



# European plant science: a field of opportunities

## European Plant Science Organization (EPSO)\*

European Plant Science Organization, Technologiepark 927, 9052 Gent, Belgium

Received 27 April 2005

The *Journal of Experimental Botany* would be pleased to receive comments, possibly for publication, either as an e-letter (see the box to the top-right of the screen when you view the manuscript online) or as an e-mail (j.exp.bot@lancaster.ac.uk).

### Abstract

Plants have a pivotal role in eco- and agricultural systems. Genomics is driving a rapid expansion of our understanding of how genes, individually and in networks, determine plant function. Technological developments in breeding and genomics are providing strategies to translate this knowledge into crop improvement. The possibilities range from improvement of existing crops and the systematic use of natural diversity through to the domestication of completely new species. As examples of possible goals, it is discussed how profiling of composition will integrate plant breeding and agronomic practice with emerging knowledge about nutrition and health, how improved and novel crops will contribute to the creation of new bio-based economies revolving around plant products, and how advances in our knowledge about plant–environment and plant–pathogen interactions will provide novel strategies to stabilize agricultural yield in a fluctuating environment and contribute to integrated approaches in which modern agriculture is carried out in concert with the environment. In addition, knowledge generated by plant science will be needed to monitor, understand, and cope with climate change and its impact on agriculture and ecosystems. Realization of these goals will require close interactions with related disciplines including agronomy and ecology. Further, it will be important to continue and deepen open support for research in the developing world.

Key words: Agronomic practice, biodiversity, domestication, ecosystems, environment, genomics, novel crops, plant breeding, plant products, yield.

### Plants are the key to life on earth

Without plants, most life on earth would cease. Plants use energy from sunlight to convert carbon dioxide and inorganic nutrients into carbohydrates, proteins, fats, nucleic acids, and tens of thousands of other organic compounds. These are required by almost all other aquatic and terrestrial organisms as a source of energy, and as raw material for growth. In addition to being the driving force for most ecosystems, plants are a major determinant of water and nutrient circulation and play a key role in stabilizing the soil and establishing the microclimate. At a global scale, the assimilation of carbon dioxide and recycling of oxygen play a key role in establishing and maintaining the atmospheric composition, with far-reaching implications for climate. The landscapes formed by plants are important for our recreation, and play a dominant role in our cultural appreciation of nature. Plants are the ultimate source of all our food, and produce natural fibres and innumerable compounds that are pivotal for industrial and medical purposes.

Plants are complex: it was a surprise for many scientists to find out that the model plant *Arabidopsis* has many more genes (*Arabidopsis* Genome Initiative, 2000) than a fly or a worm; and not many fewer than mice or humans. The number of genes in crop plants, which have more complex genomes, will be higher than in *Arabidopsis*. Plants are also different: although there are recognizable similarities between plants, fungi, and animals with respect to basic features of the biochemical and cellular machinery, there are also major differences and many aspects that are specific to plants. For example, the unicellular progenitors of plants (algae) underwent an important evolutionary step following the establishment of a second endosymbiotic relationship, resulting in the evolution of the plastid. As multicellular terrestrial plants evolved independently

\* To whom correspondence should be addressed. Fax: +32 9 331 3811. E-mail: Karin.Metzlaff@psb.ugent.be

from animals, plants possess fundamentally different anatomical and morphological structures, and have different strategies for resource acquisition and transport, communication within and between cells and organs, development, reproduction, dispersal, and survival.

Plants have never been as important to people as at the start of the 21st century. At present, 800 million people are chronically malnourished and 2 billion lack food security. Unless there are major increases in food production, the situation will deteriorate further as the world population grows from 6.3 to 8–11 billion in the next 50 years. Combating this will require that the nutritional quality of plant products is maintained and even increased. It will also require increased production. These goals need to be met without taking large additional amounts of land into agricultural use. Most of the land on the globe that is suitable for agriculture is already in use, and this precious resource is currently declining due to urbanization, erosion, and salination (Halweil, 2002). Solutions are urgently needed that will increase productivity per unit area, while safeguarding land quality and protecting surrounding natural ecosystems. Simultaneously, it will be important to decrease inputs into farming. For example, >70% of all freshwater used by mankind is consumed in agriculture, and a reduction will be essential as freshwater reserves decline (World Agriculture: Towards 2015/2030, FAO, 2002 <http://www.fao.org/docrep/005/y4252e/y4252e00.htm>). On another note, profligate use of fossil fuels is altering the composition of the atmosphere and leading to climate changes that threaten ecosystems and the well-being of mankind. A move from a fossil fuel-based to a renewable economy will require that, in addition to food, plants provide an increasingly large proportion of our requirements for energy and chemicals.

There is a tendency to view plant research as being of only marginal importance. There are many reasons for this neglect. These range from difficulties in the past in translating advances in basic knowledge about plants into better crops or a better understanding of ecosystems, through to complacency about the stability of the food supply. Further, recent controversies about transgenic plants and apprehension created by unrelated breakdowns in food production systems (for example those that led to BSE), have accentuated public concerns that parts of the food production system have developed in the wrong direction and that it is important to develop a sustainable agriculture, which places more emphasis on environmental concerns and pays more attention to the needs of the consumers and the third world.

We are convinced that continued investment in the development of the plant science research base is essential to provide the knowledge base that will be required to underpin the establishment of efficient sustainable agricultural food production systems and the quest for renewable resources in Europe and by Europeans in the 21st century. The contribution that plant science can make has already

been outlined in studies prepared by scientists in the USA (e.g. Plant/crop-based renewable resources 2020, <http://www.oit.doe.gov/agriculture/pdfs/vision2020.pdf>; The Multinational Coordinated *Arabidopsis* 2010 Project, <http://www.arabidopsis.org/workshop1.jsp>), Japan (The Rice Research Program in Japan, <http://rgp.dna.affrc.go.jp/index.html>), Australia (The Plant Functional Genomics Centre in Australia, [www.arc.gov.au](http://www.arc.gov.au)), and Canada (The Canadian Crop Genomics Initiative, [www.agr.gc.ca/science](http://www.agr.gc.ca/science)). A recent BBSRC report ([www.bbsrc.ac.uk/media/pressreleases/04\\_05\\_12\\_csr.html](http://www.bbsrc.ac.uk/media/pressreleases/04_05_12_csr.html)) analyses the problems in the United Kingdom and calls for a national strategy for crop science research.

The present document was drawn up by a set of plant scientists at a workshop initiated by the European Plant Science Organization (EPSO)<sup>†</sup>. It extends previous analyses and considers examples that illustrate, from a European perspective, why strong strategic investment in plant science will be essential to meet the major societal and environmental issues that we will be facing in the next 25 years. It does this by developing the following theses.

- (i) Advances from basic science can now be used to support plant breeding
- (ii) New technology developments and discoveries in basic research will lay the grounds for further major undertakings
- (iii) Profiling of composition will integrate plant breeding and agronomic practice with emerging knowledge about nutrition and health
- (iv) Improved and novel crops will contribute to the creation of new economies based on plant products
- (v) Advances in knowledge will provide strategies to stabilize agricultural yield in a fluctuating environment
- (vi) Changes in crops and management systems will help us to carry out agriculture in concert with the environment
- (vii) Knowledge about plants is needed to monitor, understand, and cope with climate change and its impact on agriculture and ecosystems
- (viii) A global perspective dictates strong and open support for the developing world

### **Advances in basic science enable great improvements in the efficiency of plant breeding**

Plant breeding has led to large improvements in yield and yield stability, especially by improving plant architecture and by providing resistance to plant pathogens. Plant breeding was, for a long time, an empirical art that involved carrying out crosses to generate large segregating populations, which were grown in the field and screened

<sup>†</sup> The acknowledgement lists the participants of the workshop and other major contributors to the article.

for individuals with favourable traits. Here it is usual to distinguish between 'qualitative' and 'quantitative' traits: these are traits that show either a simple segregation of distinct phenotypes or a wide spread of phenotypic variation, respectively. 'Quantitative' traits are often polygenic (i.e. determined by a large number of genes) and influenced by environment.

Plant scientists have been making advances in understanding the biochemical and molecular processes that underlie important metabolic, physiological, and developmental traits, or that affect the ability of plants to cope with unfavourable environmental conditions ('abiotic' stresses) or pathogen attack ('biotic stresses') for several decades. However, it was often difficult to exploit this information for plant breeding, because the level of understanding was not deep enough, and because necessary techniques were not available. Recent developments in plant molecular biology and genomics are greatly accelerating the speed with which knowledge gained in basic plant science can be applied to crop improvement. This is occurring via three complementary routes.

One route starts out from genes whose function is known, and uses transgenic technologies to make directed changes to attain a specific goal ('genetic engineering'). This route is based on technological breakthroughs made from 1983 onwards, when the first successful transfer of a foreign gene into a plant was reported. It came into widespread commercial use from the mid-1990s onwards as it became possible to transform a large range of important crop plants. It requires prior knowledge about the role of a gene in determining a given trait and is, at present, only applicable for traits that are determined by one or a relatively small number of genes. To date, most applications that have reached the field involve the use of heterologous genes (i.e. genes from other organisms) to engineer herbicide resistance or insect tolerance. A second generation of plants are in preparation that have a wider range of traits, including nutritional quality and abiotic resistance. This approach is viewed with caution or mistrust by many consumers, but is essential when the aim is to introduce a trait that was previously absent (e.g. tolerance against insects or herbicides, or the production of a fine chemical, a pharmaceutical, or a pro-biotic) or when a trait is recalcitrant to conventional approaches because, for example, the required genetic variation is absent from available breeding materials.

The second route uses tools from genomics to increase the speed and effectiveness of conventional breeding. Natural genetic variation within species and between related species has been and will continue to be the major resource for crop improvement. A battery of technological advances and platforms is accelerating the identification of useful genetic diversity in crops and related wild species, and enabling its introduction into plant breeding programmes. Most of these tools were developed in the last

10 years. Transgenic technology is required to validate strategies and conclusions, but not necessarily as part of the route to create the new crop line. The tools include molecular marker-assisted selection (<http://www.igd.cornell.edu/Training&Education.html>), quantitative trait loci mapping and its integration with large-scale phenotypic analysis (QTL) (Gur *et al.*, 2004) and association studies (Thornsberry *et al.*, 2001; Buckler and Thornsberry 2002). A molecular marker is a simple diagnostic test for a difference (e.g. a single base pair change, termed a 'single nucleotide polymorphism', SNP) in the DNA sequence, and QTL mapping and association mapping are different ways to search for correlations between a particular molecular marker (or markers) and a particular 'quantitative' trait. The ability to characterize routinely the genotypic composition and phenotypic traits of populations is making it possible to develop core collections and revolutionize the logistics of maintaining, extending, and using gene banks. It aids the identification of suitable material for breeding programmes, and supports the creation of tailored populations, in which useful changes are easier to detect. By coupling wide crosses (i.e. crosses between two genotypically very diverse members of a species or even between two related species) to the use of molecular markers, recombinant inbred or introgression lines can be generated in which small and defined segments of a 'donor' genome (e.g. distantly related cultivar or related wild species) are introduced into a host 'acceptor' genome (e.g. a modern cultivar). These populations can then be systematically screened to identify useful genetic variation in a large number of traits, and analysed in detail to understand the genetic and molecular basis of the variation (Fridman *et al.*, 2004).

The third route will increase the diversity in the crop package available to farmers and consumers. Enrique Sanchez-Monge, in his *Flora Agricola* (Sanchez-Monge, 1991), listed over 4000 plant species that humans have used in the past millennia as food, feed or source of other products. Almost all were abandoned, with the result that arable agriculture is currently based on a small number of species. Diversification of the species used as crops is a major future challenge for modern plant science. The domestication of crops, particularly cereals (Salamini *et al.*, 2002; Salamini, 2003), was the central achievement of the Neolithic revolution 12 000 years ago in south-east Turkey (Childe, 1953). This, and parallel events like the domestication of maize and members of the Solanaceae in pre-Columbian America and rice and soybean in East Asia, shaped all subsequent food production on the planet (Diamond, 1997). A set of complex changes occurred during crop adoption, which is known as the 'domestication syndrome' (Pozzi *et al.*, 2004). Recently, we have started to understand the genetic and molecular basis of this phenomenon. It occurred via the selection of suitable variants, often natural mutants. The types of traits that were selected

included the choice of alleles of specific genes that support an appropriate timing of seed germination, reduce the influence of the length of the day on the timing of fruit ripening, improve seed size, keep the seeds in the ears, and aid hand-threshing of ears. This, however, also resulted in a strong reduction of genetic variability because only a small subset of germplasm that was available in the natural population of a given species was domesticated (Vigouroux *et al.*, 2002). The time is ripe to go beyond understanding what happened in the past. It will soon be feasible to repeat the domestication process, allowing easier development of new crops or a better use of the wild species resource (Tanksley *et al.*, 1997). Such new crops have the potential to revolutionize agriculture.

### **New technology developments will lay the grounds for further major undertakings**

New technologies will be instrumental in allowing us to identify, characterize and use plant genetic diversity (i.e. analyse the genotypes, or ‘genotyping’) and to analyse the resulting changes in the characteristics of the plant (technically, this is termed analysis of the phenotype, or ‘phenotyping’).

Novel high-throughput genotyping technologies will play a key role in propelling large-scale analyses of large collections of plant genotypes to identify defined differences (termed DNA polymorphisms) in their genetic structure. One key development is TILLING, which combines a screen for altered DNA sequences in important (‘candidate’) genes with chemical mutagenesis (Henikoff *et al.*, 2004) to detect genotypes that carry mutations in a candidate gene that is known or thought to be important for a particular trait. This technology can also be used to survey large collections of naturally-existing populations for variation in a gene-of-interest (Comai *et al.*, 2004, this is sometimes termed ‘eco-TILLING’). Another important breakthrough is the development of increasingly cost-effective platforms for the parallel analysis of large numbers of SNPs (Hardenbol *et al.*, 2003). This will greatly facilitate the use of molecular markers (see above) in breeding. It will allow multiple markers to be analysed for multiple traits, increase the power of QTL and association mapping, and will also speed up the generation of introgression lines. Exploitation of marker or DNA or genome technology in crop plants has already led to concepts such as ‘Breeding by Design’ (Peleman and van der Voort, 2003), where a multitude of traits can be monitored and combined in breeding programmes. There are already many examples of marker-assisted breeding in commercial use, both for ‘qualitative’ traits (e.g. some types of disease resistance) and, increasingly, for ‘quantitative’ traits (e.g. yield, composition, abiotic stress resistance).

However, a further quantum leap in DNA polymorphism analysis will be required to analyse complex multigenic

traits, to understand biodiversity, and to elucidate the molecular basis of adaptive traits in the genomes of wild species and domesticated crops. QTL cloning, which is still in its infancy, will progress rapidly and provide unprecedented opportunities and a new impetus for the understanding of the genetic basis of quantitative traits and their contribution to adaptation. The recently constructed *Arabidopsis* genome tiling array (see Ishkanian *et al.*, 2004, for a general account of the technology) is already providing unprecedented and detailed insights into the organization and expression of a eukaryotic genome. The availability of the rice genome sequence has vastly improved our capacity to identify and clone candidate genes in all cereals. The genomes of other important crops will soon be sequenced, adding further opportunities to sequence-based selection. Following the sequencing of a genome for one representative cultivar of a species, tiling arrays can be used as a cost-effective approach to obtain information about the genome sequence in a large number of other cultivars. This will provide a large source of molecular markers and, as our understanding of the relation between gene sequence and function increases, important clues about the molecular basis of differences in traits between cultivars that can then be experimentally tested.

These technologies for ‘genotyping’ will be particularly powerful when they are combined with the comprehensive approaches for phenotype analysis, which are also being developed in functional genomics. Rapid advances are already being made in our ability to systematically analyse (or ‘profile’) the expression of all genes using microarrays (AtGenEXpress) or multiplexed RT-PCR (Czechowski *et al.*, 2004) and the levels of hundreds and, in the near future, thousands of proteins (Kleffman *et al.*, 2004) and metabolites (Stütt and Fernie, 2003; Kopka *et al.*, 2004), to analyse metabolic fluxes (Schwender *et al.*, 2003, 2005) and to visualize *in vivo* the localization of proteins, interactions between proteins, and the levels of ions and metabolites (Fehr *et al.*, 2005). These will allow us to analyse traits more quickly and precisely, to track genes that are responsible for these changes through breeding programmes, and to identify the genes and understand the processes that they affect. As our knowledge of plant genomes expands, novel tools will also be needed that provide a deeper understanding of the biochemical pathways, networks, and epigenetic controls that direct key developmental processes, such as flowering and grain filling. A key challenge will be to identify genetic programmes that are conserved across a wide taxonomic range, in order to prioritize research in specific crop plants to focus on genes or gene programmes that are responsible for variation between closely-related species and within species.

The analysis of plant phenotypes and physiological processes poses an even larger challenge. ‘Whole plant’ traits like allocation, shape, and architecture play key roles in many vital traits, including water and nutrient use

efficiency, yield, and susceptibility to pathogen attack. We need new tools to describe the architecture of a plant, and allow fundamental aspects of cell biology and plant physiology such as water movement, metabolite flow between source and sink, and the motion of signalling molecules directing intercellular communication to be visualized in real time. This will involve a close interaction with developments in physics and nanotechnology, as well as with developments in informatics that allow visualization of complex and dynamic processes. Understanding and visualizing plant physiology will have an enormous impact on breeding and optimizing agricultural practices.

Fundamental research is still urgently required in order to understand and decipher major unresolved questions in heredity, gene and protein regulation, cell biology, physiology, and the response of plants to environmental stresses and pathogens. In recent years, several discoveries have demonstrated that our knowledge of even the most fundamental processes is still incomplete. Examples range from the presence of major gaps in our understanding of metabolic pathways and their regulation even for a central compound like starch (see Benning and Stitt, 2004, for references), through to the revelation that the function of the vast majority of the genes in the *Arabidopsis* genome is poorly or completely unknown (*Arabidopsis* Genome Initiative, 2000), and the recognition that not only transcription factors but also epigenetics (Gendrel and Colot, 2005), and post-transcriptional regulation including micro RNAs (Jones-Rhoades and Bartel, 2004) play a major role in the regulation of gene expression. Another example is the major impact that understanding apomixis would have on plant breeding (Spillane *et al.*, 2004). In these and many other areas, advances in fundamental understanding will open the door to important possible applications.

The integration of the information generated by high throughput genotyping and high throughput phenotyping analysis will require major advances in bioinformatics and the progression to an integrated 'systems' approach that provides a global view of how plants operate and how they interact with the environment. Put more generally, the entire field of the life sciences is currently undergoing a dramatic transformation from a series of fragmented, reductionist activities towards the realization of a new integrated approach, which reunifies the molecular-based and the organism-based branches of biology (Kafatos and Eisner, 2004). Plant science is incorporating these new system-oriented approaches. The knowledge and resources gained by understanding of plant function can be transferred to other research fields like breeding, agronomic practice, and ecosystem research in which system-orientated analysis is also vital.

The following sections will discuss how advances in our understanding of plants and changes in the process of plant breeding can be combined with new priorities in the kinds of traits we select, and the way that agriculture is carried out.

### **Profiling of composition will integrate plant breeding and agronomic practice with emerging knowledge about health and nutrition**

Of the tens of thousands of chemicals in plants, a minute fraction is currently known to be beneficial or detrimental for health. The impact of the others is a matter of research, conjecture or ignorance. It can be anticipated that in the next years nutritional science, supported by human genomics, will make significant advances in extending our knowledge about the roles of many more of these metabolites for human nutrition and health. Recent rapid advances in the technologies for metabolite profiling allow 100s and potentially 1000s of metabolites to be routinely analysed (Stitt and Fernie, 2003; Kopka *et al.*, 2004). As these technologies are refined and expanded to allow analysis of a large number of important micronutrients, they will allow an increasingly exhaustive analysis of plant composition at an early stage in breeding programmes, and during the development of new storage, transport, and processing regimes. This information will make it easier to integrate emerging knowledge from nutritional and medical research into the food production chain. Simultaneously, new perspectives will emerge for interdisciplinary research on nutrition, for example, by systematically investigating the relation between the spectrum of metabolites in ingested food, the resulting changes in the blood and tissues, and the impact on cellular responses and expression patterns in animals and humans. This will contribute to a much deeper understanding of the relation between food and health. Metabolite profiling will be a particularly potent tool when it is combined with technological advances for genotyping (see above) that accelerate identification of useful genetic diversity and its introduction into plant breeding programmes. The finding that the difference in the metabolic profile between different ecotypes of *Arabidopsis* (Fiehn *et al.*, 2000) or related tomato species (Roessner *et al.*, 2001) are far larger than the difference when markedly different phenotypes are created by introducing single genes by transgenic approaches shows that a rich diversity is available in natural gene pools, which can be used to breed plants with improved nutritional value. Metabolite profiling can be used to reveal if new products—irrespective of how they are produced—differ substantially from those already present on the market, if they provide real benefits, and if they require additional safety testing.

### **Improved and novel crops will contribute to the creation of new economies based on plant products**

Higher plants synthesize tens of thousands of different low molecular weight compounds, with enormously diverse and often complex structures. They are sometimes termed

'secondary metabolites'. Correspondingly, plants have been used through unwritten and written history as a source of medicines, fragrances, spices, and colourants. Their impact has been huge, for example, 25% of all commonly prescribed pharmaceuticals are directly or indirectly (via semi-synthesis) derived from plants, notable examples including, paclitaxel, camptothecin, vincristine, morphine, codeine, and steroidal hormones, representing a market value of over €40 billion in western countries. The chemical potential of plants is however, still largely unexplored. Chemical diversity has only been analysed in about 10% of all land plants, and even here only the most abundant compounds have been well characterized. There are unprecedented possibilities for the discovery of novel chemicals, for diverse uses from pharmaceuticals through to fine chemicals. Their discovery and use will be accelerated by genomic and evolutionary analysis of the large gene families that encode the rich array of enzymes that contribute to their synthesis, by rapid advances in the analytical methods to define structures, and by the development of high throughput platforms to characterize their chemical and biological properties (Oksman-Caldentey and Inzé, 2004). Recent studies have also revealed the potential of using transcription factors to control the biosynthesis of entire pathways for valuable secondary metabolites (Van der Fits and Memelink, 2000; Bovy *et al.*, 2002; Mathews *et al.*, 2003). Compounds produced by plants can be fed into industrial processes (Herrera, 2004), decreasing the use of fossil-fuel resources, saving energy, and also opening up avenues for new and improved products. The specificity provided by enzymically-catalysed processes *in vivo* allows precise synthesis of complex structures, for example, modifications of the branching pattern of starch or site- and stereospecific desaturation of fatty acids, which are difficult or impossible to achieve by conventional chemical synthesis. In addition to producing or modifying existing compounds, novel products like high-value fine chemicals, enzymes and, in particular, pharmaceuticals will be produced.

At the other end of the scale, plants can be optimized to produce more biomass. There is great potential in annual crops and perennials, including short rotation tree species, to increase the bulk production of resources like carbohydrates, lignin, and vegetable oils. Trees are of particular interest because they produce the majority of terrestrial biomass. To date, research related to fibre as a raw material has mainly been concentrated on forest management and on timber, pulp, and paper technology. The existing biodiversity in fibre-producing plants has not been exploited, partly because their long lifespan seriously hindered improvement by breeding. Recent developments like early flowering lines and marker-assisted breeding will facilitate dramatic advances in tree breeding. This will be supported by *in vitro* propagation, in particular for long-lived or late flowering trees. Based on experience with

annual crops, we can expect that breeding will generate large advances within a few generations. It will be possible to develop new varieties of trees that have higher yield, that contain modified products, or that have a broader spectrum of genetic variability allowing higher resistance to abiotic and biotic stress and climatic fluctuations. In order to combat the prevalent use of monocultures in forest, which leads to problems of susceptibility to insects, fungi, and abiotic stress, it will be possible to grow synthetic and mixed populations with chosen properties. The challenge will be to co-ordinate tree breeding with the preservation of genetic resources, both *in vitro* (genetic banks) and *in situ* (genetic bases). It will be important to introduce remnant valuable populations of previously neglected, but economically important shrubby woods, which are important for preservation of ecosystem diversity as well as protecting against erosion, capturing dust, and aiding hydrological stability.

### **Advances in knowledge will provide strategies to stabilize yield in a fluctuating environment**

An important component of agriculture is the stabilization of yield, both in marginal environments that are more exposed to the vagaries of weather conditions and under agronomic practices that decrease the input of water, fertilizers, and pesticides. This is important at all levels, from the individual farmer through to the efficient operation of food production chains. Stability of yield and quality will be vital if plants are to take on a larger role in the delivery of energy and other raw resources. Fundamental plant science is generating major advances in our understanding of the strategies that plants use to survive unfavourable and variable environmental conditions particularly drought (Tuberosa and Salvi, 2004), and to defend themselves against pathogens (Suzuki *et al.*, 2004) and herbivores (Kessler and Baldwin, 2002).

This knowledge will open up new strategies to create crops with durable resistance against pathogens and herbivores as well as plants with increased resistance to stress or an increased capacity to maintain yield in changing abiotic and biotic conditions. For example, most farmers in Northern Europe need to spray fungicides 10–20 times per year to control potato late blight caused *Phytophthora infestans*. Resistance genes that have been isolated from wild relatives of potato could, if appropriately deployed, confer durable resistance (Song *et al.*, 2003). We will need to take advantage of transgenic approaches to accelerate the precise introgression of the rich diversity of genes from wild relatives into cultivated potato varieties, because, in this species, conventional breeding will probably be too slow. In an extension of this approach, it could be that resistance genes involved in non-host (species-level) resistance in one species could be transferred to related

species, dramatically increasing the gene pool available for crop improvement. For example, resistance genes from *Arabidopsis* could confer resistance to *Brassica* diseases, or the genomes of grass relatives of wheat and barley might be a source of resistance to important wheat diseases such as mildew and *Septoria*. Drought and heat stress or low temperature stress are major abiotic limitation on plant growth in most crop environments. Genes such as *Arabidopsis CBF1* when overexpressed confer drought and frost resistance (Jaglo-Ottosen *et al.*, 1998). It is likely that more such genes exist. However, elevated *CBF1* expression also confers a yield penalty, and a better understanding of the interactions between pathways in the plant will be required to reap the benefits of such drought-tolerance while mitigating the side-effects. Similarly, elevated jasmonic acid levels enhance insect and necrotroph resistance, but this is often also associated with reduced growth; a better understanding of interactions between defence and growth pathways may facilitate obtaining a desired trait without deleterious consequences.

Two very recent examples illustrate how advances in understanding fundamental plant physiology also open exciting possibilities in agriculture. Both involve developments that have made it possible to improve the efficiency of water use (WUE) significantly, which is a major target in a world where the pressure to reduce water use in agriculture is immense (see Abramovitz, 2002, and above). Insights into the biochemistry of photosynthesis and the regulation of carbon dioxide entry into leaves led to an understanding of the basis for discrimination against the naturally occurring carbon isotope  $^{13}\text{C}$ , which has been exploited through plant breeding to deliver new wheat varieties for the wheat cropping zone of northern Australia (Condon *et al.*, 2002). These varieties (e.g. cv. Drysdale) have an increased WUE under limited water supply and, as a result, have increased yield when the water supply is limited. In the second example, novel irrigation techniques that exploit increased understanding of long-distance chemical signalling in plants have been used to deliver substantial increases in WUE in the wine grape industry in South Australia (Loveys *et al.*, 2004). These are two examples where insights gained in basic plant biology research have been developed in little more than 10 years into fully commercial systems. Other emerging approaches to deliver high WUE include screening genotypes for oxygen isotope discrimination and producing lines with altered leaf area compared to standard cultivars (Richards *et al.*, 2002).

### **Changes in crops and management systems will help us to carry out agriculture in concert with the environment**

A major characteristic of land use in many regions of Europe is the close juxtaposition of farmed and natural

environments. These are also closely intermeshed with urban or semi-urban settlement, leading to a keen appreciation of the impact of farming practice on biodiversity and the environment on the fields themselves, in the border areas and in neighbouring non-farmed areas. In the last 50 years, the impact of farming on the natural landscape has increased greatly, reducing biodiversity and increasing environmental degradation. Europe requires a combination of strategies that will support economically-viable agriculture whilst delivering an increased range of environmental benefits. This might be termed 'increasing the stride and decreasing the footprint of agriculture', and requires a systems-based approach to food production chains.

Fundamental plant science is a vital part of the research continuum that will support this approach. This can be illustrated by two potential key contributions. Firstly, there will be a shift away from breeding purely for yield, and towards breeding for good and stable performance with lower inputs of fertilizer, herbicides, fungicides, and insecticides. This will be enabled by the large increase in the speed of breeding and the genetic diversity it can access, and by advances in our understanding of how plants function. These advances will allow breeding programmes to target important processes and genes in a direct manner. Basic research on plant nutrient metabolism, for example, can now be integrated with developmental and molecular studies to identify breeding targets to improve nitrogen use efficiency throughout crop growth (Hirel and Lemaire, 2003). Secondly, improved knowledge will allow the state of plants, fields, farms, and catchments to be continuously monitored and compared with robust mathematical models that describe nutrient and water use and the epidemiology of crop–weed and crop–pathogen interactions, allowing precision management to minimize inputs and the resulting effects on the environment. Evaluation of livestock systems using this approach shows that very significant reductions in losses of nitrogen can be achieved with a relatively small decline in animal production (Laws *et al.*, 2000). Such developments will represent a step towards developing a less costly, more environmentally-friendly and more sustainable agriculture. They will require increasingly close interactions between the development of new plant varieties and management techniques.

Farming and management build two essential elements in the conservation of the ecological equilibrium of cultural landscapes that have been created over 1000s of years in Europe. The continuation of farming is important for their maintenance. For example, deterioration of the land following abandonment of farming was one of the factors leading to the large forest fires in recent years in southern Europe. At the same time, it is clearly important that the introduction of novel types of plants is reconciled with the maintenance of cultural landscapes, due to their ecological importance, their recreational and emotional importance to

the citizens of Europe, and the economic importance of the associated tourism sector.

### **Knowledge about plants is needed to monitor, understand and cope with climate change and its impact on agriculture and ecosystems**

Human activities are having an unprecedented impact on the global environment. It is imperative to be able to detect, monitor and understand these effects, in order to identify and justify the appropriate preventive actions. Systems ecology has already developed an impressive range of technologies to monitor changes in the physical environment and vegetation cover, and integrate these in descriptive and predictive models that apply to various levels of ecosystem organization. Further large advances can be anticipated in the next 20 years including, we believe, decisive inputs from plant science.

First, the new analytic technologies developed in functional genomics for the profiling of transcripts, proteins, and metabolites, and more sophisticated approaches to analysing plant phenology will facilitate a much more precise and informative characterization of plant status in the field under changing environmental conditions (Külheim *et al.*, 2002; Bhalerao *et al.*, 2003; Wissel *et al.*, 2003). This information can readily be related to changes in genotypes and diversity, and to changes in the physical environment measured locally and using the increasingly powerful resolution delivered by satellite systems. The outputs will range from the availability of sets of diagnostic markers for different physiological states, through to an increased understanding of the physiological processes underlying ecosystem change (Osmond *et al.*, 2004).

Second, tools developed in plant genomics will be combined with advances in population genetics to provide unprecedented insights into the genetic diversity in the field. Adaptive evolution (like successful breeding) depends on the presence of genetic variation. Until now, the assessment of genetic diversity in populations of declining plant species has relied almost exclusively on the quantification of variation at putatively neutral marker loci. Over the coming 20 years, plant science will provide conservation geneticists and breeders with a range of molecular tools to identify loci of adaptive significance (Kroymann *et al.*, 2003; Ramos-Onsins *et al.*, 2004; Stinchcombe *et al.*, 2004), and will screen directly for allelic variation at them. When this is combined with genomic analyses of plant function in the context of the ecosystem, we can expect new and fundamental insights into ecosystem interactions, evolution, and the impact of climate change and environmental disturbance on plant populations. A better understanding of the genetic basis of plant adaptation to geographic variation in the biotic and abiotic environment will support the development of effective management

strategies in conservation, agriculture, forestry, and plant breeding to adjust to environmental change.

### **A global perspective dictates strong and open support for the developing world**

The novel opportunities offered by state-of-the-art plant science have to be considered in a global perspective. The knowledge obtained will be important for the competitiveness of European agriculture and industry. However, agriculture is important worldwide and most acutely for the less developed world. One of the most formidable challenges facing humanity is the rising population and the associated lack of food and unbalanced diet, and the urgent need for improvements in the standard of living in many important regions of our planet. This, in turn, leads to pressure on land and farming water and, as a consequence, the danger of land erosion and salinization, leading to the destruction of natural ecosystems that are often seen as just a short-term source of resources. This is clearly a political problem. However, appropriate developments in science and technology can contribute to finding solutions to such problems.

Europe has a long-standing tradition of collaborating with developing countries, and a duty of solidarity in developing the appropriate science and applying the new technologies to the needs of these countries through appropriate collaborative programmes. There is an urgent need to support improvements in plant breeding and agriculture in the developing world by generous cost sharing in large projects that generate, safeguard and utilize key resources, by open transfer of knowledge and by training and skill transfer. Plant breeding has already contributed varieties that are better adapted to different climate conditions such as the New Rice for Africa (West African Rice Development Association, 2001), whose breeders received the World Food Prize this year. The new approaches offered by plant genomics must be applied to traditional species, and to introduce characters important for local conditions. We also need to collaborate to preserve, manage, and characterize the corresponding wild species for the long-term benefit of mankind, and to support their use for local needs. European plant scientists should contribute by entering into close and open co-operative projects with the excellent breeding institutes located around the developing world. Examples range from the initiative to sequence the banana genome or the Brazilian sugarcane project to the Golden Rice developed by Swiss and German researchers (Xudong *et al.*, 2000), which is now being bred into local varieties in different Asian countries.

It is essential that all technological advances are open to use in the less developed world. In many cases, the infrastructure and skills can be learnt during research and training visits, and then established locally. Additional mechanisms will be needed to support open access to

international centres in cases where a technology requires extremely large-scale investment in facilities and staff. The direction in which technology develops must be guided by interdisciplinarity and by close interactions with experts from the less developed world to ensure that relevant and appropriate routes are taken. As outlined in a recent survey (Cohen, 2005), many important strategies for crop improvement are already being pursued by public research institutions in the less developed world. These have a high potential to generate useful products linking technology with the local conditions and needs. Further, the vast majority are not circumscribed by issues relating to intellectual property or worries relating to the predominant position of large agrochemical concerns. However, this survey also highlights that a large impediment to the success of these local projects is the slowness in developing a suitable regulatory environment, and in the gaining of expertise by local institutions to operate within this environment. In this direction the General Assembly of the United Nations approved a call in 2003 (Resolution 58/200 of the United Nations) that: 'Urges the relevant bodies of the United Nations system engaged in biotechnology to work cooperatively so as to ensure that countries receive sound scientific information and practical advice to enable them to take advantage of these technologies, as appropriate, to promote economic growth and development'.

### Concluding remarks

This paper has argued that recent developments in plant science are creating unprecedented possibilities to use our knowledge about plants, and illustrated this using a series of topics where our research field is generating knowledge and applications that are relevant to a series of pressing ecological, social and political questions. We are aware that the topics we have discussed are selective, and hope that colleagues will amend them and add further themes. The entire field of the life sciences including plant science is currently undergoing a dramatic transformation from various fragmented activities to a new integrated science, which reunifies the molecular-based and the organism-based branches. We believe that plant science is an important driver in this direction, not least because much of the knowledge and resources gained by understanding of plant function are applied in other research fields like breeding, agronomic practice and ecosystem research, in which system-orientated analysis is also vital. We would also welcome a contribution from colleagues in scientific areas such as taxonomy, soil science, agronomy, human nutrition, food processing, sensor technology, and field and global ecology, important disciplines with which plant sciences will need to interact increasingly closely in the future. We also stress that technological contributions from scientific research fields are options, which must ultimately be combined in a political solution.

The developments we have sketched in this paper make plant biology better prepared to contribute to a solution of some of the problems that society is facing. However, support is required to allow these options to be held open, let alone implemented. Support is needed not only to secure resources and allow their development, but also to create an atmosphere in which young scientists will continue to move into plant sciences to secure this important field for the future.

### Acknowledgements

This paper was generated during a workshop organized in Ghent (11–12 February 2004) by EPSO, at which the participants were Jon Agren, Michel Caboche, Bill Davies, Denes Dudits, Wilhelm Gruissem, Dirk Inzé, Jonathon Jones, Maarten Koornneef, Karin Metzloff, Chris Pollock, Pere Puigdomenech, Francesco Salamini, Goran Sandberg, and Mark Stitt. We also acknowledge helpful and critical input from EPSO members including Ton Bisseling, Eva Kondorosi, Helene Lucas, Ivana Machackova, Ioan Negrutiu, David Scholefield, Ulrich Schurr, Roberto Tuberosa, Wouter van Doorn, Ludger Wessjohann, Pierre de Wit, and Ulrich Wobus.

### References

- Abramovitz JA.** (ed.) 2002. *Vital signs: the trends that are shaping our future*. The Worldwatch Institute in cooperation with the United Nations Environment Programme. New York: WW Norton and Co.
- Arabidopsis Genome Initiative.** 2000. Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. *Nature* **408**, 796–815.
- Benning C, Stitt M.** 2004. Physiology and metabolism reacting to the full complexity of metabolic pathways in a post-genomic era. *Current Opinion in Plant Biology* **7**, 231–234.
- Bhalerao R, Keskitalo J, Sterky F, et al.** 2003. Gene expression in autumn leaves. *Plant Physiology* **131**, 430–442.
- Bovy A, de Vos R, Kemper M, et al.** 2002. High-flavonol tomatoes resulting from the heterologous expression of the maize transcription factor genes *LC* and *Cl*. *The Plant Cell* **14**, 2509–2526.
- Buckler ES IV, Thornsberry JM.** 2002. Plant molecular diversity and applications to genomics. *Current Opinion in Plant Biology* **5**, 107–111.
- Childe VG.** 1953. *New light on the most ancient Near East*. New York: Praeger Publishers.
- Cohen JI.** 2005. Poorer nations turn to publicly developed GM crops. *Nature Biotechnology* **23**, 27–33.
- Comai L, Young K, Till BJ, et al.** 2004. Efficient discovery of DNA polymorphisms in natural populations by Ecotilling. *The Plant Journal* **37**, 778–786.
- Condon AG, Richards RA, Rebetzke GJ, Farquhar GD.** 2002. Improving intrinsic water-use efficiency and crop yield. *Crop Science* **42**, 122–131.
- Czechowski T, Bari RP, Stitt M, Scheible WR, Udvardi MK.** 2004. Real-Time RT-PCR profiling of 1400 *Arabidopsis* transcription factors: unprecedented sensitivity reveals novel root- and shoot-specific genes. *The Plant Journal* **38**, 366–379.
- Diamond J.** 1997. *Guns, germs and steel: the fates of human societies*. London: Random House.
- Fehr M, Okumoto S, Deuschle K, Lager I, Looger LL, Persson J, Kozhukh L, Lalonde S, Frommer WB.** 2005. Development and

- use of fluorescent nanosensors for metabolite imaging in living cells. *Biochemical Society Transactions* **33**, 287–290.
- Fiehn O, Kopka J, Dörmann P, Altmann T, Trethewey RN, Willmitzer L.** 2000. Metabolite profiling for plant functional genomics. *Nature Biotechnology* **18**, 1157–1161.
- Fridman E, Carrari F, Liu YS, Fernie AR, Zamir D.** 2004. Zooming in on a quantitative trait for tomato yield using interspecific introgressions. *Science* **305**, 1786–1789.
- Gendrel AV, Colot V.** 2005. *Arabidopsis* epigenetics: when RNA meets chromatin. *Current Opinion in Plant Biology* **8**, 142–147.
- Gur A, Semel Y, Cahaner A, Zamir D.** 2004. Real time QTL of complex phenotypes in tomato interspecific introgression lines. *Trends in Plant Science* **9**, 107–109.
- Halweil B.** 2002. Farmland quality deteriorating. In: Abramovitz JA, ed. *Vital signs: the trends that are shaping our future*. The Worldwatch Institute in cooperation with the United Nations Environment Programme. New York: WW Norton and Company, 102–103.
- Hardenbol P, Baner J, Jain M, et al.** 2003. Multiplexed genotyping with sequence-tagged molecular inversion probes. *Nature Biotechnology* **21**, 673–678.
- Henikoff S, Till BJ, Comai L.** 2004. TILLING. Traditional mutagenesis meets functional genomics. *Plant Physiology* **135**, 630–636.
- Herrera S.** 2004. Industrial biotechnology—a chance at redemption. *Nature Biotechnology* **22**, 671–675.
- Hirel B, Lemaire G.** 2003. From agronomy and ecophysiology to molecular genetics for improving nitrogen use efficiency in crops. In: Basra A, Goyal S, eds. *Efficient nitrogen use in crop production*. Binghamton, New York: Haworth Food Production Press (in press).
- Ishkanian AS, Malloff CA, Watson SK, et al.** 2004. A tiling resolution DNA microarray with complete coverage of the human genome. *Nature Genetics* **36**, 299–303.
- Jaglo-Ottosen KR, Gilmour SJ, Zarka DG, Schabenberger O, Thomashow MF.** 1998. *Arabidopsis CBF1* overexpression induces *COR* genes and enhances freezing tolerance. *Science* **280**, 104–106.
- Jones-Rhoades MW, Bartel DP.** 2004. Computational identification of plant microRNAs and their targets including a stress-related miRNA. *Molecular Cell* **14**, 787–799.
- Kafatos FC, Eisner T.** 2004. Unification in the century of biology. *Science* **303**, 1257.
- Kessler A, Baldwin IT.** 2002. Plant responses to insect herbivory: the emerging molecular analysis. *Annual Review of Plant Biology* **53**, 299–328.
- Kleffmann T, Russenberger D, von Zychlinski A, Christopher W, Sjölander K, Gruissem W, Baginsky S.** 2004. The *Arabidopsis thaliana* chloroplast proteome reveals pathway abundance and novel protein functions. *Current Biology* **14**, 354–362.
- Kopka J, Fernie AF, Weckwerth W, Gibon Y, Stitt M.** 2004. Metabolite profiling in plant biology: platforms and destinations. *Genome Biology* **5**, 109.1–109.9.
- Kroymann J, Donnerhacke S, Schnabelrauch D, Mitchell-Olds T.** 2003. Evolutionary dynamics of an *Arabidopsis* insect resistance quantitative trait locus. *Proceedings of the National Academy of Sciences, USA* **100**, Supplement 2, 14587–14592.
- Külheim C, Ågren J, Jansson S.** 2002. Rapid regulation of light harvesting and plants fitness in the field. *Science* **297**, 91–93.
- Laws JA, Pain BF, Jarvis SC, Scholefield D.** 2000. Comparison of grassland management systems for beef cattle using self-contained farmlets: effects of contrasting nitrogen inputs and management strategies on nitrogen budgets, and herbage and animal production. *Agriculture, Ecosystems and Environment* **80**, 243–254.
- Loveys BR, Stoll M, Davies WJ.** 2004. Physiological approaches to enhance water use efficiency in agriculture: exploiting plant signalling in novel irrigation practice. In: Bacon MA, ed. *Water use efficiency in plant biology*. Oxford: Blackwell Publishing, 113–141.
- Mathews H, Clendennen SK, Caldwell CG, et al.** 2003. Activation tagging in tomato identifies a transcriptional regulator of anthocyanin biosynthesis, modification, and transport. *The Plant Cell* **15**, 1689–1703.
- Oksman-Caldentey KM, Inzé D.** 2004. Plant cell factories in the post-genomic era: new ways to produce designer secondary metabolites. *Trends in Plant Science* **9**, 433–440.
- Osmond B, Ananyev G, Berry J, et al.** 2004. Changing the way we think about global change research: scaling up in experimental ecosystem science. *Global Change Biology* **10**, 393–407.
- Peleman JD, Rouppe van der Voort J.** 2003. Breeding by design. *Trends in Plant Science* **8**, 330–334.
- Pozzi C, Rossini L, Vecchiotti A, Salamini F.** 2004. Gene and genome changes during domestication of cereals. In: Gupta PK, Varshney RK, eds. *Cereal genomics*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 165–198.
- Ramos-Onsins SE, Stranger BE, Mitchell-Olds T, Aguadé M.** 2004. Multilocus analysis of variation and speciation in the closely related species *Arabidopsis halleri* and *A. lyrata*. *Genetics* **166**, 373–388.
- Resolution 58/200 adopted by the General Assembly of United Nations 23 December 2003.** <http://ods-dds-ny.un.org/doc/UN-DOC/GEN/N03/506/58/PDF/N0350658.pdf?OpenElement>
- Richards RA, Rebetzke GJ, Condon AG, van Herwaarden AF.** 2002. Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. *Crop Science* **42**, 111–121.
- Roessner U, Luedemann A, Brust D, Fiehn O, Linke T, Willmitzer L, Fernie AR.** 2001. Metabolic profiling allows comprehensive phenotyping of genetically or environmentally modified plant systems. *The Plant Cell* **13**, 11–29.
- Salamini F.** 2003. Hormones and the green revolution. *Science* **302**, 71–72.
- Salamini F, Özkan H, Brandolini A, Schäfer-Pregl R, Martin W.** 2002. Genetics and geography of wild cereal domestication in the Near East. *Nature Reviews Genetics* **3**, 429–443.
- Sanchez-Monge E.** 1991. *Flora agricola. Taxonomia de las Magnoliofitas (Angiospermas) de interés agrícola, con excepción de las aprovechamiento exclusivamente ornamental o forestal*. Madrid: Ministerio de Agricultura, Pesca y Alimentación.
- Schwender J, Goffmann F, Ohlrogge JB, Shachar-Hill Y.** 2005. Rubisco without the Calvin cycle improves the carbon efficiency of developing green seeds. *Nature* **432**, 779–782.
- Schwender J, Ohlrogge J, Shachar-Hill Y.** 2003. Understanding flux in plant metabolic networks. *Current Opinion in Plant Biology* **7**, 309–317.
- Song J, Bradeen JM, Naess SK, et al.** 2003. Gene *RB* cloned from *Solanum bulbocastanum* confers broad spectrum resistance to potato late blight. *Proceedings of the National Academy of Sciences, USA* **100**, 9128–9133.
- Spillane C, Curtis MD, Grossniklaus U.** 2004. Apomixis technology development: virgin births in farmers' fields? *Nature Biotechnology* **22**, 687–691.
- Stinchcombe JR, Weinig C, Ungerer M, Olsen KM, Mays C, Halldorsdottir SS, Purugganan MD, Schmitt J.** 2004. A latitudinal cline in flowering time in *Arabidopsis thaliana* modulated by the flowering time gene *FRIGIDA*. *Proceedings of the National Academy of Sciences, USA* **101**, 4712–4717.
- Stitt M, Fernie AR.** 2003. From measurements of metabolites to metabolomics: an 'on the fly' perspective illustrated by recent

- studies of carbon–nitrogen interactions. *Current Opinion in Biotechnology* **14**, 136–145.
- Suzuki H, Xia Y, Cameron R, Shadle G, Blount J, Lamb C, Dixon RA.** 2004. Signals for local and systemic responses of plants to pathogen attack. *Journal of Experimental Botany* **55**, 169–179.
- Tanksley SD, McCouch SR.** 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* **277**, 1063–1066.
- Thornsberry JM, Goodman MM, Doebley J, Kresovich S, Nielsen D, Buckler ES IV.** 2001. Dwarfs polymorphisms associate with variation in flowering time. *Nature Genetics* **28**, 286–289.
- Tuberosa R, Salvi S.** 2004. QTLs and genes for tolerance to abiotic stress in cereals. In: Gupta PK, Varshney RK, eds. *Cereal genomics*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 253–315.
- Van der Fits L, Memelink J.** 2000. ORCA3, a jasmonate-responsive transcriptional regulator of plant primary and secondary metabolism. *Science* **289**, 295–297.
- Vigouroux Y, McMullen M, Hittinger CT, Houchins K, Schulz L, Kresovich S, Matsuoka Y, Doebley J.** 2002. Identifying genes of agronomic importance in maize by screening microsatellites for evidence of selection during domestication. *Proceedings of the National Academy of Sciences, USA* **99**, 9650–9655.
- West African Rice Development Association. (ed.)** 2001. *NERICA: rice for life*. WARDA/ADRAO, Bouaké (<http://www.warda.org/publications/NERICA.pdf>)
- Wissel K, Petterson F, Berglund A, Jansson S.** 2003. What affects mRNA levels in leaves of field-grown aspen? A study of developmental and environmental influences. *Plant Physiology* **133**, 1190–1197.
- Ye X, Al-Babili S, Klöti A, Zhang J, Lucca P, Beyer P, Potrykus I.** 2000. Engineering the provitamin A ( $\beta$ -carotene) biosynthetic pathway into (carotenoid-free) rice endosperm. *Science* **287**, 303–305.