Darwin as a botanist

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Charles Darwin on his voyage aboard H. M. S. Beagle contracted a mysterious illness that persisted throughout his life. Despite being ill, he continued his writings. He is remembered as the scientist who put-forth the theory that species are changing. A species evolves by the accumulation and preservation of successive slight favourable variations, now known as mutations. In his quest to strengthen his theory on the common origin of all life, and evolution by natural selection, he increasingly turned to plants and carried out experiments at his home-cum-laboratory, focusing on phenomena commonly associated with animals namely, movement. In plant roots, seedlings and climbing plants, he described nyctitropism, geotropism, phototropism and circumnutation. Darwin described the sleep movements in plants in which the petiole hangs down and the leaflets press together in the evening.

The year 2009 is the bicentenary of Charles Darwin (1809–1882), the author of the *Origin of Species*. In this book, he expounded evolution of species based on favourable variations[1]. His major works are available, either through reprinted editions or on the Internet[2,3]. Some journals have published tributes to Darwin, and, surely, more will be written on him – either commissioned by publishers and editors, or voluntarily. This article is in the latter category, prompted by certain postmortem notings that blot Darwin, and in some ways, make his work appear of dubious originality and technical quality. For example, in introduction to the 1964 facsimile edition titled *On the Origin of Species*, the evolutionary biologist Ernst Mayr (author of *Animal Species and Evolution*) turned himself into a critique. He commented: 'Darwin has been accused, and up to a point quite rightly, of not giving sufficient credit to his precursors. The *Origin* has no bibliography, there are no footnotes with references to literature; indeed Darwin did not proceed like the classical scholar'. Mayr adds, 'Nothing in Darwin's character would support the accusation of plagiarism or of deliberate attempt to conceal his intellectual debt to various precursors. Yet, there is little doubt that Darwin was guilty of a good deal of naïveté and a lack of generosity'. Wilkins[4] has titled a recent article 'Not saint Darwin', and Nanjundiah[5] has remarked: 'For all his fame as an explorer and student of natural history, his technical credentials as a botanist or zoologist were weak'. All these comments require close scrutiny. The allegation of plagiarism does not hold up to scrutiny. Take for example Chapter V (Laws of Variation) in *On the Origin*[1]. At least 15 persons are mentioned who provided him bits of data on variations they observed in domesticated pigeons, cats, dogs, cows or horses. Darwin obviously knew of Linnaeus' work. Darwin must have known that the richest type of vegetation in number of 'species' is found in the tropics. He had attended Henslow's lectures (1829–31) at Cambridge[6]. Indeed, Henslow was Darwin's mentor[6]; he taught him how to make herbarium specimens – a basic tool in botany those days.

I believe that it was Darwin who was on the lookout for an opportunity of seeing the richest types of vegetation first-hand before he set on the *Beagle* voyage, not the other way round; that is, the captain of the *Beagle* looking for a naturalist to go on voyage with him. Darwin went on to collect plants, carefully labelled by island and by date. I suppose that observing the shapes of the beaks in the finches in the Galapagos Islands only led to formal formulation of a theory that was already brewing in his mind, and after he had carefully examined the herbarium specimens which he had brought home.

The experimental work Darwin did with plants had led me to assume that he was blessed with good health. How wrong I was! I discovered that while on voyage, Darwin became afflicted with a mysterious disease[7,8]. The disease persisted for more than 40 years and was a cause of considerable suffering for him. Only his wife Emma knew 'the full amount of suffering he endured'. In a letter to his botanist friend J. D. Hooker (Royal Botanic Gardens in Kew, England) in 1845, Darwin said[9]: 'You are very kind in your inquiries about my health; I have nothing to say about it, being always the same, some days better and some days worse. I believe I have not had one whole day, or rather night, without my stomach having been greatly disordered, during the last three years, and most days great prostration of strength: thank you for your kindness; many of my friends, I believe, think me a hypochondriac'. The nature of Darwin's illness has been a subject of speculation and it has been suggested that this can be revealed even today by analysis of his DNA. I cite the above comments not out of sympathy, but increased appreciation of Darwin's work.

Why Darwin took to study of plants?

Subsequent to his voyage and spending 20 years or so before publishing *The Origin* in which the theory of speciation was based, primarily using examples drawn from the animal kingdom, why did Darwin take up study of plants (botany)?

While a student at Cambridge, in his botany classes, Darwin must have studied the manifold types of plants named and described by Linnaeus. Darwin needed to popularize the idea that despite their dissimilarities, animals and plants shared the same progenitor, i.e. a common descent. Hence, he set about finding animal-like features in plants. Not surprisingly, one of the first things that occupied him was to find common 'behavioural' features in plants and animals. The capture and digestion of living animal matter by insectivorous plants is the most striking manifestation of a animal behaviour (reaction to an event or stimulus). Among the carnivorous plants, Darwin was particularly fascinated by the speed and sensitivity of snap-traps in

Dionaea and *Aldrovanda*. He sought to integrate the observations by focusing on its sensory aspects. He was impressed with the remarkable sensitivity of the leaf marginal hairs responding to touch stimulus, and the secretion of digestive enzymes similar to animal glands. He wrote, 'During the summer of 1860, I was surprised by finding how large a number of insects were caught by the leaves of the common sun-dew (*Drosera rotundifolia*) on a heath in Sussex. I had heard that insects were thus caught, but knew nothing further on the subject'. Darwin studied yet another typically animal-like phenomenon: plant-root foraging and leaf movement. I suppose that it was his indifferent health that led him to publish his rather large plant work separately from *The Origin*.

With geologic record being imperfect (chapter IX of *The Origin*), and stimulated by the accounts from his botanists friends, notably Asa Gray of Harvard University and J. D. Hooker, who had been collecting and describing plants from distant areas (chapter XI in *The Origin*), Darwin became conscious of certain limitations in his theory which was based primarily on morphological characters requiring palaeontological evidence of intermediate links. He was faced with difficulty in making distinction between species and varieties. His research on plants focused on how to distinguish species from varieties (produced under domestication) and this led him to several experiments on hybridization between species/varieties of plants. He needed to explain evolution and distribution of rooted (hence, immobile) plants from a progenitor by lineal descent involving slight variation. Another question that he needed to explain was how certain plants migrated to distant quarters crossing impassable barriers, becoming naturalized there. Thus, he needed to understand the geographical distribution of plants and their means of dispersal to vast distances (chapters XI and XII), the survivability of seeds after exposure to saline oceanic waters or after ingestion by birds and their survival in droppings, and how the herbaceous forms developed into trees, diversified and spread. Darwin carried out experiments on seeds, gathered data on transportation of seeds by herons and other birds, the morphological modifications in plant life along the shores of continents, and in oceanic islands and mainland and study their peculiarities. In other words, Darwin sought a grand unified view of the extant plant species. Although Darwin published *The Origin* in 1859, he was still seeking answers until his death in 1892. Remarkably, even as he lay with illness, Darwin continued observations and experiments on plants, often using potted plants near his bedside.

Sleep movements in leaves

Darwin accepted that plants and animals may change to any extent in form and size, yet they may exhibit connectivity in essential physiological functions. He recognized that movement is the hallmark of animals. Linnaeus, Pfeffer and a few others before him had already noted that several genera of plants have leaves that extend almost horizontally during the day but hang down vertically at night. Darwin was fascinated with this behaviour, known as sleeping movement (Figure 1) or '*somnus plantarum*' by Linnaeus. Unmindful of his own sleep requirement, Darwin recorded the positions of leaves in 100 genera belonging to 28 families of plants. By fixing a fine glass filament, the size of a horse hair, to the midrib of leaves and recording the position of the filament on a graduated arc at intervals of time as the leaves moved, Darwin was able to measure the precise time period of sleep as the leaves folded and unfolded. He noted that sleeping behaviour – with respect to directionality of movement and positioning – is particularly common in the genera of plants where the leaves have a pulvinus, as for example some plants belonging to the legume family. He wrote[2] (p. 395) 'The nyctitropic movements of leaves, leaflets, and petioles are effected in two different ways: firstly, by alternately increased growth on their opposite sides, preceded by increased turgescence of the cells; and, by means of a pulvinus or aggregate of small cells, generally destitute of chlorophyll, which become alternately more turgescent on nearly opposite sides; and this turgescence is not followed by growth except during the early stage of the plant'. Darwin[2] wrote that *Averrhoa bilimbi* (Figure 2), is a wonderful spectacle to behold on a warm sunny day the leaflets one after the other sinking rapidly downwards, and again ascend slowly (Figure 3). He pointed out that leaves of *Passiflora gracilis* 'do not sleep properly'.

Figure 1. Phenomenon of sleep in plants. Darwin copied these figures of *Cassia corymbosa* from photographs. ***a***, during day; ***b***, same plant at night (from ref. 1).

Presumably, it was his observations of animal-like sleeping activity in the plants that gave him the idea that plants and animals have a common origin (evolved from the same progenitor). As mentioned above, Darwin carried out hybridization experiments (crossing) to demonstrate sterility of crosses between pure species and a method of distinguishing a species from a variety. This method of recognizing species called 'biologic species recognition (BSR)' is still followed, Darwin needed to turn to botany to fill in gaps in his theory of evolution. Some of his interesting observations are given below.

Climbers

Nearly one-fifth of all plant types comprise climbing plants. In the preface to an

Figure 2. Asleep leaf of *Averrhoa bilimbi* with leaflets pressed together (from ref. 1).

essay on climbing plants[2], Darwin wrote, 'I was led to this subject by an interesting, but too short, paper by Professor Asa Gray (1858) on the movements of the tendrils of some Cucurbitaceous plants. He sent me seeds, and on raising some plants I was so much fascinated and perplexed by the revolving movements of the tendrils and stems . . . that I procured various other kinds of Climbing Plants, and studied the whole subject', obviously with the aim of determining whether the changes are adaptive using a comparative geographical analysis. He examined the adaptive relevance of plant morphological structures, focusing on the movement of tendrils (Figure 4) – an organ highly sensitive to touch. Some of the plants he used for experiments had to be shipped from other countries, including India (Calcutta) (http://www.gutenberg.org/dirs/etext04/insec10.txt).

Darwin noted that the stem tips of all climbing plants revolve around the support (circumnutate) (see later). Such movement will allow it to contact a nearby physical support for ascending to capture light. Further, Darwin noted that the vast majority of climbers twine around the support anticlockwise for gaining ascent. In a recent study, Edwards *et al.*[10] confirmed anticlockwise twining at 17 sites in nine countries in both the northern and southern hemisphere. The adaptive significance of direction of coiling is not understood.

Darwin noted that, curiously, a twiner will not attempt to revolve around a support if the support stem is more than 4.4 inches in diameter! He said[2], 'By what means certain twining plants are adapted to ascend only thin stems, whilst others can twine round thicker ones, I do not know'. He recorded the rate of revolution in different twining plants with different support plants. He found that stem climbers revolve with an average rate of 2 h 31 min, 'but the weather was cold'. Darwin noted that after the tip of the tendril has contacted a support and fastened itself by coiling around it, the whole tendril contracts. Darwin likened twisting of climbing stems to stiffness gained by a rope by twisting.

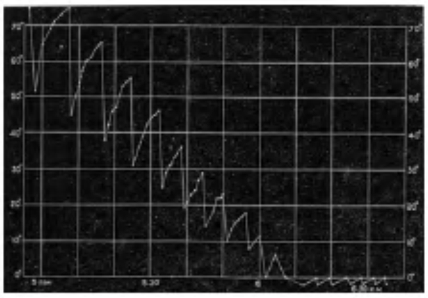

Figure 3. Sleep movement in leaflets of *A. bilimbi*. In Darwin's words, 'At 4.55 p.m. the leaflet formed an angle of 85° with the vertical . . . Shortly after 6 p.m. it hung vertically down, and had assumed its nocturnal position. Between 6.10 and 6.35 p.m. it performed a number of minute oscillations of about 2° occupying periods of 4 or 5 min. It is manifest that each oscillation consists of gradual rise, followed by sudden fall. Each time the leaflet fell, it approached nearer to the nocturnal position than it did on the previous fall. The amplitude of the oscillation diminished, while the periods of oscillation became shorter' (from ref. 1).

Figure 4. *Bryonia*. A tendril climber showing reversal in the direction of coiling from anticlockwise to clockwise (from ref. 2).

Root climbers

According to Darwin[7], the plants which do not revolve around a support are all root climbers. *Ficus repens* is a root climber. He observed that its roots produced a 'viscid fluid', obviously for attaching to a support. He conducted a simple experiment, spreading a drop of the fluid on a glass plate with some grains of sand. He left the glass exposed in a drawer during hot and dry weather and found that after 128 days the fluid still surrounded each grain! In contrast, when he placed other rootlets in direct contact with glass, they firmly cemented to the glass after 23 days. Darwin concluded (p. 106): '. . . the rootlets first secrete a slightly viscid fluid, subsequently absorb the watery part, and ultimately leave a cement'. In other work with stem climbers, Darwin found that not only a climber revolves around a support, its stem rotates (twists) around its own axis. This, then is the explanation for the helical twisting patterns of bark in some mature trees, and a special reason for us to recall Darwin's contributions which had remained unknown to us. Recently we observed pronounced twists, which we called Archimedes screw, in a liana (a woody climber) growing in the campus of the Indian Institute of Science[11]. From Darwin's writing, we can now comment on how such patterning may have arisen. The juvenile stem helically twisted on its own axis during its extension growth, unseen by us. This liana is unique in showing characteristics both of a free-standing tree and a climber. Had Darwin encountered such a liana, he would have been gladdened, as this exemplifies a transitional form between a tree and a climber. During his voyage Darwin was searching for geological and living specimens of intermediate forms that would support his theory of transmutation of species.

Circumnutation

Observing seedlings of a variety of plants from morning to dusk, Darwin[3] noted that the apex of root or shoot revolve spirally or elliptically. He explained the significance of such movement, termed circumnutation (Figure 5). A circumnutating radical can penetrate into soil through any crack and come in contact with a water film and dissolved nutrients around soil particles, whereas a

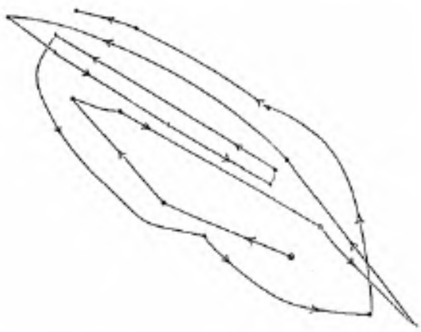

Figure 5. Conjoint circumnutation of the hypocotyl and cotyledons in a seedling of *Brassica oleracea* traced from 10.45 a.m. to 8.45 p.m. The plants were kept near a window. Darwin attached an extremely thin glass filament, to one of the cotyledons, behind which a bit of card with a black dot was fixed. The bead and the dot on the card were viewed through a vertical glass-plate, and when one exactly covered the other, a dot was made on the glass-plate with a sharply pointed stick dipped in India-ink. The bead moved seven times from side to side, and thus described 3 1/2 ellipses in 10¾ h; each being completed on an average in 3 h 4 min (from ref. 3).

continuously circumnutating hypocotyl will displace soil particles for the seedling to emerge into air. He concluded that circumnutation is of 'paramount importance in the life of every plant'. For, it would allow leaves to adjust their position under conditions of changing light conditions and minimize overlaps among leaves for maximal interception of sunlight. Darwin studied effect of age and of after-effects of light on circumnutation and discovered transmitted effects of light, referring to the work of Pfeffer and others on this subject. He says, 'All observers apparently believe that light acts directly on the part which bends, but we have seen that this is not the case'. He found no correlation between the amount of light the plant receives and degree of bending. In case of the twining species, the circumnutating movements were increased in amplitude and rendered more circular. Rather than give a teleological reasoning (that is, the stem revolves in order to find a physical support for ascending), Darwin wrote that the 'cause of this and most other variations is unknown'.

Tropic response of seedlings

Those of us who received training in plant physiology would perhaps regard Darwin's discovery of complimentary phenomenon, i.e. the curvature of coleoptiles of germinating seeds of the Gramineae (Poaceae) family towards a source of unilateral illumination as one of his most useful contributions. For this reason this may be described in more detail, at the cost of omitting some others, such as his studies of heterostyly and pollination precision in orchids, and other plants in relation to floral symmetry[12]. For want of space, I choose to say just a few words on *Drosera* (sundews), a genus comprising insectivorous plants that grows in bogs, marshes, well-drained woodlands and heaths where the soil is extremely poor in nutrients. Many are rosette plants, securing flies with sticky leaf hairs. Astonishingly, Darwin said:

'I care more for *Drosera* than the origin of species . . . it is a wonderful plant, or rather a most sagacious animal. I will stick up for *Drosera* to the day of my death.'

– Letter from Charles Darwin to Asa Gray[13].

Darwin took up studies on pollination mechanisms in flowers. He states the reason for this in a 1862 letter to Joseph Hooker: 'I have found the study of Orchids eminently useful in showing me how nearly all parts of the flower are co-adapted for fertilisation by insects, and therefore the results of natural selection, – even the most trifling details of structure'. Studying floral adaptations to pollination by insects, Darwin came to the conclusion that phenotypic selection is responsible for organic diversity. For the modern students of biology, what this means is that selection occurs at the level of final form (phenotype), not at the level of genes (genotype).

Darwin knew, as everybody, that light is essential and every plant as far as possible positions its leaves for exposure to sun. What hitherto had not been, but what he did was to investigate this phenomenon. When the grass seed germinates, the primary leaf pierces the coleoptile, a hollow, cylindrical sheath-like cotyledon that surrounds it. Darwin's son Francis put layers of muslin blinds on window of study room at home, thereby converting it into a dark room where they had seedlings, including that of *Avena sativa* (a cereal grain belonging to the wheat family of plants) growing on moist sand. They admitted light laterally through one window into the room. Darwin observed that the tip of the coleoptile curved towards light. The tip was necessary; for if it was covered by a small tube made of tin foil (an opaque cover) bending did not occur even though the rest of the coleoptile was illuminated from one side, whereas uncovered coleoptiles (control) did. Darwin concluded for a growing green plant, light is detected at the tip. Further, the response (bending) was carried out at another (the region of elongation). This implied that the tip was, in some way, communicating with the cells of the region of elongation. Darwin inferred that the stimulus (light) is perceived at one location (the tip) whereas the response (bending) is carried out at another (the region of elongation). Darwin may therefore, be given the credit for the initial discovery of a plant hormone, later called auxin.

Following Darwin's observation, subsequent workers showed that the oat (*Avena*) shoot tip is the site of production of indole-3-acetic acid (IAA). This hormone diffuses below from the laterally illuminated tip, and is displaced on the dark side causing cells on the dark side to elongate more, resulting in bending ('movement' in Darwin's terminology) of coleoptile towards light. Darwin's observation led to the development of *Avena* curvature test as a bioassay for auxin – which students are taught in botany practical classes.

Concluding remarks

Recall, Darwin had become affected with irreversible illness. How did he manage field observations? On p. 19, Darwin[2] tells 'My sons visited a hop-field for me, and reported. . .'. Sir Francis 'Frank' Darwin, FRS, who followed his father into botany, was the third son and seventh child of Charles Darwin and his wife Emma. Indeed, for the technology that existed in his time, one is surprised at the quality of Darwin's experiments. He carried out extensive correspondence with plant scientists and their comments can be enjoyably read at http://darwin-online.org.uk/content/frameset?itemID=F1452.3&viewtype=text&pageseq=301[14].

Analyzing his own observations, Darwin wrote[3] (p. 573): 'We believe that there is no structure in plants more wonderful, as far as functions are concerned, than the tip of the radicle . . . If the tip perceives the air to be moister on one side than on the other, it likewise transmits an influence to the upper adjoining part, which bends towards the source of moisture. When the tip is excited by light. . . the adjoining part bends from the light; but when excited by gravitation the same part bends towards the centre of gravity . . . It is hardly an exaggeration to say that the tip of the radicle thus endowed, and having the power of directing movements of the adjoining parts, acts like the brain of one of the lower animals; the brain being seated within the anterior end of the body, receiving impressions from the sense-organs, and directing the several movements'. This brief overview recognizes that some of the most fundamental and long-standing questions about evolution of plant adaptation remain unsolved and recognize Darwin's continued legacy. Darwin's researches and writings on plants bestow on him the mantle of one of the greatest botanists of all times.

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