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The germplasm for a cultivated crop is generally regarded as the gene pool of cultivars, species and genera that can be utilized as sources of additional genetic variation for crop improvement. When developing strategies for the optimum use of vegetable germplasm, several problems not found in field crops, ornamentals and fruits should be considered. In vegetables, a part of the immature plant is often utilized. Because it is still physiologically immature, arbitrary judgments concerning time of harvest may greatly affect yield and quality, compared to crops in which the mature seeds are harvested. Second, unlike most ornamentals, tree fruits and small fruits, many vegetables are propagated by seed rather than asexually. An efficient means of stabilizing the commercial genotype(s) must be developed before widespread use is feasible.

Peterson (22) summarized the extensive use of plant introductions. The identification and transfer of single major genes that confer disease resistance are striking examples of the successful use of germplasm. This success has been due largely to the ability to devise effective, efficient seedling screening tests for resistance and to transfer one or a few genes into a cultivar, using a conventional backcross procedure. Other notable uses of germplasm have involved one or a few genes which control traits such as sex expression in cucumber, and male sterility in onions, carrots and beets. Frequently the donor parent has been of the same species, or if not, a species having a similar ploidy level.

Despite the success of some plant breeders in enhancing certain aspects of productivity, use of vegetable germplasm in other areas has been quite limited. Three difficult situations that, however, should be particularly productive are: 1) the use of germplasm having ploidy levels different from that of the cultivars, 2) the use of exotic germplasm to improve quantitatively inherited traits, and 3) the use of germplasm for genetic variability in growth response to mineral availability for increasing crop adaptation.

Ploidy level differences

Differences in ploidy levels have usually been barriers to gene transfer, and hence a mechanism contributing to speciation. Odd-numbered ploidy levels such as triploids are often thought to be "evolutionary dead-ends", which contribute little to dynamic population changes. Contrary to these assumptions, it appears that in some plants rather simple genetic mechanisms exist which alter either meiosis, syngamy or both. An understanding of these mechanisms provides the breeder with a powerful tool to utilize much more germplasm than is otherwise possible. Recent studies of *Solanum* spp. provide an excellent example of the ability to alter ploidy levels using genetic mechanisms.

Some two-thirds of the tuberous *Solanum* species related to the cultivated potato, *S. tuberosum* grp. *tuberosum* ($4x=2n=48$), are diploid ($2x=2n=24$). Although some gene transfer from the diploids to cultivated tetraploids has been accomplished, it has been difficult and time-consuming. Following the identification of a cultivated potato haploid by Hougas and Peloquin (8), they, and their associates, have accumulated numerous such materials. Because the haploids are also $2x=2n=24$, they provide excellent materials for use in genetic and evolutionary investigations (9) and as superior breeding parents (15).

The systematic extraction of numerous haploids is facilitated by distinct differences among both seed parents and pollen parents in their abilities to produce and to induce haploids, respectively (10). The genetic control of these tendencies was further demonstrated when progenies from superior \times superior inducers produced the greatest frequency of superior inducers (5). In addition to inherent plant differences, the use of suitable pollination techniques has been important. Pollination and subsequent fruit development on stems removed from the intact plant and maintained in water-filled bottles under cool conditions, permits the development of fruits containing only a few seeds, among which are the desired haploids (21).

Haploids facilitate genetic analyses because of disomic rather than tetrasomic segregation as observed in tetraploids. However tuber yields of *S. tuberosum* haploids were usually lower than those of the best tetraploids. Tetraploidy *per se*, or the effect of sheer chromosome

number resulting from vegetatively doubling the chromosomes, has not been found to be advantageous in potato (27). The advantages of tetraploidy then, are associated with unilateral or bilateral sexual polyploidization that results from the union of 2 gametes, one or both of which contribute the somatic number of genomes (16).

The high frequency of occurrence of tetraploids from diploids by sexual reproduction is significant. Hanneman and Peloquin (6) found that many tetraploids could be recovered in either $2x \times 4x$ or $4x \times 2x$ crosses. The formation of $2n$ gametes can result from various modifications of normal meiosis, and, in potato, several mechanisms of $2n$ pollen formation having a genetic basis have been described (18).

The product of normal microsporogenesis in tuber-bearing *Solanum* species is a tetrahedron of microspores. The mechanisms of parallel spindle formation (*ps*), premature cytokinesis 1 (*pc* 1) and premature cytokinesis 2 (*pc* 2), which allow the formation of $2n$ pollen (18), have been shown to be controlled by single recessive alleles (17).

The genetic consequences of these 3 mechanisms are quite different, although similar in terms of production of $2n$ pollen. Diplandroids ($2n$ pollen) produced via *ps* are genetically equivalent to first division restitution (FDR) gametes. All heterozygous loci between the centromere and first crossover and one-half those between the first and second crossovers in the parent will remain heterozygous in the $2n$ gamete. In contrast, $2n$ pollen produced by *pc* 1 and *pc* 2 are equivalent to second division restitution (SDR) since omission of the second meiotic division is involved. Here, all heterozygous loci between the centromere and the first crossover in the parent will be homozygous in the $2n$ pollen (18). Since non-additive gene effects appear to be important for tuber yield in potato (14), the transfer of large amounts of heterozygosity intact from superior parents via the use of parallel spindle formation is a powerful breeding tool when coupled with production of tetraploids through bilateral polyploidization (Table 1).

In summary, the genetic control of modification of certain events during meiosis and hybridization provides an excellent means of reducing the barriers imposed by differences in ploidy levels. Rapid generation of haploids can be used to reduce the ploidy level, allowing ease of genetic study and facilitated gene transfer with diploid species. Single gene mutants that result in production of $2n$ gametes can be transferred to desirable breeding stocks for the production of superior polyploids via either unilateral or bilateral sexual polyploidization.

Quantitatively inherited traits.

Most quantitative or metric traits are characterized by a continuous distribution of classes and a lack of discrete segregation in a genetically variable population. This can arise from segregation of a large number of genes each having relatively small effects or from segregation of a few genes modified by a large component of non-genetic variation. Regardless of the genetic basis, metric traits often show relatively low heritability, and it is difficult to transfer a high level of expression from exotic germplasm into adapted cultivars. If many genes control expression of a quantitative trait it is not surprising to find linkages between deleterious genes and favorable alleles controlling the trait being transferred.

The main problem then, is to transfer the genes or blocks of genes from the exotic donor to a commercial cultivar or breeding line. An acceptable level of the trait must be maintained and fixed in combination with desired horticultural type.

Several examples of difficult problems can be cited, e.g. the transfer of horizontal or field resistance, the incorporation of higher yielding ability from unadapted germplasm into commercial cultivars, and the improvement of quality associated with modified levels of specific substances within the plant. The simultaneous improvement of seed protein and seed yield in common bean, *Phaseolus vulgaris* L., is an example of the use of unadapted, exotic germplasm as the primary source of new genetic variability for quantitative traits.

The percentage seed protein of common bean is affected markedly by environmental factors, however, considerable genetic variability does exist in the species (2). Heritability estimates for protein differ-

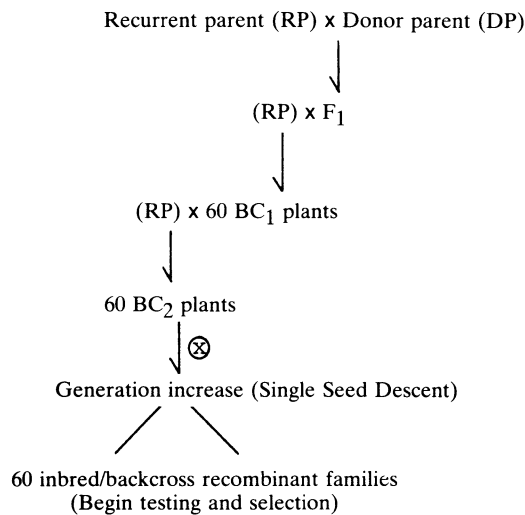


Fig. 1. Production of recombinant families using the inbred/backcross method.

ences are usually low to medium, depending on the population studied, the growing environment, and the method of estimation (11, 12, 19, 23). Most studies did not determine the consequences of selection. Since the high protein parent(s) were often poorly adapted, the question remained of whether one could select for increased seed protein and still recover high-yielding progenies that resemble a commercially acceptable dry bean.

The results of 2 selection experiments demonstrate the problem of transferring genetic control of metric traits. Tolla (29) found that 2 cycles of recurrent selection for yield and protein in a genetically broad-based population produced little evidence of improvement. He concluded that the frequency of favorable alleles for each trait was too low to expect appreciable short-term gain. Additionally, the best selections did not resemble any currently acceptable commercial class of dry beans. Even if selection for yield and protein had been successful, a useful new cultivar would not have resulted using this form of recurrent selection.

The effectiveness of pedigree selection and of modified pedigree selection using single seed descent (SSD) were also determined (1). Both methods were found to be somewhat more effective than 2 cycles of recurrent selection for producing lines with higher protein levels, but yields were variable and the seed type was still commercially unacceptable.

To obtain commercially-useful progenies using one of these 3 breeding methods would have required more selection pressure for acceptable type. This would have resulted in a lower effective selection intensity for protein and yield and would have required a longer time to achieve even the very modest gains that were seen.

The ineffectiveness of these procedures suggested that 2 important features should be included to maximize improvement of metric traits using poorly-adapted germplasm. First, the breeding procedure should offer a high probability of recovering the essential features of the commercial parent, and second, the effective measurement of quantitative differences for traits having a low heritability should be readily attainable. To accomplish the latter requires the use of replication.

A procedure that includes both these requirements is now being used. This involves a simple modification of the backcross method (Fig. 1). Instead of selecting among single plants after each backcross to the recurrent parent, one or several successive backcrosses are made to produce the desired, specified number of unique individuals (families). Advanced inbred lines are then produced by selfing and single seed descent to obtain the desired level of homozygosity. Selection is then practiced among advanced lines based on their replicated performance, with the recurrent parent being included as the standard check for estimating amount of gain.

An unadapted, high protein donor parent (M-1) was crossed to 'Sanilac', a popular navy bean cultivar which was used as the recurrent parent (Table 2). The resulting inbred/backcross population contained recombinant lines that closely resembled 'Sanilac', but were higher yielding and contained more seed protein. Among 42 recombinant lines there was segregation for plant type, with lines similar to both parents being observed (Table 3). All progenies were earlier than the donor parent M-1, with 3 being as early as 'Sanilac'. Segregation for percentage seed protein was also observed, with all lines, regardless of plant type, being equal to or better than 'Sanilac' (Table 4). None was as high as the high protein donor, suggesting that several genes are involved. Most important is the potential for identifying high yielding, high protein recombinants. None of the type 2 recombinant lines was significantly lower yielding than 'Sanilac' (Table 5). Two lines showed exceptional promise, yielding 75 g of seed per plant more than 'Sanilac', with protein levels one-fourth greater (24.1-26.0%) than the recurrent parent.

Rinke (26) suggested using a backcross procedure to improve metric traits of corn inbreds. Wehrhahn and Allard (31) proposed the essential features of the inbred/backcross procedure, described here, to produce single-gene deviate lines, for estimating the number and magnitude of action of genes controlling heading date in wheat. Reddy and Comstock (24) employed a computer simulation study to establish limits of selection and population sizes necessary for effectively improving quantitative traits using backcrossing. In addition to using this proce-

Table 1. Yield of relevant groups of 4x parents, 2x parents, and progenies (Rhineland, actual; other means, adjusted).

Location	Mean yield (kg/hill)							
	All 4x parents	All 2x parents	Male 2x parents	4x x 2x mid-parent	4x x 2x progeny	Female 2x parents	2x x 4x mid-parent	2x x 4x progeny
Rhineland	1.7	1.2	1.0	0.6	1.6	0.6	1.5	1.4
Hancock	2.0	2.0	1.6	1.9	2.3	2.2	2.1	2.0
Combined	1.8	1.6	1.3	1.5	2.0	1.8	1.8	1.7

Source: Mendiburu and Peloquin (15).

Table 2. Field performance of the recurrent parent ('Sanilac') and the donor parent (M1), Hancock, Wisconsin, 1979.

Parent	Plant type ^z		Days to 50-seed flower	Seed yield wt (g)	Seed yield (g/Plant)	Protein (%)
	2	3				
Sanilac	2	39	9.0	226	21.2	
M-1	3	59	9.2	329	28.5	

^zPlant type 2 = determinate bush; type 3 = indeterminate, prostrate.

ture to improve seed yield and protein, we are testing promising root rot resistant snap bean lines produced from cultivars crossed to resistant, unadapted donor parents of tropical origins. The same procedure is being used to improve N₂-fixation levels of dry beans.

Plant growth response to mineral availability

Increased plant growth response to mineral availability is desirable because, (1) there are large areas of land where problem soils result in low productivity due to mineral deficiency or toxicity, and (2) the rising costs of fertilizer demand that application of major elements be kept to the necessary minimum. While in animal breeding, rate of gain per unit of feed input has long been a selection criterion, higher total yield without regard to input has usually been the objective of plant breeders.

The cultivated tomato, *Lycopersicon esculentum* Mill. offers an excellent example where the available germplasm within the genus *Lycopersicon* can be utilized to alter genetically the response of cultivars to mineral stress environments. The wild relatives and cultivated forms include materials with which to produce cultivars having potential for greater productivity at reduced levels of N, P and K. The opportunity to greatly increase the range of adaptability of the tomato is substantial.

Variation in response to toxicity. Problems of increasing salinity confront irrigation agriculture on a worldwide basis. The development of salt-tolerant cultivars would not only alleviate problems, but also provide tremendous opportunity for expanded production using seawater without the cost of desalinization.

Although most cultivars of *L. esculentum* are quite sensitive to high salinity, Rick (25) reported that ecotypes of *L. cheesmanii* spp. *minor* (Hook) C.H. Mull. from the Galapagos Islands showed considerable salt tolerance. Studies by Rush and Epstein (28) demonstrated survival differences among genotypes grown in full-strength seawater, and greater growth rate at lower salinity levels. Although all salt treatments reduced growth rates of both species, some ecotypes of *L. cheesmanii* were markedly superior to cultivated types.

Segregates from progenies of crosses between *L. esculentum* and tolerant ecotypes show considerable promise for breeding (3). Following several backcrosses to a commercial cultivar of plants stress-selected at 50% seawater salinity, lines capable of germination and growth in media containing up to 70% seawater have been produced. Fruits on stress-grown plants were smaller and had more intense color and flavor components than those on non-stressed plants.

In many acid soils aluminum toxicity limits growth. Tomato is quite sensitive to Al, and some have suggested it as an indicator of aluminum availability in acid soils. Studies by Foy et al. (4) have shown genotypic differences in tolerance to low pH and to increased amounts of Al. The extent of genetic variability suggested the possibility of breeding Al tolerant cultivars for areas in which correction of soil pH is not possible because of the large amounts of lime required.

Table 3. Distribution of parents and recombinant inbred/backcross lines for days to flower and plant type. Hancock, Wisconsin, 1979.

Lines	Plant type ^z	Days to flower					x	No.
		39-41	42-44	45-47	48-50	<51		
'Sanilac'	2	5					39	5
Recombinants	2	2	1	15			46	18
"	2+	1	2	1			43	4
"	3			9	11		48	20
M-1	3					5	59	5

^zPlant type 2 = determinate bush; type 3 = indeterminate, prostrate.

Table 4. Distribution of parents and recombinant inbred/backcross lines for plant type and percentage protein.

Lines	Plant type	Protein (%)					x	No.
		20.1-2.0	22.1-24.0	24.1-26.0	26.1-28.0	28.1-30.0		
Sanilac	2	3	2				21.2	5
Recombinants	2		4	11	3		25.0	18
"	2+		3	1			23.8	4
"	3		3	14	3		25.0	20
M-1	3				2	3	28.5	5

Variation in response to major elements. When describing the response of genotypes to the major elements, several descriptive terms are necessary. Genotypes may be "efficient" or "inefficient" converters of nutrients into dry matter at different mineral levels. Efficiency should be specifically defined, since it may refer to changes in uptake, response, metabolism or dry matter production induced by increasing levels of the element in question (30).

Harvey (7) demonstrated that tomato genotypes had differential requirements for N and that these differences were heritable. O'Sullivan et al. (20) reported that efficient genotypes produced up to 45% more total dry weight than did inefficient lines under low stress conditions. However, a strain which was inefficient at low levels was also a "responder," in that relatively more dry matter was produced at higher levels of N. Genetic analyses of dry matter production in segregating progenies demonstrated that the trait was heritable. Frequency distributions suggested that few genes were responsible and that dominance and epistatic effects were of primary importance.

Parallel studies of tomatoes at low levels of potassium identified efficient genotypes, expressed in terms of a potassium efficiency ratio (KER) which is the dry weight produced per mg K absorbed. Under K stress (5 mg K/plant), efficient lines produced about 80% more total plant dry weight, while at adequate K levels the plant dry weights were similar (13). An interaction due to the effects of Na and K was seen for the efficient line no. 42, which produced a greater response to added Na at nearly all levels of K. Efficiency was found to be heritable in crosses of efficient x inefficient lines, with narrow sense heritability estimates of about 0.60, suggesting that selection should be effective.

Genotypic differences in plant dry matter production have also been found for tomato in response to low levels of phosphorus (Hochmuth, G., University of Wisconsin, Madison, personal communication). Differences were associated not only with efficiency of uptake and transport, but also with total root mass. Root morphology differences may be more important in breeding for P efficiency since P is non-mobile in the soil.

Genotypic differences for plant growth response to availability of both major and minor elements have been found in a wide range of plant species (30). The potential to develop cultivars resistant to toxic levels of certain elements and efficient in the production of greater plant dry weight at low nutrient levels appears to be considerable.

Summary

The germplasm related to a cultivated crop provides a valuable natural resource to be used in improvement programs. It can be utilized more fully when its potential value is understood and the problems related to hybridization and to effective selection within resulting progenies are overcome. The impact of ploidy level differences, which often limit transfer of important traits, may be minimized by using genetic mechanisms to reduce ploidy through haploid production and increase ploidy through sexual polyploidization. The use of unadapted germplasm to improve quantitative traits can be enhanced when methods

Table 5. Distribution of parents and type 2 recombinant inbred/backcross lines for seed yield and percentage protein.

Yield (g/plant)	Protein (%) ^z		
	221.-24.0	24.1-26.0	26.1-28.0
201-250	Sanilac	3	2
251-300	2	6	1
301-350	2	2	M-1

^zNo. of lines.

which allow accurate identification of superior progenies and a high probability of recovering the essential features of a standard cultivar are employed. Genetic variability in plant growth response to mineral availability has been identified in the germplasm of a wide range of crop plants. Incorporation of this variability into cultivars can broaden their adaptability by altering the response to mineral stress environments and increasing plant productivity at reduced levels of the major elements.

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UTILIZATION OF FRUIT AND NUT GERmplasm¹

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The National Fruit and Nut Germplasm Repository system

Future prospects for fruit and nut germplasm conservation appear more promising in 1980 than at any time in history. This fall the first of a projected 12 National Repositories for Fruit and Nut Germplasm will commence operation in Corvallis, Oregon. This accomplishment culminates 30 years of dedicated efforts on the part of many scientists and administrators in both the U.S. Department of Agriculture and the State Experiment Stations. The 12 locations were selected according to the climatic requirements of specific crops. e.g., in Corvallis, pears, fil-

berts, strawberries, blackberries, raspberries, blueberries, gooseberries, currants, hops, and mint will be maintained. Construction of the second repository will be underway soon in Davis, California, where stone fruits, grapes, walnuts, almonds, and pistachios are to be held. The erosion, and need for collection and preservation, of germplasm resources was well documented at a joint ASHS-APS Workshop on Fruit and Nut Germplasm Reserves in 1974 (19).

Following the Workshop, the next year, the National Plant Germplasm Committee took the leadership to establish 7 crop-oriented advisory committees charged with developing plans for their respective crop areas. These recommendations were then integrated into a master plan for the entire System in 1976. Details of this plan were published recently in *HortScience* (1). Fruit and nut scientists can now look with optimism toward a reversal of the alarming erosion of genetic resources and can expect an expansion and long-term maintenance of plant materials so vital to the creation of improved cultivars and rootstocks for future orchards, e.g., cultivars which (1) are more efficient producers (e.g., compact trees), and (2) have greater tolerance to stressful envir-

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