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INVITED HISTORICAL REVIEW

Darwin and seeds

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Abstract

In 2009, the bicentenary of Charles Darwin's birth on 12 February 1809 is being celebrated. For seed scientists, celebrations of the contributions of the great biologist should also mark his involvement with seeds. Darwin was interested in seeds, particularly in their role in dispersal and distribution of plant species over long distances. His studies of seeds, laid down in several books and articles, contributed to the development of his ideas on evolution and the distribution of living organisms on the planet. In this review, the place of seeds in Darwin's work is surveyed and it is shown how he referred to them to support and illustrate some of his most important ideas.

Keywords: Darwin, seeds

Darwin's theory of evolution by natural selection, first presented in July 1858 in a joint paper with Alfred Russel Wallace in London at The Linnean Society (published in August 1858) and then in 1859 in *On the origin of species*, dominates our perceptions of his work. We tend not to think of Darwin primarily as a plant biologist (indeed, he makes it clear in several letters, for example to the botanists Joseph Hooker at The Royal Botanic Gardens, Kew and Asa Gray at Harvard, that even he did not think of himself as a botanist), but very much of his research and writings were actually concerned with plants. In *On the origin of species* he uses numerous examples from the plant world to illustrate fundamental concepts concerning natural selection and, of his books, six deal specifically with plants, covering orchids, climbing plants, insectivorous plants, forms of flowers, cross- and self-fertilization and movement (the latter leading to the discovery of plant hormones), and two have major botanical content – works on plant and animal domestication and on vegetable mould. In most of these, as well as in *On the origin of species* itself, reference is made to several aspects of seed biology. Moreover, Darwin carried out a series of experiments on seeds, published in several papers and articles, which contributed to the development of his ideas on evolution and the distribution of living organisms on the planet. Most of these experiments were carried out in his garden or glasshouse, often with the assistance of his gardener.

Darwin's son, Francis, in his reminiscences about his father (Darwin, F., 1887a,b) describes the latter's daily activity:

> My father's midday walk generally began by a call at the greenhouse, where he looked at any germinating seeds or experimental plants which required a casual examination, but he hardly ever did any serious observing at this time. (Darwin, F., 1887a, p. 114)

Later in his account, Francis remarks on his father's work room:

> At his right hand were shelves, with a number of other odds and ends, glasses, saucers, tin biscuit boxes for germinating seeds … (Darwin, F., 1887a, p. 146)

And in this room Darwin seemed to have enjoyed his work with seeds:

> I can recall his appearance as he counted seeds under the simple microscope with an alertness not usually characterising such mechanical work as counting. I think he personified each seed as a small demon trying to elude him by getting into the wrong heap, or jumping away altogether; and this gave to the work the excitement of a game. (Darwin, F., 1887a, p. 147)

Darwin himself was a very keen gardener and a loyal reader of *The Gardeners' Chronicle and Agricultural Gazette* with which he frequently corresponded, often on various matters to do with seeds. He was also a prolific letter writer – in his day, letters were the means by which scientists established and maintained contact with each other – and among the several thousands

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that he sent and received were very many that exchanged information or opinions on seeds. No doubt Darwin's interest in seeds came from his awareness of their key importance in the plant life cycle and in plant evolution:

> So with plants, how remarkable it is that the organs of vegetation, on which their whole life depends, are of little signification [*sic*], excepting in the first main divisions; whereas the organs of reproduction, with their product the seed, are of paramount importance! (Darwin, C.R., 1859, p. 414)

In this article, I will survey the place of seeds in Darwin's studies and show how he referred to them to support and illustrate some of his most important ideas. Darwin's work in biology was very extensive and diverse and he frequently alluded to seeds, so to do full justice to 'Darwin and seeds' a monograph might be deserved rather than a relatively brief piece such as this. But all those aspects of Darwin's seed biology that seem to merit particular attention will be discussed – with liberal quotations from Darwin's writings – in the hope that the reader will appreciate the extent to which seeds featured in the great man's deliberations.

To show the prominence that Darwin afforded to seeds, it is appropriate first to turn to the 1858 Darwin/Wallace paper communicated to a meeting of The Linnean Society by Darwin's colleagues, Charles Lyell and Joseph D. Hooker, later to be published in the society's journal (Darwin and Wallace, 1858). This revealed Darwin as a profoundly important biological thinker and was the forerunner to the work which, just a year later, established his genius, *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. In his part of the presentation to the society Darwin wrote:

> Reflect on the enormous multiplying power inherent and annually in action in all animals; reflect on the countless seeds scattered by a hundred ingenious contrivances, year after year, over the whole face of the land; and yet we have every reason to suppose that the average percentage of each of the inhabitants of a country usually remains constant.

And then:

> If the number of individuals of a species with plumed seeds could be increased by greater powers of dissemination within its own area (that is if the check to increase fell chiefly on the seeds), those seeds which were provided with ever so little more down, would in the long run be most disseminated; hence a greater number of seeds thus formed would germinate, and would tend to produce plants inheriting the slightly better-adapted down.

He therefore chose seeds as examples to illustrate three fundamental concepts that he was developing – the ideas concerned with competition (sometimes named the 'struggle for existence'), with adaptation and with the change of species by natural selection.

Although The Linnean Society paper set the scene for his most famous work, his considerations of seeds in *On the origin of species* are largely concerned with dispersal and distribution. Darwin sought to understand the geographical distribution of plants and animals and its link with evolution. If living seeds could reach separated islands, the plants so produced in geographical isolation might eventually give rise to new species. He therefore devoted much thought and experiment to addressing the possible transport of seeds over great distances, including across the oceans. To this end, Darwin seems to have been well occupied with seeds in the years 1855–1857, if his written works can be taken as a guide. Of the 20 articles published in that period, 11 dealt specifically with seeds or seedlings, and some of the material therein was referred to shortly afterwards in the first edition of *On the origin of species*. At this time, he had his most intensive encounters with seeds, performing many experiments to throw light on seed distribution that he first published in *The Gardeners' Chronicle and Agricultural Gazette*, and which he discussed in correspondence with his friend at Kew, Assistant Director Joseph Hooker, as well as with other botanists. We should be aware, however, that his thoughts about seed distribution were aroused much earlier, during his journey as a young man on *The Beagle*. While in the East Indies, he recorded the unexpected occurrence of certain plant species on several islands and speculated that they came from other parts, by drifting of seeds across the sea. He wrote:

> It is interesting thus to discover how numerous the seeds are, which, coming from several countries, are drifted over the wide ocean. Professor Henslow [*his Professor of Botany at Cambridge and friend*] tells me, he believes that nearly all the plants which I brought from this island, are common littoral species in the East Indian archipelago … the seeds before germinating must have travelled between 1800 and 2400 miles. (Darwin, C.R., 1839, p. 542)

Darwin knew that seeds could be carried in the sea but he had no information concerning the germinability of seeds that had been exposed to salty water for many days or months. So in 1855 he set about performing a collection of experiments to resolve this problem. He kept seeds of several species in artificial seawater for various durations and then tested them for their 'vitality' as shown by their ability to germinate. On reading some of the letters that Darwin wrote about these experiments, one gets the

impression that at first he was rather apprehensive about how they would be received. On 13 April 1855 he wrote to Hooker:

> I have had one experiment some little time in progress which will, I think, be interesting, namely, seeds in salt water, immersed in water of 32°–33°, which I have and shall long have, as I filled a great tank with snow. When I wrote last I was going to triumph over you, for my experiment had in a slight degree succeeded; … It is very aggravating that I cannot in the least remember what you did formerly say that made me think you scoffed at the experiments vastly … I have in small bottles out of doors, exposed to variation of temperature, cress, radish, cabbages, lettuces, carrots, and celery, and onion seed—four great families. These, after immersion for exactly one week, have all germinated, which I did not in the least expect (and thought how you would sneer at me); for the water of nearly all, and of the cress especially, smelt very badly, … but these seeds germinated and grew splendidly. The germination of all (especially cress and lettuces) has been accelerated, except the cabbages, which have come up very irregularly, and a good many, I think, dead … I wash the seed before planting them. I have written to the *Gardeners' Chronicle*, though I doubt whether it was worth while. (Darwin, F., 1887b, p. 54)

Hooker must have replied immediately for Darwin was able to respond on the next day (14 April)

> You are a good man to confess that you expected the cress would be killed in a week, for this gives me a nice little triumph. The children at first were tremendously eager, and asked me often, 'whether I should beat Dr. Hooker!' The cress and lettuce have just vegetated well after twenty-one days' immersion. But I will write no more, which is a great virtue in me; for it is to me a very great pleasure telling you everything I do … If you knew some of the experiments (if they may be so called) which I am trying, you would have a good right to sneer, for they are so *absurd* even in *my* opinion that I dare not tell you. (Darwin, F., 1887b, p. 55)

[To digress, here is evidence of the efficiency of the English postal system of that time. Within about 24 h (13–14 April) three letters had passed between Darwin and Hooker – about 30 km apart. Even for this relatively short distance such an exchange would at the present time take at least 4 days!]. Darwin also corresponded with Asa Gray at Harvard from whom he received more encouragement than from Hooker:

> Apropos to this, many thanks for the paper containing your experiments on seeds exposed to sea water. Why has nobody thought of trying the experiment before, instead of taking it for granted that salt water kills seeds? (Asa Gray to C. Darwin, 30 June 1855. Available at http://www.darwinproject.ac.uk/darwinletters/calendar/entry-1707.html)

Darwin's doubts about the reaction of *The Gardeners' Chronicle* to his experiments were unfounded as the magazine published four notes from him in 1855, two entitled 'Does sea-water kill seeds?' (14 April, 26 May) and two, 'Effect of salt-water on the germination of seeds' (24 November, 1 December). In the first of these (14 April), Darwin announces his interest and intentions: and it is worth quoting *in toto* as it also gives some flavour of Darwin's modesty and apprehension:

> *Does Sea-Water Kill Seeds?*—I have begun making some few experiments on the effects of immersion in sea-water on the germinating powers of seeds, in the hope of being able to throw a very little light on the distribution of plants, more especially in regard to the same species being found in many cases in far outlying islands and on the mainland. Will any of your readers be so kind as to inform me whether such experiments have already been tried? And, secondly, what class of seeds, or particular species, they have any reason to suppose would be eminently liable to be killed by sea-water? The results at which I have already arrived are too few and unimportant to be worth mentioning. *Charles Darwin, Down, Farnborough, Kent*, *April* 11. (Darwin, C.R., 1855a)

In the second note (26 May) Darwin described his findings, preceded by a defence:

> As such experiments might naturally appear childish to many, I may be permitted to premise that they have a direct bearing on a very interesting problem, which has lately, especially in America, attracted much attention, namely, whether the same organic being has been created at one point or on several on the face of our globe. (Darwin, C.R., 1855b)

So to Darwin these experiments on seeds lay at the heart of the questions he was addressing concerning evolution and the origin of species. Further results were given in the note of 24 November and finally, in a presentation read to The Linnean Society on 6 May 1856, and published as a scientific paper in the following year (Darwin, C.R., 1857). Here, he included the findings of Rev. M.J. Berkeley with whom he collaborated on these saltwater experiments, together covering 87 species, many being food and garden plants. Seed germination after different durations in

salt (sea) water at various temperatures was tested, revealing a wide range of survival times from just a few days (e.g. *Linum usitatissimum*, 7 days) to several months (e.g. *Capsicum annuum*, at least 137 days). Seeds of the *Leguminosae* were particularly sensitive, but Darwin noted that these seeds were also affected unfavourably by immersion in plain water (a good control!) so their reaction to saltwater was not necessarily on account of the solutes. Darwin became aware, however, and perhaps somewhat disappointed, that seeds of many species (51 of those he experimented on) sank after a few days and he realized that this behaviour would tend to preclude their dispersal in the oceans beyond a short distance. He also tested the possibility that seeds might be transported in sea currents while still attached to floating parts of plants that had broken off. Interestingly, he remarked in a letter to Hooker on 11 May 1855, 'I begin to think the floating question more serious than the germinating one; and am making all the enquiries which I can on the subject, and hope to get some little light on it …'. But, nevertheless, in *The Proceedings* … paper he felt able to state these tentative conclusions from this series of experiments and observations:

> Some few seeds, however, do float, as I have tried with some of those cast by the Gulf Stream on the coast of Norway … and therefore I conclude, under the existing extremely scanty materials for forming any opinion, that some plants might under favourable conditions be transported over arms of the sea 300 or even more miles in breadth; and if cast on the shore of an island not well stocked with species, might become naturalized. (Darwin, C.R., 1857, p. 136)

Darwin argued that other agencies in addition to the sea could be involved in the dispersal of seeds over long distances. He suggested that birds could carry ingested seeds over the oceans, either in their normal flight patterns or when blown by high winds. He determined that many kinds of seeds were still capable of germinating even after having spent 12–24 h in the crops of certain birds, and he described finding 12 species of germinable seeds in bird excrement collected in his own garden. He also observed that fish ingest seeds, the fish are then devoured by birds and the seeds then passed by the bird, perhaps at some considerable distance from the point of ingestion. Indeed, he carried out his own experiment to show this:

> I forced many kinds of seeds into the stomachs of dead fish, and then gave their bodies to fishing-eagles, storks, and pelicans; these birds, after an interval of many hours, either rejected the seeds in pellets or passed them in their excrement; and several of these seeds retained the power of germination. Certain seeds, however, were always killed by this process. (Darwin, C.R., 1860, p. 362)

Birds could also carry seeds in the earth on their feet. Among many of his examples Darwin included this:

> Mr. Newton sent me the leg of a red-legged partridge (Caccabis rufa) which had been wounded and could not fly; round the wounded leg and foot a ball of hard earth had collected, and this when removed weighed six and a half ounces. This earth had been kept for three years, but when broken, watered and placed under a bell glass, no less than 82 plants sprung up from it: … can we doubt that the many birds which are annually blown by gales across great spaces of ocean, and which annually migrate—for instance, the millions of quails across the Mediterranean—must occasionally transport a few seeds embedded in dirt adhering to their feet? (Darwin, C.R., 1866, p. 432)

Birds alighting on wet mud would naturally pick up quantities of earth; and Darwin pointed out that such mud is rich in seeds:

> I do not believe that botanists are aware how charged the mud of ponds is with seeds: I have tried several little experiments, but will here give only the most striking case: I took in February three table-spoonfuls of mud from three different points, beneath water, on the edge of a little pond; this mud when dry weighed only 6 3/4 ounces; I kept it covered up in my study for six months, pulling up and counting each plant as it grew; the plants were of many kinds, and were altogether 537 in number; and yet the viscid mud was all contained in a breakfast cup! (Darwin, C.R., 1859, p. 387)

Readers might recall that Darwin's wife Emma was of the Wedgwood family who therefore had access to many fine breakfast cups for her husband's mud!

Darwin devoted Chapter XII of *The origin* to addressing the question of geographical distribution of organisms including 'single centres of creation', i.e. 'whether species have been created at one or more points on the earth's surface'. It is here that he marshals the information on seeds that he had collected – from his saltwater experiments, his observations on the transport of earth by birds, on fish and on mud. He added other findings concerning seed dispersal – seeds carried in drift timber, by icebergs, in carcasses of birds and even by locust swarms, and brought all this information to bear in a comprehensive discussion, concluding that the dispersal modes could account for similarities in plant population of sites separated by several hundred miles – but not by intercontinental distances.

Another consequence of this 'accidental' seed dispersal noted by Darwin is that associations existing at one site are absent at the new, colonized site:

> For instance, in certain islands not tenanted by a single mammal, some of the endemic plants have beautifully hooked seeds; yet few relations are more manifest than that hooks serve for the transportal of seeds in the wool or fur of quadrupeds. But a hooked seed might be carried to an island by other means; and the plant then becoming modified would form an endemic species still retaining its hooks, which would form a useless appendage … (Darwin, C.R., 1859, p. 392)

In Chapter III ('Struggle for existence') and Chapter IV ('Natural selection') of *On the origin of species* Darwin discusses concepts that are central to his theory; invoking many examples of seeds to illustrate his arguments. At the start of Chapter III he refers to 'exquisite adaptations of one part of the organisation to another part', mentioning as an example 'the plumed seed which is wafted by the gentlest breeze'. In the 'struggle', vast numbers of seeds fail to survive but huge numbers might be produced, which makes up for the potential loss. An absolute necessity for the preservation of a species is that the number of individuals must be greater than that of its 'enemies'; for example, 'the seeds are in great excess compared with the number of birds which feed on them'. Turning to competition, Darwin remarked, 'What a struggle between the several kinds of trees must here have gone on during long centuries, each annually scattering its seeds by the thousand …'; and, still on the subject of competition among seeds, he speculated that seed storage reserves play a role, '… it may be suspected that the chief use of the nutriment in the seed is to favour the growth of the young seedling, whilst struggling with other plants growing vigorously all around.'

In Chapter V ('The laws of variation'), Darwin devoted some attention to the 'Correlation of growth', by which he meant 'that the whole organisation is so tied together during its growth and development, that when slight variations in any one part occur, and are accumulated through natural selection, other parts become modified'. Some of his observations here are of particular interest for the seed biologist. He noted that there are frequently structural differences between the seeds of disc and ray florets of species in the *Compositae* (what we now call polymorphism), which he believed 'may be connected with some difference in the flow of nutriment towards the central and external flowers …' and later he stated that '… some correlations, occurring throughout whole orders, are apparently due to the manner alone in which natural selection can act … ', such as:

> … winged seeds are never found in fruits which do not open: I should explain the rule by the fact that seeds could not gradually become winged through natural selection, except in fruits which opened; so that the individual plants producing seeds which were a little better fitted to be wafted further, might get an advantage over those producing seed less fitted for dispersal; and this process could not possibly go on in fruit which did not open. (Darwin, C.R., 1859, p. 146)

His interest in variation and natural selection led Darwin to investigate domesticated animals and plants, culminating in the publication, 9 years after the first edition of *On the Origin of species*, of a two-volume work, *The variation of animals and plants under domestication*. Darwin realized that humans, by exploiting the variability inherent in living organisms and by imposing selection, 'may be said to have been trying an experiment on a gigantic scale'. Of the total of 25 chapters, three are devoted entirely to plants while material on plants can be found in 16 others. Scattered in these are many considerations of seeds – mostly of food plants – of which just a few will be mentioned here. He referred to the diet of native Africans, citing information about their use of the seeds of several different wild grasses, adducing this as evidence that 'there is no reason to suppose that our cereal plants originally existed in their present state so valuable to man' (Darwin, C.R., 1868a, p. 308). In his early travels in South America Darwin observed the wide diversity of maize grain types that were available as food, and later remarked on the variety in grain shape, size, colour and number per cob (Darwin, C.R., 1868a, p. 321). In contrast to the differences among seeds in the same cultivated species, such as maize or peas, he also noted the extremely slight or no differences among seeds of *Brassica* species which were vegetatively so diverse, such as cauliflowers, cabbages, Brussel sprouts, kale and broccolis.

The criteria for selection of domesticated plants and its effects are discussed at length in volume 2 of *The variation*. Several examples are given of selection for seed size, quality and vigour and for the consequential modifications to seeds that have occurred through time, but just one instance will be mentioned here. Arguing that, during domestication, organs of animals and plants might become rudimentary or disappear, Darwin refers to the case of *Carthamus*:

> … in a series of species in the genus Carthamus, one of the Compositæ, a tendency in the seeds to the abortion of the pappus may be traced extending from the circumference to the centre of the disc: thus, according to A. de Jussieu, the abortion is only partial in *Carthamus creticus*, but more extended in

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> *C. lanatus*; for in this species two or three alone of the central seeds are furnished with a pappus, the surrounding seeds being either quite naked or furnished with a few hairs; and lastly, in *C. tinctorius* [*cultivated safflower*], even the central seeds are destitute of pappus, and the abortion is complete. (Darwin, C.R., 1868b, p. 316)

There are many references in *The variation* to the effects of cross- and self-fertilization on seed vigour in cultivated plants. This is a subject which interested Darwin so much that later he devoted a book entirely to the topic (Darwin, C.R., 1876). It has been suggested that his interest was partially provoked by the fact that his wife, Emma Wedgwood, was a first cousin and that he was concerned about possible deleterious consequences of a consanguineous marriage. In Chapter IX – on the production of seeds – Darwin described his investigations on seed number, size and vigour, noting that in 10 out of 16 species the seeds of self-fertilized plants were superior in weight to those from cross-fertilization, although in some cases this may have resulted from the lower seed number per capsule in the former (p. 353). He recorded, however, that cross-fertilization often led to greater seedling vigour: and his conclusion in the final chapter is that 'cross-fertilization is generally beneficial, and self-fertilization injurious'.

In both *The variation* and *The effects of cross and self fertilisation* Darwin refers to many breeding experiments that he carried out in several species, including peas. Around 10 years prior to this work, at approximately 1000 km from Darwin's garden, in Brno, Moravia, Gregor Mendel had also carried out very many, thorough, quantitative experiments with peas. Mendel's investigations were unknown to Darwin but the latter did utilize some of the same traits (seed characters) studied by Mendel. This is what Darwin wrote on 3 November 1866 to Thomas Laxton, a 'scientific' gardener, who had also performed some crossing experiments with peas:

> I have spent some hours during the last few days in examining with the greatest possible interest your Peas But I observe in lot 1 (except one pea) & in a lesser degree in 2, & in 3. 5. 6. & 8 that the crossed peas are smooth like the paternal stock, & not wrinkled & cubical like the mother pea— Can this loss of wrinkling be due to mere variation, or to the effect of some peculiar culture, or is it the direct result of the pollen of the father? (http://www.darwinproject.ac.uk/darwinletters/calendar/entry-5267.html)

As he still thought in terms of blended inheritance, Darwin was somewhat perplexed by this apparently complete suppression of a trait. But here is a tantalizing glimpse of how close Darwin (and, to give him credit, Laxton) might have been getting to Mendel's findings on inheritance.

Considerations relevant to seed biology are scattered throughout the rest of Darwin's studies and writings. In *On the various contrivances by which British and foreign orchids are fertilised by insects* (Darwin, C.R., 1862) he discussed seed number and size in these plants. In *Insectivorous plants* (Darwin, C.R., 1875) he described his experiments on the effects of *Drosera* leaf secretions on various types of living seeds, and also the reaction of *Drosera* to thin slices of pea seeds and to extracts (e.g. legumin, gluten) from various seeds. He showed, in *The formation of vegetable mould, through the action of worms* (Darwin, C.R., 1881) that small seeds can be pulled down into their burrows by the worms, which might deceive botanists into believing that the seeds had long been buried. In *The power of movement in plants* (Darwin, C.R., 1880) he studied radicle and hypocotyl movements in newly germinated seeds. In various letters and articles he commented on seed longevity, on the 'vitality' of seeds in the soil and on the effects on seeds of steeping in manure water.

Darwin occasionally commented on how science should be done and on the proper attitudes of scientists. He advised that 'a good deal of scepticism in a scientific man is advisable to avoid much loss of time' and then continued with an amusing tale which I think is worth recounting in its entirety as we, as seed biologists, might learn something from it:

> In illustration, I will give the oddest case which I have known. A gentleman (who, as I afterwards heard, is a good local botanist) wrote to me from the Eastern counties that the seeds or beans of the common field-bean had this year everywhere grown on the wrong side of the pod. I wrote back, asking for further information, as I did not understand what was meant; but I did not receive any answer for a very long time. I then saw in two newspapers, one published in Kent and the other in Yorkshire, paragraphs stating that it was a most remarkable fact that 'the beans this year had all grown on the wrong side.' So I thought there must be some foundation for so general a statement. Accordingly, I went to my gardener, an old Kentish man, and asked him whether he had heard anything about it, and he answered, 'Oh, no, sir, it must be a mistake, for the beans grow on the wrong side only on leap-year, and this is not leap-year.' I then asked him how they grew in common years and how on leap-years, but soon found that he knew absolutely nothing of how they grew at any time, but he stuck to his belief. After a time I heard from my first informant, who, with many apologies, said that he should not have written to me had he not heard the statement from several intelligent farmers; but that he had since spoken again to every one of them, and not one

> knew in the least what he had himself meant. So that here a belief—if indeed a statement with no definite idea attached to it can be called a belief—had spread over almost the whole of England without any vestige of evidence. (Darwin, F., 1887a, p. 104)

We can see from the above account that throughout almost all of his studies Darwin acknowledged the significance of seeds. Seeds occupy an important position in his legacy to biology and it is therefore fitting that seed scientists pay special tribute to Darwin's genius in this celebratory year.

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