

Evolutionary plant physiology: Charles Darwin's forgotten synthesis

Ulrich Kutschera · Karl J. Niklas

Received: 16 April 2009 / Revised: 21 July 2009 / Accepted: 7 August 2009 / Published online: 18 September 2009
© Springer-Verlag 2009

Abstract Charles Darwin dedicated more than 20 years of his life to a variety of investigations on higher plants (angiosperms). It has been implicitly assumed that these studies in the fields of descriptive botany and experimental plant physiology were carried out to corroborate his principle of descent with modification. However, Darwin's son Francis, who was a professional plant biologist, pointed out that the interests of his father were both of a physiological and an evolutionary nature. In this article, we describe Darwin's work on the physiology of higher plants from a modern perspective, with reference to the following topics: circumnutations, tropisms and the endogenous oscillator model; the evolutionary patterns of auxin action; the root-brain hypothesis; phloem structure and photosynthesis research; endosymbioses and growth-promoting bacteria; photomorphogenesis and phenotypic plasticity; basal metabolic rate, the Pfeffer–Kleiber relationship and metabolic optimality theory with respect to adaptive evolution; and developmental constraints versus functional equivalence in relationship to directional natural selection. Based on a review of these various fields of inquiry, we deduce the existence of a Darwinian (evolutionary) approach to plant physiology and define this

emerging scientific discipline as the experimental study and theoretical analysis of the functions of green, sessile organisms from a phylogenetic perspective.

Keywords Circumnutations · Charles Darwin · Evolution · Natural selection · Plant physiology

Introduction

In the centenary year of his birth, Charles Darwin (1809–1882) is perhaps best known for his seminal book *On The Origin of Species* (1859), in which he proposed and extensively documented the theory that natural selection is the primary driving force for adaptive evolutionary innovation. It is certainly fair to say that the bulk of the primary literature dealing with his many accomplishments is either focused on biographical details surrounding the exploits that ultimately engendered the concept of adaptive evolution by means of natural selection or on the issue of whether adaptation by natural selection is prone to circular logic (Kutschera 2009a). In contrast, little is said about Darwin's scientific achievements after the publication of *The Origin* other than perhaps to recount and analyse his attempts to rebuff critics and defend his theory of organismic evolution. Yet, Darwin's 20 post-*Origin* years were in many ways as or perhaps more productive, particularly in terms of his abiding fascination with botany and plant physiology (Morton 1981; Ayres 2008).

This interest is nowhere better articulated than in the writings of his son Francis Darwin (1848–1925), who was a professional plant biologist. In a semi-autobiographical essay published one century ago, Francis describes his father's intense relationship with “sessile green organisms” as being “...of two kinds, which may be roughly distin-

This contribution is part of the Special Issue “Beyond the Origin: Charles Darwin and modern biology” (Guest editor: U. Kutschera; see Kutschera 2009a)

U. Kutschera (✉)
Institute of Biology, University of Kassel,
Heinrich-Plett-Str. 40,
34109 Kassel, Germany
e-mail: kut@uni-kassel.de

K. J. Niklas
Department of Plant Biology, Cornell University,
Ithaca, NY 14853, USA
e-mail: kjn2@cornell.edu

guished as *Evolutionary* and *Physiological*. Thus in his purely evolutionary work, for instance in *The Origin of Species* and in his book on *Variation under Domestication*, plants as well as animals served as material for his generalisations. He was largely dependent on the work of others for the facts used in the evolutionary work... And he correspondingly rejoiced in the employment of his wonderful power of observation in the [botanical] physiological problems which occupied so much of his later life.... In this physiological work he was to a large extent urged on by his passionate desire to understand the machinery of all living things.... His interests, physiological and evolutionary, were indeed so interwoven that they cannot be sharply separated” (Darwin 1909, p. 385).

Given these two opposing interests, it is not surprising that the zoologist, evolutionary biologist and philosopher Ernst Mayr (1904–2005) identified two different approaches within the biological sciences—that taken by physiologists and developmental biologists who are interested in the function and ontogeny of individual organisms and the approach taken by evolutionary biologists who analyse trans-generational (i.e. phylogenetic) events underlying adaptive evolution and diversification. Mayr went on to label the mechanistic explanations provided by laboratory scientists (physiologists and developmental biologists) as ‘proximate’ and those provided by evolutionary biologists as ‘ultimate’ explanations (Mayr 1982, 1991, 2004). Arguably, there are grounds to question this polarised view of biology, just as there are reasons to argue that neither approach, even in its purist form, can yield an ‘ultimate’ explanation for anything. And, even if we admit that the two approaches exist as a pedagogic dichotomy (an admission that we believe Darwin would never have made), it is evident that the distinction between what Mayr called the ‘two biologies’ has become blurred as deeper questions about plant genomes and developmental biology increasingly require more sophisticated interdisciplinary affiliations among researchers in widely different fields of expertise. For example, as early as the 1990s, the field of evolutionary animal physiology emerged as a widely recognised and legitimate area of study (Garland and Carter 1994) based on the explicit fusion of the two complementary approaches described by Mayr, i.e. the investigation of the evolutionary mechanisms underlying or constraining diversification of physiological mechanisms and the discrete historical patterns of physiological evolution (Feder 2002).

In light of Darwin’s synthesis of the ‘two biologies’ and of his sustained interest in plant life, it is curious that, to the best of our knowledge, no botanical analogue to evolutionary animal physiology exists (or, if it does, it is still so much in its infancy as has largely gone unnoticed by mainstream biologists). Its absence is particularly surprising

in light of the dramatic recent advances made in plant molecular biology, on the one hand, and in evolutionary biology, on the other. This vacuum where none should exist motivates this article and gives us the opportunity to review and evaluate in contemporary terms Charles Darwin as a botanist and plant physiologist. In the second part of this article, we assess current research areas emerging at the interface of the physiology and evolutionary biology of plants and try to define the discipline of evolutionary plant physiology.

Darwin as a botanist and plant physiologist

Darwin’s fascination with plants, which continued for almost 40 years after his first sketches of *The Origin*, appears to have begun with an early interest in pollination biology. We deduce this from his autobiography, wherein he wrote: “During the summer of 1839, ... I was led to attend to the cross-fertilisation of flowers by the aid of insects, from having come to the conclusion in my speculations on the origin of species, that crossing played an important part in keeping specific forms constant” (Barlow 1958, p. 127) and from various statements in his letters such as “Nothing in my life has ever interested me more than the fertilisation of ... plants” (Morton 1981; Ayres 2008). The earlier work of the German botanist Christian Sprengel (1750–1816) may have sparked this interest, particularly his book *Das entdeckte Geheimniss der Natur* in which he writes “It appears that nature has not willed that any one flower should be fertilised by its own pollen” (Sprengel 1793, p. 4). Aside from the numerous examples of adaptive evolution that could be drawn from the study of insect-pollinated species, Darwin was also keenly aware of the consequences of inbreeding from his studies of domesticated animals. He reasoned wisely that “As plants are adapted by such diversified and effective means for cross-fertilisation, it might have been inferred from this fact alone that they derived some great advantage from the process” (Darwin 1876, p. 2). Although this insight did not stop him from marrying his first cousin Emma Wedgwood (1808–1896), his botanical experiments delving into the effects of out-crossing were extensive as can be seen by reading *The Effects of Cross and Self Fertilization* (1876) and his treatment of hybridisation in chapter VIII of *The Origin of Species* (1859).

Although he published two other influential botanical books (Darwin 1862, 1877), it was his work on climbing plants such as *Bryonia dioica* (Fig. 1a) that established his career as a plant physiologist (Darwin 1867). As pointed out by his son Francis, he “... develop(ed) a broad conception of the power of climbing as an adaptation by means of which plants are enabled to reach the light.

Instead of being compelled to construct a stem of sufficient strength to stand alone, they (i.e. the climbing plants) succeed in the struggle by making use of other plants as supports” (Darwin 1909, p. 387). In his book on *Climbing Plants*, Darwin described his discovery that the habit of climbing is widely distributed through the plant kingdom and concluded that “the capacity of revolving, on which most climbers depend, is inherent, though undeveloped, in almost every plant in the vegetable kingdom” (Darwin 1867, p. 205). Based on a much more comprehensive set of observations, this work was later expanded into Darwin’s theory of circumnutations (see below).

Darwin’s botanical and physiological researches, which were published primarily in a monograph on insectivorous plants and another on floral biology (Darwin 1875, 1877), were rapidly incorporated into the leading plant biology textbooks of his day. Pfeffer (1897/1904) dwelt on Darwin’s botanical and physiological work at length, while the prominent plant physiologist, Julius Sachs (1832–1897), acknowledged Darwin’s work in his earlier publications. However, the acceptance of Darwin as a botanist and as a plant physiologist was neither unconditional nor universal. Due to controversies about experimental protocols, Sachs (1882) later disregarded many of Darwin’s achievements, and one of his students, the botanist and geneticist Hugo De Vries (1848–1935), later became the founding father of the anti-Darwinian “mutation theory for the origin of species”. Based on breeding experiments with the evening primrose (*Oenothera lamarckiana*; Fig. 2) and other plants, De Vries (1901/1903) argued that species can arise spontaneously by large mutations without natural selection or geographic separation. This concept was later adopted and amplified by Richard Goldschmidt (1878–1958) in his “hopeful monster theory”, which has received renewed interest in the context of saltational evolution in photosynthetic organisms (see Kutschera and Niklas 2008; Crepet and Niklas 2009).

Despite these historically trivial equivocations, Darwin’s botanical experiments, such as those on the phototropism of coleoptiles (which predate Fritz Went’s milestone elucidation of auxin 80 years ago), continue to cast a long shadow, indeed so much so that they are treated individually in the following sections.

The power of movements and Darwin’s theory of circumnutation

In one of his most influential monographs (which benefited from the assistance of his son Francis), Darwin (1880) described in detail the widely prevalent movements common to almost all land plants. These movements are essentially the same as those of the stem of climbing plants—

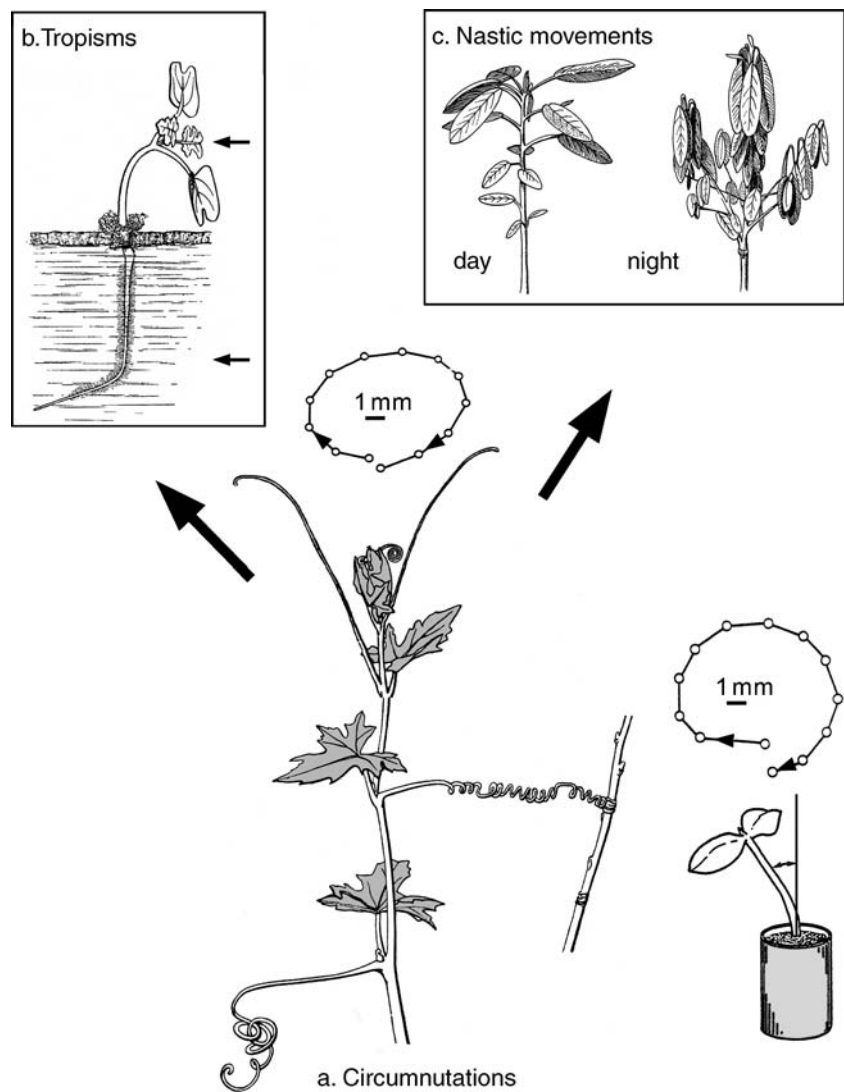
the axis bends successively in all directions, so that the tip of the shoot revolves. Sachs (1865) had named these processes “revolving movements”—a phrase later replaced by Darwin (1880) by the word “circumnutation”. Two examples of circumnutating organs, the tendrils of an adult *B. dioica* plant and the hypocotyl of a sunflower (*Helianthus annuus*) seedling, are depicted in Fig. 1a. Based on his principle of common descent with slight and successive modifications, Darwin (1880) postulated that “In this universally present movement we have the basis or groundwork for the acquirement, according to the requirements of the plant, of the most diversified movements... The leaves of various plants are said to sleep at night... through modified circumnutation... The movements of various organs to the light... and occasionally from the light... are all modified forms of circumnutation... as again are the equally prevalent movements... of roots towards the centre of the earth” (Darwin 1880, p. 3–4). In other words, the author of the *Origin of Species* proposed that tropisms and nastic movements of all types of plant organs descended, with small or large modifications, from the “archtype” of all movements in the plant kingdom, the omnipresent, non-specialised circumnutations.

In the Introduction to his book *The Power of Movements*, Darwin (1880) outlined his circumnutation theory for the origin of all plant movements (Fig. 1a–c). After a detailed description of the “circumnutation movements” in seedlings and organs of mature plants (Chaps. I to IV), Darwin devoted the remaining pages of his book to a detailed description of his novel concept. In the last chapter (XII), he recapitulated his theory as follows: “Circumnutation is of paramount importance in the life of every plant; for it is through its modification that many highly beneficial or necessary movements have been acquired” (Darwin 1880, p. 547).

Although Darwin’s conclusion that “revolving nutations” are a general property of higher plants was readily accepted by botanists throughout the world, his “circumnutation theory” was rejected. For instance, Pfeffer (1897/1904) described at length many observations and conclusions detailed in Darwin’s botanical publications, notably those summarised in his book on the *Power of Movements*, but ignored the “circumnutation theory”. As noted by Francis Darwin, “[Charles] Darwin’s view ... has not been accepted by physiologists ... [who in] fact neglect circumnutation as a factor in the evolution of movements” [italics added] (Darwin 1909, p. 398–399). Centuries of subsequent research into the mechanisms of plant organ movements has unequivocally shown that tropisms, elicited by light or gravity, and nastic movements caused by a variety of stimuli, are based on entirely different biophysical mechanisms.

Tropisms (Fig. 1b) are differential growth responses attributed to changes in the extensibilities of the walls in

Fig. 1 The power of movements in higher plants. Circumnutations in tendrils of *B. dioica* and the hypocotyl of *H. annuus* (a), phototropism in *Sinapis alba* (b) and nastic movements in the leaves of *Desmodium gyrans* (c). Horizontal arrows in (b) denote the direction of white light treatment



actively growing tissues or organs (Niklas 1992; Kutschera and Edelmann 2005), whereas nastic movements (Fig. 1c), processes whose directions are determined by the anatomy of a moving organ, are due to reversible changes in cell turgor pressure (Hart 1990). Hence, Darwin’s “circumnutation theory”, which proposes a common ancestral mode of all movements, is not supported by empirical evidence (Hart 1990).

In contrast, one sub-theory of Darwin’s unsupported unifying concept (i.e. the view that periodic growth oscillations—or “circumnutations”—have an internal driving force) has been corroborated by experiments on the space shuttle Columbia. Brown et al. (1990) investigated the behaviour of 4-day-old sunflower seedlings (Fig. 1a) in microgravity and found that 93% of these juvenile plants circumnutate, compared with 100% of the ground control that was exposed to gravity. Although the periodic growth oscillations of the spaceflight seedlings had a reduced amplitude and period compared with the control, these

results provide strong evidence for Darwin’s “endogenous hypothesis of circumnutations” published in 1880. In a more recent analysis based on novel experiments with *Arabidopsis* mutants, Kiss (2006) questioned the general significance of the so-called “endogenous oscillator model” first proposed by Darwin (1880) and later supported by the space lab experiments performed during the 1980s. Therefore, more experimental work is required to corroborate (or refute) Darwin’s hypothesis stating that circumnutations occur independent of external stimuli such as gravity or light.

Classical experiments on tropisms and evolutionary patterns in auxin action

In a subordinate chapter entitled “Sensitivity of plants to light: Its transmitted effects”, Darwin (1880) used dark-grown (etiolated) seedlings of canary grass (*Phalaris*

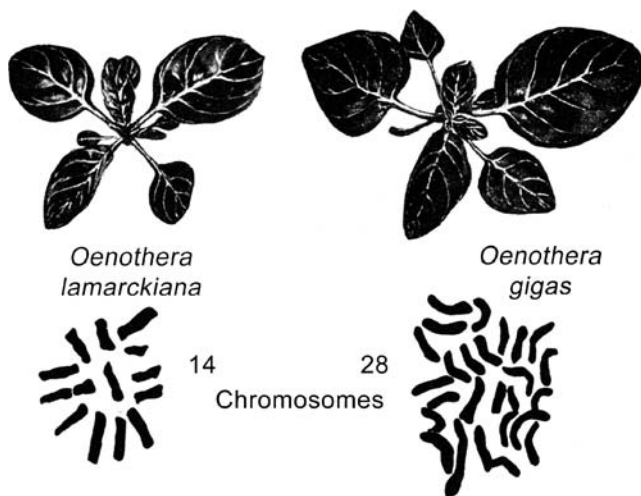


Fig. 2 From plant physiology to evolutionary biology. The botanist Hugo De Vries noticed that within populations of *O. lamarckiana*, a diploid species with 14 chromosomes, a large variant with 28 chromosomes occurs (*Oenothera gigas*) that could not interbreed with its parent species. Based on this and other observations, he postulated that species arise via spontaneous macro-mutations

canariensis) and oats (*Avena sativa*) as experimental systems for the analysis of light-mediated organ movement (phototropism; Fig. 3a). In collaboration with his son Francis, he discovered that the light stimulus is exclusively detected at the tip of the shoot. The grass coleoptile, a cylindrical sheath that surrounds the enclosed primary leaf of the juvenile plant, is dependent on an intact, un-damaged uppermost region. If this organ tip is surgically removed or shielded from the light, the seedling fails to detect the light stimulus (Fig. 3a, b). The Darwins also discovered that the bending response takes place in regions localised more than 1 cm below the tip. In another experiment, they buried the seedlings in fine black sand so that only the tip was exposed to unilateral light. The buried grass shoots bent in the direction of the light stimulus, i.e. there was no interference with the positive phototropic response of the organ. From these experiments, the Darwin father and son team concluded that "... the sensitiveness to light (is) localised in the tips of the cotyledons of *Phalaris* and *Avena*" and postulated "the transmission of some influence from the upper to the lower parts, causing the latter to bend towards the light" (Darwin 1880, p. 566). Although Charles and Francis erroneously regarded the coleoptile of the grass seedling as the "cotyledon" in accordance with the view held by Sachs (1882), Pfeffer (1897/1904), and other leading botanists, this misidentification in no way detracts from the importance of their work.

Over the subsequent five decades, the experiments and hypotheses of Darwin (1880) (Fig. 3a, b) led to the discovery of the phytohormone now known as auxin. In a series of elegant studies carried out with Darwin's exper-

imental system (i.e. etiolated oat coleoptiles), the Dutch botanist Fritz W. Went (1903–1990) proved that the intact tip secretes "Darwin's stimulus" (i.e. auxin), which is transported basipetally, where it enhances the rate of cell elongation (Went 1928; Cholodny 1928). If applied via an agar block on only one half of the coleoptile stump, organ bending is induced (Fig. 3c).

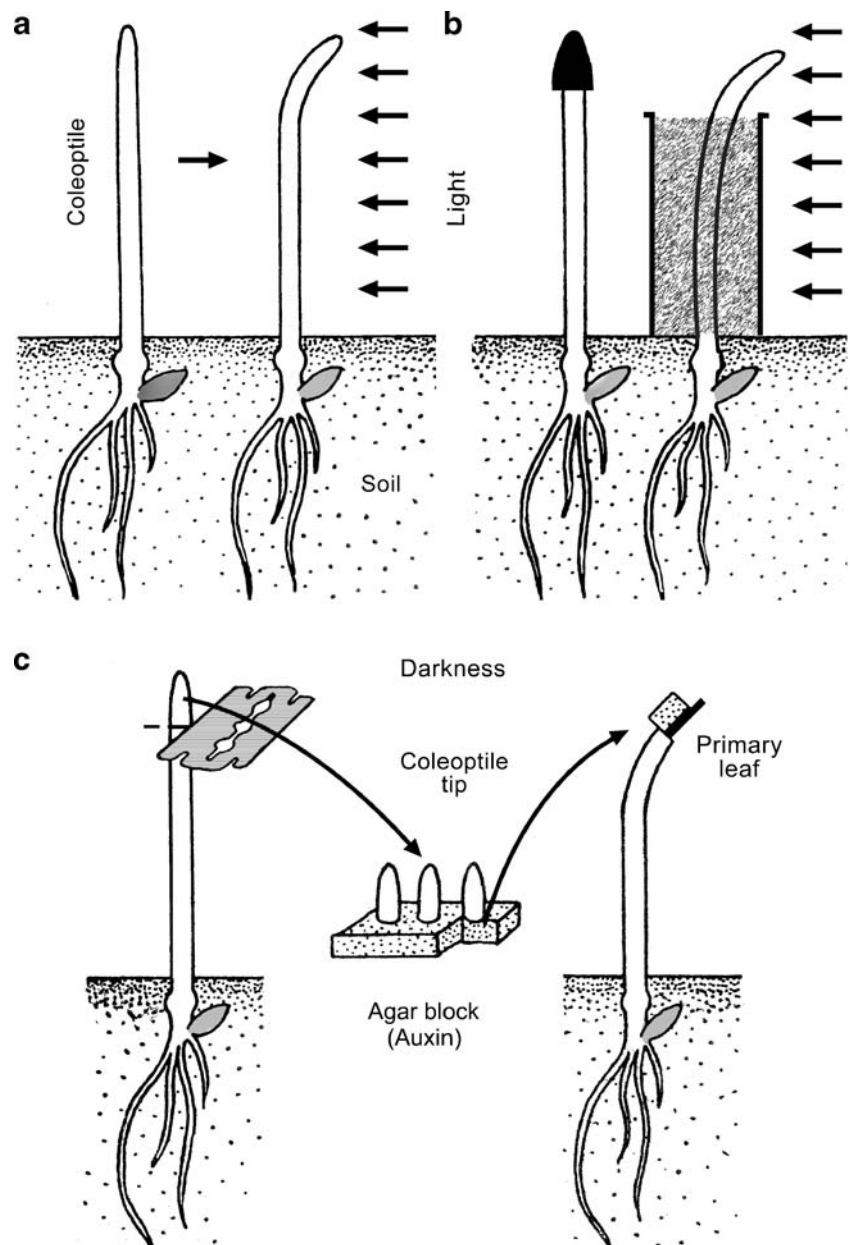
In their classical monograph entitled *Phytohormones*, Went and Thimann (1937) briefly mentioned the work of Darwin (1880) who is now acknowledged as one of the founding fathers of auxin research. The postulated mechanism(s) by which auxin causes cell elongation in coleoptiles and other axial plant organs (hypocotyls, epicotyls) have been discussed elsewhere and are beyond the scope of this article (Kutschera 2003, 2006, 2008a, b; Kutschera and Niklas 2007; Schopfer 2006, 2008). However, the evolutionary patterns in auxin action are a topic within the emerging field of evolutionary plant physiology.

Went and Thimann (1937) were the first to summarise the data on the production of auxin in "lower" organisms (bacteria, fungi) and "higher" land plants. However, they were unable to draw general conclusions due to the lack of data at that time. Sixty-five years later, Cooke et al. (2002) presented a survey of the accumulated literature on auxin action along the evolutionary "green plant lineage", which includes the charophycean algae (the closest living algal relatives of extant land plants), bryophytes (the most ancient land plants) and seed plants (which are fully adapted to grow and reproduce on land; Niklas 1997, 2000; Scherp et al. 2001). This analysis revealed that the mechanisms for the regulation of auxin levels and several hormone-mediated responses (cell elongation etc.) described for seed plants (Figs. 1, 2, 3 and 5) are also present in "lower green organisms" such as bryophytes and charophytes (Figs. 6a and 11a) but usually in a more ancient version. Cooke et al. (2002) conclude that seed plants did not evolve novel mechanisms for mediating auxin responses but are characterised by modified mechanisms that are similar to those established in early land plants.

Darwin's root-brain hypothesis

In their monograph on the *Power of Movements*, Charles and Francis Darwin not only investigated the shoot but also analysed the behaviour (i.e. gravitropism) of the growing root of developing seedlings (Fig. 4a, b). On the last two pages of their book, they postulate that the root tip (calyptra) acts like a plant brain: "We believe that there is no structure in plants more wonderful, as far as its functions are concerned, than the tip of the radicle... It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing the movements of the

Fig. 3 Charles Darwin's experiments with dark-grown grass seedlings (**a, b**) that led to the discovery of the phytohormone auxin (**c**), a growth-promoting substance produced in the cells of the light-sensitive tip of the coleoptile and transported basipetally, where it promotes cell elongation. *Arrows* denote the direction of white light treatment



adjoining parts, acts like the brain of the lower animals” (Darwin 1880, p. 572–573). This so-called “root-brain-hypothesis” (Barlow 2006) is also mentioned in Darwin’s autobiography, where he points out that he “felt an especial pleasure in showing how many and what admirably well adapted movements the tip of the root possesses” (Barlow 1958, p. 136). The stimuli mentioned that can elicit a rapid physiological response from the root tip were gravity, white light, mechanical pressure, heat and different moistures. Moreover, the Darwins observed that, after surgical removal of the tip, the sensitivity to gravity was lost (Fig. 4b). Based on these and other experiments, they concluded that “the tip can distinguish between a slightly harder and softer object, by which it is simultaneously

pressed on opposite sites” (Darwin 1880, p. 572). Father and son go on to discuss these responses with respect to the survival of the whole plant, which reproduces and leaves progeny via different organs of the shoot that are dependent on the water supply provided by the root system (Darwin and Acton 1894).

A detailed discussion of Darwin’s “root-brain hypothesis”, with reference to the pertinent literature, led to the conclusion that this plant–animal analogy is justified (Barlow 2006; Edelmann and Roth 2006). The experiments of the two Darwins are reproducible, and their speculations concerning the function of the various responses of radicles have been corroborated, notably their studies concerning root gravitropism. However, despite decades of research, we do not yet

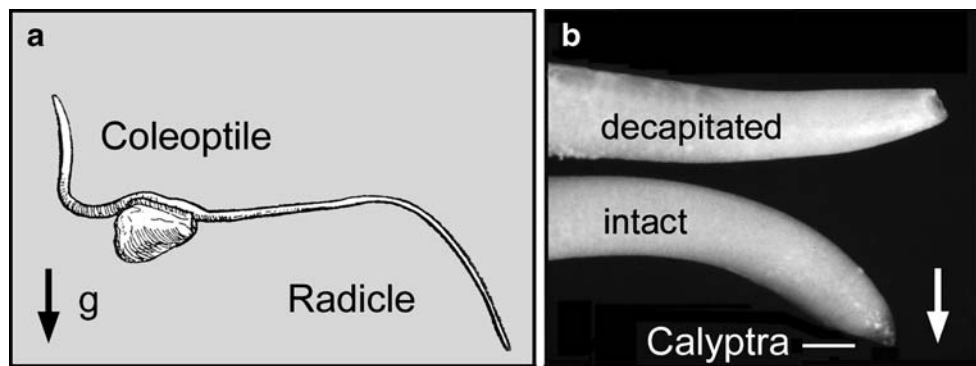


Fig. 4 Negative and positive gravitropism of the shoot (coleoptile) and root (radicle), respectively, in a dark-grown maize seedling (*Zea mays*) oriented horizontally (a). Charles Darwin analysed positive gravitropism (downward bending) of the radicle and demonstrated that

roots without tips (decapitated organs) fail to respond to gravity (b). He concluded that the perception of the gravitropic stimulus is restricted to the root tip (calyptra), whereas the growth response takes place distally. *g* vector of gravity

know by what intracellular sensors the root tip is capable of perceiving different stimuli such as mechanical pressure, light or gradients in the water potential of the soil. The field of root physiology, with reference to the “importance for the life of the (whole) plant” (Darwin 1880, p. 573) was inaugurated by the British naturalist and his son, although major questions concerning the role of phytohormones, such as auxins and ethylene, in root development are still unanswered (Kutschera and Edelman 2005; Edelman and Roth 2006).

A Darwinian approach to plant physiology: phloem structure and photosynthesis

Although more research is required to further elucidate phyletic patterns in auxin metabolism and action, particu-

larly among the charophycean algae and nonvascular land plants (see Figs. 6a and 11a, b), the Darwinian approach taken by Cooke et al. (2002) highlights the tremendous insights that can be gained when phylogenetic (cladistic) analyses are used in comparative evolutionary studies of physiological or metabolic phenomena. It is therefore surprising that our survey of the primary literature reveals few additional examples of this approach. Two of these studies are particularly noteworthy because they illustrate the tremendous potential when a Darwinian approach to plant physiology is taken.

Turgeon et al. (2001) examined the phylogenetic distribution of phloem structure and loading using a well supported molecular tree for the flowering plants and showed that extensive plasmodesmatal continuity between minor vein phloem and surrounding cells is an ancestral condition for the angiosperms. Moreover, a reduction in plasmodesmatal frequency at the interfaces between minor vein phloem and surround cell types is a general evolutionary trend, albeit one that is punctuated by noticeable reversals. These authors also report that reduced plasmodesmatal frequencies in minor vein phloem is common among crop plants and has several points of origin in the angiosperm molecular tree. The implications of this study are numerous and well beyond the scope of this paper. However, it is clear that a Darwinian (phyletic) approach to phloem structure yields significant insights into phloem loading mechanisms, which provide the “driving force” for nutrient transport by generating turgor pressure in long-distance conducting cells in plant source organs.

Likewise, the Darwinian approach taken by McKown et al. (2005) has shed light on the evolution of C4 metabolism in “yellowtops”, tropical plants of the small, inconspicuous genus *Flaveria*, which serves as a model for the ability of plants to cope with arid and hot environmental conditions (Kutschera and Niklas 2006). The vast majority of angiosperms, including most

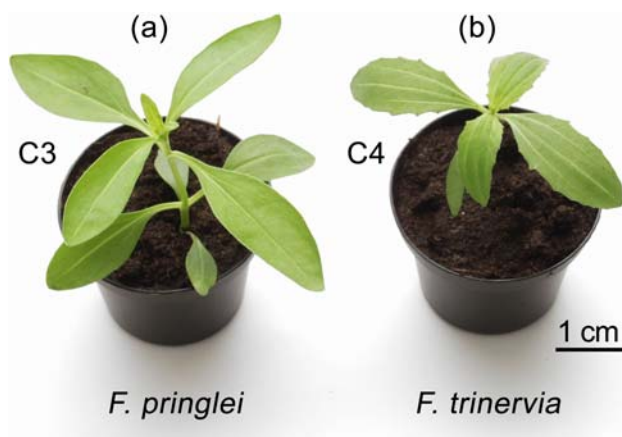
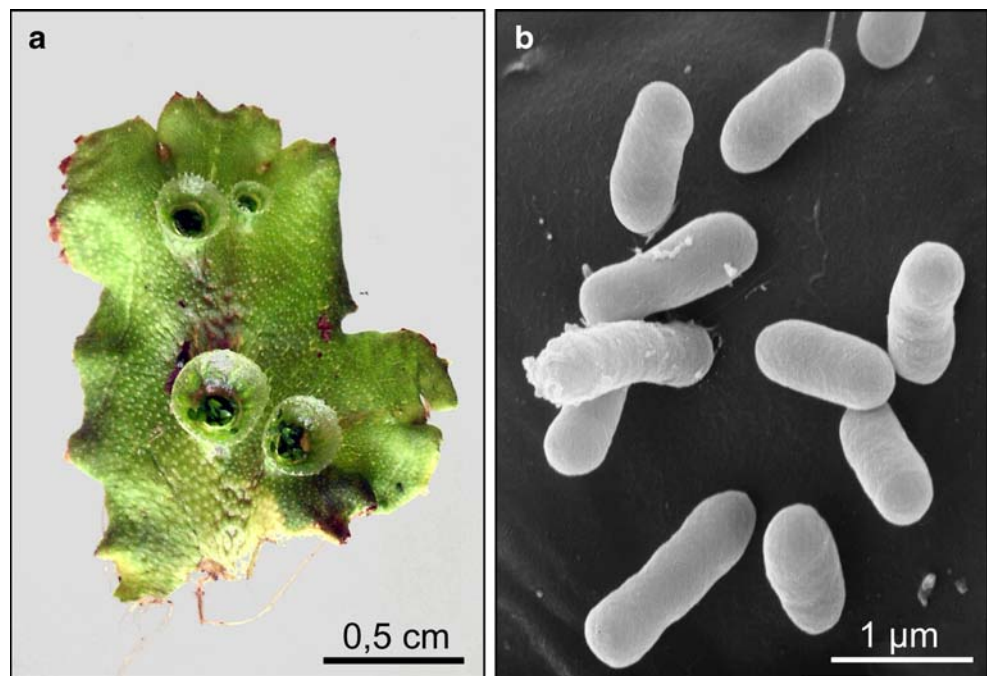


Fig. 5 Photograph of juvenile greenhouse-grown yellowtops (Asteraceae of the genus *Flaveria*). The species *Flaveria pringlei* (a) is characterised by C3 photosynthesis, whereas *Flaveria trinervia* (b) has evolved the more efficient C4 pathway of carbon assimilation. Note the three “nerves” on the upper surface of C4 leaves

Fig. 6 A fragment of the thallus of the liverwort *Marchantia polymorpha* (a) and scanning electron micrograph of plant-associated methylobacteria (*Methylobacterium mesophilicum*) growing on an agar plate (b). Under natural conditions, methylobacteria inhabit the surface of the liverwort. Since thallus growth is enhanced by these phytohormone-secreting epiphytes, the microbes have been interpreted as phytosymbionts



agronomically important crop species (such as wheat or rice) assimilate atmospheric CO₂ through the inefficient C3 pathway of photosynthesis. Under ambient conditions, C3 plants lose about 1/3 of the carbon fixed via photorespiration, arguably an energetically wasteful process that is due to the inefficiency (i.e. slow catalytic rate and substrate confusion) of the enzyme ribulose-1-5-bisphosphate-carboxylase/oxygenase (Rubisco; Kutschera and Niklas 2006).

In contrast, plants with C4 photosynthesis (such as maize) eliminate photorespiration via a biochemical CO₂ pump and thus have a higher rate of carbon gain. The genus *Flaveria* (Family Asteraceae) contains both C3 and C4 species (Fig. 5a, b). It also contains many species manifesting a C3–C4 intermediate metabolism, which appear to be evolving from an ancient C3 pathway to a fully expressed and more derived C4 metabolism. Until recently, the evolutionary significance of these C3–C4 *Flaveria* intermediates has been a matter of debate. Using a well-resolved phylogeny of nearly all *Flaveria* species, McKown et al. (2005) were able to “map” the evolutionary distribution of C3, C4 and C3–C4 species and showed that shifts from C3 to C4 metabolism were evolutionarily adaptive (as gauged by increases in relative species richness within sub-clades or by increases in geographic or ecological distribution). In a subsequent paper, the authors documented the stepwise acquisition of anatomical and leaf vein pattern traits that accompanied the gradual evolution of C4 photosynthesis in members of the genus *Flaveria* (McKown and Dengler 2007).

Endosymbioses and plant growth-promoting bacteria

Charles Darwin largely ignored the “lower unicellular forms of life”: in his books on evolution and on the biology of plants, he never once used the word “bacteria” (see Darwin 1859, 1862, 1867, 1868, 1871, 1875, 1876, 1877, 1880). Indeed, it was the “German Darwin” Ernst Haeckel (1832–1919) and the Russian biologist Constantin S. Mereschkowsky (1855–1921) who first incorporated bacteria, different “algae” (inclusive of cyanobacteria) and other unicellular microbes into their corresponding theories on the phylogenetic development of life on Earth. Mereschkowsky, the father of the concept of symbiogenesis (which was developed by Lynn Margulis and others into the theory of serial endosymbiosis for the origin of eukaryotic cells), published in 1905/1910 an “anti-Darwinian” phylogenetic scheme on the evolution of chloroplasts and photosynthesis that has been discussed elsewhere (see Niklas 1997; Kutschera and Niklas 2005, 2008 and references cited therein). Hence, long ago, the principle of endosymbiosis (i.e. the evolution of intracellular associations where the microbial endosymbiont is reduced to a domesticated partner living within a eukaryotic host cell) became part of a branch of plant physiology closely allied to photosynthesis research (Gould et al. 2008; Kutschera 2009b).

Although root nodule symbioses in legumes such as the common bean (*Phaseolus vulgaris*), pea (*Pisum sativum*) or soybean (*Glycine max*) have already been discussed by Pfeffer (1897/1904), the nature of this unique mutualistic relationship between nitrogen-fixing bacteria of the genus



Fig. 7 Classical garden experiment of Julius Sachs that led to the discovery of the reversible effect of sunlight on plant development. The tip of the green shoot of a cucumber plant (*Cucumis sativus*) was placed into a dark box. After several weeks, the tip of the pale shoot was again placed in the sunlight and growth monitored over the subsequent months (adapted from Sachs 1882)

Rhizobium and the root cells has only recently been elucidated. The intracellular uptake of free-living rhizobia and the subsequent formation of specialised, organelle-like structures (the symbiosomes) via endocytosis is an example of “endosymbiosis in action”, i.e. within the symbiosomes, which are surrounded by the peribacteroid membrane, the rhizobia differentiate into bacteroids that function as domesticated factories for nitrogen fixation (Markmann and Parniske 2009). Much has been learned about the establishment and maintenance of this unique endosymbiosis. However, one question remains largely unanswered: how do invading rhizobia evade the defence systems of their future host cells?

In contrast to the endosymbionts such as chloroplasts (i.e. domesticated ancient cyanobacteria) or bacteroids (i.e. symbiotic rhizobia), which promote growth via photosynthesis and nitrogen-fixation, respectively, plant-growth-promoting rhizobacteria (PGPR) are extracellular microbes that colonise the rhizosphere of many angiosperms. Recent studies have shown that PGPR of the genus *Paenibacillus* enhance the drought tolerance of *Arabidopsis* plants. Moreover, these soil-borne microbes, co-inoculated with a certain *Rhizobium* strain, augment body size and nodule number in bean (*P. vulgaris*) plants subjected to drought

stress (Yang et al. 2009). Like mycorrhizal fungi, some PGPR strains enhance the uptake of nutrients (nitrogen, phosphorus and potassium), possibly via a phytohormone (auxin)-mediated stimulation of root development.

In contrast to the PGPR, which are restricted to root systems, pink-pigmented facultative methylotrophic bacteria of the genus *Methylobacterium* represent the majority of microbes that colonise the above-ground phytosphere, notably leaves. These prokaryotic epiphytes are facultative methylotrophs that can grow on C1 compounds (e.g., methanol emitted via stomata). A series of studies have shown that liverworts (Fig. 6a), one of the most ancient land plant lineages, live in a symbiotic relationship with methylobacteria (Fig. 6b), which secrete phytohormones (cytokinines, auxins) that promote the growth of their thalli (Kutschera 2007). Since the seedlings of another “living fossil”, the maiden hair tree (*Ginkgo biloba*), grow more rapidly in the presence of methylobacteria compared to the aseptic control, it is conceivable that “ancient” embryophytes were dependent on phytohormones provided by epiphytic microbes, whereas evolutionarily more derived angiosperms (Crepet and Niklas 2009) are independent of these surface-dwelling bacteria. Clearly, more experimental work in juxtaposition with well-supported phyletic trees is required to corroborate or refute this hypothesis (Hellmuth and Kutschera 2008; Schauer and Kutschera 2008).

Photomorphogenesis and phenotypic plasticity

As can be seen in the forgoing sections, Darwin was fully aware of the importance of light to plant growth. Indeed, the British naturalist was one of the first to experiment with the effects of light on plant morphology and development. He was particularly interested in how light influenced plant movements. As noted, Darwin (1880) illuminated dark-grown grass seedlings to study phototropism and related phenomena (Fig. 3a, b). However, due to technological limitations, both he and his son failed to discover the specific action of visible light on organ development. To the best of our knowledge, it was Sachs (1882) who described in detail the so-called “etiolement”, i.e. changes in plant organ development due to a lack of light (Fig. 7). Unfortunately, Sachs (1882) interpreted etiolation as an “illness” of leaves and shoots. About two decades later, Pfeffer (1897/1904) summarised laboratory experiments (Fig. 8) as well as observations on a variety of plants growing under natural conditions and concluded that light exerts a “photomorphotische Wirkung” (“photomorphogenic effect”) on all above-ground organs of higher plants. Hence, the term “photomorphogenesis” (i.e. the developmental strategies of plant organs under the influence of light) originated with Pfeffer (1897/1904).

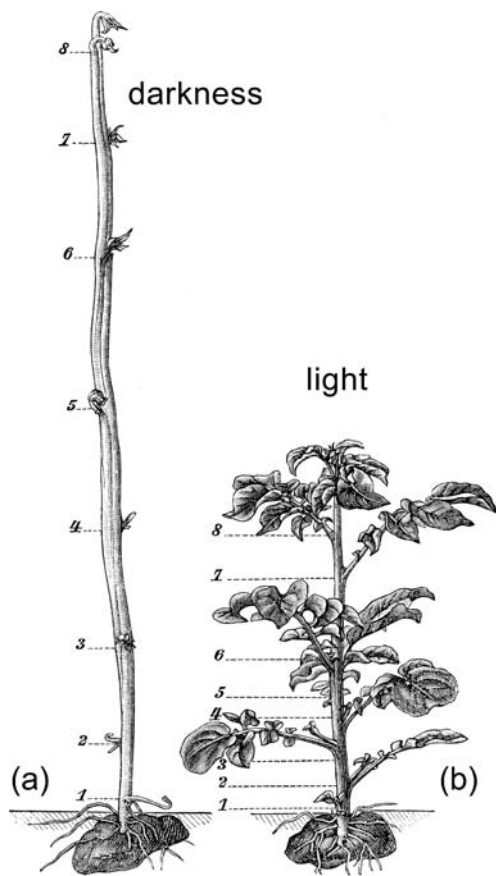


Fig. 8 Classical laboratory experiment of Wilhelm Pfeffer demonstrating the morphogenetic effect of light on the development of potato plants (*Solanum tuberosum*). Tubers from the same plant were either grown in continuous darkness (a) or under a natural light/dark cycle (b). Numbers 1 to 8: internodes of the stem counted from below. Within this context, Pfeffer noted that plant growth depended on a constant supply of atmospheric oxygen (adapted from Pfeffer 1897/1904)

Today, we know that photo- and scotomorphogenesis (i.e. plant development in the presence and absence of light, respectively) are interrelated survival strategies that occur ubiquitously within the plant kingdom (Mohr 1972; Schopfer 1986). These strategies involve complex photoreceptors (phytochromes; a variety of blue-light/UV receptors) that have been characterised in detail (Briggs and Spudich 2005) and that permit a substantial degree of phenotypic plasticity (Niklas 1997, 2009; Kutschera and Niklas 2004).

Until the mid to late twentieth century, the role of phenotypic plasticity in evolution had been comparatively neglected despite considerable interest in the “Reaktionsnorm” (“reaction norm”) and the obvious capacity of many species to manifest often dramatically alternative phenotypes in different environmental settings, a feature well known to Lamarck, Darwin and other naturalists (Sarkar 2004). A classic example, the submergence-induced modification in the phenotype of *Ranunculus fluitans*, which was discussed for

the first time by Lamarck (Burkhardt 1977), is shown in Fig. 9 (see Osborne (1984) for an experimental analysis of this phenomenon). How can the term “phenotypic plasticity” be defined? A useful working definition is “the production of alternative phenotypes by a single genotype as a consequence of environmental differences that invoke developmental changes”. Another definition is “environment-dependent (and -specific) phenotypic expression”. However, regardless of how it is defined, phenotypic plasticity can confer potential adaptive benefits, particularly to sedentary organisms that begin and end their lives in very much the same location. Indeed, Bradshaw (1965) was among the first to suggest that the sessile nature of vascular plants particularly favours phenotypic plasticity as an adaptive mechanism to environments that can vary over many different time scales (e.g. hours, days or years).

While it is true that transplant and common garden experiments have generally shown that the environment rather than the genotype causes much of the character variation observed in angiosperms, it is not always the case that phenotypically plastic responses are adaptive. Some plastic traits may be selectively neutral, while others may be maladaptive. For example, low intracellular nitrogen availability reduces leaf growth, nitrogen concentration and lamina area. Moreover, lower leaf nitrogen concentrations are correlated with reduced net photosynthetic rates (Sage and Percy 1987), and smaller leaves with lower rates of CO₂ assimilation reduce growth, which can result in smaller plants with lower fecundity (Sultan and Bazzaz 1993). It is therefore well worth noting that evolutionary theory predicts that genotypes with the ability to produce phenotypes with high relative fitness in different environments will be generally favoured over locally adapted

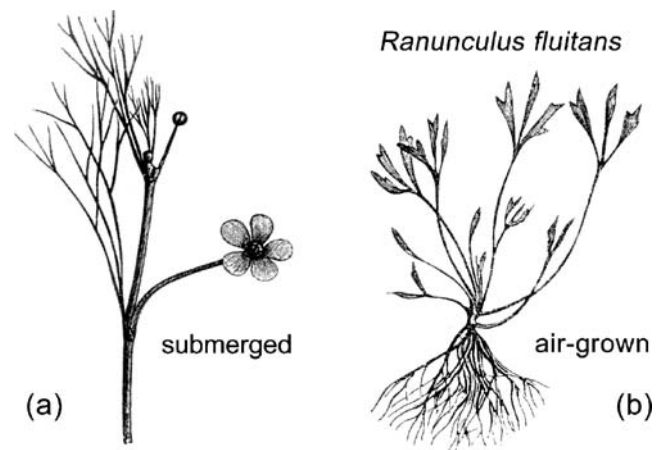


Fig. 9 Plant phenotypic plasticity illustrated by the effect of submergence on the morphology of the River water crow foot (*Ranunculus fluitans*)

genotypes that have high fitness in only one or a few environmental settings, but this prediction is only one of other alternatives when natural selection acts in the context of a spatio-temporally heterogeneous environment. Other possible outcomes include local adaptation, adaptive homeostasis and intermediate “compromise” phenotypes (Van Tienderen 1997; Callaway et al. 2003).

Nevertheless, it is true that phenotypic plasticity is nowhere better manifested nor more widely prevalent than among terrestrial plants (Figs. 7, 8 and 9). A variety of explanations can be suggested to account for this. Among the more obvious is that the embryophytes share the same basic body plan, are equipped with a similar metabolism and physiology and require very much the same essential nutrients to grow and reproduce (Niklas and Kutschera 2009). Indeed, it is obvious that all individuals, whether they are conspecifics or members of radically different species, compete among each other for the same basic resources using the same basic armamentaria. For example, most vascular plant species manifest density-dependent stem elongation, i.e. they tend to grow taller as the number of neighbouring plants increases (Weiner 1985; Jurik 1991). This response is cued by light reflected from the leaves of neighbouring plants (in many cases before individuals are large enough to be shaded by one another), which allows individuals to “anticipate” the level of subsequent competition. Because chlorophyll absorbs more red (R) than far-red (FR) light, the R/FR ratio in sunlight reflected off photosynthetic surfaces is decreased as the number of neighbouring plants increases (Franklin 2008; Ballaré 2009).

Another common feature shared among the vast majority of plant species is thigmomorphogenesis, i.e. growth responses to mechanical perturbation (for recent reviews, see Telewski 2006; Niklas 2009). The ability to sense and respond to physical stimuli, such as wind-induced stem and leaf flexure, is critical to the survival of all forms of plant life. So it is hardly surprising that most species manifest mechanoperception and developmentally adaptively respond in much the same ways. Thus, for example, mechanical bending or torsion increases the girth of stems and petiole lengths and decreases their length and elastic moduli as well as lamina surface area, which reduces the magnitudes of drag forces and bending moments and increases the ability of stems and leaves to flex.

The molecular basis for light-mediated phenotypic plasticity is largely unknown. Schlichting and Pigliucci (1993) have suggested that regulatory genes can exert environmentally dependent control over structural gene expression and thus produce plastic phenotypic responses. The environment-specific control of phenotypic expression by regulatory loci is certainly compatible with quantitative genetic models. Smith (1990) has speculated that differential gene expression of individual members of multigene

families, each under the control of its own regulatory element, provides the molecular basis for plasticity in plants. Each regulatory element is posited to respond to a different environmental signal such that the same genotype is capable of variable but predictable phenotypic responses to different environments. Although such a general model for “plasticity genes” remains viable, it is difficult to see how it can account for a graded plastic response to a continuously changing environmental variable (i.e. depicted by a continuous “reaction norm”) unless numerous “plasticity” loci are required to effect the phenotypic response involved.

Basal metabolic rate and the Pfeffer–Kleiber relationship

Although most organisms can developmentally alter their appearance in response to environmental cues, no form of life is capable of obviating the laws of chemistry or physics, a rule that Darwin (1859) already mentioned in his “species book”. This may help to explain why many if not all physiological processes manifest “scaling” relationships. Perhaps the most famous of these is known as “Kleiber’s law”, although it should be more properly called the “Pfeffer–Kleiber relationship”.

To our knowledge, Pfeffer (1897/1904) was the first to explicitly point out that plants, like animals, are aerobic organisms such that their growth and development are strictly dependent on the availability of atmospheric oxygen (Fig. 8). Indeed, he is the author of the now famous sentence “Ohne Atmung kein Leben” (“without respiration no life”). Based on his summary of all the available pertinent literature, he concluded that physiologists should determine the “spezifische Athmungstätigkeit” (“the specific rate of respiration”) of different plant organs and provide quantitative data in the unit “volume of oxygen consumed per hour and gram fresh mass”. Moreover, Pfeffer (1897/1904) described and discussed the “fire air-theory” of Anton-Laurent Lavoisier (1743–1794), which posits that the metabolism of organisms may be viewed as a combustion process. Lavoisier’s classic respiration experiments of 1784, carried out with small-sized mammals as the experimental system, later gave rise to the “fire of life” concept of animal energetics.

In a seminal paper on metabolic rate in animals, Kleiber (1932) analysed 11 species of mammals with average body masses ranging from 0.15 to 679 kg and produced his now famous “mouse-to-cattle” curve, i.e. a log–log plot of basal metabolic rate (B) versus body mass (M ; Fig. 10). From these data, Kleiber (1932, 1961) deduced his “3/4 power law”, which states that basal metabolic rates scale roughly as the 3/4 power of body mass across most if not all animals, i.e. $B \sim M^{3/4}$. With respect to animal evolution,

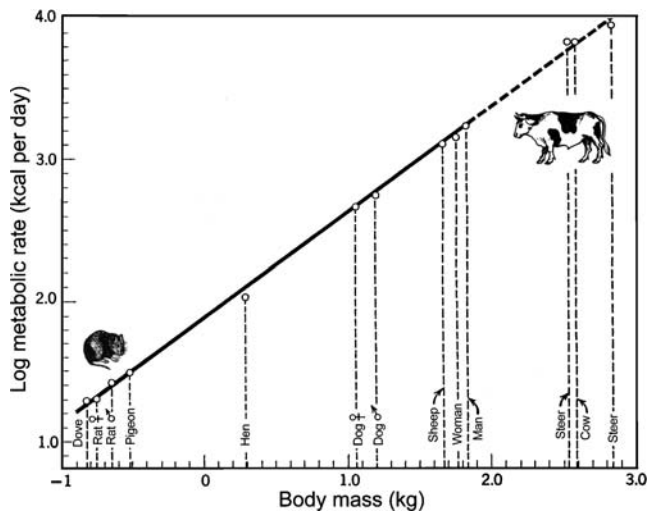


Fig. 10 The “mouse-to-cattle curve” depicting the log–log linear relationship between basal metabolic rates and body mass (adapted from Kleiber 1932)

Kleiber concluded that “In natural selection, those animals prove to be better fit whose rate of oxygen consumption is regulated so as to permit the more efficient temperature regulation as well as the more efficient transport of oxygen and nutrients” (Kleiber 1961, p. 215).

Decades later, a number of analyses indicated that annual growth rates scale roughly as the $3/4$ power of body mass across diverse plants, including algae, aquatic ferns, grasses and arborescent dicot tree species (Niklas 1994; Niklas and Enquist 2001) and that similar scaling relationships may hold true for nitrogen and phosphorus stoichiometry (Niklas et al. 2005; Reich et al. 2006). Noting that annual growth rates are a reflection of basal metabolic rates, the similarity in the scaling exponents for annual growth and basal metabolic activities with respect to body mass is not surprising. However, although many theories have been put forth to account for what some have claimed to be “universal scaling laws” (e.g., Blum 1977; see the following section), none has yet been fully accepted. Indeed, re-analyses of some of Kleiber’s data in tandem with extensive, new data sets suggest that basal metabolism actually scales as the $2/3$ power of body mass (see Dodds et al. 2001). Clearly, much more work is required to determine whether or not “universal” scaling laws exist, even for basal metabolic rates, particularly since only two out of all five kingdoms of life have thus far been explored allometrically.

Metabolic optimality and Darwinian “adaptationist” evolution

A myopic view of Darwinian “adaptationist” evolution can lead to the naive assumption that directional natural

selection invariably results in the optimisation of all physiological and metabolic processes as well as morphological phenotypic features. Indeed, Darwin (1859) frequently talks about “structures that have been perfected”. Some recent theoretical advances in allometric theory are predicated on this assumption and its consequences on the scaling of such diverse phenomena as annual growth rates, biomass partitioning to leaves, stems and roots and the effects of population density on the size frequency distributions of conspecifics in communities (e.g. West et al. 1997, 1999; Enquist et al. 1998; Brown et al. 2004). Here, we will discuss the fractal space-filling theory of G. B. West, J. H. Brown and B. J. Enquist (henceforth denoted as the WBE theory), which was developed to explain “Kleiber’s law” (Fig. 10). The WBE theory assumes that sustained natural selection has resulted in the minimisation of the time required to transport mass and energy throughout the body plan of any kind of organism and thus to have maximised or “perfected” (*sensu* Darwin 1859) internal transport efficiency across unicellular and multicellular plants and animals (West et al. 1997, 1999). This assumption in turn leads to the prediction that diverse allometric relationships are governed by scaling exponents that numerically converge on values of $1/4$ or multiples thereof. For example, according to the WBE theory (and its more recent variants), annual growth rates in biomass (G) are predicted to scale as the $3/4$ power of total body mass (M) regardless of phyletic affiliation or body size and construction (i.e. $G \sim M^{3/4}$); plant population density (N) is expected to scale as the $-3/4$ power of total body mass (i.e. $N \sim M^{-3/4}$; see West et al. 1997, 1999; Enquist et al. 1998); and overall plant (or leaf) length (L) is predicted to scale as the $1/4$ power of body (or leaf) mass (i.e. $L \sim M^{1/4}$; Price and Enquist 2007).

The WBE theory has been extensively criticised on theoretical as well as empirical grounds (Dodds et al. 2001; Cyr and Walker 2004; Li et al. 2006; Hou et al. 2008). Nevertheless, many of its predictions have withstood persistent empirical enquiry. For example, as noted in the previous section, across diverse algae and vascular plant species, annual growth rates scale, on average, as the $3/4$ power of body mass. Growth rates also scale roughly one-to-one with the ability of plants to harvest sunlight, gauged either in terms of algal cell photosynthetic pigment concentration or standing dry leaf mass (Niklas and Enquist 2001). Likewise, the biomass allocation patterns to leaves and stems observed across a broad constellation of vascular plants are statistically indistinguishable from those observed for the biomass allocation to phyllids and gametangiophores across mosses or the morphological equivalents of charophycean algae (“green lineage”, Niklas 2000; Scherp et al. 2001), such as *Nitella* and *Chara* (Fig. 11a). Perhaps more surprising than the apparent evolutionary conservation of

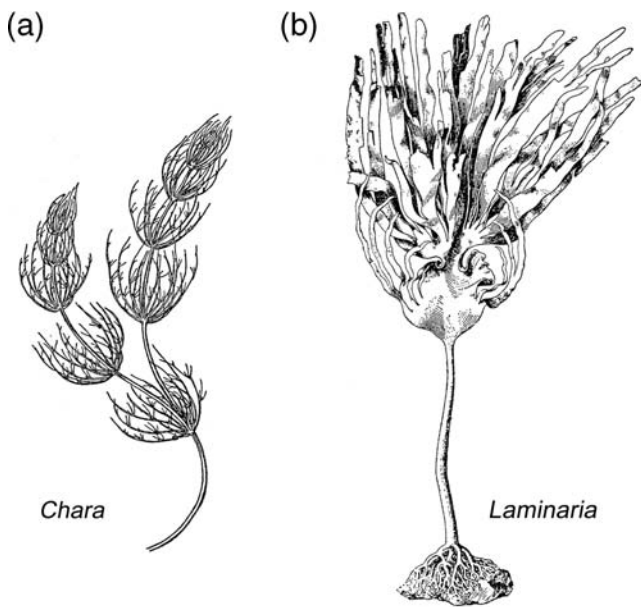


Fig. 11 Representative morphologies in the “algal” Kingdom Protocista. Stonewort (*Chara* sp.), a freshwater pondweed (Characeae) (a) and kelp (*Laminaria* sp.) (b), a member of the marine brown algae (Phaeophyceae)

biomass allocation to the functionally equivalent body parts of vascular and nonvascular embryophytes and their sister group, the charophycean algae, is the observation that this biomass allocation pattern is also indistinguishable from that observed for the foliose blades and stem-like stipes of brown algal species, such as *Laminaria* (Fig. 11b) and *Postelsia* (Niklas 2006). Statistical concordance among the interspecific biomass partitioning patterns identified for non-spermatophyte and spermatophyte lineages would provide evidence that a single “canonical” pattern may exist.

Developmental constraints versus functional equivalence with respect to natural selection

Regardless of the validity of the WBE theory, there are only two possible interpretations for a “canonical” biomass allocation pattern across such diverse plant lineages as the charophycean algae, the embryophytes *sensu stricto*, and the brown algae (Kingdom Protocista). This pattern either provides evidence for the operation of developmental constraints acting on the evolution of the morphological characters shared by these lineages or evidence for the functional equivalence of these organs across developmentally and ecologically very different taxa. The “developmental constraint” hypothesis posits that natural selection acts on different body parts in opposing directions (gauged by biomass or some linear dimension) and that developmental synergistic interactions among these parts limit the extent to which one or more body parts can change in size

evolutionarily. The “functional equivalence” hypothesis argues that particular body parts must change in size with respect to modifications in the size of other body parts to maintain comparable functional levels of performance dictated by biophysically or physiologically invariant “rules”.

Arguably, these two hypotheses are not mutually exclusive. Directional natural selection operating on the level of how well organs perform certain biological tasks can act indirectly on the developmental patterns that give rise to organ structure, shape, size, etc. (Carroll 2006; Kutschera 2008c, 2009a, b). That is to say, if form–function variants are the objects of selection, then the developmental variations that give rise to them will also be exposed to directional selection.

Certainly, organisms can neither obviate the laws of physics or chemistry nor the principles of engineering or mathematics. Thus, constraints on development have existed since the dawn of life. Nevertheless, the concepts of “developmental constraints” *sensu stricto* and “constraints on development” are different—the first posits that developmental repertoires are “internally” regulated and limited genomically; the other concept argues that the external environment limits which among possible developmental patterns persist in evolutionary time. This is not a semantic issue. The “developmental constraint” hypothesis *sensu stricto* can be rejected if the biomass partitioning patterns observed for phylogenetically unrelated lineages or ecologically and functionally diverse species groups manifest the same

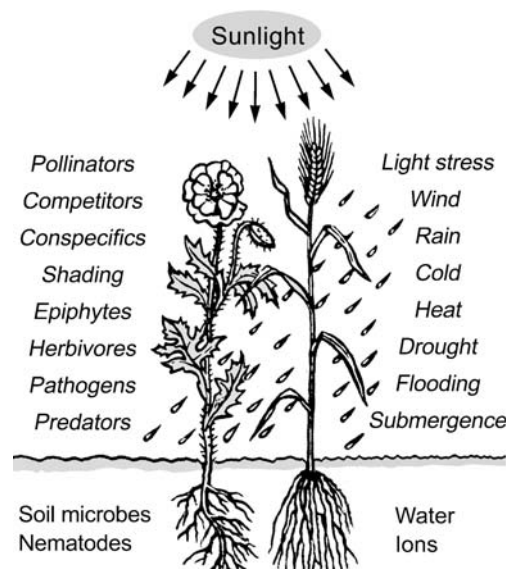


Fig. 12 Scheme illustrating the various biotic (*left*) and abiotic (*right*) factors that influence the growth, survival and reproductive success of stereotypical angiosperms. The evolutionary plant physiology paradigm argues that adaptive physiological responses have evolved via directional natural selection by the Darwinian process of descent with modification

scaling relationships because it is unreasonable to argue that the organisms within extremely divergent evolutionary lineages share the same developmental repertoires.

For this reason, the allometry of brown algae provides a yardstick with which to evaluate this hypothesis because all of the available evidence indicates that these marine photoautotrophs (Kingdom Protocista, Fig. 11b) represent a line of organismic evolution that is entirely independent of that of the green algal ancestors of the streptophiles (non-vascular plants, see Niklas 1997, 2006; Niklas and Kutschera 2009). Likewise, all of the evidence in hand indicates that the development underwriting the blade, stipe and holdfast construction of these algae is radically different from that giving rise to tracheophyte leaves, stems and roots. Accordingly, the biomass partitioning patterns that are shared across the green and brown algae and the land plants argues against the “developmental constraint” hypothesis *sensu stricto* and in favour of the functional equivalence hypothesis (Niklas 2006, 2007). In turn, this provides empirical evidence for extensive and persistent directional (Darwinian) natural selection acting on the basic metabolism and morphology of all eukaryotic photosynthetic organisms on Earth (Figs. 1, 11 and 12).

Conclusions: evolutionary plant physiology as an emerging discipline

In his famous monograph entitled *Vorlesungen über Pflanzen-Physiologie*, the eminent German botanist Julius Sachs summarised Darwin’s principle of evolution as follows: “It should be stressed that... the theory of descent with modification was deduced from the observation that new properties accumulate in different varieties. This fact, combined with the knowledge that, from the most primitive to the highest organised plants, a continuum of intermediate forms exist, led to the bold and seminal hypothesis that the most complex plants evolved gradually from lower forms via the continued production of varieties. This is the essence of the theory of descent with modification, which caused a large change in perspective among natural scientists over the last twenty years” (Sachs 1882, p. 13). Despite this general acknowledgement of Darwin’s basic idea, Sachs (1882) failed to combine his tremendous insights on the physiology of plants with the principle of evolution. Likewise, Pfeffer (1897/1904), who referred to the botanical publications of Darwin and his son Francis on many pages of his monograph, largely ignored the concept of descent with modification.

As pointed out by his son Francis, Charles Darwin was the first to attempt to combine plant physiology (i.e. the experimental analysis of processes that go on in the living

cells and organs of extant green organisms) with evolution (i.e. the cumulative changes in the characteristics of populations of plants in the course of thousands of successive generations) (Darwin 1909). Unfortunately, Darwin’s early fragmentary synthesis is largely ignored today despite technological advances that make evolutionary plant physiology a tractable and very exciting field of enquiry.

In this article, we went back to the roots of “Darwin’s forgotten synthesis” and summarised some of the most important research areas at the interface between plant physiology and evolutionary biology. As shown in Fig. 12, land plants (embryophytes) are dependent on and exposed to a variety of biotic and abiotic environmental factors. It is evident that their survival and reproduction (the two major components of Darwinian fitness of the individual plant) are to a large extent a function of numerous evolved physiological processes of sedentary photosynthetic eukaryotes. Hence, evolutionary plant physiology can be defined as the “experimental study and theoretical analysis of organismal functions from a phylogenetic perspective”. In other words, evolutionary plant physiology is the explicit fusion of two separate research agendas: the search for the general principles of how green organisms work and the broad question of how plants have been shaped by evolution to function in particular environmental contexts. This area of research represents a novel multi-disciplinary approach to a series of questions that Charles Darwin raised 150 years ago when the first edition of his book *On the Origin of Species* was published.

Acknowledgement We thank four referees for helpful comments on an earlier version of the manuscript and the Alexander von Humboldt-Stiftung (Bonn, Germany) for financial support (AvH-fellowships 2008/2009, Stanford, California, USA to U. K.).

References

- Ayres P (2008) *The aliveness of plants: the Darwins at the dawn of plant science*. Pickering & Chatto, London
- Ballaré CR (2009) Illuminated behaviour. Phytochrome as a key regulator of light foraging and plant anti-herbivore defense. *Plant, Cell Environm* 32:713–715
- Barlow N (1958) (ed) *The autobiography of Charles Darwin*. Collins St James’s Place, London
- Barlow PW (2006) Charles Darwin and the plant root apex: closing a gap in living systems theory as applied to plants. In: Baluska F, Mancuso S, Volkmann D (eds) *Communication in plants*. Springer, Berlin, pp 37–51
- Blum JJ (1977) On the geometry of four dimensions and the relationship between metabolism and body mass. *J Theor Biol* 64:599–601
- Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* 13:115–155
- Briggs WR, Spudich J (eds) (2005) *Handbook of photosensory receptors*. Wiley-VCH, Weinheim

- Brown AH, Chapman DK, Lewis RF, Venditti AL (1990) Circumnutation of sunflower hypocotyls in satellite orbit. *Plant Physiol* 94:233–238
- Brown JH, Gillooly JF, Allen AP, Savage VM, West DB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789
- Burkhardt RW (1977) The spirit of system. Lamarck and evolutionary biology. Harvard University Press, Cambridge
- Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions among plants. *Ecology* 84:1115–1128
- Carroll SB (2006) The making of the fittest. DNA and the ultimate forensic record of evolution. WW Norton, New York
- Cholodny N (1928) Beiträge zur hormonalen Theorie von Tropismen. *Planta* 6:118–134
- Cooke TJ, Poli DB, Szein AE, Cohen JD (2002) Evolutionary patterns in auxin action. *Plant Mol Biol* 349:319–338
- Crepet WL, Niklas KJ (2009) Darwin's second "abominable mystery": why are there so many angiosperm species? *Amer J Bot* 96:366–381
- Cyr H, Walker SC (2004) An illusion of mechanistic understanding. *Ecology* 85:1802–1804
- Darwin C (1859) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London
- Darwin C (1862) On the various contrivances by which British and foreign orchids are fertilised by insects. John Murray, London
- Darwin C (1867) The movements and habits of climbing plants, 2nd edn. John Murray, London
- Darwin C (1868) The variation of animals and plants under domestication (Vols 1 and 2). John Murray, London
- Darwin C (1871) The descent of man, and selection in relation to sex (Vols 1 and 2). John Murray, London
- Darwin C (1875) Insectivorous plants. John Murray, London
- Darwin C (1876) The effects of cross and self fertilisation in the vegetable kingdom. John Murray, London
- Darwin C (1877) The different forms of flowers on plants of the same species. John Murray, London
- Darwin C (1880) The power of movement in plants. John Murray, London
- Darwin F (1909) Darwin's work on the movements of plants. In: Seward AC (ed) Darwin and modern science. Essays in commemoration of the centenary of the birth of Charles Darwin and the fiftieth anniversary of the publication of The Origin of Species. Cambridge University Press, Cambridge, pp 385–400
- Darwin F, Acton EH (1894) Practical physiology of plants. Cambridge University Press, Cambridge
- De Vries H (1901/1903) Die Mutationstheorie. Band 1 und 2. Veit, Leipzig
- Dodds PS, Rothman DH, Weitz JS (2001) Re-examination of the "3/4-law" of metabolism. *J Theoret Biol* 209:9–27
- Edelmann HG, Roth U (2006) Gravitropic plant growth regulation and ethylene: an unsought cardinal coordinate for a disused model. *Protoplasma* 229:183–191
- Enquist BJ, Brown JH, West GB (1998) Allometric scaling of plant energetics and population density. *Nature* 395:163–165
- Feder ME (2002) Plant and animal physiological ecology, comparative physiology/biochemistry, and evolutionary physiology: opportunities for synergy. *Integr Comp Biol* 42:409–414
- Franklin KA (2008) Shade avoidance. *New Phytol* 179:930–944
- Garland T, Carter PA (1994) Evolutionary physiology. *Annu Rev Physiol* 56:579–621
- Gould SB, Walker RF, McFadden GI (2008) Plastid evolution. *Annu Rev Plant Biol* 59:491–517
- Hart JW (1990) Plant tropisms and other growth movements. Chapman & Hall, London
- Hellmuth J, Kutschera U (2008) The effect of growth-promoting methylobacteria on development in *Ginkgo biloba* L. *J Appl Bot* 82:26–29
- Hou C, Zuo W, Moses ME, Woodruff WH, Brown JH, West GB (2008) Energy uptake and allocation during ontogeny. *Science* 322:736–739
- Jurik TW (1991) Population distributions of plant size and light environment of ragweed (*Ambrosia trifida* L.) at three densities. *Oecologia* 87:539–550
- Kiss JZ (2006) Up, down, and all around: how plants sense and respond to environmental stimuli. *Proc Natl Acad Sci USA* 103:829–830
- Kleiber M (1932) Body size and metabolism. *Hilgardia* 6:315–332
- Kleiber M (1961) The fire of life: an introduction to animal energetics. Wiley, New York
- Kutschera U (2003) Auxin-induced cell elongation in grass coleoptiles: a phytohormone in action. *Curr Topics Plant Biol* 4:27–46
- Kutschera U (2006) Acid growth and plant development. *Science* 311:952–953
- Kutschera U (2007) Plant-associated methylobacteria as co-evolved phytosymbionts: a hypothesis. *Plant Signal Behav* 2:74–78
- Kutschera U (2008a) The outer epidermal wall: design and physiological role of a composite structure. *Ann Bot* 101:615–621
- Kutschera U (2008b) The pacemaker of plant growth. *Trends Plant Sci* 13:105–107
- Kutschera U (2008c) Darwin-Wallace principle of natural selection. *Nature* 453:27
- Kutschera U (2009a) Charles Darwin's Origin of Species, directional selection, and the evolutionary sciences today. *Naturwissenschaften* (this issue). doi:10.1007/s00114-009-0603-0
- Kutschera U (2009b) Symbiogenesis, natural selection, and the dynamic Earth. *Theory Biosci*. doi:10.1007/s12064-009-0065-0
- Kutschera U, Edelmann HG (2005) Osmiophilic nanoparticles in epidermal cells of grass coleoptiles: implications for growth and gravitropism. *Rec Res Dev Plant Sci* 3:1–14
- Kutschera U, Niklas KJ (2004) The modern theory of biological evolution: an expanded synthesis. *Naturwissenschaften* 91:255–276
- Kutschera U, Niklas KJ (2005) Endosymbiosis, cell evolution, and speciation. *Theory Biosci* 124:1–24
- Kutschera U, Niklas KJ (2006) Photosynthesis research on yellow-tops: macroevolution in progress. *Theory Biosci* 125:81–92
- Kutschera U, Niklas KJ (2007) The epidermal-growth-control theory of stem elongation: an old and a new perspective. *J Plant Physiol* 164:1395–1409
- Kutschera U, Niklas KJ (2008) Macroevolution via secondary endosymbiosis: a Neo Goldschmidian view of unicellular hopeful monsters and Darwin's primordial intermediate form. *Theory Biosci* 127:277–289
- Li H-T, Han X-G, Wu J-G (2006) Variant scaling relationship for mass-density across tree-dominated communities. *J Integr Plant Biol* 48:268–277
- Markmann K, Parniske M (2009) Evolution of root endosymbiosis with bacteria: how novel are nodules? *Trends Plant Sci* 14:77–86
- Mayr E (1982) The growth of biological thought. Diverstiy, evolution, and inheritance. Harvard University Press, Cambridge
- Mayr E (1991) One long argument: Charles Darwin and the genesis of modern evolutionary thought. Harvard University Press, Cambridge
- Mayr E (2004) What makes biology unique? Considerations on the autonomy of a scientific discipline. Cambridge University Press, Cambridge
- McKown AD, Moncalvo J-M, Dengler NG (2005) Phylogeny of *Flaveria* (Asteraceae) and inference of C4-photosynthesis evolution. *Amer J Bot* 92:1911–1928
- McKown AD, Dengler NG (2007) Key innovations in the evolution of Kranz anatomy and C4 vein pattern in *Flaveria* (Asteraceae). *Amer J Bot* 94:382–399
- Mohr H (1972) Lectures on photomorphogenesis. Springer, Berlin

- Morton AG (1981) History of botanical science. An account of the development of botany from ancient times to the present day. Academic, London
- Niklas KJ (1992) Plant biomechanics. An engineering approach to plant form and function. The University of Chicago Press, Chicago
- Niklas KJ (1994) Size-dependent variations in plant growth rates and the “3/4-power rule”. *Amer J Bot* 81:134–144
- Niklas KJ (1997) The evolutionary biology of plants. The University of Chicago Press, Chicago
- Niklas KJ (2000) The evolution of plant body plans—a biomechanical perspective. *Ann Bot* 85:411–438
- Niklas KJ (2006) A phyletic perspective on the allometry of plant biomass-partitioning patterns and functionally equivalent organ-categories. *New Phytol* 171:27–40
- Niklas KJ (2007) Sizing up life and death. *Proc Natl Acad Sci USA* 104:15589–15590
- Niklas KJ (2009) Functional adaptation and phenotypic plasticity at the cellular and the whole plant level. *J Biosci* (in press)
- Niklas KJ, Enquist BJ (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc Natl Acad Sci USA* 98:2922–2927
- Niklas KJ, Kutschera U (2009) The evolutionary development of plant body plans. *Funct Plant Biol* 36:682–695
- Niklas KJ, Owens T, Reich PB, Cobb ED (2005) Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. *Ecology Lett* 8:636–642
- Osborne DJ (1984) Ethylene and plants of aquatic and semi-aquatic environments: a review. *Plant Growth Regul* 2:167–185
- Pfeffer W (1897/1904) Pflanzenphysiologie. Ein Handbuch der Lehre vom Stoffwechsel und Kraftwechsel in der Pflanze. Band I: Stoffwechsel, Band II: Kraftwechsel. 2. Auflage. Verlag Wilhelm Engelmann, Leipzig
- Price CA, Enquist BJ (2007) Scaling mass and morphology in leaves: an extension of the WBE model. *Ecology* 88:1132–1141
- Reich PB, Tjoelker MG, Machado J-L, Oleksyn J (2006) Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* 439:457–461
- Sachs J (1865) Handbuch der Experimental-Physiologie der Pflanzen. Verlag Wilhelm Engelmann, Leipzig
- Sachs J (1882) Vorlesungen über Pflanzen-Physiologie. Verlag Wilhelm Engelmann, Leipzig
- Sage RF, Pearcy RW (1987) The nitrogen use efficiency of C3 and C4 plants. II. Leaf nitrogen effects on the gas exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). *Plant Physiol* 84:959–963
- Sarkar S (2004) From the Reaktionsnorm to the evolution of adaptive plasticity: a historical sketch, 1909–1999. In: DeWitt TJ, Scheiner SM (eds) Phenotypic plasticity: function and conceptual approaches. Oxford University Press, Oxford, pp 10–30
- Schauer S, Kutschera U (2008) Methylophilic bacteria on the surfaces of field-grown sunflower plants: a biogeographic perspective. *Theory Biosci* 127:23–29
- Scherp P, Grotha R, Kutschera U (2001) Occurrence and phylogenetic significance of cytokinesis-related callose in green algae, bryophytes, ferns and seed plants. *Plant Cell Rep* 20:143–149
- Schlichting CD, Pigliucci M (1993) Control of phenotypic plasticity via regulatory genes. *Amer Nat* 142:366–370
- Schopfer P (1986) Photomorphogenesis. In: Wilkins MB (ed) Advanced plant physiology. Longman Scientific & Technical, Essex, pp 380–407
- Schopfer P (2006) Biomechanics of plant growth. *Amer J Bot* 93:1415–1425
- Schopfer P (2008) Is the loss of stability theory a realistic concept for stress relaxation-mediated cell wall expansion during plant growth? *Plant Physiol* 147:935–936
- Sprengel C (1793) Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen. Friedrich Viehweg, Berlin
- Smith H (1990) Signal perception, differential expression within multigene families and the molecular basis of phenotypic plasticity. *Plant, Cell, Environm* 13:585–594
- Sultan SE, Bazzaz FA (1993) Phenotypic plasticity in *Polygonum persicaria*. III. The evolution of ecological breadth for nutrient environment. *Evolution* 47:1050–1071
- Telewski F (2006) A unified hypothesis for mechanoperception in plants. *Amer J Bot* 93:1466–1476
- Turgeon R, Medville R, Nixon K (2001) The evolution of minor vein phloem and phloem loading. *Amer J Bot* 88:1331–1339
- Van Tienderen PH (1997) Generalists, specialists, and the evolution of phenotypic plasticity in sympatric populations of distinct species. *Evolution* 51:1374–1380
- Weiner J (1985) Size hierarchies in experimental populations of annual plants. *Ecology* 66:743–752
- Went FW (1928) Wuchsstoff und Wachstum. *Rec Trav Bot Neerl* 25: 1–116
- Went FW, Thimann KV (1937) Phytohormones. Macmillan, New York
- West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276:122–126
- West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. *Nature* 400:664–667
- Yang J, Kloepper JW, Ryu C-M (2009) Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci* 14:1–4