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Plant Biology ISSN 1435-8603

RESEARCH ARTICLE

Disentangling the effect of growth from development in size-related trait scaling relationships

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Keywords
allometry; forks; ontogeny; plant architecture; reiteration; savanna; *Senegalia nigrescens*.

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Editor
C. Lara-Romero

Received: 19 October 2023;
Accepted: 5 February 2024

doi:10.1111/plb.13634

ABSTRACT

- In plant ecology, the terms growth and development are often used interchangeably. Yet these constitute two distinct processes. Plant architectural traits (*e.g.* number of successive forks) can estimate development stages. Here, we show the importance of including the effect of development stages to better understand size-related trait scaling relationships (*i.e.* between height and stem diameter).
- We focused on one common savanna woody species (*Senegalia nigrescens*) from the Greater Kruger Area, South Africa. We sampled 406 individuals that experience different exposure to herbivory, from which we collected four traits: plant height, basal stem diameter, number of successive forks (proxy for development stage), and resprouting. We analysed trait relationships (using standardized major axis regression) between height and stem diameter, accounting for the effect of ontogeny, exposure to herbivory, and resprouting.
- The number of successive forks affects the scaling relationship between height and stem diameter, with the slope and strength of the relationship declining in more developed individuals. Herbivory exposure and resprouting do not affect the overall height–diameter relationship. However, when height and stem diameter were regressed separately against number of successive forks, herbivory exposure and resprouting had an effect. For example, resprouting individuals allocate more biomass to both primary and secondary growth than non-resprouting plants in more disturbed conditions.
- We stress the need to include traits related to ontogeny so as to disentangle the effect of biomass allocation to primary and secondary growth from that of development in plant functional relationships.

INTRODUCTION

Scaling relationships are a core concept and area of research in plant sciences and functional ecology (West *et al.* 1999; Westoby *et al.* 2002). Understanding how different traits or the biomass of different organs scale with one another can provide insights into fundamental plant strategies, for example biomass allocation to leaves and shoots (*e.g.* Fajardo *et al.* 2020). Most studies on scaling, however, are executed at the interspecific level (*e.g.* Reich *et al.* 1999) and fail to account for variation in relationships throughout the development stages of individuals, *i.e.* through ontogeny (*e.g.* Cavender-Bares & Bazzaz 2000). This gap is particularly important when considering the scaling relationships of size-related (growth) traits, as several processes and functions have been proven to change at the intraspecific level (*e.g.* He & Yan 2018; Fajardo *et al.* 2020) and during ontogeny (Barthélémy & Caraglio 2007; Dayrell *et al.* 2018). In addition, scaling between different traits and organs may shift in response to disturbance – which is especially relevant in open biomes that are prone to frequent and long-term disturbance in the form of fire, herbivory, frost, and drought (Moncrieff *et al.* 2011; Lamont & He 2017; Pausas *et al.* 2018). In open biomes, such as savannas, most plants are therefore likely to be disturbed at least once during their ontogeny. As a result, examining plant scaling relationships while controlling for the effects of ontogeny and disturbance may provide a deeper understanding of basic scaling relationships, particularly in open ecosystems.

In plant ecology, development is often confused (if not synonymized) with growth. For example, development (*i.e.* ontogenetic) stages are routinely assessed using size-related traits, such as plant height and stem diameter. These approaches consider an individual's ontogeny as a monotonic gradient – assuming no changes in the slope of the relationship during ontogeny, implying constant growth. However, a drawback of conflating development and growth is, for instance, that in early developmental stages individuals go through an establishment phase (Tomlinson & Esler 1973; Barthélémy &

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Caraglio 2007) during which they express a sequence of differentiation characterized by an increase in the size and number of organs produced and/or the setting up of different shoot types during the stabilization of their architectural unit (Poethig 2003; see Barthélémy & Caraglio 2007 for further details on architectural unit establishment). Later, individuals start duplicating their fundamental building block (*i.e.* architectural unit) via the total sequential reiteration process (Barthélémy & Caraglio 2007). After this stage, the architectural complexity caused by vertical and lateral expansion of the crown and increased stem diameter (secondary growth) may dramatically increase. This calls for including traits able to estimate whether and how developmental variability affects size-related trait scaling relationships.

The study of plant architecture offers a viable way to assess development stages based on major branching events. Following the architectural method (*sensu* Hallé *et al.* 1978; Barthélémy & Caraglio 2007), traits such as the emergence of a new shoot type or the expression of the reiteration process, can be used as markers of developmental stages (Barthélémy & Caraglio 2007). In fact, these traits have proven useful in forestry (Bossu *et al.* 2018; Wigley *et al.* 2020), where the appearance of the first fork has been used to estimate maturity in trees as it represents the end of bole production and the beginning of the duplication of their fundamental building block (Magnin *et al.* 2022). Forks appear in tree crowns as the result of the sequential reiteration process (Barthélémy & Caraglio 2007) through which plants progress in their development. The appearance of the first fork and the number of successive forks may therefore operate as an informative and easy-to-record trait to estimate development stages, yet their usefulness in plant functional ecology, including scaling relationship studies, remains untested.

In open biomes exposed to disturbance, such as savannas, developmental events (such as the appearance of forks) may play a key role in reaching certain height thresholds to escape topkill by herbivory and/or fire (also known as disturbance traps; see Wakeling *et al.* 2011; Osborne *et al.* 2018). If individuals start forking within the disturbance trap, they have a lower chance of making it beyond the trap – as after their fifth fork plants tend to drastically reduce their height gain (Charles-Dominique *et al.* 2015a). Additionally, being able to resprout after disturbance is vital to shape individual persistence (Bond & Midgley 2001, 2003; Keeley *et al.* 2011), and may also influence scaling relationships between height and diameter because biomass allocation to stems may vary between different life histories, *i.e.* between resprouting and non-resprouting individuals. Using an architectural approach, we examine whether and how development, resprouting and disturbance exposure affect size-related trait scaling relationships (*i.e.* between plant height and stem diameter) in a common savanna woody species (*Senegalia nigrescens*) from the Greater Kruger area (including Kruger National Park [KNP]), South Africa. Specifically, we ask: (i) are size-related trait scaling relationships affected by ontogenetic stages; (ii) are scaling relationships between size-related traits as well as between growth and development affected by different life histories (*i.e.* resprouting *versus* non-resprouting individuals) and exposure to disturbance (*i.e.* more or less prone to herbivory)?

MATERIAL AND METHODS

Study area

We focused our sampling on three sites, divided in two major groups according to their disturbance by herbivores. The main differences between these two groups of sites rely on their exposure to herbivory: meso- and megaherbivores are present in Kingfischerspruit, whereas they are absent from Hoedspruit and the enclosure of the Southern African Wildlife college. On the one hand, we selected a site fully exposed to disturbances, located in the Orpen region belonging to the western central part of Kruger National Park (KNP; South Africa), in Kingfischerspruit (24°27′ S; 31°27′ E). Kingfischerspruit is part of the Timbavati gabbros geological formation, and also belongs to the Satara land system, characterized by mafic volcanic rocks (basalts) and a flat plains topography, covering around 14% of KNP (Venter *et al.* 2003). The area consists of fertile clay soils derived from gabbros interspersed between surrounding granite-gneiss. The fertile clay soil supports mixed thornveld. The average rainfall in the region ranges from 500 to 650 mm·year^{-1} (Venter *et al.* 2003), and the mean annual rainfall recorded at the nearest station of Kingfischerspruit is ~570 mm·year^{-1} (1965–2005; Yoganand & Owen-Smith 2014). The average fire interval return is 7–8 years (van Wilgen *et al.* 2000). On the other hand, we selected two sites that have a comparable fire regime but that are protected from the reach of meso- and megaherbivores. One of these sites is in the village of Hoedspruit (24°21′ S, 30°58′ E), located close to the greater Kruger region. The other site is located in the enclosure of the Southern African Wildlife College (24°32′32″ S, 31°20′08″ E), belonging to the Greater Kruger region. In these two sites, the geology and other environmental conditions, such as fire interval return (Table S1) and rainfall are comparable to those in Kingfischerspruit.

Plant material: Focal woody species and measured traits

The focal species, *Senegalia nigrescens* (Oliv.) P.J.H.Hurter (Fabaceae; World Flora Online 2022), is widespread across Eastern and Southern Africa (Dharani 2006), and is common in our study area. It is a deciduous tree producing elongated white inflorescences (from August to October; Palgrave 2002). This slow-growing tree can reach up to 30 m in height; it has thick bark and presents suberized knobs emerging from the prickles found on its shoots. It is a palatable species, representing staple food for large mammal browsers (Fornara & Du Toit 2007). For trait measurement, we randomly sampled 406 individuals of *S. nigrescens* during spring at the end of the dry season (September) of 2020, grouped by different exposure to herbivory: 200 individuals from browsed sites inside KNP (exposed to meso- and megaherbivores) and 206 individuals from unbrowsed sites outside KNP (protected from meso- and megaherbivores). On each individual, we collected data related to four morphological and architectural plant traits: plant height, basal stem diameter, presence of basal resprouts (*i.e.* presence of aboveground visible resprouted stems: yes/no), and number of successive forks. Plant height was estimated using a height pole. We measured the basal diameter of the main stem (most developed) of each individual using a flexible

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tapemeasure within 30 cm above the soil surface. For resprouting, we recorded the presence or absence of basal resprouts, older resprouted dead stems, and the presence of resprouted living stems on each individual (Fig. 1a,b). We measured a total of 143 non-resprouting individuals and 57 resprouting individuals with basal resprouts inside KNP, as well as 160 non-resprouting individuals and 46 resprouting individuals outside KNP. We identified forks following standardized protocols (Wigley *et al.* 2020); in brief, we recorded a fork if the two axes constituting the fork under evaluation had an equivalent diameter, a similar growth direction, and producing equivalent branched complexes. We also made sure that the two parts of the fork developed simultaneously, as opposed to resprouting (delayed reiteration; Wigley *et al.* 2020) or a failed fork (Fig. 1c,d). Finally, on each individual, we counted the maximum number of successive forks observable in its crown, backwards from the last fork (more distal) of the axis in the canopy towards the base of the tree (as presented in Fig. 1c,d).

Data analysis

We ran standardized major axis (SMA) linear models, which are best suited to examine scaling relationships because they do not assume any dependencies between X and Y variables (Warton *et al.* 2006). To examine whether the number of forks changed the scaling relationship between stem diameter and plant height (i), we ran the model by setting the number of forks as a grouping (*i.e.* interacting) factor. To address (ii), we ran 14 SMA linear models, sorted by two sets of seven models each. In the first set, we analysed whether different life histories affected the overall relationship between stem diameter and plant height by setting resprouting as a grouping factor (two groups: yes, no). We ran the following models for both height–number of forks and diameter–number of forks relationships. In the first couple of models, we set resprouting as a grouping factor using the entire dataset. We then subset the dataset by resprouting (*i.e.* resprouting and non-resprouting individuals separately), and grouped by site (two groups: browsed, unbrowsed). In the second set, we implemented a similar approach, but this time focusing on herbivory exposure. We ran the following models for both height–number of forks and diameter–number of forks relationships. In the first couple of models, we set site (two groups: browsed, unbrowsed) as a grouping factor using the entire dataset. We then subset the dataset by site (*i.e.* individuals from browsed and unbrowsed sites separately) and grouped by resprouting (two groups: yes, no). In all cases, we tested for differences between slopes, and whether these differed from model estimate ~1. For all models, we checked assumptions of relationship linearity, normality of data distribution, and homoscedasticity of residuals; these were met after log10-transformation of stem diameter and plant height values. We conducted all the analyses in R version 4.0.1 (R Core Team 2020), using the function 'sma' in the package *smatr* (Warton *et al.* 2012).

RESULTS AND DISCUSSION

The scaling relationship between basal stem diameter and plant height declines along ontogeny

As scaling relationships can be of different types associated with slope steepness, we followed the terminological and conceptual framework proposed by Stillwell *et al.* (2016). For relationship's slope not significantly different than 1 we refer to it as isometry, for slope significantly <1 as hypoallometry, and for slope significantly >1 as hyperallometry. The overall scaling relationship between basal stem diameter and plant height is hypoallometric (slope = 0.70) in *S. nigrescens* (inset in Fig. 2). This result shows that *S. nigrescens* fits within the overall framework of plant allometries (West *et al.* 1999) and suggests that our results may have general implications for further understanding allometric relationships observed in woody plants. By accounting for the number of successive forks, we show how the relationships between diameter and height are distinct within specific development stages (Fig. 2). Less developed individuals (zero to one fork) are distinguished by an isometric scaling (*i.e.* slope ~ 1), whereas more developed individuals (from two to seven forks) tend to be characterized by an increasingly hypoallometric scaling (*i.e.* slope decreases with higher number of forks) and by a weaker link (*i.e.* lower model

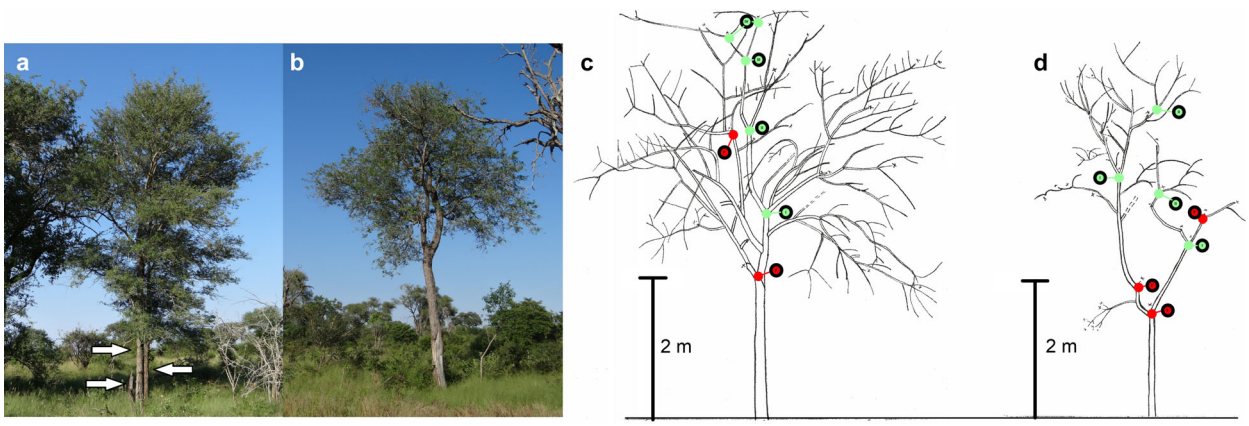


Fig. 1. Assessing resprouting individuals and forks. A resprouting individual of *S. nigrescens*; arrows point to basal resprouts (a). Non-resprouting individual of *S. nigrescens* (b). Semi-schematic representations drawn in the field (at scale) of two individuals of *S. nigrescens* with comparable height but different number of successive forks and diameters (c, d). More developed individual presenting four successive forks (c). Less developed individual presenting two successive forks (d). (I–IV): rank of the pointed fork. Green circles: successful fork; red circles: failed fork (dichasial branching with inequivalent diameter and/or bark colour following Wigley *et al.* 2020). Belowground compartment is intentionally not shown as it was not the focus of this study.

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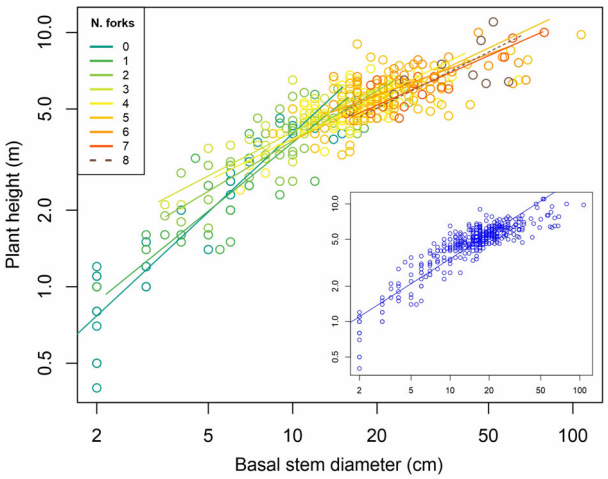


Fig. 2. Size-related trait scaling relationship and number of forks. Scaling relationship between basal stem diameter (log_{10}) and plant height (log_{10}) (inset), and this relationship broken down by accounting for the number of forks. Dashed lines indicate non-significant relationships (see Results S1 for all models' summary statistics).

R^2; Fig. 2; Supporting Information). This indicates that younger individuals tend to allocate more biomass to both primary and secondary growth than ontogenetically older individuals, which instead tend to allocate proportionally more biomass to secondary growth. The duplication of the main stem via forks considerably increases the basal stem diameter due to the anatomical functioning of this axis type (large production of wood), implying that the more a tree "repeats" its main stem by forking, the more wood it accumulates at its base (Shinozaki *et al.* 1964; Lehnebach *et al.* 2018). Foresters and plant architects (Bossu *et al.* 2018; Magnin *et al.* 2022) have long recognized that, after the first forking event, woody plants enter a different phase in ontogeny and change their functioning (as reflected in the height–diameter relationship here). We show that by using this easy-to-collect architectural trait in an ecological context we can refine the understanding of plant functioning, such as to disentangle the effect of development from growth. For instance, the more rapid height gain of less developed individuals may contribute to explaining how plants may escape the disturbance traps associated with recurrent fire and herbivory that characterize the savannas in this study (Wakeling *et al.* 2011). This varied size-related scaling along ontogeny may also have implications for how plants might be prone to ignition and burn during fires (Archibald & Bond 2003) – a task that deserves further examination.

Resprouting and disturbance exposure affect size-related trait scaling relationships once developmental stages are accounted for

While we have found that resprouting does not affect either the overall height–diameter scaling relationship (Fig. 3a) or the scaling between height and number of forks (Fig. 3b), resprouting does affect the scaling relationships between diameter and number of forks, but only weakly (Fig. 3e). Once the dataset is subset by resprouting, and the individuals grouped by site, the height–number of forks and diameter–number of forks relationships of resprouting individuals are less affected by exposure to disturbance than that of non-resprouting individuals (Fig. 3c,f cfr. Fig. 3d,g). We also observe that non-resprouting individuals from unbrowsed sites tend to grow quicker than non-resprouting individuals from browsed sites in both primary and secondary growth (Fig. 3d,g).

The overall scaling relationship between height and diameter is not affected by site (Fig. 4a), *i.e.* by exposure to herbivory. Instead, the relationship between height and number of forks and between basal diameter and number of forks differs significantly between the two levels of disturbance exposure (Fig. 4b,e): individuals growing in unbrowsed sites tend to grow faster than individuals growing in browsed sites. Once the dataset is subset by site, and the individuals grouped by resprouting, the two sites differ in their patterns. In browsed sites, where individuals are more exposed to herbivory, resprouting individuals tend to grow significantly faster than non-resprouting individuals (Fig. 4c,f), whereas no or weak differences between resprouting and non-resprouting individuals emerge at the unbrowsed sites (Fig. 4d,g).

Resprouting is an essential life-history feature of savanna woody plants, which can confer an eco-evolutionary advantage in such ecosystems (Bond & Midgley 2003; Keeley *et al.* 2011; Pausas & Keeley 2014). Despite the importance of resprouting in open biomes, whether and how resprouting influences trait scaling relationships remains under-explored. Our finding that at the site more exposed to herbivory, resprouting individuals tend to grow significantly faster in primary and secondary growth than non-resprouting individuals further corroborates the notion that resprouting constitutes an effective life-history strategy to cope with major disturbances (Clarke *et al.* 2013). The faster primary and secondary growth of younger/less developed resprouting individuals (having a small number of successive forks), benefitting from stored resources, may further contribute to explain how they can escape the disturbance traps (see Wakeling *et al.* 2011). At the same time, we reveal that the scaling relationships of non-resprouting individuals are more affected by exposure to herbivory (meso- and mega-herbivores in this case) than those of resprouting individuals, and may also indicate that non-resprouting individuals are less likely to make it through the disturbance traps. The results showing that primary and secondary growth of non-resprouting individuals are negatively affected by herbivory suggest that this disturbance may operate as a stronger top-down control on growth of non-resprouting individuals, which may not trigger basal resprouting (Clarke *et al.* 2013).

Emergence of the fifth fork as a "development milestone"

We identify – across multiple lines of evidence involving different scaling relationships – a "fifth fork threshold" (see dashed lines in Figs. 3 and 4 where most intersections between regression lines occur at or around the fifth fork). Once that threshold is reached, the growth of non-resprouting individuals of *S. nigrescens* less exposed to disturbance tends to exceed that of non-resprouting individuals more exposed to disturbance (Fig. 3d,g). This pattern implies that if non-resprouting individuals are not disturbed, they may reach greater primary and secondary growth; hence, it could be linked to the feeding of tall herbivores (such as giraffes and elephants) on browsed sites that may prevent height gain by removing the fresh herbaceous shoots present at the top of the canopy (referred to as "browse trap"; Staver & Bond 2014).

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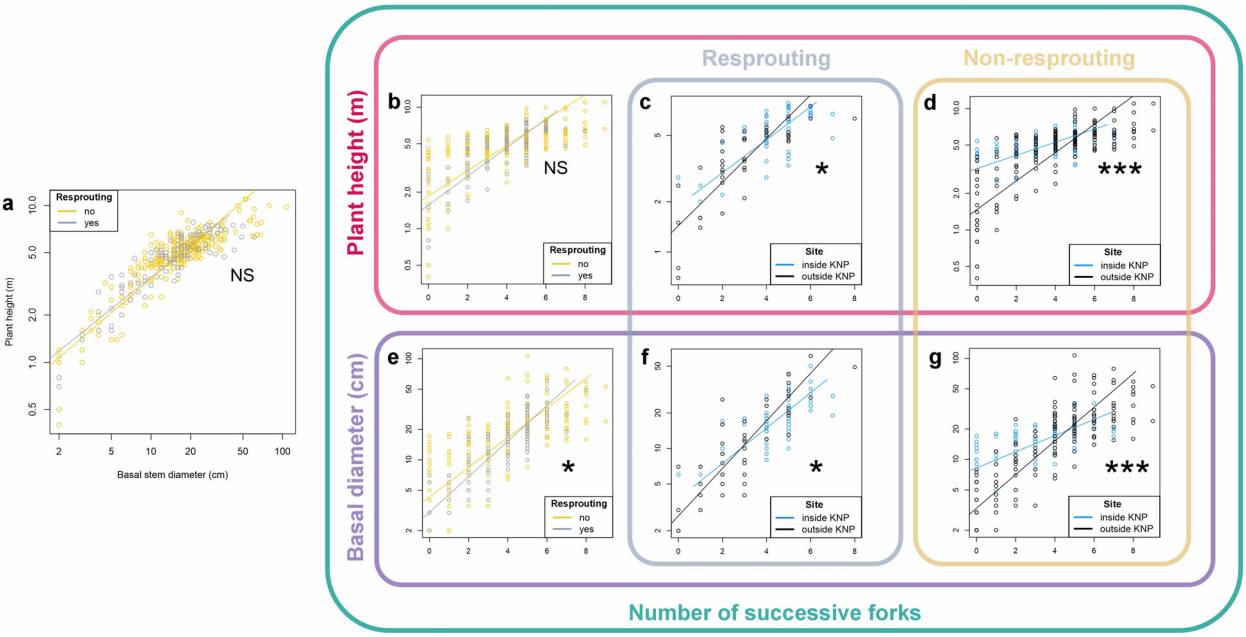


Fig. 3. Size-related trait scaling relationships and resprouting. Overall scaling relationships between basal stem diameter (x-axis: $\log_{10}$) and plant height (y-axis; $\log_{10}$) using resprouting as a grouping factor (a). Scaling relationships between plant height and number of successive forks (upper red box) and basal stem diameter and number of successive forks (lower purple box). These relationships are presented for models using resprouting as a grouping factor (b, e) and for models using subsets of resprouting (c, f) and non-resprouting (d, g) individuals, setting site as a grouping factor. Dashed lines represent the intersection point of the two regression lines in significant relationships. By "inside KNP" we refer to browsed site and by "outside KNP" to unbrowsed sites. ***$P \leq 0.001$, *$P \leq 0.05$, $^{NS}P > 0.05$.

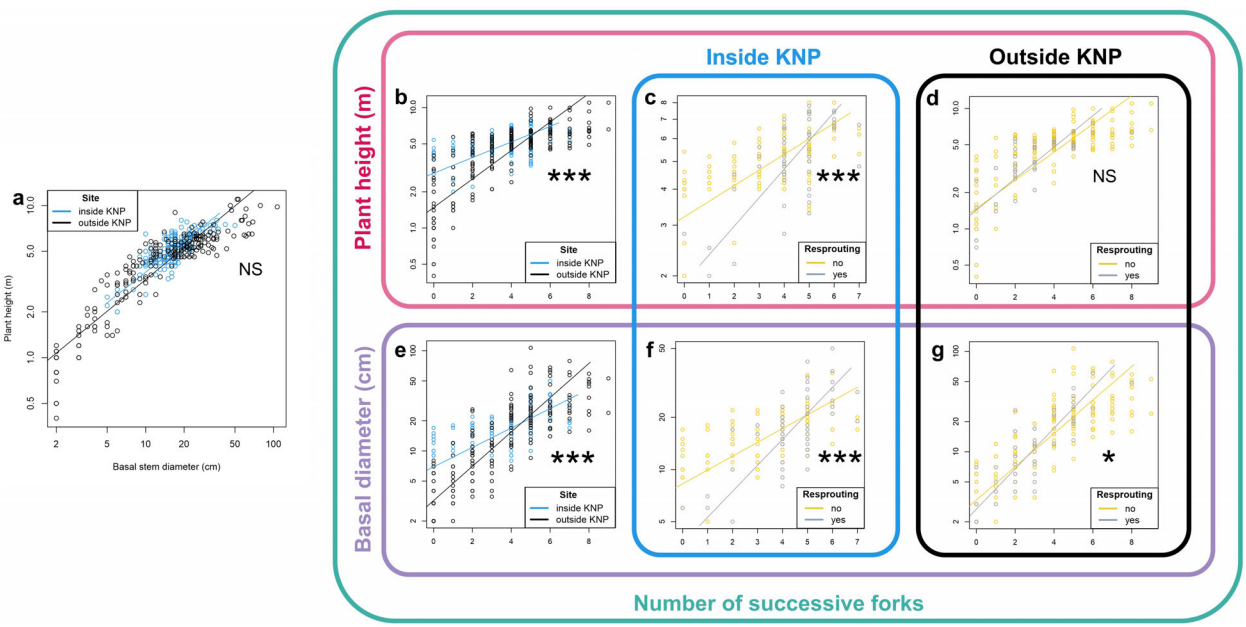


Fig. 4. Size-related trait scaling relationships and exposure to disturbance. Overall scaling relationships between basal stem diameter (x-axis: $\log_{10}$) and plant height (y-axis; $\log_{10}$) using sites as a grouping factor (a). Scaling relationships between plant height and number of successive forks (upper red box) and basal stem diameter and number of successive forks (lower purple box). These relationships are presented for models using site as a grouping factor (b, e) and for models using subsets of herbivory-exposed individuals (c, f) and herbivory-protected individuals (d, g), setting resprouting as a grouping factor. Dashed lines represent the intersection point of the two regression lines in significant relationships. By "inside KNP" we refer to browsed site and by "outside KNP" to unbrowsed sites. ***$P \leq 0.001$, *$P \leq 0.05$, $^{NS}P > 0.05$.

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Moreover, we may relate this result to the fact that gaining height is limited after the fifth fork in natural conditions (*i.e.* where all major disturbances occur, including widespread surface fires; Charles-Dominique *et al.* 2015a), while in more protected conditions this limitation could be weaker. Additionally, at the fifth fork, the growth of resprouting individuals more exposed to disturbance tends to overcome that of non-resprouting individuals (Fig. 4c,f). This indicates that the first fork in resprouting individuals appears at lower heights and smaller diameters than in non-resprouting individuals in more disturbed conditions. In development terms, this means that resprouting individuals tend to progress faster in their ontogeny than non-resprouting ones and may skip some early developmental events (Nozeran 1978; Barthélémy & Caraglio 2007).

WHERE TO FROM HERE?

Our findings stress the importance of disentangling the effect of developmental variation from that of growth variability on functional trait relationships, which are often conflated (Diggle 2002; Charles-Dominique *et al.* 2015b). Also, analysing the consequences of getting stuck in ontogeny – *i.e.* not being able to access further development stages, or being slower – may provide crucial insights for studies on population dynamics. We show that we can use forks to capture developmental stages; therefore, we should now be able to study how the forks successfully develop (or not) in the canopy, and how their set-up and its dynamics during ontogeny may impact individuals' ecological performance. Our study demonstrates that for a given height or diameter, trees could have different numbers of forks, being more or less advanced in their development (Fig. 2). Some of these tall (or thick), less developed trees often have fewer forks because their set-up failed (Fig. 1c,d). Gaining insight into the frequency, and possible causes behind such "failures" represents an interesting avenue for further studies, particularly to understand the impact of resource availability (*e.g.* water, nutrients) or biomass removal caused by disturbances on individuals' development, at least in disturbed ecosystems. Such efforts may facilitate detecting the ecological importance of the different ontogenetic stages experienced by plants. Furthermore, we acknowledge that the observed scaling relationships may have been affected by other biotic (*e.g.* plant–animal, plant–plant interactions) and/or abiotic (*e.g.* soil nutrient status and texture) factors which were not considered in this study. Also, in this research we focused on one species from one region; to further test the generality of our findings, similar approaches should be replicated and expanded to other species, regions, and biomes.

We encourage future studies to include other key plant functions, for example, whether and how architectural traits affect sexual reproduction thresholds (*e.g.* flowering onset, small or large production). The number of successive forks offers a useful tool, and also serves as a cautionary note, for future research focused on branching. In fact, it is essential to differentiate regular branching (involving morphological and functional differentiation of shoots; Barthélémy & Caraglio 2007) from the expression of sequential reiteration, which results in perennial branches duplicating the architectural unit (constituting the forks we considered in this study). Confusing these two different branching types may have far-reaching consequences for the way in which we perceive and understand plant structure, organization, and functioning.

ACKNOWLEDGEMENTS

We thank the Editors and three anonymous reviewers who provided constructive comments during the revision of this manuscript. MM, NS, HM, and SA received support from a NRF-SASSCAL grant (number 118588). MM received support from the Grant Agency of the Czech Republic (GAČR project: 22-10897S). MM and GO were supported by a long-term research development project of the Czech Academy of Sciences (RVO 67985939). GO also acknowledges the support of NBFC (National Biodiversity Future Center) funded by the Italian Ministry of University and Research, P.N.R.R., Missione 4 Componente 2, "Dalla ricerca all'impresa", Investimento 1.4, Project CN00000033 (funded by the European Union – NextGenerationEU). Open access publishing facilitated by Botanicky ustav Akademie ved Ceske republiky, as part of the Wiley - CzechELib agreement.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

MM, NS, SA designed the study. MM and HM performed the fieldwork. MM and GO conceived the research idea, analysed the data (with inputs from HB), and led the drafting of the paper. All co-authors contributed to revisions and accepted the final version of this manuscript.

DATA AVAILABILITY STATEMENT

The authors can make data available on request. Additional supporting information is available online in the Supporting Information section.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Fire history of study sites.

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