

Conclusions

Eight perennial grass varieties adapted to the conditions and the agricultural needs of the Republic of Latvia have been developed in the Skrīveri Research Institute of Agriculture during last decade. Two new grass varieties, timothy 'Varis' and festulolium 'Vizla' will be tested for DUS and VCU by the State Plant Protection Service Department this year.

During 2004 - 2006 we tested and compared newest timothy and meadow fescue varieties for different use.

Timothy 'Varis' and meadow fescue 'Vaira' delivers stable grass crops in Latvian conditions.

The new festulolium variety 'Vizla' can be used as a late season grass crop.

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JAUNĀKĀS STIEBRZĀĻU ŠĶIRNES ZEMKOPĪBAS ZINĀTNISKAJĀ INSTITŪTĀ SKRĪVEROS

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Zālāji ir viens no lētākajiem lopbarības veidiem ar augstu barības vērtību piena un gaļas ražošanā. Ilggadīgie zālāji aizņem lielāko daļu Latvijas lauksaimnieciski izmantojamās zemes.

LLU aģentūras Zemkopības zinātniskais institūts ir selekcionējis Latvijas augšņu un agroklimatiskajiem apstākļiem audzēšanai piemērotas jaunas diploīdas un tetraploīdas stiebrzāļu šķirnes, kas nodrošina labas sausnas un sēklu ražas.

Selekcijas darba rezultātā ir radītas 5 jaunas stiebrzāļu šķirnes, kas ir reģistrētas Kopējā Eiropas Savienības lauksaimniecības augu šķirņu katalogā. Šīs šķirnes ir: tetraploīdā ganību airene 'Spīdola' (4n), pļavas auzene 'Patra' (4n), pļavas auzene 'Silva' (2n), hibrīdā airene 'Saikava' (4n), agrais timotiņš 'Teicis'. Timotiņš 'Teicis' no 2007. gada līdz 2017. gadam ir iekļauts arī Lietuvas Nacionālajā Augu šķirņu sarakstā. Jaunā šķirne - vēlais timotiņš 'Varis' ir izgājis AVS testu Polijā un pēdējo gadu Latvijā atrodas SĪN testa pārbaudē. Pašlaik Polijā un Latvijā pārbaudes testus iziet mūsu jaunās šķirnes: pļavas auzene 'Vaira' (2n) un auzenairene 'Vizla' (4n).

Selekcijas darbs turpinās pie jaunas kamolzāles, pļavas lapsastes un niedru auzenes šķirņu veidošanas.

21ST CENTURY PLANT BREEDING: THE EVOLUTION OF DIRECTED EVOLUTION

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Abstract

Plant breeding began, by default, with human cultivation of plants nearly 10,000 years ago and quickly led to crop domestication as a result of natural selection toward adaptation to the new, cultivated environment. Natural selection, augmented by human preferential harvesting and planting of specific phenotypes, resulted in the creation of many locally adapted, reasonably productive landraces. These landraces were later exploited through the isolation of homogeneous populations of pure lines as varieties; this was concurrent with increased mechanization in planting, harvesting and processing operations. The discovery of Mendel's work at the beginning of the 20th century resulted in the application of genetics to plant breeding and the use of hybridization as a plant breeding tool. Thus 'directed evolution' came into being. New discoveries in genetics through the past 100 years (quantitative genetics, polyploidy, induced mutations, male sterility, understanding of DNA and molecular biology, haploidy, genetic transformation) were rapidly

applied as plant breeding tools to make the development of new varieties more effective, efficient and economical. Breeders have an ever-increasing tool chest of technology at their disposal. The challenge in breeding is to determine which of this multitude of high tech bio-tools are the most appropriate to maximize short-term, accelerated evolution for specific objectives in defined populations with limited budgets. As the 21st Century unfolds, plant breeding has evolved into a very effective, directed, evolutionary process which sustains human civilization as we now know it.

Key words: genetics, recurrent selection, male sterility, RIPE

Introduction

Evolution is geared toward improving the adaptation of a population to the environment in which it is growing and reproducing through 'survival of the fittest' (Darwin, 1859) ensuring that those individuals which are best adapted produce more progeny than those individuals which are less well adapted. As the environment changes, different traits, or expressions of a trait, will be favoured and the allelic composition of the population will change in response.

Plant breeding began, by default, with human cultivation of plants around 10,000 years ago and quickly led to changes toward better adaptation to the new, cultivated, human-managed environment as a result of natural selection. These changes were essentially an evolution toward crop domestication; changes based, in most cases, on the selection of existing characters, not the creation of new ones (Roots, 2007) and due initially to natural selection. The result was fully domesticated crops which formed the basis of the emergence of modern agrarian civilization. As knowledge of biology and genetics accumulated over time, intentional selection and eventually modern breeding evolved. The purpose of this paper is to outline the history of crop improvement and the application of basic biological principles leading to efficient and effective breeding systems capable of coping with the biological, environmental and economic challenges of the next century of human progress.

Evolution under Domestication

Natural seed dormancy and seed dispersal mechanisms essential for survival in the wild populations disappeared quickly from the early cultivated plant populations. Most plants were harvested and seeds replanted on an annual cycle so only those plants which successfully produced seed the first season contributed seed to the next growing cycle. The plants whose seeds shattered before harvest were lost from the population that was used for planting of the next generation. Selection for higher seed production came about as a result of the most productive plants contributing a higher proportion of the seed to the next generation, with a tendency toward self-pollination in most domesticated crops. Increased seed size occurred when smaller seeds were lost through the winnowing operation and through conscious selection of the larger seeds for planting. Cultivation reduced weed competition and gave crop plants a better opportunity to perform to their full genetic potential.

The selection by early farmers for types that suited their purposes better and were not negatively related to adaptation and fitness led to the emergence of free-threshing (hulless) wheats and barleys. The spontaneous mutations for these traits would have been selected and isolated from the early cultivated hulled crops. Hulless seed was a major step toward improving energy, nutrition and ease of processing as the hull was easily removed during the threshing operation itself.

Most of the crop species which we presently cultivate went through this domestication process long before recorded history. This natural selection for adaptation to cultivation, augmented by human preferential harvesting and planting of specific desirable phenotypes, resulted in the creation of many fully domesticated, locally adapted, reasonably productive landraces in ancient times. Such landraces have been cultivated by most agrarian societies for many hundreds of generations. Very few new species of crops have been domesticated in modern times.

The landraces were somewhat diverse for traits that were not directly selected for by Nature nor of specific interest to the farmers (i.e. height, maturity, seed colour). As a result of naturally occurring mutation, and occasional outcrossing, landraces accumulated many diverse, 'neutral' morphological characteristics. These landraces, with their local adaptation and basic background diversity, were excellent raw material to introduce to new environments. Seeds of such landraces

accompanied most migrating human populations and eventually many crop species were spread around the world to regions where the wild ancestors would not have been adapted.

These land races were later exploited through the isolation of single-plant derived homozygous and homogeneous pure lines as varieties. This resulted in more uniform and higher performing varieties, and occurred concurrently with increased mechanization in the planting, harvesting and processing operations. Synchrony of emergence, tillering, flowering and ripening was desired so that crop management operations could be performed on the crop on a field basis. Plants were no longer considered individually, but rather as components of a uniform population that was managed as a unit.

Genetics Applied to Plant Breeding

The discovery of Mendel's research at the beginning of the 20th century resulted in the application of basic genetic principles to plant improvement and the use of inter-varietal hybridization and selection in the segregating generations as a plant breeding technique. Thus 'directed evolution' came into being. Luther Burbank (1902) at one of the first international plant breeding conferences in New York City said "The fundamental principles of plant breeding are simple, and may be stated in few words; the practical application of these principles demands the highest and most refined efforts of which the mind of man is capable, and no line of mental effort promises more for the elevation, advancement, prosperity and happiness of the whole human race". With the understanding of the genetic basis of segregation and independent assortment and plant breeders, it became possible to predict the outcome of crosses and produce specific combinations of traits. Breeding emerged as a discipline which applied the knowledge of genetics and biological systems to maximize the short-term, accelerated evolution of defined populations for specific objectives with finite resources. In 1908, Hardy and Weinberg independently developed a mathematical method of describing the quantitative genetic dynamics of populations which met certain specific criteria, and their concepts were immediately embraced by animal breeders and many quantitative geneticists. Initially it was difficult to reconcile the differences in observed phenotypic phenomena between the Mendelian and the biometrical concepts. There was considerable support for having a completely set of different bases for genetics and the inheritance of traits in animals (quantitative) and plants (Mendelian). Eventually this was rectified when quantitative genetics was shown to be based on Mendelian behavior at each of many contributing loci which were not as easily classified due to a more complex genetic architecture, gene interactions, and environmental effects.

New Tools

New discoveries in genetics and biology over the past 100 years were rapidly applied as improved plant breeding tools to make the development of new crop varieties more effective, efficient and economical. Variations on the Hardy-Weinberg equilibrium were used to explain and predict the changes in population structure as a result of altering the assumptions toward more realistic breeding approaches. The science of quantitative genetics was developed and rapidly embraced by animal breeders, and later by plant breeders, particularly those working with cross-pollinated crops such as maize.

The discovery of polyploidy and the ability to manipulate chromosome numbers using colchicine and other mitotic control mechanisms led to the development of autopolyploidy and allopolyploidy as breeding tools. This was particularly applicable to interspecific hybridization and stimulated the creation of new species such as triticale. The occurrence of haploidy in a number of species, and methods of inducing higher frequencies of haploids through interspecific hybridization, and eventually anther culture and microspore culture, has made this a common pure line development technique in the Brassicas and some cereals.

The basis of natural mutations and the ability to induce them artificially opened up the possibility of creating 'new' genes, and hence new traits. Both chemical mutagens and radiation from various sources were extensively used in many of the small grain breeding programs in the 1950's and 1960's, especially barley. A number of dwarfing, earliness, and disease resistance genes that are widespread in modern varieties resulted from these early efforts.

Genetic male sterility as a tool for efficiently crossing normally self-pollinated crops was discovered in barley in 1940 (Suneson, 1940) and later in wheat and many other crops. Most self-

pollinated species have been found to have naturally occurring male sterile systems (Gottschalk and Kaul, 1974). Although most genetic male sterilities are recessive, some dominant male steriles have also been found in wheat (Maan and Williams, 1984; Huang and Deng, 1988). Cytoplasmic male sterility is also wide-spread in the plant kingdom, but has seen more use as a commercial hybridization mechanism than as a breeding tool, *per se*. Chemical hybridizing agents (CHA) have been developed to eliminate male fertility in a treated line that is then used as the female parent in hybrid seed production. These have been used to explore the production of hybrid wheat cultivars and, to a limited extent, in breeding programs.

The understanding of the role of DNA in inheritance, with the subsequent emergence of molecular biology, has opened up an array of techniques for monitoring and manipulating the genetic material in plants and animals for genetic studies and breeding purposes. The development of a number of DNA-based marker systems associated with allelic variation has given rise to molecular marker systems used to track genes from parents to progeny in breeding programs and to transfer specific desired alleles into recipient backgrounds. The use of quantitative trait loci (QTL) associated with traits of economic importance in breeding is fairly well developed. The ultimate application of molecular biology is in the transformation of totally new DNA segments from one species (or as wide as another kingdom) into another, well beyond the boundaries of normal sexual compatibility. Totally artificial DNA sequences can be constructed and used in transformation events to give phenotypes that have never occurred in nature. Transformation can also be thought of as 'directed mutation'.

Tools such as environmental control to create artificial environments, offseason nurseries, inoculation with diseases and pests, precise electronic measurement of numerous physical and biochemical parameters, and the use of immensely expanded computer power for analysis and data 'massaging' have made it possible to handle far more complex information than was possible in the past.

Population construction designs such as biparental crosses, diallele and half-diallele series, North Carolina Designs I and II, and convergent, conical, and composite crosses are all employed in breeding programs. Methods such as backcross breeding, the pedigree, bulk and SSD systems, and use of haploids and recurrent selection procedures are commonly used to develop pure lines from crosses for evaluation as potential varieties. Several different statistical approaches such as RCBD, lattice, moving means, nearest neighbours, periodic checks, AMMI, GGE Biplots, spacial adjustment, and honeycomb designs are used to reduce non-genetic variation in evaluation nurseries. Many different combinations of these methods have given rise to new cultivars in various breeding programs around the world.

It is evident that breeders have an ever-increasing tool chest of technology at their disposal. The challenge in breeding is to determine which of this multitude of bio-tools and technologies are the most appropriate for their particular situation. As the 21st Century unfolds, plant breeding is evolving into a very effective, directed, evolutionary process that sustains human civilization as we now know it.

Tools vs Toys

Ultimately, the application of the many new [bio]technologies must be robust enough to lead to improved cultivars in farmers' fields. To be successful, breeders must manipulate the genetic factors that they understand (and many that they do not), try to minimize (or fix) the epistatic and genotype by environment interaction effects that are unpredictable and difficult to evaluate, as well as understand the error that is always present in measuring metric traits in biological systems.

Sometimes the tool chest is overflowing and it is difficult to distinguish the tools from toys. It is challenging and rewarding to identify a new gene or marker and follow it through the generations, but it does not often lead to improved cultivars that are commercially successful. In fact, most of the traits of economic and agronomic value are quantitative in nature and are due to the cumulative effects of many, small, additive effects that cannot be individually detected, and therefore there are no QTLs for them. Perhaps we can have too much information and sometimes get caught up in generating information just because we can. Much of the molecular information generated may not be necessary, or even useful, for a breeder. Breeders can successfully manage far more complex genetic interactions via phenotypic selection among fixed lines than even the most recent molecular

approaches can explain. A breeder with a large, multi-national breeding and chemical company was recently overheard to say that they would have made much greater breeding progress if they hadn't been so 'distracted' by molecular biology. There can be too much information, and generally not enough relevant knowledge.

Breeding in the Future

We are now facing a future of global warming, the foreseeable end of economically extractable oil, and concerns about the sustainability of healthy and safe food production in degraded soils in an increasingly polluted environment. How can we address these issues through breeding in the future? In a world with a rapidly changing climate, greater variation in the weather patterns, with more severe weather events, reduced farm inputs (due to environmental concerns), and less reliance on inputs because of economics, one must explore methods that are more likely to succeed. More population buffering, better crop adaptation, with better defense mechanisms and greater stress tolerance, as well as improved productivity and stability, improved nutritional quality coupled with reduced inputs are going to be necessary in the next generation of crop cultivars. We don't need more short-term quick fixes based on single genes, we really need breeding systems that can handle a large suite of genes influencing numerous traits simultaneously. Evolution, as we now understand the mechanics of the process, is a very effective, if not particularly efficient, mechanism for bringing about population genetic change in response to such selective forces.

Evolution and Breeding

Evolution is a change in allele frequencies in a population over generations (time). There are a few basic factors that affect allele frequencies in a population over time. They are mutation and migration (gene flow) which bring new alleles into a population, and drift and selection which result in the loss of some alleles to the next generation. This loss can be random (drift) or directed by the selection process. Evolutionary response is a reaction to the environment that a population has experienced prior to reproduction and is influenced by genotype x environment interactions. The evolutionary process, as it relates to breeding, was studied extensively by Sewall Wright (1963). He explained that any evolutionary process requires the coupling of a random process to furnish the raw material of variation and a selective process to give it direction. Natural mutation coupled with phenotypic mass selection is the basic form of the evolutionary process, but adding the process of recombination, through the mechanism of sexual reproduction, to amplify the potential genotypic combinations can speed up the rate of evolutionary change enormously. He further elaborates that a predominantly self pollinating species can evolve rapidly with phenotypic selection among fixed lines, as long as there is sufficiently frequent crossing among selected lines to give recombination and new variation each generation. Cross pollinating species must be subdivided into small populations and given sufficient isolation to permit differentiation among subpopulations under the joint effects of random drift, inbreeding, and intragroup selection, as long as it is also coupled with intergroup selection. Both of the situations described by Wright (1963) for speeding up evolutionary change involve outcrossing/geneflow to promote recombination, and some form of isolation, either geographic or morphological, to promote inbreeding/fixation, followed by selection among reasonably uniform lines or sub-groups, and then further recombination among selected 'superior' individuals within/among subgroups. The cyclic systems described are essentially recurrent selection methods which can be applied to both self-pollinated and cross-pollinated crops.

These concepts were developed further by Wright's student, Jay Lush (1936) in his career in animal breeding at Iowa State University. He stated that the breeder's main tool is selection, but the choice of breeding/mating system can have a great impact on the effectiveness of those selections. The breeder needs to design a system that will increase the frequency of the desired gene combinations, and then effectively select among the resulting progeny those individuals with the highest number of desirable genes for further breeding. Lush (1936) elaborates that a breeder cannot hope for complete success and can hardly expect to put animals [or plants] together gene by gene, as a mechanic puts an automobile together. The general picture thus presented is a process of mild inbreeding to fix traits, alternating with outcrossing to recombine desirable genes and traits, both accompanied at all times by intense selection. There should be a balance between fixing and

maintaining desirable genotypes that have been created, and the evolutionary potential to create even better genotypes in the recombined progeny. Finding and maintaining this balance in the long term is a challenge for plant breeders.

Recurrent Selection

Summed up simply, recurrent selection is the best breeding system to maximize evolutionary response through an alteration between random mating (ie. genetic chaos) which creates variation, and intense inbreeding to fix various combinations of alleles in the homozygous condition for evaluation and selection. To make such a system efficient, selection must identify the best genotypes based on superior phenotype and they should be recombined in sufficient numbers to generate significant variation for the next cycle. The cycle time should be as short as possible. Very rapid response in a breeding population is possible, but is difficult to maintain. Duvick (1982) described recurrent selection as a method that is based on the probability of accumulating desirable alleles via recombination to create new genotypes which should be combined with a pedigree system to fix the new combinations rapidly through selfing to give reproducible phenotypes for evaluation and selection. Such a combination of outcrossing integrated with accelerated generation advance by selfing and early generation evaluation and selection for crossing is exemplified by the RIPE system (Falk, 2002) in barley where the complete cycle from selection of parents through evaluation of progeny involves five generations over two years.

If the objective of breeding is to change a population as much as possible for a particular trait, then the Illinois long-term recurrent selection program in corn provides an outstanding model of what is possible to achieve (Dudley and Lambert, 2004). This project was initiated in 1896 by C.G. Hopkins and has continued annually for more than 100 years, with minor modifications in population management and analytical techniques. The original population of 'Burr's White' was analyzed for oil and protein with approximately the 20% highest and lowest ears for each trait being saved to produce the next generation. The individual sub-populations were designated as Illinois High Oil (IHO), Illinois Low Oil (ILO), Illinois High Protein (IHP), and Illinois Low Protein (ILP). Mass selection for each trait was initially practiced, but later revised to ear-to-row selection for yield and ear quality followed by evaluation and selection for the specific traits. Approximately 60 ears were analyzed in each sub-population in each year and 20% (12 ears) selected for the following year. This amounts to mild selection on a small population with repeated annual cycles over many years.

The progress in selection for high oil and high protein in this population has been amazing. After 70 generations of selection, Dudley *et al.* (1974) reported that the means of the high protein (IHP), low protein (ILP), high oil (IHO) and low oil (ILO) strains were 12, 8, 27 and 10 phenotypic standard deviation (SD) units beyond the mean of the original population. They estimated that approximately 6000 ears had been evaluated in each strain; an extreme of 3.8 SD units from the mean would have been expected in an original population of that size. They reported their results as a 'vivid demonstration of the effectiveness of mild selection and recombination'. These conclusions were further supported after 100 generations (Dudley and Lambert, 2004). The physiological limits of low oil and low protein are likely being approached in the respective lines, but there is no suggestion that the upper limits have been reached in generation 99 in the high lines with the high protein line (IHP) having 26.9% protein and the high oil line (IHO) having 22.4% oil. These four subpopulations, all derived from a single open-pollinated variety from 1896, now represent the extreme expression for oil and protein for the entire *Zea mays* species. The original Burr's White population had an average of 4.7% oil and 10.9% protein, while modern hybrids generally having 7-9% protein.

Since most of the traits of economic interest in a plant breeding program are characterized by polygenic inheritance (Huehn, 1996), it makes sense to adopt quantitative and population breeding methods as the core of the breeding methodology. Lush (1936) notes that for most quantitative traits, there are some genes (often only a few) with important effects plus an uncertain, but large, number of minor modifying factors. QTL analysis may detect the few genes with significant individual effects, but will not be able to detect the multitude of minor and modifier genes which, when combined, may have a greater effect on the trait of interest.

The ultimate breeding system will be a balance between the ability to produce new gene combinations, and the new phenotypes derived from them, and the preservation of existing, successful phenotypes. Allard (1965) concludes that highly successful colonizing species of plants appear to have evolved genetic systems in which appropriate compromises are made between the high recombinational potential of outbreeders and the stability of inbreeders.

Drift may be the dominant force in very small populations or in populations where intense selection results in few individuals contributing gametes to the next generation. Small populations, which include most breeding programs, are affected not only by drift (random loss of alleles) but also by selection *per se*; the relationship of population size to both drift and selection is quite clearly illustrated by Grant (1963). He concludes that evolution is more effective in smaller populations when the force of drift is added to that of selection.

Recurrent selection has been identified by Comstock (1996) as a very natural process in most long-term, open-ended breeding programs. Recurrent selection is common, in one form or another, in both animal and plant breeding and most programs exhibit some of the features of recurrent selection (McProud, 1979). Recurrent selection results in an increase in the frequency of alleles with positive effects on the traits being selected over time. Even though the probability of an individual containing all the desired alleles may be very small at the beginning, as the frequency of the alleles increase in the population through selection and recombination, the probability of an individual occurring which has all the desired alleles increases greatly. After a sufficient number of cycles, and a significant increase in the frequency of the desired alleles, the probability of the ideal genotype being produced is large enough that it is likely to occur in a population of moderate size (Comstock, 1996). Lyrene (2004), in an attempt to adapt temperate peaches and blueberries to the subtropical conditions of Florida, concluded that recurrent selection “is the only breeding method that can accomplish the wholesale re-organization of the physiology of the plant.”

RIPE: a working model system

The process of producing and selecting the best possible lines in the existing population, then bringing in new, desirable alleles to further enhance the population, and producing the best possible new combinations is the essence of an ‘open-concept’ population breeding approach. The Recurrent Introgression for Population Enrichment (RIPE) system described for barley (Falk, 2002) details the combining of a recurrent selection system and a structured introgression mechanism to continually upgrade the potential of the breeding population. The system is based on an adapted foundation population undergoing recurrent selection at a moderate intensity with frequent recombination. Continual introgression of new material into the Elite level allows new, desirable alleles to be incorporated without disrupting the background from population structure.

Since its inception, a number of high-yielding, agronomically acceptable lines have been produced; more than 30 of them have been supported for registration on the basis of merit as cultivars by the Ontario Cereal Crop Committee, as part of the official Canadian variety registration system. The variety OAC Kawartha is currently the most widely grown barley in Ontario and has been the highest yielding six-rowed variety in each of the past five years in the Ontario Performance trial system (equivalent to National List Trials). In 2007, in official trials, more than half of the 16 six-rowed barley varieties being evaluated in the major barley producing region were from the RIPE system. These lines include the top five lines for test weight, the top line for kernel weight, and the only six-rowed lines with leaf rust resistance. They also have good powdery mildew resistance, desirable plant height, appropriate maturity, and good lodging resistance. All of them have combinations of desirable agronomic traits and disease resistance coupled with high yield. The RIPE system is producing more than just germplasm; the lines derived directly from the Elite population are fully competitive and commercially desirable varieties. They are equal (or superior) to, lines coming out of conventional and doubled haploid breeding programs being used by other breeders for the same target environments. The crosses which gave rise to the most recent lines represent about four to six cycles of recurrent selection. Many of their progeny are already in replicated, multi-location yield trials.

Thus, it has been possible to combine significant improvements in yield with advances in seed quality traits and disease resistance using the RIPE system of recurrent selection and introgression in barley in a relatively short time. The Elite population now consists of mostly high yielding

materials with large, plump grains, good plant type, and high levels of resistance to the prevalent pathogens powdery mildew and leaf rust. An attempt has been made to keep the effective breeding population size in the range of 15-20 male parents each cycle to avoid significant loss of genetic diversity. The periodic introgression of new alleles from exotic sources should also help to maintain (and increase) variability for the selected traits, ensuring that progress continues. New introgressed alleles may be giving rise to greater expression of desirable traits than would have been possible in the original Elite population by recombination alone. Walsh (2004) concluded that the Illinois high protein and high oil long-term recurrent selection populations have likely had some increase in variation due to mutation, so some of their astounding progress is also likely due to the input of new, desirable alleles through mutation, implying that new variation, either from migration or mutation, may be necessary to account for the progress exhibited.

The RIPE system, where effective recurrent selection to increase the frequency of desirable alleles in an Elite population is combined with a rapid introgression of new alleles, comes very close to meeting Wright's (1963) ideal conditions for maximizing the 'enormous evolutionary potential' of a population in the short time frame of a breeding program. Frequent opportunity for recombination through crossing of selected lines with male steriles is coupled with effective selection for yield on F3-derived F4 lines in the target environment to identify lines which will be evaluated more extensively in the following years. More importantly, selected lines are immediately used as male parents in the next round of crossing. Although some of the lines may be discontinued later in the evaluation system, many of their desirable alleles are being re-circulated in the breeding population. The superior lines that eventually are released as cultivars will have progeny in yield trials by the time their superiority is confirmed. This system addresses McProud's (1979) concerns about low numbers of founding parents, few new introductions and long cycle times in modern breeding programs. The RIPE system, as it has evolved, is highly efficient and effective in developing new high-yielding cultivars which maintain and recombine the suite of genes necessary for adaptation, and incorporate improved agronomic performance and disease resistance through accelerated introgression. This is how evolution has always worked, and how evolution and breeding will continue to do so in the foreseeable future.

Summary

Breeding high-performing crops for a more commercially competitive, and an increasingly volatile environment requires methods which can maximize the effective utilization of elite germplasm through rapid cycling recurrent selection approaches, and incorporate new, desirable alleles from the vastly under-utilized exotic germplasm collections currently stagnating around the world. The RIPE system appears to fulfill this mandate as an upgraded, updated, accelerated, and improved form of the old reliable evolution that Charles Darwin conceptualized so long ago.

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AUGU SELEKCIJA 21. GADSIMTĀ: CILVĒKA VIRZĪTĀS EVOLŪCIJAS ATTĪSTĪBA

Falk D. E.

Augu selekcija sākās, cilvēkam uzsākot augu kultivēšanu gandrīz pirms 10000 gadiem un ātri noveda pie laukaugu domestikācijas dabiskās izlases ceļā, piemērojoties augšanai kultivētos apstākļos. Dabiskās izlases ceļā, to papildinot ar ražas vākšanu izlases veidā un tikai specifisku fenotipu tālāku pavairošanu, radās daudzas vietējiem apstākļiem piemērotas, pietiekoši ražīgas vietējās šķirnes jeb landrases. Tās vēlāk tika izmantotas viendabīgu tīru līniju populāciju izolēšanai, kas kļuva par šķirnēm. Tas notika vienlaicīgi ar sējas, ražas novākšanas un apstrādes mehanizācijas palielināšanos. Mendēļa darbu atklāšanas rezultātā 20. gadsimtā augu selekcijā sāka pielietot ģenētiku un hibridizāciju. Tādējādi sāka darboties „virzītā evolūcija”. Jauni atklājumi ģenētikā pēdējo 100 gadu laikā (kvantitatīvā ģenētika, poliploidija, inducētās mutācijas, vīrišķā sterilitāte, sapratne par DNS un molekulāro bioloģiju, haploidija, ģenētiskā transformācija) tika strauji izmantoti selekcijas procesā lai padarītu jaunu šķirņu veidošanu efektīvāku un ekonomiskāku. Selekcionāriem ir pieejams aizvien lielāks jaunu tehnoloģiju klāsts. Selekcionāru uzdevums ir noteikt, kuras no šīm daudzveidīgajām augsti attīstītajām tehnoloģiskajām iespējām ir visvairāk piemērotas, lai maksimizētu īslaicīgu, strauju evolūciju noteiktās populācijās ar specifiskiem mērķiem un limitētiem budžeta līdzekļiem. Iesākoties 21. gadsimtam, augu selekcija ir izveidojusies par ļoti efektīvu, virzītu evolucionāru procesu, kas atbalsta civilizāciju.

VARIATIONS IN THE MORPHOLOGICAL CHARACTERISTICS OF WINTER WHEAT (*TRITICUM AESTIVUM* L.)

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Abstract

Estonia joined the International Union for the Protection of New Varieties (UPOV) in 2000. For that reason the requirements for a new variety changed. The law of variety protection came into