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Pierre-Éric Lauri

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Letters

Corner's rules as a framework for plant morphology, architecture and functioning – issues and steps forward

The Durian theory and Corner's rules governing plant architecture

In the middle of the twentieth century E. J. H. Corner developed 'The Durian theory' (Corner, 1949) and 'The Durian theory extended' (Corner, 1953, 1954a,b) named after the large spiny fruit of *Durio zibethinus* (Bombacaceae) containing light-brown seeds covered by a fleshy and edible white or yellow aril. Following a first intuition that 'such fruits must have been borne on massive twigs' Corner (1949) established two 'complementary principles', later referred to as Corner's rules, that were 'susceptible to mathematical treatments'. The 'axial conformity' rule states that 'the stouter, or more massive, the axis in a given species, the larger and more complicated are its appendages'. The 'diminution on ramification' rule states that 'the greater the ramification the smaller become the branches and their appendages'. These two rules delineated the poorly branched pachycaul trees with 'thick' stems and 'big' leaves and axillary organs (inflorescence, fruit) (Fig. 1a), and the highly branched leptocaul trees with 'slender primary axis and branches' and 'small' leaves and axillary organs (Fig. 1b,c).

The Durian theory was merely based on a general view on trees and encompassed an evolutionary aspect theorizing about the primitive character of pachycaul forms. Corner's hypothesis that leptocaul trees constitute an evolutionary outcome of pachycaul trees has been criticized considering that pachycaul forms may also derive from selective pressures in extreme environments (Mabberley, 1974) or questioning the plesiomorphic characteristic of the large fruits (Nyffeler & Baum, 2000).

Here, it is outlined that although this evolutionary view is discussed, Corner's rules inspired interspecific and ontogenetic studies from a morphological (organ size and shape), architectural (relations with branching) and functioning (relations with hydraulics and biomechanics) perspectives.

Corner's rules canonical relationships

Corner's rules provided a structural vision of woody plants building upon previous works on relationships among morphological traits such as the positive relationships between the diameter of the apical meristem and leaf size (Sinnott, 1921). Noticeably, Corner's rules

were at the origin of the conceptual modeling of whole-plant architecture developed by Hallé and colleagues on existing species (Hallé & Oldeman, 1970; Hallé *et al.*, 1978), recently extended by Chomicki *et al.* (2017) on Paleozoic taxa. These rules are still providing a heuristic framework for the quantification of plant form and function at various plant scales (e.g. in relation to plant hydraulics; Lehnebach *et al.*, 2018).

Most research works referring to Corner's rules are focused on two canonical relationships (Table 1). The first ones are between stem traits (namely diameter used in a majority of studies or directly derived from it, such as cross-sectional area and radius, mass, length, shape) and the number and/or size of appendages (leaf, inflorescence). The second ones are between leaf area and the number and/or size of appendages whether vegetative (branch) or reproductive (inflorescence, seed, fruit, cone). A few studies document across-scales relationships such as stem diameter or leaf area vs tree height (Table 1). Although most works are developed on woody plants a few aim at assessing these relationships on herbaceous plants (Barcellos de Souza *et al.*, 1986). Studies are developed at two main scales. The first one considers the whole-plant including the branch or the leafy shoot at the end of primary growth and is used for phylogenetic studies based on interspecific comparisons (e.g. across *Acer* accessions; Ackerly & Donoghue, 1998). The second one considers the metamer, that is, the complex formed by the internode, the attached leaf or leaves and the axillary production(s), and is used to study ontogenetic changes during the development of an individual, whether a tree (Brouat *et al.*, 1998; Brouat & McKey, 2001) or a herbaceous plant (Barcellos de Souza *et al.*, 1986).

The link with hydraulics

For a great majority of authors, the quantitative relationships between stem diameter, loosely termed stem 'size' in several articles (Brouat *et al.*, 1998; Westoby *et al.*, 2002; Westoby & Wright, 2003), and the appendages the stem supports are primarily interpreted in terms of the vascular supply joining the roots to the appendages through the stem. These relationships have been extensively discussed in past decades using the conceptual framework of the pipe model theory (Shinozaki *et al.*, 1964), including very recently by Lehnebach *et al.* (2018). This theory predicts that 'the amount of leaves existing above a certain horizontal level in a plant community (is) always proportional to the sum of the cross-sectional area of the stems and branches found at that level' (Shinozaki *et al.*, 1964). The pipe model theory does not strictly consider the process of heartwood (non-conducting wood) formation, which is independent of pipe production and deactivation, and more studies are needed to differentiate between conducting and storage sapwood (Lehnebach *et al.*, 2018). However, as a whole, this theory showed its high heuristic value in stimulating research on relations between structure and functions among plant

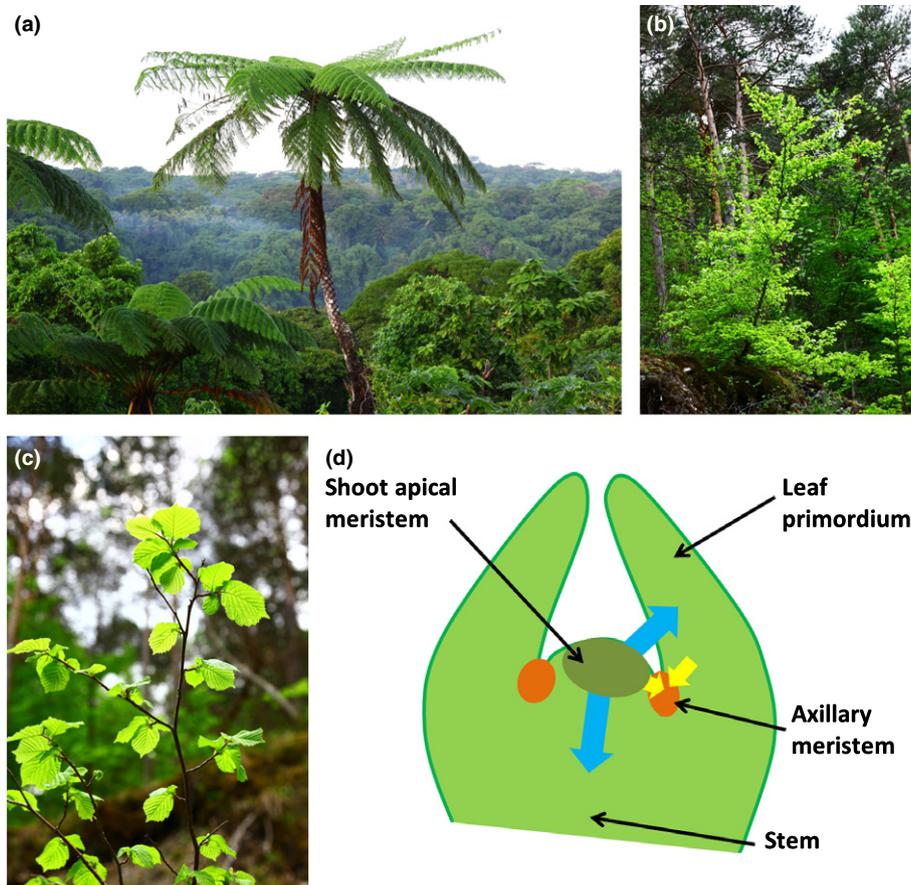


Fig. 1 Corner's rules at various scales. At the whole plant scale, (a) large and thick internodes with low slenderness are related to large leaves and no or poor branching (e.g. monocaulous pachycaul tree fern, *Cyathea* sp.), whereas (b) small and slender internodes are associated with small leaves and high branching (e.g. (b, c) leptocaul beech tree, *Fagus sylvatica*); and (d) relationships that determine the correlation space between stem and appendages are initiated in the shoot apical meristem (SAM) where cell number positively affects meristem size which, in turn, positively affects stem diameter and leaf area (blue arrows; Schnablová *et al.*, 2017). The axillary meristem, which is initiated in the boundary regions between the adaxial base of the leaf primordium and the SAM, is closely associated with leaf polarity and also results from signals from the SAM (yellow arrows; Yang & Jiao, 2016; Chomicki *et al.*, 2017). To what extent leaf and stem size and shape, and axillary production size and fate, are pre-determined in the SAM or result from later interactions among growing organs needs to be further investigated. Photograph credits: Pierre-Éric Lauri.

compartments. For example, the statement of isometry between leaf area and stem cross-sectional area is well supported by findings of Brouat *et al.* (1998) over the ontogenetic gradient on two caesalpinoid legume trees, and by Petit *et al.* (2018) on shoots of two deciduous angiosperms and of two evergreen conifers at different distances from the apex.

Further insights from Corner's rules

Based on a literature review that quantified Corner's rules among stem, leaf and appendages, it is proposed that three further insights might benefit from Corner's rules-based studies.

Insight 1. Questions raised by biomechanics: the need to consider stem shape and not only stem diameter or cross-sectional area

Beside hydraulics, the relationships between stem diameter and appendage size or number are also interpreted in terms of biomechanics. Biomechanical properties of a stem are related to

two main factors. One factor is wood density 'with denser woods being stiffer and stronger than stems with equivalent cross-section composed of less-denser wood' (Niklas & Spatz, 2012). Another factor is shape which determines that for a stem with a same weight of appendages and same construction material properties, the higher the slenderness, that is, ratio between length and diameter, the lower the mechanical stability. This limitation on length by cross-sectional area is well known by foresters in studies at the whole-tree scale to evaluate the critical buckling height (Niklas, 2013). Therefore, from the morphological point of view, considering only stem diameter (Brouat *et al.*, 1998; Fan *et al.*, 2017) as a proxy for stem biomechanical strength is misleading. In his initial articles, Corner (1949, 1953, 1954a,b, 1975) most often used the words 'massive' or 'stout' as opposed to 'slender' to qualify stems of pachycaul and leptocaul trees, respectively. These words, although imprecise, strongly suggested that to maintain same biomechanical characteristics of the stem with regards to appendages a difference in size must be accompanied by a difference in shape. Therefore, not only stem diameter, or even volume or mass, but also shape should be considered in relation to the size of appendages. Working

Table 1 Canonical relationships among morphological and architectural traits illustrating Corner's rules at various scales.

Organ	Relationships among morphological and architectural traits		Scale	
			Tree, branch or leafy shoot (also called twig)	Individual metamer
Stem	Diameter	vs inflorescence number or size vs leaf area	Bond & Midgley (1988); Midgley & Bond (1989); Normand <i>et al.</i> (2009) Bond & Midgley (1988); Westoby <i>et al.</i> (2002); Westoby & Wright (2003); Olson <i>et al.</i> (2009); Fajardo (2016); Trueba <i>et al.</i> (2016); Fan <i>et al.</i> (2017); Messier <i>et al.</i> (2017); Osada & Hiura (2017); Schnablová <i>et al.</i> (2017); Smith <i>et al.</i> (2017); Poorter <i>et al.</i> (2018)	White (1983a,b); Barcellos de Souza <i>et al.</i> (1986); Brouat <i>et al.</i> (1998); Brouat & McKey (2001)
	Mass Length Shape	vs tree height vs leaf mass vs leaf area vs leaf area	Brouat <i>et al.</i> (1998); Brouat & McKey (2001) Normand <i>et al.</i> (2008); Fan <i>et al.</i> (2017) Trueba <i>et al.</i> (2016)	Barcellos de Souza <i>et al.</i> (1986)
Leaf	Area	vs reproductive organ (seed, fruit, cone, inflorescence) size	Bond & Midgley (1988); Midgley & Bond (1989); Ackerly & Donoghue (1998); Cornelissen (1999); Westoby & Wright (2003); Duivenvoorden & Cuello (2012); Leslie <i>et al.</i> (2014)	
		vs branching intensity	Ashton (1976a,b); Yagi (2006); Takahashi & Mikami (2008); Messier <i>et al.</i> (2017); Osada & Hiura (2017)	
		vs leaf number	Fajardo (2016)	
		vs stem mass vs tree height	Yang <i>et al.</i> (2010) Hodgson <i>et al.</i> (2017)	

Only articles referring explicitly to 'Corner's rules' or 'The Durian theory' are selected.

In the case various expressions cover correlated traits or are imprecise, a single expression is retained after checking of the Materials and Methods in each article: 'stem diameter' also includes 'stem cross-sectional area' and 'radius'; 'leaf area' also includes 'leaf size'; 'branching intensity' also includes 'degree of branching'.

on a rosette-stoloniferous plant, *Callisia fragrans* (Commelinaceae), Barcellos de Souza *et al.* (1986) analyzed ontogenetic changes considering individual metamers. They showed that if, as hypothesized, leaf area was positively related to stem-cross sectional area supporting the hydraulic relations, it was negatively related to internode slenderness supporting the biomechanical relations. Variations of these three traits thus appeared as good markers of the successive stages this species goes through during its ontogeny, large leaves being associated to short internodes with a low slenderness ratio typical of the erect rosette phase, whereas small leaves were associated to long internodes with a high slenderness ratio typical of the stolon phase growing at the soil surface.

At the whole-plant and branch scales, if the relationships between stem diameter and size and number of appendages are well established (Table 1), the relations with stem shape needs to be more documented. For example, Niklas *et al.* (2006) hypothesized that the high slenderness ratio of some pachycaul species, comparable to some leptocaul species, were likely related to the absence or paucity of branching. However, this study did not detail relationships between stem traits and appendages.

Insight 2. The definition of a realistic biological-based phenotypic correlation space to better design plant architectural ideotypes

The earlier mentioned literature confirms that some main relationships, such as stem diameter vs leaf area and the coordinated

changes of these two traits, are observed from both the phylogenetic or interspecific and the ontogenetic points of view. Combined with hydraulics and biomechanics, these results support the idea that Corner's rules likely cover a universal network of biological relationships shaping plant architecture and functioning.

The definition of ideotype, that is, the best-adapted biological model in a given agricultural and socio-economic environment (Donald, 1968), is crucial to optimize plant cultivation and yield. Among architectural traits that affect yield, canopy porosity to light is a main variable governing light interception by the plant and therefore partly affects yield (Sinoquet *et al.*, 2007). In the apple, canopy porosity depends on leaf-area distribution within the canopy that is directly related to branch orientation and branching density (Willlaume *et al.*, 2004). These morphological and architectural traits can be phenotyped in progenies and can also be manipulated in the orchard through tailored precision management procedures (Lauri & Laurens, 2005). Recent attempts that aim at designing plant ideotypes to improve light interception using plant numerical models conclude on the interest of ideotypes with long internodes (e.g. tomato, Sarlikioti *et al.*, 2011; Chen *et al.*, 2014; apple, Picheny *et al.*, 2017) possibly combined with high leaf area (apple, Picheny *et al.*, 2017) and/or with narrow leaves, that is, high length to width ratio (e.g. tomato, Sarlikioti *et al.*, 2011). Such assertions confirm previous horticultural knowledge on positive relationships between light interception and stem slenderness (e.g. apple, Lespinasse, 1992; Lauri *et al.*, 1997). These works raise interest to explore further the correlation space among

morphological and architectural traits that are biologically meaningful, especially here where the extent to which stem length can be positively related to leaf number and area without endangering biomechanical and hydraulic stability. For example, in the apple case, increasing both stem length and leaf area as proposed by Picheny *et al.* (2017) is biologically realistic and agronomically relevant only up to a critical value of stem slenderness.

Beyond relationships among vegetative organs, Corner's rules also encompassed quantitative relationships between vegetative and reproductive organs (e.g. stem diameter positively correlated with the size of reproductive appendages; Midgley & Bond, 1989). It has been shown that flowering rate increases and then decreases when the bearing stem diameter (Normand *et al.*, 2009) or length (Lauri & Trotter, 2004) increases following a quadratic function. These results suggest that Corner's quantitative relationships established for mature and well differentiated vegetative and reproductive organs are likely to be prepared during floral induction and through more complex relationships.

Insight 3. The respective contributions of organogenesis and growth mechanisms in determining the phenotypic correlation space

Schnablová *et al.* (2017) working on the shoot apical meristem (SAM) conclude that stem diameter and leaf size, and in the case of a reproductive meristem seed mass, are 'linked to each other by rules such as Corner's rules'. These relationships are primarily related to cell number in the SAM from which organs are derived with a minor role of cell size (blue arrows in Fig. 1d; e.g. Gonzalez *et al.*, 2012; Schnablová *et al.*, 2017). However, we still have poor knowledge on the stage of organogenesis at which stem and leaf shape are determined, and to what extent they result from interactions at the metamer or at the whole-stem scale. Furthermore, axillary meristem initiation from which a branch or an inflorescence develops is tightly related to the boundary regions between the SAM and the leaf primordium (yellow arrows in Fig. 1d; Yang & Jiao, 2016) suggesting that the growth, and likely fate of the axillary production, is not passive but partly determined by interactions between the SAM and newly initiated organs at a very early stage. This is supported by findings on branch plagiotropy in *Araucaria* and *Coffea* likely resulting from an early SAM signal (see discussion in Chomicki *et al.*, 2017). However, results obtained on individual metamers of peach (Kervella *et al.*, 1995) and apple (Lauri & T  rouanne, 1998) show that the growth dynamics of the leaf or of both the internode and the leaf, respectively, affect the axillary bud fate (namely, latent, vegetative, floral; Lauri & Normand, 2017). The challenge is now to better investigate when and how the phenotypic correlation space is built during plant development and growth and in particular to analyze whether organ size and shape, and axillary production size and fate, are fully pre-determined in the SAM or depend on interactions among growing or mature organs at later stages.

Future directions

It is argued that agricultural plants constitute a remarkable biological material to develop Corner's rules based on

knowledge-oriented and applied research. A research agenda is proposed with two main goals.

Goal 1. Domestication effects

Most agricultural plants result from long-term domestication by human societies, which includes both selection of wild plant material and intentional breeding (Zeder *et al.*, 2006). In a majority of cases, domestication and especially breeding strategies have been oriented towards an increase of the weight of grain (e.g. wheat, Schoppach *et al.*, 2017) or fruit (e.g. apple, Cornille *et al.*, 2014) relative to the whole plant biomass. It is hypothesized that this increase in 'yield efficiency' is related to changes in size and shape of vegetative organs that support reproductive organs and likely also in branching. As a premise for such studies it is noteworthy that the decrease in trunk slenderness of domesticated *Carica papaya* is interpreted as a mechanical response to the domestication-related increase of large fruit clusters (Niklas & Marler, 2007). Such research can be extended to various agricultural plants benefiting from collaboration between geneticists, breeders and archeobotanists.

Goal 2. Environmental effects

Generally speaking, Corner's rules-based research works (Table 1) consider the plant entity without explicitly integrating the effects of the environment. Changes in environmental conditions arise from climate change and the associated global warming (Intergovernmental Panel on Climate Change (IPCC), 2014) but also result from growing conditions. This is especially true in agriculture with the development of more sustainable and diversified agroecosystems that generally increase competitions among plants for above-ground and below-ground resources (Barot *et al.*, 2017). The plasticity in responses to environmental constraints is well studied on annuals (e.g. contrasted patterns of plasticity in allocation, morphology, physiology and architecture in improving light capture or nitrogen acquisition, respectively; Freschet *et al.*, 2018) but far less on woody plants on which the abiotic (e.g. temperature) and biotic (e.g. proximity of neighboring plants) environments have a cumulative effect on tree morphology and architecture over consecutive growing seasons. It has been shown that besides their effect on budburst phenology (Legave *et al.*, 2015) mild winter temperatures compared to cold winter temperatures significantly decrease branching frequency on stems with similar size and shape (e.g. apple, Dutra Schmitz *et al.*, 2014). Similarly, shading by neighboring trees in natural or agricultural systems increases stem slenderness and decreases branching (MacFarlane & Kane, 2017). Such studies document the variation spectra of morphological and architectural traits, here stem size or shape and branching frequency, and their relationships. However, how these changes in vegetative growth are related to reproductive growth over the tree lifespan is still little studied. Works on woody plants, typically forest and fruit trees in pure stands or in multispecies systems, typically agroforestry systems, would permit an evaluation of the level of plasticity of organs size and shape and of their relationships.

Domestication and adaptation to environmental changes both address morphological and architectural relationships at stem and whole plant scales (Insights 1 and 2) with applied issues. For example, based on research works on apple tree architecture showing a relation between low branching frequency and regular flowering over consecutive years, practical guidelines are proposed for system and plant management in the context of sustainable production (Lauri & Simon, 2018; Lauri *et al.*, 2018). At a finer scale (Insight 3), it has been shown that meristem plasticity to environmental changes affects differently leaf growth and relative growth rate in *Festuca* depending on the fast- or slow-growing pattern of the species (Sugiyama & Gotoh, 2010). A further step could benefit from Corner's rules-based studies on the extent to which this environment- or domestication-related meristem plasticity also affects organ fate and growth distribution in time (ontogeny) and in space (plant architecture) with consequences for plant cultivation (e.g. onset of flowering during plant ontogeny).

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ORCID

Pierre-Éric Lauri  <http://orcid.org/0000-0002-7549-0484>

Pierre-Éric Lauri 

SYSTEM, Univ Montpellier, INRA, Cirad, Montpellier SupAgro, CIHEAM-IAMM, 2 Place Pierre Viala, Montpellier 34060, France
(tel +33 (0)4 99 61 30 54; email pierre-eric.lauri@inra.fr)

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