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Heteroblasty—A Review

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Abstract Virtually all plants show a certain degree of variation among individual metamers during ontogeny. In some cases, however, there are abrupt and substantial changes in form and function (e.g. in leaf form, leaf size, phyllotaxy, internode length, anthocyanin pigmentation, rooting ability, or wood structure). These plants were called "heteroblastic" by Karl Goebel more than a century ago, but the functional significance of this type of ontogenetic change, the evolutionary trajectories in different plant groups, even their frequency in the plant kingdom are still unresolved issues. We argue that slow progress is partly due to an on-going terminological confusion and the lack of distinction between other developmental processes such as ontogenetic drift. This review develops a conceptual framework for future scientific work, proposes a quantitative index of heteroblasty, and discusses the evidence for developmental regulation, functional significance, and evolutionary implications of heteroblasty to provide a stimulating basis for further research with this fascinating group of plants.

Zusammenfassung Fast alle Pflanzen zeigen während der Individualentwicklung ein gewisses Maß an Variabilität einzelner Metamere. Bei manchen Arten kommt es jedoch zu einer ausgeprägten und sprunghaften Änderung in Form und Funktion (z.B. in Blattform oder -stellung, Internodienlänge, Pigmentierung, Holzstruktur, oder hinsichtlich der Fähigkeit zur Bildung von Adventivwurzeln). Obwohl diese Arten von Karl Goebel schon vor mehr als einem Jahrhundert als "heteroblastisch" beschrieben wurden, sind die funktionelle Bedeutung des Phänomens, dessen Evolution innerhalb einzelner Pflanzengruppen, wie auch die Häufigkeit im Pflanzenreich immer noch weitgehend ungeklärt. Dieser schleppende Fortschritt mag mit einem weit verbreiteten terminologischen Durcheinander und dem Fehlen einer klaren Abgrenzung von anderen Entwicklungsprozessen wie der "ontogenetischen Drift" zusammenhängen. Unser Übersichtsartikel entwickelt einen klaren konzeptionellen Rahmen, um eine Basis zu schaffen für zukünftige Forschungsarbeiten dieses faszinierenden Entwicklungsphänomens. Dazu schlagen wir einen quantitativen Index der Heteroblastie vor, skizzieren den gegenwärtigen Wissensstand der Regulierung von Entwicklungsprozessen bei Pflanzen, die bisherigen Untersuchungen zur funktionelle Bedeutung heteroblastischer Veränderungen, beleuchten aber auch die evolutionären Implikationen der Heteroblastie.

Keywords Bromeliaceae · Carnivorous plants · Divaricate shrubs · Epiphytes · Evolution · Hemiepiphytes · Heterophylly · Plant hormones · Leaf development · Phase change

Introduction

The shoot system of higher plants grows by adding new modules or metamers at the shoot apex, which normally consist of an internode, a leaf or leaves, and vegetative or floral buds. Three more or less discrete temporal phases are frequently distinguished during postembryonic development: a juvenile vegetative phase, an adult vegetative phase, and a reproductive phase (Poethig, 2003). While only defined by the capacity to produce reproductive organs, more or less simultaneous changes in vegetative features such as differences in leaf shape and size, leaf arrangement, internode elongation, or the capacity for adventitious root production are frequently used as proxies to identify these phases.

Thus, plants do not merely increase in size (biomass, height, volume) during ontogeny by adding metamers, but these metamers almost universally show a certain degree of variation, in part simply because an increase in size necessitates correlated changes in shape and geometry (Niklas, 1994). This size-related variation is relatively subtle and gradual in the majority of cases, but there are also species with quite dramatic and abrupt changes. More than a century ago, Goebel (1889) described these species as "heteroblastic" to be distinguished from "homoblastic" taxa, in which changes are negligible or gradual. Classic examples of heteroblastic development (Fig. 1) are found among phyllodineous *Acacia* species (Kaplan, 1980), European ivy (*Hedera helix*, Goebel, 1913), aroid vines (Lee & Richards, 1991), *Ulex europaeus* (a leafless shrub with a leaf-bearing "juvenile" stage), or tree species with a "divaricate" initial stage, i.e. small-leaved woody shrubs that have closely interlaced branches, which are quite distinctive for the flora of New Zealand (Cockayne, 1912). Remarkably, the morphological differences between forms can be so stunning as to fool scientists into describing them as different species (Lecomte & Webb, 1981).

Since Goebel's original publication, a considerable amount of research has been dedicated to the subject, addressing a range of questions such as the proximate mechanisms behind these abrupt changes (Kerstetter & Poethig, 1998), their evolutionary implications (Tomlinson, 1970; Li & Johnston, 2000), and also their functional and ecological consequences (Jones, 2001). The older literature, mostly dealing with morphological and anatomical, but also physiological aspects of heteroblasty, was reviewed in detailed and extensive earlier reviews, e.g. by Troll, 1939, Ashby, 1948, Schaffalitzky de Muckadell, 1959, or Allsopp, 1965, while more recent reviews clearly reflect the advance of molecular techniques (Kerstetter & Poethig, 1998). There are also a considerable number of studies trying to demonstrate an extant adaptive function of these ontogenetic changes, although to date most results are negative or inconclusive (Winn, 1999; Darrow et al., 2001, 2002; Gamage & Jesson, 2007).

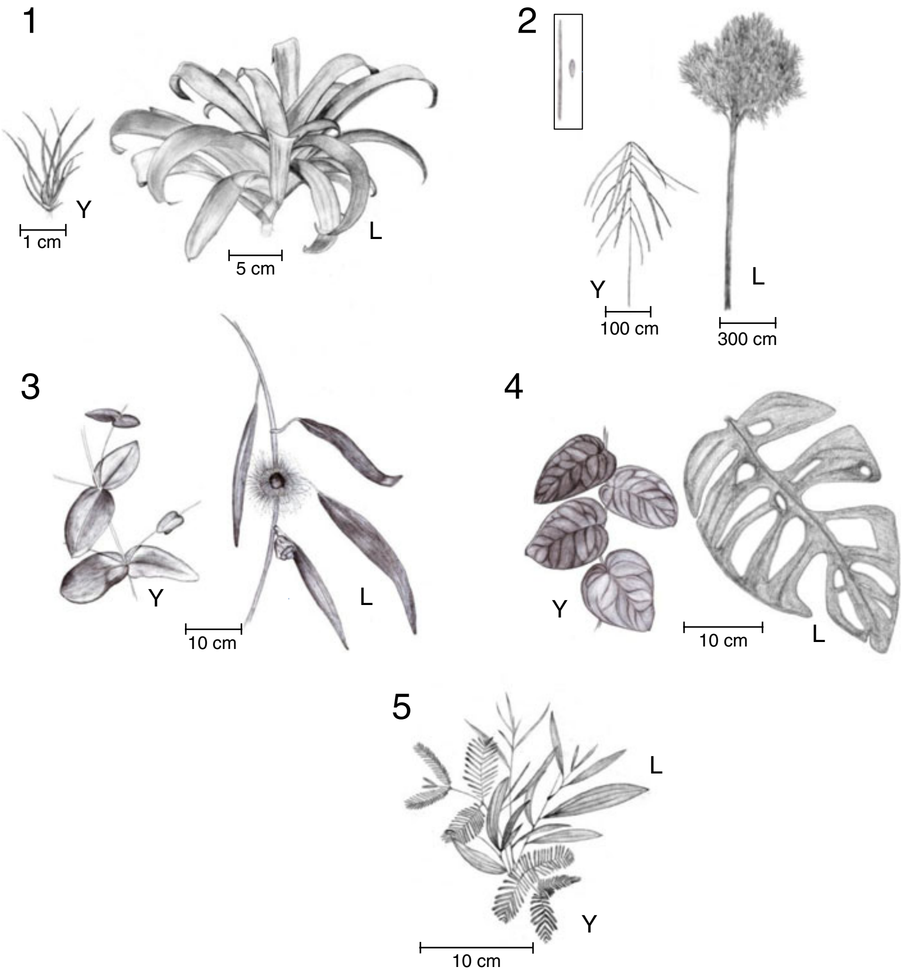

Fig. 1 Habit sketches of heteroblastic species. 1) *Vriesea heliconioides* (Bromeliaceae); 2) *Pseudopanax crassifolius* (Araliaceae), inset shows single leaves to illustrate changes in shape; 3) *Eucalyptus globulus* (Myrtaceae); 4) *Monstera dubia* (Araceae); 5) *Acacia melanoxylon* (Mimosaceae). Y = young form; L = later form. Note the different scales

However, no comprehensive recent review on heteroblasty is available. Such a review seems important not least because of a growing inconsistency in terminology in the literature, e.g. when it comes to the use of the terms heteroblastic vs. homoblastic species or heteroblasty vs. heterophylly. Although Jones (1999) has discussed major conceptual and terminological issues in an excellent essay, subsequent studies have paid little attention to her suggestions. The current review thus deals explicitly with the existing terminological ambiguity and reviews major biological aspects of heteroblasty in the hope to provide a stimulating basis for future research.

Particular emphasis is put on the functional implications of heteroblasty, starting with the assumption that it is indeed adaptive (‘all juvenile characteristics will be shown to be adaptive in certain environments’; Barber, 1965). To demonstrate that heteroblastic changes are indeed functionally important under current ecological conditions, we face a prominent problem, since different processes are likely to co-occur during ontogeny. Apart from heteroblasty, which describes a step change in vegetative features, there are gradual ontogenetic changes associated with changes in size (‘ontogenetic drift’; Evans, 1972) as well as a phase change from juvenile to adult (= reproductive) associated with maturing and possible functional physiological changes of vegetative organs. To complicate matters further, processes can be modified by phenotypic plasticity as a response to the prevailing ambient conditions within each stage or phase (Wright & McConnaughay, 2002). Unless studies distinguish between these possibilities differences may easily be ascribed to the wrong process. For example, a recent study with *Eucalyptus occidentalis* shows quite clearly that a sudden vegetative change in leaf anatomy and function and the phase change from juvenile to reproductive phase are developmentally uncoupled, i.e. these are two independent developmental processes which are under separate genetic control (Jaya et al., 2010).

Terminology

The term “heteroblastic” (condition: ‘heteroblasty’) [from Greek blastos, shoot] was originally introduced by Goebel to describe a form of plant development, in which substantial differences between earlier (“Jugendform” = juvenile form) and later stages (“Folgeform”, subsequent form) are observed as opposed to the “homoblastic” type of development with small and gradual changes (Goebel, 1898, 1913). He explicitly stated that changes could affect the entire shoot (“Gestaltung” = morph) as well as its physiology. His concept was not restricted to leaves, but also included, e.g., differences in the capacity to produce adventitious roots. Moreover, he already identified an inherent problem of his concept, the fact that there was no sharp separation between these two developmental trajectories, but his examples of heteroblasty all show a fairly abrupt and conspicuous change between stages. Although mostly applied to vegetative morphology, the concept can also be applied to reproductive features (Lord, 1979).

Unfortunately, during the last decades the usage of the term “heteroblasty” has changed considerably, and it has become customary to describe even slight changes in leaf size and/or leaf shape during ontogeny as heteroblastic (e.g. Greyson et al., 1982; Hunter et al., 2006; Hall, 2007). However, a certain degree of ontogenetic variation in (leaf) form is probably universal in plants (Wright & McConnaughay, 2002), in part simply as a structural consequence of changes in the size of the apical meristem (SAM). Thus, if heteroblasty is used for any minor change, the distinction between homo- and heteroblasty becomes virtually meaningless.

Other modifications of Goebel’s original concept seem more appropriate. For example, Philipson (1964) introduced the term “habit-heteroblastic” for cases with an abrupt (!) break in plant habit as found in a number of divaricating shrubs, which develop into a tree with a single trunk and are particularly prominent in the flora of New Zealand. A further important refinement was proposed by Ray (1990) in his treatise of climbing aroids. This author distinguished isomorphic, allomorphic and metamorphic shoot developments. The first represents a lack of ontogenetic changes in size or shape of a vegetative metamer (isomorphy), the second gradual changes in size and/or shape of varying degrees (allomorphy), and the last an abrupt change in form (metamorphosis). The major advance achieved with this scheme is the possibility of a quantitative distinction between homoblastic and heteroblastic species, morphologically or physiologically, which overcomes the vagueness of Goebel's definition (see below). In this paper, we include Philipson's and Ray's refinements, but otherwise use "heteroblasty" similar to Goebel's original definition as a "rather sudden and substantial change in form of individual metamers or plant habit during ontogeny". However, acknowledging the fact that a similar trial by Jones (1999) to disentangle decades of terminological confusion has not been very successful, we may rather take the risk of creating additional jargon and propose the term "metamorphic heteroblasty" to distinguish true heteroblasty unambiguously from allomorphy.

Similarly inconsistent is the use of the term "heterophylly" in the current literature. Heterophylly is sometimes defined extremely broadly as "variation in the size and shape of leaves produced along the axis of an individual plant" (Winn, 1999). Following this definition, all plants would be heterophyllous. Worse, heteroblasty and heterophylly are quite frequently confused, although the terms are clearly distinct conceptually (Lloyd, 1984): either one has been used as umbrella term of the other (e.g. Winn, 1999; Keller, 2004; Roberts, 2007). However, heterophylly refers exclusively to *concurrent* variation in leaf form *within* a single plant (= *sensu lato*) or, alternatively, to environmentally induced switches between either of two (or more) possible leaf morphologies (*sensu stricto*, Pigliucci, 2001), with typical examples among amphibious plants (Arber, 1919). The use of heterophylly should be confined to such cases and is then simply a special case of "phenotypic plasticity" (Alpert & Simms, 2002). In contrast, heteroblasty is not confined to leaves, although admittedly many studies on heteroblasty focus on differences in leaf form and size. Differences may also be found in phyllotaxy, internode length, anthocyanin pigmentation, rooting ability, or wood structure (Goebel, 1898; Rumball, 1963; Frydman & Wareing, 1973).

In contrast to heterophylly, heteroblastic development can only be modified, but is not driven, by environmental stimuli. Particularly remarkable creations in the literature are terms like "environmentally induced heteroblasty" or "ontogenetic heterophylly". An additional advantage of this narrow definition of heteroblasty is a clear distinction from "ontogenetic drift", i.e. a gradual ontogenetic change in phenotypic traits associated with changes in plant size (Evans, 1972). Growth not only leads to an increase in plant parts such as leaves, stem and roots, but often to a quite predictable change in the proportional distribution of biomass among these parts. For example, the root to shoot ratio is initially very high in most plants, but drops rapidly during subsequent growth. Similarly, structural changes in leaf anatomy during growth in a rosette plant may be primarily related to mechanical functions: when leaf length increases from 1 to 100 cm during ontogeny in a large tank bromeliad such as *Werauhia sanguinolenta* (Zotz et al., 2004), increasingly stiff tissues are essential to avoid buckling under the leaves' own weight, since the deflection of a leaf is proportional to the cube of its length (Niklas, 1999). Without attention to ontogenetic drift, a study with a heteroblastic species comparing "small" plants with "early" morphology with "large" plants of "late" morphology cannot separate the effects of size and heteroblastic change. For example, in a study with the epiphytic bromeliad, *Werauhia sanguinolenta*, we could show that a large proportion of the anatomical and physiological differences between small atmospherics (with linear leaves with dense trichome cover) and large tanks (with broad leaves featuring overlapping leaf bases forming a water-holding reservoir) were due to size and not at all associated with the conspicuous change in leaf form and plant habit (Zotz et al., 2004).

There is yet another terminological problem in the literature, since most studies conflate heteroblastic development and the phase change from non-reproductive (juvenile) to reproductive status (adult) (Jones, 1999). Although a change in morphological characteristics may indeed coincide with the onset of maturity, this is unlikely in some cases and at least unclear in most other cases (Poethig, 1990; Wiltshire et al., 1994; Jones, 1999). For a few taxa, e.g. *Eucalyptus occidentalis* or the *E. risdonii – tenuiramis* complex, there is even good evidence that the two processes are developmentally uncoupled (Wiltshire et al., 1998; Jaya et al., 2010). The different timing of these processes is particularly obvious when the abrupt change occurs at seedling size like in *Acacia* (Gardner et al., 2008) or heteroblastic bromeliads (Zotz, 2004), i.e. many years before minimum reproductive size is attained, but also in other cases, e.g., when large *Eucalyptus* trees are said to reproduce with a "juvenile" crown (Williams & Woinarski, 1997). At least two problems arise. First, this frequently used practice mixes two conceptually distinct processes. As already argued by Jones (1999) replacing the currently used terms "juvenile" and "adult" by "early" and "later forms" is not completely unambiguous either, but arguably such a change would be highly preferable over the current practice, which almost inevitably confuses potentially independent ontogenetic processes. In this review, juvenile and adult are put into quotation marks unless specifically referring to reproductive status (compare Jones, 2001). Secondly, when functional aspects are studied, the same argument applies as the one developed above for ontogenetic drift. Since physiological processes frequently change with reproductive status of a plant (Lambers et al., 2008), studies ignoring the reproductive status of a plant may erroneously ascribe differences between early and late forms of a species to heteroblastic changes instead of reproductive status.

A Quantitative Definition of Heteroblasty

A quantitative approach is a crucial step in advancing our understanding of the ecological and evolutionary importance of heteroblasty, which is also true for other sources of ontogenetic variation such as phenotypic plasticity (Valladares et al., 2006). Moreover, a quantitative definition of heteroblasty should allow us to avoid much of the current terminological confusion. Clearly, in spite of the complex nature of heteroblasty, the chosen quantitative trait(s) should be simple and readily measurable to allow comparisons among a larger number of species. Ray's (1990) system, originally proposed for heteroblastic vines, allows a clear distinction between homoblastic and heteroblastic species. Figure 2 illustrates a straightforward application of this scheme to a number of epiphytic bromeliads, using the leaf index (compare Tsukaya, 2002) as a readily measurable trait. Following Goebel's original definition, only the "metamorphic" species *Vriesea heliconioides* and *Guzmania lingulata* would qualify as heteroblastic species, while the other four species included in this comparison with no or subtle and gradual changes are homoblastic. This approach

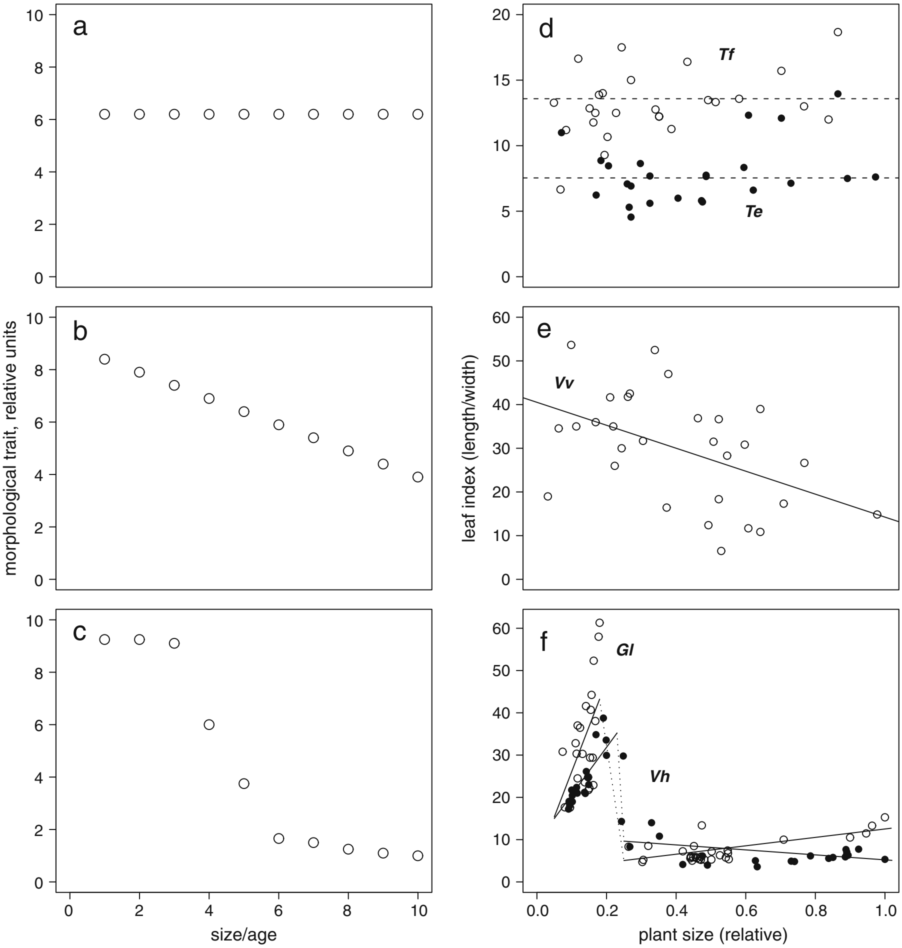

Fig. 2 Conceptual model of shoot development and its application in epiphytic bromeliads. Plots A-C depict a modified version of the scheme originally proposed by Ray (1990) for aroid vines (A = isomorphy, B = allomorphy, C = metamorphosis, i.e. heteroblasty). Plots D-F present measured values of the leaf index (compare Tsukaya, 2002) for five species of bromeliads from the lowland forest of Barro Colorado Island and the premontane Fortuna area, both Panama. Each symbol represents a different individual (K. Wilhelm, unpublished data). Species abbreviations are: *Gl* = *Guzmania lingulata*, *Te* = *Tillandsia elongata*; *Tf* = *T. fasciculata*, *Vh* = *Vriesea heliconioides, Vv* = *Vriesea vittata*

does not consider cotyledons, which would otherwise lead to an inflation of "heteroblastic" species. This exclusion is clearly justified not only from a practical point of view—cotyledons are not derived from SAM and are thus no true leaves.

Other Uses of the Term "Heteroblasty" in the Botanical Literature

The term "heteroblasty" is used here in the context of ontogenetic changes in form and function, but it has at least four additional meanings in the botanical literature.

First, orchid pseudobulbs (i.e. swollen or thickened stems) are called “heteroblastic”, when they are comprised of a single node as compared to “homoblastic”, when comprised of two or more nodes (Pridgeon et al., 1999). Second, spores from unilocular sporangia of some algae may have quite different fates and develop either into gametophytes or into sporophytes, which has been called heteroblasty by Müller (1966). This variation is largely independent of abiotic conditions (Lockhart, 1979). Third, there is an analogous phenomenon among seeds, where different germination patterns are observed within seeds of the same mother plant to identical germination conditions, which has also been called “heteroblastic” (Evenari, 1963; Datta et al., 1970; Fenner, 2000). Finally, the term is used when embryogeny is indirect and the offspring is dissimilar to the parent, producing the adult form as an outgrowth, as in *Chara* (Jackson, 1905).

Functional Significance

Goebel (1898) was the first to propose that heteroblasty is indeed adaptive and functional under current ecological conditions, a view implicitly or explicitly shared by most subsequent researchers. Heteroblasty can be seen as one possible “strategy” used by plants to cope with heterogeneous environmental conditions similar to, e.g., phenotypic plasticity (which includes heterophylly) or polymorphism (Lloyd, 1984). It is a basic assumption that heteroblasty should only evolve when there is a highly predictable difference in the abiotic or biotic conditions of “juveniles” and larger conspecifics.

Heteroblastic species include both relatively short-lived and long-lived taxa, and ecological context is likewise diverse. Not surprisingly then, we can hardly expect a single cause behind this phenomenon, which justifies the diverse and partly contradictory hypotheses put forward in the literature regarding its possible function. Moreover, since heteroblasty can be manifest in a number of different ways (e.g. habit heteroblasty, morphological changes, topic response) in phylogenetically distant plant lineages, we should expect at least some cases of heteroblasty to be functionally “neutral”. Such a non-adaptive explanation is the more likely the shorter the duration of the “juvenile” phase, e.g. when many *Acacia* species retain the ancestral compound habit in the first few plastochrons. Conversely, the longer a particular phase lasts the less likely it seems that it is not under selection under current ecological conditions.

Light and Carbon Gain

In forests, the light conditions experienced by trees, vines and lianas during ontogeny may vary substantially from deepest shade in the understory during the “juvenile” state to full sun light after reaching the forest canopy. While in the majority of plants phenotypic plasticity allows an adaptive response to such predictable changes in abiotic conditions (Valladares & Niinemets, 2008), heteroblasty may be an alternative possibility. For example, Day (1998) suggested that heteroblasty found in many tree species in New Zealand has evolved in response to such changes in light intensity. However, the evidence she presented was only indirect, e.g. morphological and anatomical resemblance of "juvenile" leaves to shade leaves (Cameron, 1970; Gould, 1993; Day et al., 1997). The only direct experimental test of this notion, with "juveniles" of 4 homoblastic and heteroblastic species pairs, failed to detect an advantage of heteroblastic species (Gamage & Jesson, 2007). Unfortunately, adult forms were not included in this experiment. Hence, it is not ruled out that heteroblasty is as adaptive a response as phenotypic plasticity to varying light conditions during ontogeny.

Some climbing aroids, e.g. *Monstera* sp. or *Syngonium* sp., are among the most conspicuous examples of heteroblastic changes in morphology among plants (Ray, 1990; Lee & Richards, 1991). Possible functional significance is usually assumed to be related to the factor light, with important differences to tree species due to their growth habit. While tree saplings invest in own stem and branches, "juveniles" of climbing plants depend on structural support from other plants for further access to the canopy. Contact can be achieved by skototropism, i.e. growth towards the shade (Strong & Ray, 1975). Once a trunk is reached, there is a switch to positively phototropic growth. This phenomenon is little studied, but suggests a change in tropic response during ontogeny in addition to any morphological variation. In *Syngonium*, plants may go through several cycles of rosettes and prostate, skototropic shoots until a trunk is encountered (Ray, 1987), highlighting the search function of "juvenile" morphology.

Although "juvenile" forms are assumed to be "adapted to the extreme shade conditions to which the plants are exposed in nature" (Lee & Richards, 1991), there is little quantitative evidence to back up this statement. To our knowledge there is a single physiological study with *Hedera helix* which shows that "juvenile" foliage resembles shade leaves, while leaves from adult plants resemble sun leaves in a common garden experiment (Bauer & Bauer, 1980). Other evidence is at odds with the notion of improved light capture efficiency by "juvenile" leaves. The "shingle leaves" produced by many "juvenile" vines (e.g. *Monstera*, but also various dicotyledonous climbers; Lee & Richards, 1991), which grow closely attached to tree trunks, intercept much less radiation then horizontally exposed leaves, which leads to a reduction of potential carbon gain of almost 50% (Oberbauer & Noudali, 1998). Alternative explanations for the "adaptive value" of this leaf type still await experimental scrutiny. Since ontogenetic development usually coincides with changes in abiotic conditions, only experimental work will allow us to differentiate between intrinsic and extrinsic reasons for the observed changes. Unfortunately, such studies are also rare for vines, although a large number of suggestions for such experiments were made by Lee & Richards (1991) almost 20 years ago. One of the few exceptions is a study by Lee (1988), although he investigated the response of *homoblastic* species to varying light quality.

Differences in photosynthetic capacity between early and late leaf forms show no consistent trend in heteroblastic woody species, early forms may show higher (Kubien et al., 2007), similar (Hansen & Steig, 1993) or lower (Bauer & Bauer, 1980) rates of net photosynthesis. On the other hand, the compound leaves of "juvenile" acacias have a consistently higher rate of photosynthesis per unit of photosynthetic investment, which arguably maximises growth during the seedling phase, while the phyllodes of later stages are physiologically superior under water stress and high irradiance (Brodribb & Hill, 1993; Hansen & Steig, 1993; Hansen, 1996; Yu & Li, 2007, Pasquet-Kok et al., 2010). This suggests an ontogenetic strategy shift.

Nutrients

Goebel already suggested a causal relationship between nutrient supply and heteroblasty, a notion that was also supported by others (e.g. Allsopp, 1965). However, the link between differences in nutrient supply and variation in plant morphology and physiology is a rather general one (Lambers et al., 2008), and no longer discussed as the proximal *cause* of the ontogenetic changes dealt with in this review. On the other hand, many cases of heteroblasty may have substantial *consequences* for the nutrient economy of such a plant. For example, the transition from atmospheric juvenile to tank form in epiphytic bromeliads should improve the supply of essential nutrients substantially from “pulse supply” in atmospheric forms to “continuous supply” (*sensu* Benzing, 1990) in plants with impounding structures. In an analogous way, the humus-collecting fronds of larger *Platycerium* or *Drynaria* individuals allow these canopy-dwelling ferns to obtain more nutrients, while juveniles only feature green fronds (Goebel, 1913). Here, a similar argument can be used as for heteroblastic bromeliads, i.e. that small “juvenile” fronds are very inefficient in capturing debris, which does not permit to pay back the structural investment, thus selecting for an alternative strategy. Finally, heteroblasty is also observed in a few carnivorous plant species, a mode of existence also associated with nutrient-poor situations. In contrast to epiphytic plants, carnivorous leaves are only developed during the early phase in these species, e.g. the tropical woody liana *Triphyophyllum peltatum,* where young plants produce a series of lanceolate leaves which alternate with a few glandular filiform carnivorous leaves (Green et al., 1979). Barthlott et al. (1987) reasoned that nutrient supply is probably improved and may be crucial for successful establishment.

Water Relations

Heteroblasty is quite common among tillandsioids in the family Bromeliaceae (Fig. 1, Benzing, 2000). In these plants, there is a conspicuous and abrupt shift from “juveniles” with the morphological characteristics of atmospherics (i.e. plants possessing non-impounding rosettes of small, linear leaves, which are densely covered with foliar trichomes) to larger conspecifics with tanks (i.e. featuring broad leaves, which overlap basally forming water-filled chambers). All these characteristics are related to plant water relations, which are known to be of most critical importance in the epiphytic habitat (Zotz & Hietz, 2001). Noteworthy, there are species with the atmospheric habit throughout their lifetime, which are typically found in more arid (micro-)environments, e.g. in drier forests or in the outer canopy of moister forests such as *Tillandsia recurvata* or *T. flexuosa*, which from early on led researchers to believe that the early atmospheric stage is primarily an adaptation to drought (Schulz, 1930). This interpretation agreed with the results of experimental work with heteroblastic *Tillandsia deppeana* (Adams & Martin, 1986a, b), and those of a quantitative assessment of tank water relations in two other, homoblastic species

(Zotz & Thomas, 1999): the efficiency of tanks to bridge rainless periods decreases in smaller plants, suggesting that the observed morphological change represents a strategy shift from drought-tolerant "juvenile" to drought-avoiding tank form. However, the already mentioned study with another heteroblastic species (*Werauhia sanguinolenta*) suggested that a simple comparison of small atmospheric and large tanks confounds the effects of heteroblasty with those of ontogenetic drift (Fig. 3, Schmidt & Zotz, 2001; Zotz et al., 2004).

Future studies should not only avoid the previously used typological approach in the study of heteroblasty, but also consider alternative hypotheses. The exclusive focus on water stress as the only selective factor ignores that many heteroblastic bromeliad species occur in the understory of moist and wet forests, compare, e.g., *Vriesea heliconioides*, *Werauhia lutheri*, or *Guzmania musaica*. In these situations, light may be similarly or even more limiting than water supply, which suggests that heteroblasty in such species may primarily reduce self-shading in "juveniles".

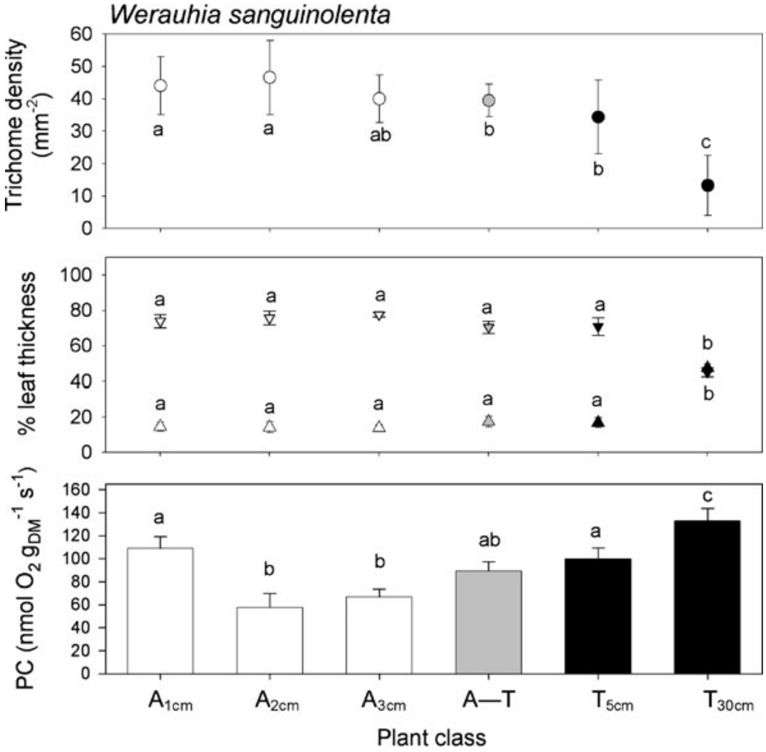

Fig. 3 Ontogenetic changes in morphological, anatomical and physiological parameters in the bromeliad, *Werauhia sanguinolenta*. Parameters are trichome density, relative tissue thickness (chlorenchyma: ▲; and hydrenchyma: ▼) and photosynthetic capacity (*bars*). Plants were of either "juvenile" morphology (A; "atmospherics", *white fill*), tanks (T; *black fill*), or in a transition stage (A-T, *grey fill*) with both "juvenile" and tank foliage. Subscripts indicate plant size as the length of the longest leaf. Data are means ± SD (n= 4–6). Significant differences between classes are indicated by different letters (ANOVA, Newman-Keuls test, p<0.05). Modified after Zotz et al. (2004)

Water stress has also been invoked as selective factor in heteroblasty of ground-rooted heteroblastic species in New Zealand (McGlone & Webb, 1981). A direct test, however, did not support this hypothesis: using pressure-volume curves, Darrow et al. (2002) found no consistent differences in plant water relations parameters between early and late stage of heteroblastic species. Noteworthy, this study was one of the few in which a homoblastic species was included to control for ontogenetic drift.

Herbivory

A possible function of heteroblasty in the defence against herbivores and pathogens has been invoked repeatedly (e.g. Greenwood & Atkinson, 1977; Givnish et al., 1994). A few studies are available which compared secondary compounds between "juvenile" and "adult" leaves of a number of heteroblastic species (e.g. Li et al., 1995; Hansen et al., 2004; Gras et al., 2005), but they failed to demonstrate major differences. Direct bioassays, on the other hand, repeatedly revealed significant effects of different leaf types of a given species on the performance of herbivorous insects (Karban & Thaler, 1999; Brennan et al., 2001). However, care should be taken to ascribe different effects of early and later leaves of a species to heteroblasty itself, since ontogenetic changes in leaf structure and leaf chemical composition are quite common in plants in general (Boege & Marquis, 2005) and the findings may thus well be due to ontogenetic drift (see discussion on the function of heteroblasty in bromeliads). Much attention has been given recently to a proposed co-evolution of herbivorous birds and heteroblastic plant species on some oceanic islands (Wood et al., 2008; Burns & Dawson, 2009; Fadzly et al., 2009). This suggestion seems particularly attractive because the proposed causal agents for the peculiar morphology of divaricate shrubs, i.e. New Zealand's Moa, Madagascar's elephant birds, or Polynesia's flightless geese (Bond et al., 2004; Bond & Silander, 2007), are now all extinct, and thus the case has a whiff of mystery ("Moas ghost", Diamond, 1990). Not surprisingly, the issue is hotly debated (McGlone & Clarkson, 1993; Howell et al., 2002).

Other Proximate Explanations

Ontogenetic changes in leaf form may be functionally related to the climbing habit. For example, in *Triphyophyllum peltatum* the leaves of older and larger plants, which are climbing into the forest canopy, are not only different in shape compared to those of smaller, self-supporting conspecifics, but feature a tip with two distinctive hooks with an obvious function in this liana (McPherson, 2008).

Darrow et al. (2001) suggested that tree seedlings and sapling were subjected to more frequent incidents of frost close to the ground. However, an experimental test with several hetero- and homoblastic species yielded no consistent support for this notion. There are a range of additional suggestions put forward in the literature (e.g. direct action of strong wind), which are discussed by McGlone & Clarkson (1993) and Howell et al. (2002).

Does Heteroblasty have an Adaptive Value Under Current Conditions?

The previous five sections reviewed the literature in regard to possible adaptive functions of heteroblastic changes under current ecological conditions. Clearly, unambiguous evidence for extant function is scarce, which does not mean, however, that the adaptionist approach failed (Gould & Lewontin, 1979). We argue that the search for function is appropriate, although a single functional explanation for all cases of heteroblasty is unlikely. As suggested above, even in a closely related group of plants such as the Tillandsioideae, heteroblasty may have completely different functional implications, e.g. for species in the understory or at exposed growing sites. Thus, an excellent understanding of natural history is needed to develop appropriate hypotheses for different groups of heteroblastic species. Since experiments frequently do not control for ontogenetic drift, crucial experiments are still to be conducted before we can accept the notion that heteroblasty may be neutral under current ecological conditions.

Molecular Control of Leaf Development - of Genes and Hormones

Excellent compilations of the morphological changes for a large number of heteroblastic species are available in the older literature (Goebel, 1898; Diels, 1906; Allsopp, 1965). In these early publications one already finds suggestions for the proximal physiological causes of heteroblastic changes. For example, Goebel (1913) hypothesized that carbohydrate deficiency results in the production of juvenile leaves, while others favoured the notion that low levels of nutrient supply were responsible for their formation (e.g. Allsopp, 1965). Since the findings of other studies were clearly at odds with these scenarios (e.g. Njoku, 1957), these earlier notions are rarely considered any more as a general explanation. There were also reports about a correlation of ontogenetic phase and genome DNA content in *Hedera helix* (Kessler & Reches, 1977), but subsequent studies suggest that the claim was based on artefacts caused by methodological problems (Greilhuber, 1998). In contrast, the involvement of particular plant hormones in heteroblastic changes, which was also demonstrated rather early for gibberellic acid (GA, Robbins, 1957), is well established: the application of GA may lead to a reversal from “adult” to “juvenile” morphology, although this artificial” rejuvenation” (Doorenbos, 1954) has only been demonstrated for a few taxa such as *Hedera helix* or *Acacia melanoxylon* (Robbins, 1957; Borchert, 1965). Not surprisingly, other hormones are involved as well (e.g. Rogler & Hackett, 1975).

Modern approaches try to understand the link between gene expression, hormonal action, and morphogenesis. However, none of the species routinely used to study the genetic framework of morphological changes is heteroblastic in the strict sense. The eudicot model plants *Arabidopsis thaliana* (thale cress) and *Antirrhinum majus* (snapdragon), but also the monocot *Zea mays* (corn) are mainly popular because of the availability of rich sources of mutants affected by developmental control genes. All three progress from juvenile to reproductive phase without major morphological changes except for internode elongation in the case of *A. thaliana*, and minor and gradual changes in leaf morphology.

Is there a Model Plant for the Study of the Genetics of Heteroblasty?

Studying the induction of heteroblasty and the regulatory cascades involved in the morphological changes associated with heteroblasty requires an organism that undergoes the ontogenetic changes described in the previous paragraphs. However, finding an organism that can serve as a genetic model system for the study of heteroblasty is rather difficult in practical terms. Ideally, genetic model organisms have a short generation time, a small genome, are amenable to genetic transformation, and can be easily grown in large amounts. Moreover, for the useful model systems, sufficient genome or transcriptome sequence information is available and a mutant collection has been set up. Unfortunately, most heteroblastic plant species are quite the opposite of a perfect model organism: many are woody species, such as eucalypts and acacias with a generation time of many years, and their genomes are largely uncharacterized. The same is true for many heteroblastic forbs, e.g. epiphytic bromeliads.

Eucalyptus grandis (flooded gum or rose gum) is a species that displays characteristics of heteroblasty as abrupt change from juvenile (ovate) to adult leaf morphology (lanceolate) (Boland et al., 1984). Moreover, *E. grandis* is of major economic value as it is one of the most widely grown hardwood trees in the tropics and subtropics. Its genome is currently being sequenced, several EST sequencing projects are under way and a substantial number of quantitative trait loci (QTL) have been mapped onto the genome (Grattapaglia & Kirst, 2008; Novaes et al., 2008; Rengel et al., 2009), and a transformation and regeneration protocol has been established (Tournier et al., 2003). The already established resources and tools for molecular biologists allow the use of *E. grandis* as a possible model organism for heteroblasty.

The well-characterized model plant *Arabidopsis thaliana* traverses with rather moderate morphological changes from a juvenile life phase characterized by rosette leaves and very short internodes to the reproductive phase. In this phase, leaf shape changes into the cauline form, internodes stretch, and the shoot apical meristem converts into an inflorescence meristem giving rise to inflorescences instead of leaves. Work with *A. thaliana* may thus help to analyze more abrupt and dramatic changes in morphology, assuming similar molecular regulation in other species. Several aspects of phyllotaxy and leaf development such as size determinants, polarity, and lobe formation have been studied in detail. These key aspects of the molecular principles of leaf development in *A. thaliana* and other well-studied species such as *Zea mays* allow at least a few general conclusions about the development in heteroblastic species.

Control of Leaf Morphogenesis—Evidence from Homoblastic Species

Phyllotaxy and Leaf Initiation

It is well established that the regular patterns in leaf initiation (phyllotaxy) are due to localized maxima of the plant hormone auxin in the SAM (Reinhardt et al., 2003). These auxin gradients are established by the action of PINFORMED1 (PIN1), a polar auxin efflux carrier localized in the cell wall of cells constituting the outer layer of the SAM. PIN1 localization at the SAM periphery allows auxin to accumulate and to promote leaf primordium formation. The new primordium subsequently acts as auxin sink, which yields a patterning mechanism for the proliferating SAM and defines the mode of phyllotaxy. Interestingly, auxin mutants in *A. thaliana* do not show phyllotactic changes suggesting that additional signalling cascades are involved in phyllotaxy.

A remarkable maize mutant, *aberrant phyllotaxy1* (*abph1*) displays a decussate phyllotactic pattern (leaves are paired at 180° and the following leaf pair develops at a 90° angle) while wild type maize develops as distichous (alternating leaf initiation) plants. *ABPH1* encodes a cytokinin-inducible response regulator and the *abph1* mutant is impaired in the crosstalk between the two hormones auxin and cytokinin shedding light on the importance of cytokinin in addition to auxin in the regulation of phyllotactic patterning (Giulini et al., 2004; Lee et al., 2009). We hypothesize that a sudden change in the phyllotaxy, which is quite conspicuous, e.g., in heteroblastic *Eucalyptus* species (Fig. 1), could be simply achieved by modulating the crosstalk between cytokinin and auxin. Conversion from distichous to decussate phyllotaxy could thus result from differential regulation of homologs of the *ABPH1* gene in heteroblastic species. Clearly, this hypothesis requires a general conservation of the molecular mechanism underlying phyllotactic patterning in angiosperms, an evolutionary aspect of plant development that has received little attention so far.

Control of Leaf Size—When to Stop Growing

While final size of leaves within most plant species is quite uniform, many heteroblastic species, e.g. the well studied *Pseudopanax crassifolius* (Clearwater & Gould, 1994), produce leaves that differ substantially in size and shape during different stages of individual development (Fig. 1). Again, understanding changes in the molecular control of rather subtle morphological changes during life phase changes of genetic model plants could be a first step to unravel the genetic processes that shape heteroblastic taxa.

Phytohormones of various classes influence organ growth in plants, e.g. plants insensitive to ethylene produce larger organs. Conversely, mutants in genes involved in auxin or brassinosteroid perception and biosynthesis are dwarfed. While auxins and brassinosteroids stimulate cell proliferation as well as cell expansion, cytokinins promote only cell proliferation but not expansion (Guzman & Ecker, 1990; Haubrick & Assmann, 2006; Sakakibara, 2006; Teale et al., 2006). Extensive cross-talk occurs between these plant hormones, for example auxin, cytokinins and brassinosteroids increase the expression of ethylene biosynthesis genes (Lin et al., 2009).

Most leaves grow first by cell proliferation and then by cell elongation once the leaf axes are established. Over the past few years, the genetic framework of leaf size control has been partially revealed when several genes involved in this process were identified (Krizek, 2009). However, most of these genes influence the timing rather than the rate of proliferation suggesting that the transition from proliferation to expansion is the crucial point in organ-size control (Anastasiou et al., 2007).The transcription factor AINTEGUMENTA (ANT) is one of the major genes promoting growth by maintaining cells in a proliferating state and is linked to auxin action, but additional genes contribute as well. Mutants in these growth-promoting genes exhibit smaller organs, jagged organ shape, or smaller narrower leaves (Mizukami & Fischer, 2000; Dinneny et al., 2004). The transition from proliferative to expansive growth is characterized by a wave of cell-cycle arrest starting from the distal and moving towards the proximal part of the leaf. *TCP* (*TEOSINTE BRANCHED1/CYCLOIDEA/PDF*) genes most likely control this process while another set of genes induces cell cycle arrest in progenitors of stomata and vascular tissue (Nath et al., 2003; White, 2006).

A wealth of genes seems to control the size of leaves in *A. thaliana* including genes required for cell cycle maintenance, genes encoding transcription factors, a gene encoding a mobile signal, as well as genes involved in phytohormone signalling (Krizek, 2009). Most of the genes known to regulate leaf size do not interact genetically suggesting that leaf size is dependent upon the concerted and well-balanced action of many pathways rather than on a single master switch inducing or repressing further growth. Similarly complex regulation of leaf size might be implemented in other plants as well. Heteroblastic plants developing leaves of substantially different size during their life time may thus draw from a rather large pool of pathways to regulate the final size of their leaves. Since different species probably regulate the same process in a different way, the rather detailed understanding of the molecular control of leaf size in *A. thaliana* yields only limited insights into analogous processes in heteroblastic species.

Regulation of Leaf Shape

Leaf shape changes dramatically in some heteroblastic species. The perforated leaf blades of the "adult" foliage of many *Monstera* species (Fig. 1) result from developmentally regulated programmed cell death (PCD), which is a rather exceptional way of achieving complex leaf shape in the plant kingdom (Gunawardena et al., 2005), and thus deviates from most other cases of heteroblastic changes in leaf shape, a classic example being *Hedera helix* that produces lobed leaves as "juvenile" and entire leaves as "adult". The "normal", PCD independent molecular determinants of leaf shape, in particular leaf dissection, have been analyzed in *A. thaliana* and other, phylogenetically distant, plants with diverse modes of leaf margin dissection, leaflet specification, and leaflet development. Compound leaves generally maintain meristematic regions at their margins which enable organogenesis of leaflets.

The organogenic activity at the leaf margins is preserved by two different pathways in seed plants which possibly reflects multiple independent origins of compound leaves. While in *Pisum sativum* (pea) the transcription factor *UNIFOLIATA* (*UNI*) is required for organogenic regions at leaf margins, plants such as *Solanum lycopersicum* (tomato) and *Cardamine hirsuta* employ class 1 homeodomain transcription factors to achieve activity of these organogenic regions (Hay & Tsiantis, 2006; Champagne et al., 2007). However, a universally conserved molecular framework required for leaf dissection and leaflet formation seems to emerge from the analysis of *S. lycopersicum, P. sativum, C. hirsuta*, and *Aquilegia*, an early branching eudicot. It seems that the *NAM/CUC3* genes are required for leaf dissection and leaflet formation in compound leaves in all the above mentioned species as they pattern the interleaflet boundary (Blein et al., 2008). As the phylogenetic range of the plants shown to employ the *NAM/CUC3*-like genes for specifying interleaflet boundary extends from early branching eudicots to rosids and asterids, it can be assumed that heteroblastic taxa that develop simple and dissected leaves during their lifetime (e.g. *Hedera*) might use the same switch to turn on their leaf dissection program, by simply activating the *NAM/CUC3* pathway in the very early stages of leaf development. This regulatory potential could be achieved during evolution if the promoter of the *NAM/CUC3*-like genes in heteroblastic species acquired a regulatory element active in a specific life phase only. When inactive, this would lead to simple leaves and when active e. g. in the "adult" phase of a heteroblastic species, dissected leaves would be generated by the action of *NAM/CUC3*-like genes.

Evolutionary Implications

Goebel (1913) already noted that heteroblastic changes may shed light on evolutionary relationships among species. A classic example are phyllodineous *Acacia* species, where the compound leaves of juveniles are seen as an evolutionary legacy of an ancient, leaf-bearing progenitor (Kaplan, 1980; Gardner et al., 2008). Many other and less well-known examples exist, e.g. among some fern groups (Kato & Setoguchi, 1999) or in the Maloideae (Phipps et al., 1991). Inclusion of "juvenile" forms is also useful in chemotaxonomy (Li et al., 1995). In many other cases, the resemblance of "adults" of closely related species with the early forms of heteroblastic species is interpreted as indications of neoteny. This is the case for atmospheric species in the tillandsioids (Tomlinson, 1970), aroid vines such as *Monstera tuberculata*, which produces only saucer-shaped leaves throughout their life time (Lee & Richards, 1991), life-long carnivorous plants as descendents of species, in which carnivory was originally restricted to the early stages of ontogeny as in a few extant species (Barthlott et al., 1987), or divaricate shrubs that may have arisen from heteroblastic trees after losing the original adult state (Day, 1998). Alternatively, heteroblastic species may be the result of hybridization events. Godley (1985) proposed that at least some heteroblastic species may have arisen in this manner, one example being heteroblastic *Pittosporum turneri* as the hybrid between a divaricating shrub (*P. divaricatum*) and a non-divaricating tree (*P. colensoi*). A recent study using both molecular and morphological methods provided some support for this notion, but overall the results were inconclusive (Carrodus, 2009).

Our understanding of the evolution of heteroblasty would certainly benefit substantially from a consensus of a quantitative definition of heteroblasty. This would enable us to make broad-scale correlative analyses of heteroblasty, ecological conditions, and phylogenetic relatedness. Crayn et al.'s (2004) work is a good example for the power of this type of analysis. They compared the occurrence of crassulacean acid metabolism (CAM) and epiphytism among bromeliads in a phylogenetic context. They were able to show that both CAM and epiphytism have evolved multiple times within the family, and that both arose independently. The analogous question, i.e. how often heteroblasty has evolved within this family and whether there is a connection with the transition from terrestrial life style to epiphytism cannot be addressed at the moment. Even in smaller taxa, our understanding of the evolution of heteroblasty is quite limited. An analysis of the phylogeny of the 12 species in the small genus *Pseudopanax* did not yield sufficient resolution to reconstruct the evolution of heteroblasty in this genus (Perrie & Shepherd, 2009).

Similarly important for evolutionary considerations would be a better understanding of the molecular mechanisms causing heteroblastic changes. As heteroblasty has evolved many times independently in the plant kingdom it is parsimonious to assume that already existing regulatory networks have been adopted and modified, rather than supposing the de-novo generation of developmental programs. Candidate genes for changing the mode of phyllotaxy, the size or the shape of leaves could be identified and used to manipulate morphogenesis in genetic model plants. Possibly, life-phase dependent control of networks directing differential modes of developmental programs could play a major role for the evolution of heteroblasty. For the animal kingdom, such an adoption of pre-existing control elements and layering of new elements onto already existing ones to create new developmental patterns has been just recently demonstrated (Werner et al., 2010)

Even plant species with subtle morphological changes between life phases traverse through at least two different developmental programs, the vegetative and reproductive phase. The shoot apical meristem active during vegetative development acquires inflorescence and, later, floral meristem fate. In *Arabidopsis*, these meristem identity shifts are induced by the differential expression of only a handful of genes, such as *LEAFY* conferring inflorescence meristem identity and *APETALA1* required for floral meristem identity (Sablowski, 2007). In heteroblastic species, a similarly simple genetic switch may be sufficient for transition between vegetative stages.

Strategy shifts, e.g. from “pulse-supplied” juveniles in epiphytic bromeliads to “continuously supplied” later stages (*sensu* Benzing, 2000) lend themselves to quantitative modelling exercises in the framework of life history theory: quite a few studies have dealt with the question of the optimal size and/or age for metamorphosis in animals (Hentschel, 1999; Rudolf & Rodel, 2007). The same logic could be applied to heteroblastic plants: for example, when is the optimal time for a small bromeliad to switch to tank form? Can the transitional stage, which may last for several months (Zotz, 2004) be considered a life history bottleneck? Plasticity in the timing of heteroblastic changes could also be exploited in experiments because the timing of the change from “juvenile” to “adult” form normally shows considerable variation. This approach was used by Burns (2005) in a study with heteroblastic *Senecio lautus*. He hypothesized that heteroblasty was related to shade and high winds in this species, and indeed, the juvenile-adult transition was slowed in shaded conditions. Care must be taken, however, to distinguish between changes in the timing of a switch between leaf types and the response of individual leaves (Jones, 1995).

Outlook

Heteroblastic species offer fascinating research opportunities for the study of general ecological and evolutionary questions concerning developmental regulations, plant adaptation and speciation. Unfortunately, the terminology of ontogenetic changes in plants has developed in a very inconsistent way in the last decades, which quite likely reflects a similar confusion of concepts. For further progress in the field it seems essential to clearly distinguish the step changes observed in heteroblastic species from both (gradual) ontogenetic changes in form and function that are associated with increases in size (i.e. ontogenetic drift and allometric changes) and those associated with a (similarly abrupt) phase change. Conceptual clarity is a prerequisite for an increased understanding of the developmental, functional, and evolutionary dimensions of a phenomenon that has attracted scientific attention for more than a century. Currently, we are not even able to provide a rough estimate of the number of heteroblastic plants in the plant kingdom, in contrast to other "peculiar" groups such as carnivorous plants, parasitic plants, or plants with crassulacean acid metabolism. We hope that this review will help to change this situation.

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Appendix I

A diverse body of literature that deals with heteroblasty has accumulated over the last 100 or so years. Unfortunately, the older literature is hardly covered in data bases such as WOS, in part because quite a few contributions were made in monographs, in dissertations, or in journals, which are not indexed. Other studies are not readily accessible due to terminological confusion. To assist in future research we have done an extensive literature search and compiled the following list of research articles, books and book chapters that deal with heteroblasty. Also included is a selection of general textbooks, which provide different definitions of "heteroblasty", "heterophylly" and/or "phase change".

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