1 GREEN THREADS ACROSS THE AGES: A BRIEF PERSPECTIVE ON THE DARWINS' BOTANY

Plants have determined man's history and they will determine his future. Whether they were suspended in the primeval soup of the oceans, or more firmly anchored after their emergence onto land, plants modified the earth's early atmosphere, fixing carbon dioxide (CO_2) and releasing oxygen (O_2), making possible the evolution of primitive animal life and, much later, of man himself.[1] Plants are at the base of every food chain, supplying us with both building and clothing materials, with wood for cooking and heating, and with fuels to generate power. Such green threads connect our most fundamental activities yet, despite this, we have until very recently taken plant growth and health for granted. Many aspects of plant physiology remain a mystery to us, particularly where they concern plants under the variable conditions of the field – away from the controlled conditions of the laboratory. Still in its infancy is the study of how the physiology of an individual plant is modified when it functions as a member of a community in a natural environment. One concern of the greatest current interest is the extent to which plants, with their capacity to fix CO_2, might ameliorate changes in the composition of the earth's atmosphere that threaten our safe and familiar world.

Given the importance and urgency of the latter, it is salutary to review the progress we have made in our scientific understanding of plant growth and to reflect that our understanding began less than three centuries ago. And this is where the Darwin family comes in.

A strong green thread ran through that family, connecting different generations across two hundred years. Erasmus Darwin (1731–1802), his grandson, Charles (1809–82), and his great grandson, Francis (1848–1925), were all botanists of distinction, each fascinated by the movements of plants as they seek light, nutrients and water.

Mention of the name Darwin has for too long conjured an image of just one of them, Charles, his theory of evolution, fossils, struggles for survival in the animal world, and man's origins with the apes. As this book will reveal, the image is misleading where Charles in concerned. It is moreover unfair both to Erasmus and, particularly, to the previously forgotten Francis, each of whom deserves to be better remembered.

The popular image of Charles is misleading simply because he studied plants as much as animals, finding their study satisfying and rewarding. He wrote that 'It has always pleased me to exalt plants in the scale of organised beings' and, in a letter to J. D. Hooker dated 3 June 1857, that he found 'any proposition more readily tested in botanical works ... than zoological.'[2]

It is unfair because Erasmus led 'a life of unequalled achievement',[3] not least when he was popularizing botany and writing about plant function with extraordinary prescience. It is unfair because Francis continued and with great vision enlarged upon Charles's botanical works. The Darwins' botany has borne fruit in many areas; its outcomes are easily recognizable in many of today's horticultural and agricultural practices (see Chapter 11). But what is most remarkable is that the culmination of the Darwins' fascination with movements, and its extension by Francis's young colleague in Cambridge, Frederick Frost Blackman, has provided the very foundations upon which our modern studies of interactions between plants and the atmosphere are based. Thus, Francis was a pioneer in the study of the movements of stomata – pores in the otherwise impermeable surface of the leaf whose daily opening and closing regulates entry of CO_2 into the leaf, and the escape of water from it (Figure 1.1) – while Blackman complemented Francis's work by defining the way in which the levels of key environmental factors, CO_2, temperature, and irradiance limit the rate at which carbon is fixed.

To understand how water was lost by transpiration – or perspiration as Erasmus called it – and how plants obtained most of their dry weight from the air (not from the soil or, indeed, by transforming water) proved fundamental to understanding their growth, that most basic task facing those early botanists

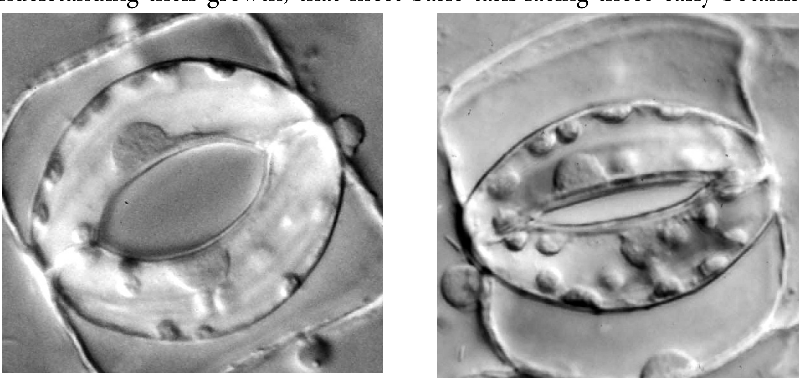

Figure 1.1: In epidermis detached from a leaf of *Commelina communis*, an open (left) and almost closed stomatal pore (right) are seen from above. Each pore is surrounded by two kidney-shaped 'guard cells' whose swelling and shrinking determine the pore area. Reproduced by permission of Dr Mark Fricker, Plant Sciences University of Oxford

interested in more than merely naming and describing plants. Later chapters will describe the progress they made and the connections they revealed between water and movements. But why should those basic subjects, transpiration and photosynthesis, be so important for today's botanists (or plant scientists as they prefer to be known)? At the heart of the answer lies the subject of energy and its transformation. Pigments in plants, such as the green chlorophylls, trap solar energy in the first stage of a process that has become known as known as photosynthesis. In the second stage, which is independent of light, that energy is used to drive a series of chemical reactions during which CO_2 is used, with other chemicals, to make sugars and energy-rich compounds, respectively, the building blocks and fuel needed for growth.

Photosynthesis occurs in specialized bodies, chloroplasts, located deep within the cells of leaves and green stems. In order to get from the atmosphere to those cells, CO_2 has to diffuse through stomatal pores in the epidermis or surface layer of cells of the plant. The composition of our atmosphere has been continually changing over millions of years. Today its concentration of CO_2 is around 382 parts per million (ppm = 0.0382 per cent) and rising fast, perhaps by as much as 2 ppm per year.[4] In a recent but pre-industrial age it was 273 ppm. Our way of life is threatened because CO_2 in the atmosphere stops some of the solar energy that strikes the earth's surface from being immediately re-radiated back into space; the higher the concentration of CO_2 in the atmosphere the more energy that is retained. The energy is trapped in the form of heat under the thickening blanket. Higher CO_2 levels are not in themselves a direct threat to life but they contribute to global warming. Among the forecast consequences of warming are large but unpredictable changes in climatic factors, such as amounts of rainfall, probably leading to hugely increased areas of aridity that are totally unsuitable for plant growth which, of course, would in turn affect climate.

And here is a conundrum: at higher CO_2 concentrations more carbon dioxide diffuses into the leaf, and the rate of photosynthesis is higher, than at lower more 'normal' concentrations. Furthermore, at high CO_2, less water is lost per unit of carbon captured – in other words 'water use efficiency' is increased. So, in theory, plants *can* cope with anthropogenic rises in CO_2 levels, and even ameliorate those increases, but the question is, *will* they do so in practice? We cannot yet answer this question with any certainty because we are still learning about the limits of plants' capacity to respond to ever increasing CO_2 concentrations. It is clear that while photosynthesis in most plants increases as CO_2 levels rise to about 600 ppm – if water is freely available and the temperature is suitable – photosynthesis shows less and less response as concentrations rise above 600 ppm. Even below 600 ppm there are variations between plant types, with many annual crop plants responding to higher CO_2 levels less than woody crops, such as cotton, or many tree species, for reasons that are not yet entirely clear.[5]

The Darwins' individual contributions to the evolution of botany (plant science) are laid out in the following chapters, as are the connections between the three men. Each man has his own intrinsic interest but, seen in a wider context, the differences between their working lives illustrate contemporary sociological changes that were affecting the study of plants, such as the battle between 'country house' and laboratory science, the professionalization of science, and the rise of women in the laboratory. The story of the Darwin family is the story of the evolution of plant science.

The Darwins were not *the* founders of plant science but individually and collectively they made an unique contribution to its early development. Along with a handful of others, they played major parts in the growth and sustenance of its core area – physiology – which is concerned with the functioning of organs or systems in relation to their structure. Quantitative, that is measurement-based, experimental plant physiology began with the Reverend Stephen Hales in 1727. Its forward march stuttered through the next hundred years, but then accelerated. The scientific story originates therefore with Hales and ends with the death of Francis Darwin in 1925, or, to be more exact, a few years *after* his death, for, in order to appreciate the Darwins' scientific legacy, it is necessary to follow forwards in time the particular subjects on which they worked. What is indisputable is that by the period between the two world wars botany had become an independent and rigorous, laboratory-based science.

Before exploring the botany of the Darwins, however, it is necessary know more about the family and its fortunes, for these strongly influenced the ways in which Erasmus, Charles and Francis approached the study of plants. Among those who influenced the Darwins, or were influenced by them, one of the most significant was the German botanist, Julius von Sachs. Like him, I trust that, 'I may sometimes have overrated the merits of distinguished men, but have never knowingly underestimated them'.[6]