occurred through both the autophagy and ubiquitin–proteasome pathways.

## Concluding Remarks

Taken together these findings not only reveal exiting new molecular mechanisms in the battle between viruses and their host, but may also offer novel opportunities for plant antiviral strategies. For instance, activation of autophagy could be used to enhance plant resistance to several DNA viruses, as indicated by Haxim *et al*. [7], or engineering AGO1 to make it resistant to P0-mediated degradation could possibly protect plants from poleroviruses.

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Forum

# On Plant Modularity Traits: Functions and Challenges

Gianluigi Ottaviani,[1,*] Jana Martínková,[1] Tomáš Herben,[2,3] Juli G. Pausas,[4] and Jitka Klimešová[1]

**On-spot persistence, space occupancy, and recovery after damage are key plant functions largely understudied. Traits relevant to these functions are difficult to assess because of their relationships to plant modularity. We suggest that developing collection protocols for these traits is feasible and could facilitate their inclusion in global syntheses.**

## Plant Modularity Traits and Related Functions

After several decades of data collection, broad-scale analyses of plant functional traits (e.g., specific leaf area, plant height, seed size) are emerging as formidable tools for understanding plant ecological strategies [1–3]. Coordination and trade-offs among traits prevail, with a large proportion of the intra- and interspecific trait variability explained by two dimensions [2]: competitive ability and resource acquisition, retention and use strategies (see Glossary). Other important functions and associated ecological strategies, however, are not captured by these trait axes and are consequently overlooked in current global functional analyses [4]. For example, in addition to reproducing sexually, plants can also reproduce vegetatively through clonal growth, which increases plant longevity and fitness [5]. Also, damaged plants may regenerate not only from seed banks but also from bud banks [6]. Plant size and competitive ability may be related not only to vertical growth (as in trees) but also to horizontal growth, as in clonal plants. By means of spacers such as rhizomes and stolons, clonal plants can explore and forage for resources far from the maternal plant [7].

There are other key functions related to plant–plant interactions and plant–environment relationships that have long been considered essential for plant community ecology, yet they are unexplored. These include on-spot persistence, space occupancy, and recovery after damage [4]. Traits related to these functions – plant modularity traits (Figure 1 and Box 1) – are underrepresented in global trait databases, with a few exceptions from Central Europe (e.g., CLO-PLA, LEDA; with information on plant clonality) and from fire-prone regions (e.g., BROT; with information on resprouting). This gap has precluded global comparisons and is

### Glossary

**Leaf economics spectrum [1]:** leaf traits are correlated in a manner such as to generate a functional continuum. On one end, leaves are thin and large, photosynthetically efficient, high in nutrient content, short-lived, palatable, and easily decomposable. On the other end, leaves have the opposite traits.

**Global spectrum of form and function [2]:** the relationships among six functional plant traits and growth form reveal that trait space is not randomly or uniformly filled; instead, traits are coordinated with each other along two main dimensions. The first axis is related to plant size (from herbs to trees) while the second dimension refers to the leaf economics spectrum. The traits used in this global-scale study are adult plant height, stem-specific density, leaf area, leaf mass per leaf area, nitrogen content per unit of leaf mass, and diaspore mass.

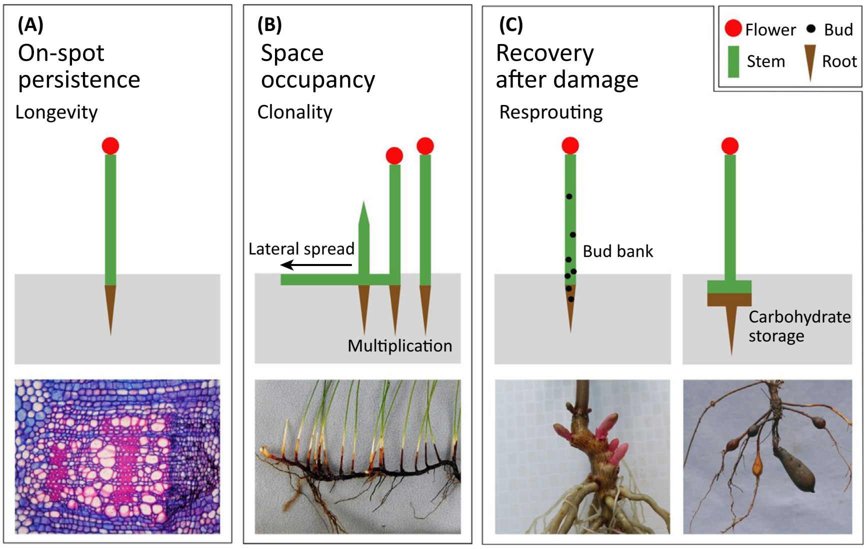


Figure 1. Plant Ecological Functions and Relevant Modularity Traits. (A) On-spot persistence is associated with plant longevity. Photograph: Transverse section of 3-year-old rhizome segment of *Filipendula ulmaria* (Rosaceae), 200× magnification (photograph credit: F.H. Schweingruber). (B) Space occupancy can be explored by clonality, which involves lateral spread, clonal growth organs, and multiplication rate. Photograph: Rhizome of *Ficinia nodosa* (Cyperaceae) with multiple shoots and roots (photograph credit: J. Martínková). (C) Recovery after damage depends on resprouting ability, which is made possible by two plant resources: reserves of buds and storage of carbohydrates. Left photograph: Root buds induced by injury in *Euphorbia illirica* (Euphorbiaceae) (photograph credit: J. Martínková). Right photograph: Storage root tubers in *Filipendula vulgaris* (Rosaceae) (photograph credit: Š. Janeček).

likely to reflect the lack of standardized protocols for measuring plant modularity traits [8]. The vast diversity and variability of clonal growth forms, the difficulty in identifying and locating the different modules, and their plasticity have limited the incorporation of modularity traits into plant functional handbooks.

We propose that such limitations can now be overcome by changing the way we look at individual plants; instead of looking at organs like leaf, seed, and root, we should consider plant modules (Box 1). With this view we can understand how individual modules (e.g., shoots) are added or replaced, how long they persist, where they are located, and whether they are capable of becoming independent. With this 'modular perspective', we suggest operational protocols for describing traits relevant to the key functions of on-spot persistence, space occupancy, and recovery after damage.

## Ecological Relevance and Operational Challenges

The greatest challenge in standardizing plant modularity traits lies in the definition of the sampling units; that is, the modules for which traits must be assessed (Box 1). Relevant modules may differ among growth forms. Therefore, the correct determination of modules for the standardization of these traits is crucial. Below, we identify methods and challenges for the collection and standardization of key modularity traits related to: (i) longevity (on-spot persistence); (ii) clonality (space occupancy); and (iii) resprouting (recovery after damage) (Figure 1). We also include examples of successful attempts to dealing with these functions.

### Longevity

Longevity refers to the lifespan of different plant modules and provides information on the time interval during which a plant occupies an area, acquiring, retaining, and sharing resources; it is thus indicative of overall plant persistence. Several longevity traits can be described using anatomical and morphological methods for dating modules (herbchronology, dendrochronology) and for detecting connections among clonal offspring (Figure 1). By considering the longevity of structures other than leaves, we can improve our understanding of plant strategies (e.g., how longevity correlates among different modules and differs between modules and organs [9]?). Determining the age of clonal plants is challenging when the oldest parts are decaying or when the growth rings are obscured. Age may be estimated, however, by indirect approaches based on demographical techniques [10].

### Clonality

Clonality is the capacity to produce physically independent ramets, which promotes vegetative reproduction when conditions hinder seed production or seedling establishment. The ability to spread laterally by means of spacers enables plants to explore and colonize new environments, compete with neighbors, and forage for nutrients [7]. Additionally, the ability of ramets connected by rhizomes to share resources in heterogeneous environments may be beneficial under stressful conditions. Key traits describing clonality include the type of clonal growth organs, the lateral spread, and the multiplication rate (Figure 1). Standardizing the descriptions of clonal growth organs is difficult because of the different morphological typologies used (e.g. [11]). Furthermore, clonality exhibits both high intraspecific plasticity and interspecific variability, with many species combining several modes of clonal growth. Examples of successful implementation of a common, shared typology for clonal organ description across biomes are still lacking, whereas definitions of individual clonal traits exist regionally and may serve as a foundation for broader standardization [11].

## Box 1. Plant Modularity: Basic Concepts

Plant modules are defined as any repeating architectural unit of a plant body. Clonal and non-clonal plants can be formed by different modules (Figure I), determining their architecture and associated functions. Four major modules are identified.

- Genet: Product of a zygote (the rooting unit in non-clonal plants).
- Ramet: Potentially independent part of a genet (a rooting unit in clonal plants).
- Rooting unit: The smallest plant part capable of independently surviving as the root and shoot systems are connected (i.e., a ramet of clonal plants, the genet of non-clonal plants).
- Shoot: The product of apical meristems; its growth is usually terminated by flowering and fruiting structures. Examples are ramets in clonal herbs and twigs in trees.

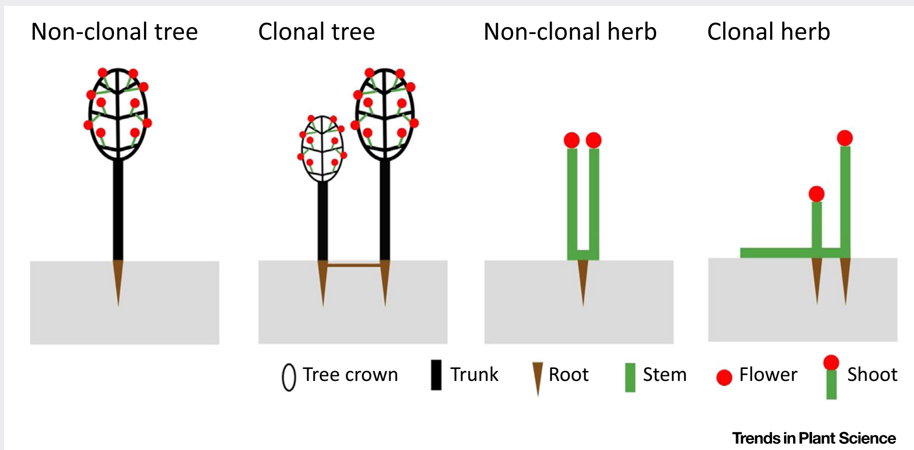


Figure I. Modular Structures in Non-clonal and Clonal Trees and in Non-clonal and Clonal Herbs. In these examples, the non-clonal tree and non-clonal herb are formed by one rooting unit (i.e., the rooting unit is the genet) but their clonal counterparts are formed by two rooting units (the rooting unit is a ramet).

### Resprouting

Resprouting – the ability to generate new shoots after the elimination of part or all of the aboveground biomass – is probably the most-studied strategy related to plant modularity worldwide, due to its relevance in fire-prone environments [6,12]. Resprouting allows plants to recover after seasonal rest or after injury caused by environmental pressures or disturbances. Most studies have recorded resprouting ability as a binary trait (presence/absence), but there is much more variability in the probability and the vigor of resprouting at the global scale [12]. Resprouting depends on two resources, buds and carbohydrates [6,7,12], and their numbers and quantities can be used as proxies for resprouting potential. Traits deserving focus include bud bank size, distribution of buds in relation to the soil surface, bud protection by plant structures (e.g., bark), and carbohydrate amount and concentration in roots and in specialized storage organs (Figure 1). The main challenge in sampling these traits is the belowground location of most bud-bearing organs, where they are hard to extract and often intermingled among plants, making any quantitative determination rather difficult. Another challenge is standardizing the resprouting ability or vigor across different disturbance regimes. The knowledge gained in fire-prone ecosystems [6,12] might serve as a basis for the development of standardization protocols.

## Concluding Remarks

We suggest that the gathering of comparable data on plant modularity traits is now an important and reachable target in plant ecology. By building on the above-mentioned expertise gained regionally regarding longevity, clonality, and resprouting traits, we are aiming at developing a large research network that would allow us to combine this knowledge into a handbook of standardized protocols. These procedures could then be applicable worldwide, considering these traits from different regions and biomes, which will increase our mechanistic understanding of plant fitness, strategies, and community assembly. Therefore, standardized methodologies could facilitate the inclusion of key, yet poorly studied, ecological dimensions into global syntheses.

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