

TECHNICAL ARTICLE

Leaf mechanical resistance in plant trait databases: comparing the results of two common measurement methods

Lucas Enrico^{1,*}, Sandra Díaz¹, Mark Westoby² and Barbara L. Rice^{2,‡}

¹Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC) and FCEFyN, Universidad Nacional de Córdoba, CC 495, 5000 Córdoba, Argentina and ²Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

*For correspondence. E-mail lenrico@com.uncor.edu

‡Deceased June 2009.

Received: 10 April 2015 Returned for revision: 8 June 2015 Accepted: 17 August 2015

● **Background and Aims** The influence of leaf mechanical properties on local ecosystem processes, such as trophic transfer, decomposition and nutrient cycling, has resulted in a growing interest in including leaf mechanical resistance in large-scale databases of plant functional traits. ‘Specific work to shear’ and ‘force to tear’ are two properties commonly used to describe mechanical resistance (toughness or strength) of leaves. Two methodologies have been widely used to measure them across large datasets. This study aimed to assess correlations and standardization between the two methods, as measured by two widely used apparatuses, in order to inter-convert existing data in those global datasets.

● **Methods** Specific work to shear (W_{SS}) and force to tear (FT) were measured in leaves of 72 species from south-eastern Australia. The measurements were made including and excluding midribs. Relationships between the variables were tested by Spearman correlations and ordinary least square regressions.

● **Key Results** A positive and significant correlation was found between the methods, but coefficients varied according to the inclusion or exclusion of the midrib in the measurements. Equations for prediction varied according to leaf venation pattern. A positive and significant ($r = 0.90$, $P < 0.0001$) correlation was also found between W_{SS} values for fresh and rehydrated leaves, which is considered to be of practical relevance.

● **Conclusions** In the context of broad-scale ecological hypotheses and used within the constraints recommended here, leaf mechanical resistance data obtained with both methodologies could be pooled together into a single coarser variable, using the equations provided in this paper. However, more detailed datasets of FT cannot be safely filled in with estimations based on W_{SS} , or vice versa. In addition, W_{SS} values of green leaves can be predicted with good accuracy from W_{SS} of rehydrated leaves of the same species.

Key words: Comparative plant ecology, force to tear, leaf biomechanics, leaf tensile strength, leaf toughness, leaf venation, specific work to shear, plant trait databases, work to shear.

INTRODUCTION

Previous work in comparative plant ecology has identified mechanical resistance (either toughness or strength) of leaves as a key indicator of the relative carbon investment in structural protection of photosynthetic tissue against abiotic (e.g. wind, drought) and biotic (e.g. chewing, trampling) mechanical damage. Leaf mechanical resistance depends on different properties of leaves (Westbrook *et al.*, 2011), such as leaf age (Nichols-Orians and Schultz, 1989), density (Onoda *et al.*, 2011; Westbrook *et al.*, 2011) or venation pattern (Niklas, 1999; Roth Nebelsick *et al.*, 2001; Zhang *et al.*, 2004), as well as on the environment where the leaf is growing (i.e. sun or shade; Onoda *et al.*, 2008; Kitajima *et al.*, 2013). Because plants with hard leaves can survive longer in habitats with low availability of soil nutrients or water (Grubb, 1992; Cornelissen *et al.*, 1997, 2003; Grime *et al.*, 1997; Wright and Westoby, 2002; Balsamo *et al.*, 2006; Kitajima and Poorter, 2010), leaf mechanical resistance has been identified as one of the fundamental traits defining the conservative versus acquisitive plant strategies that influence local ecosystem processes such as trophic transfer, decomposition and nutrient cycling (Cornelissen *et al.*, 1999; Pérez-Harguindeguy *et al.*, 2000, 2003, 2013; Díaz *et al.*, 2004;

Read and Stokes, 2006). This has resulted in a growing interest in including leaf mechanical properties in large-scale databases of plant functional traits.

Tearing and shearing tests are two common methods to quantify overall leaf mechanical resistance (i.e. comprising epidermis, mesophyll and veins). The variables measured in such tests are force to tear (an indicator of leaf strength, or the mechanical resistance to a pulling-apart force, hereafter FT) and specific work to shear (an indicator of leaf toughness, or the mechanical resistance to a perpendicular shearing force, hereafter W_{SS}), respectively. FT has been measured widely (approx. 3600 species, Onoda *et al.*, 2011; Pérez-Harguindeguy *et al.*, 2013; TRY database, <https://www.try-db.org/TRYWeb/Home.php>) and the apparatus used to do most of the measurements (approx. 2700 species, from more than 15 countries) is low-tech, hand-cranked (no source of electrical power required), inexpensive and highly portable (for a detailed description see Hendry and Grime, 1993). There are various W_{SS} measurement apparatuses (see Wright and Illius, 1995; Darvell *et al.*, 1996; Aranwela *et al.*, 1999; Wright and Cannon, 2001) that have been proved to produce similar W_{SS} values in standard materials (Onoda *et al.*, 2011). Unlike apparatus for FT

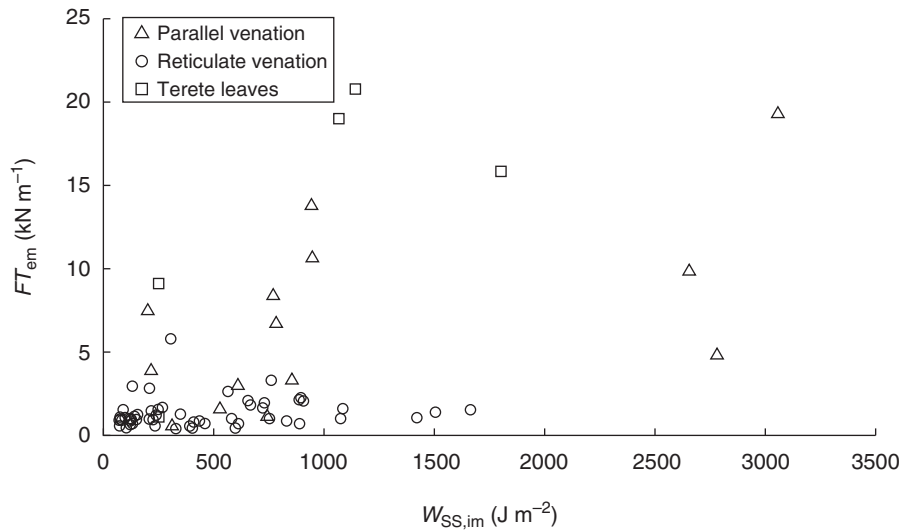


Fig. 1. Relationship (untransformed data) between specific work to shear ($W_{SS,im}$, including midrib) and force to tear (FT_{em} , excluding midrib) of fresh leaves with parallel venation, reticulate venation or terete leaves (as indicated in the key).

measurement, W_{SS} measurement devices allow control of cut angle and speed (increasing measurement precision), but they are electronic devices that tend to be more difficult to construct and transport, and fairly expensive (Moles *et al.*, 2011; Pérez-Harguindeguy *et al.*, 2013). As a consequence, existing W_{SS} measurements, although numerous (approx. 1200 species, Onoda *et al.*, 2011), are geographically more restricted. A cross-calibration between studies using these two methods is therefore of obvious interest for several researchers worldwide focusing on comparative plant ecology as well as on vegetation and biogeochemistry modelling (Sanson *et al.*, 2001; Cornelissen *et al.*, 2003; Kattge *et al.*, 2011; Pérez-Harguindeguy *et al.*, 2013).

The main objective of this work was to carry out a comparison and build a cross-calibration between FT as measured with the apparatus presented by Hendry and Grime (1993) and W_{SS} as measured by the apparatus presented by Wright and Cannon (2001). In view of the logistical problems involved in carrying this particular W_{SS} apparatus to different field sites (Moles *et al.*, 2011), a second objective was to look for a correlation between values of W_{SS} for fresh and rehydrated (previously collected and air-dried) leaves. A good correlation between both W_{SS} values could provide the opportunity to collect leaves in sites far from the laboratories in which the few existing apparatuses are normally located, allowing researchers to measure W_{SS} in a wider range of species around the world.

MATERIALS AND METHODS

Species collection

From a total of 72 species (listed in Supplementary Data Table S1) from south-eastern Australia, we collected four young but fully expanded, hardened and outer-canopy leaves from each of six plant individuals. We collected leaves of a variety of sclerophyllous species, involving different families and growth forms (grasses, shrubs and trees) as well as different leaf shapes and venation patterns. Leaves were placed in previously water-

sprayed plastic bags, and stored in a cool box until measurement. In cases where the major photosynthetic organs were not leaves (e.g. phyllodinous members of the genus *Acacia*) we considered those organs as leaves and treated them accordingly. We classified leaves into three categories according to their venation pattern: parallel veined, reticulate veined or teretes (for those acicular leaves without a clear pattern of venation to the naked eye).

Force to tear (FT)

We measured the force needed to tear a leaf or leaf fragment divided by its width (Cornelissen and Thompson, 1997), expressed in kN m^{-1} , using the apparatus described by Hendry and Grime (1993). From the group of leaves previously collected, six leaves per species, from different individuals, were cut parallel to the main axis, at the central part of the leaf. From the central section of each leaf, two fragments were obtained, one of them excluding the midrib (for a graphical representation see Onoda *et al.*, 2011, fig. 1b) and the other one including it. While the first way of measuring FT (excluding midrib) is the one recommended by Pérez-Harguindeguy *et al.* (2003) and has been applied in most existing FT databases worldwide, standard W_{SS} measurement methodology includes the midrib (Wright and Cannon, 2001). Consequently, we wanted to test if a possible lack of correlation between the methods could be related to the exclusion of the midrib in one and its inclusion in the other. For species that lack a distinctive midrib, such as some graminoids and species with acicular or parallel veined leaves, FT was measured only in one fragment, and the value obtained was then used in both sets of data (FT including midrib, hereafter FT_{im} , and FT excluding midribs, hereafter FT_{em}). For this reason, these species were not included in correlations between values of FT_{im} and FT_{em} (see Table 1) for which we only used species with an evident midrib.

Some previous publications (e.g. Pérez Harguindeguy *et al.*, 2000; Cornelissen *et al.*, 2003; Díaz *et al.*, 2004) have referred

TABLE 1. Spearman correlation coefficients (r) between force to tear (FT ; in kN m^{-1}) and specific work to shear (W_{SS} ; in J m^{-2})

	FT_{im}	FT_{em}	$W_{SS,im}$	$W_{SS,em}$
FT_{em}	0.79*** $n = 43^\dagger$			
$W_{SS,im}$	0.71*** $n = 72$	0.47*** $n = 72$		
$W_{SS,em}$	0.75*** $n = 72$	0.58*** $n = 72$	0.91*** $n = 42^\dagger$	
$W_{SS,rim}$	0.76*** $n = 55$	0.47** $n = 55$	0.90*** $n = 55$	0.86*** $n = 55$

Abbreviations: im, including midrib; em, excluding midrib; rim, rehydrated, including midrib. ** $P \leq 0.001$; *** $P \leq 0.0001$.

† Calculated only for those species in which a midrib was apparent. Values of FT and W_{SS} are shown in Supplementary Data Table S1.

to FT as ‘leaf tensile strength’ (expressed in kN m^{-1} , or most commonly its equivalent, N mm^{-1}). However, strictly speaking, leaf tensile strength includes one more variable, leaf thickness, and it is expressed in kN m^{-2} (or its equivalent N mm^{-2}).

Specific work to shear (W_{SS})

We measured the work per unit cross-section area needed to fracture a leaf with a single blade, at a constant speed and shearing angle of 20° , using the apparatus described by Wright and Cannon (2001). From the group of leaves previously collected, five leaves per species, from different individuals, were cut at right angles to the midrib, at the widest point along the lamina (or halfway between base and tip if this was difficult to determine). W_{SS} values were expressed in J m^{-2} . As in FT , we measured each species including and excluding midrib. For those species with apparent midribs, values of W_{SS} excluding midrib were obtained by detecting and subtracting the signature of midrib portions of the leaf in the output files.

Specific work to shear in rehydrated leaves

We selected a subset of 55 species from those in Supplementary Data Table S1, representing as many families and genera as possible. From the same pool of leaves used for FT and W_{SS} measurements, we set aside five leaves per species, from different individuals. These leaves were air-dried for 15 d and then rehydrated by wrapping them in moist paper and putting them in sealed plastic bags in the fridge for 24 h (Pérez Harguindeguy et al., 2013). We then measured W_{SS} in five leaves, in the same way as in fresh leaves.

Data analysis

We compared the mechanical resistance values obtained with the two methods, as well as W_{SS} for fresh and rehydrated leaves, by using Spearman correlation analyses. To find an equation to inter-convert mechanical resistance values obtained with the two methods, we analysed the relationship between FT and W_{SS} data using ordinary least square (OLS) regressions. The most functionally meaningful comparisons would be between FT and W_{SS} both with midrib on the one hand, and between FT and W_{SS} both without midrib. However, the vast majority of datasets contain FT without midrib (e.g. Díaz et al.,

2004) or W_{SS} with midrib (e.g. Wright and Westoby, 2002), so comparison of these was also relevant. A first exploration of the data showed different relationships between these variables according to the venation pattern of the leaves (parallel-venated, reticulate-venated or tereted). Therefore, we included the categorical variable ‘venation type’ in the analysis by incorporating dummy variables in the regression analysis. We therefore present correlation coefficients and the inter-conversion equations for all these possible combinations of FT and W_{SS} , with and without midrib.

RESULTS

Across the 72 species measured, FT values ranged from 0.34 kN m^{-1} (*Astrotricha floccosa*) to 20.8 kN m^{-1} (*Hakea tephrosperma*), while W_{SS} ranged from 60 J m^{-2} (*Senna artemisioides*) to 3058 J m^{-2} (*Xanthorrhoea arborea*). Mean FT values (both including and excluding midrib) of reticulate veined leaves (mainly from trees and shrubs) were significantly lower than those of terete and parallel veined leaves (from some trees and grasses) (Fig. 1). Mean W_{SS} values differed significantly only between reticulate and parallel veined leaves (data not shown). In general, FT measurements were less sensitive in detecting differences among relatively more tender leaves (mostly reticulate leaves, towards the left end of the x -axis in Fig.1) than W_{SS} measurements (see left extreme of Fig. 1).

Positive association between FT and W_{SS}

All possible correlations between FT and W_{SS} either including midrib (FT_{im} , $W_{SS,im}$) or excluding it (FT_{em} , $W_{SS,em}$) were significant and positive (Table 1). The strongest associations involved FT_{im} vs. $W_{SS,em}$ ($r=0.75$) and FT_{im} vs. $W_{SS,im}$ ($r=0.71$). The association between FT_{em} and $W_{SS,im}$ was weaker but still significant ($r=0.47$).

All species whose leaves were measured with and without midrib showed the expected displacement to lower mechanical resistance values when the midrib was excluded (Supplementary Data Table S1). Table 1 shows also that FT_{im} and FT_{em} are strongly correlated ($r=0.79$), as are $W_{SS,im}$ and $W_{SS,em}$ ($r=0.91$). This indicates that even when the midrib influences leaf mechanical resistance by increasing resistance to fracture, its inclusion or exclusion does not account for the relatively low correlation between values obtained using the two devices.

The linear regression equations to obtain W_{SS} values from FT values and vice versa are shown in Table 2. The most practically relevant relationship in terms of comparison of pre-existing databases is $W_{SS,im}$ vs. FT_{em} ; this is therefore displayed in Fig. 2. Although the one with the lowest R^2 value (0.71), the relationship to obtain FT_{em} from $W_{SS,im}$ was significant. The opposite calculation to obtain $W_{SS,im}$ from FT_{em} , however, showed a low R^2 (0.32). A complete list of the equations is shown in Table 2.

W_{SS} of fresh vs. rehydrated leaves

We found a strong association between W_{SS} values of fresh ($W_{SS,im}$) and rehydrated ($W_{SS,rim}$) leaves ($r=0.90$, Table 1 and Fig. 2). On average, rehydrated values were twice as high as fresh values. $W_{SS,rim}$ values were higher than $W_{SS,im}$ values for the same species in all but three cases (*Hakea dactyloides*,

TABLE 2. Linear regression equations and coefficients (R^2) between force to tear (FT ; in kN m^{-1}) and specific work to shear (W_{SS} ; in J m^{-2}) for leaves with different venation types

Parallel veined	Reticulate veined	Terete	R^2
W_{SS} to FT			
$FT_{im} = 2.499 + 0.0053 W_{SS,im}$	$FT_{im} = 0.753 + 0.0029 W_{SS,im}$	$FT_{im} = 5.019 + 0.009 W_{SS,im}$	0.79
$FT_{em} = 3.426 + 0.003 W_{SS,im}$	$FT_{em} = 1.165 + 0.0003 W_{SS,im}$	$FT_{em} = 5.019 + 0.009 W_{SS,im}$	0.71
$FT_{im} = 2.859 + 0.0055 W_{SS,em}$	$FT_{im} = 0.554 + 0.0044 W_{SS,em}$	$FT_{im} = 5.173 + 0.0108 W_{SS,em}$	0.80
$FT_{em} = 3.446 + 0.0034 W_{SS,em}$	$FT_{em} = 1.030 + 0.0008 W_{SS,em}$	$FT_{em} = 5.173 + 0.0108 W_{SS,em}$	0.72
FT to W_{SS}			
$W_{SS,im} = -24.913 + 134.697 FT_{im}$	$W_{SS,im} = 139.108 + 156.8648 FT_{im}$	$W_{SS,im} = 110.686 + 60.3918 FT_{im}$	0.65
$W_{SS,em} = -147.754 + 136.534 FT_{im}$	$W_{SS,em} = 100.527 + 118.107 FT_{im}$	$W_{SS,em} = 145.936 + 45.201 FT_{im}$	0.74
$W_{SS,im} = 387.709 + 104.0166 FT_{em}$	$W_{SS,im} = 384.4506 + 61.8438 FT_{em}$	$W_{SS,im} = 110.686 + 60.3918 FT_{em}$	0.32
$W_{SS,em} = 227.72 + 111.6817 FT_{em}$	$W_{SS,em} = 246.454 + 75.9719 FT_{em}$	$W_{SS,em} = 145.936 + 45.201 FT_{em}$	0.43

Equations were obtained from regression analysis from the model with dummy variables including the three types of venation. $n = 72$; im, including midrib; em, excluding midrib.

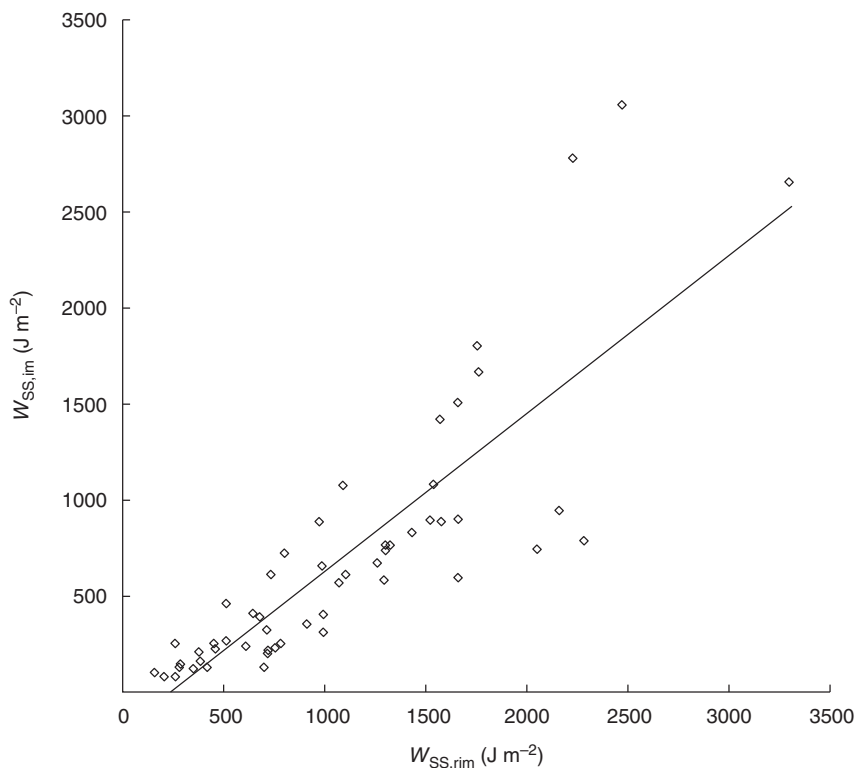


FIG. 2. Relationship between W_{SS} predicted from rehydrated leaves ($W_{SS,rim}$) and W_{SS} for green, fresh leaves ($W_{SS,im}$) both including midribs.

Xanthorrhoea arborea and *Macrozamia communis*, Supplementary Data Table S1). The OLS regression between these variables showed a high predictive capacity of $W_{SS,im}$ values on the basis of $W_{SS,rim}$ ($R^2=0.82$, $P<0.0001$, $n=55$). The equation obtained for such a conversion was:

$$\log_{10} W_{SS,im} = -0.804 + 1.181 \log_{10} W_{SS,rim}$$

DISCUSSION

Relationships between FT and W_{SS} at the species level

Both FT and W_{SS} are good indicators of leaf mechanical resistance and structural robustness (Cornelissen and Thompson,

1997; Wright and Cannon, 2001; Pérez Harguindeguy *et al.*, 2013). Our results show that they are also positively correlated. Edwards *et al.* (2000) and Read and Sanson (2003) also found a positive and significant correlation between FT and W_{SS} values for sclerophyllous leaves of Australian heath and forest systems, albeit using instrumented devices, different from those involved in the present study. However, our results indicate that values of one indicator cannot be safely predicted with precision from values of the other, particularly when trying to predict W_{SS} from FT . Predictive capacity is improved by the use of different equations for leaves with different venation patterns. In this sense we conclude that, as a general rule, individual datasets with missing values for one of these indicators cannot be safely ‘filled in’ by predicting them on the basis of the other, when available. Nevertheless, within the constraints mentioned above,

broad comparisons are possible and are the subject of the next section.

We originally suspected that a major factor affecting the fit between methods could be the exclusion of leaf midribs from most *FT* measurements and their inclusion in the W_{SS} procedure. This was confirmed when we included data of *FT* from leaves with midribs. The correlation coefficients were higher when *FT* included midribs than when *FT* excluded them (independently of including or excluding the midribs in W_{SS}). Nevertheless, the inclusion or exclusion of midribs in the case of W_{SS} seemed not to greatly alter the correlation coefficients for any of the two *FT* sets of values.

We also detected a difference in sensitiveness between the methods. In particular, *FT* seems to be less sensitive than W_{SS} in detecting differences between more tender leaves. Although highly significantly correlated, the methods compared do measure different mechanical properties, which are connected in different ways to leaf anatomy and architecture (Roth-Nebelsick *et al.*, 2001; Zhang *et al.*, 2004). The difference in sensitivity could be related to the fact that the most tender leaves in our dataset had reticulate venation, while tougher leaves had parallel venation or were terete (as in *Hakea teretifolia* and *H. tephrosperma*). A greater number of veins per unit width, orientated parallel to the main axis of the leaf, should lend more resistance to a tearing force than to a shearing force (Zhang *et al.*, 2004).

Calculation of W_{SS} values from rehydrated leaves

Based on the good fit detected between W_{SS} values for fresh and rehydrated leaves, we conclude that W_{SS} of green leaves can be predicted with good accuracy from W_{SS} of rehydrated leaves. This opens up a new practical advantage, namely to obtain W_{SS} values by air-drying leaf samples of interest and measuring at those laboratories where the W_{SS} measurement apparatus is available. Note, however, that we could not successfully measure W_{SS} in the more tender-leaved species of our dataset (see Supplementary Data Table S1) because when rehydrated and cut, these leaves tend to be dragged between the blade and the anvil of the apparatus. Therefore, the good correlation detected in the mostly sclerophyllous species that are common in the Australian flora (Tallis, 1991) may not apply to more tender-leaved plants. As a point of reference, in a preliminary test on a set of 34 Argentine species, those softer than 0.40 kN m^{-1} in the tearing test could not be successfully rehydrated and tested for W_{SS} because they were dragged during the measurement process. Another note of caution relates to drying history of rehydrated leaves. The material used here was air-dried shortly (15 d) before rehydration. We do not yet know whether the good fit between fresh and rehydrated leaves would persist if the latter were dried using other methods (e.g. fast drying in an oven) and/or had remained dry for long periods of time (e.g. in herbaria), as recently found for other leaf traits such as specific leaf area (Torrez *et al.*, 2013).

Combining *FT* and W_{SS} in global databases

The lack of a good enough fit between *FT* and W_{SS} to accurately predict one from the other in detailed studies does not

mean that there is no hope of ‘compiling’ these two properties in a useful way as general indicators of leaf mechanical resistance in broad-scale comparisons. There is now growing international interest in using large, communal databases to test ecological hypotheses and to inform regional- to global-scale vegetation models (e.g. the TRY database, <https://www.try-db.org/TryWeb/Home.php>; Kattge *et al.*, 2011). Leaf mechanical resistance is considered an important trait in the assessment of several ecosystem properties, such as decomposition, canopy longevity or trophic transfer to herbivores (Gallardo and Merino, 1993; Cornelissen *et al.*, 1999; Pérez-Harguindeguy *et al.*, 2000, 2003; Díaz *et al.*, 2004; Vaieretti *et al.*, 2005; Read and Stokes, 2006), and therefore highly valued in these initiatives; yet the number of leaf mechanical resistance records is comparatively low. For example, there are only about 2819 species in the largest compilation for leaf mechanical resistance published so far in a single work, measured in at least three different ways (Onoda *et al.*, 2011). In this context, and considering the new global datasets available, the ability to interconvert measurements taken with different methods could dramatically increase the number of records. Can we use the equations developed in this article to achieve this? We conclude that the answer depends on the question at hand. If one is to predict with accuracy the mechanical resistance value for a particular species, so that it could be regarded by other users of the databases as the ‘true’ value for the species for future study, and be incorporated permanently in collective data repositories, then we do not recommend their application. However, if the question at hand is about general leaf mechanical robustness and its links to ecosystem properties at the broad scale (e.g. with decomposition, herbivory and nutrient turnover rates), and the purpose is to identify broad leaf mechanical resistance categories (e.g. very tender, intermediate, very tough), then data of leaf mechanical resistance obtained with both methodologies could be pooled together into a single, rough, ad hoc ‘leaf mechanical resistance’ variable, using the equations provided in this article. If used within the constraints recommended here, this approach could significantly contribute to increase the representation of a highly relevant component of leaf strategy in broad-scale functional trait studies.

How should we maximize inter-convertibility in future measurements of leaf mechanical resistance via *FT* or W_{SS} ? Our findings offer little hope for shortcuts. The most suitable way, according to our results, would be to obtain *FT* on the basis of W_{SS} values (either including or excluding midrib for both parameters), rather than the opposite (to calculate W_{SS} on the basis of *FT* values), which would have been more practical considering restrictions due to the different portability of the apparatuses. The practical advantages of estimating *FT* on the basis of W_{SS} include the ability to measure how easily leaves will tear off when being pulled by, for example, a grazer, in those datasets created for originally different purposes. Regarding new databases, considering the high portability and low cost of the *FT* measurement apparatus, we recommend running *FT* measurements directly on the same species that are to be subjected to the W_{SS} determinations, either by transporting an *FT* apparatus to laboratories where W_{SS} measurements are to take place, or by measuring *FT in situ*, and transporting dehydrated leaves to such places.

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of Table S1: mean leaf mechanical resistance values.

ACKNOWLEDGEMENTS

We thank Tanja Lenz, Fiona Scarff and Kate Hughes for field assistance, Ian Wright for advice on W_{SS} measurements and supplementary W_{SS} data, Fernando Casanoves for statistical support and Tina Lohitharajah for measurement of W_{SS} in some rehydrated leaves. This work was supported by the Australian Research Council (ARC), by the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET, Argentina) through its research grants PIP 01532CO and 00103CO, PICT-2013-0554 and the Inter-American Institute for Global Change Research SGP-CRA2015 (which were supported by the National Science Foundation grants GEO-0452325 and GEO-1138881).

LITERATURE CITED

- Aranwela N, Sanson G, Read J. 1999. Methods of assessing leaf-fracture properties. *New Phytologist* **144**: 369–383.
- Balsamo RA, Vander Willigen C, Bauer AM, Farrant J. 2006. Drought tolerance of selected *Eragrostis* species correlates with leaf tensile properties. *Annals of Botany* **97**: 985–991.
- Cornelissen JHC, Thompson K. 1997. Functional leaf attributes predict litter decomposition rate in herbaceous plants. *New Phytologist* **135**: 109–114.
- Cornelissen JHC, Werger MJA, Castro-Díez P, Van Rheenen JWA, Rowland AP. 1997. Foliar nutrients in relation to growth, allocation and leaf traits in seedlings of a wide range of woody plant species and types. *Oecologia* **111**: 460–469.
- Cornelissen JHC, Pérez-Harguindeguy N, Díaz S, et al. 1999. Leaf structure and defence control litter decomposition rate across species, life forms and continents. *New Phytologist* **43**: 191–200.
- Cornelissen JHC, Lavorel S, Garnier E, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335–380.
- Darvell BW, Lee PKD, Yuen TDB, Lucas PW. 1996. A portable fracture toughness tester for biological materials. *Measurement Science and Technology* **7**: 954–962.
- Díaz S, Hodgson JG, Thompson K et al. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.
- Edwards C, Read J, Sanson G. 2000. Characterising sclerophylly: some mechanical properties of leaves from heath and forest. *Oecologia* **123**: 158–167.
- Gallardo A, Merino J. 1993. Leaf decomposition in two Mediterranean ecosystems of Southwest Spain – influence of substrate quality. *Ecology* **74**: 152–161.
- Grime JP, Thompson K, Hunt R, et al. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**: 259–281.
- Grubb PJ. 1992. A positive distrust in simplicity lessons from plant defences and from competition among plants and among animals. *Journal of Ecology* **80**: 585–610.
- Hendry GAF, Grime JP. 1993. *Methods in comparative plant ecology. A laboratory manual*. London: Chapman & Hall.
- Kattge J, Ogle K, Boenisch G et al. 2011. A generic structure for plant trait databases. *Methods in Ecology and Evolution* **2**: 202–213.
- Kitajima K, Poorter L. 2010. Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytologist* **186**: 708–721.
- Kitajima K, Cordero RA, Wright SJ. 2013. Leaf life span spectrum of tropical woody seedlings: effects of light and ontogeny and consequences for survival. *Annals of Botany* **112**: 685–699.
- Moles AT, Wallis IR, Foley WJ et al. 2011. Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytologist* **191**: 777–788.
- Nichols-Orians CM, Schultz JC. 1989. Leaf toughness affects leaf harvesting by the leaf-cutter ant *Ana cephalores* (L.) (Hymenoptera: Formicidae). *Biotropica* **21**: 80–83.
- Niklas KJ. 1999. A mechanical perspective on foliage leaf form and function. *New Phytologist* **143**: 19–31.
- Onoda Y, Schieving F, Anten NPR. 2008. Effects of light and nutrient availability on leaf mechanical properties of *Plantago major*: a conceptual approach. *Annals of Botany* **101**: 727–736.
- Onoda Y, Westoby M, Adler PB et al. 2011. Global patterns of leaf mechanical properties. *Ecology Letters* **14**: 301–312.
- Pérez-Harguindeguy N, Díaz S, Cornelissen JHC, Vendramini F, Cabido M, Castellanos A. 2000. Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant Soil* **218**: 21–30.
- Pérez-Harguindeguy N, Díaz S, Vendramini F, Cornelissen JHC, Gurvich DE, Cabido M. 2003. Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology* **28**: 642–650.
- Pérez-Harguindeguy N, Díaz S, Garnier E et al. 2013. New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167–234.
- Read J, Sanson GD. 2003. Characterizing sclerophylly: the mechanical properties of a diverse range of leaf types. *New Phytologist* **160**: 81–99.
- Read J, Stokes A. 2006. Plant biomechanics in an ecological context. *American Journal of Botany* **93**: 1546–1565.
- Roth-Nebelsick A, Uhl D, Mosbrugger V, Kerp H. 2001. Evolution and function of leaf venation architecture: a review. *Annals of Botany* **87**: 553–566.
- Sanson G, Read J, Aranwela N, Clissold F, Peeters P. 2001. Measurement of leaf biomechanical properties in studies of herbivory: opportunities, problems and procedures. *Austral Ecology* **26**: 535–546.
- Tallis JH. 1991. *Plant community history. Long-term changes in plant distribution and diversity*. London: Chapman & Hall.
- Torrez V, Jørgensen PM, Zanne AE. 2013. Specific leaf area: a predictive model using dried samples. *Australian Journal of Botany* **61**: 350–357.
- Vaieretti MV, Pérez Harguindeguy N, Gurvich DE et al. 2005. Decomposition dynamics and physico-chemical leaf quality of abundant species in a montane woodland in central Argentina. *Plant and Soil* **278**: 205–221.
- Westbrook JW, Kitajima K, Burleigh JG, Kress JW, Erickson D, Wright SJ. 2011. What makes a leaf tough? Patterns of correlated evolution between leaf toughness and demographic rates among 197 shade-tolerant woody species in a Neotropical forest. *American Naturalist* **177**: 800–811.
- Wright IJ, Cannon K. 2001. Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. *Functional Ecology* **15**: 351–359.
- Wright IJ, Westoby M. 2002. Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytologist* **155**: 403–416.
- Wright W, Illius AW. 1995. A comparative study of the fracture properties of 5 grasses. *Functional Ecology* **9**: 269–278.
- Zhang JM, Hongo A, Akimoto M. 2004. Physical strength and its relation to leaf anatomical characteristics of nine forage grasses. *Australian Journal of Botany* **52**: 799–804.