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The Inheritance of Iodine Value in Rice and Its Association With Other Characters.

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THE INHERITANCE OF IODINE VALUE IN RICE AND
ITS ASSOCIATION WITH OTHER CHARACTERS

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
in
The Department of Agronomy

by
Ramaswamy Seetharaman
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ABSTRACT

Inheritance of amylose content in rice in terms of iodine value was studied in the \( F_1 \), \( F_2 \) and \( F_3 \) generations of a cross between a low iodine variety, Texas Patna and a high iodine variety, Toro. The lower the iodine value, the higher is the amylose content. The materials were grown at the Rice Experiment Station, Crowley, Louisiana and iodine value determinations were made at the Rice-Pasture Experiment Station, Beaumont, Texas, by a method involving use of a starch-iodine blue test.

The mean iodine values of the parents in 1957 were 15.0 for Texas Patna and 56.3 for Toro. The mean of \( F_1 \) plants was 22.8, a value close to the low iodine parent and indicating partial dominance for low iodine. A mean of 28.5 was obtained for 470 \( F_2 \) plants, which also indicates that low iodine value was partially dominant in this cross. Although the frequency distribution curve for the 470 \( F_2 \) plants was continuous, it was distinctly bimodal with a large group of low iodine plants and a smaller group of high iodine plants. An approximate 3:1 ratio was obtained in \( F_2 \) between low iodine plants like the Texas Patna and \( F_1 \) compared to high iodine plants that resembled Toro. This evidence suggested that the parents differed by one pair of genes. However, the occurrence of plants in iodine value classes intermediate between the \( F_1 \) and Toro provided evidence for the presence of minor genes which
had a modifying effect on the major pair. Transgressive segregation occurred only for high iodine value.

In $F_3$, it was possible to group the lines into three general classes. Lines included in the first and the third group were relatively homozygous for low and high iodine value, respectively. Lines belonging to the second group segregated for iodine value and were heterozygous. This tended to confirm the conclusion that the parents differed by one major pair of genes. However, differences were apparent between lines included in any one group and these differences were explained as being due to the influence of the minor genes. All evidence from $F_2$ and $F_3$ therefore indicated that the parents differed by one pair of major genes and several modifiers.

A heritability value of 95 per cent was obtained from the regression of $F_3$ means on $F_2$ plant values, indicating that selection for iodine value on an individual plant basis would be highly effective.

Significant correlation coefficients of -.44 and -.59 were obtained in $F_2$ and $F_3$, respectively, for the association between iodine value and data of heading, indicating a moderately strong relationship of some importance. However, plants or lines with low or moderately low iodine values varied widely in maturity with no association, whereas plants or lines with moderately high or high iodine values showed a strong tendency to be early in maturity. The correlation was therefore suggested to be due mainly to the strong tendency for the plants with high
iodine values to be early in maturity. The value for their genetic correlation was -.49.

A correlation coefficient of .41 in F<sub>2</sub> indicated an association of moderate strength between iodine value and apiculus colour. It is probable that one or more of the genes for both traits are linked. The correlation coefficient was much lower in F<sub>3</sub>.

Low correlation coefficients of -.13 and -.02 were obtained in F<sub>2</sub> and F<sub>3</sub> generations, respectively, between iodine value and hull colour.
INTRODUCTION

Rice breeding has been in progress for a considerable period of time in almost all of the major rice producing countries of the world. The first objective in breeding in these regions was the improvement of rice through increase in yielding ability. Although this is still true in some countries where acre yields are comparatively low, in several other countries breeding programmes have been broadened to include other objectives, such as grain length, resistance to lodging, relative date of maturity and suitability for combine harvesting. As a result, not until recent times has much attention been given to improvement in the quality of rice.

Even in countries where breeding programmes have included improvement in the quality of rice, this has been confined largely to the milling and processing aspects of rice. However, within the past few years there has been a diversion of attention and considerable importance has been attached to the cooking quality of rice from the standpoint of chemical composition. In fact a recent addition in the breeding programmes in the United States has been improvement in the cooking quality based on the chemical composition.

In general, two main types of rice have been recognized for many years based on the cooking quality. These are the short and long grained types. The kernels of short grained types adhere to each
other on cooking and have a moist, sticky texture, whereas in the long
grained types the kernels are dry and fluffy after cooking and their indi-
vidual grains do not split or stick together. The varieties of medium
grain length tend to be intermediate in these respects.

Preference for any particular type of rice is based on the cooking
characteristics of the variety and the choice of the consumer. Thus in
some countries, such as India, Indonesia and The Philippines, long
grained types are preferred, while in certain other countries, like
Japan and Korea, people generally prefer short grained types. Hence,
what constitutes desired cooking quality depends on the country and the
preferences of the consumer. Further varietal preference is also de-
pendent on the flavour and appearance.

The situation in the United States in regard to cooking quality is
not as well defined as in India or Japan. For many years the bulk of the
rice grown and consumed in this country has been of medium grain length
and it has been generally assumed that a majority of consumers pre-
ferred this type. However, in the past few years there has been a con-
siderable increase in the production of long grain varieties, resulting
probably from the development of such new, superior varieties as Blue
Bonnet and Texas Patna, and the consumption of long grain types is in-
creasing. This, plus the fact that housewives are willing to pay a
premium price for the long grain types, indicate that the cooking charac-
teristics described earlier for long grain rices probably represent the
most highly desired types in the United States. It is certainly true that,
when the American housewife buys long grain rice she expects it to cook relatively dry and fluffy.

Since the short and long grained types differ distinctly in the behaviour of their kernels after cooking, it has been a general assumption that cooking quality is controlled directly by grain length in some manner and that all long grained types or all medium and short grained varieties have similar cooking quality. However, it is known through experience with new varieties developed by hybridization between types which differ in grain length that major differences in cooking characteristics may occur among varieties having the same grain length. Thus, not all long grained types have the desirable cooking qualities generally associated with this group. The actual relationship between grain length and cooking characteristics of rice is uncertain.

Recent studies conducted in India and the United States indicate that the chemical composition of the starch may be an important factor in the cooking behaviour of rice varieties, irrespective of their grain length. Since milled rice as consumed consists of 90 to 94 per cent starch, differences in the cooking quality were assumed in these researches to be determined most probably by variation in their starch components. Rice starch, like any other cereal starch, consists of amylose and amyllopectin fractions. These fractions differ from one another both in physical properties and in chemical behaviour. Amylose is a straight chain fraction while amyllopectin has a branched structure. The amylose molecule consists of roughly 500 or more dextrose units
whereas more than 1,000 dextrose units are contained in an amylopectin molecule. Amylose forms a complex with iodine; amylopectin does not form any complex. They also differ in the nature of their acetate film and in their capacity to form a firm gel.

The starch of the medium and long grained rice varieties grown in the United States contains approximately 12 to 26 per cent amylose. Even higher levels of amylose may be available in some introductions. From a general comparison of the amylose content and the grain type, it appears that the long grained types tend to possess a high percentage of amylose than the medium and short grained types. However, there are exceptions to this general tendency.

It is generally agreed that rice varieties with a high amylose content have good cooking qualities in that their grains remain fluffy after cooking and that differences in degree of stickiness after cooking are governed largely by the percentage of amylose in the starch. It has been suggested that samples analysing at least 20 per cent amylose are the most satisfactory from the standpoint of giving fluffy and non-sticky product when cooked. Thus, the desirable cooking quality possessed by the long grained rice varieties has been attributed to their high amylose content.

The available information strongly indicates that the amylose content, or probably the ratio of the amylose to the amylopectin in the starch, is mainly responsible for the differences in the cooking characteristics. The higher the amylose content or lower the amylopectin content, the better is the cooking quality. But methods for the chemical determination
of amylose content are tedious, time consuming and require large samples of grain. Therefore these methods would be of no practical use to the rice breeder since he must test a large number of plants within a short period. Absence of a simple and rapid method for the estimation of amylose content necessitated the attempts of several workers to devise a method that would be of practical help in the breeding programme.

Based on the differential iodine-blue reaction of the amylose fraction, a simple method was developed by Halick and Keneaster to provide an estimate of the relative amylose content in the samples. This method was described by them in 1956. The method is simple, does not require much special equipment, uses only a small amount of grain per sample and is rapid. These features permit its use in a rice breeding programme.

A consistent relationship between iodine values obtained by this method and the actual amylose content obtained by chemical determination indicates the reliability of the iodine method for the estimation of amylose content. A good correlation between the results of this method and actual cooking tests was also reported by the authors who had described the method. All of this information indicates that the iodine method provides a sufficiently reliable estimate of amylose content and cooking quality to justify its extensive use in rice breeding. The iodine test has been in use in the United States since 1955. The fact that in 1957 alone 7175 samples were evaluated for cooking and processing behaviour using this iodine test would show how extensively this test has been
utilized to detect differences in the varieties in the United States.

In spite of its wide application in rice breeding programmes in the United States, knowledge concerning the genetic and breeding behaviour of iodine value is very limited. The little information that has so far been available has been from highly selected populations and even here studies have not been systematic. However, it is well known that major differences in starch fractions are hereditary. Being so, a knowledge concerning the genetics of amylose content in terms of iodine value and the breeding behaviour would definitely improve the effectiveness of the breeding programmes. Any new information obtained through a systematic study would itself add to the present knowledge. It is therefore the intention of the present study to obtain information concerning the inheritance of amylose content as indicated by the iodine test.

This study was conducted with the parents \( F_1, F_2, \) and \( F_3 \) generations of a cross between Toro, a variety with a high iodine value (low amylose content), and Texas Patna, a variety with a low iodine value (high amylose content). Both parents are long grained types. Since these two varieties also differed in respect to date of maturity, apiculus colour and colour of hull, a study was made of their association with iodine value.
REVIEW OF LITERATURE

Iodine Value

Literature dealing with the inheritance of iodine value is limited being mainly reported from the Rice-Pasture Experiment Station, Beaumont, Texas. To make the information complete, studies conducted with different aspects of amylose content have also been reviewed.

Sanjiva Rao, et al. (1952) compared the amylose content of different Indian varieties with their swelling number calculated by them. The amylose content was determined by them analytically. They concluded that the swelling number increased along with an increase in amylose content. Varieties with high amylose content exhibited high swelling number. They attributed this to the structure of the amylose fraction and suggested that as a result of the loose structure possessed by the linear chain component, the kernels were less rigid and were able to absorb more water. The swelling number was described as the weight of water imbibed by 100 grams of rice when cooked in water at 98°C under standard conditions. They also used the swelling number as the indicator of cooking quality of rice and reported that varieties having high swelling number were preferred by consumers since these varieties became soft when cooked.
The linear and branched components of starch have also been synthesized. Thus Cori and Cori and Hanes, both cited by Brautlecht (1953), working independently disclosed the synthesis in vitro of the linear component utilizing the substrate glucose-1-phosphate and an enzyme phosphorylase.

Peat, Bourne, Haworth and associates, cited by Brautlecht (1953), later disclosed the Q-enzyme which, in the presence of a suitable substrate, is capable of converting the linear component into the branched component.

Williams, et al. (1955) in their study involving distribution of the different fractions of starch in rice suggested that samples analyzing at least 20% amylose content are satisfactory from the cooking point of view.

Halick and Keneaster (1956) made a comparative study of the iodine value and the swelling number of different American rice varieties. Among the long grained varieties it was not possible to detect differences in their amylose content by means of their swelling number. On the other hand swelling number of short, medium and long grained varieties showed differences indicating differences in their amylose content. On the basis of these observations the authors concluded that the swelling number determinations could not be used as a reliable estimate of the amylose content in American long grained varieties. In the same study they also determined the iodine value of some of the American varieties of known cooking quality. On comparing the iodine value with
their known cooking behaviour, these authors concluded that a low iodine value (high amylose content) was associated with good cooking and processing characteristics of long grained rice. The same authors (1956) reported a comparison between iodine test and a simple cooking test. The criteria used by these authors for testing the quality were the general appearance of the cooked rice after a period of soaking in distilled water and the presence or absence of longitudinal splits. In their procedure the samples consisting of a certain quantity of milled rice together with a known amount of distilled water were cooked in an autoclave in a steam atmosphere without pressure for 20 minutes. A portion of the cooked rice was then placed in a petri dish and kept submerged in distilled water overnight. The samples were then carefully examined. Varieties whose cooked grains had uniform appearance and were without any longitudinal splits were considered to possess good cooking quality. The cooking test was conducted with 200 samples and in 86% of the samples, the results of the cooking test were in agreement with the iodine test.

Beachell and Halick (1957a) studied the inheritance of iodine value in some crosses. In one of their studies the F₁ plants of a cross between Century Patna 231 and Texas Patna were back-crossed to both parents. When Texas Patna was used as the recurrent parent, all of the plants of the first back-cross generation had low or intermediate iodine values. When the recurrent parent was Century Patna 231, about fifty per cent of the plants belonging to the first back-cross progeny had high iodine
values similar to Century Patna 231. On the basis of these observations the authors concluded that the high iodine value of Century Patna 231 was probably controlled by a single gene.

Transgressive segregates with iodine values lower than the low iodine parent Texas Patna were obtained in the first backcross generation of the cross (Century Patna 231 x Texas Patna) x Texas Patna. Results similar to this were obtained by them in a few other crosses. However, no transgressive segregation for low iodine value was obtained when the F₁ plants of the cross Bluebonnet 50 and Texas Patna were back-crossed to Texas Patna.

Yet in another cross between Century Patna 231 and C. I. 9359 these authors (1957a) obtained a wide range of types in the F₂ population with iodine values ranging from 17 to 92%. They concluded that two or more genetic factors may be involved although they were unable to establish any ratio.

Further studies on the inheritance of iodine value were made by the same authors (1957b) in advanced selections and unselected bulk population of a cross between Century Patna 231 and Bluebonnet 50. In these studies the authors observed that most individual plant selections with iodine values of 30% or below produced progenies with low mean readings and selections with 75% or above tended to produce progenies with higher values in subsequent generations. Progenies of plants with intermediate iodine values showed segregation for low, medium and high values. Similar results were also obtained by them in several other
crosses. In some instances selections with high iodine values were recovered from the bulk population of families having low iodine values.

Williams, et al. (1958) presented evidence for the association between iodine value and amylose content in their study of the amylose content of a number of rice varieties. The amylose content of different varieties was obtained both at Louisiana State University and at Southern Utilization Research and Development Division, New Orleans. These values were compared with the iodine values obtained by the starch-iodine blue test. Here, too, varieties with high iodine values had relatively low amylose content. When the percentage iodine transmission values were converted into absorbances, a coefficient of correlation of .916 was obtained between amylose data obtained by Louisiana State University workers and the values obtained from the starch-iodine blue test. Based on the general trend exhibited by some of the samples studied by them, it was suggested that amylose content may be responsible for the general processing characteristics of different varieties.
MATERIALS AND METHODS

The material selected for this study consisted of parents, \( F_1 \), \( F_2 \) and \( F_3 \) generations of a cross between Toro and Texas Patna, two long grained varieties of rice. Despite their similarity in grain length, these varieties were known to differ greatly in iodine value and were chosen for this reason.

Toro is a midseason, long grained variety developed at the Rice Experiment Station, Crowley, Louisiana and released in 1955. It is a selection from crosses involving three varieties, Rexoro, Blue Rose and Bluebonnet. Toro is known to have a low amylase percentage and a correspondingly high iodine value.

Texas Patna is a late maturing, long grained selection from a cross between Rexoro and C. I. 5094. It was developed at the Rice-Pasture Experiment Station, Beaumont, Texas and distributed in 1942. This variety was selected as a parent in the study because of its very high amylase content and consequent low iodine value.

The cross made in 1955 by Mr. Nelson E. Jodon at the Rice Experiment Station, Crowley, Louisiana, and a single \( F_1 \) plant was grown at Crowley in 1956. The author was generously given the seeds from this \( F_1 \) plant for continuation of the study by Mr. Jodon. The seeds from the \( F_1 \) plant were spaced singly in rows in 1957 at the Rice Experiment Station, Crowley, to provide the \( F_2 \) population. Toro was
grown alongside in a single row consisting of 24 plants. Similarly, 28 plants of Texas Patna were also grown in another row. The planting was done on May 11, 1957, and the F2 population consisted of 551 plants. Every tenth plant was tagged both in the F2 population and in the parental lines. The actual number of the plant was marked on the tag with waterproof ink.

The date of heading was recorded for each plant in the F2 population and in the parental rows. The date of heading was taken as the date on which the first panicle emerged from the flag leaf. To facilitate analysis the date of heading was later converted to number of days to head from the date of seeding.

The colour of the apiculus was also recorded for each plant in the field as the plants headed. The F2 plants were later grouped into two classes, i.e., coloured and colourless apiculus.

After the plants had matured, the colour of the hull was recorded in the field for each plant in the F2 population. The F2 plants could be grouped into two classes, i.e., plants with straw coloured hull and plants with gold hull.

After the data described previously had been obtained in the field, each F2 and parental plant was harvested and threshed individually.

Enough seeds for running the iodine test were available from only 470 plants in the F2 population. All plants of the parents were also tested individually. The procedure followed in the iodine test was similar to the one described by Halick and Keneaster (1956) to
determine differences among rice varieties. The tests were conducted at the Rice-Pasture Experiment Station, Beaumont, Texas.

For each plant tested 4 grams of rough rice were dehulled in a McGill sheller. The brown rice was then placed in a test tube with a spoonful of fine sand. The test tube was closed tightly and placed in a milling device in which the tube was shaken at a speed of 500-600 rpm. Thorough shaking was continued for 30 minutes. The sample was then run through a sieve of .135 inch gauze to remove the broken particles. The whole kernels were collected and rubbed with a piece of clean cloth to remove the sand particles that might have been sticking on the surface of the grains. The clear white grains were ground to a fine powder in a small grinding machine.

One gram of this powder was transferred to a conical flask and 100 cc. of distilled water were added to the flask. The flask was thoroughly shaken. Twenty flasks at a time, including two controls consisting of Texas Patna and Century Patna were then placed in five specially built holders and these were kept in a hot water bath maintained at 77°C for 45 minutes. The flasks were kept gently closed in the water bath. After this period, the flasks were removed from the bath and allowed to cool at room temperature for 15 minutes. The suspension was then filtered.

Ten cc. of this filtrate were pipetted into a 100 cc. flask which already contained 1 cc. of an iodine solution (made from 2 grams of iodine and 20 grams of potassium iodide in one litre of distilled water),
1 cc. of 30 per cent hydrochloric acid and 65 cc. of distilled water. The volume of the solution in the flask was then made up to 100 cc. and the contents were allowed to stand for 30 minutes. The intensity of blue colour was then determined in a photo-electric calorimeter at 600 mu. Per cent transmission of each experimental solution was determined in relation to a control consisting of 1 cc. of the iodine-potassium iodide solution and 1 cc. of the hydrochloric acid solution in 100 cc. of distilled water. The transmission of the control was set at 100. Any set in which the reading for Texas Patna exceeded 18 was discarded and the iodine test was run once again with these samples.

The cross between Toro and Texas Patna was remade in 1957 and in 1958 five F₁ plants were grown along with the parents. Each parental line consisted of nine plants. The parents and the F₁ plants were sown on May 13, in that year. The date of heading and observations on apiculus colour and colour of the hull were recorded on an individual plant basis in the field in a similar manner to that of the previous year. After maturity of the plants, they were harvested and threshed individually. The F₁ plants and plants belonging to both parents were tested individually for iodine value.

After completion of the F₂ analysis in 1957, 112 F₂ plants out of the 470 tested for iodine value were taken for progeny testing as F₃ lines in 1958. The selection of the 112 F₂ plants was not at random. They were selected to include several plants from each iodine class found in the F₂ population. The seeds of 112 F₃ lines and the parents
were drilled on April 4, 1958. The sowing was intentionally done at an early date to provide a maximum period for the plants to develop. Each parent and F₃ line was planted in separate rows. Each row was 12.0 feet in length and in each row the plants were spaced 6 inches apart with the result that each row had twenty-five plants. The rows were spaced 9 inches apart. Each F₃ line and parent was replicated three times in the form of a randomized block design. In each block the lines were arranged by the use of a randomization table. In each row, every tenth plant was tagged and the number of the plant was marked on the tag.

Records taken in the field for the parents and F₃ lines included date of heading, apiculus colour and colour of the hull. These records were made on the basis of individual plants and were taken in the manner described for the 1957 populations. After all records had been completed in the field, ten plants from the first replication of each F₃ line, starting from the 4th plant in the row, were harvested individually.

Seventy-three of the F₃ lines and the two parents harvested in this manner were tested for iodine value. The iodine value was determined for each plant by the method used in 1957 and described earlier.

In the laboratory the date of heading for all the plants in each F₃ line was assembled from the three replications. The date of heading was converted to number of days to head from the date of seeding. The mean value for each line was subsequently obtained. Similarly the data for all the plants in each F₃ line in respect to apiculus colour and hull colour were assembled.
The data collected from the parents, F₁, F₂ and F₃ generations were analyzed to provide information on the nature of inheritance of iodine value, its heritability and effectiveness of selection in F₂ and its association with the other characters.
EXPERIMENTAL RESULTS AND DISCUSSION

Iodine Value

The inheritance of iodine value was studied in the parents, $F_1$, $F_2$ and $F_3$ generations of a cross between Toro and Texas Patna. The cross was originally made in 1955 and a single $F_1$ plant was grown in 1956. An $F_2$ population derived from the single $F_1$ plant was grown in 1957 together with the parents. The frequency distributions of plants belonging to the parents, $F_1$ and $F_2$ generations for iodine value are given in Table I. Their mean iodine values are also included.

Texas Patna - This parent population consisted of 28 plants and all were tested for iodine value. The iodine values for these plants ranged from 12% to 20% with a mean value of 15.6%. This mean iodine value obtained for Texas Patna is close to values reported for different samples of Texas Patna in other tests, which vary between 16% and 20%. The relatively low iodine transmission value for Texas Patna is presumed to indicate a high amylose content since the blue color resulting from the reaction between amylose and iodine acts to inhibit transmission of light. Chemical determinations of amylose content have shown that Texas Patna possesses around 23% of amylose fraction (Williams, et al. 1958). Compared to other long grained varieties of rice, the amylose content of Texas Patna is high and, with the possible exception of Rexoro, no long
Table I. Frequency distribution of plants in iodine value classes for the parents, F₁ and F₂ populations of a cross between Toro and Texas Patna.

| Iodine Value Classes | 5-10 | 11-15 | 16-20 | 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | 61-65 | 66-70 | 71-75 | 76-80 | Total | Mean |
|----------------------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Texas Patna          | 13   | 15    | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 1     | 28    | 15.6 |
| Toro                 |      |       | 1     | 11    | 10    | 2     |       |       |       |       |       |       |       |       |       |       |       | 24    | 56.3 |
| F₁                   |      |       | 4     | 1     |       |       |       |       |       |       |       |       |       |       |       |       |       | 5     | 22.8 |
| F₂                   | 1    | 34    | 148   | 147   | 32    | 3     | 3     | 12    | 19    | 18    | 14    | 18    | 15    | 3     | 3     | 470   | 28.5  |
grained American variety tested so far has a higher amylose content. As a result of the high amylose percentage, the cooking quality of Texas Patna is good.

Toro - A total of 24 plants belonging to the Toro parent were tested for iodine value. This parent had a comparatively wider range than Texas Patna, from 50% to 62%, and a mean value of 56.3%. This wider range in the iodine value indicated that there was considerable influence of environment on the expression of iodine value of Toro. Previous tests had also shown that the iodine value of this parent was subject to considerable environmental variation. The mean value obtained in this study for Toro was close to values reported in other studies. The mean iodine value of Toro is relatively high, especially for a long grained rice. Most long grained varieties have considerably lower values. This suggests that the amylose fraction of the starch in Toro is low. The actual amylose content of starch in Toro has been reported to be only 14% (Williams, et al. 1958), which is much lower than most long grained types. Thus, Toro is not a typical long grained rice in respect to amylose content and would be expected to behave differently from the average long grained rice in cooking characteristics. This has been found to be true. Due to its low amylose content the cooked rice of Toro is less flaky than Texas Patna and is somewhat sticky.

Rice is a self fertilized plant and since the variation within each parent is not extremely great it is assumed that this variation is only
environmental and that the parents were homozygous.

Toro is one of the varieties that possesses a comparatively high iodine value and hence a low amylose content. On the other hand Texas Patna has a very low iodine value and consequently high amylose content. Thus the difference in the parents in the amylose content, indicated by a mean difference of 40.7% in their iodine value, can be considered to represent almost the maximum difference known at present in rice.

The iodine value for the single $F_1$ plant was not obtained in 1956. The cross was, however, made again in 1957 and $F_1$ plants were grown in 1958 along with the parents. The mean iodine values for each of the parents when grown in 1957 and 1958 were more or less identical. In 1957 Texas Patna had a mean iodine value of 15.6% while in 1958 its mean iodine value was 18.3%. Toro had a mean iodine value of 56.3% in 1957 while its mean iodine value in 1958 was 56.0%. Since the iodine values of the parents did not differ appreciably in the two years, it was assumed that the results from the $F_1$ plants grown in 1958 can be compared validly with the parents and $F_2$ grown in 1957. The frequency distributions of the $F_1$ plants for iodine value are given in Table I.

The iodine values for the 5 $F_1$ plants showed a range from 20.5% to 26.0%. The mean iodine value was 22.8%. This narrow range exhibited by the $F_1$ plants indicated that the influence of environment on the expression of iodine value in the $F_1$ plants was no greater than for the low iodine Texas Patna parent. The mean iodine value 22.8% of the $F_1$ plants was closer to the mean of the low iodine parent, Texas Patna.
This indicated partial dominance for low iodine value. With absence of dominance the mean of the F$_1$ should have been nearer to 35.9%, the average of the parents. Further, assuming complete dominance of low iodine value the F$_1$ plants should possess a similar range and frequency as that of Texas Patna. However, in the present study, the frequency distribution of the F$_1$ plants was in continuation of the low iodine parent and there was no overlapping. This indicated that dominance of low iodine value was only partial.

The evidence in the F$_1$ generation, therefore, indicated that low iodine value showed partial dominance in the present study. Dominance of low iodine value was also observed by Beachell and Halick (1957a) in their studies.

Only 470 of the 551 plants belonging to the F$_2$ population were tested for iodine value as sufficient seeds to run the iodine test were not available from the remaining plants. The F$_2$ population showed a wide range with plants having iodine values as low as or lower than the low iodine parent and others with iodine values much higher than the high iodine parent. This extremely wide range indicated that considerable genetic variation was present in the F$_2$ population. The mean of the F$_2$ was 28.5%. This low F$_2$ mean value despite a wide range again indicated partial dominance for low iodine value.

The distribution in F$_2$ was continuous from a minimum value of 8% to a maximum of 78%. However, the distribution of the F$_2$ plants, though continuous, was in a way unusual in that only six plants were
obtained in the range of 31 to 40. Except for these six plants, the distri-
bution would have been discontinuous.

The frequency distribution curve for the 470 F$_2$ plants is given in
Figure 1. A normal curve was not obtained. Instead, the data gave an
essentially bimodal curve with one mode between 11 and 30 and another
between 41 and 70. Thus, 362 of the 470 F$_2$ plants tested for iodine
value were within the range of Texas Patna and the F$_1$ and had low to
moderately low iodine values. This also indicated partial dominance
for low iodine value.

If the remaining F$_2$ plants are assumed to be like Toro, approxi-
mately 3/4 of the F$_2$ plants were within the range of the low iodine parent
Texas Patna and F$_1$ and approximately 1/4 in the range of high iodine
parent, Toro.

The bimodal distribution of plants in the F$_2$ population, virtual
absence of F$_2$ plants in the range 31 to 40 (an area not represented by
the parents or F$_1$) and the approximate 3/4 : 1/4 ratio between F$_2$ plants
like the Texas Patna and F$_1$ compared with those resembling Toro sug-
gest segregation for one pair of major genes for iodine value in this
cross with partial dominance for low iodine value.

In addition, the F$_2$ data also suggest segregation for minor genes
having a modifying effect on the major pair. One evidence was the
presence of 18 plants in the range 31 to 45. These few plants, occupy-
ing an intermediate range between the F$_1$ and the Toro parent, appear
Figure 1. Frequency distribution curve for iodine value in the parents, $F_1$, and $F_2$ populations of a cross between Toro and Texas.
to have differed in respect to the minor genes only. Segregation for the minor genes resulted in these plants possessing iodine values between those of the F₁ and Toro.

In the F₂ distribution, only two plants had iodine values lower than the lowest value for the low iodine Texas Patna parent. The percentage of such plants was extremely low and, in view of the influence of environment, it appears probable that no F₂ plant with a genotype for lower iodine value than Texas Patna occurred. The F₂ distribution provided therefore no evidence for the occurrence of transgressive segregation for low iodine value. This would in turn indicate that the high iodine parent Toro probably did not possess any modifiers for low iodine value. In the present study it appears that there were no plants in the F₂ in which the genetic potential for amylose content of the starch was greater than the amount present in Texas Patna.

On the other hand 32 of the F₂ plants exceeded the maximum value obtained for any plant of Toro (62%). These plants would represent transgressive segregates for high iodine value and probably obtained minor genes from the low iodine parent. From the point of view of chemical composition of starch, the amylose content of starch in such plants would be expected to be lower than that of Toro. This is probably true for part of these F₂ plants but it appears that a factor other than amylose content also affected iodine transmission among the F₂ plants.

Among these 32 transgressive segregates for high iodine value, six
plants exceeded the maximum value of Toro by approximately 10 to 20 units. These plants did not appear to have any amylose since the colour was essentially yellow. In this respect they resembled the behaviour of the long grained variety Century Patna 231, which has been found to have an extremely high iodine value. Chemical tests have indicated that Century Patna 231 does contain about 12% amylose and that the extremely high iodine value is due to a high gelatinization temperature. Century Patna 231 does not become gelatinized at the temperature used in the iodine test, 77°C. It is possible that the six $F_2$ plants with iodine values higher than 70 represent segregates for high gelatinization temperature. If this is the case, it is not possible to estimate their amylose content from their iodine values. They may have had low amylose like Century Patna 231 or it may have been moderate to low.

The occurrence of such segregates with extremely high iodine values, probably due to high gelatinization temperatures, from a cross between two parents which did not possess this characteristic indicates that these segregates were probably due to some type of gene interaction.

Thus, the behaviour of iodine value was in several ways peculiar. Presence of partial dominance for low iodine value as indicated in the $F_1$ and $F_2$ generations and an essentially bimodal frequency distribution curve in $F_2$ indicated that iodine value behaved as a simply inherited qualitative character. An additional evidence was the occurrence of approximately $3/4$ of the $F_2$ plants within the range of the Texas Patna parent and $F_1$ and $1/4$ in the range of the Toro parent. However, iodine
value also possessed features characteristic of quantitative traits. The expression of iodine value was subject to considerable environmental influence like any other character quantitative in nature. There was a continuous variation in the $F_2$ population. The presence of segregates in the $F_2$ population with iodine values higher than the higher iodine parent indicated transgressive segregation, a condition observed only in the study of a quantitative character.

These lines of evidence, therefore, indicated that iodine value behaved neither as a typical qualitative character nor as a typical quantitative trait but resembled more a qualitative character than a quantitative one.

Seventy-three $F_3$ lines and the parents were tested for iodine value in 1958. In each of these $F_3$ lines and the parents ten plants were harvested individually for the iodine test. The frequency distributions of plants for iodine value in both parents and in $F_3$ lines are given in Table II. The mean values for the lines are also included along with the respective values of their $F_2$ plants from which these lines were derived. The lines are arranged in increasing order of their mean values and to facilitate easy reference they are numbered serially from 1 to 73.

The iodine values for the plants belonging to the Texas Patna parent ranged from 14% to 17% with a mean of 16.1%. These values were essentially similar to the values obtained in 1957 for Texas Patna and indicated that early sowing in 1958 had practically no influence on the
Table II. Frequency distribution of plants in iodine value classes for the parents and 73 F₂ lines of a cross between Toro and Texas Patna.

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Table II. Continued:

| Line No. | 11-15 | 16-20 | 21-25 | 26-30 | 31-35 | 36-40 | 41-45 | 46-50 | 51-55 | 56-60 | 61-65 | 66-70 | 71-75 | 76-80 | 81-85 | 86-90 | 91-95 |
|----------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|          |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 55       | 1     | 3     |       | 2     |       | 1     |       |       |       |       |       |       |       |       |       |       |
| 56       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 57       | 1     | 2     | 6     | 1     |       |       |       |       |       |       |       |       |       |       |       |       |
| 58       | 1     |       | 2     | 3     | 1     | 1     | 1     |       |       |       |       |       |       |       |       |       |
| 59       |       | 2     |       | 3     | 1     |       |       |       |       |       |       |       |       |       |       |       |
| 60       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
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| 66       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 67       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 68       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 69       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 70       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 71       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 72       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |
| 73       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |       |

Number of Plants in Iodine Value Classes

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|               | 69.8  | 70.3  | 71.7  | 72.1  | 72.4  | 72.6  | 72.9  | 73.1  | 73.7  | 74.8  | 75.7  | 76.2  | 76.7  | 77.2  | 78.6  | 80.3  | 81.9  | 82.3  | 82.9  | 83.9  | 85.8  | 87.5  | 88.6  |
|---------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|               | 72    | 69    | 69    | 71    | 64    | 60    | 58    | 68    | 61    | 61    | 9     | 76    | 69    | 67    | 63    | 60    | 59    | 66    | 59    | 66    | 69    | 71    |

Mean Value: 72.1

Group: VIII
expression of iodine value in this low iodine parent.

The behaviour of Toro parent in 1958 was, however, somewhat different from 1957. This parent in 1958 had a range from 65% to 70% and a mean of 67.1%. This mean value was higher than the corresponding value obtained for Toro in 1957 which was 56.3%. Further, whereas in 1957 the maximum value for any plant of Toro was 62%, the maximum value in 1958 was 70%. The minimum iodine values were 50% and 65%, respectively, in 1957 and 1958. Thus early sowing in 1958 resulted in an increase in the range as well as in the mean value for the high iodine parent.

Starting from the lowest mean value of 15.4% as exhibited by F₃ line 1, there was a gradual and continuous increase in the mean values of the lines up to the maximum value of 88.6% exhibited by line 73. Thus, the mean values for the different lines showed a continuous range. It can be noted from Table II that some of the F₃ lines resembled the low iodine parent, Texas Patna, while certain others resembled the high iodine parent, Toro. For example, lines 1 and 2 both in their mean value and in the range resembled Texas Patna while lines 45, 46, 47, 48, 49, and 50 strongly resembled the high iodine parent, Toro.

The continuous range in distribution of the F₃ lines on the basis of their means suggests that iodine value was quantitative in inheritance and that the large parental difference was probably governed by several pairs of genes. However, despite the continuity in range of mean values among the lines, the F₃ results, like those obtained in F₂, did not
resemble those of a typical quantitative trait. Based on distribution of plants within the lines and line means, the 73 F₃ lines could be separated broadly into three general groups, in which all lines within a group showed certain common characteristics which were not shared with lines in other groups.

In the first group the lines had the lowest mean iodine values of those tested (15.4% to 25.9%) and contained no plants with moderately high or high iodine values. Nine lines were included in this group. These are lines 1 through 10 in Table II, with the exception of line 9. The highest individual plant value for any of these nine lines was 34%. Thus all lines of this group were relatively uniform in iodine values of individual plants. Furthermore, these lines were derived from F₂ plants which themselves had low iodine values, ranging from 8% to 25%. Considering the low mean values of these lines and the fact that they were uniform for low or moderately low iodine values, it is concluded that these lines were relatively homozygous for low iodine value.

The second group consists of lines which contained plants which ranged from low to high in iodine values. In these lines, some of the plants were as low as the Texas Patna parent while other plants were as high as Toro. Intermediate plants also occurred. Eighteen F₃ lines, lines 11 through 30 in Table II excluding 25 and 28 were included in the second group. The lines of this group were obviously segregating widely for iodine value and many of them resembled the F₂ population. The
mean values of the lines in this group ranged from a moderately low 27.2 for line 11 to a high 56.4 for line 30. These lines were derived from $F_2$ plants which had low to intermediate iodine values.

Lines with mean values ranging from 57.1% to 88.6% were included in the third group and involved lines 31 through 73 in Table II. These lines did not contain any plant with low or even moderately low iodine values. The lowest iodine value of any individual plant in this group was 47%. Though many of the lines included in this group were much more variable than the high iodine parent, all of the plants had high iodine values. Furthermore, these lines were derived from $F_2$ plants which had intermediate to high iodine values. Because of the absence of plants with low or intermediate iodine values in this group of lines and their high mean values, it was concluded that these lines, though not entirely homozygous, were not segregating for the genes necessary for low iodine values.

Ordinarily the number of $F_3$ lines in each phenotypic class can be used to determine a ratio that is useful in the genetic interpretation of the results provided the lines were derived from randomly chosen $F_2$ plants. Since this was not the case in the present research and approximately the same number of $F_2$ plants was taken from each class for progeny testing in $F_3$ regardless of their frequency, then the number of lines in each of the three groups described previously had no genetic significance.

In general therefore, the lines in the first group had all low iodine
values and appeared to be relatively homozygous for low iodine values; lines in the second group showed considerable variation as a result of segregation and indicated that they were heterozygous for low and high iodine; and lines in the third group had high iodine values like the high iodine parent Toro.

Thus, the results obtained from the F<sub>3</sub> data supported the general conclusion reached from the F<sub>2</sub> data that the parents differed by one major pair of genes.

Although their general behaviour enabled the grouping of these lines into three broad classes, differences among the lines included in the same group were obvious in many instances. For example, lines 1 and 2 included in the first group had low iodine values similar to other lines that were included in the same group and yet in the frequency distribution of plants they showed a distinct difference from other lines in this group. Similarly, though all lines included in the second group showed segregation, the mode of segregation was different in different lines. Differences between lines were also observed in the third group as is evident from comparing lines 31 and 60. In fact, considerable variation was observed among the lines included in this third group. These differences among lines within the same group appeared to indicate that the results in F<sub>3</sub> could not be fully explained on the basis of one pair of genes.

However, these results can be explained adequately by assuming that the parents also differed in several pairs of genes having a minor
or modifying effect on the expression of iodine value. Thus, lines which were homozygous for the major gene from Texas Patna for low iodine might differ appreciably from one another and from Texas Patna due to the presence of varying numbers of these minor genes for high iodine from Toro. Under this assumption the very low mean iodine value of Texas Patna is due to the presence of a major gene for low iodine combined with several minor genes also tending to produce low iodine transmission, while the very high iodine figure of Toro is caused by a major gene for high iodine in combination with minor genes which also tend to produce high iodine. If this assumption is correct, it appears that lines homozygous for the major gene for iodine value from Texas Patna may vary in mean values from approximately 15 to 26. Some of these lines would probably have the same cooking characteristics as Texas Patna but some of the higher ones may not.

On the assumption that the Texas Patna and Toro parents differed by several minor genes affecting iodine value as well as one major pair, it should be possible to recognize more than the three general classes of F3 lines described earlier. In fact, on the basis of mean values and the frequency distribution of plants within lines, the 73 F3 lines could be divided into 9 phenotypic groups. The lines in these groups are identified with Roman numerals at right side of Table II.

Group I: Lines 1 and 2 were included in this group. These lines had as low iodine values as the low iodine parent, Texas Patna and in
the distribution of plants they also resembled this parent. It was concluded, therefore, that these lines were homozygous for the major gene as well as minor genes present in Texas Patna. These lines appear to represent recovery of the Texas Patna genotype for iodine value in respect to both the major and minor genes.

Group II: Three lines (lines 3, 4 and 5) were included in this group. Their mean values, though low, were slightly but significantly higher than the mean values of the lines belonging to the first group. In the nature of distribution also these lines differed from lines 1 and 2. However, the three lines of this group were as uniform as the Texas Patna parent and hence were concluded to be homozygous. These lines were, therefore, considered to be homozygous and identical with Texas Patna in the major gene but were assumed to possess one or more minor genes for slightly higher iodine value from Toro.

Group III: Lines 6 to 10, with the exception of line 9, belonged to this group. These lines had relatively low mean values ranging from 19.8 to 25.9. Their frequency distribution indicated that these lines were slightly more variable genetically than lines belonging to groups I and II and did not appear to be completely homozygous. Considering their low mean values and the relatively narrow range possessed by these lines, it was concluded that they were homozygous for the major gene for low iodine value but were heterozygous for minor genes. As a result of the segregation for the minor genes these lines possessed a greater range than Texas Patna. Thus groups I, II and III were assumed
to be identical in respect to the major gene but to differ in minor genes.

Group IV: Lines with moderately low to moderately high iodine values (27.2 to 56.4) were included in this group. This group consisted of eighteen lines (lines 11 to 30, excluding 25 and 28). All lines in group IV segregated for low and high iodine values. In certain lines like 12 and 13 segregation was comparatively sharp while in some others like lines 26 and 30 the range was continuous. These lines exhibited maximum variability. Considering their intermediate mean values, occurrence of segregation in these lines and consequently the variability possessed by these lines it was concluded that these lines were heterozygous for the major gene pair derived from the two parents. Some of the lines also were probably heterozygous for minor genes.

Group V: Fourteen lines were included in this group. Their mean values (55.8 to 63.9) were close to but slightly below the mean value of the high iodine parent. These lines also had a relatively narrow range but somewhat greater than the parents. On the basis of their mean values and their range it was concluded that these lines were homozygous for the major gene for high iodine value but were segregating for one or more of the minor genes. The presence of minor genes from Texas Patna for low iodine value would account for the somewhat lower means than found for Toro.

Group VI: This group was represented by a single line (35). Its mean value 58.5 was close to the mean value of Toro. Like Toro this line occupied a small range but differed from this parent in the classes
occupied by their plants. Plants belonging to Toro occupied classes of 61 to 70 while this line occupied classes 56 to 65. It was concluded that line 35 was not only homozygous for the major gene for high iodine value but also homozygous for the minor genes. The slightly lower mean for line 35 than for Toro is probably due to the presence of one or more minor genes from Texas Patna.

Group VII: Six lines (lines 45 to 50) were included in this group. The mean values of these lines (64.5 to 67.1) were either very close to or identical with the mean value of Toro. Almost all plants included in each line occupied the frequency classes similar to Toro. Thus both in their mean value and in their range these lines resembled very closely the high iodine parent, Toro. It was, therefore, concluded that these lines were probably similar in genetic constitution to Toro in being homozygous for the major gene for high iodine value as well as minor genes present in Toro. They are probably the recoveries of the genotype of Toro parent for iodine value.

Group VIII: In this group were included seventeen lines (51 to 70 excluding lines 52, 56 and 59) which had mean values higher than the high iodine parent and in which the range in iodine values was from high to extremely high. No plant with a low iodine value was obtained in any of these lines. It was concluded that these lines were homozygous for the major gene for high iodine value from Toro but were segregating for other genes which led to extremely high iodine values, considerably above that of Toro. These exceptionally high iodine plants appeared to be the result
of some form of gene interaction apparently involving other genes than the major pair or modifiers found in the previous lines. These plants probably were the result of the same condition that led to the extremely high iodine plants found in $F_2$.

Group IX: These lines had extremely high iodine values and appeared to be homozygous. The reaction of their starch solution with iodine indicated that these lines probably had a high gelatinization temperature, too, and that they were homozygous for the genes that led to high gelatinization temperature. On the basis of the extremely high iodine values possessed by these lines and the fact that these lines differed from the rest in the reaction of their starch solution with iodine it was concluded that these lines belonged to a separate group. It was not possible to be certain of their genotype for the major and minor genes for iodine value due to the complicating influence of high gelatinization temperature.

In summarizing it can be said that lines belonging to groups I through III were all homozygous for the major gene for low iodine value and that differences between lines belonging to different groups were due to the minor genes; lines in group IV were all heterozygous for the major gene as well as minor genes obtained from both parents; and lines included in groups V through VIII were homozygous for the major gene for high iodine value and differences between lines belonging to these groups were due to minor genes. It is significant to note in this connection that none of the lines included in the first three groups produced a single plant
with a high iodine value and furthermore not a single line included in the last four groups produced a plant with a low iodine value.

Thus the $F_3$ data appeared to confirm the tentative conclusion reached from $F_2$ that the difference between Texas Patna and Toro in iodine value is governed by one pair of major genes and an undetermined number of modifiers.

Absence of transgressive segregates for low iodine value indicated that probably Toro did not possess minor genes for low iodine value. In addition, the $F_3$ data indicated that the parents contained genes of a complementary nature which, when combined, led to a higher gelatinization temperature than either parent.

In the discussion of $F_2$ behaviour it was suggested that plants with high gelatinization temperature probably had low amylose content. Evidence in support of this was available from the $F_3$ data. There were 19 $F_3$ lines which contained one or more plants with high gelatinization temperature. None of these 19 lines contained a single plant with low iodine value. Since it is known that plants with high iodine values had generally low amylose content, it is obvious that these plants or lines too had low amylose content.

In a breeding programme that utilizes the iodine test for the estimation of amylose content, it is natural that lines which had iodine values as low as Texas Patna would be most desirable. In the present study only two lines that definitely resembled the low iodine parent were obtained. The occurrence of only two lines that could be considered as
recoveries of the genotype of the low iodine parent suggested that homozygosity for the major gene for low iodine value alone would not be sufficient to obtain lines with low iodine values as low as Texas Patna. What is further needed is the presence of several minor genes in a homozygous condition. Thus, for any variety to possess a good cooking quality similar to Texas Patna it should possess the major gene for low iodine value as well as the several modifiers in a homozygous condition. The minor genes or modifiers have therefore considerable influence on the expression of iodine value. Fortunately, the fact that at least a few of the F₃ lines resembled the low iodine parent, indicated that the number of such minor genes is not great.

In any breeding programme for low iodine value it is therefore necessary for the breeder to grow a large population of the early segregating material to permit him to select such plants which would be homozygous for the major gene as well as for several of the minor genes. Otherwise, his chances of obtaining lines with low or very low iodine values are very low.

Under certain conditions the segregates with high gelatinization temperature could complicate a breeding programme. Had no selection for iodine value been practiced in the early segregating generations, these plants would have been included by chance in his selected material. In this way it would be possible to release as a new variety a strain having a high gelatinization temperature and hence an undesirable cooking quality. Century Patna 231 might represent an example of this type.
Soon after its release it was observed that this variety did not possess desirable cooking quality and as a result, this variety has never been grown since then on a large scale. Under these circumstances it is essential for the breeder to eliminate as many plants as possible on the basis of iodine test and retain only those which possessed low or moderately low iodine values. Only by practicing selection on the basis of iodine test would the breeder be able to avoid any such complication.

Heritability is that portion of the total variance that is due to genetic effects. The value of heritability indicates how much reliance could be placed on the selection of the genotype based on the phenotypic expression. The higher the heritability value for any trait the more effective would be the selection for any genotype of that trait based on its phenotypic expression. Generally, quantitative characters possess low to moderately high heritability values, while high heritability values are characteristic of qualitative traits. Since this value gives an indication of the effectiveness with which selection of genotypes can be based on the phenotypic expression, information regarding heritability is important in most of the breeding programmes. In the present study from the F2 data the heritability was calculated by using the following formula:

\[ \text{Heritability} = \frac{S^2_G}{S^2_G + S^2_E} \]

where

\[ S^2_G = \text{mean square of variance due to genetic causes} \]
\[ S^2_E = \text{mean square of variance due to environment} \]
Environmental variance was obtained by averaging the variances of both parents. A measure of genetic variance was obtained by subtracting the environmental variance from the total variance in $F_2$.

A value of .97, or 97 per cent when expressed in percentage, was obtained from the $F_2$ data. This was a very high value and suggested that most of the variation occurring in the $F_2$ population was genetic and that individual plant selection for iodine value should be effective. This high value further indicated that iodine value behaved more like a qualitative trait than as a quantitative one.

Since in $F_3$ the individual $F_2$ plants are progeny tested, the association between $F_2$ plant value and the means of the $F_3$ lines derived from such plants should be a more reliable measure of heritability than that obtained in $F_2$. A scatter diagram of 73 $F_2$ plants and means of $F_3$ lines derived from them in respect to iodine value is given in Figure 2.

Values of heritability were obtained by (i) calculating the correlation coefficient between $F_2$ plant values and means of $F_3$ lines derived from them and (ii) calculating the regression of progeny means in $F_3$ on individual plant values in $F_2$. A highly significant value of .94 was obtained for the correlation coefficient. This was a very high value and indicated a very close agreement between iodine values for the $F_2$ plants and means of $F_3$ lines derived from them. Thus, plants with low iodine values produced lines whose mean values were also low; and lines with moderately high or high iodine values were derived from plants which themselves had moderately high or high iodine values. This close association is
clearly brought out in Figure 2.

The heritability value obtained by the calculation of regression of means of $F_3$ lines on $F_2$ plant values was .98 which was also significant. This value is exceptionally high and close to values of heritability obtained by other methods and indicated that selection on an individual plant basis in $F_2$ for iodine value would be highly effective.

Thus all values of heritability were extremely high and indicated that selection for iodine value on an individual plant basis would be very effective.

Despite the high heritability possessed by iodine value, the behaviour of some of the $F_3$ lines indicated that it is important to select not only those plants which had very low iodine values but also some of the other plants which had moderately low iodine values. Some of these plants with moderately low iodine values did in fact produce plants in $F_3$ which resembled Texas Patna in having low or very low iodine values. For example, lines 16, 19, 23 and 27 had some plants in $F_3$ which resembled Texas Patna in their iodine value and yet those lines had been derived from $F_2$ plants which had iodine values of 26%, 22%, 30% and 34% respectively. Presence of such plants resembling Texas Patna in some of the $F_3$ lines which had been derived from $F_2$ plants with moderately low iodine values indicated that these plants also should be selected since they are also capable of producing plants with low or very low iodine values like Texas Patna. The inclusion of such plants would definitely increase
Figure 2. Scatter diagram of 73 $F_2$ plants and means of $F_3$ lines derived from them in respect to iodine value.
the chances of obtaining plants with low iodine values in subsequent generations. The present study indicates that it would be advantageous to select those plants which had iodine values up to 34% with a reasonable chance of obtaining segregates with iodine values as low as Texas Patna.

In general, the main object of the breeder is to combine as many of the useful characters from different varieties in a single or a few established varieties. Some of these characters in which the breeder is interested may be associated with other characters and this association may either facilitate or prove disadvantageous to the transfer of the useful characters, depending upon the nature of association. As a result, a knowledge of the association of the particular character in which the breeder is interested with other characters would help the breeder in determining his manner of selection.

Determination of iodine value was done at the laboratory after plants had been harvested individually in the field. Harvesting of the materials and the subsequent procedures followed prior to the running of the iodine test involve considerable work and still the breeder is not certain of the percentage of plants that would possess the desirable iodine value. In such cases, if the breeder is aware of any association between iodine value and any character for which selection could be made in the field, depending upon the nature of the association, the breeder could within reasonable limits make indirect selection for the first character by selecting the plants for the second trait. This should enable him to discard at least some of the undesirable plants. However,
the success of such selection would entirely depend upon the magnitude of
the association. Any correlation coefficient less than .4 irrespective of
significance is not considered to be of any importance in a breeding pro-
gramme. Since selection of plants for iodine value could not be practiced
in the field, under certain circumstances a knowledge of relationship be-
tween iodine value and other characters would be of importance to the
breeder.

In the F₂ population the correlation coefficients of iodine value with
date of heading, apiculus colour and hull colour were calculated to deter-
mine the degree of association. Correlation coefficients for the associa-
tion between iodine value and the other three characters are shown in
Table III. In the F₂ population, to calculate the correlation coefficient
for the association between iodine value and apiculus colour an arbitrary
value of 2 was given to the plants with colourless apiculus and the plants
with coloured apiculus were given an arbitrary value of 1. Likewise
plants with gold hull were assigned a value of 2 while a value of 1 was
assigned to plants with straw hull.

Iodine value and date of heading. A highly significant correlation
coefficient of -.44 was obtained between iodine value and date of heading.
The magnitude of the association indicated that this association was of
moderate importance in a breeding programme. The negative association
in turn indicated that the association was between low iodine value and
late maturity or high iodine value with early maturity. This would be
expected since the early maturing parent, Toro, had a high iodine value
Table III

Correlation coefficients for iodine value with other characters among 470 $F_2$ plants of a cross between Toro and Texas Patna

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<tbody>
<tr>
<td>Iodine Value with</td>
<td></td>
</tr>
<tr>
<td>date of heading</td>
<td>-.44**</td>
</tr>
<tr>
<td>apiculus colour</td>
<td>.41**</td>
</tr>
<tr>
<td>hull colour</td>
<td>-.13**</td>
</tr>
</tbody>
</table>

Level of Significance required

for 400 degrees of freedom at .05 (5%) level  .098
for 400 degrees of freedom at .01 (1%) level  .128
and the late maturing parent, Texas Patna, had a low iodine value. The association between iodine value and date of heading among 470 F$_2$ plants is shown as a scatter diagram in Figure 3.

As shown in Figure 3, the association was peculiar in nature. There was a very strong tendency for plants with high iodine values to be early in maturity. On the other hand, no tendency of any nature was observed among the low iodine plants. Thus, of the 53 plants which had iodine values of 56% and higher, all except three were relatively early in maturity. Even plants with iodine values 30% and above were early in maturity. Therefore, of a total of 110 plants with iodine values 30% and above, 107 plants were earlier than the late maturing parent, Texas Patna. On the other hand, 360 plants which had iodine values of 29% and below showed a wide distribution in regard to date of heading. Some of these plants were very early and headed only 99 days from the date of sowing whereas some others headed after 130 days. Others were intermediate. Thus plants with low and moderately low iodine values showed a continuous range in regard to date of heading from early to late while plants with iodine values 30% and above showed a very strong tendency to be early in maturity.

A similar trend was also observed among the 73 F$_3$ lines. Correlation coefficients for the associations involving iodine value and other characters among F$_3$ lines are given in Table IV. Figure 4 shows the association between mean iodine values of the 73 F$_3$ lines and their respective mean values for number of days to head as a scatter diagram.
Figure 3. Scatter diagram showing the association between iodine value and date of heading among 470 F$_2$ plants.
Figure 3. Scatter diagram showing the association between iodine value and date of heading among 470 F₂ plants.
Table IV

Correlation coefficients for iodine value with other characters among 73 \( F_3 \) lines of a cross between Toro and Texas Patna

<table>
<thead>
<tr>
<th>Variables Correlated</th>
<th>( r )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iodine Value with</td>
<td></td>
</tr>
<tr>
<td>date of heading</td>
<td>(-.59^{**})</td>
</tr>
<tr>
<td>apiculus colour</td>
<td>(+.29^{*})</td>
</tr>
<tr>
<td>hull colour</td>
<td>(-.02)</td>
</tr>
</tbody>
</table>

Level of Significance required

- for 70 degrees of freedom at .05 (5%) level \( .232 \)
- for 70 degrees of freedom at .01 (1%) level \( .302 \)
Figure 4. Scatter diagram showing the association between iodine value and date of heading among 73 F$_2$ lines.
As in the $F_2$ a negative highly significant correlation coefficient of .59 was obtained. The magnitude of this correlation was higher than the value for the correlation coefficient for these two characters calculated among the 470 $F_2$ plants. In Figure 4 all of the 61 $F_3$ lines which had mean iodine values of 30% and above were early to moderately early in maturity. However, of the 12 lines with mean iodine values less than 30, some lines were as early or earlier than the early maturing parent, Toro, while others were as late or later than the late maturing parent, Texas Patna. Thus in $F_3$ also, lines with low or moderately low mean iodine values showed a wide range in regard to maturity whereas lines with iodine values 30% and above showed a very strong tendency to be early in maturity.

The evidence from $F_2$ and $F_3$ indicated that the association between iodine value and date of heading was of importance in a breeding programme. That this association was genetic was indicated by the genetic correlation calculated for the two characters. This was calculated by the formula proposed by Comstock and used by Burton (1951)

$$ \text{Genetic correlation} = \frac{cv_{XYF_2} - cv_{XYF_1}}{\sqrt{(vXF_2 - vXF_1)(vYF_2 - vYF_1)}} $$

where

- $cv$ = covariance
- $v$ = variance
- $X$ = measurement of one variable
- $Y$ = measurement of the second variable
- $F_1$ = first generation
- $F_2$ = second generation
A value of -.49 was obtained which suggested that the association between iodine value and date of heading was genetic.

The genetic association between these two characters may be suggested to be due to linkage. But the distribution of $F_2$ plants and $F_3$ lines as shown in Figures 3 and 4 for iodine value and date of heading did not completely support the presence of linkage. Despite the fact that there were 29 early maturing plants with low iodine values in $F_2$, there were only 3 plants which were late in maturity and had high iodine values. Had the association been due to linkage, there should have been more late maturing plants with high iodine values. Further, the uneven distribution of $F_2$ plants indicated that the association was not due to linkage.

In the absence of a clear evidence for linkage, it is suggested that the degree of association indicated by correlation studies was due to a strong tendency exhibited by the plants with moderately high and high iodine values to be early in maturity. This tendency on the part of such plants to be early in maturity is indicated by the general distribution of plants and lines in $F_2$ and $F_3$ generations respectively. As stated earlier, in the $F_2$ generation of the 110 plants which had iodine values 30% and above, with the exception of 3 plants, all were earlier in maturity than Texas Patna. The Texas Patna parent headed after 113 days. Likewise in $F_3$, 61 lines which had mean iodine values of 30% and above were earlier in maturity than Texas Patna which headed after 135 days. Thus these plants or lines showed a strong tendency to be earlier in maturity.
In contrast to these plants or lines, both in $F_2$ and in $F_3$ generations, plants or lines with iodine values less than 30% showed a continuous range in regard to date of heading. Their actual distribution showed no indication of any association between iodine value and date of heading. In fact, the plants within any particular iodine value class had a continuous range in regard to maturity.

Thus, in the present study, the evidence from the $F_2$ and $F_3$ generations indicated that the correlation between iodine value and date of heading was due mainly to a strong tendency exhibited by plants possessing moderately high and high iodine values to be early in maturity and not due to any association between low iodine value and date of heading. In this respect the association between iodine value and date of heading was unusual and the cause for this unusual relationship was not apparent in the present study. It is likely that environment may have a certain degree of influence on the expression of iodine value.

It is obvious from the above data that late maturity was not necessary for low iodine value. It is also apparent that early maturity was not necessary for high iodine value.

From the breeding point of view the data suggest that despite a negative correlation, it should be possible to obtain lines with low iodine values belonging to different maturity periods. In fact, the data indicated the possibility of obtaining lines with low iodine values in any maturity group.

The test for iodine value is a recent addition. Prior to this the
breeder had been selecting plants on the basis of maturity and milling. While selecting for early maturity probably they were also selecting individuals with moderately high and high iodine values. But for some reason, their selection for late maturing plants had in almost all cases ended with types with low iodine values. This had resulted in the release of late maturing types with low iodine values and early maturing types with high iodine values without obtaining any early types with low iodine value.

This is borne out by the fact that the present commercial varieties in the United States of America which have low iodine values are late in maturity while the early maturing varieties have comparatively high iodine values.

It would thus appear that in his selection of plants based on maturity and milling, the breeder had been in certain instances discarding those very lines in which he is primarily interested.

The present study, therefore, indicates that in any future breeding programme intended to evolve varieties with good cooking qualities and other desirable characters it is essential to practise selection for iodine value before any attempt is made to select plants for maturity.

Though evidence in the present study failed to indicate a clear linkage between genes for iodine value and date of heading, reports of linkage between a gene for waxy endosperm and a gene for maturity are available. Jodon (1940) observed linkage between these two genes with a recombination percentage of 41. Ramiah and Rao (1953) had reported
recombination values in different cases as varying from 8.8 per cent to 24 per cent. However, the classification of endosperm was broad and included only two classes, i.e. starchy and glutinous. Further, in grouping plants for maturity, the plants were grouped into two classes, i.e. early and late.

Iodine value and apiculus colour. A highly significant correlation coefficient of -0.41 was obtained in F2 between iodine value and apiculus colour, which indicated that the association was of moderate strength. A positive correlation showed that the association was between low iodine value and coloured apiculus and this would be expected since the low iodine parent, Texas Patna, has coloured apiculus while the high iodine parent, Toro, has colourless apiculus. In the F3, however, the correlation (+0.29), though significant at the 5 per cent level, was too low to be considered of any importance. It is likely that the correlation of moderate importance obtained in F2 might have been due to the influence of other characters on one or both traits.

Linkage between endosperm and apiculus colour has been reported. Chao (1928) in his studies reported a recombination percentage of 22.4. Jodon (1940) noted linkage between a gene for starch endosperm and a gene for apiculus colour with a recombination percentage of 22.5. In subsequent studies Jodon and Chilton (1946) reported recombination percentages of 16 and 17. Nagao (1951) noted that one of the complementary genes for apiculus colour, C, was linked with gl. He reported a recombination value of 23 per cent. Ramiah and Rao (1953)
reported a recombination value of 29 per cent.

Iodine value and hull colour. A highly significant correlation coefficient of -.13 was obtained between iodine value and hull colour. Though significant, the value was too small in magnitude to be considered of any importance. This negative association is possible since the low iodine parent, Texas Patna, has gold hull and the high iodine parent, Toro, has straw hull. The correlation coefficient in $F_3$ (.02) was extremely low and was insignificant. Thus, both the $F_2$ and $F_3$ data indicated absence of any important association between iodine value and hull colour. These results are in agreement with those of Jodon and Chiltor (1946). They observed independent assortment of genes governing endosperm character and hull colour.
A study of the inheritance of iodine value in rice and its association with three other characters namely, date of heading, apiculus colour and hull colour was made with the parents, $F_1$, $F_2$ and $F_3$ generations of a cross between Toro and Texas Patna. The iodine value is a relative estimate of the amylose content in the endosperm of rice kernels. The higher the amylose content of the grain the better is its cooking quality. Texas Patna has a low iodine value, resulting from a high amylose content, while Toro possesses a high iodine value, indicating low amylose content.

Iodine value determinations for the individual plants belonging to the parents and $F_2$ generation were made in 1957 and in 1958 iodine value determinations were made for the individual plants belonging to the parents, $F_1$ and $F_3$ generations. The mean iodine values of the Texas Patna and Toro parents were 15.6 and 56.3, respectively. A low mean of 22.8 obtained for the $F_1$ indicated partial dominance for low iodine value, or high amylose content. A range of approximately 10 units occurred in each parent and the $F_1$ population, presumably due to environmental variation.

The mean value of the $F_2$ population was 28.5, which also indicated that low iodine value was partially dominant. Although continuous, the frequency distribution curve in $F_2$ was bimodal with a large group of
low iodine plants and a relatively small group of high iodine plants.

The bimodal nature of the curve in $F_2$ and the approximately 3:1 ratio between $F_2$ plants like Texas Patna and $F_1$ compared to plants that resembled Toro in iodine value indicated that the parents differed by one major pair of genes. Occurrence of plants in intermediate range between the $F_1$ and the high iodine parent, Toro, indicated also the presence of minor genes. Though there was no evidence in $F_2$ for the occurrence of transgressive segregation for low iodine value, several plants were considerably higher than any plant of the Toro parent and some of the segregates had extremely high iodine values.

The general behaviour of the $F_3$ lines supported the conclusion arrived at from the $F_2$ data that the two parents differed by one pair of major genes and several modifiers. The $F_3$ lines could be divided into three general groups, those homozygous for low iodine value, those segregating like the $F_2$ and those homozygous for high iodine. Some range among means of lines within groups appeared to be due to the effects of modifiers. No transgression for low iodine value occurred indicating that the high iodine parent, Toro, probably had no minor genes influencing low iodine value.

The occurrence of only two lines in $F_3$ out of 73 lines tested for iodine value that appeared identical to the low iodine parent, Texas Patna, indicated that minor genes have considerable influence on the expression of iodine value. This also indicated that for any line to possess iodine value as low as Texas Patna it should have not only the
major gene for low iodine value but also all of the minor genes.

A few $F_3$ lines were homozygous for extremely high iodine values. The occurrence of these extremely high iodine plants in $F_2$ or lines in $F_3$ generation indicated that these are due to some form of gene interaction. These plants probably had high gelatinization temperature.

A high heritability value of above 90% was obtained from the regression of $F_3$ means on $F_2$ plant values. This high value for heritability indicated that selection for iodine value on an individual plant basis should be very effective.

In $F_2$ a significant correlation coefficient of -.44 was obtained between iodine value and date of heading indicating the moderate importance of this association. In $F_3$ the correlation coefficient was -.59 which was also significant. The distribution of plants for iodine value and date of heading in $F_2$ and in $F_3$ generations indicated that this association was mainly due to a strong tendency exhibited by plants or lines with moderately high or high iodine values to be early in maturity. On the other hand, plants or lines with low or moderately low iodine values varied widely in maturity with no association. This unusual relationship indicated that it should be possible to obtain lines with low iodine values belonging to different maturity groups despite a negative correlation. Genetic correlation between iodine value and date of heading was -.49.

A low positive correlation was found between iodine value and apiculus colour, probably due to linkage of genes for both traits.
A significant but low correlation coefficient of -.13 in \( F_2 \) and an insignificant value of -.02 in \( F_3 \) indicated that there was practically no association between iodine value and hull colour.

In general, the behaviour of the \( F_3 \) lines segregating for low and high iodine values and the unusual relationship between iodine value and date of heading suggested that it would be advantageous to advance plants or lines with even moderately low iodine values for further testing. Also evident was the fact that in order to obtain lines with high amyllose content and hence with a good cooking quality it is necessary to practise selection on the basis of iodine test prior to making final selection for any other attribute.


VITA

Ramaseswamy Seetharaman was born July 19, 1927, in Tirunelveli district, Madras State, India. He passed the Matriculation examination in 1944 and the Intermediate examination in 1946. He enrolled in 1946 in the Science College, Banaras Hindu University, Banaras, Uttar Pradesh and received the Bachelor of Science degree in 1948 and Master of Science in 1950.

In 1951 he was appointed Research Assistant in the Rice Hybridization Scheme sponsored by the F. A. O. and was stationed at the Central Rice Research Institute, Cuttack, India. He was transferred to the Department of Botany in 1953 and was working until 1956 when he was awarded a fellowship by the Rockefeller Foundation for advanced studies in breeding and genetics of rice under Dr. M. T. Henderson, Professor of Agronomy, Louisiana State University and Mr. N. E. Jodon, Agronomist, United States Department of Agriculture at the Rice Experiment Station, Crowley, Louisiana.

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Major Field:

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Approved:

M. T. Henderson
Major Professor and Chairman

Richard J. Russell
Dean of the Graduate School

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Date of Examination: January 22, 1963