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Editorial

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The past 10 years have seen a radical transformation of biology, including plant sciences. 1997 marked the beginning of large-scale genome-level sequencing, with the completion of the genome sequence of brewer's yeast, *Saccharomyces cerevisiae*. It seems difficult to believe today that *Nature* devoted an entire supplement to this achievement, with a separate article about each of the nine chromosomes that had not been previously published! By that time, sequencing of the *Arabidopsis thaliana* genome was already well under way; a major milestone was the publication in 1998 of 1.9 Mb of contiguous genomic sequence from chromosome 4, soon followed by sequences of the entire chromosomes 2 and 4 in 1999, all culminating in the release of the remaining three chromosomes along with an analysis of the entire genome sequence in 2000 [1]. Since then, three more land plant genomes have been announced, those of rice, the first monocot and a key crop plant; of poplar, the first tree; and, very recently, grape, the first dicot crop. In addition, several more genomes are available in draft form, such as sorghum and the genomes of non-vascular plants, including *Chlamydomonas*, a green alga, *Physcomitrella*, a moss, and *Selaginella*, a fern and more genome drafts are on the way (<http://www.jgi.doe.gov/>).

While these plant genome sequences have provided us with various parts lists, they have, perhaps more importantly, been a tremendous boon to everyday tasks in the plant molecular biology laboratory. One example is positional cloning, which no longer requires the painful assembly of overlapping clone contigs by repeated rounds of library screening nor sequencing of candidate regions. Similarly, the amazing rapidity with which genes responsible for Quantitative Trait Loci (QTL) are identified is fueled to a large extent by the availability of genome sequences. During the past few years, the advances in QTL cloning have led to the isolation of many genes responsible for traits associated with domestication, particularly in cereals [2].

Another critical and broadly used set of functional genomics tools derived from plant genome sequences blurs the line between 'forward' and 'reverse' genetics. Collections of sequence-indexed mutant collections, knockout mutations, in almost any gene in *A. thaliana*, are today only a mouse click away, and TILLING resources can provide missense or nonsense alleles of thousands more genes. It is probable that all major model plants, including rice and maize, will soon feature similar resources. These collections will enable the establishment of unimutant arrays, allowing systematic genetic screens that are no longer restricted to qualitative traits, but can incorporate statistical analysis of replicated mutant individuals. We can expect that mutations with much smaller phenotypic effects can thus be isolated in forward genetic screens.

Just as for genome sequences, it is difficult to imagine modern plant biology without microarrays. In fact, the first microarrays were developed using *A. thaliana* cDNA clones [3], and plant biologists have been systematically applying microarrays to a very large spectrum of questions. There are impressive community resources such as Genevestigator, with which the expression of any gene can be studied *in silico* in only a few seconds and over a much wider set of tissue and conditions than possible in an individual laboratory. For many of the samples so queried, these data have higher accuracy and confidence, because all the experiments were performed on plants grown under uniform conditions. We caution, however, that these sorts of *in silico* tools are only as good as the primary data that went into them. One exasperating problem is that much of the expression data is heterogeneous and not easily amenable to cross comparisons. Users of 'gene expression atlas databases' should, of course, wonder what the 'meta-data' are and whether or not, or how, the comparisons provided by the database have been validated.

All these resources are of course not ends in themselves but serve to help us understand how plants function throughout their life cycle. It is difficult to list all the major breakthroughs that the mechanistic analyses of plant function, powered largely by genetics, have seen in the past 10 years (simply read this journal!). Among them must be the discovery of receptors for nearly all of the major plant hormones (with none of these proteins having close similarity to animal hormone receptors); a detailed understanding of how these receptors control subsequent outputs; knowledge of how exposure to winter-like temperature, vernalization, and the correct photoperiod leads to flowering; how flowers are built; how roots are built; how leaves are built; and how the plant immune system controls the interplay of the different lines of pathogen defense. Even the elusive mobile signal controlling flowering, florigen, has come within reach [4].

Perhaps the largest impact that plant biology has had outside our field comes from the discovery of small RNAs as the active principle of RNA interference (RNAi). While many of our non-plant biology colleagues appreciate this, it remains remarkable that the past 10 years have seen two Nobel prizes for discoveries in humans or animals that had previously been made in plants, namely the finding of a hormone in gas form (NO, 1998, about a century after the discovery of ethylene) and RNAi (2006).

In many ways, much of what we take for granted today would have occurred only in our wildest dreams in 1997 (although some of the everyday experimental struggles persist, such as pesky cloning problems or obtaining decent antibodies, which seems to be just as difficult today as it was 10 years ago). This should warn us how dangerous it is to speculate about the future, except that

we can be reasonably certain that in another 10 years, many things that sound like science fiction today will have come true.

Some of the more obvious and immediate advances can be expected in the area of genome sequencing. Rather interestingly, only the rice genome has been finished to the same high standard as *A. thaliana* [5], and it is unclear when we will (again) see genome sequences of the same quality. On the contrary, the price for conventional sequencing using the Sanger method has decreased tremendously; a human genome can be sequenced today for less than 1% of the cost for the first human genome sequence. With the arrival of the new sequencing-by-synthesis methods, price tags have dropped by one to two further orders of magnitude. The \$1000 human genome can only be a few years off. Let's be clear though, these technologies are for re-sequencing of individuals across a species for which a high quality reference sequence already exists; they are not, at least yet, for the sorts of high quality reference draft sequencing that the plant biology community needs.

Why is this? The sequencing of all animal genomes, including platypus, serves as a comparative platform to inform, in the final analysis, human biology. Hence, 'animal genomics' is directional and ultimately human health related. But because humans use so many different plants, derived and domesticated across huge evolutionary distances, we will need many more high quality drafts, if we are to fully realize the potential of plant genomics in crop improvement. Hence, one important challenge is to define the key species for quality draft sequencing and to convince funding agencies that these still relatively expensive efforts are important. An interesting and important challenge that will help our cause in this regard will be the development of computational tools, and perhaps combinations of traditional sequencing and next generation sequencing methods, that will allow the cost benefits of the new technologies to impact the generation of high quality draft genomes. The key here is *de novo* assembly of very short sequence reads; one might expect that the first solutions to this problem will come from the microbial genomics community.

Nevertheless, the incredible power of the next generation sequencing technologies means that we can look forward to many more plant genomes, both from different species and from many individuals from within a species. There are already efforts underway to re-sequence hundreds of *A. thaliana* accessions and at least a dozen rice strains, for example. Somewhat paradoxically, substantial strides have already been made in plant species such as maize, rice, and *A. thaliana* to record within-species sequence diversity, while sequences from closely related species have been lacking. The latter type of information has been extremely useful for identifying, for example,

conserved regulatory sequence elements in fungi and animals. We hope that it will take at most a couple of years until we are in a similar situation as our fungal or animal colleagues, who are beginning to enjoy the fruits of rather detailed evolutionary comparative genomics. Further into the future, we envision that plant scientists, like Doctor 'Bones' McCoy of Star Trek fame, will be able to use tricorder-like devices to obtain complete genome sequences, and RNA information, within minutes in the field.

Progress in DNA sequencing and the many applications that follow from it, such as expression profiling, genome-wide studies of DNA–protein interactions, or DNA modifications, are inevitable; these will deepen in both their descriptive volume and explanatory power as larger, more uniform data generation platforms are merged with hypothesis testing. However, a key challenge for years to come will be to obtain single-cell or even subcellular resolution of important processes in the plant. Plant biologists have been at the forefront of recording expression profiles at the level of individual cell types [6], but the study of subcellular events is still much less common in our field compared with animal cell biology. Much of this, of course, has to do with the rigid and substantial wooden box encasing plant cells, which makes imaging often very challenging.

From the few examples we have, however, it is clear that live imaging has tremendous potential [7], and we hope that it will be used much more widely. Information on individual cells combined with data from live imaging is a prerequisite for the creation of models that are both explanatory and predictive (e.g. [8,9]). As before in bioinformatics, targeted programs to foster the interactions with physicists and mathematicians need particular encouragement from the community and the funding agencies.

Finally, we are very excited about the prospects of plants as a source of renewable materials and energy. While it is still unclear how much biofuels can contribute to the

solution of our energy and carbon emission problems, plant sciences have become much more prominent in the public sphere during the past couple of years. Furthermore, with the competition between food and other uses for plants, prices at the farm gate have risen in many places, something that is sure to help the economies of developing countries. The public will soon realize that the days of a limitless and often ridiculously cheap supply of plant products, both geologically ancient and contemporary, are over, which in turn should provide many new opportunities for creative research in the plant sciences. Our job, as plant scientists, is to engage that public often and factually; to be in the schools and in front of civic and professional groups of all kinds to teach them that plant science matters more now than ever before.

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