Apomixis: A social revolution for agriculture!

Among the many other advantages, apomictic food crops could eliminate the need of farmers in developing countries for yearly purchases of new hybrid seed. Richard Jefferson argues that especially public domain research into apomixis could generate new and versatile breeding strategies, available to the resource-limited plant improvement community.

Shaping agriculture for both human needs and for environmental health can be greatly accelerated by properly developing the trait of apomixis. Apomixis is the phenomenon by which certain plants produce 'seeds without sex'. Introduction of this trait to crop plants would allow the immediate fixing of the genetic make-up of any individual plant that responded particularly well to a given environment or social need by producing seed with identical genetic properties to the parent. This tool would enable us to adapt plants to the environment, rather than the current necessity for adapting the environment to the plants through intensive agricultural practice. In contrast to today's hybrid technologies, it would make grain and seed once again the same, restoring farmers to their role as innovators. The introduction of this trait into crop plants would herald perhaps the single greatest change in agricultural practice since the dawn of cultivation.

To achieve such a revolutionary impact, and to ensure that the impact is both environmentally and socially sound, the trait must be developed to have certain characteristics, and must be accessible to all people. We should develop a concerted, focused and strategic international research programme within the public domain to generate the trait *de novo* using molecular techniques.

What is apomixis

Plant reproduction occurs by complex and diverse mechanisms. Sexual reproduction is most common in flowering plants of agricultural importance. Male and female gametes (the pollen and the egg cells respectively) are separately produced with half the normal chromosome number. These combine during fertilization and further develop to give rise to a seed. This seed contains genes derived from both parents in a form that is distinct from both parents so that once that seed germinates a plant of unique genetic constitution is generated. By contrast, apomixis produces seeds through asexual processes. The genetic make-up of the seeds is identical to that of the mother plant. If the mother plant is well adapted to a particular environment or purpose, so will be the offspring.

Although many wild plants are naturally apomictic, for instance the common dandelion (*Taraxacum sp.*), very few crop species are apomictic. This is perhaps not surprising. Over the last thousands of years today's crop species were selected from amongst the numerous edible or fibrous plants by farmers. The criteria for such a choice almost certainly included the plant's ability to segregate variation: to reassort traits through sexual reproduction, and thus to improve under mass selection. This is the very property that apomixis prevents. Thus our small collection of modern day crops probably represents a biased population in favour of sexuality.

Potential impacts of apomixis

When apomixis is developed to meet stringent criteria the impact on agriculture could be sweeping and profound. Changes that could ensue are:

- preparation of almost limitless numbers of hybrid cultivars from newly apomictic crop species, thus greatly expanding the diversity of utilized genetic resources and providing the benefits of hybrid vigour to numerous crops that have never previously had hybrid technology available;
- maintenance of heterozygous genotypes including those made through wide crosses, opening up completely new breeding strategies and methods in both sexual and vegetatively propagated crops. Thus, plant breeding could become extremely quick and responsive to micro-environments, cropping conditions, pathogen or pest populations, and markets. This in turn could stimulate diverse strategies for agro-ecosystem management and optimization. It could, in effect, encourage 'boutique breeding' of crops to suit the environment, since a single well adapted plant, which is chosen for its performance in a micro-environment, could directly give rise to a successful cultivar.
- propagation of hybrid seed directly by the farmer. Seed from an apomictic hybrid will not lose its genetic make up through sexual crossing, and thus will 'breed true'. By contrast, seed obtained from a conventional (i.e. sexual) hybrid does not give rise to the same genotype or performance as the parent plant, obliging the farmer to purchase new hybrid seeds for each planting.
- propagation through seed of crops that are currently vegetatively propagated such as cassava, potato, sweet potato and yams - with concomitant elimination or reduction of propagule-borne disease, substantial increases in germplasm flows, and expansion of potential growing regions;
- elimination of crop losses related to the 'mechanics' of sexual reproduction, such as failure of pollination or fertilization, This failure can occur through both biotic and abiotic stresses, and constitutes a major cause of unpredictable reductions in crop yield and reliability;
- substantial increases in yield in some crops due to photosynthate availability through elimination of male flowers/flower parts.

A fringe area of research?

This list of possible impacts is so striking that it well worth considering apomixis, if developed to achieve the goals for a broad and diverse group of users, as being the most important target for international agricultural research. And yet apomixis is almost always viewed as comprising a 'fringe' element within agricultural research community. It has never been the subject of a concerted effort. Why is this?

Few existing organizations in either the private or public sector are structured to benefit from the changes as would ensue from this innovation. For instance, some members of the hybrid seed industry will view apomixis as a threat to their ability to be compensated for their research investments, which currently relies on the necessity for annual purchase of hybrid seed. This logic, however, is faulty.

Turning to the computer industry for our lessons, operating systems such as DOS, UNIX and Windows, and public-domain programming languages, together with revolutions in decentralized hardware, stimulated the creativity, productivity and profitability of the computer industry. This has allowed many thousands of new programmes tailored to particular users to be generated rapidly by hundreds of new companies, using the newly-available tools. Few of these programmes are copy-protected (unlike the situation with hybrid seeds), simply because the competition to innovate is so intense, that only with new and improved products can these firms retain their market share. Importantly, however, this competition is coupled to the technical ability to innovate. Apomixis would provide just such tools for innovation, and could thus stimulate user driven breeding.

An additional reason for the limited attention for apomixis is that the extraordinary promise of apomixis has been unmet by conventional methods. As a consequence, the assessment of its potential is compromised by a perception that it is not achievable. Traditional approaches to developing apomictic crops are limited to breeding in apomictic traits from wild, but sexually compatible relatives. Few, if any, of these relatives will have the optimum apomictic characteristics. Hence, this approach has met with limited success, with a few notable exceptions on the horizon (see box).

Shaping apomixis by a transgenic mechanism

It is becoming clear that *de novo* generation of the trait, i.e. synthesis of a suitable controllable apomixis through molecular biology, is a viable and productive avenue. Molecular biology and genetic engineering are often seen largely as tools to introduce an existing trait or gene into sexually incompatible species. However, the real power of these approaches lies in the ability to prise apart the underlying mechanism(s) of biological processes. With this level of understanding, adjustment and modification of biological processes by molecular intervention can lead to generation of entirely new traits.

For example, envision a scenario in which an apomictic gene 'cassette' can be generated through molecular biology that addresses the key constraints and opportunities outlined above. This cassette could be introduced into diverse crops where it would function to: (a) produce a fully functional egg cell with a full set of maternal chromosomes; (b) block the development of male sexual structures to avoid wastage of the plant's resources and to prevent uncontrolled spread of the trait; (c) allow development of the seed without any requirement whatsoever for pollination to avoid problems of pollination failure; (d) be conditional, where the default state is apomictic, but upon application of a non-proprietary, inexpensive natural compound, the trait is fully suppressed so that crosses can be performed in either direction.

With the increase of information about the biology of plants and other organisms, we can now see our way forward to realizing this scenario. For instance the structure and function of most of the genes involved in the critical decision to make a reduced egg cell have already been identified in yeast, a higher organism that is very simple to work with in laboratories. Many similar genes are being identified in plants.

Additionally, choice of the proper 'model' apomictic plant to analyze both at the molecular and cellular level, will have a major impact. Recently, there has been very substantial progress in Australia and New Zealand using the apomictic weed *Hieracium* (see box).

Conditional apomixis

To maximize the benefits to the agricultural community, it is crucial to retain the ability to introgress (insert) numerous genetic combinations into the apomictic background. Without this ability, apomixis would be restricted to a limited set of cultivars. Introgression of new genes requires sexuality in the plant, and therefore the apomictic trait must be able to be switched off temporarily. This could be achieved using compounds that can be applied to induce or repress defined gene cassettes that have been engineered. Some promoter control systems of this type have been described, including a number by laboratories in the pri-

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Ongoing research towards molecular apomixis

A joint ORSTOM-CIMMYT project in Mexico, led by Y. Savidan, on the introgression of apomixis from *Tripsacum* into Maize reportedly is nearing fruition, and should prove itself in the next few years.

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W. Hanna and colleagues, at the US *Department of Agriculture*, Georgia are making substantial progress on introgressing apomixis into pearl millet.

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J. Miles and J. Tohme at CIAT, Colombia, have recently made important progress in molecularly mapping a gene or gene complex associated with apomixis in the tropical apomictic forage *Brachiaria.*

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In New Zealand, R. Bicknell has pioneered the use of the important model apomict, *Hieracium.* He developed the suite of tools necessary to make *Hieracium* a laboratory system, including genetic transformation, anther culture, tissue culture, transposon mutagenesis and others. In a collaboration with A.M. Koltunow of the *CSIRO*, Adelaide, strides are made in the molecular and cellular biology of autonomous apospory - the most promising mechanism.

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A. Chaudhury, of the *CSIRO*, in Canberra, has obtained numerous mutants of the versatile genetic system, *Arabidopsis thaliana* which have components of apomixis, and will shed light on the underlying mechanisms.

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CAMBIA, Canberra, through its *International Molecular Apomixis Project* (IMAP), in which many of the above mentioned researchers participate, is in the process of securing funding to carry this work forward. The *Food and Agriculture Organization* (FAO) will be working with CAMBIA in bringing together the expertise in all fields necessary to analyse possible outcomes and to shape future research, ownership and application.

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vate sector using proprietary agrochemicals. However, improved systems need to be available to even the most resource-limited of the plant improvement community.

Public domain: the way forward

The form that the development of apomixis takes will determine who will benefit from it. However, the increasing commoditization of agricultural production and the concomitant privatization andcentralization of agricultural research instills legitimate fears that key methodology and opportunities will become restricted. This would be particularly tragic in the case of apomixis, which could have an important impact if it were broadly available to the agricultural research and production sectors, This is especially true in the less developed nations that are struggling with the problem of reconciling the desperate needs for environmental preservation, enhancement of agricultural production, and managing increasing populations. It is therefore imperative to move forward with research into apomixis in the public domain before it is too late. ◆

Richard A. Jefferson (CAMBIA, Australia)

Interview with Richard Jefferson, director of CAMBIA

Richard Jefferson, director of the Center for *the Application of Molecular Biology to International Agriculture* (CAMBIA) explains the organization’s unorthodox view on the application of biotechnology.

Q. *The word* CAMBIA *is an acronym and in Spanish means it changes . Is there special significance to this? Does it in some way reflect your own thinking?*

A. The Spanish word ‘cambia’ basically sums up our ideas - we *must* change the way we approach the world. If you look at the words the acronym contains, I could explain them as follows: Biotechnology invokes a technological fix to issues that are fundamentally social, and which can best be approached through management changes. We would rather focus on using the powerful tools of *Molecular Biology* to increase ‘heuristic’ value, or the ability to see changes in the environment, and on making these available to people who have local knowledge, insights and commitment to solving problems. So, our approach will be based on molecular biology, but will not require molecular biology for its use. *Application* is chosen to make a careful distinction from purely knowledge-driven work. *International* is chosen to recognize that the problems in agriculture and environment affect us all, but can be felt more acutely in those societies that are poorer and with less buffering capacity in their economies and environments. We chose *Agriculture,* because it is there that reductionist thinking, reducing a complex local structure to a simple simulacrum of nature has proven so devastating to both societies and environments. Center is obviously because to create such different and powerful tools requires a critical mass of diversely skilled and interested individuals.

Q. *CAMBIA’s stated goal is to encourage us to look beyond model systems* and *put the power of modern science in the bands of farmers. How does it plan to do this?*

A. Well, certain examples may clarify this. I will describe these examples as being related to four classes of question. What is out there? How is it performing? How can it be improved? How can we be involved in the process? These are the fundamental questions in agriculture. CAMBIA is developing methods to allow these questions to be answered by the people who should be answering them, such as farmers and the research community whose job is to support these farmers.

For instance, “What is out there?” is basically a statement of our ignorance of genetic diversity. We are all driven by the need to experience - usually to see - the world before we can do anything about it. If we had ways of looking with high resolution and clear vision at the genetic diversity *within* a population of organisms, we could then use this vision and information to predict, to verify and to sustain productive systems. But first we have to see it. So, CAMBIA is catalyzing the interactions of a number of governments in Asia and Latin America, scientific instrument companies, research organizations and United Nations specialized agencies, to create a consortium to develop new, affordable instruments and methods that will allow robust, inexpensive DNA-based fingerprints and taxonomically valid information to be developed for our existing biodiversity *by* and *for* those with stewardship responsibilities: typically the developing countries of the tropics and subtropics. This group is called the GRIT *(Genetic Resource Indexing Technologies)* Consortium.

Understanding *how* things work can give us important short cuts if we are wise enough not to assume we have all the answers. For example, research has shown that in tropical legumes, including mung bean, common beans, soya beans etc. the nitrogen that is derived from the fixation of atmospheric nitrogen by symbiosis with rhizobia, is transported in the plant as a set of signature compounds (ureides), while the nitrogen absorbed from soil reserves or fertilizer is transported in other forms. Under laboratory conditions, we can measure these compounds, and their ratio shows the efficiency with which crop is fixing nitrogen a very important parameter for measuring the health of a plant. However, we really need to do this in the field, and cheaply, so that any farmer can then use methods of their choice (many of which we cannot even guess) to manipulate the system to improve the efficiency. For instance by changing management strategies, germplasm combinations, rotations, irrigation etc.. CAMBIA thinks we can do this by using molecular biology to genetically ‘engineer’ plants *not* to fix nitrogen better-we are miles from this but rather to produce two enzymes that give vivid colours on the living plant whose levels are proportional to these compounds. By visualizing the colours, one could then be able to estimate this crucial ratio, and assess the efficacy of an empirically adjusted system! This is a tangible example of developing living ‘bioindicators’ or ‘sentinels’, through using molecular biology.

Q. *Haven t farmers during the past millennia not been able to develop their own bioindicating skills?*

A. Absolutely! As in any profession, there are good farmers and bad farmers. The good ones have certainly developed substantial knowledge and intuitions that encompass bioindicators of all types. But we must not think that the need for innovation has ended. The types and varieties of crops grown, the growing conditions, and the environmental, population and economic pressure that exist today in most parts of the world are unprecedented. Our contribution is to provide new tools with which to improve the existing types of bioindicators as developed by the ‘good farmers’. ◆

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