

University of Dundee

## Future opportunities for crop physiology in fruit production

Jones, H. G.

*Published in:*

International Symposium on Physiological Principles and Their Application to Fruit Production

*DOI:*

[10.17660/ActaHortic.2017.1177.6](https://doi.org/10.17660/ActaHortic.2017.1177.6)

*Publication date:*

2017

*Document Version*

Peer reviewed version

[Link to publication in Discovery Research Portal](#)

*Citation for published version (APA):*

Jones, H. G. (2017). Future opportunities for crop physiology in fruit production. In *International Symposium on Physiological Principles and Their Application to Fruit Production* (Vol. 1177, pp. 59-71). (Acta Horticulturae; Vol. 1177). International Society for Horticultural Science . <https://doi.org/10.17660/ActaHortic.2017.1177.6>

### General rights

Copyright and moral rights for the publications made accessible in Discovery Research Portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from Discovery Research Portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain.
- You may freely distribute the URL identifying the publication in the public portal.

### Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

# **Future opportunities for crop physiology in fruit production**

Hamlyn G. Jones  
Division of Plant Science, College of Life Sciences  
University of Dundee at the James Hutton Institute  
Invergowrie, Dundee, DD2 5DA, UK  
*and* School of Plant Biology  
University of Western Australia, Crawley 6009  
West Australia, Australia

email: h.g.jones@dundee.ac.uk

**Keywords:** automation, crop physiology, decision support, fruit, remote sensing, stress diagnosis

## **Abstract**

**This paper outlines some of the challenges and opportunities for whole plant and crop physiology to contribute to enhanced and more efficient fruit production in the coming years. The rapid advances in molecular biology provide both an opportunity (especially to improve understanding of physiological processes in crop production) and a challenge (to use this knowledge to advance production in real farm situations). Similar or even greater opportunities are being provided by other developing technologies, especially the rapidly increasing power and availability of powerful computing and communications technology and smartphones which provide real opportunities to contribute to improved crop and farm management. In addition the rapid development of novel ‘remote’ or ‘proximal’ sensing technologies, including the use of Unmanned Aerial Vehicles and on-tractor sensors for crop monitoring and stress diagnosis also holds great promise. These and other advances are discussed in the context of their potential for improving both crop breeding and orchard management, drawing on examples from a wide range of crops. The potential of these scientific advances will be put in the context of other factors relating to the advance of horticultural knowledge including the availability of funding and the training of young scientists.**

## **INTRODUCTION**

In my invitation letter I was asked to look forward over the next twenty to thirty years to give a foresight into the future for whole plant physiology of fruit crops. I would not presume to be able to predict the future with any accuracy; all soothsayers/prophets from Nostradamus to modern weather forecasters (who probably have less excuse) inevitably seem to get their predictions wrong. Therefore I shall only attempt to draw some parallels with the past, and perhaps to identify some areas where there seems to be to be particular scope or need for future development with specific application to the fruit industry.

## **THE PAST**

Before looking forward, it is useful to consider how much has changed in the past 20 years, or even the past 40 or 60 years. When I started out in research, more than 40

years ago, we seem to have been asking many of the same questions and indeed highlighting many of the same requirements as we are today (e.g. the need to manipulate tree growth more effectively; the development of improved pruning and training systems; the improvement of irrigation and irrigation scheduling systems; the need to know more about roots and their distribution and dynamics; the need to understand and regulate carbohydrate partitioning, etc.). Even at that time these topics had all been of major concern for many years, with some aspects having been central to the work of fruit research stations such as the New York State Agricultural Experiment Station, Geneva, NY (established 1880), Long Ashton Research Station (established 1903) and East Malling Research Station (established 1913) and since their earliest days.

Changes in the research equipment and technologies available to us have been dramatic over the past 40 years. Although we were starting to understand the roles of growth regulators in the 1960s and 70s, and they had been used since the 1930s for plant propagation, analytical methods were primitive in comparison with modern chromatography and mass spectrometry. Similarly, computing power was almost non-existent (some were still doing calculations on mechanical calculators, though the first electronic calculators were coming available). Any computing was done on main-frame computers often based many miles away using tape or cards as inputs and the consequential daily turnaround meant that a whole extra day was required if one made any tiny error. The Personal Computer was only introduced in the early 1980s; I recollect introducing the Apple IIe (with its pitiful 64 kb of RAM) to East Malling in 1983 and using it successfully for many years as an effective field data-logger and for data analysis using simple spreadsheets. At this stage there were no commercial porometers or photosynthesis systems and researchers had to have the skills and ability to construct their own, often but not always based on published designs (Parkinson & Legg, 1972; Slatyer & Jarvis, 1966). Now all this has changed with readily available commercial instruments for the study of stomatal conductance, photosynthesis, light interception, soil moisture, hormone content, etc.; though there is the associated disadvantage that young researchers are less likely to understand the underlying basis of the measurements with the increasing likelihood that they will be unable to recognise erroneous data. Interestingly, the use of Unmanned Aerial Vehicles (UAVs) is still at this earlier phase where users have to do much of the development work themselves, both in relation to construction and for image handling and map construction; only now are turn-key systems starting to become available (e.g. [precisionhawk.com](http://precisionhawk.com); [farmaerial.co.uk](http://farmaerial.co.uk); [www.aeroscout.ch](http://www.aeroscout.ch); [www.cropcam.com](http://www.cropcam.com)).

There have been many successes over the past few decades (as reported in other papers from this conference) in areas as diverse as irrigation sensing, scheduling, and other aspects of crop management including the introduction of approaches such as Regulated Deficit Irrigation (RDI; Chalmers *et al.*, 1981; Fereres & Soriano, 2007; Mitchell & Chalmers, 1982) and partial root-zone drying (PRD; see e.g. Sadras, 2009; Stoll *et al.*, 2000), the use of light climate manipulation using coloured films or netting (Schettini *et al.*, 2011), improved understanding of dormancy and chill requirements (Atkinson *et al.*, 2013), the use of hormone/PGR treatments for thinning (Davis *et al.*, 2004), growth control and improvement of fruit quality (Lawes & Woolley, 2001), while there have been substantial advances in other aspects of crop management (e.g. in planting and training systems, pruning, ground cover, nutrition, etc.), often dependent on advances in technology becoming available to growers. Not all the innovative ideas proposed in the 1970s and 1980s have had the impact that had been hoped: for example

exciting new concepts such as meadow orchards where a form of biennial cropping requiring extremely high density planting (e.g. 70,000 trees per hectare), extensive use of plant growth regulators and a harvesting system more akin to that for cereal crops were being proposed (Luckwill & Child, 1973). Nevertheless, even though such systems may never have been widely adopted, several of the concepts introduced provided the stimulus for modern high density cropping, columnar apples and fruit wall systems (Erez, 1984; Luckwill, 1978).

## **THE FUTURE**

In some ways it is easier to answer the question: “where is horticulture going?” than “where is fruit physiology going?”. Developments in horticulture are very largely driven by external drivers such as energy prices, consumer (or more likely Supermarket) demands, food fads (often rather little supported by rational science), together with a range of other economic or indeed political (e.g. “green”) considerations and by external factors such as climate change and its perception. Such drivers tend to be very fickle and are notoriously difficult to predict and are likely to be the main force determining future developments in fruit growing. The actual advances in physiology, on the other hand, are more likely to be driven by advances in technology or understanding developed in other fields. Foremost among these I would highlight the rapid advances in computing, communication technology, global positioning (GPS), informatics and “big data”, together with parallel advances in remote sensing, robotics and sensor technology, leading to the development of what have been called “smarter farming systems” (Pedersen *et al.*, 2006). These developments will lead to enhanced opportunities for individual plant care, with variable-rate and spot treatment technologies being used, rather than conventional agronomy where whole orchards are treated the same. Though such precision farming approaches are becoming more and more widely used in broad-acre agriculture they have yet to be adopted at any scale in fruit cultivation; though I expect it to come, and to come soon. Equally important for fruit crops as for other crops are the tremendous recent advances that have been made in genetics, molecular biology and the “Omics” technologies.

Notwithstanding all these rapid technological advances all the real developments that will benefit the fruit industry will depend crucially on an understanding of crop physiological principles; for example as we shall see below, the potential impacts of molecular biology will only be achieved when crop physiologists and molecular geneticists work together. I will discuss each of these areas in more detail below.

### **Technology and “smarter farming systems”**

All farming and horticulture is highly dependent on the engineering and other technological tools that are available to growers. Here the recent developments in computing, robotics and remote sensing, including the widespread availability of global positioning systems, information and communications technology coupled with the enormous computing power and wireless communication ability that we now have, and the development of sensor technologies for providing real time information on distributed systems are all going to have increasing impact on the way crops are grown. This information technology and its ready accessibility on smartphones and tablets in the field and its integration with guidance systems on tractors and data-bases and maps in the office provides and unprecedented power for farm managers. This technology is allowing farmers to move well beyond the capacity of the earliest expert systems (though they may

have been around for 30 years, they are yet to make the impact they should). Fruit growers are generally rather behind advances in large area field crops in the adoption of these technologies which comprise a linked set of systems: sensor systems and data acquisition (including soil properties, crop status using remote sensing, and yield mapping); data integration, interpretation and mapping making use of weather forecasts, crop modelling and economic modelling; through to feedback to precision targeted farm management and potentially individual tree treatments. Optimal use of the new technologies for crop management will depend on a combination of advanced sensing techniques with models of crop development. For example, combination of sensor data with crop models and weather data will allow the generation of useful yield predictions. The trend will be for these complex systems to be incorporated into novel farm information management systems (Sorensen *et al.*, 2010) with increasing numbers of commercial systems coming available.

A likely key component of these smarter farming systems will include a range of autonomous robots that will autonomously and routinely sense crop status and apply appropriate management responses such as weed removal, localised spraying against disease, and so on (Pedersen *et al.*, 2006).

### **Remote sensing**

Advances in non-contact sensing of crop status and function are developing rapidly and are becoming rapidly incorporated into precision farming technologies. Opportunities range from the use of satellites through the use of sensors on airborne, balloon and unmanned aerial vehicle (UAV) platforms through to fixed or mobile ‘in-field’ sensors for what is known as ‘proximal’ sensing. Satellites are increasingly powerful with improving spatial resolution and rapidly falling costs with the advent of constellations of SmallSats and even NanoSats. Currently around 12-14 new civilian missions are launched each year (Belward & Skøien, 2014). Unfortunately, although satellites are crucial both for regional studies, such as for weather forecasting and for estimates of regional water use, and for ‘inventory’ functions such as mapping of crop extent, their use by fruit growers is not likely to grow as rapidly as is the use of proximal and UAV sensing platforms because the latter technologies are not limited by cloud cover and can provide the much improved spatial (and temporal) resolution that will be required for crop management. Although the use of balloons can provide relatively cheap means of suspending sensors over an orchard, their deployment is severely limited by high winds, so they cannot be recommended for general use. Even higher resolution and precision can be achieved by mounting sensors on in-field platforms such as tractors or even by using fixed sensor networks with data uploaded to a central server (possibly in the ‘cloud’) by telemetry. The increasing sophistication of UAVs and their ready availability at surprisingly low cost (generally less than \$10,000 including all the control gear) means that UAVs are likely to soon become the platform of choice for many applications. Software is now readily available that allows one to mosaic a whole series of images from a micro-UAV to generate an ‘image’ of the whole field or orchard; it is even possible to generate stereographically a high precision digital elevation model that can be used to estimate canopy height and extent using cheap RGB cameras. The advantages and disadvantages of different platforms for remote sensing are outlined in Table 1.

Although UAVs offer tremendous potential for precision agriculture and general farm management, it is worth pointing out that most currently available rotary wing UAVs (quadrocopters, hexacopters, etc.) have very limited payloads (often <1 kg),

limited endurance (often restricted to about 15 min flying time) and range (usually less than about 500 m to remain within good view of the pilot). Such systems would probably only be able to map up to 10 ha per hour with multiple battery changes. This range limitation may be less of a problem to fruit growers than for broad-acre agriculture and can be partially overcome by the use of larger (but more expensive) fixed wing UAVs. Although many commercial systems are currently available, they are largely set up solely for mapping purposes using simple RGB cameras; where one seeks more sophisticated measurements of use for advanced crop management (such as thermal) further development or modification is normally required.

Considerations in the choice of sensor platform include: cost of data acquisition and subsequent analysis; timeliness and frequency of image availability (satellites such as Landsat only overfly any one spot every 16 days – even then clouds may obscure the image); spatial resolution (for some purposes pixels need to be the same size as individual leaves – i.e. a few cm – while larger pixels will contain mixed pixels from which it may be difficult to extract information about the leaf component) (Jones & Sirault, 2014); flexibility of data acquisition in relation to farm requirements is also critical.

In order to get some idea of the potential capacity of such technologies to revolutionise fruit culture it is necessary to consider the range of sensors that are available and their potential application to different aspects of crop management or crop improvement. Available sensor technologies are outlined in Table 2. Optical sensors (including RGB cameras and multi- or hyperspectral sensors) depend on reflection from the vegetation and especially on the characteristic low reflectance of leaves and canopies in the visible or red (R) and high reflectance in the near infrared (NIR). This behaviour is quite different from that of alternative targets such as soil where reflectance changes rather slowly with wavelength, and provides the basis for many of the ‘vegetation indices’ that have been proposed (see e.g. Jones & Vaughan, 2010). The best known example of a vegetation index is the normalised difference vegetation index ( $NDVI = (NIR - R)/(NIR + R)$ ). This provides a useful measure of canopy greenness or vegetation cover when applied to satellite data. By making use of the characteristic reflection spectra of various metabolites and biochemicals in leaves, indices composed of other wavelength combinations, particularly when narrow-band hyperspectral sensors are available, are increasingly being developed for diagnosis and monitoring of changes in plant or tissue water status or biochemical content (Blackburn, 2007; Jones & Vaughan, 2010). It is even possible to monitor processes such as photosynthesis using hyperspectral indices such as the photochemical reflectance index (PRI) which is based on the detection of the epoxidation state of xanthophyll pigments in chloroplasts as a measure of photosynthesis (Gamon *et al.*, 1992), by the use of solar induced chlorophyll fluorescence measurements (Meroni *et al.*, 2009) or by using laser induced fluorescence transients (LIFT; Kolber *et al.*, 2005). Although many of these techniques work well in controlled environments where one may be viewing only single leaves, when applied in tree canopies in the field it is necessary to take account of the varying illumination from leaf to leaf, possibly by means of radiation transfer models such as SAIL (Jacquemoud, 1993). This will be a continuing challenge in future developments of proximal remote sensing for crop management.

Similar considerations affect the use of thermal sensors in the field, as leaf temperature is a function of local environmental conditions, including especially irradiance, with sunlit leaves tending to be much warmer than shaded leaves. Nevertheless, where suitable methods are adopted to correct for environmental variation,

such as the use of physical or virtual reference surfaces (Guilioni *et al.*, 2008; Jones, 1999), it is possible to get good estimates of stomatal conductance or evaporation rate as proxy indicators of plant water stress. Combining thermal estimates of transpiration rate with estimates of photosynthesis from chlorophyll fluorescence or the hyperspectral PRI could in principle even allow estimation of water use efficiency in the field, though thus far this approach has only been successfully applied in the laboratory (McAusland *et al.*, 2013).

Proximal sensors mounted on tractors or other in-field platforms can provide valuable information on crop canopy structure and even estimates of crop yield. Stereo photography allows reconstruction of detailed 3D canopy structure, while increasingly the availability of mobile Lidar scanners as well as Time-of-flight cameras and even ultrasonic sensors has greatly enhanced the repertoire of tools available for real-time generation of canopy structure maps to guide crop management (Jones & Vaughan, 2010).

Although remote sensing provides an extremely powerful tool for crop managers, it is necessary to note that a number of precautions must be taken when applying such technologies. Perhaps the most obvious is the mixed pixel problem where it can be difficult to extract the critical information from pixels containing both leaf and background soil; a number of techniques are available to improve the extraction of relevant information, such as canopy temperature, but none are perfect (Jones & Sirault, 2014). It is also true that too small a pixel can be as bad, or worse than, too large a pixel, as variability increases as pixels get smaller and the exponential increase in data volume can lead to problems in data management so that inevitably some data reduction will be required to allow effective data processing. Another common problem with remote sensing of crop characteristics or function can be the difficulty of obtaining accurate predictions from the proxy measures obtained remotely. For example, Jones (2014b) showed that even when one has a good correlation ( $r^2 > 0.9$ ) between a proxy measure such as NDVI and a physiological character such as canopy nitrogen content (N), prediction of N from NDVI can be subject to substantial errors.

### **Molecular biology and ‘Omics technologies**

Not entirely separate from the technological and big-data considerations discussed above are the capabilities provided, especially to plant breeders, but also to crop managers, of the new genetic tools. Molecular biology is revolutionising the way we can do things, but unfortunately too many recent graduates who might call themselves plant physiologists may have rather little understanding of the physiology of how plants function in the field and the natural compensatory mechanisms that can occur. There is still often a too-naïve belief in the simplicity of inserting single ‘magic’ genes to achieve improvements in yield or stress tolerance. The problem is well illustrated by a recent meta-analysis of over 500 reports of attempts to improve drought tolerance by gene manipulation (Blum, 2014). Although more than 100 separate genes have been used in attempts to improve drought tolerance, they have often been selected in inappropriate experiments in artificial environments (see Table 1) that take no account of the real interactions and compensations between genes that occur in the field. The result has been that extremely few putative drought tolerant GM lines have thus far been released to farmers or growers even in cereal crops which are far ahead of fruit crops.

Any physiologist would recognise that drought tolerance in terms of crop yield under limited water supply involves a complex interaction (Jones, 2014a) between one or more of the following component mechanisms:

- (a) conservation of water (through stomatal closure, cuticular modifications, changes in leaf area, etc.)
- (b) improved water uptake (though altered rooting patterns)
- (c) maintenance of cell function at lower  $\psi_{\text{tissue}}$  (e.g. by osmotic adjustment )
- (d) changes in harvest index/partitioning
- (e) improved survival

Thus the conventional molecular geneticist's tools of selecting genes with differing expression under artificial conditions such as desiccation of tissue on a bench, or total withholding of water until death are unlikely to identify the real key genes controlling yield under drought. A few years ago I reported (Jones, 2007) on a rather simple survey of molecular papers at that time that related to drought tolerance and showed that especially in the more molecular plant journals (*Plant Cell*, *Plant Physiology*, *Plant Journal* and *Plant Molecular Biology*) over 55% of papers had no measure of plant water status by which to evaluate any physiological responses. Furthermore, in most of these cases the drought treatments used were far removed from natural drought progression in the field. In order to see if anything has improved in the past eight years I conducted an even briefer sample survey, taking the first 20 papers from a search (on 10 March 2014) of the Plant Physiology website (<http://www.plantphysiol.org/search>) that came up in response to a search for "drought" in the title. After eliminating the two non-molecular papers on plant water relations, the remaining molecular papers included only 4 (22%) that had any measure of plant water status and only 66% measured physiological responses such as stomatal aperture or photosynthesis (Table 3). On the other hand, the situation regarding severity of treatment has somewhat improved over the intervening eight years with only about 33% of the papers only using extreme drought treatments with the remainder including some attempt at more moderate water deficit treatments (Table 3). Nevertheless, only one paper (Harb *et al.*, 2010) took any explicit account of the potential effects of differing plant size or stomatal conductance on the rate of drought development to ensure that all genotypes had achieved comparable soil or tissue water stress, others generally assumed that drought severity was simply a function of time (or soil moisture content); assumptions that can lead to very misleading results.

I would argue that the most rapid progress with molecular studies on drought tolerance can only be achieved when the researchers actually measure plant water status and compare plants under similar tissue water status. As has been cogently argued by Blum (2014) progress in breeding for drought tolerance will only speed up when the approaches used take more recognition of how plants adapt and respond under natural conditions. At least there is evidence that molecular biologists are now starting to recognise that drought tolerance is complex and that genetic engineering solutions will need to recognise this, with one paper stating that "*We propose that one significant challenge will be to unravel the complex mechanisms of drought resistance in crops through more intensive and integrative studies . . . .*" (Hu & Xiong, 2014).

Future progress in fruit physiology research will depend on effective collaboration between molecular biologists and physiologists. Molecular biology provides a set of fantastic tools; these are not just the ability to insert genes to change some particular crop characteristic, but probably even more importantly the ability to use transgenic plants and reverse genetics as tools to improve our understanding of physiological responses and the underlying mechanisms. Molecular biology should therefore not be regarded as a 'bogey man' and our efforts need to be concentrated on helping molecular scientists design better and more discriminatory molecular experiments, avoiding the pitfalls inherent in doing



simple molecular screens in atypical environments as discussed above.

### **Some other opportunities**

There are a wide range of other scientific opportunities that have unrealised potential to impact on fruit production in the coming years. These will include further advances in many of the areas in which there have already been substantial improvements in the past couple of decades, including for example further improvements in irrigation, nutrition and soil management as well as in the use of plant growth regulators. There is also much unrealised potential in topics that have been known for many years but which have not yet found wide application: I will just highlight one here. This is the use of microbial assistant species including growth-promoting soil rhizobacteria (Belimov *et al.*, 2008) and fungi (Windham *et al.*, 1986). Recent increases in understanding of the mechanisms by which such organisms can promote growth suggest that their wider application and the development or selection of improved genotypes could potentially have significant impact in the future fruit crop production.

### **OTHER ASPECTS IMPACTING ON HORTICULTURAL RESEARCH**

As I outlined above, the future of horticultural research and development depends critically on external socio-economic factors. One such is that significant advances in horticultural science of fruit crops will depend critically both on adequate funding for research and on the availability of well trained scientists to do the research and on appropriately trained growers and agronomy specialists to ensure that these advances are developed in a ways that can be adopted by the industry.

### **Research Funding**

The availability of research funding is determined both by government policy and by grower sentiment is a key factor that determines both the general fields of research conducted and increasingly the detail. Historically the more basic and fundamental science has been funded by government or government agencies, while the more practical application largely depends on funding from growers. Unfortunately, to my mind, there has been too much of a shift away from funding for ‘blue skies’ or even basic research towards short-term problem solving and technology transfer, especially that driven by the withdrawal of government funding and its increasing replacement by a need for grower funding. Although this is a world-wide trend the degree does vary substantially between countries. Not surprisingly growers are primarily concerned with short-term solutions to current problems and less willing to underpin the longer term projects that are likely to lead to the major advances.

The research funding climate has changed substantially over the past 40 years, first in the UK, and then in many countries worldwide, following publication of the Rothschild report in 1971 (Rothschild, 1971), which reversed the earlier Haldane principle (the idea that decisions on research funding should be made by researchers rather than politicians – named after the report of the Haldane committee (Haldane, 1918)) and where funders aimed to support the best scientists. A similar principle in Germany under laid the Kaiser Wilhelm Society (from its establishment by Adolph von Harnack in 1911) though to its successor the Max Planck Society which continues the tradition of its predecessor institution with the structural principle of the person-centered research organization (<http://www.mpg.de/183251/portrait>). Following Rothschild, there has been much greater concern worldwide for an increasing proportion of government

research funding to be directed at solving specific practical problems, and as an economic tool to drive economic growth (e.g. by getting industry involved to take on the basic ideas and develop them into new products and wealth). Admittedly the UK has often been seen as a good example of a research system producing the new ideas, but where others have made the money from them.

This shift has occurred in spite of the fairly wide recognition that many advances have been made entirely serendipitously (e.g. the world-wide-web, Teflon, monoclonal antibodies, etc.), while in fruit cultivation many plant growth regulators were not developed with fruit as a target. Interestingly, earlier, when Rothschild was head of the Agricultural Research Council (ARC) in Britain he gave a speech at the 50<sup>th</sup> anniversary of LARS in 1955 (Rothschild, 1953) where he was particularly proud of the fact that the ARC had aimed to fund the best scientists without constraining their work quoting as examples Fisher, Yeates, Darlington, etc.; this is in direct contrast to his later proposals. There are continuing calls to reinvigorate the current funding models to encourage better support for young scientists and to improve funding stability while freeing up scientists to spend a greater proportion of their time on research than is currently possible (Alberts *et al.*, 2014).

### **Training**

The quality and availability of good and appropriate training both for young scientists and for farmers and extension workers is crucial for future development of the fruit industry. Unfortunately there is an increasing problem with the level and content of training in many current plant science courses. There is a shift towards a greater emphasis on molecular studies almost to the exclusion of more physiological components of the subject, with many researchers trained in the top universities now having only superficial understanding of the complexity of plant functioning. This is illustrated by the common rather naive expectation among many (see Blum, 2014) that simple single gene solutions exist to breeding improved crops with enhanced drought tolerance as we discussed above. Similarly there is a real need to instil an understanding that results in controlled environments and even less those *in vitro* do not generally represent those expected in the field, while in many cases even pot size plays a crucial role on determining the results obtained (Poorter *et al.*, 2012). This shift in plant science courses towards molecular studies may be related to the perception that agronomy and whole-plant studies are often considered to be second-class studies, partly because work in these fields tends to be published in less-cited journals than does the more molecular research. Associated with this is the perception that agronomy is low on the list of preferred careers and in many places it is difficult to attract the best students.

A second problem that results from limited training in conventional plant physiology is that often students, and indeed the teachers, are not well versed in the older physiological literature published before the internet age. This is partly because much of the older literature is not as readily available on the internet as are publications since c.1997. At least in the UK, many libraries and universities do not subscribe to archival databases that cover the older literature, though encouragingly, in Australia both the organisations with which I am associated (CSIRO and the University of Western Australia) do subscribe to these older archives. I consider that it is crucial for researchers to learn from history and to read older papers before designing and starting new projects to ensure that we benefit from the lessons learned and avoid much wasted effort and repetition of mistakes that have been made before.

## CONCLUSIONS

There is every reason to expect that the pace of developments in fruit crop physiology will increase in the coming years, primarily as a result of developments in areas such as information technology and remote sensing, but also as a result of developments in molecular biology that will enhance the rate of increase of our understanding of the endogenous mechanisms involved in the control of plant growth. The impact of molecular biology will, however, only be optimal if there is a true collaboration between molecular biologists and physiologists; methods must be found to ensure that effective collaborations are encouraged. I would expect the most rapid advances only if we can encourage more scientists with vision who are willing to 'go out on a limb' with speculative, or even wacky, ideas of the same scale as Luckwill's meadow orchard. But this will only occur if funders allow a significant proportion of speculative science in their portfolio.

It will also be important to ensure that horticulture does not lag any further behind other plant sciences. There are several steps that will be needed to ensure the future of horticultural research, among which I would argue that there is a need for us to improve the rigour in horticultural journals. Currently there are too many papers published that lack the presentation of broader unifying concepts and simply represent large amounts of undigested data, and often lack rigorous experimental design. It will also be necessary to improve systems for archiving and access to all raw experimental data to allow effective meta analysis and to ensure that unnecessary repetition of experiments is avoided. All authors should be required to archive their raw data on appropriate online databases.

It will also be necessary in the future to convince the public that crop improvements including genetic manipulation are of positive benefit to the consumer. In 1972, at the time of the proposal of meadow orchards, John Craven, then a young reporter on the BBC's Points West programme, asked the Long Ashton Research Station director, John Hudson: "*Do you think this messing about with nature could be harmful?*"

"*Oh no, not at all,*" answered Hudson. "*We're not messing about with nature, we're improving on nature.*"

This response holds as well today, even in the era of genetic modification, as it did then.

## ACKNOWLEDGEMENTS

I am very grateful to the organisers of the ISHS Symposium "Physiological Principles and Their Application to Fruit Production" for their invitation to present this paper, and to all my many colleagues over more than 40 years for their support and many stimulating discussions.

## Literature Cited

- Alberts B, Kirschner MW, Tilghman S, Varmus H (2014) Rescuing US biomedical research from its systemic flaws. *Proceedings Of The National Academy of Sciences of The United States of America* **111**, 5773-5777.
- Atkinson CJ, Brennan RM, Jones HG (2013) Declining chilling and its impact on temperate perennial crops. *Environmental and Experimental Botany* **91**, 48-62.
- Belimov AA, CDodd IC, Hontzeas N, Theobald JC, Safronova VI, Davies WJ (2008) Rhizosphere bacteria containing 1-aminocyclopropane-1-carboxylate deaminase increase yield of plants grown in drying soil via both local and systemic hormone

- signalling. *New Phytologist* **181**, 413-423.
- Belward AS, Skøien JS (2014) Who launched what, when and why; trends in global land-cover observation capacity from civilian earth observation satellites. *ISPRS Journal of Photogrammetry and Remote Sensing*  
<http://dx.doi.org/10.1016/j.isprsjprs.2014.03.009>.
- Blackburn GA (2007) Hyperspectral remote sensing of plant pigments. *Journal of Experimental Botany* **58**, 855-867.
- Blum A (2014) Genomics for drought resistance – getting down to earth. *Functional Plant Biology*.
- Bu Q, Lv T, Shen H, Luong P, Wang J, Wang Z *et al.* (2014) Regulation of drought tolerance by the F-box protein MAX2 in Arabidopsis. *Plant Physiology* **164**, 424-439.
- Chalmers DJ, Mitchell PD, Vanheek L (1981) Control of peach-tree growth and productivity by regulated water supply, tree density and summer pruning. *Journal of the American Society for Horticultural Science* **106**, 307-312.
- Chen J-H, Jiang HW, Hsieh EJ, Chen H-Y, Chein CT, Hsieh HL, Lin T-P (2012) Drought and salt stress tolerance of an Arabidopsis glutathione S-transferase U17 knockout mutant are attributed to the combined effect of glutathione and Abscisic Acid. *Plant Physiology* **158**, 340-351.
- Davis KJ, Stover E, Wirth F (2004) Economics of fruit thinning: A review focusing on apple and citrus. *HortTechnology* **14**, 282-289.
- Du H, Wang N, Cui F, Li X, Xiao J, Xiong L (2010) Characterization of the b-Carotene hydroxylase gene DSM2 conferring drought and oxidative stress resistance by increasing xanthophylls and Abscisic Acid synthesis in rice. *Plant Physiology* **154**, 1304-1318.
- Erez A (1984) Peach meadow orchards. In *International Conference on Peach Growing. Acta Horticulturae* **173**, 405-412.
- Fereres E, Soriano MA (2007) Deficit irrigation for reducing agricultural water use. *Journal of Experimental Botany* **58**, 147-159.
- Gamon JA, Peñuelas J, Field CB (1992) A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment* **41**, 35-44.
- Guilioni L, Jones HG, Leinonen I, Lhomme JP (2008) On the relationships between stomatal resistance and leaf temperatures in thermography. *Agricultural and Forest Meteorology* **148**, 1908-1912.
- Haldane V (1918) *The Haldane Report (1918). Report of the Machinery of Government Committee under the chairmanship of Viscount Haldane of Cloan. London: HMSO. HMSO, Ondon.*
- Harb A, Krishnan A, Ambavaram MMR, Pereira A (2010) Molecular and physiological analysis of drought stress in Arabidopsis reveals early responses leading to acclimation in plant growth. *Plant Physiology* **154**, 1254-1271.
- Hu H, Xiong L (2014) Genetic engineering and breeding of drought-resistant crops. *Annual Review of plant Biology* **65**, 715-741.
- Jacquemoud S (1993) Inversion of PROSPECT + SAIL canopy reflectance model from AVIRIS equivalent spectra: Theoretical study. *Remote Sensing of Environment* **44**, 281-292.
- Jeong JS, Kim Y, S., Baek KH, Jung H, Ha S-H, Choi YD *et al.* (2010) Root-specific expression of OsNAC10 improves drought tolerance and grain yield in rice under

- field drought conditions. *Plant Physiology* **153**, 185-197.
- Jones HG (1999) Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. *Plant Cell and Environment* **22**, 1043-1055.
- Jones HG (2007) Monitoring plant and soil water status: established and novel methods revisited and their relevance to studies of drought tolerance. *Journal of Experimental Botany* **58**, 119-130.
- Jones HG (2014a) *Plants and microclimate: a quantitative approach to environmental plant physiology*. (3rd. ed.). Cambridge University Press, Cambridge.
- Jones HG (2014b) The use of indirect or proxy markers in plant physiology. *Plant, Cell & Environment* **37**.
- Jones HG, Sirault XRR (2014) Scaling of thermal images at different spatial resolution: the mixed pixel problem. *Agronomy* (**submitted**).
- Jones HG, Vaughan RA (2010) *Remote sensing of vegetation: principles, techniques, and applications*. Oxford University Press, Oxford.
- Kakumanu A, Ambavaram MMR, Klumas C, Krishnan A, Batlang U, Myers E *et al.* (2012) Effects of drought on gene expression in maize reproductive and leaf meristem tissue revealed by RNA-Seq. *Plant Physiology* **160**, 846-847.
- Klinkenberg J, Faist H, Saupe S, Lambertz S, Krischke M, Stingl N *et al.* (2014) Two fatty acid desaturases, STEAROYL-ACYL CARRIER PROTEIN D9-DESATURASE6 and FATTY ACID DESATURASE3, are involved in drought and hypoxia stress signaling in Arabidopsis crown galls. *Plant Physiology* **164**, 570-583.
- Kolber Z, Klimov D, Ananyev G, Rascher U, Berry J, Osmond BA (2005) Measuring photosynthetic parameters at a distance: laser induced fluorescence transient (LIFT) method for remote measurements of photosynthesis in terrestrial vegetation *Photosynthesis Research* **84**, 121-129.
- Lawes GS, Woolley DJ (2001) The commercial use of plant growth regulators to regulate fruit development. *Acta Horticulturae* **553**, 149-150.
- Luckwill LC (1978) Meadow orchards and fruit walls. *Acta Horticulturae* **65**, 237-244.
- Luckwill LC, Child RD (1973) The meadow orchard – a new concept of fruit production based on growth regulators. *Acta Horticulturae* **34**, 213-220.
- McAusland L, Davey PA, Kanwal N, Baker NR, Lawson T (2013) A novel system for spatial and temporal imaging of intrinsic plant water use efficiency. *Journal of Experimental Botany* **64**, 4993-5007.
- Meroni M, Rossini M, Guanter L, Alonso L, Rascher U, Colombo R, Moreno J (2009) Remote sensing of solar-induced chlorophyll fluorescence: Review of methods and applications. *Remote Sensing of Environment* **113**, 2037-2051.
- Mitchell PD, Chalmers DJ (1982) The effect of reduced water supply on peach tree growth and yields. *Journal of the American Society for Horticultural Science* **107**, 853-856.
- Ning Y, Jantasuriyarat C, Zhao Q, Zhang HR, Chen S, Liu J *et al.* (2011) The SINA E3 ligase OsDIS1 negatively regulates drought response in rice. *Plant Physiology* **157**, 242-255.
- Parkinson KJ, Legg BJ (1972) A continuous flow porometer. *Journal of Applied Ecology* **17**, 457-460.
- Pedersen SM, Fountas S, Have H, Blackmore BS (2006) Agricultural robots—system analysis and economic feasibility. *Precision Agriculture* **7**, 295-308.

- Phung T-H, Jung H-I, Park J-H, Kim J-G, Back K, Jung S (2011) Porphyrin biosynthesis control under water stress: Sustained porphyrin status correlates with drought tolerance in transgenic rice. *Plant Physiology* **157**, 1746-1764.
- Poorter H, Bühler J, van Dusschoten D, Climent J, Postma JA (2012) Pot size matters: a meta-analysis of rooting volume on plant growth. *Functional Plant Biology* **39**, 839-850.
- Prasch CM, Sonnewald U (2013) Simultaneous application of heat, drought, and virus to Arabidopsis plants reveals significant shifts in signaling networks. *Plant Physiology* **162**, 1849-1866.
- Riboni M, Galbiati M, Tionelli C, Conti L (2013) GIGANTEA enables drought escape response via abscisic acid-dependent activation of the florigens and *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1*. *Plant Physiology* **162**, 1706-1719.
- Rothschild L (1953) The jubilee lecture: Agricultural research 1953. In: *Science and fruit* (eds Wallace T & Marsh RW), pp. 1-10. Bristol University Press, Bristol.
- Rothschild L (1971) *The Rothschild Report (1971). A Framework for Government Research and Development*. HMSO, London.
- Sadras VO (2009) Does partial root-zone drying improve irrigation water productivity in the field? A meta-analysis. *Irrigation Science* **27**, 183-190.
- Savchenko T, Kolla VA, Wang C-Q, Nasafi Z, Hicks DR, Phadungchob B *et al.* (2014) Functional convergence of oxylipin and abscisic acid pathways controls stomatal closure in response to drought. *Plant Physiology* **164**, 1151-1160.
- Schettini E, De Salvador FR, Scarascia-Mugnozza G, Vox G (2011) Radiometric properties of photoselective and photoluminescent greenhouse plastic films and their effects on peach and cherry tree growth *Journal of Horticultural Science & Biotechnology* **86**, 79-83.
- Seiler C, Harshavardhan I a VT, Reddy PS, Hensel G, Kumlehn K, Eschen-Lippold L *et al.* (2014) Abscisic acid flux alterations result in differential ABA signalling responses and impact assimilation efficiency in barley under terminal drought stress. *Plant Physiology* **164**, 1677-1696.
- Slatyer RO, Jarvis PG (1966) Gaseous-diffusion porometer for continuous measurement of diffusive resistance of leaves. *Science* **151**, 574-576.
- Sorensen CG, Fountas S, Nash E, Pesonen L, Bochtis D, Pedersen SM *et al.* (2010) Conceptual model of a future farm management information system. *Computers and Electronics in Agriculture* **72**, 37-47.
- Stoll M, Dry P, Loveys B, Stewart D, McCarthy M (2000) Partial rootzone drying. Effects on root distribution and commercial application of a new irrigation technique. *Australian & New Zealand Wine Industry Journal* **15**, 74-76.
- Tang N, Zhang HR, Li X, Xiao J, Xiong L (2012) Constitutive activation of transcription factor OsbZIP46 improves drought tolerance in rice. *Plant Physiology* **158**, 1755-1768.
- Van Houtte H, Vandesteene L, López-Galvis L, Lemmens L, Kissel E, Carpentier S *et al.* (2013) Overexpression of the trehalase gene AtTRE1 leads to increased drought stress tolerance in Arabidopsis and is involved in Abscisic Acid-induced stomatal closure. *Plant Physiology* **161**, 1158-1171.
- Windham MT, Elad Y, Baker R (1986) A mechanism for increased plant growth induced by *Trichoderma* spp. *Phytopathology* **76**, 518-521.
- Yu L, Chen X, Whang Z, Wang S, Wang Y, Zhu QJ *et al.* (2013) Arabidopsis *Enhanced*

*Drought Tolerance1/HOMEODOMAIN GLABROUS11* confers drought tolerance in transgenic rice without yield penalty. *Plant Physiology* **162**, 1378-1391.

Zhou XF, Jon YH, Yoo CY, Lin X-L, Kim WY, Yun D-J *et al.* (2013) CYCLIN H;1 regulates drought stress responses and blue light-induced stomatal opening by inhibiting reactive oxygen species accumulation in Arabidopsis. *Plant Physiology* **162**, 1030-1041.

## Tables

Table 1. The advantages and disadvantages of different remote sensing platforms

Platform	Features
Satellite	Cloud-limited (ex. radar); low spatial resolution (trade-off with frequency/cost); good for weather/mapping; poor for crop management
Airborne (piloted) UAV	Below cloud; higher resolution; flexible deployment v. high resolution; very flexible deployment; low cost; generally excellent potential; but low payload and short range
Balloon	Rarely useable because of wind
Tractor-mounted	Readily incorporated into on-farm management; v. high resolution
Fixed sensor network	Limited coverage; need to correct for perspective if mounted on single sites; capital cost.

Table 2. Remote sensing sensor technologies and their potential applications to fruit production.

Sensor	What measured	Application
RGB cameras	Visible reflectance	Canopy size, cover, LAI
Spectral reflectance	Visible/NIR reflectance	Cover, pigments, chl, N, etc.
Thermal infrared	Temperature	Evaporation, stomata, stress
Microwave (Radar)	Water; canopy structure	Water content
Lidar	Canopy structure	Canopy structure, height
'Time-of-flight' cameras	Canopy structure	Canopy structure
Ultrasonic sensors	Canopy structure	Canopy height
Fluorescence	Emitted visible/NIR	Photosynthesis, pigments

Abbreviations: chl – chlorophyll; LAI – leaf area index; N – nitrogen; NIR – near infrared



Table 3. The 18 molecular papers retrieved by a search (10 Mar 2014) on “drought” on the website of *Plant Physiology* (after excluding two water relations papers).

Reference	Drought imposition	Water status measurement
Bu et al., (2014)	M – S (drying on bench and withholding water)	None (stomatal aperture; water loss rate of leaves)
Chen et al., (2012)	S (withholding water 10d)	None (water loss by leaves; ABA)
Du et al., (2010)	M – S (survival) by withholding water <b>ii. M Field</b>	<b>RWC</b> (water loss; gas-exchange; chl fluorescence)
Harb et al., (2010)	M (30% field capacity - gravimetric)	None (gas-exchange; ABA; SMC)
Jeong et al., (2010)	i. S (survival) ii. S (air dried tissue) <b>iii. M in field (yield components)</b>	None (measured survival; chl fluorescence; SMC; yield in field)
Kakumanu et al., (2012)	M (withholding water 21.5% SMC)	<b>RWC</b> (gas exchange; chl fluorescence; SMC)
Klinkenberg et al., (2014)	Unclear (humidity?)	None
Lakshmanan et al., 2013	Unclear (?osmotic)	None
Ning et al., (2011)	i. S (dried on filter paper) ii. S (no water for >6 d) (survival)	None
Phung et al., (2011)	M – S (withholding water)	$\psi_{\text{stem}}$ (bomb); <b>RWC</b> (chl fluorescence)
Prasch & Sonnewald, (2013)	<b>M – watered to 30% field capacity (soil probe)</b>	$\psi_{\text{leaf}}$ (psychrometer)
Riboni et al., (2013)	M – watered to 30% RSWC (gravimetric)	None
Savchenko et al., (2014)	S? (no water for 10d)	None (stomata aperture; PS)
Seiler et al., (2014)	S (10% SMC – soil probe)	None (gas analysis)
Tang et al., (2012)	S? (withholding water)	None (leaf water loss rate)
Van Houtte et al., (2013)	M? (watered to 22% SMC)	None (SMC; stomatal aperture; thermal imagery)
Yu et al., (2013)	<b>i. M? (pot withholding water)</b> <b>ii. M (field trial)</b>	None (cut leaf water loss rate; ABA; gas exchange)
Zhou et al., (2013)	M? (withholding water)	None (water loss rates; stomatal aperture)
Summary		Tissue water status: 4 Physiological responses: 12

Abbreviations: M – moderate; S – severe; ABA – abscisic acid; chl - chlorophyll; PS – photosynthesis; RWC – relative water content; SMC soil moisture content;  $\psi$  water potential