Albersheim's discovery of inhibitors affecting polygalacturonase and other enzymes which affect the cell wall (1) creates new possibilities in raw material control and processing manipulation. Of particular interest are perhaps the protease inhibitors that are discussed by Dr. Liener in another paper in this symposium. The biological function of these inhibitors has been the subject for much speculation since the discovery of the first protease inhibitor by Ham and Sandstedt in 1944 (5). Until quite recently, all the known inhibitors were primarily active against animal or fungal proteses, and there was a natural tendency to assign a protective role to the inhibitors. In 1971, however, Kirsi and Mikola (6) were able to show that a protease inhibitor system from barley which inhibits trypsin and an *Aspergillus* protease, also inhibits a barley protease. During germination the latter inhibitor disappears while the former two remain. Here we have the first indication of a biological control function ascribable to the protease inhibitors. We have in our laboratory obtained evidence for the existence in the potato of an inhibitor active against a series of plant enzymes similar to papain. These developments herald perhaps a new insight into the problems of biochemical control systems in the plant. Obviously the food processor will benefit by being given new means of quality control and an increased opportunity of predicting and controlling the textural characteristics of his products.

Literature Cited

1. Albersheim, P., and Anne J. Anderson. 1971. Protein from plant cell walls inhibit polygalacturonase secreted by plant pathogens. *Proc. Nat. Acad. Sci.* 68:1815-1819.
2. Atwater, W. O. 1895. Methods and results of the investigation of the chemistry and economy of foods. *U. S. Dept. Agr. Expt. Sta. Bul.* 21.
3. Barrios, E. P., D. W. Newsom, and J. C. Miller. 1963. Some factors influencing the culinary quality of Irish potatoes. II. Physical characteristics. *Amer. Pot. J.* 40:200-208.
4. Bartolome, Linda G., and J. E. Hoff. 1972. Firming of potatoes: biochemical effects of preheating. *J. Agr. Food Chem.* 20:266-270.
5. Ham, W. E., and R. M. Sandstedt. 1944. A proteolytic inhibiting substance in the extract from unheated soy bean meal. *J. Biol. Chem.* 154:505-506.
6. Kirsi, M., and J. Mikola. 1971. Occurrence of proteolytic inhibitors in various tissues of barley. *Planta* 96:281-291.
7. Linehan, D. J., and J. C. Hughes. 1969. Texture of cooked potato. II. Relationships between intercellular adhesion and chemical composition of the tuber. *J. Sci. Food Agr.* 20:113-119.
8. Personius, Catherine J., and P. F. Sharp. 1939. Adhesion of potato-tissue cells as influenced by pectic solvents and precipitants. *Food Res.* 4:299-307.
9. Pressey, R. 1966. Separation and properties of potato invertase and invertase inhibitor. *Arch. Biochem. Biophys.* 113:667-674.
10. Rathsack, K. 1935. Der speisewert der kartoffel. Berlin.
11. Reeve, R. M. 1954. Histological survey of conditions influencing texture in potatoes. II. Observations on starch in treated cells. *Food Res.* 19:333-339.
12. Schwartz, J. H., R. B. Greenspun, and L. W. Porter. 1961. Chemical composition of potatoes. II. Relationship of organic acid concentrations to specific gravity and storage time. *Food Technol.* 15:364-366.
13. Van Buren, J. 1968. The chemistry of snap bean blanching. *N.Y. Food Life Sci.* 1(3):17-19.

THE INFLUENCE OF MULTIPLE QUALITY REQUIREMENTS ON THE PLANT BREEDER

M. Allen Stevens[1]
University of California, Davis

Traditionally, plant breeders have been concerned with characteristics such as yield and disease resistance which can be evaluated subjectively or by straightforward objective methods where differences are qualitative and maximum manifestation of the trait is desired. Quality has not been a principal objective in most plant breeding programs; frequently, it has been an afterthought. Once the other desired characteristics have been achieved, there is an attempt to select for adequate quality. The attention that quality characters have received varies greatly among the numerous quality traits. Color, for example, has received considerable attention because of its importance to appearance and consequently salability. In contrast, nutritional value and flavor have been mainly neglected by plant breeders.

Developing a new cultivar is difficult even when the goals can be well stated. Often, quality characteristics cannot be clearly defined. Quality has many facets, and it often means different things to the various groups concerned with a new cultivar. The consumer wants the best appearance and flavor for the money he is willing or able to pay. The processor wants a raw product that will give him maximum case yields of a finished product that sells well and gives maximum return. This may represent high quality, not in absolute terms, but only relatively. Frequently, quality and price are closely related, and the consumer may not be able to afford highest quality. If breeders are able to increase quality of predominant cultivars, higher quality at a reduced price should result. The grower wants a product that meets the grade requirements of the processor or shipper. If the primary requirements are color and freedom from physical defects, these are his chief concerns.

The needs of consumers, processors, and growers are interrelated, and presumably, since the consumer is king, his needs and wishes should have priority. Obviously, this has not happened, as some of the consumer's primary concerns have been almost completely ignored by breeders.

One commonly hears that foods, including fruits and vegetables, are bought not for their nutritional value, but for taste and appearance, and the enjoyment they provide. This situation appears to be changing and through the efforts of various groups, people are becoming more aware of nutrition, and, in the future, there will probably be increased insistence by the consumer that foods have good nutritional value. As a consequence, cultivars which provide this will be more popular.

There is evidence that breeders supported by public funds will have to be more actively concerned with the consumers' needs if they intend to maintain that support. Urban-oriented legislators feel that there are more pressing problems than further increases in production, particularly when overproduction is already a problem. Many of these legislators are skeptical of research they feel will mostly benefit corporate farmers and large processors. However, when a breeder has a program to improve flavor and nutritional value, the benefits to everyone become more apparent.

COMPLEXITY OF BREEDING PROGRAMS

A number of factors contribute to the plant breeder's lack of attention to quality. Most of these are related to the complexity of breeding programs. A major factor is the effect that hybridization and selection for additional traits has on the complexity of a program, which increases exponentially with the number of genes being manipulated (Table 1). From a cross segregating for 21 genes a perfect population of tomatoes, which is one in which each phenotype occurs at least once, would require over 420,000 acres of tomatoes.

To keep a breeding program manageable requires setting priorities. It is simply not possible to develop a cultivar with all of the desired characteristics. The best tasting, most nutritious cultivar is doomed to failure unless it has yield, disease resistance, and the other characters essential to growers and processors. Thus, most quality characteristics necessarily greatly complicate breeding programs. To be successful a high-quality cultivar must also possess all the characters that make

Table 1. Kinds of phenotypes possible in F_2 generation from parents differing by various allelic pairs.

Number of Allelic Pairs	No. of phenotypes in F_2 (additive genic effects)
1	3
2	9
4	81
10	59,049
21	10,460,353,203

[1]Department of Vegetable Crops.

money for growers, shippers, or processors at an acceptable price to the consumer. Quality then becomes an adjunct and, often an afterthought. Develop as much quality as possible, but not at the expense of yield or shipping and processing characteristics.

Maturational and environmental effects

A further complication in breeding for quality is that fruits and vegetables are usually harvested when the edible portion is undergoing rapid change in composition. Furthermore, it is usually difficult to pinpoint a definable stage of maturity. Thus, in a breeding program where it is often desirable to evaluate single plants, sampling becomes a major source of error. It is difficult to determine whether observed differences are due to environment, stage of maturity, or genetic variation. Therefore, even when constituents can be accurately and readily measured, data obtained may not represent genetic potential. In the tomato, acid concentration changes dramatically during fruit development and maturation (12). It increases during early development, reaches a maximum near incipient color, then decreases until well beyond prime maturity. The magnitude of change is dependent upon the genetic constitution of the plant, some lines maintaining acid concentration better. Tomato acidity is also affected by the nutritional and moisture status of the plant. A potash deficiency causes a decrease in acidity, whereas moisture stress causes an apparent increase, partially because of a concentrating effect (8).

Evaluation and definition

Another factor complicating efforts to breed for quality is the difficulty describing and measuring some quality characteristics. Objective measurement of some quality characters, e.g. color, is relatively simple because instruments are available which provide data that are easy to obtain and reliable, and which give the breeder the information he needs (4). Other quality characteristics are rather nebulous. It is not only difficult to describe good flavor, it may be troublesome to get people to agree on what is best flavor, because of personal preferences. Agreement that flavor is bad is usually considerably less difficult. There is no easy, reliable way to measure flavor objectively. Nor can a breeder use gross, subjective evaluation techniques to select for flavor and nutritional value. Rather the individual components which make important contributions and are responsible for the variations must be selected objectively.

As already indicated, definition of certain quality characteristics can be a major problem. What is good flavor in a peach, a strawberry, a snap bean or a tomato? Almost everyone has an acquired concept of what tastes good and, depending on background, personal preferences vary greatly. In a study of snap bean flavor using an evaluation panel composed of staff and graduate students we found that most of the American panelists preferred the flavor of the 'Blue Lake'; but there was a number of graduate students from the Middle East on the panel and, almost to the man, they preferred the stronger flavor of the 'Romano'.

Because flavor differences are often subtle, they sometimes tend to be considered unimportant. There are still people, including processors, who believe that differences in raw product flavor are not really very important. Fortunately, this feeling is not widespread, and there seems to be increasing awareness of the importance of raw product flavor.

The breeder is faced with the problem of defining the flavor he wants to improve. A good procedure for him is to use, as a standard, a cultivar that has been widely used, and is noted for its quality. By studying the concentrations of important flavor compounds in this standard, the breeder can often make considerable progress in defining this elusive character.

Flavor is frequently determined by relationships among components, and the desired concentration of a compound will depend upon the concentrations of other compounds. A good example of this interrelationship is the effect of sugar/acid ratio on the flavor of several fruits. A prime factor determining intercultivar variation in tomato flavor is the sugar and acid content (10, 11). The relative and absolute quantities of fructose plus glucose and citrate plus malate are major factors in tomato flavor and processing characteristics.

REDUCED QUALITY IN NEW CULTIVARS

A brief discussion of the solids and acids of tomatoes will help illustrate some of the difficulties that can be encountered. The development of tomato cultivars suitable for machine harvest resulted in many changes in fruit and vine characteristics. These were related primarily to increasing yield with a once-over harvest, and the ability of the fruits to withstand the rigors of machine harvest. Development of mechanically harvested tomatoes has had an adverse effect on quality, as the characters considered essential for mechanical harvesting are in opposition to the ones needed for high solids (Table 2). As a consequence of changes in plant morphology and setting ability, most machine-harvest tomato cultivars have less solids than do hand-pick types. Hand-pick cultivars generally have a large vine and scattered fruit-set, which results in a relatively low fruit/leaf ratio. Machine-harvest cultivars have a reduced vine and heavier, more concentrated fruit-set. This results in a very heavy load on available photosynthetic area over a reduced time period. Obviously unless assimilation efficiency is improved dramatically, either yield or stored photosynthate has to decrease. Actually, yield increased, but fruit solids, primarily sugars, decreased. This reduction has had an adverse effect on the flavor of tomatoes, and has also resulted in reduced case yield of all products sold on the basis of solids content.

Table 2. Factors contributing to high solids in tomato fruits.

Indeterminate growth habit	Low yield
Low fruit:leaf ratio	Small fruit size
Dispersed fruit-set	Restricted moisture availability
Late maturity	

The processing tomato industry is now changing to bulk handling, which requires fruits that are firmer and tougher than those of most current cultivars. The lines that appear to be well suited for this type of handling have thick walls and a reduced locular area. These characteristics have an adverse effect on tomato acidity, as the acid concentration of the locular area is higher than that of the walls or interlocular area. Acid concentration and pH are important factors in tomato flavor and processability. A pH less than 4.4 is necessary to avoid problems with thermophylic organisms, such as *Bacillus coagulans.* In newer cultivars it has not been possible, because of low solids, to maintain the sugar/acid ratio needed for good flavor, and at the same time maintain the pH needed for safe processing. It appears that a sugar/acid ratio of about 8.5 will contribute to good flavor, providing solids are not so low that an insipid taste results. Total solids of about 5.5% are necessary to assure a pH of 4.35 and a sugar/acid ratio of 8.5. Most of the California processing cultivars do not have total solids of 5.5% or a sugar/acid ratio of 8.5. Some of the new firm-fruited lines do have a sugar/acid ratio of 8.5, but they have poor flavor and processing characteristics because of low solids, low acidity, and high pH.

ASSIMILATION EFFICIENCY

As breeders develop cultivars with the traits needed for once-over harvest, the problem of assimilation efficiency becomes important. Yield and quality depend on this efficiency, and when efforts are made to increase the photosynthetic load of crops, efficiency becomes an important consideration.

Photosynthetic efficiency of horticultural crops has received little attention. In a study of photosynthetic efficiency of the bean, Izhar and Wallace (5) found that differences among certain cultivars are determined by the dark reactions of photosynthesis and controlled by a relatively few genes. A difference in water content of the leaves was the only consistent difference observed among the cultivars studied, and the authors postulated that differences may exist because of variation in water availability for the photosynthetic process.

BREEDING EFFICIENCY

The efficiency of a plant breeder is determined by a number of factors, many of which are related to his understanding of the breeding material available. A prime factor influencing efficiency is efficacy of selection technique. A breeder manages most easily those characters that have a high heritability and for which there is a rapid, objective screening technique. Frequently there is little understanding of the genetics, chemistry, or physiology of the trait being selected. In such instances, plant breeding becomes an art and selection efficiency may be nil.

Heritability

Only a few studies have been made on the inheritance of concentrations of quality components. Studies of gross characteristics, such as total acidity and solids, have often indicated multigenic control (9). Conversely, study of several individual compounds has revealed that concentration differences are frequently under simple genetic control. Since these compounds normally result from complicated biochemical pathways in which many genes are involved, quantitative differences apparently are sometimes controlled by one or a few major mutations.

Intuitively one might expect that differences between closely related lines would be controlled by few genes, whereas differences between widely divergent line would be more complex. However, differences between lines from widely different sources and with great variation in concentration, have been shown to be simply inherited. Study of 'Tondo Liscio' from Italy and PI 263713 from Puerto Rico indicated that differences in citrate and malate concentrations of tomato fruits are controlled by a single gene for each compound, with dominance for low concentration of malate and for high concentration of citrate (12). Also, a study of the inheritance of of concentrations of volatile compounds among tomato and snap bean cultivars showed that they are simply inherited.

Chemistry

To cope effectively with some quality characteristics, e.g. flavor, the breeder must have an understanding of the chemistry of important components, as the composition of fruits and vegetables is greatly affected by environment and postharvest treatment. Many important flavor compounds are formed by enzymatic oxidation of nonvolatile precursors after tissue damage. Forss et al. (3) reported that nona-2,6-dienal, which has a cucumber-like aroma, is a prime factor in cucumber flavor. Fleming et al. (2) noted that this compound, is formed by enzymatic oxidation of linolenic acid. The C_6 aldehydes, which are important in fruit and vegetable flavor, are frequently formed by enzymatic oxidation of fatty acids after tissue damage (6).

The compound 2-isobutylthiazole, which is important in intercultivar differences in tomato flavor, is present in intact tissue and appears to be little affected by enzymatic activity. Conversely, 6-methylhept-5-en-2-one, citrals, geranylacetone, β-ionone, and farnesylacetone, which are also important tomato flavor compounds, are greatly affected by postharvest treatment, and appear to result from oxidation of carotenoids. The pectins and cellulose of tomatoes are rapidly destroyed by enzymatic activity after the cells are ruptured during evaluation or processing.

Evaluation

An understanding of compound formation is crucial to the development of evaluation techniques. To screen breeding populations effectively, the researcher must use analytical short cuts, because large numbers of samples must be evaluated in a short time. Sometimes quality characteristics can be evaluated indirectly. An example is the use of other characters to select for the high-pigment and crimson genes in tomatoes (7). Both of these genes improve the color to tomato fruits and they appear to be valuable quality assets. An F_2 population segregating for these two characters can be selected for the high-pigment character by germinating the seeds in the dark and keeping only seedlings having anthocyanin in the hypocotyls. Progeny with the high-pigment character can be evaluated for orange flower color in a cool temperature, and selected for the crimson gene. Thus assured that progeny have both of these genes, the breeder can then evaluate them for other characteristics.

Frequently, simple procedures can be used to measure compound concentration. Numerous straightforward and relatively simple techniques have been developed for accurate assessment of many compounds. These procedures can be of great value to the plant breeder.

The rapid changes in handling procedures for vegetables and fruits that have occurred recently have put many demands on breeders. The requirements for cultivars to meet the rapidly changing technology have often resulted in reduced quality. Generally, before a breeder can effectively develop high quality, it must be defined and objective evaluation techniques developed. It is likely that much can be done to improve quality after it becomes an active part of a breeding program.

Literature Cited

1. Allard, R. W. 1960. Principles of plant breeding. John Wiley and Sons. New York.
2. Fleming, H. P., W. Y. Cobb, J. L. Etchells, and T. A. Bell. 1968. The formation of carbonyl compounds in cucumbers. *J. Food Sci.* 38:572-576.
3. Forss, D. A., E. A. Dunstrone, E. H. Ramshaw, and W. Stark. 1962. The flavor of cucumbers. *J. Food Sci.* 27:90-93.
4. Francis, F. J. 1970. Color measurement in plant breeding. *HortScience* 5:102-106.
5. Izhar, S., and D. H. Wallace. 1967. Studies of the physiological bases for yield differences. III. Genetic variation in photosynthetic efficiency of *Phaseolus vulgaris* L. *Crop Sci.* 7:457-460.
6. Kazeniac, S. J., and R. M. Hall. 1970. Flavor chemistry of tomato volatiles. *J. Food Sci.* 35:519-530.
7. Kerr, E. A. 1965. Identification of high-pigment, *hp*, tomatoes in the seedling stage. *Canadian J. Plant Sci.* 45:104.
8. Lee, F. A., and C. B. Sayre. 1946. Factors affecting the acid and solids content of small fruited tomatoes. N. Y. Agr. Expt. Sta. Tech. Bul. 278.
9. Lower, R. L., and A. E. Thompson. 1967. Inheritance of acidity and solids content of small fruited tomatoes. *Proc. Amer. Soc. Hort. Sci.* 91:486-494.
10. Simandle, P. A., J. L. Brogdon, J. P. Sweeney, E. O. Mobley, and D. W. Davis. 1966. Quality of tomato varieties as affected by some compositional factors. *Proc. Amer. Soc. Hort. Sci.* 89:532-538.
11. Stevens, M. Allen. 1972. Relationships between components contributing to quality variation among tomato lines. *J. Amer. Soc. Hort. Sci.* 97:70-73.
12. ______. 1972. Citrate and malate concentrations in tomato fruits: Genetic control and maturational effects. *J. Amer. Soc. Hort. Sci.* 97:655-658.

NATURALLY OCCURRING TOXICANTS OF HORTICULTURAL SIGNIFICANCE[1]

Irvin E. Liener[2]
University of Minnesota, St. Paul, Minn.

While Nature has generously provided man with a liberal supply of plants which can serve as a source of food, it is ironic to note that she has at the same time seen fit to endow many of the plants with the genetic capacity to synthesize a wide variety of chemical substances, which, because of their toxicity to insects, nematodes, grazing animals, and even man, have permitted plants to survive in a hostile environment. When chemicals are added to foods, we rely on appropriate governmental agencies to enact legislation to protect the consumer. But, unlike chemicals which are deliberately added to foods, natural toxicants cannot be legislated out of existence. Furthermore, unlike a chemical additive which should be assumed to be toxic unless proved otherwise, a natural food is generally assumed to be safe if it has been consumed by man for centuries with apparent impunity.

It would be manifestly impossible for me to include here a detailed coverage of all of the deleterious substances that are known to be present in plant materials. I shall concern myself here only with those plants whose seeds have present or potential value as a source of protein for human feeding, since experts are agreed that our hope for feeding the exploding world population of the future will rest largely on the expanded use of plants as a source of protein. I have in mind such high protein containing plants as the soybean, peanut, and cottonseed, and a large variety of legumes which constitute an important component of the daily diet for large segments of the world's population.

As a biochemist I am inclined to view the natural toxicants of plants in terms of their chemical structure. In doing so I find it convenient to classify them into three main categories:

1. proteins and amino acid derivatives
2. glycosides
3. a miscellaneous group of substances of diverse and, in many cases, unknown chemical structure.

Proteins and amino acid derivatives

Trypsin inhibitors. Perhaps the best known, and certainly the most studied, of all of the antinutritional factors which may be categorized

[1]A portion of the work reported in this paper has been supported by Grant AM13869 from the National Institutes of Health.

[2]Department of Biochemistry, College of Biological Sciences.