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Letters

One hundred important questions facing plant science research

Introduction

Plant science has never been more important. The growing and increasingly prosperous human population needs abundant safe and nutritious food, shelter, clothes, fibre, and renewable energy, and needs to address the problems generated by climate change, while preserving habitats. These global challenges can only be met in the context of a strong fundamental understanding of plant biology and ecology, and translation of this knowledge into field-based solutions.

Plant science is beginning to address these grand challenges, but it is not clear that the full range of challenges facing plant science is known or has been assessed. What questions should the next generation of plant biologists be addressing? To start to answer this question we set out to compile a list of 100 important questions facing plant science research.

We had three main goals.

(1) We aimed to stimulate discussion amongst the plant science and related communities, and identify areas of research that would have a substantial impact.

(2) We hoped to encourage plant scientists to think beyond the limits of their own sphere of research and consider the most important research that could possibly be carried out.

(3) We sought to illustrate the importance and potential of plant science to the broader public.

This paper addresses aims 1 and 2, but questions were selected with all three aims in mind. This is intended to be a starting point. Research priorities and challenges change continuously and unpredictably as new concerns and needs arise, and new knowledge is revealed, and it will be important to review and reassess this list in the future. Here we present, with brief explanations of their significance, our list of the important questions facing plant science research today.

Methods

Questions were invited online over a 3-month period at http://www.100plantsciencequestions.org.uk/index.php. The website was publicized by email using distribution lists of plant scientists in the UK and abroad, on websites aimed at plant scientists and farmers, and in a press release, which led to coverage by some news websites and newspapers. The questions submitted to the website are listed in full at http://www.100plantsciencequestions.org.uk/viewquestions.php, along with the names of the people who submitted them, apart from a few cases where submitters chose to be anonymous. The online consultation process allowed input from contributors with a range of nationalities and experience. The full list of 350 questions was provided in advance to a panel of 15 individuals (Steve Barnes, Ruth Bastow, Mark Chase, Matthew Clarke, Claire Grierson, Alastair Fitter, Don Grierson, Keith Edwards, Graham Jellis, Jonathan Jones, Sandy Knapp, Giles Oldroyd, Guy Poppy, Paul Temple and Roger Williams) representing the academic, commercial and public service communities that produce or benefit from plant science research, and able to take part in a 2-d workshop at Bristol (UK) in 2009. During the process the list was reduced to 96 questions by mutual agreement, which we hope will stimulate more local variants particularly adapted to research and societal priorities in both the developing and developed world. Before the panel meeting the full list of 350 submitted questions was roughly organized into groups according to topic. Each panel member independently selected their top 20 questions and these lists were combined. During this process other possible questions under each topic were suggested and considered for inclusion. Each question selected by a panel member was discussed by the whole panel, along with other questions that addressed similar issues. The most important question on each topic was agreed upon by the whole panel and a final wording chosen. In some cases the panel decided that a new question was required, and the panel worked together to produce the wordings for these new questions.

Results and Discussion

As plant science is a broad and diverse field, we provide brief explanations of the background, context and prospects for addressing each question with the aim of making the questions accessible to the broadest possible audience.

There is no ideal way to divide the questions into topic areas. Many questions inevitably and desirably span more than one category, and some particularly substantial topics merit multiple questions. For the purposes of this paper, the panel decided to categorize the questions into five broad areas that reflect the breadth and depth of plant research discussed during the 2-d workshop: Society, Environment and adaptation, Species interactions, Understanding and utilizing plant cells, and Diversity.

A. Society

Here we consider the overall significance of plants and plant science to human society in general. We open with 10 questions that the panel felt encapsulated the most burning societal issues that should be addressed by plant science, followed by other societal questions selected by the panel. More specific biological questions in plant science follow in later sections.

The 10 questions most important to society

A1. How do we feed our children's children?

By 2050 the world population will have reached *c.* 9 billion people. This will represent a tripling of the world population within the average lifetime of a single human being. The population is not only expanding, but also becoming more discerning, with greater demands for energy-intensive foods such as meat and dairy. Meeting these increasing food demands over the years to come requires a doubling of food production from existing levels. How are we going to achieve this? Through the cultivation of land currently covered in rainforests, through enhanced production from existing arable land or by changing people's habits to change food consumption patterns and reduce food waste? The reality is probably a combination of all three. However, if we are to reduce the impact of food production on the remaining wilderness areas of the planet then we need significant investment in agricultural science and innovation to ensure maximum productivity on existing arable land.

A2. Which crops must be grown and which sacrificed, to feed the billions?

The majority of agricultural land is used to cultivate the staple food crops wheat (*Triticum aestivum*), maize (*Zea mays*) and rice (*Oryza sativa*), the oil-rich crops soy (*Glycine max*), canola (*Brassica napus*), sunflower (*Helianthus* spp.) and oil palm (*Elaeis guineensis*) and commodity crops such as cotton (*Gossypium* spp.), tea (*Camellia sinensis*) and coffee (*Coffea* spp.). As the world population expands and meat consumption increases, there is a growing demand for staples and oil-rich crops for both human needs and animal feed. Without significant improvements in yields of these basic crop plants, we will experience a squeeze on agricultural land. It is therefore essential that we address the yield gap; the difference between future yield requirements and yields available with current technologies, management and gene pools. Otherwise we may be forced to choose between production of staple food crops to feed the world population and the production of luxury crops, such as tea, coffee, cocoa (*Theobroma cacao*), cotton, fruits and vegetables.

A3. When and how can we simultaneously deliver increased yields and reduce the environmental impact of agriculture?

The first green revolution of the late 1950s and early 1960s generated unprecedented growth in food production. However, these achievements have come at some cost to the environment, and they will not keep pace with future growth in the world population. We need creative and energetic plant breeding programmes for the major crops world-wide, with a strong public sector component. We need to explore all options for better agronomic practice, including better soil management and smarter intercropping, especially in the tropics. Finally, we need to be able to deploy existing methods of genetic modification that reduce losses to pests, disease and weeds, improve the efficiency of fertilizer use and increase drought tolerance. We also need to devise methods to improve photosynthetic efficiency, and move the capacity for nitrogen fixation from legumes to other crops. These are all desirable and, with public support, feasible goals.

A4. What are the best ways to control invasive species including plants, pests and pathogens?

Invasive species are an increasingly significant threat to our environment, economy, health and well-being. Most are nonindigenous (evolved elsewhere and accidentally introduced) and have been removed from the constraints regulating growth in their native habitat. The best method of control is to prevent establishment in the first place or to quickly identify establishment and adopt an eradication programme. However, if an invasive species becomes established many of the options for removal can cause environmental damage, for example chemical control or mechanical excavation. Biological control (introduction of a natural predator/pathogen) can work well as long as the control organism targets only the invasive species. Otherwise there is a risk that the control organism might also become an invasive species. Alternatives, such as manipulating existing natural enemies and/or the environment to enhance biological control, are also being developed. Sustainable solutions are required if we are to deal with the continually growing problem of invasive species.

A5. Considering two plants obtained for the same trait, one by genetic modification and one by traditional plant breeding techniques, are there differences between those two plants that justify special regulation?

The products of traditional plant breeding are subject to no special regulations, even though the wild sources of germplasm often used by breeders may contain new components that have not been assessed before. A plant derived by genetic modification, however, is highly regulated, even though the target genotype and the modification itself may both be highly characterized and accepted as innocuous for their intended use. This is a major exception to the norm for safety regulation in food and other areas, which is normally based on the properties of the object being regulated. It is important for food safety and for the public's perception of science and technology in general to establish whether there are any objective differences between these groups of products that justify the different approaches to their regulation.

A6. How can plants contribute to solving the energy crisis and ameliorating global warming?

Plants use solar energy to power the conversion of CO_2 into plant materials such as starch and cell walls. Plant material can be burnt or fermented to release heat energy or make fuels such as ethanol or diesel. There is interest in using algae (unicellular aquatic plants) to capture CO_2 emissions from power stations at source. Biomass cellulose crops such as *Miscanthus* × *giganteus* (Poaceae) are already being burnt with coal at power stations. There is understandable distaste for using food crops such as wheat and maize for fuel, but currently 30% of the US maize crop is used for ethanol production, and sustainable solutions are being found. Sugarcane (*Saccharum officinarum*) significantly reduces Brazil's imports of fossil fuels. Agave (*Agavea fourcroydes*) in hot arid regions can provide very high yields (> 30 T ha^{-1}) of dry matter with low water inputs compared with other crops. To ameliorate global warming, CO_2 must be taken out of the air and not put back. There is considerable interest in 'biochar' in which plant material is heated without air to convert the carbon into charcoal. In this form, carbon cannot readily re-enter the air, and, if added to the soil, can increase fertility. Carbon markets do not currently provide sufficient incentive for farmers to grow crops simply to take CO_2 out of the air.

A7. How do plants contribute to the ecosystem services upon which humanity depends?

Ecosystem services are those benefits we human beings derive from nature. They can be loosely divided into supporting (e.g. primary production and soil formation), provisioning (e.g. food, fibre and fuel), regulating (e.g. climate regulation and disease regulation) and cultural (e.g. aesthetic and recreational) services. Plants are largely responsible for primary production and therefore are critical for maintaining human well-being, but they also contribute in many other ways. The Earth receives virtually no external inputs apart from sunlight, and the regenerative processes of biological and geochemical recycling of matter are essential for life to be sustained. Plants drive much of the recycling of carbon, nitrogen, water, oxygen, and much more. They are the source of virtually all the oxygen in the atmosphere, and they are also responsible for at least half of carbon cycling (hundreds of billions of metric tons per year). The efficiency with which plants take up major nutrients, such as nitrogen and phosphorus, has major impacts on agricultural production, but the application of excess fertilizers causes eutrophication, which devastates acquatic ecosystems. Plants are already recognized as important for sustainable development (e.g. plants for clean water) but there are many other ways that plants might contribute. A combined approach of understanding both the services provided by ecosystems and how plants contribute to the functioning of such ecosystems will require interdisciplinary collaboration between plant scientists, biogeochemists, and ecologists.

A8. What new scientific approaches will be central to plant biology in the 21st Century?
Biologists now have a good general understanding of the principles of cell and developmental biology and genetics, and how plants function, change, and adapt to their environment. Addressing the questions in this list, including those related to generating crops that can deal with future challenges, will require detailed knowledge of many more processes and species. New high-throughput technologies for analysing genomes, phenotypes, protein complements, and the biochemical composition of cells can provide us with more detailed information in a week than has ever been available before about a particular process, organism or individual. This is delivering a deluge of information that is both exhilarating and daunting. The challenge is to develop robust ways of analysing and interpreting this mountain of data to answer questions and deliver new insights. The skill sets required to make full use of the new information extend far beyond those previously expected from biologists. There is general agreement that we need a new era of collaboration between all types of plant scientists, geographers, geologists, statisticians, mathematicians, engineers, computer scientists, and other biologists to evaluate complex data, find new relationships, develop and test hypotheses, and make discoveries. Challenges include understanding complex traits and interactions with the environment, generating 'designer crops', and using modelling to predict how different genotypes will cope with alterations in the climate.

A9. (a) How do we ensure that society appreciates the full importance of plants?
Plants are fundamental to all life on Earth. They provide us with food, fuel, fibre, industrial feedstocks, and medicines. They render our atmosphere breathable. They buffer us against extremes of weather and provide food and shelter for much of the life on our planet. However, we take plants and the benefits they confer for granted. Given their importance, should we not pay plants greater attention and give higher priority to improving our understanding of them? Awareness could be increased through the media, school education, and public understanding of science activities, but a major step-change in activity will be required to make a substantial difference.

A9. (b) How can we attract the best young minds to plant science so that they can address Grand Challenges facing humanity such as climate change, food security, and fossil fuel replacement?
Everyone knows that we need doctors, and the idea that our best and brightest should go into medicine is embedded in our culture. However, even more important than medical care is the ability to survive from day to day; this requires food, shelter, clothes, and energy, all of which depend on plants. Beyond these essentials, plants are the source of many other important products. As is clear from the other questions on this list, plant scientists are tackling many of the most important challenges facing humanity in the 21st Century, including climate change, food security, and fossil fuel replacement. Making the best possible progress will require exceptional people. We need to radically change our culture so that 'plant scientist' (or, if we can rehabilitate the term, 'botanist') can join 'doctor', 'vet' and 'lawyer' in the list of top professions to which our most capable young people aspire.

A10. How do we ensure that sound science informs policy decisions?
It is important that policy decisions that can affect us all, for example environmental protection legislation, are based on robust and objective evidence underpinned by sound science. Without this, the risk of unintended consequences is severe. Ongoing dialogue between policy makers and scientists is therefore critical. How do we initiate and sustain this dialogue? How do we ensure that policy makers and scientists are able to communicate effectively? What new mechanisms are needed to enable scientists to respond to the needs of policy makers and vice versa?

The Supporting Information, Notes S1, provides explanatory text for the remaining questions.

A11. How can we translate our knowledge of plant science into food security?
A12. Which plants have the greatest potential for use as biofuels with the least effects on biodiversity, carbon footprints and food security?
A13. Can crop production move away from being dependent on oil-based technologies?
A14. How can we use plant science to prevent malnutrition?
A15. How can we use knowledge of plants and their properties to improve human health?
A16. How do plants and plant communities (morphology, colour, fragrance, sound, taste etc.) affect human well-being?
A17. How can we use plants and plant science to improve the urban environment?
A18. How do we encourage and enable the interdisciplinarity that is necessary to achieve the UN's Millennium Development Goals which address poverty and the environment?

B. Environment and adaptation

Plants have evolved to cope with changes in their environment but their adaptability has not necessarily been preserved as crops have been developed from wild species. Assessing and utilizing the capacity of plants to adapt should help to increase the use of more marginal land for cultivation, and enhance agricultural production despite changes in climate.

B1. How can we test if a trait is adaptive?
B2. What is the role of epigenetic processes in modulating response to the environment during the life span of an individual?
B3. Are there untapped potential benefits to developing perennial forms of currently annual crops?
B4. Can we generate a step-change in C_3 crop yield through incorporation of a C_4 or intermediate C_3/C_4 or crassulacean acid metabolism (CAM) mechanism?
B5. How do plants regulate the proportions of storage reserves laid down in various plant parts?
B6. What is the theoretical limit of productivity of crops and what are the major factors preventing this being realized?
B7. What determines seed longevity and dormancy?
B8. How can we control flowering time?
B9. How do signalling and cross-talk between the different plant hormones operate?
B10. Can we develop salt/heavy metal/drought-tolerant crops without creating invasive plants?
B11. Can plants be better utilized for large-scale remediation and reclamation efforts on degraded and/or toxic land?
B12. How can we translate our knowledge of plants and ecosystems into 'clever farming' practices?
B13. Can alternatives to monoculture be found without compromising yields?
B14. Can plants be bred to overcome dry land salinity or even reverse it?
B15. Can we develop crops that are more resilient to climate fluctuation without yield loss?
B16. Can we understand (explain and predict) the succession of plant species in any habitat, and crop varieties in any location, under climate change?
B17. To what extent are the stress responses of cultivated plants appropriate for current and future environments?
B18. Are endogenous plant adaption mechanisms enough to keep up with the pace of man-made environmental change?
B19. How can we improve our cultivated plants to make better use of finite resources?
B20. How do we grow plants in marginal environments without encouraging invasiveness?
B21. How can we use the growing of crops to limit deserts spreading?

C. Species interactions

Cultivated plants interact directly with other species, including pathogens, pests, symbionts and weeds. Some interactions are beneficial, whereas others can cause devastating agricultural losses. It remains a challenge to control deleterious species without causing significant environmental damage, and there is untapped potential in developing improved interactions with beneficial species, such as mycorrhizal fungi.

C1. What are the best ways to control invasive species including plants, pests and pathogens?
C2. Can we provide a solution to intractable plant pest problems in order to meet increasingly stringent pesticide restrictions?
C3. Is it desirable to eliminate all pests and diseases in cultivated plants?
C4. What is the most sustainable way to control weeds?
C5. How can we simultaneously eradicate hunger and conserve biodiversity?
C6. How can we move nitrogen-fixing symbioses into nonlegumes?
C7. Why is symbiotic nitrogen fixation restricted to relatively few plant species?
C8. How can the association of plants and mycorrhizal fungi be improved or extended towards better plant and ecosystem health?
C9. How do plants communicate with each other?
C10. How can we use our knowledge of the molecular biology of disease resistance to develop novel approaches to disease control?
C11. What are the mechanisms for systemic acquired resistance to pathogens?
C12. When a plant resists a pathogen, what stops the pathogen growing?
C13. How do pathogens overcome plant disease resistance, and is it inevitable?
C14. What are the molecular mechanisms for uptake and transport of nutrients?
C15. Can we use nonhost resistance to deliver more durable resistance in plants?

D. Understanding and utilizing plant cells

Plant structure and function depend on the composition and behaviour of plant cells. A lot of progress has been made towards identifying cellular components (including DNA, RNA, proteins, cell wall components and membranes) and understanding how they contribute to specific processes (such as development, metabolism, and pathogen resistance). The early questions in this section address frontiers in our understanding of plant cells, and potentially timely applications are tackled later.

D1. How do plant cells maintain totipotency and how can we use this knowledge to improve tissue culture and regeneration?
D2. How are growth and division of individual cells coordinated to form genetically programmed structures with specific shapes, sizes and compositions?
D3. How do different genomes in the plant talk to one another to maintain the appropriate complement of organelles?
D4. How and why did multicellularity evolve in plants?
D5. How can we improve our understanding of programmed developmental gene regulation from a genome sequence?
D6. How do plants integrate multiple environmental signals and respond?
D7. How do plants store information on past environmental and developmental events?
D8. To what extent do epigenetic changes affect heritable characteristics of plants?
D9. Why are there millions of short RNAs in plants and what do they do?
D10. What is the array of plant protein structures?
D11. How do plant cells detect their location in the organism and develop accordingly?
D12. How do plant cells restrict signalling and response to specific regions of the cell?
D13. Is there a cell wall integrity surveillance system in plants?
D14. How are plant cell walls assembled, and how are their strength and composition determined?
D15. Can we usefully implant new synthetic biological modules in plants?
D16. To what extent can plant biology become predictive?
D17. What is the molecular/biochemical basis of heterosis?
D18. How do we achieve high-frequency targeted homologous recombination in plants?
D19. What factors control the frequency and distribution of genetic crossovers during meiosis?
D20. How can we use our knowledge about photosynthesis and its optimization to better harness the energy of the sun?
D21. Can we improve algae to better capture CO_2 and produce higher yields of oil or hydrogen for fuel?
D22. How can we use our knowledge of carbon fixation at the biochemical, physiological and ecological levels to address the rising concentrations of atmospheric CO_2?
D23. What is the function of the phenomenal breadth of secondary metabolites?
D24. How can we use plants as the chemical factories of the future?
D25. How do we translate our knowledge of plant cell walls to produce food, fuel and fibre more efficiently and sustainably?

E. Diversity

It is currently estimated that there are at least a quarter of a million species of flowering plant in the world, the vast majority of which have not been tested for useful properties. Questions in this section address the need to identify plants with potential for human benefit that have yet to be recognized, and to do so in a sustainable and responsible manner. The resulting knowledge and natural resources could then be used to tackle new challenges as they arise.

E1. How much do we know about plant diversity?
E2. How can we better exploit a more complete understanding of plant diversity?
E3. Can we increase crop productivity without harming biodiversity?
E4. Can we define objective criteria to determine when and where intensive or extensive farming practices are appropriate?
E5. How do plants contribute to ecosystem services?
E6. How can we ensure the long-term availability of genetic diversity within socio-economically valuable gene pools?
E7. How do specific genetic differences result in the diverse phenotypes of different plant species? That is, why is an oak tree an oak tree and a wheat plant a wheat plant?
E8. Which genomes should we sequence and how can we best extract meaning from the sequences?
E9. What is the significance of variation in genome size?
E10. What is the molecular and cellular basis of plants' longevity and can plant life spans be manipulated?
E11. Why is the range of life spans in the plant kingdom so much greater than in animals?
E12. What is a plant species?
E13. Why are some clades of plants more species-rich than others?
E14. What is the answer to Darwin's 'abominable mystery' of the rapid rise and diversification of angiosperms?
E15. How has polyploidy contributed to the evolutionary success of flowering plants?
E16. What are the closest fossil relatives of the flowering plants?
E17. How do we best conserve phylogenetic diversity in order to maintain evolutionary potential?

Conclusions

Plant science is central to addressing many of the most important questions facing humanity. Secure food production and quality remain key issues for the world in the 21st Century, and the importance of plants extends well beyond agriculture and horticulture as we face declining fossil fuel reserves, climate change, and a need for more sustainable methods to produce fuel, fibre, wood, and industrial feedstocks. There is also untapped potential in optimizing the nutritional properties of foods, and in identifying novel plant products such as medicines. Tackling these frontiers will require new scientific methods and collaborations as existing approaches are delivering incomplete answers.

Many of the most important questions that we have identified can only be addressed by the integrated efforts of scientists with diverse expertise. For example, many require close cooperation between scientists working to improve crops and those working on environmental stability and ecosystem services. Funding mechanisms, scientific publishing and conferences could be more effective in supporting and encouraging the efficient transfer of knowledge between different areas of plant science and this should be addressed. In the longer term, changes to higher education may be required to ensure that future researchers have the most suitable background knowledge and skill sets to address the research challenges that they are likely to face.

As plant science becomes increasingly important, we need to attract the brightest and best to careers in plant research. School education does not include the most interesting or relevant aspects of plant science, and discourages young people from studying the subject at university. This is indefensible in a world with such a strong requirement for outstanding plant scientists, and steps should be taken to put it right.

Research moves quickly, and our questions and suggestions about the ways that they might be tackled will require revision, but in the meantime we hope that they will stimulate discussion, and encourage plant scientists to think beyond the limits of their own specific fields about the most important research that can conceivably be carried out, the most promising approaches that can be developed and applied, and the most significant discoveries that can possibly be made.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Notes S1 Explanatory text for questions A11–E17.

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