana</i>	Mantovani et al. 2012

<i>Quesnelia</i>	<i>strobilispica</i>	Pereira et al. 2011
<i>Racinaea</i>	<i>aerisincola</i>	Gomes-da-Silva et al. 2012
<i>Racinaea</i>	<i>dyeriana</i>	CUBG
<i>Ronnbergia</i>	<i>neoregelioides</i>	Aoyama and Sajo 2003
<i>Tillandsia</i>	<i>balbisiana</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>bergeri</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>brachycaulos</i>	CUBG
<i>Tillandsia</i>	<i>bulbosa</i>	CUBG
<i>Tillandsia</i>	<i>butzii</i>	CUBG
<i>Tillandsia</i>	<i>caput-medusae</i>	CUBG
<i>Tillandsia</i>	<i>complanata</i>	Leoni 2022
<i>Tillandsia</i>	<i>fasciculata</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>gardneri</i>	Scatena and Segecin 2005
<i>Tillandsia</i>	<i>geminiflora</i>	Scatena and Segecin 2005
<i>Tillandsia</i>	<i>harrisii</i>	MSBG
<i>Tillandsia</i>	<i>ionantha</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>junccea</i>	CUBG
<i>Tillandsia</i>	<i>leiboldiana</i>	CUBG
<i>Tillandsia</i>	<i>linearis</i>	Scatena and Segecin 2005
<i>Tillandsia</i>	<i>lithophila</i>	RBGE
<i>Tillandsia</i>	<i>loliacea</i>	Proença and Sajo 2007
<i>Tillandsia</i>	<i>mallemontii</i>	Scatena and Segecin 2005

<i>Tillandsia</i>	<i>malzinei</i>	Gomes-da-Silva et al. 2012
<i>Tillandsia</i>	<i>paleacea</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>paucifolia</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>pohlana</i>	Proença and Sajo 2007
<i>Tillandsia</i>	<i>polystachia</i>	Gomes-da-Silva et al. 2012
<i>Tillandsia</i>	<i>recurvata</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>schiedeana</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>setacea</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>stricta</i>	Scatena and Segecin 2005
<i>Tillandsia</i>	<i>tenuifolia</i>	Proença and Sajo 2007
<i>Tillandsia</i>	<i>usneoides</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>utriculata</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>valenzuelana</i>	Loeschén et al. 1993
<i>Tillandsia</i>	<i>xerographica</i>	RBGE
<i>Vriesea</i>	<i>arachnoidea</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>biguassuensis</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>bituminosa</i>	Arruda and da Costa 2003
<i>Vriesea</i>	<i>carinata</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>corcovadensis</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>correia-araujoi</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>erythrodactylon</i>	RBGE
<i>Vriesea</i>	<i>fenestralis</i>	CUBG

<i>Vriesea</i>	<i>flammea</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>fosteriana</i>	Arruda and da Costa 2003
<i>Vriesea</i>	<i>gigantea</i>	CUBG
<i>Vriesea</i>	<i>guttata</i>	CUBG
<i>Vriesea</i>	<i>incurvata</i>	RBGE
<i>Vriesea</i>	<i>lubbersii</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>microrachis</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>neoglutinosa</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>poenulata</i>	Gomes-da-Silva et al. 2012
<i>Vriesea</i>	<i>rubens</i>	Gomes-da-Silva et al. 2012
<i>Werauhia</i>	<i>sanguinolenta</i>	CUBG
<i>Werauhia</i>	<i>viridiflora</i>	RBGE
<i>Wittrockia</i>	<i>gigantea</i>	Pereira et al. 2011

Table S2. Mean anatomical parameters for all bromeliad species used in this investigation. NA = data not applicable or not measured.

Genus	Species	Subfamily	Photosynthetic pathway	<i>d</i> (μm)	LT (μm)	H (μm)	C (μm)	C: H	IAS (%)	A (μm)
<i>Acanthostachys</i>	<i>strobilacea</i>	Bromelioideae	CAM	28.77 ± 0.44	3079.47 ± 24.21	2248.75 ± 18.15	830.72 ± 4.05	0.37	NA	14082 ± 11.30
<i>Aechmea</i>	<i>alba</i>	Bromelioideae	CAM	34.69 ± 0.21	812.65 ± 7.24	65.62 ± 0.54	747.03 ± 2.66	11.38	NA	13110 ± 11.09

<i>Aechmea</i>	<i>bromeliifolia</i> var <i>albobracteata</i>	Bromelioideae	CAM	47.89 ± 0.35	2370.44 ± 18.99	597.95 ± 3.21	1772.49 ± 11.09	2.96	NA	92331 ± 52.06
<i>Aechmea</i>	<i>bromeliifolia</i> var <i>bromeliifolia</i>	Bromelioideae	CAM	50.20 ± 0.72	1437.42 ± 13.96	145.75 ± 0.92	1291.67 ± 10.43	8.86	NA	68975 ± 42.31
<i>Aechmea</i>	<i>capixabae</i>	Bromelioideae	CAM	37.79 ± 0.22	867.96 ± 5.20	514.35 ± 3.01	353.61 ± 2.88	0.69	NA	7243 ± 12.04
<i>Aechmea</i>	<i>carvalhoi</i>	Bromelioideae	CAM	21.39 ± 0.28	387.41 ± 3.89	153.82 ± 1.17	233.59 ± 1.78	1.52	NA	6461 ± 10.01
<i>Aechmea</i>	<i>castanea</i>	Bromelioideae	CAM	39.69 ± 0.40	1850.56 ± 14.41	264.37 ± 1.85	1586.19 ± 12.04	6.00	NA	115935 ± 66.91
<i>Aechmea</i>	<i>conifera</i>	Bromelioideae	CAM	50.21 ± 0.33	1537.57 ± 12.02	NA	1537.57 ± 10.65	NA	NA	67041 ± 52.33
<i>Aechmea</i>	<i>corymbosa</i>	Bromelioideae	CAM	61.00 ± 0.37	838.21 ± 5.06	NA	838.21 ± 4.50	NA	NA	NA
<i>Aechmea</i>	<i>digitata</i>	Bromelioideae	CAM	52.21 ± 0.25	3657.24 ± 33.53	1138.88 ± 9.85	2518.36 ± 19.91	2.21	NA	351516 ± 94.09
<i>Aechmea</i>	<i>fasciata</i>	Bromelioideae	CAM	41.10 ± 0.26	584.08 ± 4.87	215.74 ± 1.04	368.34 ± 3.04	1.71	9.01 ± 0.22	6542 ± 9.76
<i>Aechmea</i>	<i>glandulosa</i>	Bromelioideae	CAM	35.45 ± 0.11	684.49 ± 6.76	187.68 ± 1.31	496.81 ± 2.89	2.65	NA	13118 ± 15.50
<i>Aechmea</i>	<i>hostilis</i>	Bromelioideae	CAM	34.70 ± 0.14	1492.36 ± 12.66	173.11 ± 1.56	1319.25 ± 10.31	7.62	NA	NA
<i>Aechmea</i>	<i>lamarchei</i>	Bromelioideae	CAM	38.01 ± 0.19	921.07 ± 3.12	112.46 ± 0.87	808.61 ± 5.41	7.19	NA	48800 ± 26.76
<i>Aechmea</i>	<i>leucolepis</i>	Bromelioideae	CAM	28.97 ± 0.24	1835.98 ± 14.57	396.83 ± 2.66	1439.15 ± 11.30	3.63	NA	177634 ± 72.44

<i>Aechmea</i>	<i>maasii</i>	Bromelioideae	CAM	34.56 ± 0.21	1190.43 ± 10.10	59.52 ± 0.26	1130.91 ± 10.19	19.00	NA	40354 ± 53.01
<i>Aechmea</i>	<i>perforata</i>	Bromelioideae	CAM	45.86 ± 0.20	2270.34 ± 18.83	328.88 ± 3.04	1941.46 ± 14.47	5.90	NA	NA
<i>Aechmea</i>	<i>racinae</i>	Bromelioideae	CAM	34.70 ± 0.29	317.54 ± 2.55	NA	317.54 ± 2.87	NA	NA	2008 ± 12.08
<i>Aechmea</i>	<i>rodriguesiana</i>	Bromelioideae	CAM	62.90 ± 0.41	2112.00 ± 17.80	143.00 ± 1.22	1969.00 ± 14.32	13.77	NA	96736 ± 56.79
<i>Aechmea</i>	<i>rubens</i>	Bromelioideae	CAM	60.79 ± 0.45	1527.64 ± 12.02	215.16 ± 2.07	1312.48 ± 10.10	6.10	NA	109072 ± 43.09
<i>Aechmea</i>	<i>saxicola</i>	Bromelioideae	CAM	51.23 ± 0.50	1855.14 ± 16.03	265.81 ± 2.18	1589.33 ± 14.43	5.98	NA	NA
<i>Aechmea</i>	<i>triangularis</i>	Bromelioideae	CAM	42.37 ± 0.36	1523.39 ± 13.33	129.44 ± 0.99	1393.95 ± 12.76	10.77	NA	54528 ± 40.02
<i>Aechmea</i>	<i>victoriana var discolor</i>	Bromelioideae	CAM	45.56 ± 0.35	772.27 ± 4.04	423.16 ± 3.35	349.11 ± 3.24	0.83	NA	14028 ± 33.99
<i>Aechmea</i>	<i>warasii</i>	Bromelioideae	CAM	48.59 ± 0.48	1394.47 ± 10.06	728.69 ± 6.14	665.78 ± 5.50	0.91	NA	19598 ± 56.65
<i>Aechmea</i>	<i>weberbaueri</i>	Bromelioideae	CAM	23.42 ± 0.20	774.86 ± 4.25	297.21 ± 1.00	477.65 ± 3.87	1.61	NA	21121 ± 34.40
<i>Aechmea</i>	<i>weilbachii</i>	Bromelioideae	CAM	40.88 ± 0.21	553.78 ± 5.61	86.87 ± 0.65	466.91 ± 3.91	5.38	NA	25546 ± 39.95
<i>Alcantarea</i>	<i>burle-marxii</i>	Tillandsioideae	C3	10.87 ± 0.11	680.63 ± 3.08	183.03 ± 1.03	497.60 ± 3.22	2.72	NA	40178 ± 33.42
<i>Alcantarea</i>	<i>duarteana</i>	Tillandsioideae	C3	14.24 ± 0.09	1413.77 ± 11.19	959.34 ± 6.66	454.43 ± 3.08	0.47	NA	70183 ± 55.90
<i>Alcantarea</i>	<i>extensa</i>	Tillandsioideae	C3	11.79 ±	988.17 ±	323.99 ±	664.18 ± 4.50	2.05	NA	95933 ± 62.03

				0.11	6.76	1.04				
<i>Alcantarea</i>	<i>farneyi</i>	Tillandsioideae	C3	11.45 ± 0.04	892.84 ± 4.82	484.68 ± 3.85	408.16 ± 3.90	0.84	NA	42551 ± 41.45
<i>Alcantarea</i>	<i>geniculata</i>	Tillandsioideae	C3	10.75 ± 0.06	841.77 ± 4.45	500.89 ± 3.90	340.88 ± 3.21	0.68	NA	41989 ± 49.03
<i>Alcantarea</i>	<i>glaziouana</i>	Tillandsioideae	C3	12.51 ± 0.10	718.71 ± 3.87	315.80 ± 2.76	402.91 ± 2.86	1.28	NA	38102 ± 28.76
<i>Alcantarea</i>	<i>nahoumii</i>	Tillandsioideae	C3	12.50 ± 0.08	984.80 ± 9.09	372.63 ± 2.34	612.17 ± 5.16	1.64	NA	79244 ± 30.05
<i>Alcantarea</i>	<i>nigripetala</i>	Tillandsioideae	C3	10.10 ± 0.09	762.77 ± 4.32	392.94 ± 2.41	369.83 ± 3.21	0.94	NA	30890 ± 50.20
<i>Alcantarea</i>	<i>patriae</i>	Tillandsioideae	C3	10.77 ± 0.03	1041.59 ± 9.98	440.26 ± 3.66	601.33 ± 5.11	1.37	NA	70301 ± 64.43
<i>Alcantarea</i>	<i>roberto-kautskyi</i>	Tillandsioideae	C3	10.24 ± 0.05	802.47 ± 4.41	388.29 ± 3.75	414.18 ± 2.98	1.07	NA	73300 ± 32.09
<i>Alcantarea</i>	<i>trepida</i>	Tillandsioideae	C3	11.86 ± 0.06	928.04 ± 3.05	377.33 ± 2.98	550.71 ± 4.07	1.46	NA	79293 ± 48.18
<i>Alcantarea</i>	<i>vinicolor</i>	Tillandsioideae	C3	12.45 ± 0.07	1168.22 ± 10.22	527.25 ± 4.04	640.97 ± 5.55	1.22	NA	113390 ± 90.54
<i>Ananas</i>	<i>comosus</i>	Bromelioideae	CAM	32.78 ± 0.18	1518.88 ± 9.98	576.13 ± 4.12	942.75 ± 5.41	1.64	6.21 ± 0.11	37870 ± 40.32
<i>Araeococcus</i>	<i>micranthus</i>	Bromelioideae	CAM	39.77 ± 0.24	2648.59 ± 18.81	1726.65 ± 10.05	921.94 ± 3.99	0.53	NA	18897 ± 12.19
<i>Araeococcus</i>	<i>parviflorus</i>	Bromelioideae	CAM	24.99 ± 0.20	418.11 ± 2.00	227.23 ± 1.88	190.88 ± 1.30	0.84	NA	3665 ± 8.85
<i>Billbergia</i>	<i>distachia</i>	Bromelioideae	CAM	35.39 ±	738.02 ±	339.81 ±	398.21 ± 2.25	1.17	NA	12260 ± 14.47

				0.29	5.44	2.45				
<i>Billbergia</i>	<i>euphemiae</i>	Bromelioideae	C3	48.26 ± 0.36	1400.03 ± 12.11	738.76 ± 2.31	661.27 ± 3.64	0.90	NA	28614 ± 22.25
<i>Billbergia</i>	<i>porteana</i>	Bromelioideae	CAM	47.42 ± 0.40	2003.37 ± 18.10	928.65 ± 5.07	1074.72 ± 8.08	1.16	NA	NA
<i>Bromelia</i>	<i>antiacantha</i>	Bromelioideae	CAM	33.94 ± 0.41	1022.02 ± 9.76	189.65 ± 1.09	832.37 ± 6.67	4.39	NA	63308 ± 42.45
<i>Bromelia</i>	<i>arenaria</i>	Bromelioideae	CAM	35.75 ± 0.32	3100.69 ± 28.84	1537.32 ± 11.34	1563.37 ± 10.11	1.02	NA	80195 ± 61.00
<i>Bromelia</i>	<i>balansae</i>	Bromelioideae	CAM	48.50 ± 0.33	1492.81 ± 12.21	367.79 ± 2.67	1125.02 ± 8.99	3.06	NA	29939 ± 23.54
<i>Bromelia</i>	<i>binotii</i>	Bromelioideae	CAM	20.82 ± 0.38	1046.90 ± 8.66	214.96 ± 1.89	831.94 ± 4.41	3.87	NA	73535 ± 49.05
<i>Bromelia</i>	<i>goyazensis</i>	Bromelioideae	CAM	44.60 ± 0.40	2701.73 ± 24.51	1149.32 ± 10.05	1552.41 ± 10.16	1.35	NA	46927 ± 23.39
<i>Bromelia</i>	<i>humilis</i>	Bromelioideae	CAM	35.61 ± 0.32	1871.93 ± 14.07	843.21 ± 5.66	1028.72 ± 9.75	1.22	6.44 ± 0.10	55667 ± 44.67
<i>Bromelia</i>	<i>morreniana</i>	Bromelioideae	CAM	31.35 ± 0.33	456.26 ± 3.31	76.04 ± 0.43	380.22 ± 2.14	5.00	NA	16598 ± 29.08
<i>Bromelia</i>	<i>reversacantha</i>	Bromelioideae	CAM	18.37 ± 0.06	1017.73 ± 9.76	162.40 ± 1.13	855.33 ± 4.47	5.27	NA	15522 ± 14.98
<i>Bromelia</i>	<i>scarlatina</i>	Bromelioideae	CAM	34.15 ± 0.25	610.10 ± 5.20	260.19 ± 1.49	349.91 ± 2.09	1.34	NA	33933 ± 38.56
<i>Catopsis</i>	<i>berteroniana</i>	Tillandsioideae	C3	11.85 ± 0.06	571.83 ± 4.87	408.45 ± 3.00	163.38 ± 1.33	0.40	12.39 ± 0.15	16354 ± 27.77

<i>Catopsis</i>	<i>floribunda</i>	Tillandsioideae	C3	11.77 ± 0.10	506.86 ± 4.46	374.64 ± 2.65	132.22 ± 1.04	0.35	15	5287 ± 9.09
<i>Catopsis</i>	<i>juncifolia</i>	Tillandsioideae	C3	12.09 ± 0.08	586.72 ± 4.30	476.02 ± 3.80	110.70 ± 0.98	0.23	NA	NA
<i>Catopsis</i>	<i>morreniana</i>	Tillandsioideae	C3	11.95 ± 0.11	316.12 ± 3.04	189.67 ± 0.95	126.45 ± 1.03	0.67	14.2 2 ± 0.17	6818 ± 10.13
<i>Catopsis</i>	<i>nitida</i>	Tillandsioideae	C3	11.78 ± 0.04	259.04 ± 2.15	188.39 ± 1.14	70.65 ± 0.54	0.38	NA	NA
<i>Catopsis</i>	<i>paniculata</i>	Tillandsioideae	C3	18.95 ± 0.05	575.14 ± 4.95	226.57 ± 2.21	348.57 ± 2.77	1.54	NA	21011 ± 25.04
<i>Catopsis</i>	<i>sessiliflora</i>	Tillandsioideae	C3	10.08 ± 0.06	450.10 ± 3.87	310.78 ± 2.46	139.32 ± 1.20	0.45	NA	NA
<i>Cryptanthus</i>	<i>acaulis</i>	Bromelioideae	CAM	36.61 ± 0.24	422.11 ± 3.42	251.26 ± 2.09	170.85 ± 1.55	0.68	6.83 ± 0.11	12010 ± 14.45
<i>Cryptanthus</i>	<i>bivittatus</i>	Bromelioideae	CAM	33.17 ± 0.27	392.42 ± 2.07	237.83 ± 1.90	154.59 ± 1.40	0.65	6.01 ± 0.06	11225 ± 26.98
<i>Deuterocohnia</i>	<i>brevifolia</i>	Pitcairnioideae	CAM	29.33 ± 0.30	1444.16 ± 13.75	948.19 ± 4.63	495.97 ± 3.94	0.52	7.18 ± 0.05	12122 ± 24.55
<i>Deuterocohnia</i>	<i>lorentziana</i>	Pitcairnioideae	CAM	35.16 ± 0.28	1612.05 ± 12.01	1083.46 ± 8.91	528.59 ± 4.28	0.49	5.11 ± 0.12	13087 ± 19.05
<i>Deuterocohnia</i>	<i>meziana</i>	Pitcairnioideae	CAM	32.19 ± 0.30	1503.71 ± 10.09	981.92 ± 9.02	521.79 ± 3.90	0.53	NA	15430 ± 31.37
<i>Deuterocohnia</i>	<i>scapigera</i>	Pitcairnioideae	CAM	17.38 ±	695.80 ±	598.14 ±	97.66 ± 0.43	0.16	NA	NA

				0.14	3.74	3.58				
<i>Dyckia</i>	<i>bracteata</i>	Pitcairnioideae	CAM	22.42 ± 0.19	1189.46 ± 8.56	624.47 ± 4.01	564.99 ± 2.38	0.90	NA	11585 ± 26.43
<i>Dyckia</i>	<i>choristaminea</i>	Pitcairnioideae	CAM	26.01 ± 0.14	1665.25 ± 10.01	1080.86 ± 8.76	584.39 ± 4.19	0.54	NA	2701 ± 8.08
<i>Dyckia</i>	<i>rariflora</i>	Pitcairnioideae	CAM	31.84 ± 0.24	1597.18 ± 13.71	1009.60 ± 7.88	587.58 ± 4.40	0.58	NA	9760 ± 21.08
<i>Dyckia</i>	<i>remotiflora</i>	Pitcairnioideae	CAM	24.78 ± 0.22	1438.22 ± 9.70	892.69 ± 4.51	545.53 ± 4.48	0.61	4.43 ± 0.14	5661 ± 11.19
<i>Dyckia</i>	<i>tuberosa</i>	Pitcairnioideae	CAM	54.25 ± 0.39	1569.20 ± 10.22	781.96 ± 3.25	787.24 ± 3.20	1.01	NA	10424 ± 30.02
<i>Encholirium</i>	<i>pedicellatum</i>	Pitcairnioideae	CAM	41.73 ± 0.34	4085.72 ± 23.64	2962.68 ± 19.20	1123.04 ± 9.05	0.38	NA	NA
<i>Fascicularia</i>	<i>bicolor</i>	Bromelioideae	C3	30.22 ± 0.31	2240.13 ± 10.01	1909.62 ± 14.54	330.51 ± 2.88	0.17	5.91 ± 0.12	NA
<i>Fosterella</i>	<i>albicans</i>	Pitcairnioideae	C3	13.01 ± 0.10	553.71 ± 4.21	416.99 ± 3.22	136.72 ± 1.04	0.33	NA	1888 ± 8.05
<i>Fosterella</i>	<i>chiquitana</i>	Pitcairnioideae	C3	15.58 ± 0.17	1175.77 ± 9.95	1017.49 ± 8.80	158.28 ± 1.26	0.16	NA	47007 ± 48.71
<i>Fosterella</i>	<i>cotacajensis</i>	Pitcairnioideae	C3	11.41 ± 0.05	1385.37 ± 12.01	1222.39 ± 10.41	162.98 ± 1.70	0.13	NA	1645 ± 6.55
<i>Guzmania</i>	<i>claviformis</i>	Tillandsioideae	C3	20.71 ± 0.18	630.42 ± 3.88	259.58 ± 2.09	370.84 ± 2.95	1.43	NA	39011 ± 32.08
<i>Guzmania</i>	<i>lingulata</i>	Tillandsioideae	C3	17.08 ± 0.14	480.82 ± 2.35	279.19 ± 1.54	201.63 ± 1.80	0.72	19.42 ±	27234 ± 55.21

									1.06		
<i>Guzmania</i>	<i>monostachia</i>	Tillandsioideae	C3-CAM	17.01 ± 0.09	494.12 ± 2.65	262.50 ± 2.30	231.62 ± 1.94	0.88	18.02 ± 0.94	11992 ± 20.10	
<i>Guzmania</i>	<i>paniculata</i>	Tillandsioideae	C3	19.71 ± 0.13	616.69 ± 3.09	376.51 ± 3.33	240.18 ± 2.37	0.64	NA	20853 ± 31.38	
<i>Guzmania</i>	<i>retusa</i>	Tillandsioideae	C3	11.10 ± 0.04	365.33 ± 3.10	162.37 ± 0.87	202.96 ± 1.88	1.25	NA	40152 ± 38.90	
<i>Guzmania</i>	<i>sanguinea</i>	Tillandsioideae	C3	19.38 ± 0.14	591.67 ± 3.45	318.16 ± 1.43	273.51 ± 2.35	0.86	NA	42103 ± 41.22	
<i>Guzmania</i>	<i>ventricosa</i>	Tillandsioideae	C3	11.20 ± 0.10	365.50 ± 2.78	173.76 ± 1.49	191.74 ± 1.02	1.10	NA	13434 ± 30.20	
<i>Guzmania</i>	<i>wittmackii</i>	Tillandsioideae	C3	14.11 ± 0.07	300.55 ± 2.91	153.22 ± 1.01	147.33 ± 1.56	0.96	NA	9785 ± 8.70	
<i>Lutheria</i>	<i>glutinosa</i>	Tillandsioideae	C3	16.22 ± 0.13	461.08 ± 3.06	295.56 ± 2.24	165.52 ± 1.09	0.56	12.12 ± 0.71	12122 ± 27.15	
<i>Lutheria</i>	<i>splendens</i>	Tillandsioideae	C3	15.04 ± 0.12	440.62 ± 3.41	277.36 ± 2.54	163.26 ± 1.32	0.59	8.29 ± 0.13	10815 ± 22.04	
<i>Lymania</i>	<i>corallina</i>	Bromelioideae	CAM	31.03 ± 0.30	434.26 ± 3.87	133.62 ± 1.07	300.64 ± 2.87	2.25	NA	NA	
<i>Lymania</i>	<i>globosa</i>	Bromelioideae	CAM	45.01 ± 0.32	724.93 ± 2.09	258.45 ± 2.26	466.48 ± 2.34	1.80	NA	15339 ± 31.40	
<i>Mezobromelia</i>	<i>capituligera</i>	Tillandsioideae	C3	11.56 ± 0.02	384.43 ± 1.90	180.20 ± 1.08	204.23 ± 2.00	1.13	NA	34141 ± 49.94	
<i>Mezobromelia</i>	<i>pleiosticha</i>	Tillandsioideae	C3	19.49 ±	708.03 ±	333.19 ±	374.84 ± 2.08	1.13	NA	38852 ± 42.80	

				0.13	5.61	3.17				
<i>Ochagavia</i>	<i>carnea</i>	Bromelioideae	C3	31.03 ± 0.12	2124.06 ± 18.76	1370.36 ± 11.19	753.70 ± 4.34	0.55	NA	NA
<i>Ochagavia</i>	<i>elegans</i>	Bromelioideae	C3	28.16 ± 0.22	1930.66 ± 14.39	1295.33 ± 10.54	635.33 ± 3.28	0.49	5.00 ± 0.06	NA
<i>Ochagavia</i>	<i>litoralis</i>	Bromelioideae	C3	30.39 ± 0.31	2006.16 ± 17.71	1310.36 ± 12.22	695.80 ± 5.04	0.53	NA	NA
<i>Pitcairnia</i>	<i>crystalinensis</i>	Pitcairnioideae	C3	12.90 ± 0.08	728.13 ± 4.56	441.29 ± 2.33	286.84 ± 2.22	0.65	NA	6472 ± 4.55
<i>Pitcairnia</i>	<i>encholirioides</i>	Pitcairnioideae	C3	12.38 ± 0.07	553.44 ± 3.27	307.47 ± 1.09	245.97 ± 2.18	0.80	NA	6682 ± 5.09
<i>Pitcairnia</i>	<i>imbricata</i>	Pitcairnioideae	C3	10.87 ± 0.05	612.31 ± 3.19	436.31 ± 2.22	176.00 ± 1.19	0.40	15.3 ± 1.00	13371 ± 18.74
<i>Pitcairnia</i>	<i>integrifolia</i>	Pitcairnioideae	C3	11.12 ± 0.05	644.92 ± 4.78	449.94 ± 3.08	194.98 ± 1.53	0.43	16.3 ± 0.87	15043 ± 22.90
<i>Pitcairnia</i>	<i>paniculata</i>	Pitcairnioideae	C3	9.25 ± 0.02	525.98 ± 2.98	304.98 ± 2.10	221.00 ± 1.98	0.72	NA	10334 ± 25.16
<i>Pitcairnia</i>	<i>xanthocalyx</i>	Pitcairnioideae	C3	9.30 ± 0.04	585.17 ± 3.76	382.61 ± 3.08	202.56 ± 1.74	0.53	15.8 ± 1.03	12133 ± 14.45
<i>Puya</i>	<i>alpestris</i>	Puyoideae	C3	19.47 ± 0.13	1395.56 ± 11.10	899.20 ± 5.52	496.36 ± 3.42	0.55	4.16 ± 0.09	NA
<i>Puya</i>	<i>chilensis</i>	Puyoideae	C3-CAM	18.81 ± 0.14	1414.52 ± 12.04	924.88 ± 2.78	489.64 ± 4.04	0.53	5.84 ±	NA

									0.11	
<i>Puya</i>	<i>mirabilis</i>	Puyoideae	C3	20.56 ± 0.21	1201.03 ± 10.05	810.96 ± 7.90	390.07 ± 3.00	0.48	7.87 ± 0.08	NA
<i>Puya</i>	<i>venusta</i>	Puyoideae	CAM	18.31 ± 0.16	1371.22 ± 12.41	912.32 ± 6.76	458.90 ± 4.20	0.50	4.55 ± 0.07	NA
<i>Quesnelia</i>	<i>arvensis</i>	Bromelioideae	CAM	23.26 ± 0.20	947.98 ± 7.67	223.05 ± 1.04	724.93 ± 2.39	3.25	NA	59453 ± 63.37
<i>Quesnelia</i>	<i>edmundoi</i>	Bromelioideae	CAM	34.36 ± 0.33	794.46 ± 6.98	31.78 ± 0.24	762.68 ± 3.98	24.00	NA	23905 ± 21.38
<i>Quesnelia</i>	<i>seideliana</i>	Bromelioideae	CAM	23.75 ± 0.25	934.73 ± 6.65	521.09 ± 1.45	413.64 ± 2.87	0.79	NA	8546 ± 17.70
<i>Quesnelia</i>	<i>strobilispica</i>	Bromelioideae	CAM	44.98 ± 0.42	770.46 ± 5.40	347.25 ± 1.98	423.21 ± 3.06	1.22	NA	9055 ± 10.04
<i>Racinaea</i>	<i>aerisincola</i>	Tillandsioideae	C3	25.09 ± 0.22	423.62 ± 2.29	274.46 ± 2.05	149.16 ± 1.09	0.54	NA	13511 ± 26.90
<i>Racinaea</i>	<i>dyeriana</i>	Tillandsioideae	C3	23.09 ± 0.20	418.05 ± 3.64	293.76 ± 2.23	124.29 ± 1.08	0.42	11.93 ± 0.86	13022 ± 24.45
<i>Ronnbergia</i>	<i>neoregeloides</i>	Bromelioideae	NA	22.97 ± 0.15	558.78 ± 2.00	303.80 ± 2.98	254.98 ± 2.22	0.84	NA	4457 ± 3.76
<i>Tillandsia</i>	<i>balbisiana</i>	Tillandsioideae	CAM	78.56 ± 0.38	1301.82 ± 9.89	387.03 ± 3.56	914.79 ± 5.13	2.36	NA	NA
<i>Tillandsia</i>	<i>bergeri</i>	Tillandsioideae	CAM	124.16 ± 0.46	2444.89 ± 14.42	NA	2444.89 ± 18.90	NA	NA	NA
<i>Tillandsia</i>	<i>brachycaulos</i>	Tillandsioideae	CAM	57.12 ±	622.34 ±	340.34 ±	282.00 ± 1.76	0.83	7.93 ±	NA

				0.28	5.04	2.99			0.21	
<i>Tillandsia</i>	<i>bulbosa</i>	Tillandsioideae	CAM	70.13 ± 0.39	904.14 ± 6.39	579.58 ± 4.06	324.56 ± 2.20	0.56	6.01 ± 0.09	NA
<i>Tillandsia</i>	<i>butzii</i>	Tillandsioideae	CAM	52.77 ± 0.33	613.04 ± 4.90	406.14 ± 3.11	206.90 ± 1.55	0.51	5.16 ± 0.19	NA
<i>Tillandsia</i>	<i>caput-medusae</i>	Tillandsioideae	CAM	68.03 ± 0.42	1455.91 ± 12.70	433.31 ± 1.32	1022.60 ± 8.87	2.36	5.14 ± 0.21	9556 ± 8.04
<i>Tillandsia</i>	<i>complanata</i>	Tillandsioideae	C3	11.54 ± 0.05	306.06 ± 2.88	153.03 ± 1.83	153.03 ± 1.31	1.00	NA	NA
<i>Tillandsia</i>	<i>fasciculata</i>	Tillandsioideae	CAM	63.34 ± 0.29	1795.88 ± 15.60	1172.16 ± 9.56	623.72 ± 4.05	0.53	6.15 ± 0.48	36031 ± 24.15
<i>Tillandsia</i>	<i>gardneri</i>	Tillandsioideae	CAM	43.41 ± 0.30	349.00 ± 2.43	243.75 ± 1.00	105.25 ± 0.95	0.43	NA	NA
<i>Tillandsia</i>	<i>geminiflora</i>	Tillandsioideae	CAM	45.76 ± 0.38	468.35 ± 2.22	208.16 ± 1.54	260.19 ± 1.89	1.25	NA	5067 ± 9.24
<i>Tillandsia</i>	<i>harrisii</i>	Tillandsioideae	CAM	24.29 ± 0.26	1147.66 ± 8.75	590.23 ± 3.88	557.43 ± 4.77	0.94	NA	18550 ± 31.35
<i>Tillandsia</i>	<i>ionantha</i>	Tillandsioideae	CAM	122.22 ± 0.44	2241.61 ± 19.01	991.86 ± 6.09	1249.75 ± 10.13	1.26	6.20 ± 0.22	47677 ± 52.26
<i>Tillandsia</i>	<i>juncea</i>	Tillandsioideae	CAM	41.22 ± 0.36	501.33 ± 5.22	211.09 ± 0.98	290.24 ± 2.05	1.38	4.71 ± 0.17	NA
<i>Tillandsia</i>	<i>leiboldiana</i>	Tillandsioideae	C3	24.12 ±	436.11 ±	290.74 ±	145.37 ± 1.31	0.50	10.53 ±	11899 ± 35.43

				0.20	2.70	2.10			0.77	
<i>Tillandsia</i>	<i>linearis</i>	Tillandsioideae	CAM	37.94 ± 0.18	226.11 ± 1.86	131.29 ± 0.65	94.82 ± 0.54	0.72	NA	1135 ± 6.07
<i>Tillandsia</i>	<i>lithophila</i>	Tillandsioideae	CAM	36.92 ± 0.24	1700.93 ± 11.67	1026.42 ± 8.54	674.51 ± 5.21	0.66	NA	NA
<i>Tillandsia</i>	<i>loliacea</i>	Tillandsioideae	CAM	74.07 ± 0.45	1160.71 ± 10.59	NA	1160.71 ± 8.98	NA	NA	NA
<i>Tillandsia</i>	<i>mallemontii</i>	Tillandsioideae	CAM	40.15 ± 0.31	423.77 ± 3.64	NA	423.77 ± 3.26	NA	NA	728 ± 2.04
<i>Tillandsia</i>	<i>malzinei</i>	Tillandsioideae	C3	15.05 ± 0.04	363.90 ± 3.30	249.84 ± 2.44	114.06 ± 1.04	0.46	NA	4627 ± 4.15
<i>Tillandsia</i>	<i>paleacea</i>	Tillandsioideae	CAM	74.12 ± 0.41	1085.42 ± 8.48	393.27 ± 1.05	692.15 ± 5.42	1.76	NA	NA
<i>Tillandsia</i>	<i>paucifolia</i>	Tillandsioideae	CAM	90.11 ± 0.36	2110.77 ± 16.31	1045.24 ± 7.74	1065.53 ± 8.09	1.02	5.75 ± 0.23	NA
<i>Tillandsia</i>	<i>pohliana</i>	Tillandsioideae	CAM	59.72 ± 0.33	598.44 ± 5.22	235.10 ± 1.80	363.34 ± 2.24	1.55	NA	9245 ± 5.66
<i>Tillandsia</i>	<i>polystachia</i>	Tillandsioideae	CAM	23.56 ± 0.09	757.82 ± 4.01	417.92 ± 2.35	339.90 ± 2.76	0.81	6.29 ± 0.19	18203 ± 22.54
<i>Tillandsia</i>	<i>recurvata</i>	Tillandsioideae	CAM	96.58 ± 0.38	2394.00 ± 20.13	827.83 ± 8.04	1566.17 ± 12.12	1.89	NA	NA
<i>Tillandsia</i>	<i>schiedeana</i>	Tillandsioideae	CAM	86.38 ± 0.40	1765.67 ± 14.54	718.59 ± 6.22	1047.08 ± 8.87	1.46	NA	NA
<i>Tillandsia</i>	<i>setacea</i>	Tillandsioideae	CAM	51.22 ± 0.36	1654.54 ± 11.18	1020.21 ± 8.00	634.33 ± 5.43	0.62	NA	NA

<i>Tillandsia</i>	<i>stricta</i>	Tillandsioideae	CAM	49.21 ± 0.28	545.30 ± 3.76	216.88 ± 2.01	328.42 ± 2.09	1.51	7.01 ± 0.21	5490 ± 11.17
<i>Tillandsia</i>	<i>tenuifolia</i>	Tillandsioideae	CAM	43.34 ± 0.27	382.82 ± 3.29	122.06 ± 0.87	260.76 ± 1.90	2.14	NA	2758 ± 4.65
<i>Tillandsia</i>	<i>usneoides</i>	Tillandsioideae	CAM	94.42 ± 0.38	802.72 ± 4.65	NA	802.72 ± 4.45	NA	NA	NA
<i>Tillandsia</i>	<i>utriculata</i>	Tillandsioideae	CAM	72.95 ± 0.34	1148.67 ± 10.05	574.34 ± 4.03	574.34 ± 3.22	1.00	4.50 ± 0.11	19657 ± 24.34
<i>Tillandsia</i>	<i>valenzuelana</i>	Tillandsioideae	CAM	46.40 ± 0.41	788.28 ± 4.09	492.68 ± 4.11	295.61 ± 1.09	0.60	NA	NA
<i>Tillandsia</i>	<i>xerographica</i>	Tillandsioideae	CAM	34.60 ± 0.35	1787.92 ± 14.16	573.90 ± 4.89	1214.02 ± 9.65	2.12	NA	46635 ± 47.65
<i>Vriesea</i>	<i>arachnoidea</i>	Tillandsioideae	C3	15.76 ± 0.13	461.15 ± 3.26	320.80 ± 1.94	140.35 ± 1.00	0.44	NA	4672 ± 3.21
<i>Vriesea</i>	<i>biguassuensis</i>	Tillandsioideae	C3	13.82 ± 0.10	366.68 ± 2.41	194.12 ± 0.98	172.56 ± 1.43	0.89	NA	12320 ± 16.87
<i>Vriesea</i>	<i>bituminosa</i>	Tillandsioideae	C3	13.46 ± 0.11	480.78 ± 1.59	193.30 ± 1.45	287.48 ± 2.33	1.49	NA	62922 ± 59.65
<i>Vriesea</i>	<i>carinata</i>	Tillandsioideae	C3	20.08 ± 0.16	170.73 ± 1.44	96.75 ± 0.33	73.98 ± 0.65	0.76	NA	404 ± 1.18
<i>Vriesea</i>	<i>corcovadensis</i>	Tillandsioideae	C3	12.94 ± 0.10	545.46 ± 3.78	302.43 ± 2.76	243.03 ± 2.30	0.80	NA	12197 ± 11.22
<i>Vriesea</i>	<i>correia-araujoi</i>	Tillandsioideae	C3	10.53 ± 0.04	348.46 ± 3.02	205.65 ± 1.87	142.81 ± 1.11	0.69	NA	12027 ± 31.08
<i>Vriesea</i>	<i>erythrodactylon</i>	Tillandsioideae	C3	16.52 ±	243.26 ±	127.42 ±	115.84 ± 0.90	0.91	NA	12126 ± 30.55

				0.09	2.00	1.04				
<i>Vriesea</i>	<i>fenestralis</i>	Tillandsioideae	C3	18.11 ± 0.16	523.17 ± 2.15	352.70 ± 3.22	170.47 ± 1.24	0.48	13.6 8 ± 0.91	11007 ± 26.73
<i>Vriesea</i>	<i>flammea</i>	Tillandsioideae	C3	12.57 ± 0.04	548.73 ± 2.76	346.29 ± 3.04	202.44 ± 1.87	0.58	NA	13675 ± 22.45
<i>Vriesea</i>	<i>fosteriana</i>	Tillandsioideae	C3	20.82 ± 0.08	642.45 ± 4.09	256.98 ± 2.45	385.47 ± 3.20	1.50	15.8 6 ± 1.13	86664 ± 89.94
<i>Vriesea</i>	<i>gigantea</i>	Tillandsioideae	C3	19.04 ± 0.14	531.04 ± 4.98	362.66 ± 3.01	168.38 ± 1.54	0.46	12.4 2 ± 0.97	10556 ± 12.31
<i>Vriesea</i>	<i>guttata</i>	Tillandsioideae	C3	17.17 ± 0.12	487.43 ± 3.98	341.20 ± 2.89	146.23 ± 1.02	0.43	9.36 ± 0.81	13041 ± 25.54
<i>Vriesea</i>	<i>incurvata</i>	Tillandsioideae	C3	18.67 ± 0.12	269.15 ± 3.24	146.81 ± 1.20	122.34 ± 1.30	0.83	NA	8352 ± 12.43
<i>Vriesea</i>	<i>lubbersii</i>	Tillandsioideae	C3	21.15 ± 0.10	378.54 ± 3.33	238.77 ± 1.15	139.77 ± 1.06	0.59	NA	8993 ± 4.56
<i>Vriesea</i>	<i>microrachis</i>	Tillandsioideae	C3	11.89 ± 0.10	469.44 ± 3.75	221.23 ± 1.09	248.21 ± 2.09	1.12	NA	23026 ± 35.67
<i>Vriesea</i>	<i>neoglutinosa</i>	Tillandsioideae	C3	14.55 ± 0.13	520.44 ± 3.90	314.43 ± 2.07	206.01 ± 1.88	0.66	NA	14303 ± 13.54
<i>Vriesea</i>	<i>poenulata</i>	Tillandsioideae	C3	14.28 ± 0.05	591.20 ± 4.41	319.38 ± 2.55	271.82 ± 1.97	0.85	NA	13650 ± 22.08
<i>Vriesea</i>	<i>rubens</i>	Tillandsioideae	C3	13.57 ± 0.07	382.10 ± 3.20	196.21 ± 2.01	185.89 ± 1.43	0.95	NA	15257 ± 28.90

<i>Werauhia</i>	<i>sanguinolenta</i>	Tillandsioideae	C3	15.22 ± 0.08	395.60 ± 3.44	237.36 ± 1.76	158.24 ± 1.20	0.67	14.0 1 ± 0.91	12716 ± 31.38
<i>Werauhia</i>	<i>viridiflora</i>	Tillandsioideae	C3	15.08 ± 0.04	315.89 ± 2.71	131.12 ± 1.04	184.77 ± 1.04	1.41	NA	28105 ± 34.75
<i>Wittrockia</i>	<i>gigantea</i>	Bromelioideae	CAM	28.54 ± 0.22	748.42 ± 5.05	56.70 ± 0.34	691.72 ± 5.45	12.20	NA	34855 ± 42.66

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