American Journal of Botany

American Journal of Botany 99(11): 1756–1763. 2012.

The leaf-area shrinkage effect can bias paleoclimate and ecology research[1]

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- *Premise of the Study:* Leaf area is a key trait that links plant form, function, and environment. Measures of leaf area can be biased because leaf area is often estimated from dried or fossilized specimens that have shrunk by an unknown amount. We tested the common assumption that this shrinkage is negligible.
- *Methods:* We measured shrinkage by comparing dry and fresh leaf area in 3401 leaves of 380 temperate and tropical species and used phylogenetic and trait-based approaches to determine predictors of this shrinkage. We also tested the effects of rehydration and simulated fossilization on shrinkage in four species.
- *Key Results:* We found that dried leaves shrink in area by an average of 22% and a maximum of 82%. Shrinkage in dried leaves can be predicted by multiple morphological traits with a standard deviation of 7.8%. We also found that mud burial, a proxy for compression fossilization, caused negligible shrinkage, and that rehydration, a potential treatment of dried herbarium specimens, eliminated shrinkage.
- *Conclusions:* Our findings indicate that the amount of shrinkage is driven by variation in leaf area, leaf thickness, evergreenness, and woodiness and can be reversed by rehydration. The amount of shrinkage may also be a useful trait related to ecologically and physiological differences in drought tolerance and plant life history.

Key words: dry area; fresh area; leaf area; leaf mass per area; leaf size; shrinkage specific leaf area; stomatal density; vein density.

Leaf area is a fundamental plant trait that influences a wide range of biological processes. The area of a leaf directly influences its energy and water balance (Givnish, 1987) and helps determine the scope of interactions between species (Mopper and Simberloff, 1995; Ritchie and Olff, 1999). Leaf area is correlated with plant size and rates of metabolism (Price and Enquist, 2007), climate (Ackerly, 2004), elevation (Cordell et al., 1998), and latitude (Li et al., 1998). Additionally, leaf area can be a useful character for plant taxonomy (Dilcher, 1974) and paleoclimate reconstruction (Peppe et al., 2011). Leaf area is

[1]Manuscript received 7 February 2012; revision accepted 15 October 2012.

The authors thank the Editorial Office staff, G. Jordan, and L. Kouwenberg for a thoughtful and productive review process. Colorado samples were collected with research permits and support from the Rocky Mountain Biological Laboratory (RMBL), Colorado National Monument (COLM-2011-SCI-0004); Black Canyon of the Gunnison National Park (BLCA-2011-SCI-0002); Colorado State Parks; and the U.S. Forest Service Region 2 (FS-2400-8). Costa Rica samples were collected with research permits and support from the Instituto Nacional de Biodiversidad Costa Rica, Ministerio del Ambiente y Energía and Area de Conservación del Pacífico Central. Hawaii samples were collected with research permits and support from the National Tropical Botanical Garden, Kaua'i State Parks (K71707); Hawaii Department of Land and Natural Resources (P-158); Department of Defense Pōhakuloa Training Area, Hawaii Volcanoes National Park (HAVO-2010-SCI-0039); Haleakalā National Park (HALE-2011-SCI-0001); The Nature Conservancy; and the U.S. Fish and Wildlife Service (TE-30445A-0). B. Blonder was supported by a National Science Foundation (NSF) GK-12 teaching fellowship, an RMBL research fellowship, and a National Geographic Young Explorers grant. V.B. and B.J.E. were supported by an NSF Advancing Theory in Biology award to B.J.E. I.S. was supported by a Fulbright fellowship. B. Boyle was supported by The iPlant Collaborative.

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doi:10.3732/ajb.1200062

necessary to calculate many other functional traits based on per-area measures, such as leaf mass per area (whose inverse is specific leaf area; Wright et al., 2004), stomatal density (Jordan, 2011), and vein density (Brodribb and Jordan, 2011). A problem is that leaves may have shrunk by an unknown amount before measurement, which can be relevant for dried or fossilized specimens. Indeed, botanical studies that use leaf area or per-unit-area measures implicitly assume that drying or fossilization does not influence leaf area (Peñuelas and Matamala, 1990; Ackerly, 2004; Buswell et al., 2011). Although the physiological relevance of fresh leaf area is commonly recognized, its relationship to dried leaf area has rarely been measured. Measurements of dried or fossilized leaves have been used interchangeably with fresh leaf area, despite the expectation that leaves from herbarium sheets and many types of fossils may yield underestimates of leaf area (but see Ackerly [2004] for a contrasting opinion).

Biases due to leaf shrinkage are conceivably large enough to influence physiological and climate models. For example, model output can depend on nonlinear leaf area or per-unit-area terms that are logarithmic (Royer et al., 2007; Blonder et al., 2011), quadratic (Gottschalk, 1994) or other powers (Brodribb et al., 2007; Price and Enquist, 2007), or even exponential (Verwijst and Wen, 1996). Thus, some models will be especially sensitive to biases in leaf-area measures (e.g., precipitation reconstructions based on leaf morphology; Wilf et al., 1998). For example, atmospheric [CO_2] reconstructions based on leaf data (Jordan, 2011) often use proxies like stomatal index (number of stomata divided by number of cells in a given area) in which all components of the proxy shrink at the same rate (McElwain, 1998).

Empirical data on shrinkage are rare. For fossils, evidence from one uniquely formed Carboniferous compression fossil with a single leaf spanning two different types of matrix shows that changes in leaf area between matrix types can reach 30% (Laveine, 1987). However, experimental investigations of compression fossilization have found that either expansion or contraction can also occur (Rex and Chaloner, 1983), depending on the type of matrix (Rex, 1986). For dried leaves, we are unaware of other studies of modern leaf shrinkage that would be relevant to herbarium specimens, but note that the drying process is also relevant to taphonomy. Leaves from some temperate deciduous trees are shed dry before fossilizing (Spicer, 1981; Greenwood, 1991).

Here, we quantify the amount by which leaves shrink and assess the causes of this shrinkage. Our goal is to estimate the potential bias from unaccounted-for leaf shrinkage in existing studies, to recommend corrections for "the shrinkage effect." We define shrinkage as $100 \times (1 - \text{final area/fresh area})$, so that shrinkage ranges from 0% (no loss of area) to 100% (total loss of area).

We address three key questions. First, how large is the shrinkage effect? To address this question, we created a global data set for fresh and dry areas for 3401 leaves from 380 temperate and tropical species within 94 families. Second, what variables predict shrinkage? To address this question, we determined whether shrinkage was correlated with a suite of potential measurable predictors: morphological variables (leaf mass per area, leaf thickness, succulent/not succulent, evergreen/not evergreen, woody/not woody), climate variables (mean annual precipitation, mean annual temperature), and evolutionary history. Third, under what conditions does the shrinkage effect need to be considered? To address this question, we conducted an experiment in which we subjected 274 leaves of four species to one of four treatments: (1) drying (a control); (2) drying, then rehydration (a common prefossilization process, and potential way to reverse shrinkage for dried leaves); (3) hydration, then drying (a control, and inverse of the previous treatment); and (4) burial in mud (a key preliminary step for compression fossilization; Greenwood, 1991). We then measured pre- and post-experiment leaf area, mass, and thickness to determine shrinkage and potential correlates.

MATERIALS AND METHODS

***Observational study*—**To understand the importance of shrinkage in herbarium specimens, we studied leaves from angiosperm plants spanning a wide climate range (Costa Rica, Hawaii, and Colorado).

In Costa Rica, we sampled 175 species from forest communities at four sites, ranging from tropical moist forest at 65 m elevation to tropical wet montane forest at 3200 m elevation. At each site, we established ten 50-m line transects, sampling approximately five healthy mature leaves from woody plants with ≥2.5 cm diameter at breast height. All plants were identified to species or genus level. Shortly after collection, we obtained a 300-dpi image of each leaf using a digital flatbed scanner (Canon LiDE 210). We then applied an Otsu threshold to binarize each image and so determine fresh leaf area (cm^2; ImageJ; http://rsbweb.nih.gov/ij/). We also measured leaf thickness (mm) using a digital micrometer (Tresna, 211-101F) by averaging measurements of three points on the lamina; these points were located at evenly spaced intervals between the base and apex of the leaf, midway between the midrib and the distal margin, and avoided major veins. Leaves were then pressed flat in small coin envelopes (i.e., the pressure applied during herbarium specimen preparation) and dried at 60°C for at least 72 h, after which masses were determined with a digital balance. We then measured dry leaf area using the same procedure as for fresh leaf area.

In Colorado, we sampled 188 woody and herbaceous species at 51 sites. These sites ranged in elevation from low desert at 1440 m to alpine at 4390 m. At each site, we sampled up to five leaves from up to five individuals of easily accessible plants. All plants were identified to species level. We then measured fresh and dry leaf area using the same protocol as previously described for Costa Rica, but we did not measure leaf thickness.

In Hawaii, we sampled 17 species in the silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia* [Asteraceae]) at 12 sites. These sites were located on Hawaii, Maui, and Kaua'i and spanned an elevational range of 880–2890 m. We collected up to five leaves from up to 10 individuals of each species. We measured fresh leaf area by tracing leaf outlines onto paper immediately after collection and later digitized these tracings using the same scanning protocol as in Costa Rica. We also measured the thickness, dry area, and dry mass of each leaf using the same protocol as in Costa Rica. Site locations are intentionally deleted in Appendix S1 (see Supplemental Data with the online version of this article) to protect the habitat of several threatened or endangered species.

For all three data sets, we obtained site-level measurements of mean annual temperature and precipitation using 30-arcsecond-resolution WorldClim GIS layers (Hijmans et al., 2005) and site latitudes and longitudes (GDAL and MATLAB). We then obtained mean shrinkage values for each species at each site, and for each species across sites. We generated a phylogenetic tree that included all species using Phylocom's phylomatic and an angiosperm consensus tree (Davies et al., 2004; Webb et al., 2008). We used the bladj tool to estimate branch lengths using fossil ages (Wikström et al., 2001) as calibration points. We also assigned species-level traits (woody/not, evergreen/not, succulent/not) based on expert classification by B. Boyle.

All analyses were conducted in R (http://www.r-project.org/). Predictive modeling with random forest algorithms (Liaw and Wiener, 2002) was implemented by the 'randomForest' package. Phylogenetic analyses were implemented the 'ape' and 'picante' packages. Mixed models were implemented with the 'nlme' package.

***Manipulative experiment*—**As part of a National Science Foundation GK–12 program to enrich K–12 science classrooms, we conducted the manipulative experiments with four middle school science classes at Miles Exploratory Learning Center in the Tucson Unified School District. Each student was supervised and was personally responsible for several leaves of each of four species; each class performed a different treatment, resulting in a 4×4 fully crossed

factorial design. Students were trained to properly use equipment before collecting data for this project.

We collected leaves from four woody species (*Citrofortunella mitis* [hereafter CIMI], *Dalbergia sissoo* [DASI], *Eucalyptus microtheca* [EUMI], and *Populus mexicana dimorpha* [POME]) shortly after dawn on 28 and 29 November 2011. These species were chosen because they were easily obtained from the University of Arizona Campus Arboretum and their entire margin and large size made them easy for middle school students to handle. We used only undamaged mature leaves from irrigated plants. Leaves were stored in plastic bags with a moist paper towel and kept in a refrigerator for 2 to 4 h before initial measurements.

We made pretreatment measurements: leaf thickness was measured at three random points on the lamina using the same protocol as for Costa Rica; leaf mass was measured three times using a digital balance; and leaf area was determined by photocopying each leaf in the school office, later scanning each image at 150-dpi resolution, and then applying a median filter, Otsu threshold, and hole-filling algorithm (in MATLAB) to obtain a silhouette of each leaf from which a pixel count could be made.

We then applied a treatment to each leaf. For drying, leaves were pressed flat between paper sheets and dried at 60°C for 7 d. For drying followed by rehydration, fresh leaves were pressed flat between paper sheets and dried at 60°C for 3 d, placed in a sealed plastic bag with ~100 mL of water at room temperature for 4 d, and then patted dry with a paper towel. For hydration followed by drying (a control for the previous treatment), the order of the previous treatment was reversed. For mud burial, fresh leaves were placed in a plastic bag (to facilitate leaf identification) into which was put ~250 mL of mud at room temperature. Bags were sealed and left to sit with no additional applied pressure for 7 d. Leaves were then taken out of the bags, rinsed in water, and patted dry. Mud was obtained by mixing dirt from a schoolyard (silt loam: 45% sand, 50% silt, 5% clay) with water. The difference in drying times between treatments should not matter because drying is typically complete within 48 h (Cornelissen et al., 2003).

Posttreatment measurements of leaf mass, area, and thickness were made using the pretreatment protocol. All data were entered into a spreadsheet at Miles Exploratory Learning Center. To ensure data quality, all measurements were triple checked. Individual measurements that were too variable (outside a plausible range, or with coefficients of variation >0.3 when calculated for repeated measurements) were replaced with NA values ($n = 56$ leaves). Data from fragmented or mishandled leaves were also excluded from the study ($n = 9$ leaves). In total, usable data were available for $n = 274$ leaves, yielding an average of 17.1 ± 3.1 (SD) leaves per species-treatment factor.

RESULTS

***Observational study*—**Species-mean area shrinkage was highly variable, ranging from a minimum of –9.9% to a maximum of 81.5%, with a mean of 21.9%. Negative shrinkage values were from five species (*Agropyron cristatum*, *Chrysothamnus* sp., *Chrysothamnus viscidiflorus*, *Pentaphylloides floribunda*, and *Trifolium dasyphyllum*) and are attributed to measurement errors.

We assessed the role of categorical species traits in predicting species-mean area shrinkage (Fig. 1). Shrinkage was significantly different between woody (mean = 15.0%) and herbaceous (mean = 33.8%) taxa, as well as between evergreen (mean = 15.0%) and deciduous (mean 27.4%) taxa (unpaired two-sided Wilcoxon rank-sum test, both $P < 10^{-13}$). However, shrinkage was only marginally different between succulent (mean = 28.2%) and nonsucculent (mean = 21.6%) taxa (same test, $P = 0.05$).

We next assessed the role of quantitative functional traits in predicting species-mean area shrinkage (Fig. 2). Shrinkage was negatively associated with $\log_{10}$ leaf area ($P < 10^{-15}$, $R^2 = 0.25$) and positively associated with $\log_{10}$ leaf thickness ($P < 10^{-14}$, $R^2 = 0.36$) but not significantly associated with $\log_{10}$ leaf mass per unit area (LMA) ($P = 0.15$). We then determined the role of climate in predicting species-at-site-mean area shrinkage (Fig. 3). We observed a significant negative relationship ($P < 10^{-15}$) with shrinkage for both mean annual temperature ($R^2 = 0.21$) and mean annual precipitation ($R^2 = 0.17$).

We also assessed the role of evolutionary history and phenotypic plasticity in constraining shrinkage. A phylogenetic analysis of angiosperm species ($n = 380$ in 94 families) also showed that shrinkage is significantly more evolutionarily labile (Blomberg's $K = 0.43$, $P = 0.001$) than expected ($K = 1$) under a Brownian evolution model (Fig. 4). Thus, evolutionary history is not especially helpful for predicting shrinkage. Indeed, a variance partitioning of species-mean shrinkage showed that 40.5% of variation occurred between species whereas 59.5% occurred within species, indicating some trait variation not explained by taxonomy. The between-species average of the standard deviation of within-species shrinkage was 5.9%; this number directly estimates the within-species between-leaf variation.

We then constructed a predictive model of area shrinkage. We constructed a 10000-tree "random forest," using LMA, leaf area, leaf thickness, woody/not, evergreen/not, and succulent/not as predictors of species-mean area shrinkage. This is a bootstrapping approach that builds multiple regression trees on subsets of the data and makes predictions and error estimates based on the ensemble of trees. We obtained a forest that explained 54.0% of

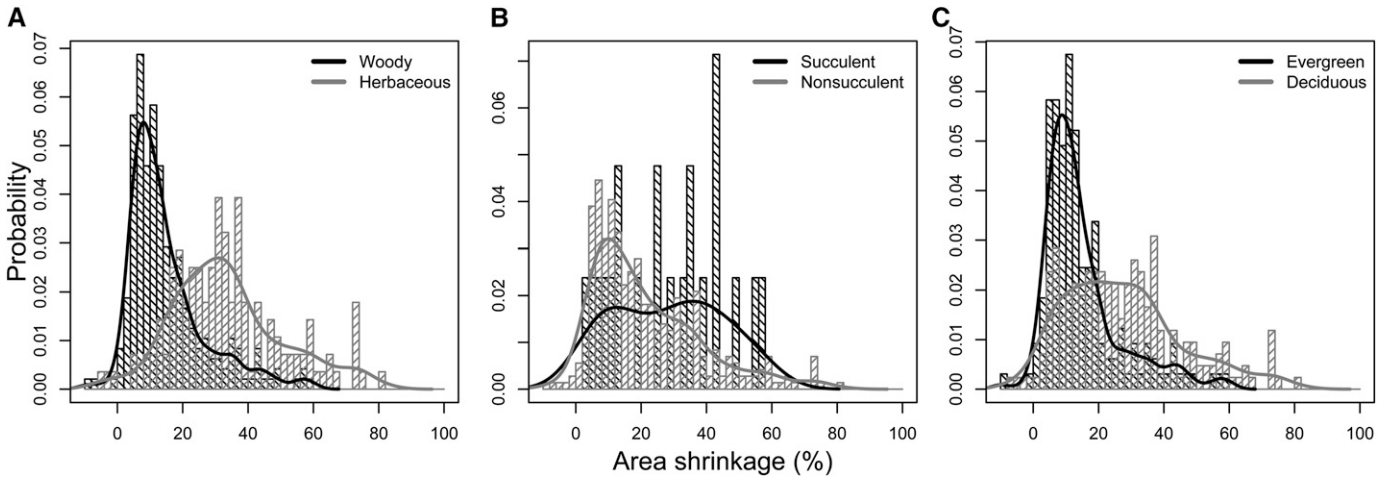

Fig. 1. The distribution of species-mean leaf shrinkages varies with multiple species-level predictors: (A) woody vs. herbaceous species, (B) succulent vs. nonsucculent species, and (C) evergreen and deciduous species. Lines are smoothed estimations of the probability density.

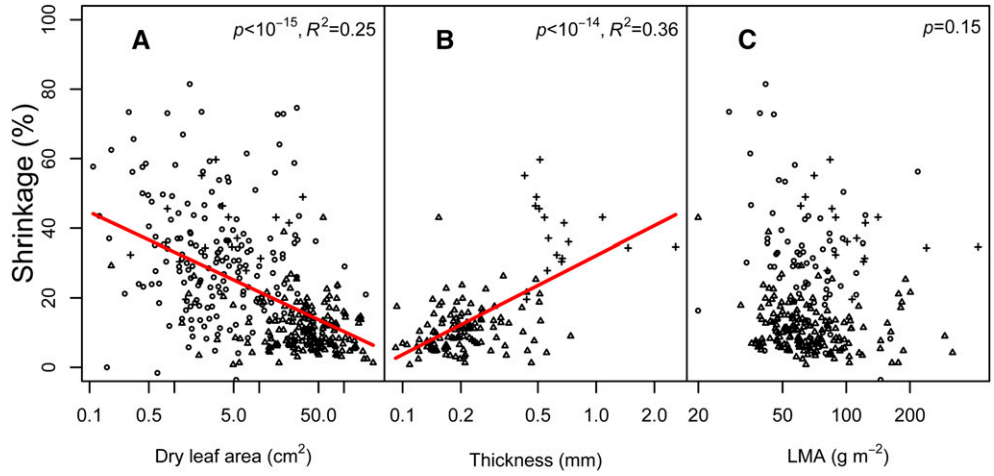

Fig. 2. The relationship between leaf shrinkage and leaf functional traits is strong for (A) leaf area and (B) thickness but not for (C) leaf mass per unit area (LMA). Each point is a species-at-site mean value; regression lines are shown when significant at $\alpha = 0.05$. Circles indicate Colorado species, triangles Costa Rica species, and crosses Hawaii species.

the variance in area shrinkage, with a mean square error of 61.0, corresponding to a prediction standard deviation of 7.8%, assuming no bias. Because random forests are not easily interpreted, we have included the R code as supplemental information for investigators who wish to predict shrinkage for other taxa (Appendix S1). Thus, an investigator with trait measurements for leaves of a different species can put these values into our model and obtain a prediction for shrinkage of each leaf in that species.

***Manipulative experiment*—**Because we were primarily interested in the effect of each treatment, we analyzed the data using a linear mixed model of area shrinkage with a fixed effect of treatment and a random intercept for each species. Area shrinkage was significantly affected by the species intercept ($F_{1,261} = 340$, $P < 0.001$) and treatment ($F_{3,261} = 678$, $P < 0.001$) (Fig. 5). The two treatments that finished with drying had similar effects: drying yielded the largest shrinkage (14.3 ± 0.4% [SE]) and was matched closely by adding water and then drying (11.7 ± 0.4%). By contrast, drying and then rehydrating yielded very low shrinkage (0.8 ± 0.4%), as did mud burial (0.1 ± 0.4%). Table 1 presents details by species of thickness and mass shrinkage. These results indicate that area shrinkage can be (1) slightly

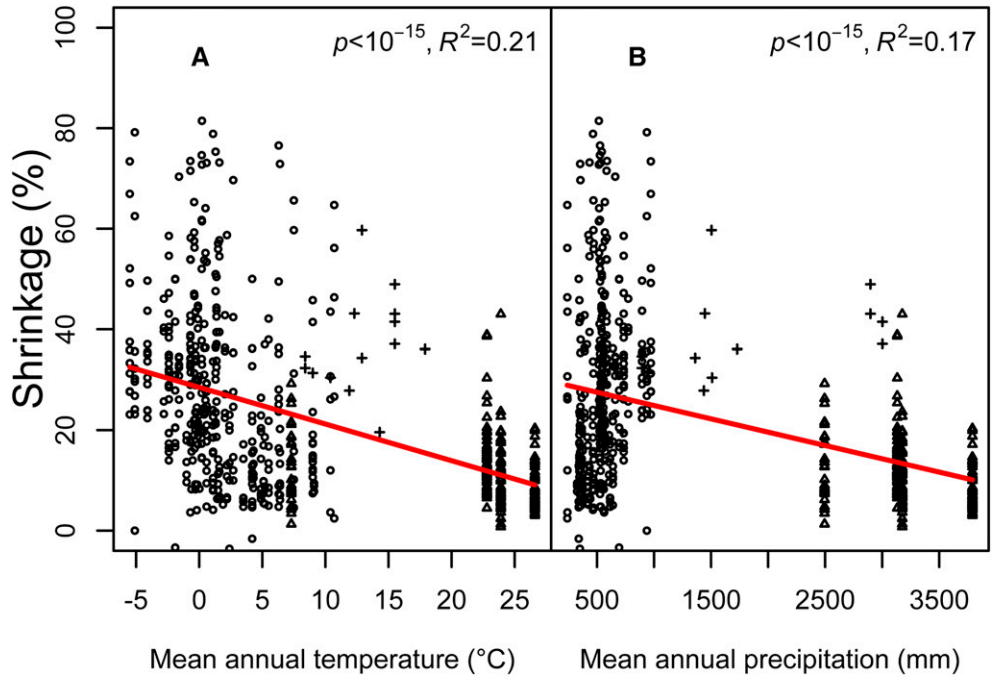

Fig. 3. The relationship between leaf shrinkage and climate at the location of leaf collection is strong for (A) temperature and (B) precipitation. Each point is a species-at-site mean value; regression lines are shown when significant at $\alpha = 0.05$. Circles indicate Colorado species, triangles Costa Rica species, and crosses Hawaii species.

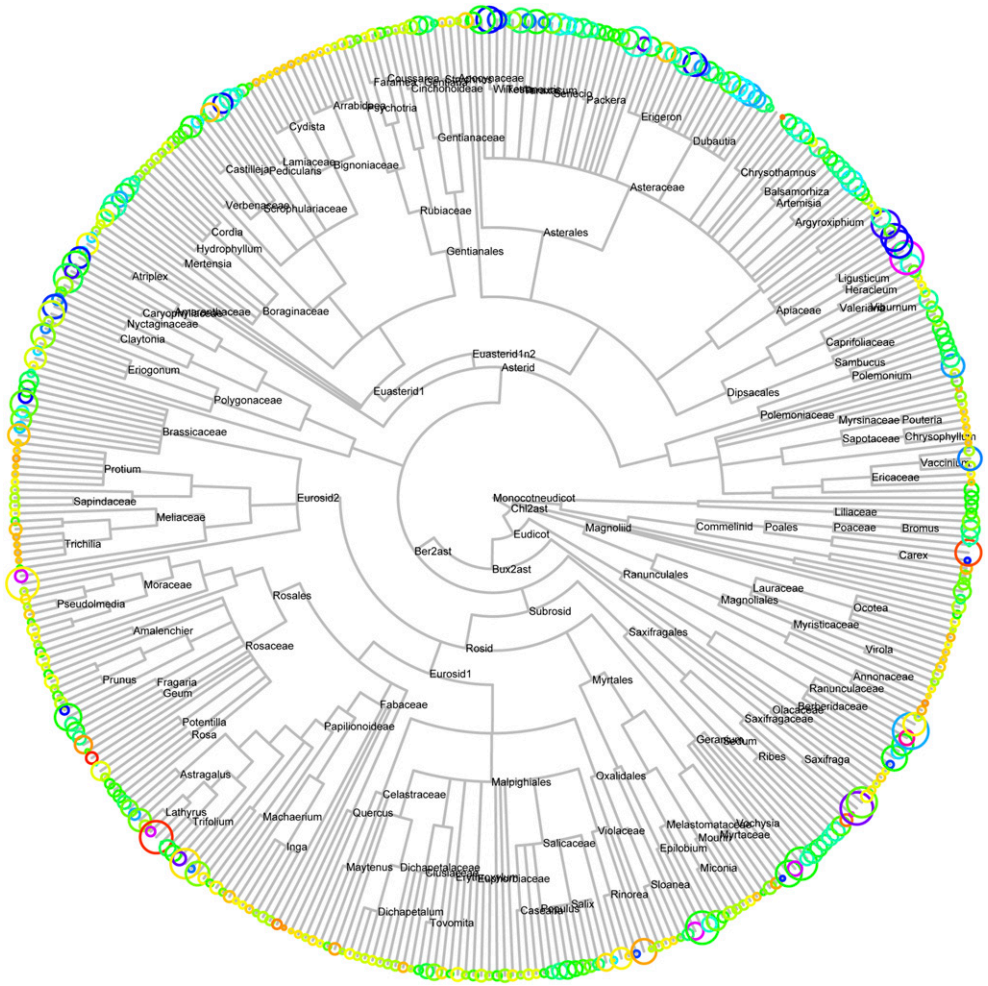

Fig. 4. The distribution of leaf shrinkages across the angiosperms does not show a strong phylogenetic signal. The radius and color of circles at node tips represent the relative magnitudes of shrinkage for each species. Branch lengths are proportional to inferred clade age.

reduced if leaves are hydrated before drying, (2) greatly reduced if leaves are rehydrated after drying, and (3) greatly reduced if leaves are immediately buried in mud.

We also further assessed the morphological correlates of area shrinkage using pooled data for drying and adding water followed by drying. We found that shrinkage was significantly negatively correlated with leaf dry matter content (LDMC; dry mass/fresh mass) for DASI, EUMI, and POME (all $P < 0.002$, all r^2 in 0.33–0.36) but not for CIMI ($P = 0.29$) (Fig. 6). Results for tissue density (dry mass/fresh area × fresh thickness) were weaker: DASI and POME had significant relationships (both $P < 0.006$, $r^2 > 0.23$), but CIMI and EUMI did not (both $P > 0.15$). Area shrinkage was also not consistently related to thickness shrinkage: DASI, EUMI, and POME had significant relationships (all $P < 0.02$, r^2 in 0.07–0.30) but CIMI did not ($P > 0.73$). The proximate causes of shrinkage therefore remain ambiguous.

DISCUSSION

We quantified the shrinkage effect across a broad sampling of angiosperms from a wide range of climates because of the potentially large consequence for systemic bias in measurement of leaf area and derived traits. We found that the shrinkage effect can be large (up to ~80% and typically about 10–30%). This result indicates that potential biases must be considered when using dried or fossil leaf areas as proxies for fresh leaf area in climate, comparative biology, and ecological research. Leaf-area shrinkage is likely to be a less serious problem in fossil leaves obtained from some taxa, such as evergreen woody species. Thin herbaceous leaves may also be less likely to enter the fossil record because their weak tissue promotes degradation and the short stature of herbaceous species prevents long-distance transport of leaves.

We found that higher values of leaf-area shrinkage are associated with taxa with smaller, thinner, or lower dry-matter-content leaves, as well as taxa with deciduous leaves or a nonwoody growth form. These predictors are consistent with an understanding of shrinkage as being driven primarily by cell contraction after water loss. Other potential predictors, including evolutionary history and climate, were not important. Our random forest model integrates each of these different variables to provide a robust method for predicting leaf shrinkage with a standard deviation of 7.8%, suggesting that investigators confronted with unknown specimens have the ability to infer fresh leaf area from dried leaf area. Moreover, our study provides

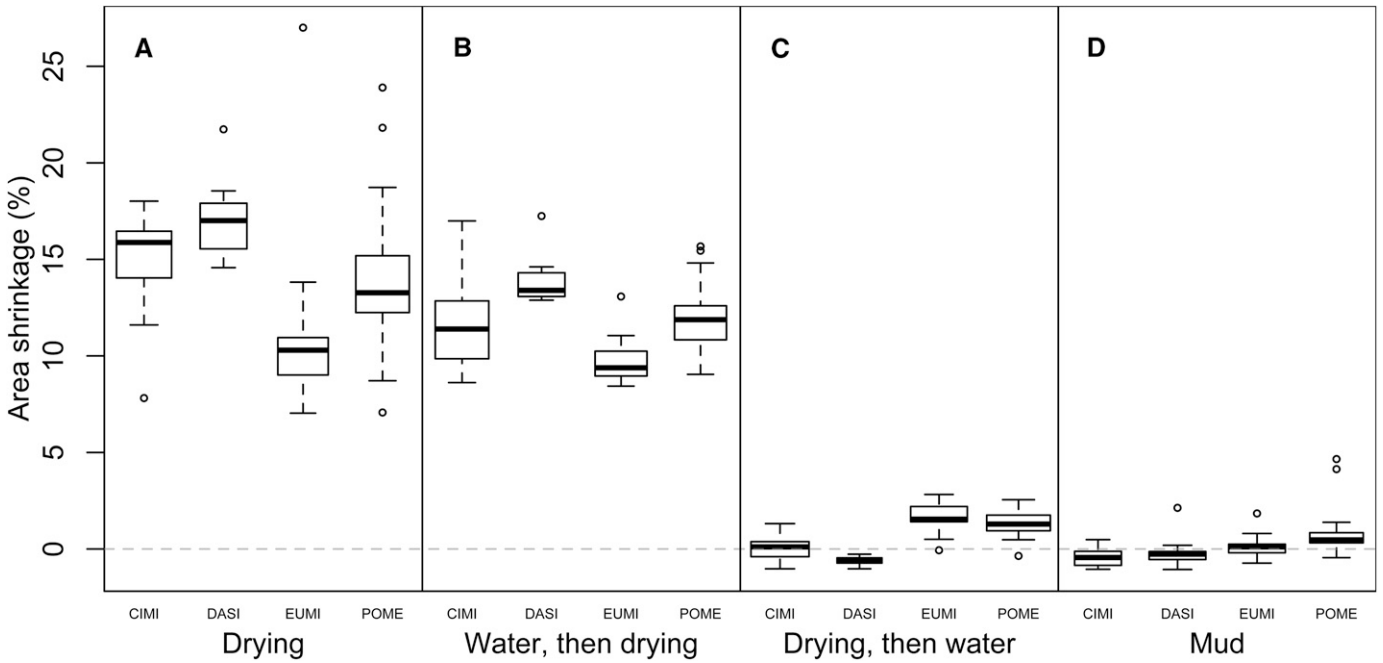

Fig. 5. Shrinkage is highly variable across different experimental treatments: (A) drying; (B) added water, then drying; (C) drying, then rehydration; and (D) burial in mud. Results were also variable between the four species studied (CIMI = *Citrofortunella mitis*, DASI = *Dalbergia sissoo*, EUMI = *Eucalyptus microtheca*, and POME = *Populus mexicana dimorpha*).

empirical shrinkage measurements (Appendix S1) for more than 300 tropical and temperate species (all angiosperms; further work is needed to calibrate this model for nonangiosperm taxa). The observed shrinkages for these species can be used directly as correction factors and also to provide uncertainties about leaf-area measurements that can be propagated through the inferences of previously published studies.

One interesting aspect of our work is that the amount of shrinkage may also be a useful trait in and of itself and reflective of important differences in plant water-use strategies. There is reasonable evidence suggesting that differences in leaf cell shrinkage may be related to the stiffness and rigidity of plant cell walls and tissue (Cheung et al., 1975; Jones, 1992) and that stiffness of plant leaves may be related to the drought tolerance of a species (Knapp, 1984; Lawlor and Cornic, 2002; Bartlett et al., 2012). With decreases in water, plant leaves correspondingly lose water, and physiological functions will decline with further reductions in water supply until the "permanent wilting point," where all physiological control is lost and the plant does not recover. However, as the availability of water declines with drought, different leaf traits can differentially influence the physiological responses of plants to drought. In particular, certain traits enable plant to tolerate increasing drought. Plants that wilt sooner during drought appear to be characterized by less rigid cells and leaf tissue (Knapp, 1984; Bartlett et al., 2012). Although we did not measure leaf rigidity (the elastic modulus), we measured other key traits (leaf thickness and dry matter content) that are strongly correlated with the elastic modulus (Cheung et al., 1975; Zimmermann, 1978). Leaves with higher LDMC tend to have thicker and more rigid cell walls, which enable the maintenance of turgor at a lower leaf water potential (Markesteijn et al., 2011). Further, larger leaves tend to be more prone to drought and hydraulic failure (Markesteijn et al., 2011). Together, our results show that

TABLE 1. Summary of shrinkage experiments (means ± SE). Negative values indicate increases in size.

Measure	Treatment	Citrofortunella mitis	Dalbergia sissoo	Eucalyptus microtheca	Populus mexicana dimorpha
Area	Drying	15 ± 0.6	17.1 ± 0.5	11.2 ± 1.1	14.0 ± 1.0
	Drying, then water	0.0 ± 0.1	−0.6 ± 0.1	1.7 ± 0.2	1.3 ± 0.1
	Mud	−0.4 ± 0.1	−0.3 ± 0.2	0.1 ± 0.1	1.0 ± 0.3
	Water, then drying	11.8 ± 0.6	13.8 ± 0.3	9.7 ± 0.3	12 ± 0.5
Mass					
	Drying	65.3 ± 1.0	66.2 ± 1.4	54.0 ± 2.5	68.2 ± 0.8
	Drying, then water	−27.3 ± 16.1	−10.8 ± 1.6	9.8 ± 2.8	21.1 ± 1.3
	Mud	−12.0 ± 2.1	−9.6 ± 5.1	−10.9 ± 11.8	−17.4 ± 13.5
	Water, then drying	64.5 ± 0.9	62.7 ± 0.5	55.4 ± 0.7	65.2 ± 0.5
Thickness					
	Drying	21.5 ± 5.2	29.3 ± 2.8	33.1 ± 4.1	32.0 ± 3.7
	Drying, then water	28.5 ± 4.1	0.2 ± 3.1	12.5 ± 2.5	28.6 ± 3.2
	Mud	13.7 ± 2.3	14.0 ± 4.5	3.1 ± 5.6	14.3 ± 4.7
	Water, then drying	27.1 ± 3.0	24.2 ± 1.4	33.0 ± 2.3	35.0 ± 1.8

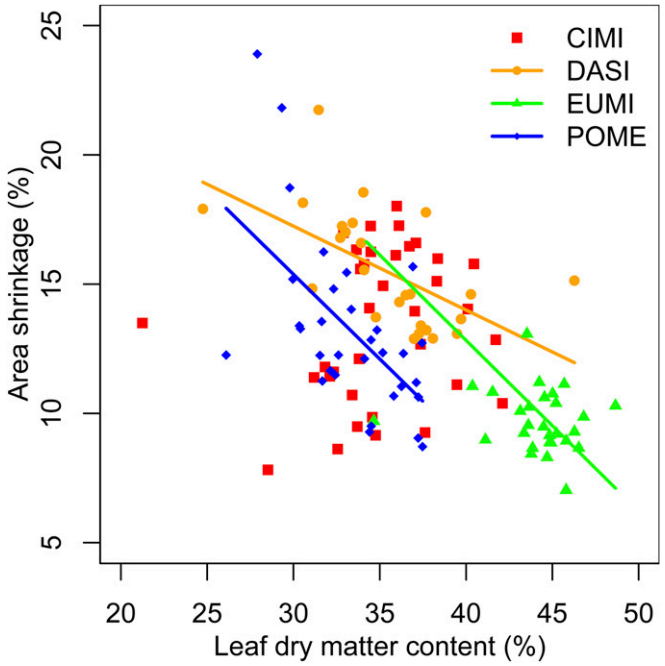

Fig. 6. Leaf dry-matter content is negatively correlated with shrinkage for three of four species studied. Each point is an individual leaf from either the drying or the added-water-then-drying experiment; regression lines are shown when significant at $\alpha = 0.05$. Species codes are the same as in Figure 5.

LDMC as well as leaf size are predictors of leaf shrinkage. Because drought tolerance is also correlated with rates of stomatal conductance, hydraulic conductance, and photosynthetic gas exchange (Abrams and Kubiske, 1990; Mitchell et al., 2008), the amount of shrinkage may also be reflective of a suite of physiological responses to the environment. Future studies should assess the possibility that the amount of leaf shrinkage may be a measure of drought tolerance.

Our experimental study provides guidelines for understanding and controlling the processes that cause shrinkage. Our mud-burial experiment, though limited, showed that shrinkage may not be a problem for fossils that are initially formed in a moist matrix. This treatment was a reasonable short-time model of a preliminary step of fossilization in riverine and lake systems, where sediments remain wet and diagenesis does not drive out all water from the matrix. However, fossils form under diverse conditions (variation in moisture, pressure, charcoalification, pH, etc.), so it is not yet possible to provide general guidance on shrinkage in fossils. Our experiments also show that area shrinkage could be completely reversed for dried leaves via subsequent rehydration (though thickness shrinkage could not be reversed). The ability of leaves to reabsorb water is supported by work on fresh leaves, but the proximate mechanisms of water gain remain unclear (Maass et al., 1995; Garnier et al., 2001; Vaieretti et al., 2007). This surprising result suggests that fossils commonly originating from dried leaves shed by trees (Spicer, 1981) may be subject to little or no shrinkage effect if initially formed in damp conditions. More strongly, this result also provides a simple solution to correct for the area shrinkage of pressed dried leaves commonly found in herbaria: put them in water and rehydrate. This rehydration approach may also be useful for fossil leaf cuticles.

Together, our results show that the area shrinkage effect is a potentially serious problem for many types of studies. Nonetheless, the amount of leaf shrinkage is predictable on the basis of several functional traits. As a result, the problem posed by using dry leaf areas in climate models and comparative biology is not an unsolvable one. Our results also suggest that the amount of leaf shrinkage may be a useful and relatively easy trait to quantify that is reflective of differential water-use strategies of plants and their susceptibility to drought.

LITERATURE CITED

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