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THE NATURE AND BREEDING FOR PHYSIOLOGICAL STRESS RESISTANCE IN SWEET POTATO

F.W. Martin, J. Santiago and R. Ruberté*

USDA-ARS, Tropical Agriculture Research Station
Mayaguez, Puerto Rico.

ABSTRACT

Stress is defined and progress in studies of physiological stress in sweet potato is reviewed, with emphasis on breeding. Sweet potatoes were bred in the heavy clay soils of Mayaguez by selecting seedlings that had grown in such soil and by polycrossing. The population so developed increased in tolerance to the soil, and outstanding clones were found. These clones were shown to have considerable yield stability in better soils. Seedlings were also grown in pots in the greenhouse and subject to several stresses: flooding, drought, soil acidity, shade, salinity, poor fertility, and competition with other plants. Selections for stress resistance were made and selections were polycrossed. Stress resistance increased in populations and outstanding clones were produced that outyielded standard clones in field trials under stress. Stresses reduced plant growth and resulted in some cases in characteristic responses to stress. Components of yield were explained. Increased yields occurred chiefly due to increased storage root size. Selection for stress results in simultaneous selection for genes for high yield, and for resistance to the stress in question. Prospects for further progress are excellent.

INTRODUCTION

The population of the world is continuing to increase even though we cannot feed now the people who are here. How are we going to feed these new people? Obviously there are economical and political answers to this question, but in addition, to feed more this world has to produce more. It is doubtful that agriculture can be expanded by opening new lands. As pointed out by Christiansen (1979), increased food production must be accomplished by producing more on lands now used for agriculture, or producing on marginal lands not now in use. In both cases it will be necessary to consider the limits imposed by physiological stresses and to breed new cultivars tolerant to physiological stress.

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* The senior author is a USDA Collaborator, formerly a Research Horticulturist, TARS, Mayaguez, Puerto Rico.

What is a stress? It is any factor that reduces growth from the optimum. In practice it is very difficult if not impossible to define optimum growth conditions. Yet, it is easy to define and to name the opposite extremes, the factors that impede growth. The physiological stresses are those related with climate, including drought, excess water, insufficient light, excess heat, and cold, and those involved with soil, such as poor soil structure, infertility, and acidity or alkalinity. In addition to physiological stresses, plants are subject to biological stresses, the effects of other living organisms, including bacteria, fungi, viruses, nematodes, insects, and other plants.

It is probable that every plant is subject to some stress during growth. Minor stress conditions may limit highest possible yields, but strong stresses can even limit the practice of agriculture. In general, yield may be thought of as an integration of the effects of many factors affecting growth, each functioning in time and space according to circumstances. Seldom is it possible to separate completely the effects of these many factors and to assign a specific amount of yield to each.

Agricultural scientists are becoming aware of the need to breed crop plants for resistance to physiological stresses. The cultivars of the future, 25, 50, and 100 years from now will have to have more stress resistance. As the famous tomato breeder Jack Hanna used to say, that the plant breeder must breed varieties for needs 25 years in advance. It will take that long to develop such varieties.

BREEDING SWEET POTATOES FOR STRESS RESISTANCE

In breeding sweet potatoes at the Tropical Agriculture Experiment Station, in Mayaguez, Puerto Rico, we were concerned with breeding for stress resistance. One rapidly learns that stress resistance is also related to adaptation, yield, and yield stability. Let us look at some generalities first, and then we want to present to you some results and make some interpretations. From these we wish to point out the ways sweet potatoes should be bred for the long term future.

Adaptation is the ability of a plant to live and grow in a particular environment. Some plants have very wide adaptation, are common, and are found everywhere. No better examples exist than weeds. Some plants have very narrow adaptations, such as most orchids. They often grow in very unusual environments and may be difficult to cultivate elsewhere. Adaptation can be genetic, influenced by many genes, some of which have visible and describable effects. We can take it as an axiom that wide adaptation includes tolerances of commonly found stresses.

The plant breeder is interested in adaptation in the sense of yield. A crop plant might grow very well in a particular environment and still not yield well. If high yields are obtained for a particular genotype in many distinct environments, it is said to possess yield stability, something that can be measured statistically. In interpreting stress resistance we must be aware that we are imposing our judgement of what success is, yield, on the plant's situation, where survival and growth might be far more indicative of adaptation. We think that yield stability is related to a collection of stress resistances.

We bred for stress resistance in sweet potatoes at TARS by two methods. In the first, we grow sweet potato seedlings in a highly stressed situation, (the soil of Mayaguez), and selected those seedlings capable of highest yields under these conditions. In addition, we bred sweet potatoes for stress resistance by growing the seedlings in the greenhouse in pots where they were subjected to controlled stress conditions, and in there we made selections. In both cases we cross pollinated the selections in polycrosses and retested seedlings. In this fashion we increased the genes for stress resistance in populations.

SELECTING IN THE FIELD

Let us take the first breeding method and examine techniques and results in more detail. The production of seeds in polycrosses, the germination of seeds after scarification, and the establishment of the seedlings in small pots are typical techniques used in sweet potato breeding. We then planted seedlings in the TARS fields in a Cialitos clay soil. This soil is a heavy clay, acidic soil of poor fertility, with poor oxygenation, and easily water-logged during the rainy season. This is a very poor soil for sweet potatoes. Puerto Rican sweet potatoes yield about 1/3 in this soil compared to the soils of Fortuna and Isabela.

We planted with irrigation in April and harvested four and a half months later. Thus, the seedlings experienced the stresses of the soil, and matured during the rainy season. During eight years of selection of sweet potatoes, followed by polycrossing, sweet potato clones were produced that were very tolerant to the soil of Mayaguez. This response was evidenced by the harvest, after weeks of heavy rains, when unbelievably large and sound sweet potatoes were removed directly from the mud. Yields in the Mayaguez soil were as high as 35 tons per hectare.

A series of clones outyielding local and introduced varieties were produced. These were then tested in Isabela under very favorable conditions, frequently in Fortuna as well, and once in St. Croix under conditions of drought stress. We found that sweet potato clones bred as high yielders in Mayaguez tended to be great yielders in other environments as well (Table 1).

When tests for yield stability were made by a student, Nestor Flores, it was verified that sweet potatoes high in yield stability had been produced in the Mayaguez soils. Furthermore, in an unconventional analysis derived from the yield stability data, Mayaguez was shown to be a key location where high yields under stress are suggestive of yield stablility, and of even higher yields in less stressful soils (Martin et al., 1988).

Table 1. Yields of 12 superior selections of sweet potato under stress conditions (Mayaguez) and under good conditions (Isabela) as compared to those of control varieties.

	------Kg./plant------	
Cultivar or clone	Mayaguez	Isabela
Miguela	0.3	1.4
Gem	1.3	2.6
SPV 43	1.2	3.0
SPV 55	1.1	4.1
SPV 56	1.3	3.7
SPV 64	2.0	4.8
SPV 72	1.2	4.7
SPV 73	1.5	5.4
SPV 75	1.9	3.5
SPV 79	1.3	4.5
SPV 80	1.4	3.0
SPV 83	1.4	3.8
SPV 84	1.5	3.6
SPV 88	2.2	5.2

What happened in breeding sweet potatoes at Mayaguez? The following are our conclusions:

We accumulated genes in the populations for tolerance of Mayaguez soil.

We selected individual clones that outyielded standard varieties.

We obtained considerable yield stability in these clones.

Did we actually develop stress tolerance? In part yes, but this conclusion has to be modified by later findings. Nevertheless, there is the clear suggestion that one can best breed for high yields under stress conditions by both polycrosses and mass selection, and by selecting under field conditions that represent the stresses in question.

SELECTING IN THE GREENHOUSE

In the second breeding effort, stresses were set up in the greenhouse. Cuttings were potted in four inch pots, and then were subjected to stress during growth for four months. The principal stresses tested and the techniques for giving stress were as follows:

Excess water or flooding. The pots were placed in a basin where water was maintained at the level of 2.5 cm.

Drought. The pots were allowed to dry to the point of excess wilting, and were then watered to run-off.

Shade. The pots were kept in a plastic shed that permitted about 20% of normal sunlight to enter.

Competition. Three corn seeds were planted in each pot and one plant was allowed to grow in competition with the sweet potato.

Acidity. The pots were watered daily with acidified water.

Salinity. The pots were watered weekly with salty water.

Poor fertility. The potting soil was beach sand.

The controls were grown in the same size pots, in greenhouse soil, with adequate sunlight and water.

Each of these conditions reduced the growth of sweet potatoes and resulted in smaller storage roots. In fact, most seedlings did not produce storage roots at all under these stress conditions. The highest yielding seedlings from each treatment were selected, considered tentative selections, and polycrossed to produce the next generation of seed. During several generations of polycrossing, the number of seedlings producing storage roots under stress, and the size of these roots increased. This is not surprising. Mass selection and polycrossing are powerful tools for the improvement of cross-pollinated crops.

There was always a question about what indeed we were selecting for. Stresses in the greenhouse situation might be distinct from those in the field. However, in the case of three stresses, result in the field confirmed what we had developed in the greenhouse.

We tested for production under the stress of flooding by growing flood resistant selections and controls during wet summer and early fall months in a field with exceptionally poor drainage and excess flooding after rains. Yields were drastically reduced. Yet, selections for resistance to flooding far outyielded controls and other cultivars.

We tested for production under the stress of shade by planting under young mango trees, with controls. The yield of all materials was drastically reduced, but those that yielded best were our selections for shade resistance.

We tested for production under the stress of competition by planting in a field where weeds were not controlled. Yields were drastically reduced. However, the best yields were obtained by selections for competition resistance.

Thus, with respect to three stresses, the evidence is that by selecting in the greenhouse for stress tolerance, we obtained clones which yielded well under similar stresses in the field.

Did we, in fact, produce stress resistant clones? The answer is, "Yes, in part." We must qualify that answer because of other information we began to acquire, which eventually led to a theory of the genetic control of stress tolerance in sweet potato.

In an earlier piece of work we studied the tolerances of 288 sweet potato seedlings to stress conditions, flooding, drought, acidity, shading, salinity, competition for space, competition with corn, weevils, and heavy soils. We generated a great deal of data which was analyzed by Dr. Samuel G. Carmer at the University of Illinois (Martin and Carmer, 1985). In this study, using storage root weight as an indication of stress resistance, there were several interesting findings.

We were surprised to find that stress resistances, as we measured them, tended to occur together. There were significantly more plants with multiple stress resistances, two, three, or even four stress resistances in one clone, than would be expected by chance alone. Thus tolerance of one stress appeared to be related to tolerance of another stress. We began to suspect that we were measuring something of a general nature, which we can call yielding ability. Clones with high yielding ability under one stress tended to be high in yielding ability under another.

We also measured the correlations among individual pairs of stress resistances. Of the 36 pairs of correlations, four were significant and eight were highly significant. However, these correlations were small, ranging from 0.12 to 0.33. When this paper was published clearly it was evidenced that we were selecting for one trait, yielding ability, but we failed to realize the significance of the low correlations. This suggested that other factors were also causing differences in yields. These factors undoubtedly included chance variation, but because of our success in producing clones resistant to stress, We strongly suspect now that individual stress tolerances were also being measured.

Our conclusions are, first, that stress tolerances were developed by testing in the greenhouse followed by polycrossing.

Second, when selecting for stress tolerance one selects for two separate and unrelated sets of genes, one set for yielding ability, and another set for the specific tolerance.

CHARACTERISTICS ASSOCIATED WITH STRESS RESISTANCE

During this research we were able to observe characteristics associated with several stress tolerances. For example, when testing for flood resistance, we saw that the roots growing from the base of the pots into water, floated on the surface and proliferated many fine roots. In addition, roots grew up through the water-soaked soil, and actually penetrated the soil and surfaced. These are clearly adaptations permitting better aeration of the roots. Lenticels on the surface of the storage root proliferate and enlarge, forming an aerenchymous tissue believed to facilitate gas exchange (Martin, 1983).

In the case of shading, the plant is modified by producing longer internodes, larger, more succulent leaves, which are greener in color, and increased tendency to climb. These characteristics favor increased reception of light and increased efficiency in its use (Martin, 1985).

Drought resistance in plants is often related to the extent of growth of the root system. In sweet potato, planted as cuttings without roots, drought resistance might be related to the ability to form root readily. We compared 40 clones for rootability of cuttings and found significant differences among them for all rooting indices (Martin et al., in press). We also found that extensive rooting gives protection from drought. We identified the first two weeks after planting as a critical time for water, and cuttings that suffer from drought at this time, never completely recover. We found that drought during the final month of growth had little or no effect on storage root yields, and in some clones appeared to stimulate yields. We found that rooting of sweet potato cuttings is not related to thickness of the stem under good conditions, but under poor conditions cuttings with thin stems do not form roots or survive as well as those with thick stems. Many of the best sweet potato cultivars have very thick stems.

In regard to resistance to competition from other plants we found that sweet potato reduces the growth of corn in the same pot, as might be expected. But even after harvest of the sweet potato, the soil inhibits the growth of corn, a suggestion of allelopathy. This information has not yet been published.

YIELDS

It became obvious to us that to understand stress tolerance we had to know something about other factors responsible for yields of storage roots. The leaves themselves are the factories which produce the photosynthate responsible for life and growth of the plant. It appears that a coverage of leaf surface equal to about three times the soil surface is optimum for production of photosynthate. If foliage is excessive, then lower leaves do not get enough light to produce, and become net users. This reduces the amount of photosynthate that can be stored as starch in the roots. The condition of excess foliage is called in Latin America "el vicio" and several ways to treat it involve destruction of part of the foliage. Excess nitrogen as well as excess water in the soil will stimulate foliar growth at the expense of root growth. Related to this physiological problem is the postponement of storage root production under conditions of lush growth. Extending the season results in less yield at the normal harvest time, and more chance for insect damage if harvest is delayed.

During the normal life of the sweet potato there occurs a shift in production of foliage to production of storage root. This little understood physiological change is gradual. During storage root growth low nitrogen but high potassium is desirable, and drought may not only be tolerated but might be useful. Thus, yields are influenced by these factors that reflect the nature of the sweet potato itself.

The genetic nature of the root and shoot influence the partitioning of photosynthate, and thus yield. By grafting it is easy to test the influence of a series of foliages on a standard root. As one might expect the shoots differ in their influence on yield, and this influence depends on the leaf surface area as well as intrinsic factors such as photosynthesis per unit area. A factor much more important in determining yield potential is the ability of the root to accept and store starch. This is easily demonstrated by grafting the roots of different varieties with one standard shoot. We have done this with 40 clones (Martin and Ruberté, unpublished manuscript). The differences in storage roots are undoubtedly related to the components of yield in sweet potato.

The components of yield in sweet potato are number of storage roots, size of storage roots, and density or dry matter content of storage roots. These components are interrelated so that an increase in one tends to decrease the others. Extremes of each are characteristic of particular clones, and thus under genetic control.

At a very early stage after planting of cuttings distinctive roots are formed with the capacity to become storage roots (Wilson and Lowe, 1973). These roots, often grouped around the first node below the soil, may not tuberize if conditions are adverse, but under good growing conditions, they will slowly enlarge until storage root growth begins in earnest. Later, other roots can also tuberize, including those on stems that are far from the crown of the plant. This tendency, too, is under genetic control. There are surprising differences among clones in the average number of storage roots per plant, the limits being 1 to 20 or more.

The size of the storage root is more important as a factor in yield that is the number of roots. Size depends on the amount of cell division that occurs in the meristems, and thus is under hormonal control and is genetically determined.

The density of the root depends on the degree to which starch is stored in a given amount of space. While this is genetically controlled, the mechanism for high density has not been identified.

There is a further component of yield determined by man's own choice, the portion of yield which is usable, and this depends on size, shape, irregularity, surface features, and those judgements man makes of these characteristics. Furthermore, climate, soil, insects and virus as well as intrinsic factors control shape and surface characteristics. In fresh markets of the USA both small and very large sweet potatoes are rejected, although they may be used for processing. In calculating yields it is useful to measure both total yield and marketable yield.

FACTORS INFLUENCING YIELD

In the last study before my retirement we attempted to understand the influence of various measurable factors on yield. Using our standard 40 cultivars we measured yield at Mayaguez and Isabela in terms of number of tuberous roots, weight per root, and total weight. We calculated the correlations with yield of 17 indices, measurements, or observations. These included five ways of calculating overall stress tests results, four ways of measuring rootability, four estimates of foliage quantity or quality, three characteristics of the foliage, and one physiological characteristic, flowering. Furthermore, we calculated multiple correlations, taking two or three factors at a time. These data have given us further insights into the factors related to yield.

We have summarized the extensive correlations in tables 2-4. In interpreting the correlations, one must not forget that since yield is influenced by many factors, individual correlations are expected to be small, but significant.

Thus, in table 2 one can see that with respect to number of storage roots per plant, stress test results were related to yields in both Mayaguez and Isabela. Number of roots of cuttings in a standardized test is related to number of storage roots produced, and thus this simple measurement is a way to estimate rapidly the number of storage roots that will later be produced.

In table 3 one sees that the weight of the storage root is most highly related to flowering. Apparently flowering is inversely related to root weight, for it competes with tuberization in the use of photosynthate. Light penetration in the field, related to canopy thickness, is negatively correlated to storage root weight.

In table 4 we see that total storage root weight, which is the product of number of roots, and weight per root, is most influenced by canopy thickness, followed closely by stress test results and then by flowering.

We would like to mention briefly the findings obtained by multiple correlations. Multiple correlations have great resolving power in showing how two or more factors work together to influence a character. What we want to show here are the differences between number of roots and weight per root. In Mayaguez, eight of the 17 factors accounted for 50 percent of the variation in number of storage roots. The three factors of most importance were rootability of cuttings as measured by their length, stress test results, and leaf size. In Isabela 59 percent of the variation was associated with eight factors. The most important were again rootability and stress test results. With respect to weight per storage root, eight factors accounted for only 25 percent of the variation, especially stress test results and canopy thickness. In Isabela eight factors were responsible for 38 percent of the variation. The most important were again stress test results, canopy thickness, and flowering. Thus, these extensive data suggest that many factors acting together are responsible for each of the components of yield in sweet potato.

CONCLUSIONS

We would like to try to summarize all of the available information with respect to yields and stress tolerances in the sweet potato, as follows:

1. The sweet potato is a hexaploid with 90 chromosomes. This means that most if not all genes are represented by as many as 6 alleles. As an obligatory outcrossing species, the degree of heterozygosity is naturally very high.

2. In our breeding work we used a very broad germplasm base consisting of seeds from major sweet potato producing areas around the world. Such a broad base permits selection for any trait desired.

3. Yield, which is a complex character integrating the influences of many genetic and environmental factors, is not highly correlated to any one factor. Furthermore, it appears that stress resistances, which might be associated with some observable characteristics, are also controlled by many genes.

4. Given this complexity, it is remarkable that progress with stress resistance was made in so few years of breeding.

5. The success of breeding for stress resistances was related to three techniques, the use of polycrossing after mass selection, the use of large numbers of seedlings, and selection techniques in the greenhouse and field that permitted the identification of stress resistant individual clones.

6. Nevertheless, the development of superior varieties, those varieties of the future of which we spoke, will need a much longer period of breeding, probably a lifetime. Possibly the most important factor is still lacking, the will of an agency, private or public, to commit the funds and personnel to do the job.

7. We have found the sweet potato an excellent and responsive material to work on these problems.

Table 2. Most important factors related to number of tuberous roots in Isabela and Mayaguez.

Factor	Correlation Coefficient	
	Isabela	Mayaguez
Stress test, root weight	0.34 *	0.52 ***
Stress test, number of roots	0.38 **	0.45 ***
Number of roots of cuttings	0.46 ***	0.29 *
Leaf size	-0.06 NS	0.31 *

Table 3. Most important factors related to weight of tuberous root in Isabela and Mayaguez.

Factor	Correlation Coefficient Isabela	 Mayaguez
Light penetration in the field	-0.20 NS	-0.31 *
Flowering	-0.30 *	-0.35 *

Table 4. Most important factors related to total yields of sweet potato in Isabela and Mayaguez.

Factor	Correlation Coefficient Isabela	 Mayaguez
Stress test, root weight	0.34 NS	0.34 *
Stress test, number of roots	0.24 NS	0.37 *
Field canopy thickness	0.42 **	0.34 *
Flowering	-0.38 *	-0.26 *

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