

that synthetic rubber is at least equivalent to the natural; the chemist's goal is not necessarily to synthesize a duplicate of natural rubber, but it is certain that whatever properties rubber has that are needed will not only be duplicated, but radically improved and new ones added. Synthetic rubber is superior to natural rubber in gasoline, oil and chemical resistance. The synthetic product is more stable to light and air, and has greater wearing properties. Some trucks using synthetic rubber tires have gone over 35,000

miles. Sidewall tire strength is greater, meaning greater safety and better road gripability. The latter property has been tested out thoroughly on wet and muddy roads. Tests on hills with different trucks have shown that the synthetic rubber-tired vehicle goes up a hill with very little side-slipping, whereas the tires of natural rubber slipped all over the road. On curves when operating the car at high speeds, the synthetic tire is safer than the natural.

(To be concluded)

INFLUENCE OF THE ENVIRONMENT ON THE EXPRESSION OF HEREDITARY FACTORS IN RELATION TO PLANT BREEDING¹

By Dr. S. H. YARNELL

CHIEF, DIVISION OF HORTICULTURE, TEXAS AGRICULTURAL EXPERIMENT STATION, A. & M. COLLEGE OF TEXAS

ENVIRONMENTAL influence on the expression of hereditary factors has many aspects. To the geneticist this is the cause of non-hereditary variation. To the experimental taxonomist it helps to explain the status of geographic races. To the breeder it may represent the opportunity to provide adaptability. To the horticulturist interested in cultural problems, differential varietal response to the environment is being increasingly recognized as an important factor in making cultural recommendations. Each aspect has as its fundamental basis the response of the hereditary factors or genes, either singly or more commonly in groups, to the many conditions external to the organism, under which it develops. These outside influences are usually rather complex and difficult to control experimentally. Those most frequently studied are temperature, light intensity and duration, soil and air moisture, wind movement and a variety of nutritional factors.

One of the first careful studies of the effect of the environment on the expression of the gene was made by T. H. Morgan and reported by him in 1915. A strain of *Drosophila* was found in which the abdomen was defective. This was shown to be sex-linked and to be due to a single mendelian factor. The remarkable thing about it was that only the flies that hatched while the colony was young had the defect, while flies emerging later were normal in every respect. By suitable tests it was shown that flies developing from larvae whose food had been moist had the defective abdomen, while flies whose larval stage was spent on drier food were normal.

A second component of the environment that has received considerable attention from the geneticists working with fruit-flies is temperature. Zeleny in 1923 showed that an increase of 1° C. during the larval stage decreases the number of facets of bar eye by 10 per cent., of ultra-bar by 8 per cent. and of normal flies by 2.5 per cent. He pointed out that the same effect can be obtained either by increasing the temperature or by adding another bar gene.

Passing on to another insect, the Hymenopterous parasite of the oriental fruit moth (*Trichogramma minutum*) consists of several morphologically similar races that carry different factors for body color which are entirely dependent upon an appropriate temperature for their expression. According to Peterson, when the average daily temperature exceeds 62° F. the females of one race have a distinct lemon-yellow body color, but when the temperature drops below this average these same individuals become a metallic brown. Flanders finds that four races of this parasite can be identified on a basis of color when raised at the same temperature, but when raised at different appropriate temperatures they are indistinguishable. Temperature with this insect not only affects body color but also influences the length of the life cycle, an important character in determining adaptability to climate.

The effect of temperature on the expression of hereditary factors is by no means limited to insects. In Canna, Honing finds that the anthocyanin pigment producing "old purple" is recessive to another factor for yellow. Plants that are homozygous recessive for old purple and heterozygous for yellow (ssWw) are completely yellow during the heat of summer, but later flowers of the same plant developing during cool weather in the fall have a bluish cast. *Primula sinensis* has a form in which the flower is red

¹ Condensed address of the retiring chairman of the Southern Section of the American Society for Horticultural Science, presented at the Memphis meeting on February 5, 1942. Citations to literature have been published with the complete paper in Volume 41, Proceedings, Amer. Soc. Hort. Sci., 1942.

at 20° C. but white at 30°. A genetically distinct type has a white flower at both temperatures.

The effect of low temperature on the flowering of biennials depends upon (a) the temperature employed, (b) length of time exposed, (c) stage of development, (d) kind of plant, (e) photoperiod and (f) later growing conditions. All of us are familiar with the necessity of many fruits and ornamentals for cold during the dormant period in order to bloom and fruit normally in the spring. Varieties differ widely in their cold requirements. The use of cold in vernalization treatments to hasten fruiting would seem to be a variation of this same theme. The bearing of these differential responses of plant varieties to heat or to cold on the problems of plant breeding may not be immediately evident to those who handle plants in an environment for which their crops have long been bred or selected. Once these plants are grown outside of their accustomed environment the necessity for hereditary factors that will permit them to grow and produce as an economic crop are soon apparent.

The same may be said of the responses of plants to light. The literature concerning the reactions of plants to photoperiod has become rather extensive. The interest of southern plant breeders in this subject arises from the shortness of the days experienced during both summer and winter compared to the day-length of the normal growing season farther north where many of our commercial varieties were developed.

Often environmental factors other than or in addition to temperature and light make a significant contribution to the appearance or behavior of a plant. Platenius and Knott found that onions on peat are twice as pungent as those grown on sand, and onions on loam are intermediate in this respect. Pungency tends to increase with increased temperature. More sulfur in the soil increases pungency, but more soil moisture decreases it. In spite of these environmental effects, with comparable conditions some varieties are three times as pungent as others.

Available sugars inside the plant are an important factor in the formation of anthocyanin pigmentation. Environmental factors influencing the accumulation of sugars therefore affect plant color. These include soil nutrients, light, temperature, water, available nitrogen and altitude. Owen reports increased mottling of soybean seeds on heavy, rich soil, and sometimes with wider spacing, while increased nitrogen decreased mottling. Ratsek has been able to reduce the intensity of color of red roses to nearly white by defoliation and by pruning away carbohydrate reserves.

Work on the manipulation of a multitude of nutritional factors has now assumed enormous proportions. It is all based on the assumption that the complex of

hereditary factors affecting growth and yield are influenced in their expression to a considerable degree by the environment. To return to *Drosophila*, the vermilion brown stock lacks the amount of eye pigment of normal flies. When the 70-hour larvae are placed on a partial starvation diet the intensity of color is greatly increased. It is estimated that this treatment stimulates the production of the eye color hormone by "not less than a hundredfold" according to Beadle, Tatum and Clancy. In studying a stock of the bent nose Norway rat in which about half of the individuals had this defect when fed a home-made diet, Heston was surprised to get only normal rats when the stock was placed on Purina Fox Chow. It was found that a certain calcium-phosphorus ratio and vitamin D do not allow genes for bent nose in the rat to express themselves.

Work on the effect of nutrients on the fruiting of plants has produced rather striking results. Many fungi are induced to produce sexual spores on artificial media only with great difficulty or not at all. Sax grew field beans with white and with colored seed coats on rich and on poor soil. Factors linked with color gave the higher yield under unfavorable conditions, while factors linked with white seed gave a higher yield under favorable conditions.

A somewhat different type of effect of environment on gene expression is found in its influence on disease resistance. Walker and Smith report a decreased resistance of commercial varieties of cabbage resistant to yellows, with increased soil or air temperature to 28° C. It would seem that both host and pathogen might share in this measurable response in their relationship.

For plant breeders faced with problems of adaptability, as many of us in the South and West are, a good deal of the work in experimental taxonomy has a direct bearing on our problems. It makes no real difference whether the characters that fit a plant for a particular environment are inherited under other conditions or not. Whether the valuable characteristic represents an "environmental variation" from what may be considered the normal type elsewhere, or represents a new genetic combination that can maintain its individuality under other conditions makes a difference only if the climatic conditions the plant breeder faces are so variable that the usefulness of the so-called "environmental variation" is nullified. One of the difficulties in discussions of this kind is the almost universal human error of assuming that the familiar is the only true norm and that all other forms are "off-type." This suggestion obviously has its limitations, as the familiar tends to be the modal type, and environmental variation as observed in the laboratory or under field conditions tends to be continuous. In the widest sense, distinct forms resulting from the

interaction of a genetic complex with contrasting environments do have genetic meaning both for the taxonomist and for the plant breeder.

The problem of adaptation among both wild and cultivated plants is a matter of finding genes whose expression under a particular set of conditions favor growth and maintenance. The essential differences in the two cases lie in the numbers of individuals involved, in the methods of selection and to no small extent in the economic motivation of the breeder. A better understanding of the processes of nature should be of value to the latter.

Vavilov has developed the idea of parallel variation among geographic races and species, calling this the "law of homologous series in variation." He suggests that where plant breeders observe adaptive characteristics in species related to the material they are working with, there might be a reasonable chance of finding or developing the character from their own or the more closely related wild material. The crossing of genetically distinct geographic races may make it possible to transcend the limits of ordinary types.

The work of Massart provides an example of very marked response of a single genotype to different environments. *Polygonum amphibium* may be readily adapted as a land plant, a water plant or a dune type merely by growing divisions of a single individual under these distinct conditions. Each one would be considered a definite geographic race, which is the normal type for each environment.

In discussing the origin of genes responsible for well-adapted climatic races Goldschmidt credits Davenport and Cuenot with the suggestion that genes useful in a new environment arise by mutation and may be carried along by chance until they have an opportunity to express themselves and contribute to the survival of the species under the new conditions. This has been called preadaptation. He even goes so far as to say ". . . we must regard such preadaptational mutations as a prerequisite for the spreading of a species into new areas with different conditions, which would be inaccessible to the original forms. . . ." White discusses the possibility of the existence of genes for cold hardiness among tropical species and those having a southern range. He cites the case of a native Texas pecan that was found to be fully hardy in Canada. Three species of *Iris* native to Texas proved to be hardy in New York. Occasional mutations for hardiness in tropical plants are likely to be lost if there is no change of climate to give them selective value.

There may be a lesson for the plant breeder in Fisher's theory of the origin of dominance. He supposes that most mutations originally have some effect in the heterozygous condition, *i.e.*, they are partially dominant to their wild-type allele. As this effect is

unlikely to be beneficial to the organism, any combination of genetic factors tending to cover up the effect of the new gene will have survival value, and eventually this will become the normal wild type with the new gene fully recessive. Such a complementary effect might be made use of by the plant breeder in outcrosses of valuable but not fully adapted material to secure new genetic combinations that favor the development of the desired characteristic under a particular set of environmental conditions. The value of such a method will depend entirely upon the material available. It should be remembered that the breeding situation among the crop plants is different from that among wild species both in the matter of the effective number of breeding individuals and in the basis of selection. The opportunity for crosses with wild types in many instances permits the incorporation of such recessive genes in the plant breeder's stocks.

Some of the most important characteristics the plant breeder interested in adaptability has to deal with may be classed as physiological. Nilsson-Ehle found that an apparently uniform variety of wheat would become more resistant to cold through the natural elimination of those individuals with genetic factors for tenderness. McKinney and Sando have crossed spring wheat, which requires long warm days, with winter wheat, which first needs cool short days. In order to classify the segregation in the F_2 they found it necessary to grow populations both in the spring and in the fall. Heyne and Laude have tested the resistance of inbred lines of corn to high temperature in the laboratory, securing differential response that checks with field experience. They conclude that "the testing of seedlings for heat resistance can be relied upon with considerable assurance for distinguishing genetic differences in the drought tolerance of larger plants of different strains of maize." Hawthorn has been able to select lines of Bermuda onion less apt to split and double. The point of chief interest to us in connection with this work on wheat, corn and onions is that varieties that are to all appearances entirely uniform, do carry valuable hereditary factors that can express themselves only under suitable environmental conditions.

Before drawing the moral for plant breeders inevitable to such a discussion as this let us review briefly some of the points that have been made: (1) single mendelian factors that have been studied genetically have been found to vary widely in their expression because of differences in environmental conditions; (2) under one set of conditions it may be impossible to distinguish between distinct genetic types while under other conditions they may be quite different in appearance; (3) factors of the environ-

ment that are responsible for these differences include moisture, temperature, light, nutrition and many geographic and cultural conditions that affect these things; (4) there must be appropriate environmental conditions before any gene or combination of genes can have selective value, either natural or in plant breeding, otherwise they may be entirely lost; (5) in tests, suitable conditions may have to be provided artificially; (6) the cumulative effect of modifying factors under a particular set of environmental conditions can be taken advantage of by the plant breeder in improving the adaptability of selections having special market appeal; (7) the value of any heritable character under a particular set of conditions may bear no relation to its development or lack of development under other environmental conditions; (8) work in experimental taxonomy encourages the belief that the adaptability of many crops for southern and western conditions can be materially improved by breeding and selection even though they have been developed primarily for other regions with quite different conditions; (9) improvement might be expected in some cases through intervarietal crosses by accumulating genes from different varieties that may have a favor-

able effect directly or in combination; and finally (10) in other cases more rapid progress may be expected by outcrossing to wild forms where these are available or by making wide crosses among cultivated forms. Perhaps this summary carries its own moral. As a matter of fact much of the breeding work in the South and Southwest has been and still is in line with these considerations.

This interest in breeding for increased adaptability to southern conditions evident in the past ten years is very encouraging. As the work progresses we may expect an even larger accumulation of hereditary factors favoring quality and production under our conditions. This will make it increasingly easy to synthesize a variety according to certain specifications. There is still a good deal of spade work to be done. This means that we must discover new genes judging their value to us not by their expression under a different environment, but by what they can do under conditions peculiar to our own locality, both as individual hereditary factors and in new combinations. With these it seems reasonable to expect that we can provide the plant material basis for an increasingly prosperous southern horticulture.

SCIENTIFIC EVENTS

RECENT DEATHS

HERMAN STABLER, since 1925 chief of the conservation branch of the U. S. Geological Survey, died on November 24, at the age of sixty-three years.

DR. REUBEN PETERSON, until his retirement in 1931 with the title emeritus for thirty years professor of obstetrics and gynecology at the University of Michigan, died on November 25, at the age of eighty years.

DR. SAMUEL HANFORD MCKEE, ophthalmologist at the Montreal General Hospital, formerly clinical professor of ophthalmology at McGill University, died on November 25. He was sixty-seven years old.

A RECENT message received through the American Red Cross announces the death in Germany on July 5 of Professor Oskar Bolza at the age of eighty-five years. He was a reader in mathematics at the Johns Hopkins University in 1888-89, associate at Clark University, 1889-93, associate professor at the University of Chicago, 1893-94, and professor, 1894 to 1910. For many years past he had been non-resident professor living in Freiburg.

DR. RICHARD B. GOLDSCHMIDT, professor of zoology at the University of California, writes: Mrs. L. Goldschmidt, widow of the crystallographer, Professor Victor Goldschmidt, of Heidelberg, who had been professor there for about forty years and had be-

queathed his fine art collection with a large endowment to Heidelberg University, recently committed suicide at the age of eighty-two years, when the Nazis wanted to deport her to a Polish ghetto.

TRANSFER TO THE UNITED STATES OF THE HEADQUARTERS OF THE INTER- NATIONAL SOCIETY OF SURGERY

By a vote of the delegates from all the affiliated societies of the Americas, representing Argentina, Brazil, Canada, Cuba, Ecuador, Guatemala, Mexico, Paraguay, Peru, the United States, Uruguay and Venezuela, the headquarters of the International Society of Surgery has been provisionally transferred from Brussels to the United States.

In explaining the need for the change Dr. Rudolph Matas, of New Orleans, acting secretary and treasurer, said:

The German occupation of Belgium and the Nazi devastation of the rest of Europe and all the other war-torn nations had virtually restricted the international relations of the society to the Western Hemisphere, where its fellowship is widely spread through its affiliated branches in North, Central and South America.

The Executive Committee of the United States Division, the largest, most active contributor to the transaction, felt it their duty conjointly with their Latin American colleagues to rescue the society from the perils of the Euro-