Towards 3D basic theories of plant forms

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Allometric, metabolic, and biomechanical theories are the critical foundations for scientifically deciphering plant forms. Their concrete laws, however, are found to deviate for plenty of plant specimens. This phenomenon has not been extensively studied, due to technical restrictions. This bottleneck now can be overcome by the state-of-the-art three-dimensional (3D) mapping technologies, such as fine-scale terrestrial laser scanning. On these grounds, we proposed to reexamine the basic theories regarding plant forms, and then, we case validated the feasibility of upgrading them into 3D modes. As an in-time enlightening of 3D revolutionizing the related basic subject, our theoretical prospect further sorted out the potential challenges as the cutting points for advancing its future exploration, which may enable 3D reconstruction of the basic theories of plant forms and even boost life science.

Introduction: The established basic theories of plant forms show law deviations

In plant science, form, also termed appearance, shape, architecture, structure, or morphology, has long been followed with wide interest1,2—ranging from its measurement3 to its attribution4. For quantitative characterization and ecological analysis of its diversity and development, scientists have creatively developed multiple basic theories5. Allometric6, metabolic7, and biomechanical8 approaches can collectively outline the characteristics of plant forms. Such already-established basic theories have been able to generally shed light on the underlying patterns and reasons how and why plants show their distinctive forms9.

The allometric theory, alias the allometric scaling theory, can characterize the size relations of the body parts that constitute the integrative forms of plants10–12 and facilitate metering the different properties of plants in a relatively easy way. The metabolic theory, also termed the metabolic scaling theory, is aimed at quantitatively deriving the scaling of metabolic rate as a function of body sizes and environmental factors (e.g., in the scaling forms based on Cauchy’s theorems)13–16, in favour of learning the inner processes of plants through their forms. As for the biomechanical theory, it examines the forms and functions of plants in a mechanical way17,18 such as explaining the strategies used by plants for avoiding windbreaks, being self-supporting, and retaining their growth habits19.

These basic theories on the apparent structure, internal physiology, and external adaptability of plants, in principle, can elucidate their respective effects in modulating plants to grow into specific forms6,20–22. Flexible combinations of these theories have also been validated for explaining the multifold aspects of form-related characteristics for diverse plant species23. For generalizing and characterizing such functions, many “universal”-purposed models such as the Geometric Similarity model24, the West/Brown/Enquist (WBE) model13, and the Auto-Stress-regarded Bending model25 have been developed. Such models can act as bridges for probing why the anatomical and physiological scaling exponents of plants scale as quarter-powers of mass, such as the popular WBE model performing with the scaling exponent = 3/4 for gross photosynthetic rate, metabolic rate, and resource use26.

However, for many species with complex forms, specific laws under the frameworks of these basic theories have been found with various deviations, which may be caused by plant species differences27, plant self-shading28, crown ratio influencing29, or plant-plant interaction30.
For example, scientists observed that the scaling exponent of 3/4 for the metabolic relationships is not common for some woody plant species. Till now, it is still uncertain whether such law deviations are special phenomena or general modes for plants. The reason is the lack of systematic studies focusing on this question. This shortage is rooted in another technical limitation that is typically unavoidable in traditional plant measurements, namely, almost no efficient techniques for in-situ mapping the full structure of plants.

The state-of-the-art mapping technologies supply a new perspective

The state-of-the-art mapping technologies such as terrestrial laser scanning (TLS) can survey and represent plant forms in a three-dimensional (3D) manner. This is illustrated by the point cloud in Fig. 1a and the multi-cylinders-based branch modelling in Fig. 1b, respectively. This advantage can bring about a 3D revolution in how we look at trees and tree communities. By extension, TLS can supply a new 3D perspective on the complex structures of plants and their communities. This reasoning is rooted in the fact that TLS has proved to be able to support deriving crown structural properties, classifying species, and estimating biomass, which all serve as the foundations for a comprehensive understanding of plant forms. So far, these endeavours were mainly dedicated to bringing changes to the traditional plant phenotyping fields or providing supplementary points to the existing knowledge base, not paying attention to the fundamental scientific questions that are explicitly involved in the basic theories of plant forms. Still, the scarce emergences of TLS-based attempts to gain further insight are inspiring, and we review these below.

For the allometric basic theory, a couple of studies based on TLS characterizing plants have detected its law deviations or even totally new laws in some specific scenarios. As a case study indicated, the conventional allometric equations are inadequate for estimating the biomass of a temperate species-mixed forest, while TLS-based tree stem modelling can serve as a potential solution of deriving non-destructive allometric equations for updating allometry and reducing the uncertainties in landscape-scale biomass estimations. TLS was also used in an attempt to quantify the allometric variations of Quercus mongolica in semi-arid forests, and its derived allometric situation of low height but large canopy (as illustrated in Fig. 1c) matched just a low percentile of the derivations from the common Dynamic Global Vegetation Models (DGVMs). More such TLS-based studies exploring plant allometric modes and determinants would have implications for supporting from plant hydraulics analysis to DGVM improvement, and include 3D reexamining the allometric basic theory on plant forms.

**Fig. 1 The background of inspiring a rethink of the basic theories of plant forms.** Illustration of (a) the TLS-collected point cloud and (b) characterized 3D structure of a woody plant, with the high potential for boosting reexaminations of the deviations from its related (c) allometric scaling laws, (d) metabolic scaling laws, and (e) biomechanical laws. Note that (a) and (b) were generated based on published TLS data and Quantitative Structure Model software, (c) was generated based on the published formulas of allometric scaling, (d) was generated by following the published formulas of metabolic scaling, i.e., scaling exponent = 1.131 for gross primary productivity, scaling exponent = 0.602 for gross photosynthesis ability, and scaling exponent = 3/4 ~ 1 as derived from the adapted WBE model, and (e) was generated in accordance to the published formulas of biomechanics (in terms of lean angle) before and after tree thinning. The integration of the five images that reflect the kernel aspects of 3D reexamining the basic theories of plant forms draws the schematic framework to guide future studies.
In regard to the metabolic basic theory, some plans based on the TLS-mapped plant data have been proposed for exploring its new performance laws in special situations. As illustrated in Fig. 1d, the metabolic scaling laws of some plant species proved to show deviations from the simulations based on the WBE model. To explain such deviations, it is needed to recheck the physiological assumptions regarding how the fractions and activities of the metabolically active tissues vary in organisms, and exploiting the key sources of this uncertainty relies on an accurate assessment of the surface areas of relatively smaller branches and twigs that make a disproportionate contribution to the total woody surface area. TLS is applicable to finishing this basic task, and hence, it was supposed that TLS can help to test the existing allometric assumptions and give rise to new significant insights. This hypothesis was verified by the finding that the TLS-measured scaling exponents of branch radius scaling ratio $a$ and branch length scaling ratio $\beta$ proved to diverge from the theoretical exponents of the WBE models. Therefore, it was argued that TLS can be adopted as a useful tool for making comprehensive studies of plant biophysical processes and metabolic theories in ecology, certainly covering the metabolic basic theory on plant forms.

As for the biomechanical basic theory, some endeavours based on the TLS-collected plant data have detected novel laws of biomechanical modes in some situations. As compared in Fig. 1e, the ecological effect of tree thinning can affect its biomechanical performance in terms of lean angle. However, more comprehensive explorations of plant biomechanical properties, in terms of four typical biomechanical traits (such as two safety traits against wind and self-buckling, and two motricity traits involving how to sustain an upright position—tropic motion velocity and posture control), require more detailed information about plant forms. For this need, TLS has proved to be a potential solution for deriving plant structural features, and such parameters can inspire more studies on plant biomechanical natures. A representative TLS-based biomechanical study proved to generate the answers to the specific questions on plant structure-wind ecological interactions, such as what decides critical wind speeds and whether trade-offs lie between such speeds and plant growth rates. Such applicability of TLS can no doubt be extended to 3D reexamining the biomechanical basic theory on plant forms.

**3D reexamining the basic theories of plant forms: allometric case study**

As it is not sufficient to only propose the feasibility of 3D reexamining the basic theories of plant forms, we performed an allometric case study. Specifically, we proposed a new concept of 3D allometry instead of its traditional mode, as illustrated by the principle transition from Fig. 2a, b. The theoretical foundation of making such a proposal is that growth direction, in addition to the often used parameter of its magnitude, can better re scale the answers to the specific questions on plant form-structural-functional links. Under this 3D allometric principle framework, the pitfalls in traditional analyses of biomass allocation modes in plants can be addressed, and more specific 3D patterns of biomass allocations in branches of various inclination angles can be reflected. Such specified 3D allometric laws may mean that it is quite possible to quell the traditional allometry-derived debates. Further, 3D allometry may bring breakthroughs to the often-assumed laws on plant form, re-understanding the basic theories on plant allometry, and even open the totally new fields on plant structure. In all, the proposed 3D allometric concept may...
start 3D revolutions of plant form-structural-functional sciences in the future.

3D upgrading the basic theories of plant forms is of potential but challenging

This allometric case study suggested that 3D reexamining the basic theories of plant forms is of high potential for promoting their 3D upgrading and, thereby, disclosing more secrets about plant forms. This potential is valid not only for the three cardinal kinds of basic theories as considered in this study but also many other kinds aiming at the different aspects involving plant forms. Such aspects may include plant physiology, biophysics, biochemistry, and biosystematics. Their basic theories after 3D reexaminations will bring critical revolutions to the related fields as well, and this will be of considerable implications for refreshing our knowledge on plant forms to updating the foundation for global ecosystem understanding, even possibly projecting a new field.

The identified potential, however, does not mean that stepping forward from 3D reexamining to 3D theorizing is easy, as this process will be challenging. The challenges include more than the technical gaps between TLS data collections and the possible laws of the new 3D allometric, metabolic, and biomechanical basic theories. How to derive such potential laws may be the key challenges in this theoretical-level analysis. This can be mitigated by re-asking the questions that have been unclear under the traditional frameworks of the allometric, metabolic, and biomechanical basic theories of plant forms. For example, can biomechanical or optimal allocation theories better make accurate estimates of reproductive allometries for special plant species? How is it possible to balance the weight of allometric scaling and resource limitation in predicting maximum heights and other features of plants? Can the changes in plant structure anatomy serve as the evidence of plant “liberations”? To what degree can plant morphologic plasticity explain the law deviations from the metabolic scaling theory in special situations? On the other hand, how can biomechanical performance constrain plant forms? How can biomechanical design decide the long-term stability of plants in terms of the balance between weight increase and gravitropic reaction? How can the common framework of structural mechanics account for the evolution of the whole geometry due to plant growth processes? What can theoretically cause their diversities? Collectively, the possible challenges may involve dealing with plant structural traits from the perspective of their forming mechanisms and coordinating the derived laws between the different kinds of new basic theories.

The challenges discussed above indicate that the existing basic theories of plant forms are far from being perfect, particularly for woody plant species that commonly grow with complex structures. However, the compilation of these challenges is useful for figuring out the potential cutting points for launching the future studies in this direction.

Prospect: towards 3D basic theories of plant forms

To upgrade the basic theories of plant forms to 3D will ultimately lead to their 3D versions. This prospect is based on its viability in...
principle, as evidenced by Fig. 3, which illustrates its physical demand and mechanistic foundation. Substantially, developing 3D basic theories of plant forms is equivalent to returning to their 3D growth space. At the same time, the process of plant growth is in a 3D manner, ranging from carbon capture, carbon allocation, to carbon sequestration66. These physiological functions working within a 3D vascular structure engender 3D apparent patterns of metabolic scaling, biomechanical coordinating, and allometric scaling, integrally performing with coherent inner relationships. As specifically explained in Fig. 3, this facilitates systematically 3D reexamining and -reconstructing the basic theories of plant forms, even to the structure of plant collection67. The total picture in Fig. 3 provides an instructive framework for developing 3D basic theories of plant forms.

Overall, this study proposes the state-of-the-art in-situ 3D mapping technologies such as fine-scale TLS, for 3D reexamining the basic theories of plant forms. This work may promote more future explorations, particularly on plants with more diverse forms in the wild, towards 3D basic theories of plant forms. This trend may bring 3D critical changes and even breakthroughs to the scientific cognitions of plant forms and, in a broader sense, biological forms. All such merits will be of fundamental significance further for revealing more biological and mechanistic mechanisms for advancing life science from the bottom up.

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Y.L. conceived the study and conducted the case testing. Y.L. and J.H. wrote the manuscript.

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