

2

Who Are Plant Breeders, What Do They Do, and Why?

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Even though plant breeders have an intuitive sense of what they do and what function they perform, the general scientific community and the public at large have little understanding of the essential nature of plant breeding. The first section of this chapter reviews historical trends relating to numbers of plant breeders. However, a great deal is left unsaid by merely reviewing survey results or historical patterns. So, while the first section provides a necessary starting point for a discussion about the plant-breeding profession, the more interesting issues—why do plant breeders do what they do, and should they even try to do it—are left hanging. Therefore, the last two sections address the more fundamental issues of what plant breeding actually accomplishes and how it fits in with the modern era of genomic science.

Who are the plant breeders, and how many are there?

There has been a recent increase in private plant-breeding expenditures in industrialized countries to the extent that private investment may now surpass public expenditures by a considerable margin (Heisey et al., 2001). This trend is particularly acute in the United States Based on Frey's National Plant Breeding Study — I (Frey, 1996); in 1994 there were a total of 2,241 science person years (SYs) devoted to plant-breeding research and development in the U.S. Of these, 1,499 were in the private sector, and 742 were in the public sector. From 1990 to 1994, the net loss from state agricultural experiment stations (71% of the total public sector involvement) was estimated to be 2.5

SY/year, while private industry increased at 32 SY/year. Over this period, private industry spent approximately \$338 million on plant-breeding research annually (61%), while the public sector spent approximately \$213 million/year (39%). There are many reasons for these trends, and among them are the following: (1) there is an increasing emphasis on basic (versus applied) research in the public sector because of the need to attract funds from federal granting agencies; (2) new organizations with single-interest focus (environment, consumer, etc.) are diluting the public-funding base; (3) funding for public agricultural research has not kept pace with increasing research and development costs; and (4) intellectual property restrictions have lessened public access to elite germplasm.

The consequences of the decrease in public sector plant breeding may be particularly severe for minor crops. As the public sector shrinks, many of the minor agronomic and horticultural crops risk becoming plant-breeding orphans. The private sector has embraced biotechnology to the extent that its near-term focus must be on relatively simply inherited traits and on major crops grown in the developed world as a necessary strategy to recoup the substantial research investments made in recent years. Given the negative public sentiment toward biotechnological innovations such as genetic transformation, those crops directly consumed by humans, many of which are classified as minor crops, will probably not receive much attention in the near future. Unfortunately, despite the moniker “minor,” most minor crops are important components of the agricultural system, for example, perennial grasses and forage legumes, and

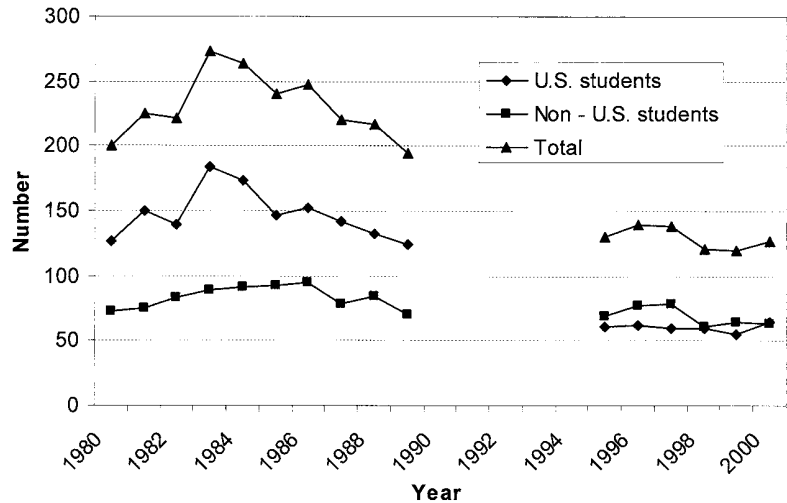


Figure 2.1 Plant-breeding graduate degrees awarded by U.S. universities from 1980 to 1989 (Collins and Phillips, 1991) and from 1995 to 2000 (Guner and Wehner, 2003).

many so-called minor crops can become major crops in a relatively short time, for example, alfalfa and soybeans.

One of the more ominous features of the Heisey et al. study (2001) and the Frey (1996) survey is that the public infrastructure supporting the education of plant breeders destined for either public or private service appears to be eroding. There have been a number of surveys of graduate training over the past several decades addressing this issue, but two of the most recent best depict the current situation—the Collins and Phillips (1991) survey performed over the 1980–1989 time period and the Guner and Wehner (2003) survey, which focused on 1995–2000.

The Collins and Phillips (1991) survey was sent to all public land grant and 1890 colleges. Responses were received from 84 departments from 46 institutions in 42 states. Institutions in 2 states did not respond, and 6 indicated no plant-breeding activity. The Guner and Wehner (2003) survey was sent to 71 land grant universities, and 52 indicated that they had capacity for plant-breeding training. In contrast to the Collins and Phillips (1991) survey, the Guner and Wehner (2003) survey had a specific statement requesting that students working mostly in molecular genetics not be counted as involved in plant-breeding research. Responses were received from 82 departments from 47 institutions in 47 states. Institutions in 3 states did not respond, and 7 reported that they had no degree programs involving plant breeding.

Based on the coverage and response rates, the

two surveys seem roughly comparable, and they are graphed together in Figure 2.1. Collins and Phillips (1991) reported that there was no real change in numbers of graduate students from 1980 to 1989, but there was a trend upward in early 1980s followed by a downward trend toward the end of the decade. Collins and Phillips (1991) were not certain that the latter trend was real. The Guner and Wehner (2003) survey appears to support the downward trend starting in the mid-1980s, but from 1995 on there was little change. Some caution is needed comparing trend lines, however. In particular, it is difficult to determine what effect the molecular genetics disqualifier had in the Guner and Wehner (2003) survey and whether a similar statement would have affected the earlier survey.

One trend does seem obvious. The number of non-U.S. graduate students in plant breeding in the period from 1995 to 2000 equals or exceeds U.S. students, whereas in the 1980s there were nearly twice as many U.S. students as non-U.S. students. There may be several reasons for this. Non-U.S. graduate students in plant breeding are often funded by their home institutions, making them very attractive to cash-strapped U.S. plant-breeding programs. But also, many U.S. plant breeders may find non-U.S. students better acquainted with agricultural issues and better motivated to perform the public service of plant breeding.

Thirty-seven institutions were common to the two surveys, and the figures were broken down by institution for the two time periods (Figure 2.2).

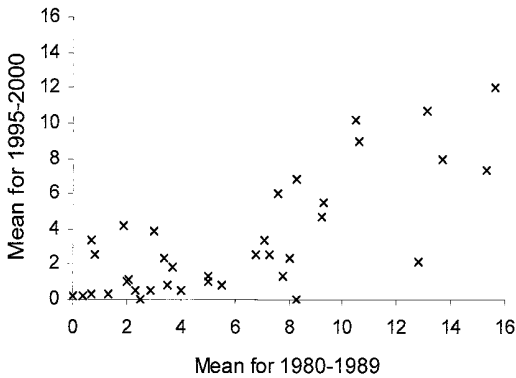


Figure 2.2 Number of plant-breeding graduate degrees awarded per year at 37 U.S. universities. Data for 1980–1989 are from the survey of Collins and Phillips (1991), and data from 1995 to 2000 are from the survey of Guner and Wehner (2003). The 37 land-grant universities are those in common for the two surveys. The institutions in the circle are the 10 that produced the highest number of plant-breeding graduate degrees (master's and doctorate degrees for both U.S. and non-U.S. students) based on the 1995–2000 survey.

Most of the major plant-breeding training institutions in the 1980s remained strong in the late 1990s, although most experienced a decrease in the number of graduate degrees awarded. Fortunately, the top 10 institutions in 1995–2000 represented a diversity of regions in the United States, with the possible exception of the far western United States. It also seems that several institutions may have downsized their plant-breeding programs to a considerable extent.

One final way to quantify trends in plant-

breeding activity is to review registration articles in *Crop Science* as tallied by the Germplasm Retrieval Information Network (GRIN, 2003). Since 1926 there have been over 10,000 such registration articles. Many plant breeders in the United States and elsewhere publish brief registration manuscripts in *Crop Science* and then deposit the referenced germplasm in the U.S. National Plant Germplasm System (NPGS). From an academic standpoint, registration manuscripts count in the tally of a public sector scientist's publications, which encourages registration, especially among young scientists seeking promotion. On the other hand, individuals also receive professional credit for registering intellectual property with their university's intellectual property office, which may preclude registering germplasm (along with the required seed deposit in the NPGS). In other words, some caution is needed when interpreting these data.

For all classes of registrations and for all crops combined, registration activity leveled off sometime in the early to mid-1990s (Figure 2.3). If it were not for the addition of the genetic stock category, the trend would be downward. Surprisingly, this is not due to a lessening of cultivar or parental line releases, which are the most adapted and immediately useful germplasm. These classes have remained relatively stable over a long period beginning in the 1970s. Instead, germplasm registrations leveled off beginning in the mid-1990s.

If the so-called major and minor crops (as defined by the National Agricultural Statistics Service,

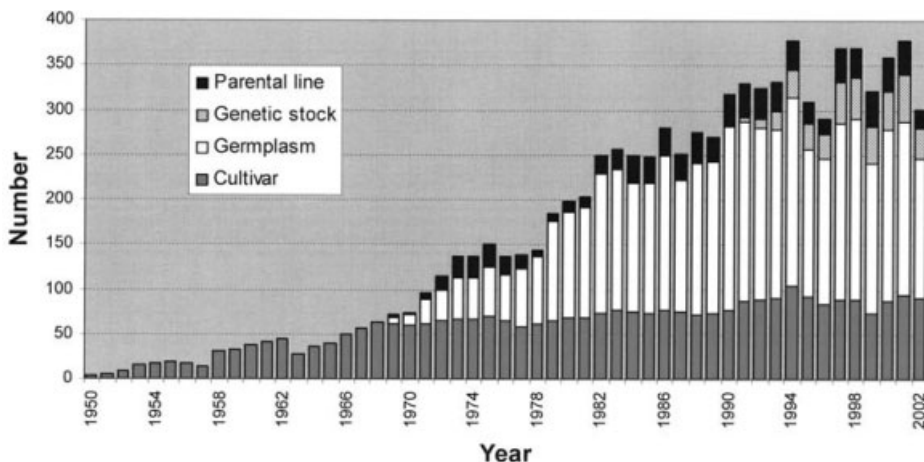


Figure 2.3 *Crop Science* registration manuscripts published from 1950 to 2002. Data presented are five-year trailing means for all crops (GRIN, 2003).

USDA) are separated out, the trends are somewhat similar for the two categories (data not provided). The germplasm class peaked sometime in the early to mid-1990s for the minor crops, perhaps a little earlier than that for major crops. However, the number of minor crop cultivar registrations trends slightly upward up to the present time, which is encouraging relative to the recommendations for increased public effort for minor crops coming from the National Plant Breeding Studies of Frey (2000).

Six crops, alfalfa, cotton, maize, soybean, sorghum, and wheat, make up about two-thirds of the total of 4,739 germplasm registrations from 1967 (the year the germplasm category came into use) to 2002. Germplasm registrations for alfalfa, cotton, and maize have trended downward from the mid-1990s, while sorghum, soybeans, and wheat remain level or have increased slightly. These trends reflect somewhat the relative importance of public and private sector plant-breeding involvement. Molecular genetic approaches may also be supplanting germplasm enhancement activities for those crops experiencing a decrease in germplasm registrations.

Why do plant breeders do what they do?

Operational model

There has been a substantial transformation in how genetics relates to plant breeding. Until recently, the focus was on plants and phenotypes, and phenotypic selection was the *raison d'être* for plant breeders. Plant breeders relied on disciplines such as statistical genetics that, in some vague but nonetheless effective manner, helped improve germplasm. The operational model was that of form follows function; that is, select on the basis of phenotype (function), and changes in the underlying genotype (form) would follow.

The focus of current plant genetics is mostly on genes and genotypes. We are in the era of gene sequencing, mapping, transformation, functional genomics, proteomics, and metabolomics. The underlying assumption of most current plant geneticists is that if the genotype is well enough understood, improved plants and phenotypes will follow without undue exertion. The new vision of a plant breeder is that of a true engineer who assembles the appropriate set of nucleotide sequences in the construction of an ideal genotype. The engineer-

ing approach to plant improvement most closely follows the function follows form model. The ultimate goal is to engineer plants from the sequence up, locus by locus, rather than, as some would claim, work backward by using plants and their phenotypes to modify the underlying genotype.

What is not often recognized is that the change from the form follows function model to that of function follows form is a profound philosophical transformation in how scientists view the biological world. Form follows function clearly has been the Darwinian operational model underlying evolutionary advance starting with the first replicating molecule over 3 billion years ago. Only in the last several decades has it become conceivable to work from the genetic sequence back up to the whole organism. This transformation seems to be happening by default, without any discussion or challenge.

What is the real relationship between the genotype and phenotype? This is a particularly acute issue for students intrigued with the promise of the plant breeding and plant genetics disciplines. Recent generations of students have been generally highly disciplined academically, and most new students have broad and thorough understanding of genetic technology, far surpassing that of any past generation. Current students now also typically come from biological rather than agricultural disciplines. They have grown up mostly in air-conditioned urban settings; they tend to have little understanding of agriculture in general; and their notion of the "environment" is relatively unsophisticated. Most new students have the optimistic sense that the genotype is now directly controllable or it shortly will be. Understanding the genotype has become the essential and ultimate target.

Past plant-breeding students, on the other hand, had an ingrained and practical sense of the environment since many came from rural areas and many were involved directly with farming. To them, every season was a new season, and they knew that in any season no sequence of environmental events is ever repeated again. They also knew what a phenotype was. They helped plant, cultivate, harvest, and sell phenotypes. However, they faced a vexing limitation in that the genotype was only a concept. They knew it existed and that quantitative genetic models could be used to help breeders select more efficiently, but that was the end of it.

This transition is not particular to students. It has also occurred for their faculty mentors. What are the implications of this transition, and more to the point, what has plant breeding now become?

What is plant breeding in the modern era?

Typically, most discussions of how plant-breeding works start with the idea of a breeding population from which adapted cultivars are derived. A breeding population might be a broad-based population or a narrow-based population, such as an F₂ generation of a cross between two lines. Plants derived from the breeding population might then be improved by pedigree selection to create the adapted cultivar. Some breeding approaches more tightly focus on trait introgression, and the breeding population used to start the process may actually be single inbred lines or even single plants. Backcrossing or some form of molecular genetic transformation can be used to insert one or few genes of value. The essential feature common to all approaches is that there is a starting germplasm source and that adapted varieties are to be derived from it in some fashion.

Trait introgression has become very important in the current era. It is now mostly a gene-oriented, mechanistic approach, and, as such, it is intellectually attractive and regarded as a more rational approach than merely relying on chance events inherent to the sexual cycle (segregation and recombination). Trait introgression uses *a priori* structural knowledge of genes and proteins and provides predictable outcomes. It also works well, for the most part.

But both pedigree selection and trait introgression are one-dimensional approaches, and plant breeders must work in at least two dimensions. Not only is it important to develop adapted cultivars from current breeding populations, plant breeders must also provide future generations a continuous supply of ever-improved breeding populations. Breeding populations, in whatever form, serve as the base platform for plant improvement, either by means of selection or trait introgression, and they will remain in this role for the foreseeable future.

We don't know all we need to know about the genetic control of even the most well-defined and simple metabolic pathways, so the notion that merely adjusting the genetic architecture of a common, stagnant germplasm base will suffice is sim-

ply foolish, although there is tremendous commercial reward for operating in exactly this fashion. Recycling selected materials to form new breeding populations has been a major long-term responsibility of plant breeders, but since reliance on the sexual cycle is now regarded as somewhat suspect, and perhaps even irrational, at least relative to modern genetic approaches, fewer and fewer plant breeders seem to want to do it.

As Knight (2003) points out, other forces are also at work that undermine the plant-breeding profession. In both the public and private sectors, reward structures are strongly skewed toward short-term objectives, for example, gene discovery, papers, patents, and promotion, rather than addressing more substantive and long-term problems. Knight glibly suggests redefining plant breeders as "open-source molecular agronomists," as a means of providing some sort of professional cachet, but much more is needed.

What is required is that there be a thorough re-examination and reinvigoration of the intellectual foundation of the plant-breeding discipline. The basic problem is that conventional plant breeding is not usually considered an overly scientific pursuit. To a large extent, success relies on factors of chance such as mutation, recombination, genetic drift, and the environment. Chance events cause the most problems for the current scientific generation. Under the engineering operational model, how can random events serve any purpose? The sexual cycle is inexact and, therefore, outmoded. Why rely on random recombination and mutation, if we can ultimately assemble the precise base sequences we need?

Plant breeders must recognize that their strength lies in what are now two unique attributes: (1) respect for the phenotype, and (2) an understanding of the creative power of selection. The challenge is to bring new intellectual rigor to the understanding of the phenotype and selection in an appealing and fruitful way.

What is the scientific rationale for plant breeding?

Ironically, the most intriguing justification for the plant-breeding approach to problem solving comes from disciplines closely tied to engineering and computational programming (e.g., artificial intelligence, evolutionary computation, and computational ecology). These disciplines are attempting to use the current understanding of molecular

genetics, developmental biology, and evolutionary biology to address some of the most complex engineering/computational issues of the day. They do so by evoking the concept of evolvability as a way of embracing mechanisms promoting productive change.

The concept of evolvability

To a plant breeder, evolvability is an organism's capacity to generate heritable phenotypic variation. More generally, evolvability can be thought of as the process by which complex systems acquire the capacity to discover and perpetuate beneficial adaptations (Stewart, 1997). Living organisms are exquisitely evolvable, and many researchers in nonbiological disciplines are intrigued by the possibility of harnessing evolvability on a broader scale.

Computer programmers dealing with highly complex tasks such as prediction of climatic change or those in artificial intelligence who want to imbue computer code with the ability to learn are designing systems of computer algorithms in such a manner that one can use genetic operations to more efficiently arrive at optimal code than would be possible by a standard programming approach (Wagner and Altenberg, 1996). To greatly simplify, the goal of evolutionary computation is to design code such that it can handle random coding variants. One can then choose among the variants based on how efficiently programs accomplish some computational task. Selected variants are then recombined in some fashion to create the next round of possible solutions for continued improvement. Repeated iterations of this procedure can provide increasingly efficient solutions for highly complex tasks. The analogies to selective breeding are obvious. The computer code is the genotype, the function performed by the code is the phenotype, random coding mistakes or variants represent mutations, and random replacement of algorithms among selected variant systems of code represents recombination. Most intriguing is the fact that the operational model has shifted from function follows form to form follows function. These disciplines have the power plant geneticists so desperately want—the ability to create the underlying code specifying precisely any outcome—yet they are looking at evolutionary paradigms to more efficiently achieve their goals.

Obviously, the situation has been oversimpli-

fied. Computer code will not respond to an evolutionary approach unless programs are suitably designed (Marrow, 1999). Random coding mistakes and scrambling of algorithms are not, in and of themselves, creative forces and will quickly disable most computer programs. Conditions must be appropriate for such random forces to be creative rather than destructive. Those involved with evolutionary computation have recognized that a thorough understanding of evolutionary biology is needed to provide some perspective on what these conditions might be.

What enhances evolvability?

There are many core biological processes that have been highly conserved across eukaryotes and even all life forms. For example, based on extensive evaluations of genomic synteny across plant taxa, it is becoming clear that perhaps more than 90% of plant genes in any given species have close homologs within most other plant genomes (Bennetzen, 2000). But what does this really mean? Darwin would be pleased to know that we now have ample genetic evidence that all organisms trace back to a common source. The more important question, though, is what is it about genome organization that starts with such homology yet provides such immense diversity in plant morphology and adaptation. The conventional view is that conserved features have been selected for efficient function and optimal design. However, as we learn more about metabolic systems, it is beginning to look like a significant number of “highly conserved developmental mechanisms are characterized by not being programmed for a particular specialized job and in some cases by profligate inefficiency” (West-Eberhard, 1998).

Just as with complex computer code, genes provide the instructions for carrying out specific functions in a complex living system. If molecular requirements for gene function are numerous and extremely precise, the system becomes highly constrained. Changes in amino acid or base sequence are likely to be catastrophic. Something must be acting to deconstrain systems of core biological processes such that organisms can evolve.

Deconstraining mechanisms

There are a number of likely deconstraining mechanisms that ultimately shape the genotype–phenotype map in such a way as to preserve a great deal

of phenotypic plasticity even though the underlying genetic systems may be highly conserved. Those interested in these issues use concepts such as “exploratory behavior,” “hierarchical redundancy,” “modularity,” and “weak linkage” to explain how evolvable systems come about.

Exploratory behavior is well covered by the excellent review of evolvability by Kirschner and Gerhart (1998). Of course, the sexual cycle is inherently exploratory. It is a fundamentally stochastic process of creating variants and allowing selection to pick among the most successful. But the sort of exploratory behavior that Kirschner and Gerhart (1998) refer to occurs across all developmental stages and levels of organization. One example involves the kinetics of mitotic microtubule formation during the process of cell division, a highly conserved process throughout eukaryotes. Spindle microtubules connect to the kinetochores of chromosomes and mediate chromosomal segregation to the spindle poles. However, the process is far from straightforward. Spindle microtubules are dynamic and turn over with a half-life of 60–90 s. There is a rapid transition of microtubule ends from polymerizing to depolymerizing states. Since chromosomes are located somewhat randomly throughout the cell, random microtubule searches are required, and far more microtubules must be initiated than there are chromosomes. If a polymerizing microtubule contacts a kinetochore, fine; otherwise the microtubule depolymerizes, and the search goes on.

The dynamic structure of microtubule searches provides a very robust system because it reaches a functional state regardless of initial arrangement of chromosomes. It is a highly flexible system because it tolerates different cellular arrangements, and it allows an unlimited range of alternative cellular conformations. The process is fundamentally stochastic rather than mechanistic, and this is typical of exploratory behavior. There is an overproduction of random variants followed by selective use of only a few. In a more general sense, exploratory behavior is characterized by a system of random events that promote epigenetic variation that can become fixed by somatic selection (Kirschner and Gerhart, 1998).

Hierarchical redundancy seems to be a universal property of living organisms. Gene duplication is a well-known mechanism allowing divergence of gene function, but less well appreciated is the mul-

tiplicity of redundant systems at all levels of organization that serve essentially the same purpose—allowing divergence of function in response to varying internal and external conditions. Redundancy is particularly effective in concert with modularization. For example, repetition of morphological modules allows populations of cells to become independent. The evolution of multicellular organisms (Metazoa) is a case in point. For the first 3 billion years all life was unicellular. At some point, though, a number of independent single-celled organisms came into closer and closer contact, and some cells diverged slightly and took on specialized functions in response to particular microenvironmental stimuli. Once this happened and there was some benefit to the larger group, the race toward cellular specialization and new multicellular morphologies began. It was probably no mere coincidence that the Cambrian explosion closely followed the appearance of multicellular organisms (Gould, 1990).

Plants are really nothing more than repeating morphological modules termed phytomers. Repetition of morphological modules provides a degree of compartmental independence. Compartmentation allows weakly linked components to change function slightly (through mutation, epigenetic variation, and transcriptional regulation) and begin exploring alternate roles. Repetition of morphological modules allows populations of cells to become independent, reducing the deleterious effects of mutations, and increasing the potency of selection within modules. Phytomers represent a higher-order redundancy that provides a means of phenotypic accommodation that is very robust, yet also highly evolvable because any given change in extracellular or intracellular signal is not likely to cause a catastrophic failure in overall enzymatic, cellular, or morphological organization (West-Eberhard, 1998).

The nature of interactions, either among genes, molecules, pathways, or higher-order modules such as phytomers, strongly influences the evolvable potential of an organism. In general, as a biological system becomes more and more complex, interactions among components must become weaker (Conrad, 1990). Multiple weak interactions are complementary to redundancy in that if any one connection is broken, the system can remain functioning. Weak interactions allow for gradual transformation of function rather than complete

dysfunction in the presence of mutation or some other genetic or environmental challenge.

Kirschner and Gerhart (1998) use the comparison of transcriptional regulation between prokaryotes and eukaryotes to highlight the more weakly linked (i.e., less-constrained and more evolvable) nature of the latter. In order to initiate gene expression, RNA polymerase is activated and bound to the transcription initiation site, but this process depends upon the binding of other components. In prokaryotes, there is a high degree of binding specificity for these components, the binding sites must be near the transcriptional initiation site, and the overall regulatory system is relatively simple and the control quite stringent. The eukaryotic system has a great many more transcriptional inputs involving proteins binding at multiple enhancer sequences located both near and far from the initiation site. The binding specificity can be relatively low. Multiple inputs are essential to regulate genes in response to the variable conditions eukaryotic organisms face during development. But individual inputs are less well linked to the regulatory network than that which is typical with prokaryotes.

Evolvable Features of the Lignin Pathway

The lignin pathway provides several examples of how an evolvable system of organization operates for a single metabolic process in plants that is important for both breeders and geneticists. Lignin is a core component of plant cell walls, and it is important for a number of reasons including water transport, structural integrity, rigidity, and pest resistance. High levels of lignin typically reduce the nutritional quality of forages and increase the difficulty in pulping of forest products. Lignin is under intense scrutiny by plant breeders and geneticists interested in altering lignin composition (Baucher et al., 1998).

Lignin is a highly complex molecule typically formed from three monolignols, sinapyl, coniferyl, and *p*-coumaryl alcohols. Lignification occurs in three discrete steps. First is the biosynthesis of monolignols. The enzyme peroxidase then converts monolignols to free radicals, which are transported to the cell wall. Finally the monolignols in the cell wall are polymerized by an oxidative coupling process (Hatfield and Vermerris, 2001).

Monolignol precursors of lignin can be formed by any of several interconnected metabolic routes.

In the past several years, many of the enzymes involved in the lignin biosynthesis have been sequenced and cloned and their function well characterized (Chabbert et al., 1994b; Halpin et al., 1998; Lapiere, 1993; Li et al., 2000; Marita et al., 2003; Vermerris and Boon, 2001; Vignols et al., 1995). Several researchers have attempted to limit monolignol production by down-regulating certain enzymes such as cinnamoyl-CoA reductase, caffeic acid *O*-methyl transferase, or cinnamyl alcohol dehydrogenase. However, it has been difficult to predict with certainty the result of any given enzymatic perturbation in the monolignol pathway. In some instances even novel phenolic components can be recruited as substitute monolignols, and the resulting lignin polymer may well have nearly the same properties as the original form (Marita et al., 2001; Ralph et al., 1998, Ralph et al., 2001). In more general terms, the system is weakly linked, and the genotype-to-phenotype map is imprecise. It appears from recent lignin research that weak linkage between gene function and metabolic outcome may actually be advantageous, since it may enhance the tolerance, flexibility, and robustness of metabolic regulation.

Peroxidase activity underlies the second step in lignin formation, the conversion of monolignols to free radicals. Peroxidase is highly conserved across bacteria, fungi, plants, and animals. In plants, peroxidase is a flexible enzyme used for many functions apart from the lignin pathway. In corn (*Zea mays* L.), for example, there are at least 13 different peroxidase genes having many distinct roles and different tissue specificities (Maize GDB, 2003). Peroxidase is typical of many redundant, flexible, and versatile proteins that have broad target specificity and can impose varying levels of inhibition/activation, depending on external conditions. These sorts of flexible and versatile proteins contribute to evolvability because they make it easier to develop new targets and regulatory roles than it would be to change highly specific and constrained proteins.

Once peroxidase converts monolignol precursors to free radicals, and these precursors are transported to the cell wall, the complex cross-linking in the plant cell wall to form the final lignin polymer may be controlled by little more than chemical conditions at the time the free radicals are formed. There may be few regulating enzymes of any sort (Hatfield and Vermerris, 2001; Ralph et al., 2001).

This is highly contentious research that has led to the so-called “lignin war” (Rouhi, 2001). Some researchers are very skeptical. How can nature be so haphazard in the assembly of the second most-abundant biopolymer in plants (Davin and Lewis, 2000)? The response is that haphazard processes may actually be essential for such critical functions as those involved in the structural integrity of many different tissues, as well as defense against a large array of plant pests. Exploratory mechanisms that have low systematic requirements for achieving highly complex functional outcomes contribute greatly to the overall evolvability of living organisms. And, of course, the most evolvable metabolic systems are those that now exist.

Should plant breeders continue breeding plants?

Plant breeders should take heart that those in fields such as artificial intelligence or evolutionary computation, who have the sort of knowledge and tools geneticists most covet, the complete understanding of the underlying controlling code, and the ability to modify it at will, have become intrigued with the power plant breeders already possess, the use of the sexual cycle and selection, to address some of the most complex technological issues of the day.

Exploratory behavior, hierarchical redundancy, modularity, and weak linkage have provided clues to those in evolutionary computation on how to imbue coding systems with the capacity to discover and perpetuate beneficial adaptations. What are the implications for plant breeders and geneticists? There are at least five:

1. The function performed by evolvable systems of complex code must be only imperfectly and, in some cases, even haphazardly related to the underlying coding sequence itself.
2. The genotypic–phenotypic map is necessarily inexact or evolvability is not possible.
3. Phenotypic plasticity and loosely drawn genotypic–phenotypic maps will not make functional genomics any easier.
4. Highly evolvable traits will probably not be the initial focus of functional genomics simply because these sorts of traits will be the most difficult to handle.

5. Highly evolvable traits would probably be those most directly affecting reproductive fitness, and these are usually the traits of most interest to plant breeders (e.g., plant vigor and seed yield).

We are dealing with a biological world in which stochastic processes have reigned supreme for more than three billion years. The Darwinian revolution showed us how, even in the face of such forces, or perhaps more accurately stated, precisely because of them, biological life has achieved the remarkable ability of self-organization. Furthermore, this self-organization is fundamentally based on flexibility and plasticity at all levels. The acknowledgment of this is what truly distinguishes plant breeders from genetic engineers. It is a deeply profound distinction that few appreciate or comprehend. As Conrad (1990), a computer scientist, so aptly comments:

The organizations that are best suited to evolution are precisely those that are the most ill suited to the classical standards of scientific description.

Plant breeders already know that multiple phenotypes can be conditioned by a single genotype, and multiple genotypes can give rise to the same phenotype. There is not a one-to-one correspondence between genotype and phenotype, nor should there be. Plant breeders know that the phenotype is what matters in the end and that selection based on the phenotype is precisely the process that has given rise to the evolvable nature of the plants they work with. Plant breeders know that sex is an admittedly disruptive process, but one that, when coupled with selection, is extremely creative.

The challenges confronting public plant breeders are not due to any deficiencies in their application of genetics or defects in their traditional approaches, but rather to economic, sociological, and philosophical factors that are diverting them from the task of creating novel plant germplasm. For the foreseeable future the biological justification for continuing conventional selection remains intact, and the practical consequences of shifting course are disturbing.

All of humankind has benefited greatly from one of the most cost-effective technologies ever devised, plant breeding. The benefits have been widely distributed to both the developed and the

developing world. Recent biotechnological approaches to plant improvement have come at great expense, and the benefits appear to have a more limited distribution. Many would argue that we are only in the initial phase of developing exciting new technologies with tremendous future potential. Perhaps, but it seems that we should more closely evaluate the nature of this argument and better examine its underlying premise.

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