

## NO LARGE BIAS WITHIN SPECIES BETWEEN THE RECONSTRUCTED AREAS OF COMPLETE AND FRAGMENTED FOSSIL LEAVES

ERIC R. HAGEN,<sup>1</sup> DANA L. ROYER,<sup>1</sup> RYAN A. MOYE,<sup>1</sup> AND KIRK R. JOHNSON<sup>2</sup>

<sup>1</sup>Wesleyan University, Department of Earth and Environmental Sciences, Middletown, Connecticut 06459, USA

<sup>2</sup>Smithsonian Institution, National Museum of Natural History, Washington, D.C. 20013, USA

email: [ehagen@wesleyan.edu](mailto:ehagen@wesleyan.edu)

**ABSTRACT:** Taphonomic processes may filter in a biased manner the tiny fraction of leaves preserved as fossils. A common perception is that large leaves are underrepresented; this is based both on intuition (large leaves are more likely to break apart) and some observations of extant vegetation. Characterizing leaf area correctly is critical for reconstructing climate and for studying evolutionary and biogeographic patterns. In extant dicotyledonous angiosperms, leaf area generally scales with the inverse of second-order vein density. This scaling offers the potential to test if fossil leaf fragments were derived from leaves that were larger than complete (or nearly complete) fossil leaves of the same species. Here we test vein scaling on 573 complete leaves from the latest Cretaceous Hell Creek Formation and earliest Paleocene Fort Union Formation in the Williston Basin of western North and South Dakota. We find a strong scaling similar to extant vegetation, with a somewhat shallower slope (1.67 vs. 2.04) and lower  $r^2$  (0.64 vs. 0.80). We apply these two scalings to 41 species-site pairs from the Williston Basin that are each represented by complete ( $n = 355$ ) and fragmented ( $n = 387$ ) leaves. With both scalings, the reconstructed leaf areas of fragments are on average 10% larger ( $\pm 36\%$   $1\sigma$ ) than their complete companions. This small but noisy signal means that the underrepresentation of large leaves, as captured by our study design, is probably not critical for most fossil applications. Comparing directly the reconstructed areas of complete and fragmented leaves appears reasonable, thus expanding the usefulness of fossil leaf fragments.

### INTRODUCTION

Most leaves do not fossilize, and those that do are commonly fragmented. It may be expected that complete (or nearly complete) leaves are on average smaller than the original population for the simple reason that large leaves are more likely to break apart (e.g., Greenwood 1991). This pattern is sufficiently intuitive that it is often stated without citation (e.g., Wolfe 1977; Hill and Gibson 1986). Leaf area is an important functional trait that provides insight about taxonomy and biogeography (e.g., Merkhofer et al. 2015). Also, in many species, leaf area scales with mean annual precipitation (MAP) (Wright et al. 2017); this allows for the reconstruction of MAP from fossil floras, a technique called leaf-area analysis (Wilf et al. 1998; Peppe et al. 2011). Leaf area is used in other proxies for climate (Carpenter et al. 1994, 2012; Yang et al. 2015) as well as for economic traits such as leaf mass per area (Royer et al. 2007; Blonder et al. 2014). If the fossil record is biased towards small leaves, interpretations based on leaf area may be biased as well (e.g., Roth and Dilcher 1978; Greenwood 1994). For example, MAP reconstructions may be chronically low.

The fossilization process potentially includes many steps in which candidate leaves can break apart or escape fossilization altogether (Fig. 1). Among non-herbaceous plants, leaves first abscise and become airborne. Leaves high in the canopy are more likely to encounter higher wind speeds and travel farther (Ferguson 1985; Greenwood 1992, 1994). Sun leaves are common high in the canopy and, within species, are usually smaller than shade leaves (Wylie 1951; Talbert and Holch 1957; Sack et al. 2006). Sun leaves also tend to have a higher leaf mass per area (Hanson 1917; Koch et al. 2004; Sack et al. 2006) and should be more resistant to physical decay. Together, these factors could lead to the preferential fossilization within

species of smaller complete leaves, especially for deposits that are associated with considerable transport such as large lakes and stream channels.

Present-day observations are mixed (Ferguson 1985). In Australian rainforests, Greenwood (1992) reported that litter in both stream-bed and forest floor sites contained smaller leaves relative to surrounding vegetation, perhaps reflecting a disproportionate representation of sun leaves. In contrast, in southern Mexico, Burnham (1989) found no difference in leaf area between those in unlithified levee sediment and those in the regional vegetation; leaves from channel sediment, however, were smaller than the regional vegetation, implying a selection for small leaves with river transport (see also Steart et al. 2002; Ellis and Johnson 2013). Similarly, Christophel and Greenwood (1989) observed that leaves collected from streams tended to be smaller than leaves collected from litter on neighboring terra firma. We know of no study comparing leaf area in lake sediment directly to the surrounding standing vegetation. Roth and Dilcher (1978) found smaller leaves in sediment near a lake center relative to the lake margin, implying transport-mediated selection for small leaves, but others found no striking difference between leaves from lake-bottoms versus neighboring litter traps (Spicer 1981; Astorga et al. 2016).

A limitation of present-day taphonomic studies is that post-burial processes are not captured (Fig. 1). Thus, fossil studies comparing complete and fragmented leaves may provide new information about leaf-size biasing, but with the caveat that the leaf-size distribution of the original vegetation cannot be recovered. As such, neither present-day nor fossil studies provide a complete picture; instead, they complement one another.

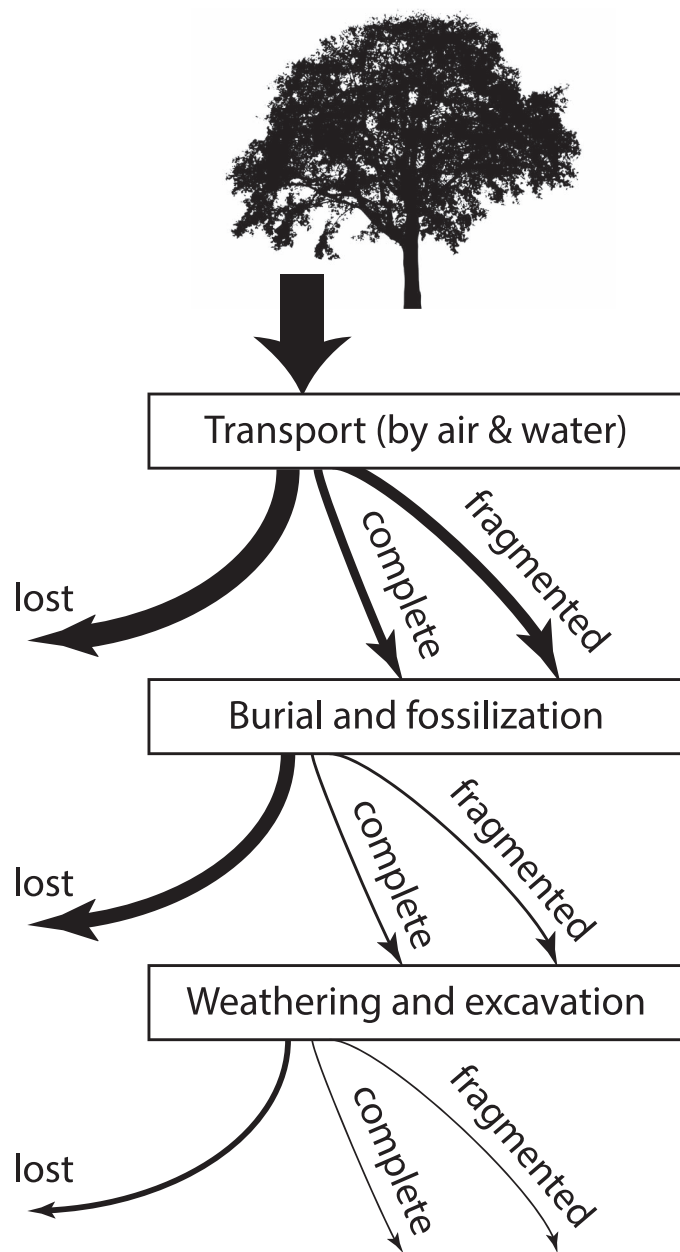


FIG. 1.—Some taphonomic processes for the fragmentation of leaves. Most leaves are never captured as fossils, and many are not captured in their complete forms.

### Vein Scaling

Until recently, quantifying the original leaf area represented in leaf fragments was an impossible task. Sack et al. (2012) found a strong global scaling in dicotyledonous angiosperms (386 species) between leaf area and the inverse of second-order ( $2^\circ$ ) vein density (see also Li et al. 2018). First-order ( $1^\circ$ ) veins (including midveins) are thick and originate at the leaf base;  $2^\circ$  veins are thinner and typically radiate from  $1^\circ$  veins, and so on, up to seven orders for some dicots (Ellis et al. 2009). The scaling between vein density and leaf area is underpinned by leaf development: early on inside the bud, leaves undergo a “slow” phase, followed by a “rapid” phase during the latter stages of bud development and after budbreak. The  $1^\circ$  and  $2^\circ$  veins form during the slow phase, and higher-order veins arise mostly during the rapid phase. As a leaf expands after budbreak,  $1^\circ$  and  $2^\circ$  vein

density declines, much like a balloon with lines drawn on it. Since higher-order veins form mainly during the rapid phase, their density is mostly insensitive to leaf size (Sack et al. 2012). Leaf area scales most strongly with  $1^\circ$  veins, but the quantification of this correlation requires complete leaves. For fragments,  $2^\circ$  vein density is the best choice (Sack et al. 2012).

This vein scaling opens the door for reconstructing leaf area from fossil fragments. To our knowledge, Merkhofer et al. (2015) is the one study to date to explore this new tool. Their primary interest was understanding the biogeographic history of plants from Laguna del Hunco, an early Eocene flora from Argentina preserved in lake sediments. Some species at this site are known only from fragments, and their inclusion increased the across-species mean leaf area by 7%; this revised leaf-area “fingerprint” was a good match to present-day subtropical Australian forests. Merkhofer’s data identify a leaf-size biasing, namely that leaves of species preserved only as fragments tend to be larger, on average, than leaves of species with complete preservation. A different question, and one that perhaps addresses leaf-size biasing more directly, is whether—within-species—fragments have different reconstructed areas than complete leaves.

### Study Aims

We sought to test if the original areas of leaf fragments were larger than complete leaves of the same species. To carry out this test, we analyzed 960 leaves from the Upper Cretaceous Hell Creek and lower Paleocene Fort Union Formations in southwestern North Dakota and northwestern South Dakota (Johnson 2002). First, for the subset of complete leaves, we tested whether the inverse of  $2^\circ$  vein density scales with leaf area. We then divided the data set into morphospecies (called morphotypes) by site. For the 41 morphotype-site pairs with sufficient representation of complete and fragmented and leaves ( $\geq 3$  each), we tested for a leaf-size bias.

### MATERIALS AND METHODS

#### Williston Basin Floras

The fossils used in this study come from 65 sites in the Hell Creek and overlying Fort Union Formations in the Williston Basin (Johnson 2002). The sites range in age from  $\sim 67$  to  $\sim 65$  Ma and span the Cretaceous–Paleogene boundary, which generally occurs within 0–2.5 m of the formational contact (Johnson 2002).

The Hell Creek Formation is comprised of mudstone and sandstone that were originally deposited in freshwater (Moore 1976; Murphy et al. 2002). Most Hell Creek fossils used here come from channel deposits: 86% of sites and 90% of specimens. Sandstone, mudstone, and coal beds comprise the Fort Union Formation in the Williston Basin (Johnson 2002). Similar to the Hell Creek, most of our fossils come from channel deposits: 80% of sites and 83% of specimens.

#### Data Collection

We photographed fossils at the Denver Museum of Nature and Science and the Yale Peabody Museum. We took care to include a balance of complete leaves and leaf fragments for each morphotype at each site. Every photo included a scale bar as well as the fossil’s associated information card, which contained site information, a morphotype ID, and a specimen ID.

To analyze the photos, we first made a digital copy of each leaf in Adobe Photoshop CS6. For complete or nearly complete leaves, we traced the leaf outline with the polygonal lasso tool, correcting any minor defects in the margin along the way, and then rendered the outline with the stroke command. For bilaterally symmetric leaves with substantial damage on one half, the intact half was traced and the final area doubled.

For all leaves (complete and fragmented), we next drew boxes with the rectangle tool in ImageJ (<http://imagej.nih.gov/ij/>) following the protocols

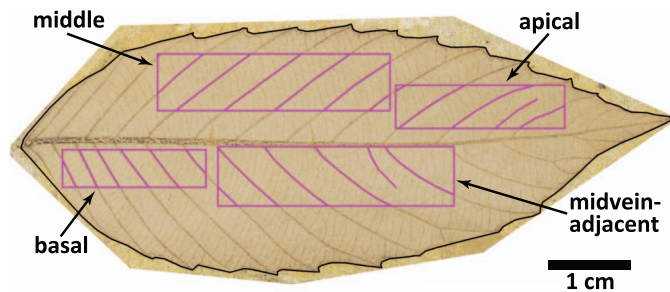


FIG. 2.—Vein density boxes drawn on a fossil leaf using ImageJ. One box is shown in each of four areas: apical, middle, basal, and midvein-adjacent. The highlighted lines inside the boxes are 2° veins and the midvein is the 1° vein. The black line is the leaf outline, which is used to calculate leaf area for complete specimens.

of Sack et al. (2012) and Merkhofer et al. (2015) (see Fig. 2 for example). All boxes contained at least two 2° vein segments and were similar in proportion to the boxes shown in Figure 2. Intersecondary veins were included (Sack et al. 2012; Merkhofer et al. 2015), which have a similar architecture to regular 2° veins but are smaller in gauge (Ellis et al. 2009). Up to four boxes were drawn per leaf, corresponding to different regions of the leaf: apical, basal, middle, and midvein-adjacent (Fig. 2; Merkhofer et al. 2015). In each box, we traced the length of each 2° vein segment with the segmented line tool.

We used ImageJ to calculate areas and vein lengths. For area we used the threshold tool and for vein length the segmented line tool. Vein density is defined as the sum of vein lengths divided by the rectangular area ( $\text{cm cm}^{-2}$ ) (e.g., Sack et al. 2012). Because we did not find strong differences in vein density among the four box positions, we computed the mean vein density of each leaf. The Online Supplemental File contains all measurements.

#### Analysis of Leaf Size Bias

We tested the strength of the vein-scaling relationship among 573 complete leaves using ordinary least-squared regression. Following Sack et al. (2012), we used  $\log_{10} \text{cm}^2$  units for leaf area. We analyzed 355 complete and 387 fragmented leaves for the 41 morphotype-site pairs with at least three complete and three fragmented specimens. By convention (e.g., Wilf et al. 1998), we expressed these leaf areas in units of  $\ln \text{mm}^2$ . We tested the scaling between the areas of complete and fragmented leaves across morphotype-site pairs using standardized major axis (SMA) regression. SMA regression incorporates uncertainty in both x- and y-variables, unlike ordinary least-squares regression that only incorporates uncertainty in the dependent variable. SMA is appropriate when no causality is assumed between the two variables, as is the case here. If there is no size difference between complete and fragmented leaves, the slope of the SMA regression should be 1 and the y-intercept 0. We tested these null hypotheses using the R package SMATR (Warton et al. 2012).

To quantify user error associated with measuring vein density and leaf area, two student assistants and the lead author measured both 2° vein density and area five times for ten separate leaves. From these trials, the median standard deviation across the ten leaves was computed. For directly measured areas of complete specimens, the user error ( $0.024 \ln \text{mm}^2$ ) was added to the standard error of the morphotype-site population (median =  $0.18 \ln \text{mm}^2$ ) via quadrature. For inferences of area from the inverse of 2° vein density, we propagated four uncertainties with Monte Carlo simulations: the user error ( $0.096 \log_{10} [\text{cm cm}^{-2}]^{-1}$ ), the standard error of the morphotype-site population (median =  $0.039 \log_{10} [\text{cm cm}^{-2}]^{-1}$ ), and the standard errors of the slope and intercept terms from the ordinary least-squares regression.

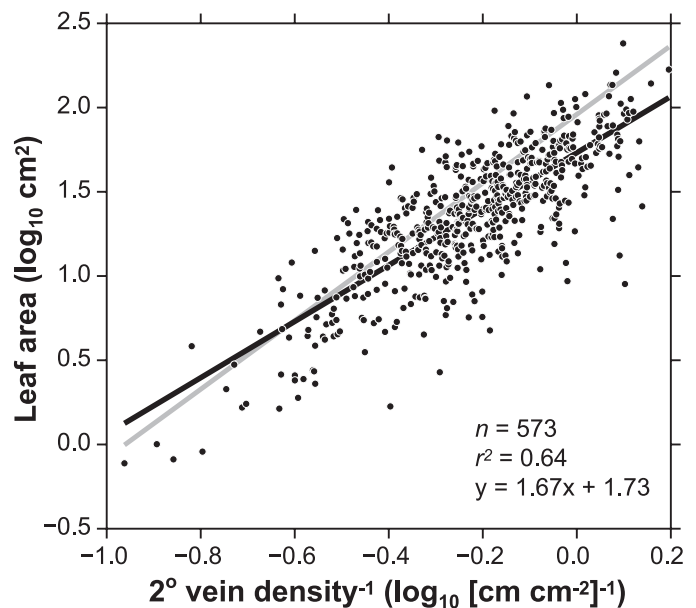


FIG. 3.—Relationship between second-order vein density and leaf area. These data were used to create the Williston Basin regression (black line). Gray line is the regression based on extant vegetation from Sack et al. (2012) ( $y = 2.04x + 1.96$ ;  $n = 386$ ;  $r^2 = 0.80$ ).

To test how leaf-size biasing may effect estimates of MAP, we used the leaf-area analysis regression of Wilf et al. (1998):  $\ln(\text{MAP}) = 0.548 \times \ln(A) + 0.768$ , where A is leaf area ( $\text{mm}^2$ ) and MAP has cm units.

## RESULTS

### Strength of Vein Scaling Relationship

We observe a strong relationship between the inverse of 2° vein density and leaf area in our 573 complete leaves (Fig. 3):  $A = 1.67 \times \text{SVD}^{-1} + 1.73$ , where A is leaf area ( $\log_{10}[\text{cm}^2]$ ) and  $\text{SVD}^{-1}$  is inverse 2° vein density ( $\log[\text{cm cm}^{-2}]^{-1}$ ). We call this the Williston Basin (WB) regression. The relationship is not affected by vein architecture (pinnate vs. palmate), age (Hell Creek vs. Fort Union Formations), or sedimentary facies (e.g., channel, pond) (see the Online Supplemental File). The regression  $r^2$  is 0.64 and standard error is  $0.235 \log_{10}(\text{cm}^2)$ , or +72% / -42% relative to the mean in linear space. This relationship is similar to, but not quite as strong as, the relationship observed by Sack et al. (2012) in extant vegetation (slope = 2.04; y-intercept = 1.96;  $n = 386$ ,  $r^2 = 0.80$ , standard error = 0.235).

### Leaf-Size Bias

The Sack et al. (2012) regression has a tendency to overpredict leaf area over most of the range in 2° vein density captured in our fossil data set (compare gray and black lines in Fig. 3). Indeed, for the 41 morphotype-site pairs, the Sack et al. (2012) regression overpredicts leaf area in the complete specimens by 35% on average (Fig. 4). This means that, for our fossil data set, it is not appropriate to compare leaf areas that have been directly measured to leaf areas that have been inferred with the Sack et al. (2012) regression. Instead, we use vein-scaling to infer area from both complete and fragmented leaves. In this way, any model artifacts should be present in both calculation sets, leading to a more accurate comparison, albeit with less precision because—for complete leaves—inferring area from vein scaling is less precise than direct measurements (compare x- and y-axis errors in Fig. 4). This problem is not present in the WB regression

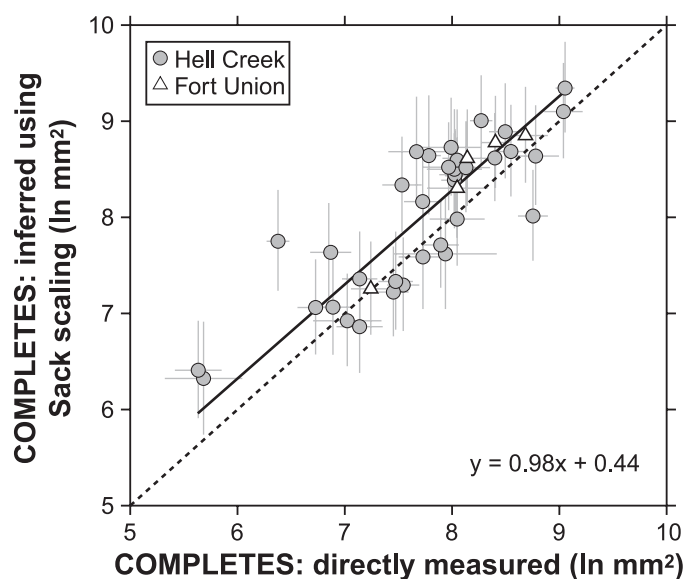


FIG. 4.—Scaling for complete leaves between directly measured leaf area and inferred leaf area using the regression from Sack et al. (2012). Each symbol is a morphotype-site pair. Error ranges correspond to the 16<sup>th</sup> and 84<sup>th</sup> percentiles. The SMA regression is the solid black line; its equation is in the bottom right. Dashed line is  $y = x$ . The Sack et al. (2012) regression generally over-predicts leaf area in Williston Basin fossil sites.

because all of the complete leaves comprising the morphotype-site pairs are also present in the regression itself. Nonetheless, in order to maintain a uniform methodology (but with the trade-off of less precision), we adopt a similar strategy when assessing leaf-size biasing with the WB regression.

We find a small bias in the areas of complete versus fragmented leaves (Fig. 5). Within morphotype-site pairs, on average we reconstruct fragmented leaves to be larger than complete leaves: 11% using the Sack et al. (2012) regression and 9% using the WB regression. The consistent

result between the two regressions is encouraging, considering the regression slopes and y-intercepts are somewhat different. However, the signal is noisy: the average standard deviation is  $\pm 36\%$ . As a result, a paired-sample t-test applied to the data shown in Figure 5 reveals that we cannot reject the null hypothesis that leaf areas inferred from complete and fragmented specimens are the same ( $P = 0.11$  for both Sack and WB regressions). Similarly, for both SMA regressions (black lines in Fig. 5) we cannot reject the null hypotheses that the slope = 1 and y-intercept = 0 ( $P > 0.80$  for all tests). We also note that the average size difference is even smaller (4%) if fragments reconstructed with the WB regression are instead compared to directly measured complete leaves. Lastly, we observe that with greater sampling effort the magnitude of the size bias tends to diminish (Fig. 6), suggesting a signal:noise problem with results based on fewer leaves.

In sum, we detect a small but statistically insignificant size bias, and the true bias may be even smaller in light of our analysis of sampling effort. Nonetheless, if we assume that fossil fragments were originally 10% larger than their complete companions, then MAP's estimated from leaf-area analysis should be adjusted by +6%. This adjustment is considerably smaller than the standard error associated with the proxy (+43% / -30%; Wilf et al. 1998).

## DISCUSSION

The lack of a statistically significant size bias between complete and fragmented fossil leaves in the Williston Basin is somewhat surprising in light of some (but not all) observations in present-day forests, where fresh litter is often skewed towards smaller leaves relative to nearby vegetation (Roth and Dilcher 1978; Burnham 1989; Christophel and Greenwood 1989; Greenwood 1992). Furthermore, most of our fossils come from channel deposits, and so may be expected to have experienced stronger size-sorting via water transport relative to fossils preserved in (para)-autochthonous deposits (see Introduction). We think this disconnect is caused by fossil and extant studies capturing different, but partly overlapping, taphonomic processes (e.g., Fig. 1). Fossil studies such as ours capture the full set of taphonomic processes—starting when the leaves

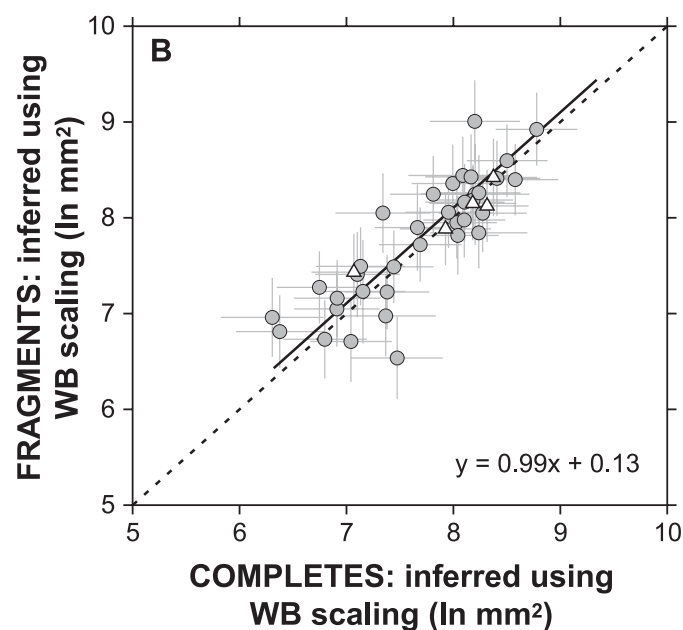
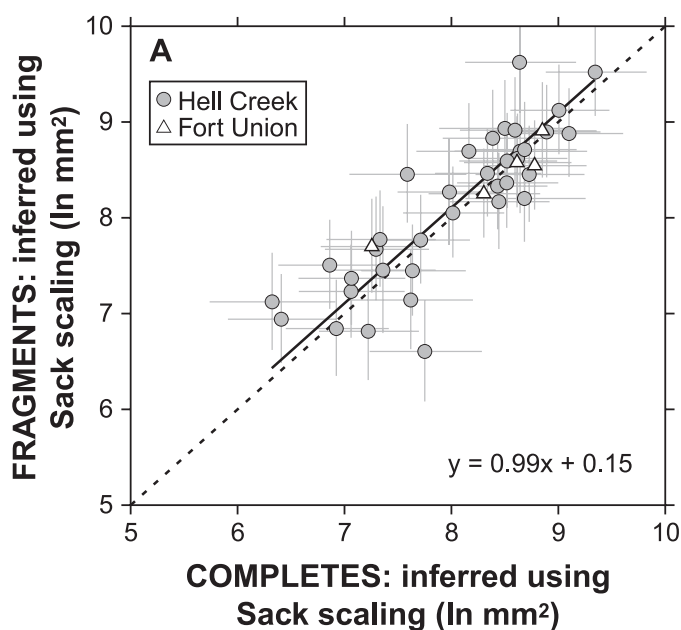


FIG. 5.—Comparing inferred area from complete leaves against inferred area from fragmented leaves with the (A) Sack et al. (2012) regression and (B) Williston Basin (WB) regression. Each symbol is a morphotype-site pair. Error ranges correspond to the 16<sup>th</sup> and 84<sup>th</sup> percentiles. The SMA regressions are the solid black lines, with the corresponding equations in the bottom right. Dashed lines are  $y = x$ .

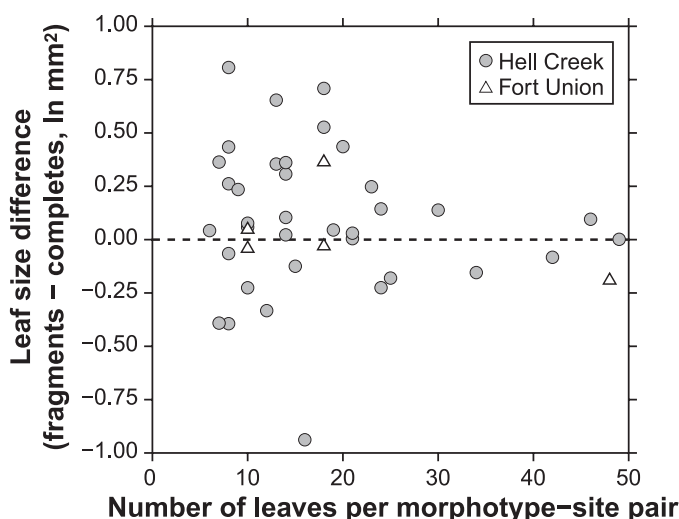


FIG. 6.—The impact of sampling effort on the magnitude of the leaf-size bias. The leaf-size differences come from Figure 5B. Dashed line corresponds to no size difference. With greater sampling, the leaf-size bias generally diminishes.

were alive and ending when excavated from rock—but only for the (small) subset of leaves that actually fossilized. Leaves that do not fossilize are lost (a “known unknown”); unlike in extant studies, we do not know the original leaf-size distribution of the forest. Thus, it is possible that fossilized leaves—both complete and fragmented—are smaller in general than the original stock of living leaves. This interpretation could be strengthened with further work on vein scaling at other fossil sites, as well as more litter studies in extant forests.

Our Williston Basin localities comprise a robust initial case study because most of the leaves preserve 1° and 2° veins and because the interpreted depositional settings are mostly the same (channel deposits; see Methods). Thus, any taphonomic sorting should be consistent. Care should be taken if comparing leaves from different depositional settings. A separate issue is diagenetic shrinkage (Blonder et al. 2012). Shrinkage should be minimal when burial occurs in water-saturated conditions (Blonder et al. 2012) such as the channel deposits in our study, but could be substantial when this condition is not met, for example in some ash-fall deposits or charcoalfied floras. Importantly, shrinkage should not bias the construction of a calibration based on complete leaves (e.g., Fig. 3), nor the comparison between complete and fragmented leaves with the same taphonomic history (e.g., Fig. 5), because shrinkage proportionately affects leaf area and vein density equally. But shrinkage would bias comparisons of area with present-day leaves, along with any associated climatic or evolutionary information. A final issue is sampling effort. Because the calibration between vein density and measured leaf area has large uncertainties (Fig. 3), our conclusion of little-to-no size-biasing depends strongly on analyzing a large number of species-site pairs (Fig. 5) and a large number of leaves within each species-site pair (Fig. 6).

In summary, in the Williston Basin we find that fossil fragments do not provide any new information about original leaf size for species that are already represented by complete specimens (beyond greater sampling), although the comparison is noisy ( $1\sigma = \pm 36\%$ ). If this pattern is generally true, we see at least two positive and important implications. First, previous interpretations of climate and evolutionary history based only on the areas of complete leaves do not suffer from the type of size-biasing tested in our study. Second, complete and fragmented leaves can be analyzed together to create a more integrated and robust understanding of leaf area. Merkhofer et al. (2015), for example, leveraged this advantage in their biogeographic study of site-mean leaf area at Laguna del Hunco. Ultimately, applications

such as these may be the lasting legacy of inferring leaf area from vein scaling (Sack et al. 2012).

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#### SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive: <http://www.sepm.org/pages.aspx?pageid=332>.

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