Research paper

Plant Functional Traits: an Ecophysiological Perspective

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【 Summary 】

A new, ecophysiologically focussed approach to quantifying plant functional traits is described, including brief descriptions of techniques for measurement. Traits included relate to sun/shade adaptation, adaptation and exposure to drought stress, adaptation to salt stress, photosynthetic pathways, adaptations to temperature extremes, and adaptation to low elemental availability stress. These functional traits are not necessarily intended to supplant those currently in use, but are instead intended to improve the functional characterization of an ecological unit of vegetation. Thus, these more ecophysiologically-relevant traits might be used alone or in addition to morphological and other traits currently in use, depending on the questions being addressed by the investigator. An attempt has been made to propose the use of traits that are relatively time-independent, taxon-independent, and that can be compared to other major ecophysiological groupings of plants (*e.g.*, sun/shade plants, mesophytes/xerophytes, stressed/nonstressed plants). A number of the traits are stress-related, yet can be used to gain insight into plant adaptations to local environmental/microenvironmental conditions, regardless of stress level.

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研究報告

從生態生理學觀點看植物機能性特徵

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摘　要

　　本篇說明一種新穎、聚焦於生態生理學的方法以定量植物機能性特徵，也包括相關量測技術的簡短說明。植物特徵包括與日照/遮蔭適應、對於乾旱逆壓暴露的適應、對鹽份逆壓的適應、光合作用途徑、對極端溫度的適應以及對低元素供應逆壓的適應等。這些機能性特徵並非試圖取代目前已在使用者，而是作為改善一生態單元內植生機能性界定之目的。因此這些更為生態生理學相關的特徵可予單獨應用或是附加於目前使用的形態與其他特徵；端視研究者探討的問題為何而定。本篇並嘗試提出利用一些相對不隨時間改變、不因分類群差異，且可與其他主要生態生理學群組比較之植物特徵(例如，日照/遮蔭植物、中生植物/乾生植物、受逆壓/未受逆壓之植物)來進行研究。其中一些特徵是與逆壓有關，但不論逆壓的程度，可用以獲取植物對局部環境/微環境條件適應的更深入了解。
關鍵詞：適應、葉綠素、δ¹³C、δ¹⁵N、生態學、養份、逆滲透壓、光合作用途徑、溫度。
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INTRODUCTION

　　Plant ecologists have long sought ways to categorize plants according to functionally relevant features or traits in order to better characterize plant communities in ways that provide greater insight into the structure and function of such communities (*e.g.*, Raunkiaer 1918; Smith *et al*. 1997; Tilman *et al*. 1997; Schulze *et al*. 2002). Such approaches are deemed superior to describing plant communities based solely or primarily on taxonomic or gross physiognomic (*e.g.*, forbs, grasses, shrubs, trees, etc.) approaches. Functionally relevant traits typically used in such ways include anatomical features, biomass, fruit and seed dimensions, growth form, growth rates, leaf area, leaf area index (LAI), leaf dimensions (*e.g.*, width, length), phenological events, photosynthetic pathway, photosynthetic rate (instantaneous), plant size and shape, transpiration rate (instantaneous), and other features that are relatively easily mea-sured or easily obtained from the literature (Baraloto *et al*. 2012; de Lima *et al*. 2012; Seyoum *et al*. 2012; Cayssials and Rodríguez 2013; Wang and Chen 2013; Bradford *et al*. 2014; Cornelissen *et al*. 2014).

　　In this paper, an attempt is made to offer a more direct and integrative functional approach, as opposed to a "functionally relevant" approach, based on plant physiological and ecophysiological characteristics of plants, that should provide a more useful and ecophysiologically meaningful tool for plant ecologists, yet while also maintaining relative technological simplicity in experimental techniques required to address the questions being posed in studies of community and ecosystem function.

　　This is not the first treatment directed toward a more ecophysiological approach. There have recently been others, yet most of these use ecophysiological characteristics ("traits") that are highly variable, temporally, spatially,

and phylogenetically. For example, Everwand *et al*. (2014) used instantaneous photosynthetic rate, respiration rate, stomatal conductance, and leaf elemental nutrient concentrations, all of which are highly variable and depend on time (minutes to days) of measurement, microhabitat features, and species identity. In the current treatment, an attempt is made to avoid these dependencies; thus, the physiological characteristics ("traits") proposed here should vary little over short time scales, over small variations in habitat, and among species. Of course, perfect fidelity to to reducing all such variability is impossible, given unavoidable and natural variability in all such features, yet this treatment reflects an attempt to reduce, to the degree possible, such variability.

Furthermore, each of the following measurements should provide insight, in a quantitative and comparative manner, into the degree of adaptation of a species to a particular environmental stress. Of course, one measurement can not fully quantify how well or how poorly adapted a species is to a particular stress, but the variables described here were chosen with this in mind, and such variables have been found to be reliably general indicators of such adaptations and are especially useful in comparisons of the adaptations of a species with others, both in the same community/ecosystem and in others described in other studies.

Sun/Shade Adaptation
Leaf chlorophyll a/b ratio

The chlorophyll *a/b* ratio of a leaf provides an excellent indicator of a plant's ability to adapt to sun or shade. The chlorophyll *a/b* ratio reflects two characteristically adaptive responses of plants to high and low light: the quantity of light (number of photons) absorbed by the light-harvesting apparatus, as well as the spectral quality of the light

absorbed (Boardman 1977; Bjorkman 1981; Evans 1988).

Although best used in a comparative fashion (*e.g.*, sun *vs*. shade plants, both related or in the same area), the chlorophyll *a/b* ratio can often be used independently of such comparisons. For example, in general, a chlorophyll *a/b* ratio above 2.5 is usually characteristic of a sun plant, whereas a value less than 2.5 is typically found in shade plants (Grahl and Wild 1972; Brown *et al*. 1973, 1974; Lewandowska *et al*. 1976; Alberte *et al*. 1976; Šesták *et al*. 1978; Rühle and Wild 1979; Wild and Wolf 1980; Martin and Churchill 1982; Martin *et al*. 1985; Martin *et al* 2010).

There are many methods to extract and quantify chlorophylls *a* and *b* from plant leaves, but the simplest (but perhaps not safest or cheapest) is that of Moran (1982).

Adaptation to Drought Stress
Leaf osmotic potential

The osmotic potential (Ψ_π) of a leaf quantifies the total solute concentration of that leaf, and more important here, its value represents the *lowest* (most negative) *survivable water potential* (Ψ) of a plant. The latter is true because most plant cells die from plasmolysis when they lose turgor, and when the cell turgor pressure is zero, the Ψ of the plant is equal to its Ψ_π (Taiz and Zeiger 1998; Nobel 1999; Larcher 2003). As a result, plants that grow in constantly moist or wet areas have relatively high (less negative) osmotic potentials (*e.g.*, above -2 MPa), whereas those that grow in more arid environments (or microenvironments) have much more negative osmotic potentials (*e.g.*, below -2 or -3 MPa; Larcher 2003). Notable exceptions exist, such as succulents that have very high osmotic potentials, yet grow in arid environments (Nobel 1999). Halophytic plants might also be considered as exceptions (Larcher 2003), given

their extremely low Ψ_π, yet moist habitat (but see below).

There are a number of methods available to measure the osmotic potential of leaf cells (Koide *et al.* 1991; Beadle *et al.* 1993), unfortunately the best of which require relatively expensive and specialized instrumentation. On the other hand, a simple and inexpensive technique for measuring the Ψ_π of a leaf is the Shardakov (Chardakov) method (Slavík 1974), using frozen and thawed leaves or extracted leaf liquid ("sap"). Using intact leaf tissue, freezing is necessary to eliminate the contribution of turgor pressure to the leaf Ψ, as this method measures the latter, so, in the absence of turgor pressure, Ψ_π is measured. Because plants that are well-adapted to arid environments or habitats can change (decrease) their osmotic potential when drought-stressed, a phenomenon known as osmotic adjustment, measurements of leaf Ψ_π should ideally be made when plants are not suffering from drought stress, unless, of course, the latter is a desired aspect of the trait measured.

Adaptation to Salt Stress
Leaf osmotic potential

Tissues of plants adapted to highly saline soils typically have very low (highly negative; often much more negative than -3.0 MPa) osmotic potentials, which reduces the Ψ of such plants, allowing the uptake of water from salty soils that have low water potentials (Nobel 1999; Larcher 2003). Thus, values of leaf Ψ_π can also indicate the salt tolerance or adaptation of plants to saline soils, especially if the saline nature of the soil where the plants of interest grow is known.

Degree of Exposure to Previous (Drought) Stress
Stable Carbon Isotope Ratio

Not only will the $\delta^{13}C/^{12}C$ value of a plant help indicate its photosynthetic pathway (see below), this value will also reflect the recent history of (primarily drought) stress of a C_3 plant (Griffiths 1993; this does not usually hold for C_4 and CAM plants). This value must, however, be used with caution and, at best, in a comparative fashion, as many factors can influence the $\delta^{13}C$ value of a plant. Nonetheless, if other factors are comparable, especially if two individuals of the same species are compared, a higher (less negative) stable carbon isotope value indicates that the plant has closed its stomata (partially) more often and/or for longer periods of time than a comparable plant with a lower (more negative) $\delta^{13}C$ value, at least over the life span of the leaf measured. Variations in this value are often interpreted as reflecting the "intrinsic water-use efficiency" (WUE) of a plant, because more frequent stomatal closure increases the water-use efficiency of a plant; however, extrapolation of the $\delta^{13}C$ value to the WUE of a plant can lead to erroneous conclusions if the plant has not experienced drought stress or, if past stress effected full stomatal closure during the time period of interest. Furthermore, a plant with a low (more negative) $\delta^{13}C$ value might be interpreted as having exerienced little stress, yet this conclusion might be incorrect if the plant had experienced stress that damaged the photosynthetic apparatus, yet had little effect on the stomata. Nevertheless, $\delta^{13}C$ values can provide useful insight into the past (over the life span of the leaf measured) stress exposure, if these caveats are heeded. In other words, if differences in $\delta^{13}C$ values are found among plants, it can be reasonably assumed that those with less negative values were more stressed than those plants with more negative $\delta^{13}C$ values. Difficulties in interpretation of these values may arise, however, when no differences in $\delta^{13}C$ values are observed among plants, and one is

tempted to conclude that all such plants were not or were equally stressed.

Adaptation to High or Low Temperature Stress

Temperature Limits of Leaf Cell Integrity

Many physiological processes decline at sub- and supraoptimal temperatures; however, most such processes are difficult to detect without sophisticated instrumentation and/or elaborate experimentation. On the other hand, the loss of cell integrity, *i.e.*, rupture of the cell plasmalemma, marks an easily measured response to lethally low and high temperatures for a plant. Furthermore, a simple and inexpensive method exists to determine such lethally high and low temperature limits: the vital stain neutral red will be absorbed only by cells with intact outer membranes (Onwueme 1979). Thus, treatment (often a using temperature-controlled water bath) of leaves or other plant tissues at a range of low or high temperatures, then staining thin tissue slices with neutral red, followed by obervation of cell color with a compound microscope will reveal the temperature tolerances of the plant.

Photosynthetic Pathway

Stable carbon Isotope Ratio, Anatomy, and Tissue Acidity Changes

Although many and often glaring exceptions exist, each of the three photosynthetic pathways often generally reflects the environmental (including microenvironmental) conditions to which a plant is best adapted. For example, most C_3 plants are best suited to shady or at least less-exposed, cooler, and moister environments, whereas C_4 and CAM plants are usually better suited to sunny, exposed, warm-to-hot, arid conditions. The best predictor of the occurrence of C_4 plants is often high temperature, while drought intensity and frequency is a better predictor of the occurrence of CAM plants. It is important to keep in mind that some plants in all three photosynthetic pathway groups can be found growing successfully in nearly all types of habitats.

Determining the photosynthetic pathway of a plant is fairly straightforward, but may require several different measurements. First, the stable carbon isotope ratio of a leaf will reveal much in this regard (Ehleringer and Osmond 1991; Griffiths 1993). If the $\delta^{13}C$ value is substantially (more than a few per mil) more negative than -20‰, the plant is most likely a C_3 plant. In contrast, if the value is less negative than -20‰, the plant is likely a C_4 or CAM plant (Edwards and Walker 1983; Winter and Holtum 2002). In the case of the latter twp plant types, if anatomical inspection of a leaf cross-section reveals Kranz anatomy, then the plant uses the C_4 photosynthetic pathway. If the plant with a high (not very negative) delta-^{13}C value lacks Kranz anatomy, yet exhibits an overnight increase (or diurnal decrease) in acidity of the photosynthetic tissue, the plant is a CAM plant.

Adaptation to Soil Nutrient Availability

Leaf/Soil Elemental Concentrations

Leaf elemental composition, especially concentrations of nitrogen, potassium, and phosphorus, is informative and can be compared with published values for plants in a wide variety of conditions, but these concentrations reflect two parameters, the elemental composition of the soil and the ability of a plant to extract the elemental nutrients from that soil (Binkley and Vitousek 1991; Chapin and Van Cleve 1991). Both parameters are of considerable interest, but in studies of plant functional traits, the latter is usually of greater interest than the former. As a result, simple leaf elemental concentrations are likely inadequate. A more useful measure of a plant's

ability to acquire nutrients is its response to nutrient additions. Therefore, it is proposed here that leaf elemental concentrations be compared with soil concentrations for the same element, with both values expressed on a dry mass basis. Although not a perfect comparison, this plant: soil concentration ratio should provide comparative approximations of the ability of different plants to obtain essential elements from the soil, even if such plants are growing in soils with different nutrient contents.

$^{15}N/^{14}N$ ratio

The stable nitrogen isotope ratio can provide great insight into the source of nitrogen of a plant, especially differentiating nitrogen from N_2-fixing organisms vs. soil nitrogen derived from other sources in the plant community (Virginia and Delwiche 1982; Ehleringer and Osmond 1991; Viana *et al*. 2011). This information may be useful in characterizing ecosystem function, as it indicates whether the plants in the ecosystem depend on soil and litter for their nitrogen or provide nitrogen themselves, at least in association with symbiotic, N_2-fixing microorganisms. As a result, an ecosystem with more plants having the nitrogen-fixing trait is less likely to suffer from malfunction due to low nitrogen for all critical plant functions.

CONCLUSIONS

Although some of the criteria described above may fail to meet the goals stated earlier, these criteria approximate those goals and were selected for this reason and, in part, for their relative ease of measurement.

A number of the proposed traits are stress-related, yet quantification of such traits is intended to provide insight into the ability of a plant to adapt to different environmental

or microenvironmental conditions, regardless of the level of stress - or lack thereof - at the time of measurement.

If all - or many - of the above measurements were made on the dominant species (as many as practicable) of the different plant communities to be compared, the resultant data should provide great insight into the nature and severity of different abiotic stresses encurred by plants in each community, as well as the degree to which plants in each community have adapted to such stresses and physiological demands associated with growing in the communities under comparison. To wit, this will allow more detailed comparisons and analyses of community or ecosystem function.

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