

Letters

Understanding ecological variation across species: area-based vs mass-based expression of leaf traits

This article discusses the paper by Lloyd *et al.* (2013, in this issue of *New Phytologist*, pp. 311–321), a paper that sets out to criticize the leaf economic spectrum (LES) described by Wright *et al.* (2004). Table 1 identifies the two key arguments from Lloyd *et al.* (2013) and responds to them.

The LES is a dimension of ecological variation across plant species. It concerns construction and maintenance costs of leaves, and duration of photosynthetic returns from those investments (Reich *et al.*, 1997; Wright *et al.*, 2004). The LES is underpinned by a positive relationship between leaf mass per area (LMA, reflecting investment costs) and leaf lifespan (LL, reflecting

duration of the revenue stream arising). Variation among species in LMA reflects underlying variation in quantitative anatomy such as thickness of cuticle, mesophyll and other cell layers, and the degree of structural reinforcement (Niinemets, 1999).

Photosynthetic rate on a leaf-area basis (A_{area}) does not vary nearly so widely across species as does leaf mass per area LMA (c. 40-fold vs 100-fold, in the glopnet dataset provided by Wright *et al.*, 2004 and re-analysed by Lloyd *et al.*, 2013). Also, photosynthetic rate on a mass basis (A_{mass} ; 140-fold variation) decreases with increasing LMA across species. These two statements are equivalent to each other because A_{area} divided by LMA is the same as A_{mass} . Hence, if A_{area} graphed against LMA is a horizontal relationship or nearly so, then a relationship between A_{mass} and LMA will be sloped downwards. The two statements are inter-convertible.

Lloyd *et al.* (2013) are concerned with the equivalence between these two statements. They carry out several statistical manoeuvres, but they all boil down to the fact that mass-based and area-based data contain the same evidence and can be inter-converted. They seem especially concerned that high r^2 between LMA and mass-based assimilation rate or nitrogen (N) content can equally be

Table 1 The two main arguments put by Lloyd *et al.* (2013, in this issue of *New Phytologist*, pp. 311–321) (left-hand column) as to why mass-based representation of leaf trait data should be regarded as misleading, together with our comments or responses (right-hand column)

Argument from Lloyd <i>et al.</i> (2013)	Our comments or responses
<p>Argument 1: Photosynthesis is naturally an area-based process. When it is expressed on a mass basis, the dominant axis of variation then mainly reflects leaf mass per area (LMA) variation rather than leaf-area (A_{area}) variation.</p>	<p>Response 1.1: Indeed it is true that the leaf economic spectrum (LES) reflects variation in LMA and leaf lifespan. The LES expresses differences across species in the cost of investing in a unit leaf area and in the duration of the revenue stream that arises from the investment. That is the reason why we called it the leaf economic spectrum rather than, say, the photosynthetic metabolism spectrum.</p> <p>Response 1.2: More generally we (Wright <i>et al.</i>, 2004) advocate looking at variation across species both on an area basis and on a mass basis, since both can be enlightening in complementary ways. For example, both leaf structure (LMA and associated traits) and biochemistry (e.g. nitrogen (N)) affect leaf carbon exchange processes, with these effects being partially or entirely independent of one another (Reich & Walters, 1994; Reich <i>et al.</i>, 1998; Peterson, 1999). Gas exchange occurs through surfaces (area basis), while growth over time is most often expressed on a mass per mass basis, and there are good reasons for both choices.</p> <p>Response 1.3: There is no reason to regard A_{mass} as a derived measurement vs A_{area} as a primary measurement. When assimilation A is measured in a gas cuvette, typically mass of the leaf sample and area of the leaf sample are each measured separately. A_{mass} is just as fundamental a measurement as A_{area} is. There are three primary measurements (assimilation, sample leaf mass, sample leaf area), but since the size of the sample is not informative about the biology, the variables reported are always the three ratios A_{area}, A_{mass}, LMA. Any two of these ratios can be used to calculate the third. This point extends to further measurements involving leaf N, which typically is measured on a dry mass basis in the first instance, but can be expressed as N_{mass} or N_{area}.</p>
<p>Argument 2: If there were random or 'error' variation in LMA, then this would propagate during conversion of A_{area} into A_{mass}, giving rise to negative correlation across species between A_{mass} and LMA even when there is no correlation between A_{area} and LMA.</p>	<p>Response 2.1: Certainly it is true that much if not all of the negative correlation between A_{mass} and LMA can be seen as a result of dividing A_{area} through by LMA. To put that another way, what is biologically enlightening is that A_{area} is not much correlated across species with LMA; at least as enlightening as that A_{mass} is strongly negatively correlated with LMA.</p> <p>Response 2.2: In any event, high r^2 among photosynthetic and nutrient-concentration traits and LMA is not a primary basis for identifying the LES. The primary basis is the logic of investment costs and returns on investment, and the wide spread of LMA and leaf lifespan across species, including species coexisting within the same habitat.</p> <p>Response 2.3: One of the points made by Lloyd <i>et al.</i> (2013) is that these scaling relationships depend strongly on the variances of the (log-scaled) variables relative to each other. Indeed it was for this reason that Wright <i>et al.</i> (2004) expressed relationships between variables via the standardized major-axis slope, which is the ratio of the standard deviations of the two variables, rather than via ordinary least-squares regression, where slopes are different depending which variable is treated as x and which as y.</p>

interpreted as low correlation between LMA and area-based assimilation or N. But high r^2 among traits is not the main pillar supporting the LES concept. Rather the LES rests on the logic of the trade-off between construction cost and duration of revenue from a unit of leaf area deployed.

Mass-based vs area-based data presentation has actually been under discussion over decades (Field & Mooney, 1986; Reich & Walters, 1994; Reich *et al.*, 1997, 1998, 1999; Peterson, 1999). Wright *et al.* (2004), in the paper proposing the LES, provided a page-long section titled 'Area vs mass basis of expression', elaborating what can be learned from the different presentations of equivalent data.

Central to Lloyd *et al.* (2013) is their view that area-based statements are genuine and mass-based statements are in some sense derived or artefactual. They write '... the relevant question is which of the two is the "parent" correlation: that is, the one justified on theoretical or logical grounds'. They call mass-basis data spurious (though with a degree of ambivalence): 'correlations [between A_{mass} and LMA] may be considered "spurious": Yet only spurious in the sense ... the correlations themselves are real ... [yet] requiring careful insights for their interpretation'. They coin a new term 'lulu-effect', seemingly with the intention this may sound less derogatory than 'spurious'.

The crux of the argument put forward by Lloyd *et al.* (2013) is this: 'Given that the main function of leaves is to intercept light for which the rate of arrival of photons into the plant canopy has a natural dimension of flux density (i.e. flux per unit area), then an area-based metric seems to us to be the more logical one'. In response and surely with equal logic, it can be argued that a main function of leaves is to deliver a profitable return on the investment that has been made in constructing the leaf. Since investment and return are naturally expressed in units of mass, then a mass-based representation will correspond to this argument. Perhaps the first argument will appeal more to people interested in photosynthetic physiology, and the second more to people interested in plant growth and economics. But both points of view deserve respect.

Looking at leaf metabolism and gas exchange as rates at a point in time is complementary to looking at leaves as investments, made for the purpose of a growth process over time. They are two views of the same elephant. It makes biological sense that assimilation rates on an area basis would vary across species within somewhat constrained bounds. There must be an upper bound set by the supply of light and by the problems of exchanging water for CO₂ across a surface. Low assimilation rates on an area basis are presumably disadvantaged by competition. By contrast, LMA and LL associated with a leaf surface can and do vary more widely across species. Low LMA together with short LL (and high N_{mass} and P_{mass}) is a trait-constellation capable of producing competitive returns on investment over a leaf's lifetime, but so also is high LMA together with long LL (and low N_{mass} and P_{mass}). It is this spread of LMA-strategies that is expressed by the LES. Clearly, leaves are under natural selection to meet two key criteria: considered day-by-day, they need to intercept light and carry on photosynthesis at a competitive rate; considered over the leaf's lifetime, they need to provide a positive return on the investment costs for the leaf. Investment and return are measured most obviously in units of dry matter, but it is also relevant to think about returns per unit N or phosphorus (P) invested in the leaf.

We agree with the main statistical point of Lloyd *et al.* (2013), that strong r^2 between LMA and mass-based leaf traits can correspond with the same leaf traits on an area basis being uncorrelated with LMA, or only weakly so. This point is not new. That mass- and area-bases for expression are complementary and can be interconverted via LMA is well known, as is the use of multiple regression approaches to quantify assimilation–N relationships independent of LMA (Reich *et al.*, 1998; Peterson, 1999; Wright *et al.*, 2004). Consequently the position of Lloyd *et al.* (2013), that mass basis is somehow misleading and should not be adopted, is, in our view, a step backwards rather than forwards. And we do not give credit to Lloyd *et al.*'s complaint that Wright *et al.* (2004) has somehow hindered researchers from looking at data on a leaf-area basis. That is simply untrue. Wright *et al.* (2004) explicitly advocated looking at leaf traits from both perspectives.

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References

- Field C, Mooney HA. 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ, ed. *On the economy of plant form and function*. Cambridge, UK: Cambridge University Press, 25–55.
- Lloyd J, Bloomfield K, Domingues TF, Farquhar GD. 2013. Photosynthetically relevant foliar traits correlating better on a mass vs an area basis: of ecophysiological relevance or just a case of mathematical imperatives and statistical quicksand? *New Phytologist* 199: 311–321.
- Niinemets Ü. 1999. Components of leaf dry mass per area – thickness and density – alter leaf photosynthetic capacity in reverse directions in woody plants. *New Phytologist* 144: 35–47.
- Peterson AG. 1999. Reconciling the apparent difference between mass- and area-based expressions of the photosynthesis–nitrogen relationship. *Oecologia* 118: 144–150.
- Reich PB, Ellsworth DS, Walters MB. 1998. Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology* 12: 948–958.
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- Reich PB, Walters MB. 1994. Photosynthesis–nitrogen relations in Amazonian tree species. 2. Variation in nitrogen vis-a-vis specific leaf area influences mass-based and area-based expressions. *Oecologia* 97: 73–81.
- Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA* 94: 13730–13734.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS, Cornelissen JHC, Diemer M *et al.* 2004. The world-wide leaf economics spectrum. *Nature* 428: 821–827.

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