

days. This strain was put in competition with unselected *melanogaster* in two cages, 12 and 13. The results are given in table 3 and in the lower left graph of figure 1. It was necessary to terminate these cages after the 325-day sample was collected. It would appear from the results that the 329-day strain of *simulans* was superior to the 229-day strain in competitive ability and it is certainly far better than the unselected *simulans*.

The experiments were continued one step further. Adult females were isolated from cage 13 on the 171st day. From these a strain of *simulans* was obtained that had been selected through competition with *melanogaster* for a total of 500 days. These were put into competition with stock *melanogaster* (cages 26 and 27) and control experiments of stock *melanogaster* with stock *simulans* (cages 24 and 25) were also conducted. It was not possible to continue these cages after the 100-day sample was taken. The results are shown in the lower right graph of figure 1. The selected *simulans* are definitely superior to the unselected *simulans* but it is not clear if the 500-day strain is better than the 329-day strain of the previous experiment.

The results taken as a whole indicate that flies with improved competitive ability can be developed by selection and that this can be done in relatively short periods of time. The importance of this ability for the survival of a species is clear. In a species not living near the limits of its ecological tolerances, competition with other species is one of the main factors influencing its existence. For survival a species must compete successfully. Probably the usual solution is adaptation to a particular niche that becomes its own and thus to limit the ecological area in which it must compete. In the present case it is likely that *simulans* has become better adapted, through selection, to a niche in which *melanogaster* is still superior.

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## A MORPHOLOGICAL BASIS FOR HIGHER NIACIN IN SUGARY MAIZE\*

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Previous studies have shown that sugary (*su*<sub>1</sub>) maize endosperms or kernels contain about twice as much niacin as those of the normal starchy (*Su*<sub>1</sub>) allele.<sup>1-3</sup> The data in this paper show that the higher niacin has a morphological basis in that sugary kernels have more niacin-rich aleurone tissue than starchy. This finding makes suggested biochemical explanations<sup>4-5</sup> of the carbohydrate-niacin differences unnecessary.

*Methods.*—The niacin assays were carried out by use of *Lactobacillus arabinosus* according to the method of the Association of Vitamin Chemists.<sup>6</sup> Assay figures are given on the basis of samples dried at 50°. Carbohydrate was determined as glucose by the Somogyi-Benedict method<sup>7</sup> following acid hydrolysis of samples. Protein values were obtained by multiplying per cent nitrogen by 6.25, the nitrogen being determined by Nesslerization after sulfuric acid-peroxide digestion.

*Results and Discussion.*—Inasmuch as an ear segregating for sugary and normal shows higher niacin content in both whole and degermed sugary kernels than in the normals, the increase of niacin is not due to the embryos. Nor can it be a difference in the pericarps, since the pericarp is maternal tissue and therefore the same for all kernels of the segregating ear. Therefore differences in niacin distribution were looked for within the starchy and sugary endosperms. Heathcote, Hinton and Shaw<sup>8</sup> who have recently reported data on dissected kernels found approximately 60 per cent of the niacin in the one-cell thick aleurone layer of the endosperm. Unfortunately they did not examine comparable starchy and sugary lines.

In the separation of pericarp, aleurone, inner endosperm, and embryo there was the possibility of niacin diffusion from one tissue to another if water soaking of mature dried kernels was used to prepare seed for dissection. Consequently a different dissection technique was adopted. Two almost mature segregating ears were used which, although sufficiently mature to permit distinguishing the two kernel phenotypes, had not dried too much for peeling off the pericarp and clean removal of the embryo. Studies of niacin in developmental stages of starchy and sugary kernels by Teas, Cameron and Newton<sup>9</sup> indicate that niacin levels at the stage of development of these two selected ears, estimated at 38 days after pollination, would differ little from those at maturity. Both of the ears selected for dissection carried factors for purple aleurone color. Niacin determinations of the kernel fractions are shown in table 1. Pericarps of starchy and sugary are seen to be identical in niacin concentration and almost the same in micrograms of niacin contributed per kernel. Embryos of sugary kernels from both ears had somewhat higher niacin. Sugary inner endosperm from both ears showed almost twice the niacin concentration of starchy, although the contribution of this tissue to the content of the whole kernel is 20 per cent or less. Sixty to 70 per cent of the niacin of the kernel was found in the aleurone. Calculation from these data showed that 89 and 94 per cent of the "extra" niacin by which sugary endosperm exceeds starchy endosperm is localized in the aleurone. Moreover, in the aleurone the increased niacin is not a consequence of higher concentration, but rather of increased amount of aleurone in sugary, there being about twice (1.98 times) as much aleurone in sugary endosperm of ear number 1 and 1.7 times as much in ear number 2 as in the corresponding starchy endosperms.

In interpreting assays of aleurone which represent a separated single cell layer there arises immediately the question of whether sugary and starchy samples are both pure aleurone. The use of colored aleurone stocks should have assured completeness of aleurone removal. However, some contamination of aleurone with the underlying inner endosperm tissue is unavoidable. It seemed possible that because of different endosperm

TABLE 1

NIACIN IN DISSECTED FRACTIONS OF STARCHY AND SUGARY KERNELS FROM TWO SEGREGATING EARS

Each starchy or sugary sample represents a composite from 10 dissected kernels

| EAR NO. | KERNEL PART           | WEIGHT % DISTRIBUTION |           | NIACIN MICROGRAMS PER GRAM <sup>a</sup> |           | NIACIN MICROGRAMS PER KERNEL PART |           |
|---------|-----------------------|-----------------------|-----------|-----------------------------------------|-----------|-----------------------------------|-----------|
|         |                       | <i>Su</i>             | <i>su</i> | <i>Su</i>                               | <i>su</i> | <i>Su</i>                         | <i>su</i> |
| 1       | Pericarp              | 5.4                   | 8.0       | 7.8                                     | 7.8       | 0.103                             | 0.111     |
|         | Aleurone              | 2.2                   | 6.0       | 545                                     | 372       | 2.940                             | 3.982     |
|         | Inner endosperm       | 81.6                  | 68.8      | 3.2                                     | 6.3       | 0.647                             | 0.779     |
|         | Embryo                | 10.8                  | 17.2      | 18.8                                    | 23.7      | 0.498                             | 0.728     |
| 2       | Pericarp <sup>b</sup> | ..                    | ..        | ..                                      | ..        | ..                                | ..        |
|         | Aleurone              | 2.1                   | 5.4       | 289                                     | 220       | 1.590                             | 2.090     |
|         | Inner endosperm       | 86.9                  | 76.3      | 2.8                                     | 4.9       | 0.627                             | 0.658     |
|         | Embryo                | 11.0                  | 18.3      | 17.5*                                   | 18.4      | 0.505                             | 0.589     |

<sup>a</sup> Micrograms of niacin calculated for whole kernel samples of *Su* and *su* are 17.1 and 31.4 for ear number 1 and 10.4 and 19.3 for ear number 2.

<sup>b</sup> Not assayed. Pericarp omitted in calculations of ear number 2.

TABLE 2

CARBOHYDRATE AND PROTEIN CONTENT OF ALEURONE AND INNER ENDOSPERM OF STARCHY AND SUGARY KERNEL FRACTIONS

| EAR NO. | KERNEL PART     | OBSERVED % CARBOHYDRATE |           | CALCULATED <sup>a</sup> % CARBOHYDRATE, <i>Su</i> | OBSERVED % PROTEIN |           | CALCULATED <sup>a</sup> % PROTEIN, <i>Su</i> |
|---------|-----------------|-------------------------|-----------|---------------------------------------------------|--------------------|-----------|----------------------------------------------|
|         |                 | <i>Su</i>               | <i>su</i> |                                                   | <i>Su</i>          | <i>su</i> |                                              |
| 1       | Aleurone        | 19.7                    | 23.3      | 44.0                                              | 26.0               | 23.8      | 20.0                                         |
|         | Inner endosperm | 71.8                    | 68.8      |                                                   | 12.1               | 13.9      |                                              |
| 2       | Aleurone        | 22.8                    | 22.3      | 40.1                                              | 24.0               | 23.6      | 20.6                                         |
|         | Inner endosperm | 62.6                    | 63.7      |                                                   | 12.8               | 16.1      |                                              |

<sup>a</sup> Calculated concentration is that per cent expected if the extra amount of aleurone in sugary were a result of contamination of the sample with sugary inner endosperm.

texture the "extra" sugary aleurone might have arisen from contamination with a considerable amount of inner endosperm. If this were true it would be expected that an uncontaminated sample of sugary aleurone would weigh approximately the same per kernel and have about the same composition as a sample of starchy. One should be able to decide by chemical analysis if aleurone of sugary is contaminated with an almost equal weight of inner endosperm, since there is an appreciable difference in the

nitrogen content of aleurone and inner endosperm, and a considerable difference in carbohydrate content. As shown in table 2, the greater amount of aleurone in sugary cannot be explained by differential contamination because such contamination would require that carbohydrate of sugary aleurone be 44.0 and 40.1 per cent, and protein 20.0 and 20.6 per cent. Some differential contamination of sugary aleurone may have occurred in the case of ear number 1, but the amount is inadequate to account for the extra aleurone.

The aleurone layer is completely laid down about 21 days after pollination,<sup>10</sup> at which time starchy and sugary kernels are by visual observation and actual measurement very similar in volume. Since the size of the kernels is approximately the same until they dry with approaching maturity,

TABLE 3  
MEASUREMENTS OF ALEURONE CELL THICKNESS IN STARCHY AND SUGARY KERNEL SECTIONS

Thickness in microns of aleurone cells. Each figure given represents the average of ten consecutive cells on each of four sections.

| SOURCE OF KERNELS           | KERNEL PHENOTYPE | POSITION IN KERNEL |        |      |
|-----------------------------|------------------|--------------------|--------|------|
|                             |                  | CROWN              | MIDDLE | SIDE |
| Segregating ear             | <i>Su</i>        | 47.5               | 35.0   | 54.5 |
|                             | <i>su</i>        | 48.5               | 45.0   | 72.0 |
| Segregating ear             | <i>Su</i>        | 34.6               | 32.0   | 42.4 |
|                             | <i>su</i>        | 48.8               | 46.0   | 73.9 |
| New occurrence of <i>su</i> | <i>Su</i>        | 38.4               | 31.4   | 43.7 |
|                             | <i>su</i>        | 43.0               | 39.8   | 58.0 |
| TB-4a sugary ear            | <i>Su</i>        | 36.5               | 36.3   | 40.8 |
|                             | <i>su</i>        | 52.3               | 54.9   | 58.2 |
| Segregating ear             | <i>Su</i>        | 28.1               | 27.0   | 46.3 |
|                             | <i>su</i>        | 50.5               | 51.6   | 68.7 |
| Mean                        | <i>Su</i>        | 46.2               | 32.4   | 45.6 |
|                             | <i>su</i>        | 60.7               | 47.4   | 67.0 |
| Ratio of means              | <i>su/Su</i>     | 1.31               | 1.45   | 1.47 |

differences in the amount of aleurone per kernel should reflect differences in aleurone thickness. This was tested directly by measuring the thickness of aleurone cells. Starchy and sugary kernels from five segregating ears were fixed, dehydrated, embedded and sectioned according to the procedure developed by Larkin, *et al.*,<sup>11</sup> for maize seed. Kernels were cut before fixation in order to speed up penetration of reagents. Each kernel was divided into halves by a median cut, then divided further by a transverse cut. The two pieces representing the crown of each of three or four kernels were mounted on cardboard by the method of Randolph<sup>12</sup> to assure proper orientation. Sections were cut at 15-25 microns through the central region of the kernels in a plane at right angles to the original median and transverse cuts. Each section therefore represented aleurone cells from

the center of the crown to about half way to the apex of the kernel. Slides were coded and cell measurements taken with an ocular micrometer at a magnification of 440. The thickness of 10 consecutive aleurone cells at the top (center of crown), middle, and side (toward the embryo) portions of each section was recorded. Two sections were examined from each of two slides from each sample of starchy and sugary kernels. Figure 1 is a camera lucida drawing of typical aleurone cells of the two types. The averages for the three classes are shown in table 3. In all cases the sugary aleurone cells averaged thicker than starchy ones. This difference in aleurone thickness was clearly demonstrated by a starchy-sugary conate (twin) kernel sectioned in a longitudinal plane that included the two embryos. In this case the adjacent starchy and sugary aleurone tissue was strikingly different in thickness as seen side by side in the same microscope field. The discrepancy between the measured thickness of sugary aleurone, approximately 1.4 times (table 3), and the amount by weight, about 1.8 times, may be due to differences in thickness of aleurone in the basal half of the kernel which was not included in the sections measured.

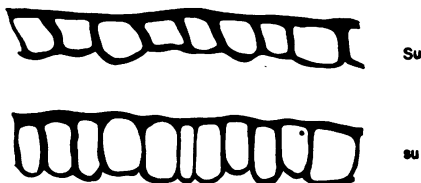


FIGURE 1

Camera lucida drawings of typical starchy and sugary aleurone cells.

It is anticipated that other "pleiotropic effects" of the sugary-starchy alleles may owe their origin to differences in aleurone thickness, and also that selection of high niacin maize may involve, at least in part, a selection for thicker aleurone.

*Summary.*—Approximately 90 per cent of the higher niacin of sugary maize has been found to have a morphological basis in that sugary kernels have a thicker niacin-rich aleurone layer than starchy kernels.

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## THE FOURIER HEAT EQUATION IN RIEMANNIAN SPACE\*

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1. Let a certain body, capable of absorbing heat, occupy a region of  $n$  dimensional Riemannian space  $V_n$  whose metric is defined by the positive quadratic differential form  $ds^2 = g_{ij} dx^i dx^j$ . Suppose that this body is heated by conduction in any manner. The situation can be visualized as a flow of heat from the warmer to the cooler parts of the body.

The rate of flow of heat within the body can be depicted as a vector field  $X^i(x; t)$  or  $X_i(x; t)$ , where  $X^i = g^{ij}X_j$  and  $X_i = g_{ij}X^j$ . At the position  $x$  within the body for the particular instant of time  $t$ , the vector  $X$  is in the direction of the flow of heat and its magnitude is the rate of flow of heat. It is assumed that this vector field  $X^i(x; t)$  or  $X_i(x; t)$  is single valued and continuous with continuous partial derivatives of first order over the given region and in a given interval of time.

The lines of flow of heat are the integral solutions of the system of  $n$  ordinary differential equations of the first order

$$\frac{dx^i}{dt} = X^i(x; t). \quad (1)$$

In general, there are  $\infty^n$  lines of flow of heat.

2. There are two fundamental assumptions which characterize a given flow of heat.<sup>1</sup> These may be described in the following manner.

*Assumption I.*—The velocity of the flow of heat at any position  $x$  in the body for any given instant of time  $t$ , is proportional to the rate of decrease of the temperature  $U$  at the position  $x$  for the given instant of time  $t$ . That is

$$X_i = -k \frac{\partial U}{\partial x^i}. \quad (2)$$

The factor of proportionality  $k$  is the conductivity of the body. In certain bodies such as crystals, this  $k$  depends not only on the position of the point  $x$  and the time  $t$ , but also on the direction through the point  $x$ . We