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REVIEW ARTICLE

From Charles Darwin's botanical country-house studies to modern plant biology

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ABSTRACT

As a student of theology at Cambridge University, Charles Darwin (1809–1882) attended the lectures of the botanist John S. Henslow (1796–1861). This instruction provided the basis for his life-long interest in plants as well as the species question. This was a major reason why in his book *On the Origin of Species*, which was published 150 years ago, Darwin explained his metaphorical phrase 'struggle for life' with respect to animals and plants. In this article, we review Darwin's botanical work with reference to the following topics: the struggle for existence in the vegetable kingdom with respect to the phytochrome-mediated shade avoidance response; the biology of flowers and Darwin's plant–insect co-evolution hypothesis; climbing plants and the discovery of action potentials; the power of movement in plants and Darwin's conflict with the German plant physiologist Julius Sachs; and light perception by growing grass coleoptiles with reference to the phototropins. Finally, we describe the establishment of the scientific discipline of *Plant Biology* that took place in the USA 80 years ago, and define this area of research with respect to Darwin's work on botany and the physiology of higher plants.

INTRODUCTION

In the third English edition of the famous book *On the Origin of Species by Means of Natural Selection* published in April 1861, Charles Darwin (1809–1882) added a 'Historical Sketch of the Recent Progress of Opinion on the Origin of Species', which attempted to place the original text of 1859 within a prior tradition of the notion of descent with modification. In this short review, which was reproduced in later reprints of the first and all five subsequent editions of his seminal work, Darwin (1859) pointed out that Jean-Baptiste de Lamarck (1744–1829) was the first to postulate that all extant species, including man, may have descended from pre-existing forms of life. Lamarck's concept of evolution, published in detail in his *Philosophie Zoologique* (1809), is fully acknowledged in Darwin's 'Historical Sketch', but another earlier student of evolution, his grandfather Erasmus Darwin, is only briefly mentioned in a footnote to the section on Lamarck (1809). A wealthy physician, Erasmus Darwin (1731–1802) published a pre-Lamarckian version of the principle of evolution in his *Zoonomia* of 1794, and examined green plants as photosynthetic sessile organisms. Two years before his death, he published another book entitled *Phytologia*. Based on his own botanical studies as well as those of Hales, Lavoisier, Priestley and others, the book provided a summary of the state of botanical knowledge in the year 1800. Erasmus Darwin's *Phytologia* became a standard text on botany in Britain and may have influenced his famous grandson more than he ever admitted (Desmond & Moore 1991; Browne 2002; Ayres 2008).

During his years as a student of theology at Cambridge University, Charles Darwin (Fig. 1) attended the lectures on botany by his mentor Professor John S. Henslow (1796–1861). He recommended the young Darwin, who was inspired by the writings of Alexander von Humboldt (1769–1859), as naturalist to Captain James FitzRoy on the HMS *Beagle* expedition to the Southern Hemisphere (Jackson 2009). A detailed analysis of the Darwin–Henslow relationship revealed that the close contact with this

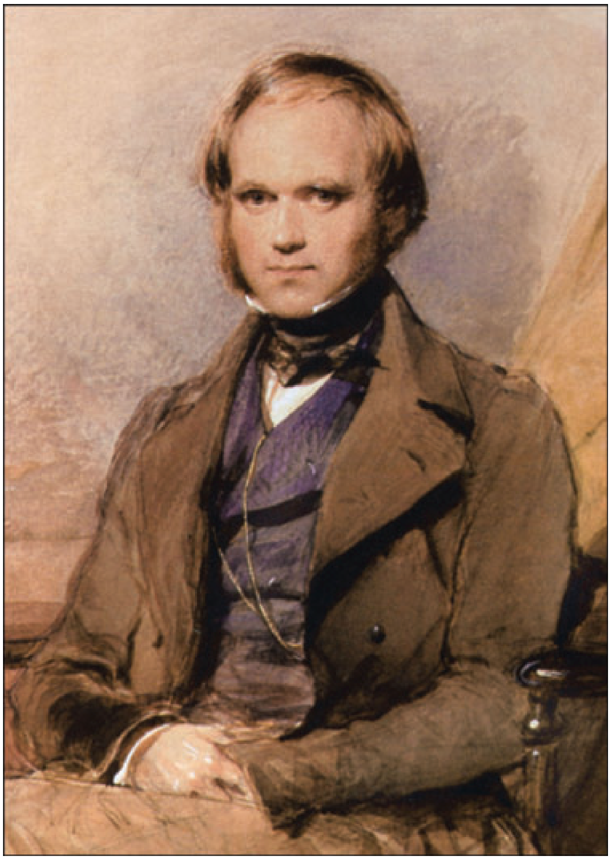


Fig. 1. The British naturalist Charles Darwin (1809–1882). Even if he had never published one sentence on biological evolution, Darwin would be remembered today as one of the greatest botanists and zoologists of the nineteenth century (adapted from a painting by George Richmond, 1840).

famous botanist provided the basis not only for Darwin's subsequent life-long botanical studies but also for the development of his post-Lamarckian evolutionary thought (Kohn *et al.* 2005). In addition to his well-known books on the 'transmutation of species', Charles Darwin published six influential monographs on botanical issues, ranging from floral biology to plant developmental physiology (Darwin 1862, 1867, 1875, 1876, 1877, 1880).

In this article, we briefly outline the major achievements of the 'country-house' botanist and plant physiologist Charles Darwin, comment on his conflict with Julius Sachs (1832–1897) and describe the development of his seminal ideas with respect to modern botanical research. In addition, we briefly outline the significance of the work of Darwin's son Francis (1848–1925) and explore the history and meaning of the term *Plant Biology*.

THE STRUGGLE FOR EXISTENCE IN THE VEGETABLE KINGDOM

In popular articles and books dealing with Charles Darwin's *Origin of Species* one can regularly read statements such as the 'theory of our descent from the apes', *etc.* However, the reader of Darwin's book will look in vain for references to humanity. With the exception of the sentence 'Light will be thrown on the origin of man and his history', the 'human animal' is absent in this monograph on the theory of descent with modification by means of natural selection. Darwin illustrated his principle of natural selection, or the 'universal struggle for life', to a large extent with references to the survival and reproductive strategies of higher plants. According to Darwin (1859), the term 'struggle for existence' should be used in a metaphorical sense, including dependence of one being on another, which enhances the success in leaving progeny. In chapter III, entitled 'Struggle for existence', more references to the 'Vegetable Kingdom' are made by the author than to wild animals that may in fact sometimes fight: 'Two canine animals in a time of dearth, may be truly said to struggle with each other which shall get food and live. But a plant on the edge of a desert is said to struggle for life against the drought, though more properly it should be said to be dependent on the moisture. A plant which annually produces a thousand seeds, of which on average only one comes to maturity, may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground' (Darwin 1859, p. 50).

These and many other examples clearly document that Darwin's *Origin of Species* was written from a zoological and a botanical perspective. The 'struggle for life' in natural populations of organisms and the resulting selection of those varieties that are better adapted than their competitors is 'the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms' (Darwin 1859; p. 51). Hence, the popular translation of the word 'struggle' as 'Kampf' (*i.e.* fight) is not correct, since plants, as sessile photoautotrophic organisms, are hardly able to fight. However, within populations, essential resources such as light, water, nutrients, *etc.* are often limiting so that the individuals compete with each other in their 'struggle' for growth and reproduction (Kutschera 2009a; b). One of the most impressive examples of Darwin's 'struggle for (individual) existence' in the plant kingdom is the phytochrome-regulated 'shade-avoidance behaviour' documented in a number of selected angiosperms. The sunlight passing through leaves, or reflected from leaves, is strongly depleted in red light through chlorophyll absorption, but not in far-red light. As long as the individual does not perceive the transmitted or reflected far-red light from neighbours, the stem elongates at a moderate rate. However, if the plant perceives the red-depleted (and therefore relatively far-red enriched) shade or reflected light from its competitors, the rate of growth increases and the 'struggle for a top place in the sun' commences (Ballaré *et al.* 1990; Ballaré 2009). The far-red-absorbing form of phytochrome, which inhibits stem elongation, is driven back to the red-absorbing form by the dominating far-red light and inhibition is reduced.

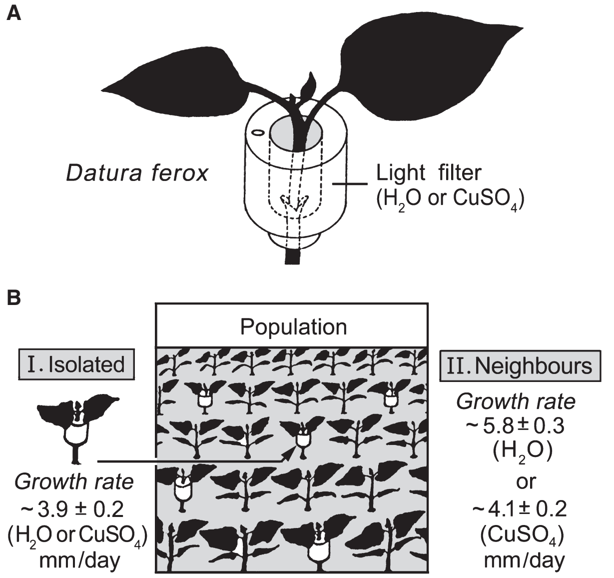


Fig. 2. Experimental demonstration of the 'struggle for life' in a population of seedlings of *Datura ferox*. Single plant with annular filter (A) that either contains water (H_2O, control) or a solution of copper sulphate ($CuSO_4$), a filter to remove far-red radiation from the surrounding light. (B) A seedling (I) and the same individual after transfer into a population of conspecifics (II). Note that the average rate of internode elongation in isolated and far-red 'blinded' seedlings is about 4.0 mm per day, whereas plants that perceive the far-red light reflected by their neighbours (within a population) elongate much faster (*ca*. 5.8 mm per day). This 'shade avoidance reaction' was recorded 3 days after transfer of the seedlings (adapted from Ballaré *et al.* 1990).

Elegant experiments with seedlings of long-spined thorn apple (*Datura ferox*) have shown that 'blinded' individuals that are unable to perceive far-red light, either transmitted or reflected from neighbours, *via* phytochrome photoreceptors, do not engage in this form of competition (Fig. 2A, B) (Ballaré *et al.* 1990). Hence, Darwin (1859) was right when he concluded that sessile plants and mobile animals behave, under certain conditions, in analogous ways: as soon as the supply of resources becomes limited only the best-adapted individuals in the corresponding populations survive and reproduce. Over thousands of subsequent generations, this selection pressure may result in descent with modification (*i.e.* evolution), notably if there is a gradual change in environmental conditions during those many generations (Niklas 1997; Kutschera & Niklas 2004; Kutschera 2009b).

THE BIOLOGY OF FLOWERS AND *XANTHOPAN MORGANI PRAEDICTA*

Only 3 years after Darwin's *Origin of Species* was published, another book by the author appeared in print that was devoted to the fertilisation of orchids by insects and the positive effects of inter-crossing. Together with a subsequent monograph on a similar subject, these two seminal works (Darwin 1862, 1877) led to the establishment of a new botanical discipline, which was later called *Floral Biology* (Osche 1972, 1983).

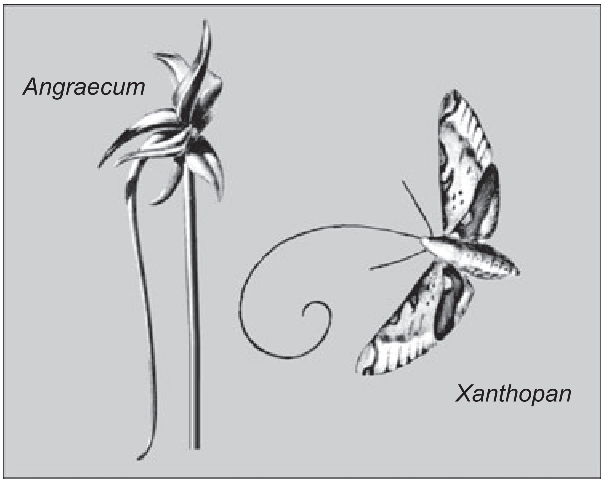


Fig. 3. Charles Darwin's plant–insect prediction: the orchid *Angraecum sesquipedale* from Madagascar and the butterfly *Xanthopan morgani praedicta*, a large moth with a long proboscis that pollinates it (adapted from Osche 1972).

According to Kritsky (2008), the British naturalist not only discovered and described the intimate relationships that exist between certain species of orchids and their pollinators, but, moreover, implicitly postulated the principle of plant–insect co-evolution (Osche 1983). The most famous example analysed by him, which later became known as 'Darwin's Madagascan hawkmoth prediction', is illustrated in Fig. 3. At the beginning of the 1860s, biologists studied a bizarre Madagascan plant, which is known today under common names such as star of Bethlehem, Christmas star, comet- or rocket orchid. This endemic member of the Orchidaceae, which inhabits certain lowland forests of Madagascar, has a nectar tube of 10–12 inches (25–30 cm) in length and was therefore named *Angraecum sesquipedale* (Etymology: lat. *sesquipedale* = 1½ feet long). Charles Darwin analysed the strange morphology of the sesquipedalian flower of *Angraecum* and wrote in his book on orchids that 'In several flowers which Mr. Bateman sent to me, I found nectaries of eleven inches and a half in length, with only the inch and a half lower filled of a very soft nectar. It is however surprising that an insect is able to reach nectar: our English sphinges have horns as long as their body; but in Madagascar there must be butterflies with horns capable of an extension in length ranging between ten and eleven inches!' (Darwin 1862; p. 162). In the 'Concluding Remarks' of his monograph, we read the following prediction: 'We know that certain Orchids require certain insects for their fertilisation … In Madagascar, *Angraecum sesquipedale* must depend on some gigantic moth' (Darwin 1862, p. 282).

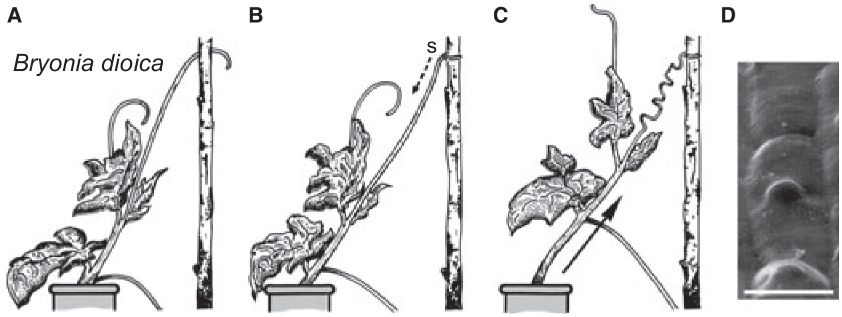


Fig. 4. The behaviour of a freshly cut shoot of the climbing plant *Bryonia dioica* that was kept in a solution of 0.1 mM KCl and 0.5% (w/v) glucose. Searching movements (circumnutations) of the upper tendril (A), coiling of the tip upon mechanical contact with a piece of wood (B), release of a gaseous chemical signal (s, 12-oxo-phytodienoic acid, a biosynthetic precursor of jasmonic acid, *dashed arrow*), free coiling in the lower part of the tendril, and climbing response of the shoot (*arrow*, C) (original experiment). The scanning electron micrograph (D) of the touch-sensitive region of a tendril shows the tactile protrusions on the epidermal surface (bar = 10 μm) (adapted from Engelberth *et al.* 1995).

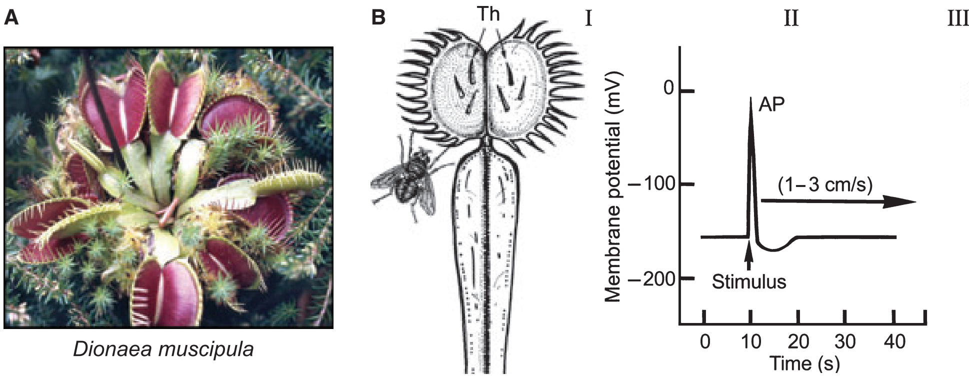
If we combine these two quotes, it becomes apparent that Darwin concluded that since the nectar was at the bottom of the spur, a pollinator must exist with a tongue as long as or even larger than the spur; otherwise, this orchid species could not be pollinated. At first, Darwin's prediction was ridiculed or ignored. However, in 1903, *i.e.* four decades later, the predicted pollinator was discovered: a hawkmoth now named *Xanthopan morgani praedecta* (*i.e.* as predicted by Darwin). It had a correspondingly long proboscis capable of extending 11 inches (28 cm). Under natural conditions, this giant moth pollinates *A. sesquipedale*, which depends on this large nocturnal moth for its survival as a species (Kritsky 2008).

The broader implications of Darwin's detailed studies of plant–insect interactions can be summarized as follows. In a famous letter of 22 July 1879 from Charles Darwin to Joseph Hooker, wherein Darwin described the origin, rapid diversification and subsequent rise to dominance of the flowering plants (angiosperms) as an 'abominable mystery', he mentioned for the first time his 'co-evolution hypothesis' as follows: 'Saporta believes that there was an astonishingly rapid development of higher plants, as soon as flower frequenting insects were developed' (Crepet & Niklas 2009). A detailed analysis of paleontological data recently revealed that the first appearances of key floral traits and insect families in the fossil record are significantly correlated, as are the numbers of angiosperm species and insect families (Crepet & Niklas 2009). However, this positive correlation of course provides no evidence for a causal relationship. Hence, the 'co-evolution hypothesis', proposing that the insect–plant connection provided the major 'driving force' for the evolutionary success of the angiosperms, is only weakly supported by the data currently available. Nevertheless, Darwin's work on floral biology is still of considerable significance and discussed at length in current literature on the evolution of flowers (Pauw *et al.* 2008; Penet *et al.* 2008; Crepet & Niklas 2009).

CLIMBING PLANTS AND THE DISCOVERY OF ACTION POTENTIALS

In 1867, Charles Darwin published an article in Volume 9 of the *Journal of the Linnean Botanical Society* that described in detail the structure and unique behaviour of climbing plants, such as European white bryony (*Bryonia dioica*) (Fig. 4). The paper was later updated and supplemented so that in 1875 a book was published on the topic that was of general interest. In this monograph (Darwin 1867/1875), the author postulated that climbing must be viewed as an adaptation by means of which certain flowering plants are enabled to reach the light. Instead of being compelled to develop a stem of sufficient mechanical strength to stand upright, climbing species succeed in the 'struggle for life' by making use of other, lignified, plants as mechanical supports. A detailed analysis of the function of the tendrils in *Bryonia dioica*, which can reach a height of up to 10 m without the construction of a rigid, erect stem, led to the identification of a novel group of gaseous plant hormones such as the jasmonates and related compounds (Schaller & Weiler 2002). It is obvious that the descriptive work of Darwin (1867/1875), wherein the discovery that the habit of climbing is widely scattered throughout the plant kingdom was published, formed the basis for these elegant physiological–biochemical analyses (Engelberth *et al.* 1995; Schaller & Weiler 2002).

In 1875, a second monograph authored by Charles Darwin appeared in print, exploring the sensitivity of certain plant organs towards mechanical stimuli, notably touch. In his book *Phytologia*, Darwin's grandfather Erasmus had described the behaviour of a selection of European insectivorous plants, such as sundew (*Drosera rotundifolia*), a species he called the 'Queen of the marsh'. In a letter to the American botanist Asa Gray (1810–1888), Charles Darwin pointed out that '[*Drosera*] is a wonderful plant, or rather a most sagacious animal' (Ayres 2008). However, the study of another insectivorous plant, the Venus flytrap (*Dionea muscipula*) (Fig. 5A), which the British 'country-house



Dionaea muscipula

Fig. 5. Photograph of an adult Venus flytrap (*Dionaea muscipula*), a plant that responds to environmental stimuli similar to an animal (A). Experiment to demonstrate the occurrence of action potentials after a twofold mechanical stimulus of one or two trigger hairs, elicited by a fly (B). Fly trap open (I), change in membrane potential after stimulation (II), trap closed (response) (III). AP = action potential, Th = trigger hair (adapted from Hodick & Sievers 1988).

botanist' described as 'one of the most wonderful [plants] in the world' (Darwin 1875; p. 231), led to the discovery of action potentials in the vegetable kingdom (Brenner *et al.* 2006). After detailed studies of the rapid closure of the trap in response to touch, Darwin (1875) speculated that this insectivorous plant might be equipped with a kind of nervous system analogous to that of animals. Since, in his country house, he did not have the equipment to test this revolutionary idea, Darwin handed the 'Venus project' to the physiologist Johns Burdon-Sanderson (1828–1905), an eminent medical scientist who was working at the University College of London.

Burdon-Sanderson placed electrodes on the surface of the trap lobes and recorded that each time a trigger hair was touched, a wave of electrical activity similar to 'nerve impulses' or action potentials in animals is fired. His classic research paper (Burdon-Sanderson 1873) later led to the discovery of the sophisticated system of a localized receptor potential in the cells of the trigger hairs of the trap, which, if sufficiently large, fires a fast-moving electrical wave (Jacobson 1965; Williams and Pickard 1972). This electrical wave is a true action potential that rapidly spreads across the lobe and, if a second action potential is fired (the first one is 'remembered' by the cells), the trap shuts (Hodick and Sievers 1988; 1989; Forterre *et al.* 2005) (Fig. 5B). Hence, Charles Darwin's observations during the early 1870s, which he summarized in his monograph published in 1875, led to a series of important experimental studies that ultimately created the highly complex and sophisticated modern field of plant electrophysiology (Brenner *et al.* 2006). The convergent evolution of carnivory in a variety of angiosperms with reference to Darwin's seminal contributions has been summarized by Ellison & Gotelli (2009).

THE POWER OF MOVEMENTS AND DARWIN'S CONFLICT WITH JULIUS SACHS

One hundred and thirty years ago, Charles Darwin announced the completion of a major botanical work in the following words: 'Together with my son Francis, I am preparing a rather large volume on the general movements of Plants, and I think that we have made out a good many new points and views. I fear that our views will meet with a good deal of opposition in Germany' (from a letter to Victor Carus on 17 July 1879, see De Chadarevian 1996).

In the late 1870s, when *Movements and Habits of Climbing Plants* (Darwin 1867/1875) was out of print, a revised and extended version of this popular monograph was scheduled. Darwin's son Francis, who had assisted his father with editing, became the subordinate co-author of this last botanical book that was published under a new title, *The Power of Movements in Plants* (Darwin 1880). As documented by Ayres (2008), Francis' mark can be seen in this monograph as well as in all later editions of his father's books, since the younger Darwin was trained (1878/1879 and 1881) in the 'modern' laboratory of the eminent German plant physiologist Julius Sachs, where specialized equipment and exact measurements were the norm (Browne 2002). In addition, citations of the pertinent publications of others became part of new standards for scientific publication. Darwin's large new botanical monograph published one year before his death met these standards.

Why did Charles Darwin nevertheless fear strong opposition from Germany? One reason may have been Darwin's new theory on the origin of organ movements in higher plants, which states that endogenous revolving nutations, which the author documented at length and called 'circumnutations' (see Fig. 4A), may be the 'evolutionary precursor' of all forms of tropisms and nastic movements in the vegetable kingdom. This theory of circumnutation was neglected by most plant physiologists because there was, and still is, no solid empirical evidence for this postulated evolutionary origin of all plant movements (Hart 1990). In addition, Darwin (1880) may have feared the phenomenon of the 'invasion of turf', since his comprehensive monograph contained many novel observations on the

Fig. 6. The German botanist Julius Sachs (1832–1897) was one of the founders of the discipline of experimental plant physiology. Although Sachs acknowledged Charles Darwin's principle of evolution, he did not accept the physiological work of the Darwins, which he described as 'amateurish county-house experiments' (adapted from an unfinished painting by Maria Sachs, published in Gimmler *et al.* 2003).

physiology of higher plants, a subject that Julius Sachs (Fig. 6) described in detail in his outstanding papers and books. Although Sachs (1868, 1882) fully acknowledged Darwin's principle of descent with modification with respect to the plant kingdom (this phylogenetic view, an expression of Eduard Strasburger (1844–1912), opened novel and unifying perspectives), the leading plant physiologist of the nineteenth century regarded Darwin's last botanical work with contempt. For instance, in his *Vorlesungen über Pflanzen-Physiologie* he commented on the sophisticated 'root experiments' of the Darwins (1880) as follows: 'In such experiments with roots not only is great precaution necessary, but also the experience of years and extensive knowledge of vegetable physiology, to avoid falling into errors, as did Charles Darwin and his son Francis, who, on the basis of experiments which were unskilfully made and improperly explained, came to the conclusion, as wonderful as it was sensational, that the growing point of the root, like the brain of an animal, dominates the various movements in the root' (Sachs 1882, p. 843).

According to the detailed historical analyses of Junker (1989) and De Chadarevian (1996) it was Darwin's 'root tip hypothesis' that sparked Sachs's fierce opposition. Darwin (1880) documented that it is the tip of the root that is sensitive to gravity as well as other stimuli, and through the transmission of a signal causes the adjoining part of the radicle to bend towards the centre of the Earth. The 'Down House root experiments' were later repeated, with positive results, so that Wilhelm Pfeffer (1842–1920) fully acknowledged the physiological work of the Darwins. In his *Handbuch der Pflanzenphysiologie* (Pfeffer 1879/1881), which was called by Sachs a 'mere heap of undigested facts' (De Chadarevian 1996), the author extensively described and referred to Darwin's work, which later became a classic in the field of plant developmental physiology.

In addition, a critical evaluation of the 'Darwin–Sachs controversy' published by a leading historian of the botanical sciences should be quoted here: 'The fact was, that Sachs was a bit shocked by what seemed to him the amateurish methods of the Darwins. He was used to quite elaborate apparatus like the clinostat, and precise physical and chemical methods, and he had some of the professional's distrust of county-house experiments' (Morton 1981, p. 444). This benign judgement is in contrast to the harsh words of Sachs (1882) quoted above, but Morton (1981) may be correct in pointing out that Sachs, the German founder of experimental plant physiology (Gimmler 1984; Gimmler *et al.* 2003), may have been unable to accept the non-institutionalized, relaxed way of carrying out experiments by the famous British naturalist and his gifted son Francis. Based on their modest approach philosophy, the Darwins made all their outstanding discoveries (Browne 2002). Finally, it should be mentioned that Darwin's 'root cap hypothesis', which postulates that the tip of the radicle reacts to a variety of stimuli such as touch, gravity and light, has been thoroughly corroborated by subsequent experiments (Barlow 2002; Edelmann & Roth 2006).

It has long been known that most organisms on Earth are exposed to ultraviolet (UV)-B irradiation, which is an integral part of natural sunlight. Over three decades ago, the photoreceptor phytochrome was shown to be present in the root cap of *Avena sativa* (Pratt & Coleman 1974) and the corresponding organ of several other grass seedlings, including maize (Pratt & Coleman 1974). Red light treatment of maize roots induces increased positive gravitropic curvature, a response reversible by far-red light (Mandoli *et al.* 1984). More recently, Tong *et al.* (2008) reported a UV-B-sensing mechanism in the roots of *Arabidopsis* seedlings that may be involved in the regulation of organ development. This finding goes back to the observation that the radicle is a light-sensitive organ in the juvenile plant (Darwin 1880). A mutation in the *RUS1* gene (function unknown) leads to exquisite sensitivity to UV-B irradiation, with roots killed by the amount of UV-B present in ordinary fluorescent lamps. Although the exact location of the UV-B photoreceptor is unknown, *RUS1* itself is expressed in the root tip just below the root apex and it is reasonable to expect that the photoreceptor is similarly located (Tong *et al.* 2008).

GRASS COLEOPTILES, LIGHT PERCEPTION AND PHOTOBIOLOGY

Even more important than the 'root cap studies' outlined above was Darwin's introduction of the coleoptile of grass seedlings (Fig. 7) as research material. The coleoptile later became one of the standard objects of plant physiological investigations. It is fair to say that the establishment of this system is equivalent to Thomas H. Morgan's (1866–1945) introduction of the fruit fly *Drosophila* into the emerging field of animal genetics.

The Darwins analysed the phototropic response of the coleoptile of dark-grown seedlings of two species of Gramineae (canary grass, *Phalaris canariensis*, and oats, *Avena sativa*) and documented their results in detail (Fig. 7). They either covered coleoptile tips with opaque caps or buried the seedlings in fine sand, so that just the tips were exposed, and then illuminated them from one side. Those with the tips exposed developed curvature in the portion of the coleoptile that was buried, causing the coleoptile to make a small furrow in the sand. However, when the tips were capped, little curvature developed. Thus the coleoptile tip perceived the light stimulus and transmitted the information to lower growing regions. The latter did not need to be irradiated for curvature to occur. Based on this experimental analysis, the authors concluded that, 'These facts … all indicate that light acts on them (*i.e.* the coleoptiles of *Phalaris*) as a stimulus, … and not in a direct manner on the cells or cell walls, which by their contraction or expansion causes their curvature' (Darwin 1880, p. 461). Although it is well known that these experiments on phototropism led to the discovery of auxin (Went 1928; Went & Thimann 1937; Kutschera 2004), it is little appreciated that the Darwins (1880) introduced three additional theoretical concepts: the light stimulus hypothesis, which implicates the presence of photoreceptors in plant cells (Briggs & Spudich 2005); the notion that a signal induced in the coleoptile tip would be transmitted to lower regions of the coleoptile to induce the differential growth leading to phototropic curvature; and the notion that cell wall expansion is a major cause of plant organ growth (Kutschera 2001, 2004, 2006, 2008; Schopfer 2006).

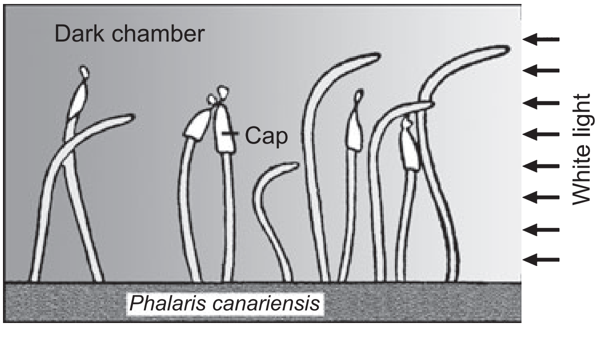


Fig. 7. Darwin's light stimulus experiment: Phototropism in dark-grown grass (*Phalaris canariensis*) seedlings irradiated from one side with continuous white light. Some seedlings were covered with tinfoil caps; these individuals failed to respond to unilateral light, indicating that the tip represents the light-sensitive region of the coleoptile.

Two major research areas emerged from the seminal studies of the Darwins on growth and phototropism of dark-grown (etiolated) grass coleoptiles: (i) analysis of the mechanism of organ elongation with reference to the growth hormone auxin, which is produced in the tip of the organ and actively transported basipetally, where it causes cell enlargement; and (ii) the search for photoreceptors that are localized in the auxin-secreting uppermost cells of this protective organ sheath. Biophysical and cytological studies on coleoptiles of maize, oats and rye have shown that auxin causes organ elongation *via* a loosening process in the sturdy outer epidermal wall, which represents the growth-limiting structure of this ephemeral organ (Kutschera 2001, 2004, 2008; Schopfer 2006; Kutschera & Niklas 2007). A detailed description of this hormone-mediated wall weakening reaction, inclusive of a discussion of the postulated biochemical events, is beyond the scope of this historical essay.

Since the Darwins were the first to demonstrate that phototropism could be caused by light perceived by one part of the plant leading to transmission of the signal to another part (which led to the discovery of auxin, see above), we focus on the search for a photoreceptor. Although the investigator who first noted that it was blue light that induced phototropic curvature preceded the Darwins by several decades, long before the 1880 publication of *The Power of Movements in Plants* (see Briggs 2006; Whippo & Hangarter 2006), it was over 100 years later that the first blue light receptor was finally characterized (Ahmad & Cashmore 1993). These novel sensor pigments were ultimately designated cryptochromes. Ironically, cryptochromes turned out not to be the photoreceptor for phototropism and another 6 years passed before identification of the photoreceptors mediating phototropism in stems and coleoptiles of etiolated seedlings (Huala *et al.* 1997; Christie *et al.* 1998). The two members of this family in the model plant *Arabidopsis thaliana* were subsequently designated phototropins. The Darwins were clearly aware of the earlier work (although they did not cite it) as they used a red safelight to set up plants for their experiments. They wrote, '… and they were first illuminated by light from a paraffin lamp passing through a solution of bichromate of potassium, which does not induce heliotropism' (the earlier term for phototropism) (Darwin 1880, p. 462).

As early as 1936, Wald and du Buy (1936) first proposed that the light-absorbing portion of the photoreceptor (the chromophore) was a carotenoid. Thirteen years later, Arthur Galston's laboratory proposed that the chromophore must be a flavin, on the basis that a flavoprotein could mediate light-activated destruction of auxin (Galston 1949; Galston & Hand 1949). However, Went (1928) had previously presented evidence that unilateral light sufficient to induce curvature of oat coleoptiles caused an increase in the amount of auxin flowing down the shaded side and a decrease on the illuminated side, and suggested that the mechanism involved light-induced lateral transport of auxin away from the light source. Briggs *et al.* (1957) then demonstrated that no auxin destruction occurred as a consequence of phototropic induction and questioned the flavin hypothesis. In a detailed study that was based on previous publications (Briggs *et al.* 1957; Briggs 1960, 1963), Iino & Briggs (1984) analysed blue light-mediated organ bending in etiolated maize coleoptiles (Fig. 8). Consistent with the reported lateral redistribution of auxin, they found a decrease in growth of the illuminated side of the coleoptile, a compensatory increase in growth of the shaded side, and no net overall change in the rate of organ elongation.

Although these experiments eliminated auxin destruction as a possible mechanism of phototropism, they did nothing to help identify the chromophore. Action spectroscopy was no help because the action spectra for phototropism had characteristics both of the absorption spectrum of carotenoids and that of flavoproteins (Curry 1957). The flavin *versus* carotenoid controversy raged in the literature for an additional 50 years before it was resolved in favour of flavins with the characterization of the phototropins (Christie *et al.* 1998; see Briggs 2006; Whippo & Hangarter 2006). All of this work can be traced back to the Darwins' original observations on the phototropism of coleoptiles (Fig. 7).

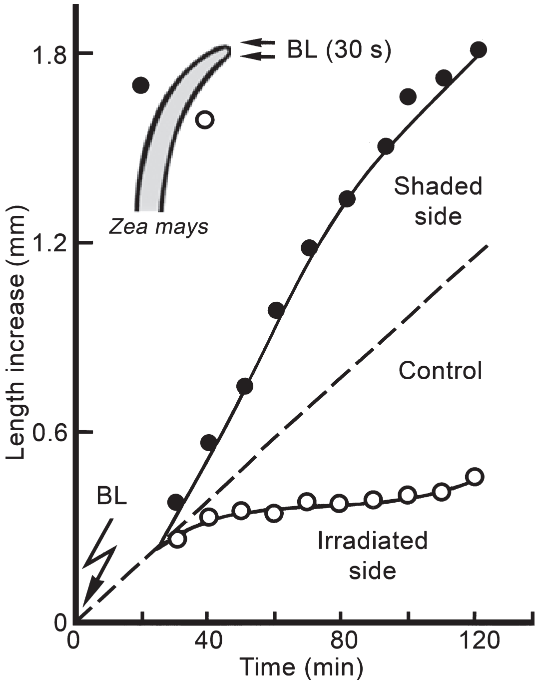


Fig. 8. Experimental analysis of phototropism in maize (*Zea mays*) coleoptiles. Time-course changes of elongation increments on irradiated and shaded sides of the intact organ. After these two sides of the coleoptiles were marked, the tips were unilaterally irradiated for 30 s with blue light (BL, fluence = 5.0 $\mu mol \cdot m^{-2}$); thereafter, the seedlings were placed under dim red light and growth of the illuminated and shaded sides was monitored over the subsequent 2 h (adapted from Iino & Briggs 1984).

CONCLUSIONS

The establishment of *plant biology* 80 years ago

The facts summarized above document that Charles Darwin, who maintained contact with his peers in Europe and the United States of America, was not only an evolutionary biologist with a focus on animals, but also an outstanding botanist and plant physiologist. Since his books are still quoted in the most recent primary literature (see, for instance, Pauw *et al.* 2008; Penet *et al.* 2008), we have to conclude that most of the seminal concepts of this nineteenth century naturalist on a variety of botanical topics are still alive today. It should be mentioned that, after his father's death (1882), Francis Darwin moved to Cambridge, where he became university lecturer in botany and started to teach plant physiology. Based on his experience as an academic teacher, he published, with a co-author, the first British textbook that was exclusively devoted to the physiology of higher plants (Darwin & Acton 1894) and later became a leading scientist in this field (Loftfield 1921; Briggs 2006). Hence, Charles Darwin established, *via* his son Francis, the discipline of plant physiology in the universities of his home country.

It is well known that the term *Pflanzen-Physiologie* (plant physiology), introduced and popularized by Sachs (1882) and others, has been replaced in recent years by *Plant Biology*. For instance, the 'American Society of Plant Physiologists' (ASPP), founded in 1924, was re-named 'AS of Plant Biologists' (ASPB) in 2001; likewise, the 'Annual Review of Plant Physiology', founded in 1950, since 2002 is published under the new title 'Annual Review of Plant Biology' *etc.* What are the differences between the terms 'botany, plant physiology, and plant biology'? The German word *Botanik* means *Pflanzenkunde*, with a focus on morphology, anatomy and systematics of members of the kingdom Plantae. As a result of the works of Sachs (1868, 1882), Pfeffer (1879/1881) and Darwin (1880), the novel discipline of *Experimental Plant Physiology* emerged, which aimed to elucidate the functions of model plants raised and analysed in the laboratory.

To the best of our knowledge, the term *Plant Biology* was introduced in its modern sense by the Carnegie Institution of Washington (re-named Carnegie Institution for Science in 2007), a non-profit organisation founded in 1902 by Andrew Carnegie (1835–1919). In 1903, the Institution's 'Desert Laboratory' became the headquarters of

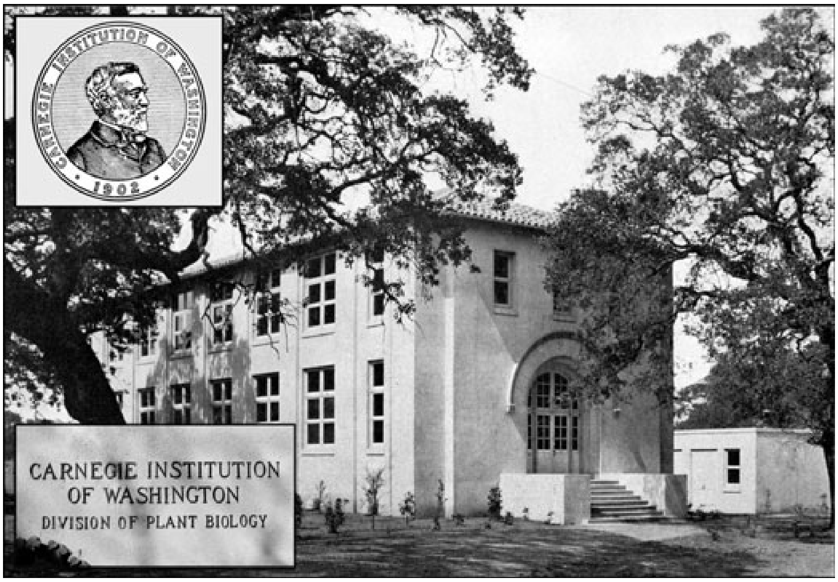


Fig. 9. Historical picture of the new central laboratory of the Division of Plant Biology (15 July 1929) at the Carnegie Institution of Washington on the Stanford University campus (California, USA) and photograph of the name sign of this building taken on 10 March 2009 (lower inset). In addition, the original logo of the institution is included, depicting Andrew Carnegie (1835–1919) (upper inset). The term *Plant Biology* was coined 80 years ago with the establishment of this division (now department) of the Carnegie Institution.

the Department of Botanical Research (established in 1905). The name was changed to Laboratory for Plant Physiology in 1923, and re-organised in 1928 as the Division of Plant Biology. As described in detail by Spoehr (1929), the headquarters for the new division on the campus of Stanford University (California, USA) was ready for occupation on 15 July 1929 (Fig. 9). Hence, *Plant Biology*, as an independent branch of the natural sciences, was established 80 years ago. What was the aim of the new division (later re-named 'department') within the Carnegie Institution? As the first acting chairman H.M. Hall pointed out, the 'activities of the Division of Plant Biology center around two basic biologic problems, one concerned with energy transformation in connection with living protoplasm, the other having to do with origins, modifications, and development of life or, in short, with organic evolution' (Hall 1931, p. 239). Two decades later, Carnegie Director S.C. French provided an even more precise definition: 'The means by which plants manufacture organic food and the evolutionary mechanisms by which they have reached their great variation in form, size, and distribution have, as in past years, been under investigation by the Division [of Plant Biology]' (French 1950, p. 83). Hence, the two major topics of *Plant Biology* centre on the physiology, biochemistry/molecular biology and evolutionary relationships of pigmented, photosynthetic organisms (cyanobacteria, algae and plants). These areas of research are largely identical with the main interests of Charles Darwin, who was an evolutionary biologist and physiologist with a strong focus on the secret life of plants.

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