*New Idea***Reducing size to increase number: a hypothesis for compound leaves****Lonnie W. Aarssen***Lonnie W. Aarssen (aarssenl@queensu.ca), Dept. of Biology, Queen's University, Kingston, ON, Canada, K7L 3N6***Abstract**

Adaptive advantages of the compound leaf form in flowering plants have so far remained elusive. A novel idea—proposed here—is that there are no direct advantages; the compound leaf evolved instead as a trade-off of selection in favour of something else: greater leafing intensity. Producing more leaves per unit of supporting shoot or plant body size generates a larger ‘bud bank’: an aggregate of axillary meristems available for optimal deployment in strategies for growth, survival, and reproduction, and also facilitating capacity (through DNA replication errors) for generating novel adaptive mutations that can be transmitted through the germ line. But, higher leafing intensity requires that individual leaf mass be smaller. Transition from a simple leaf (the ancestral form in angiosperms) to a compound leaf, therefore, may represent one mechanism whereby individual leaf mass was reduced within some angiosperm lineages. Compound leaves, however, are rare in angiosperms, I suggest, because more parsimonious mechanisms for mass reduction in a simple leaf are likely to involve straightforward reductions in overall dimensions (i.e. length, width), or increased lobing.

Keywords: bud bank, branching intensity, leafing intensity, leaf size, lobed leaves, meristems, size/number trade-off.

The first angiosperms had simple leaves (Bharathan and Sinha 2001), and the vast majority still do. Plant ecologists have long wondered, therefore, why—within some lineages—simple leaves evolved into compound leaves. The interesting speculation, of course, is that compound leaves conferred some sort of adaptive

advantage. Four main hypotheses have been proposed (reviewed by Warman et al. 2011): (i) compound leaves may confer advantages in capturing light while minimizing overheating and water loss; (ii) they may represent economical units for disposal (compared with a woody branch) under adversity, e.g. during seasonal drought; (iii) as ‘ramification surrogates’ for more costly woody branches, compound leaves might allow greater energy allocation to vertical growth under competition for light; and (iv) compound leaves may represent adaptation to herbivory, by presenting several small (and hence less apparent) leaflets—where damage can be limited (compared with a single large lamina), or where chemical defenses can be deployed differentially (with indirect defense for neighbouring leaflets and thus more energetically efficient investment in defense). While plausible and intriguing, these hypotheses have so far enjoyed scant empirical support, prompting recent calls for further research (Warman et al. 2011). As part of these future investigations, I propose adding another hypothesis—one in which the compound leaf is interpreted merely as a trade-off, with no direct fitness advantage. Specifically, compound leaves, I suggest, could have evolved from ancestral simple leaves because the result was a leaf with smaller mass, which represents a trade-off of selection that favoured the production of more of them.

Several recent studies have shown that—just as for seeds—variation in the sizes and numbers of leaves produced by plants is determined by a very precise and inevitable resource allocation trade-off relationship; i.e. species that produce leaves with smaller mass can produce more of them per unit of supporting shoot or plant body size/mass, commonly involving a proportional

(isometric) scaling relationship. In other words, having smaller leaves allows higher ‘leafing intensity’ (Kleiman and Aarssen 2007, Ogawa 2008, Yang et al. 2008, Milla 2009, Li et al. 2009, Xiang et al. 2009, Whitman and Aarssen 2010, Xiang et al. 2010, Milla and Reich 2011). The same is also true for different plants within a species (Scott and Aarssen 2012), and even for different shoots within a plant (Dombroskie and Aarssen 2012).

According to this ‘leafing intensity premium’ hypothesis, therefore, most angiosperms have relatively small individual leaf mass because small leaf mass is the trade-off necessary for maximizing leafing intensity—and the latter has been widely favoured by natural selection because producing more leaves generates a larger ‘bud bank’, i.e. more axillary meristems per unit of supporting shoot or plant body size (Kleiman and Aarssen 2007, Whitman and Aarssen 2010). Having a larger bank of meristems means that more of them (per unit body size) are available to be engaged in DNA replication, hence facilitating greater localized capacity (through replication errors)—per unit body size—for generating novel adaptive mutations for transmission through the germ line. Having a larger bud bank also means that more meristems are available for strategic deployment—e.g. in the expression of architectural/growth-form plasticity (including for branching intensity), or as a ‘reserve’ for survival and compensation following tissue loss to herbivores or disturbance, or for maximizing fecundity per unit shoot or plant body size. The latter is likely to facilitate potential for smaller reproductive size thresholds (Tracie and Aarssen 2011), and hence for greater reproductive economy (Aarssen 2008), i.e. capacity to produce at least some offspring despite severe body size suppression due to impoverishment, physical disturbance, herbivory, or competition/crowding effects from neighbours—which describes the chronic condition experienced by the vast majority of resident plants within most natural vegetation (Harper 1977). These interpretations are consistent with recent evidence, for herbaceous plants, indicating that both smaller species (Whitman and Aarssen 2010), and smaller plants within species (Scott and Aarssen 2012) have higher leafing intensity—and also evidence indicating that the vast majority of offspring available for the next generation within natural populations of herbaceous species are routinely produced by individuals that—despite being severely suppressed by neighborhood crowding—belong to the smaller half of the body-size range of resident plants (Chambers and Aarssen 2009). Taken together, these considerations provide plausible inference to the best explanation for recent analyses indicating that most episodes of species origination within angiosperm lineages have generally involved favouring effects of natural selection associated with relatively small leaf size, as well as relatively small plant body size (Dombroskie and Aarssen 2010).

The leafing intensity premium hypothesis is also employed here for interpreting the evolution of the compound leaf form—as well as leaf lobing. Higher leafing intensity—and hence a larger bud bank—could be realized, I suggest, from three distinctly different consequences of selection involving reduced individual leaf mass (Figure 1). Within each hypothetical lineage—(a), (b), and (c) in Figure 1—the ancestral leaf is assumed to be simple, unlobed, and larger in mass. The derived lobed (b) and compound (c) forms are adaptive only indirectly; i.e. they facilitate reduced individual leaf mass, thus promoting elevated leafing intensity, resulting in turn from selection for a larger bud bank (shown as black circles, representing axillary meristems

Figure 1. Three different hypothetical outcomes of selection for higher leafing intensity, involving a bio-mass allocation shift to more leaves per unit of supporting shoot mass (indicated by thick horizontal lines)—but smaller individual leaf mass as a tradeoff: (a) reduced leaf dimensions (length and/or width); (b) increased lobing; or (c) transition from a simple leaf to a compound leaf. Note that total leaf mass and total shoot mass are both unaffected by selection. After selection (on the right sides of arrows), however, axillary meristems (buds, represented by small black circles) are twice as numerous (per unit of supporting shoot mass) because individual leaf mass is half as large. (Ancestral simple leaf size outline is delineated by dotted lines). See text for explanation.

Figure 2. Hypothetical data distribution for angiosperm genera or families containing both compound-leaved species and simple-leaved species—predicted if compound leaves evolved from simple leaves as a mechanism for reducing individual leaf mass (with each point representing a pair of con-generic species): (a) leaf lengths for the species with the longest simple leaf versus the species with the longest compound leaf; (b) leaf widths for the species with the widest simple leaf versus the species with the widest compound leaf. Such data would normally be log-transformed since leaf size distributions are generally strongly right skewed. Dashed line is shown only to indicate the 1:1 line. See text for explanation

in Figure 1). Reduced leaf mass may (or may not) also be associated with fitness benefits of ramification (greater branching intensity), made possible by the larger bud bank. In other words, having smaller leaves may not only enable greater ramification (because they permit more leaves, thus conferring more axillary meristems that can be deployed for branching)—but in turn, these smaller leaf sizes may then be regarded as directly adaptive, because the ancestral heavier leaf size would no longer be supported efficiently on the now thinner twigs (Corner's rules; Olsen et al. 2009).

This model predicts, therefore, that relatively few angiosperms have evolved compound leaves (Figure 1c), simply because Figures 1a and 1b represent generally more parsimonious structural/archetypal modifications for reducing individual leaf mass. It should be possible, from phylogenetic analyses, to examine whether there has been a general trend of decreasing leaf size/mass over time within angiosperm lineages—as hypothesized in Figure 1. This seems likely given that analyses of extant species within genera indicate strongly right-skewed leaf size distributions (Dombroskie and Aarssen 2010). If indeed 'small is generally better', then the origin of the compound leaf form (from an ancestral simple leaf) is unlikely to have been associated with an increase in leaf dimensions (length, width). Accordingly, we might predict a relationship like that hypothesized in Figure 2, where (when controlling for phylogeny) the dimensions of simple leaves and compound leaves for closely

related species are positively correlated across higher taxa (e.g. genera, families)—and may not be significantly different (e.g. for con-generic species), with the compound leaves therefore possibly having less mass per unit length and/or per unit width (e.g. see Figure 2 in Bharathan and Sinha 2001). Importantly, however, it is conceivable that all three possible selection products generating reduced leaf mass (Figure 1) could have commonly evolved within some lineages, resulting in a general tendency for simple leaves to have smaller overall dimensions (Figure 1a) compared with con-generic species that have compound leaves (Figure 1c). In this event, a paired t-test in Figure 2 would indicate a data distribution significantly above the dashed lines (i.e. with compound leaves being generally longer and/or wider than simple leaves within a given genus or family).

Finding conclusive empirical tests with potential for rejecting (or supporting) hypotheses involving historical effects of natural selection is typically challenging. Some possibilities are suggested above—but for solving the mystery of the compound leaf, more new ideas may be needed as much as more data.

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Response to referee

Rubén Milla (2012) raises an important issue. What if the compound leaf—rather than evolving from dissection of a simple leaf—evolved instead from developmental modifications allowing precursor leaves/leaflets to produce additional leaflets? Some recent molecular evidence, as Milla (2012) points out, supports the latter 'leaflet iteration' hypothesis. Few taxa have so far been studied in sufficient detail, and Efroni et al. (2010) caution that it would be premature to generalize at this point. Either way, however, the essential question presently is whether the outcome of historical developmental modifications (whatever they were) that resulted in compound leaves was generally associated with an increase or a decrease in individual leaf mass. The 'leaflet iteration' hypothesis implies that derived compound leaves should be larger—or at least not smaller—in mass than the ancestral simple form. If corroborated generally, this would certainly provide sufficient evidence to reject the 'leafing intensity premium' hypothesis for compound leaf evolution.

I completely agree with Milla (2012) that, in the history of angiosperm evolution, natural selection is

likely to have favoured (and disfavoured, and sometimes subsequently favoured again) various traits associated with leaf size and morphology, as well as leafing intensity. And the compound leaf is likely to have conferred several kinds of fitness advantages, evolving independently in different lineages. Deciphering these fitness consequences, and the selection mechanisms involved in the evolution of leaf traits, and the interactions/relationships/trade-offs between traits, will of course require future empirical studies. The most promising progress is likely to come from those that can integrate ecological, physiological, developmental, molecular, phylogenetic, and paleobotanical data. The aim of the present contribution (and of IEE in general) is to promote theory maturation, by providing inspiration for formulating (and revising) key questions and hypotheses that have potential for guiding this future research.

Milla, R. 2012. Compound leaves and the evolution of leaf size and display. *Ideas in Ecology and Evolution* 5: 6–8. [CrossRef](#)