Levin SA, Durrett R. 1996. From individuals to epidemics. *Philosophical Transactions of the Royal Society of London, Series B – Biology Sciences* **351**: 1615–1621.
Michael E. 1993. Mathematical modelling of disease epidemiology. *Parasitology Today* **9**: 397–399.
Mollison D, Levin SA. 1995. Spatial dynamics of parasitism. In: Grenfell BT, Dobson AP, eds. *Ecology of infectious diseases in natural populations*. Cambridge, UK: Cambridge University Press, 384–398.
Shea K, Thrall PH, Burdon JJ. 2000. An integrated approach to management in epidemiology and pest control. *Ecology Letters* **3**: 150–158.
Swinton J, Gilligan CA. 1998. Theory, data and experiments in heterogeneous transmisssion. *Trends in Microbiology* **6**: 50–51.
Thompson JN. 1994. *The coevolutionary process*. Chicago, IL, USA: Chicago Univeristy Press.
Thrall PH, Burdon JJ. 1997. Host-pathogen dynamics in a metapopulation context: the ecological and evolutionary consequences of being spatial. *Journal of Ecology* **85**: 743–753.
Van der Plank JE. 1963. *Plant diseases: epidemics and control*. New York, USA: Academic Press.
Zadoks JC, Shein RD. 1979. *Epidemiology and plant disease management*. New York, USA: Oxford University Press.
Zhu YY, Chen HR, Fan JH, Wan ZH, Mundt CC. 2000. Genetic diversity and disease control in rice. *Nature* **406**: 718–722.

Key words: fungal spread, epidemics, spatial structure, percolation model, soil-borne disease.

Timelines

The birth of cell biology

1804–1881: the bicentenary of the birth of Matthias Jakob Schleiden

Matthias Schleiden was, along with Theodore Schwann, one of the formulators of the classical 'cell theory' of organism structure. Schleiden had a complex life: his belief that he had failed in his first career as a barrister led him to attempt suicide by shooting himself in the head. After recovering, he re-trained as a scientist. Whilst this could be construed to mean one needs a complete brain even to fail as a lawyer but a fraction of a brain to be a famously successful scientist, a sample size of one and no proper controls prevents us from reaching such a conclusion.

Formulating the 'cell theory'

In 1665, Robert Hooke published *Micrographia* in which he gave the first description of the 'cells' of cork (Box 1). While this may have been the first use of the word 'cell' in a histological context, he was actually describing cellulose walls that no longer contained any living components. Unwittingly therefore Hooke was the first to record the effect of programmed cell death on plant development. Following this, Nehemiah Grew, in 1682, gave a description of the 'cells or bladders' of root parenchyma and accompanied this with detailed engravings of his observations (Turner, 1890; Gall, 1996). Building on these descriptions, several advances were made – such as the discovery of the nucleus in the early eighteenth century – before the synthesis of the 'cell theory' in the 1830s.

Box 1 A brief history of Cell Biology

1642	Death of Galileo Galilei – credited as the father of the scientific method.
1665	Robert Hooke publishes '*Micrographia*'.
1683	Anton van Leeuwenhoek writes to the Royal Society of London describing the presence of 'animalcules' in the plaque of his own teeth. This was among the first descriptions of living bacteria ever recorded.
1776	Lazzaro Spallanzani demonstrates that an organism is derived from another organism.
1831	Robert Brown coins the term 'nucleus'. Brown also discovered Brownian motion.
1838	Matthias Schleiden states that plants are composed of cells.
1839	Theodore Schwann states that animals are composed of cells and that 'the elementary parts of all tissues are composed of cells'
1857	Carl Zeiss sells his first compound microscope.
1876	Ernst Haeckel credited with coining the term 'plastid'.
1882	Walther Flemming introduces the term 'mitosis'.
1898	Carl Benda names 'mitochondria' and Camillo Golgi discovered the organelle that bears his name.
1931	Ernst Ruska builds first Transmission Electron Microscope (TEM) at Siemens.
1944	Keith Porter, credited as the father of modern cell biology, and his colleague Albert Claude take first picture of an intact cell with the TEM. Porter coins the term 'endoplasmic reticulum'. Porter is also responsible for developing the microtome.
1994	Martin Chalfie and colleagues first to use GFP as a marker for gene expression.

In 1833, Robert Brown published a paper highlighting the presence of nuclei in plant cells, in doing so bemoaning the fact that, while they had been described previously, they were accorded little attention (Hughes, 1959). This was rectified by Schleiden, who proposed that the nucleus was an elementary organ in plants, and closely linked to their development (Schleiden, 1838; in Turner, 1890). His observations of nuclei included descriptions of 'spots or rings', which were later named nucleoli by Schwann. In his 1838 article, Schleiden reached the now famous conclusion that the basic structural element of all plants was the cell. This was followed only a few months later by Schwann's statement 'That there is one universal principle of development for the elementary part of organisms, however, different, and that this principle is the formation of cells' (Schwann, 1839 – translated from German, 1847). These conclusions by Schleiden and Schwann are generally considered to mark the official formulation of the 'cell theory'.

Developing concepts

While they were in agreement over the principle that cells were the basic unit of life, Schleiden and Schwann had differing theories regarding the formation of new cells. Schwann believed that new cells could be formed in the extracellular fluid surrounding existing cells, while Schleiden held that new daughter cells could only form from within pre-existing parent cells. From his incorrect observations that mature cells had no nuclei, Schleiden also contended that the nuclear membrane of the parent went on to form the cell wall of the daughter (Hughes, 1959).

The idea of cells being the 'elementary parts' of organisms gained wide acceptance after the initial work on 'cell theory' was published. The 'preformationist' ideas of Schleiden, however, were gradually eroded and attacked, notably by Darwin's champion T.H. Huxley & in 1853 (Richmond, 2000). By the end of the 19th century, microscopist William Turner could state with confidence that new cells arose from division of a parent cell, rather than emerging from within one (Turner, 1890). The fact that microscopy had moved on to such an extent, allowing these observations to be made, can also be attributed in no small way to Schleiden.

In *Micrographia*, Hooke (1665) predicted that the minute structures of plant cells would be detectable by 'some diligent observer, if help'd with better microscopes'. Schleiden played his part in confirming this prediction by persuading a young Carl Zeiss to dedicate himself to the study of optics. The work of Zeiss and colleagues heralded a revolution in microscopy with the development of his first compound microscope, first sold in 1857, followed by fruitful collaboration with Ernst Abbe who developed optical theory and helped apply this to the development of better microscopes. The 20th century saw the development of the transmission electron microscope in the 1930s and the coming of age of fluorescence microscopy with the introduction of FITC as a fluorescent label in 1958 (Riggs *et al.*, 1958). However, it is the application of green fluorescent protein to cell biology research (Chalfie *et al.*, 1994) that has led to the latest revolution: the ability to visualise fundamental cell biological phenomena at the molecular level in living tissue and in real time.

Perspectives

Over the years much of the detail of Schleiden's and Schwann's 'cell theory' has been found to be erroneous, such as their views on cell formation, and their belief that cells were anatomically and physiologically independent. However, the impact their work has had on cell biology can be attributed to the power of the original hypothesis which stimulated many research endeavours. Indeed 'cell theory' is an excellent example of the importance of traditional hypothesis forming and testing that is a classical tenet of scientific research. As Schwann wrote 'A hypothesis is never hurtful, so long as one bears in mind the amount of its probability, and the grounds upon which it is formed. It is not only advantageous, but necessary to science, that when a certain cycle of phenomena have been ascertained by observation, some provisional explanation should be devised as closely as possible in accordance with them; even though there be a risk of upsetting this explanation by further investigation; for it is only in this way that one can rationally be led to new discoveries, which may either confirm or refute it.' (Schwann, 1839 – translated from German, 1847). Certainly, the doctrine of 'cell theory' as advocated by Schleiden and Schwann signalled the birth of cell biology and was instrumental in helping cell biology become the dynamic science it is today.

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References

Chalfie M, Tu Y, Euskirchen G, Ward WW, Prashner DC. 1994. Green fluorescent protein as a marker for gene expression. *Science* **263**: 802–805.

Gall JG. 1996. *A pictorial history: views of the cell.* Bethesda, MD, USA: The American Society for Cell Biology

Hooke R. 1665. *Micrographia*. (1961 facsimile reproduction of original, 1st edn published by Dover Inc, NY, USA). London, UK: Royal Society of London.

Hughes A. 1959. *A history of cytology*. London, UK: Aberlard-Schuman.
Richmond ML. 2000. T.H. Huxley's criticism of German 'cell theory': an epigenetic and physiological interpretation of cell structure. *Journal of the History of Biology* **33**: 247–289.
Riggs JL, Seiwald RJ, Burckhalter JH, Downs CM, Metcalfe TG. 1958. Isothiocyanate compounds as fluorescent labelling agents for immune serum. *American Journal of Pathology* **34**: 1081–1097.
Schleiden MJ. 1838. Beiträge zur Phytogenesis. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medici.* **13**: 137–176.
Schwann T. 1839. *Mikroskopische Untersuchungen über die Übereinstimmung in der Struktur und dem Wachstum der Thiere und Pflanzen*. Berlin, Germany: Sander'schen Buchhandlung.
Schwann T. 1847. *Microscopical researches into the accordance in the structure and growth of animals and plants* (translated by Henry Smith). London, UK: Name of publisher.
Turner W. 1890. *The cell theory past and present – Inaugural Address to the Scottish Microscopical Society*. Edinburgh, UK: Neill and Co.

Key words: Cell theory, cell biology, microscopy, TEM, green fluorescent protein, plastid, golgi, endoplasmic reticulum.

Books

Forest biotechnology – thriving despite controversy

Molecular genetics and breeding of forest trees

Edited by S. Kumar and M. Fladung. The Haworth Press (www.haworthpress.com), 2004.
ISBN 1-56022-959-4, $59.95

It was the summer of 1999, and as the organizers of the semiannual international conference on molecular biology of forest trees sent emails around the globe in final preparations for the upcoming meeting at the University of Oxford, UK, the wheels started to come off. The train-wreck that was crop biotechnology in the UK started to spread to the previously obscure field of forest biotechnology. Major news articles in the UK and elsewhere in the EU tarred forest biotechnology in the same way they had already done to agricultural biotechnology. A protest was carried out at the July meeting, and to the shock of all the scientists the meeting began with the announcement that a pioneering field experiment with lignin-modified poplar trees, also in the UK, had been cut down the night before by vandals. The scientists at the meeting scratched their heads and wondered how science and 'society' could be so out of whack in Europe.

'In 2001 vandalism of field sites or arson was directed against forest biotechnology research sites in the United States'

But this was not the end. After this watershed event, several of the mutinational environmental organizations issued reports that generally demonized forest biotechnology, and called for various forms of moratoria. and in 2001 vandalism of field sites or arson was directed against forest biotechnology research sites in the United States – clearly this form of terrorism was not going to be restricted to Europe. Given this turmoil, what is the state of the science that underlies biotechnology? Has the political upheaval, which has certainly set back field research in Europe, driven researchers and research funds from the field? Are the scientists out of ideas? Has there been substantive progress?

A read of this book, which has about half its chapters by researchers from biotechnology-embattled Europe, make it clear that the science is moving ahead impressively. The editors have carefully crafted it to include the major scientific thrusts in forest biotechnology. These span genomic maps and markers as supplements to traditional breeding, through to novel means for altering the characteristics of wood and tree reproduction, with the goal of enabling novel kinds of highly domesticated, biosafe plantations to be employed.

Arabidopsis upward

All of the chapters are written by authorities in their fields, including many of the long-standing leaders in forest biotechnology – such as Jouanin, Boerjan, Davis, Ebinuma, Walter and Fladung. All of these provide literature reviews that are comprehensive and up to date, and many move fluidly between knowledge of the genes in model plants, especially *Arabidopsis*, and trees, as any modern intellectual analysis of tree genetics should. The age where breeders need to be educated only about breeding methods in trees is clearly over. Moreover, if the extraordinary potential of poplar as a model organism is fully capitalized upon, the combination of its genome sequence and transformability will soon allow scientists to know the consequences of modifying vast numbers of genes on development of trees, not just taxonomically distant annual plants.