Mr. Bell, referring to the masking of symptoms of leaf-scald, mentioned that with S.J. 7, a highly susceptible variety, one cutting was selected from each of six apparently healthy plants, and only one healthy stool resulted. In the case of one of the other stools germination did not take place for four months, and symptoms did not show for ten months. This stool was under daily observation.

Mr. W. Cottrell-Dormer presented his paper, "The Variability of Plant Pathogens."

The Variability of Plant Pathogens.*

by

W. COTTRELL-DORMER,
Research Officer, Fairymead Sugar Company, Bundaberg, Queensland.

It has been said that the most invariable thing in nature is variation, and belief in the immutability of species is no longer taken seriously. Nevertheless the importance of the variability of plant pathogens in crop improvement and protection does not perhaps always receive the recognition which is its due. Other papers in these Proceedings already draw attention to this matter; it is the purpose of this paper further to emphasise the practical significance of this aspect of plant pathology and to encourage a full discussion at this Conference. While no attempt has been made to give anything approximating a full review of the literature, the examples taken from sugar-cane pathology have been amplified by some taken from other sources. For the sake of clarity these examples have been grouped as occurring in fungi, bacteria, and viruses, and some suggestive cases of variation in varietal resistance have also been included.

Variability in Fungi.

Perhaps the best known example of variability in fungi is to be found in *Puccinia graminis* Pers. The forms of this rust fungus are of two types: 1. the so-called biologic forms or varieties of *P. graminis tritici*, *P. graminis secalis*, *P. graminis avenae*, etc., which differ from each other principally in their ability to attack different genera of the Gramineae, and 2. physiologic forms or strains which differ from each other chiefly in their ability to attack different varieties of wheat, rye, or oats, etc., as the case may be. Some idea of the extent to which this physiologic variation may be carried within one species of fungus is gained by the fact that in the single biologic form *P. graminis tritici* 128 physiologic forms were known in 1933 [21] and the list has been

* The writer wishes to express his sincere thanks to Mr. S. F. Ashby of Kew, England, Mr. A. F. Bell and Dr. J. V. Duhig of Brisbane, Mr. J. P. Martin of Hawaii, Professor E. C. Stakman of Minnesota, and Mr. Eaton M. Summers of Louisiana for having very kindly supplied suggestions or notes or literature or all three; and also to Dr. H. W. Kerr, Director of the Bureau of Sugar Experiment Stations for permitting the use of notes made by the writer while on the staff of the Bureau.
slowly augmented since. Most forms appear to have arisen by hybridization but Stakman, Levine, Cotter, and Hines [23] report having observed two definite cases of mutation in parasitism.

The existence of physiologic forms has also been demonstrated in most of the cereal smuts. Owing to the fact that smuts have a saprogenic phase during which some of them can be grown on artificial media it has been possible to obtain more information concerning their variability than has been the case with the rusts. A very comprehensive study of mutation and hybridization in Ustilago zeae was carried out by Stakman, Christensen, Eide, and Bjorn Peturson [22]. In cultures from single sporidia large numbers of sectors and some patches were obtained which differed sometimes very widely from the parent in appearance. These sectors and patches were sub-cultured and frequently the phenomenon repeated itself. In this manner 162 different strains were obtained from one monosporidial line and 70 from another. The strains varied from the parents in appearance, in physiological characters (ability to liquefy gelatine, reduction of nitrates, etc.), and in pathogenicity in either direction. The rate of appearance of strains in any given line appeared to be considerably affected by nutrients and by temperature. The smuts and other higher fungi show many of the cytological characters of the higher plants and animals in that their cells contain definite nuclei which show reasonably well defined mitotic and meiotic phenomena. The cultures in which the sectors appeared were the result of propagation of single haploid sporidia. For these and other reasons the authors considered that they were dealing with “true mutation.” Further work by Christensen [22, Pt. II.] involving hybridization supported this view.

The fungus Fusarium moniliforme Sheldon, the causal agent of pokkah boeng, is another good example of variability. Leonian [13] in a study of the species, obtained from corn, found it to exhibit almost every conceivable form of variation—variation in morphology, physiology, and pathogenicity. Sectoring was a more or less constant factor in nearly all of the single spore colonies studied and there was only a slight tendency towards fixation when frequent selection was practised. In this case the author preferred to call the various strains “dissociants” rather than mutants. He considered them to be merely different manifestations of the species which are observable when the environment happens to be favourable to their appearance. He suggests that the concept of species is usually far too rigid and that if any given species could be studied under suitable conditions it would be found to dissociate in some manner.

Rands and Dopp [17] have shown Pythium arrhenomanes Dreschler, the well known cane root parasite, to be very variable in morphological, cultural, and pathogenic characters. It would appear also that the species contains a number of physiologic forms. The authors suggest that this variability of the species may be due to hybridization between different forms.
The existence of physiologic forms of the red rot fungus *Colletotrichum falcatum* Went. has been demonstrated by Abbott [1] who has dealt further with the subject in a paper in these Proceedings.

The following relevant remarks concerning *Helminthosporium sacchari* Butler have been submitted to the writer by Mr. J. P. Martin in a personal communication: “A number of years ago a very virulent strain of the eye spot fungus was isolated at this Station and with inoculation studies exceptionally large lesions resulted on the cane leaves; this form of the disease has at times been referred to as giant eye spot disease. In more recent years we have obtained in our eye spot isolation studies cultures which did not appear to be uniform in colour and development with our standard culture.”

**Variability in Bacteria.**

The marked morphological variation which occurs in bacterial cultures of different ages and on different media is familiar to all pathologists and has been made the subject of a monograph by Henrič [11]. He attributes this phenomenon to the perfectly normal differentiation of the cells, the degree of differentiation being governed by environment just as it is in multicellular organisms. However the significance of morphological variation and its relation to pathogenicity are not known and perhaps never will be known owing to technical difficulties.

Variations in the cultural and physiological characteristics of bacteria have for many years been known to exist though it is only in comparatively recent times that they have received much attention, and that more particularly in the case of bacteria pathogenic to man of which an excellent summary has been given by Arkwright [2]. A well known example is found in *Bact. typhosus* in almost any casual isolation of which may be found a rough ‘R’ variant which will remain fixed for many generations; this ‘R’ form is very much less virulent than the normal smooth ‘S’ form. Similar strains are found in plant bacteria. *Aplanobacter michiganense*, the causal agent of bacterial canker of tomato, usually produces abundant, fluid, spreading growth; on whey agar Bryan [5] has observed another type of colony which is small, round, and highly convex; the latter form is very weakly parasitic as compared with the normal type. By growing *Bacterium tumefaciens* (hop strain) and *Bacillus phytophthora* by a special technique in broth at pH 6 and pH 7 Quirk [16] claims to be able to produce smooth or rough colonies at will; the smooth colonies are virulent and the rough non-virulent.

The “sectorial differentiation” of bacterial colonies is the subject of an instructive and well illustrated paper by Nirula [15]. This writer working with cultures of saprophytic bacteria obtained from swede-turnips observed the more or less frequent appearance of sectors in colonies. Single-cell cultures were prepared from these sectors and in most cases the “new races” remained constant on different media, at different temperatures, and at different pH. The term “saltant,” which was suggested by Brown for dissociants in *Fusaria,*
Fig. 1.—Colonies of *B. albilineans*, showing sectors (x 2½).

Fig. 2.—Two types of sector of *B. albilineans*: A—smooth, B—rough. Upper photographs by reflected, lower by transmitted light.

Face Page 714.
is applied to these newly observed strains. In all cases they arose suddenly and apparently independently of cultural conditions. It is suggested that new species may arise in this way and that cases of reversion reported by other writers may have been due to admixtures of strains.

Passing now to sugar-cane bacteria we find ample evidence of variation in the different species in which we are interested. First of all the writer will deal with some hitherto unpublished observations made while on the staff of the Sugar Experiment Stations. During the time spent in the Brisbane laboratory many hundreds of cultures passed through the writer's hands. Sectoring was observed in colonies of the leaf-scald, gumming, and mottled stripe organisms and daughter colonies frequently appeared on old slopes of the red stripe bacterium. Owing to the importance of leaf-scald in Queensland and the many peculiarities presented by the disease some little attention was paid to the phenomenon of sectoring in \textit{B. albilineans}. Pressure of other work prevented the study from being carried very far. The following observations are however of interest:

\textbf{Sectoring in Cultures of \textit{B. albilineans}.}

Sectors were first observed in "giant" and large colonies, on Wilbrink's medium containing 1 per cent. glucose and 1 per cent. sucrose, of a stock isolate from E.K. 28; their general appearance is indicated in Fig. 1. Two main types were observed: A, smooth, almost hyaline, and usually rapidly growing; inner angle of sector usually distinctly rounded, highly refractile, and with clear cut demarcation between it and parent growth. B, rough, fine to coarsely granular; growth rate varying but sometimes very slow and leading to the formation of distinct bights in margin of parent colony; inner angle of sector sharply and finely tapering into parent growth where it eventually becomes lost. Both types are seen in Fig. 2. In no case did sectoring occur until during the third week after inoculating the medium. The inclusion of glucose in the medium favoured sectoring and sectors grew to a larger size than when sucrose was the only carbohydrate provided. By means of very fine glass threads minute portions of growth were taken from sectors and used for preparing dilution plates by Paine's mapping pen method. Highly varying types of colonies were obtained which were transferred to slopes. Attempts to make single-cell cultures by means of a micro-manipulator and specially designed moisture chambers were unsuccessful as in no instance could growth be initiated in spite of variations in media and in other respects. Experiments with inoculations of cuttings of E.K. 28 with various strains and with parent culture in an effort to determine their relative virulence all failed; it might be added that this is not an uncommon experience in leaf-scald studies. Very rough forms were found to be somewhat smaller and more curved than the smooth forms which quite resembled the parent. That these forms which differ in cultural appearance also differ physiologically is indicated by their reaction to certain toxic ions as an example of which the following two experiments have been abstracted from notes:
Exp. I.: Exposure of strains to lithium nitrate solutions.
Inoculum: 0.2 ml. of 3-day old liquid culture per 10 ml. of solution.
Cultures: one 4 mm. loop of inoculated solution plated out in 5 ml. of agar at end of exposure.

Exp. II.: Inclusion of lithium nitrate in medium.
Inoculum: 0.3 ml. of 2-day old liquid culture suspended in 5 ml. of sterile water.
Cultures: one 4 mm. loop of suspension plated out in 5 ml. of agar to which the correct amount of lithium nitrate had previously been added.

Strains used: 702 smooth rapid growing.
708 very rough moderate growing.

Results: these are shown in Table I.

<table>
<thead>
<tr>
<th>Experiment I</th>
<th>Experiment II</th>
</tr>
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<tbody>
<tr>
<td>% LiNO₃</td>
<td>702</td>
</tr>
<tr>
<td>12</td>
<td>+</td>
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<tr>
<td>16</td>
<td>+</td>
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<tr>
<td>18</td>
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<td>20</td>
<td>+</td>
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<td>22</td>
<td>+</td>
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<td>24 hour exposure</td>
<td>-</td>
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<td>4</td>
<td>+</td>
</tr>
<tr>
<td>Water</td>
<td>+</td>
</tr>
</tbody>
</table>

All attempts to maintain rough forms in a pure condition failed. In every case sectors and patches sooner or later appeared and overran the cultures. Experiments and observations were made before this apparent reversion was perceptible. Whether reversion actually did occur or whether the reappearance of the smooth form was due to mixed inoculum could not be ascertained without reliable single-cell cultures.

Further evidence of variation in sugar-cane bacteria is found in the literature. Ashby [3] observed cultural and physiological differences between cultures of B. vascularum from St. Kitts and from Australia and obtained indications that the Australian form is rather more virulent than that from St. Kitts. In a personal communication dated 5th April, 1935, this writer makes the following statement: 'Although I recorded the isolation sent by Mr. North as a variety distinct from my isolation from St. Kitts, it deserved perhaps to be considered as a separate species and it may be that you have in New South Wales and Queensland two diseases characterised by a production of bacterial gum in
the xylem vessels of the stalks. This would seem to be indicated by the differences in cultural characters between North's organism and that isolated and described by Erwin F. Smith from 'gummed' Australian cane, both being pathogenic. No evidence has come to the notice of the present writer of the existence of two different gumming diseases in Australia but that different strains or varieties of the one organism do exist seems beyond doubt. Differences are found in the cultural characters of various isolates, in the color of the gum which oozes from the stems, and perhaps in varietal pathogenicity. The color of oozing gum varies considerably in Porto Rico also. Cook [8, p. 160] states that this variation ranges "from perfectly clear to milky white, to many shades of yellow, and occasionally orange, red and brown." Such color changes might of course be due to variations in the host.

The red stripe organism would not seem to be quite the same in different countries. Thus, whereas gelatine is definitely liquified by Phytoponas rubrilinea in Java [4] and in Hawaii [12], no evidence of liquefaction has been obtained in Queensland [9]; the reaction of 1 per cent. glucose beef-extract agar is reported as being "partly acid" in Hawaii, whereas in Queensland and in Java an alkaline reaction is recorded. Similar observations may be made concerning P. rubrisubalbicans which causes mottled stripe. In Louisiana [7] the organism is reported as producing indol and as forming no acid from glucose or mannite; diametrically opposite results were obtained by the writer in Queensland.

Many theories have been put forward to explain the manifold types of variation found in bacteria. Arkwright [2, p. 369], after discussing the matter at some length, concludes as follows: "The view that bacteria, since they are unicellular and without any definite nucleus, are simple forms which can comparatively easily be modified by the environment and can pass on such changes to their offspring appears to be the most acceptable view."

In dealing with fungi considerable emphasis was placed upon the existence of physiologic forms. There is evidence which suggests that this state of affairs also exists among bacteria. Stakman [20, p. 1316] expresses this opinion in the following words: "Many so-called species of bacteria are in reality nothing but physiologic forms. This seems to be true of the group of organisms causing soft rot of vegetables and consisting of such species as Bacillus carotovorus, B. atrosepticus, etc. Unpublished studies made by Leach at Minnesota strongly indicate the correctness of this assumption." Domeaster [10] points out that the recorded ratio of occurrence in cases of meningitis of the four agglutination types of Meningococcus corresponds very closely with the ratio of occurrence of the four iso-agglutinin groups of blood in a normal human population; which would also seem to be evidence of the existence of physiologic forms in bacterial species.
Variability in Viruses.

Evidence of the existence of variants in viruses is not lacking. Smith [19, p. 287] in a discussion of this aspect of virus diseases writes as follows: "Perhaps the best illustration of the existence of two apparently independent strains of a plant virus is afforded in the case of aster yellows and celery yellows. Severin, working with the virus of aster yellows in California, found it easy to transmit the disease by means of its vector, the leaf hopper Cicadula sexnotata, to celery, while Kunkel, working in New York with a local strain of aster yellows, found that celery was apparently immune or at least highly resistant to the virus. Kunkel obtained from Severin a sample of Californian aster yellows and found that it was transmissible to celery under New York conditions, while the local strain under similar conditions was not transmissible to celery. In every other respect of symptoms, incubation period in the plant and identity of insect vector the two viruses are identical. Here then is apparently a case of a virus having 'mutated' or adapted itself to a new host plant in one district and after sojourn in this host has acquired the ability to infect it as easily as any other plant in its host range. Such a virus may be regarded merely as a slightly different strain of aster yellows, or it may be regarded as a different entity and be referred to as 'celery yellows.' It is also possible that celery yellows is a stage in the evolution of an entirely new virus. In the writer's opinion slight differences in host range do not justify the separation into distinct viruses of entities which are otherwise identical."

Summers [24] last year drew attention to the occurrence in Louisiana of three or four types of sugar-cane mosaic which differed markedly from each other in symptoms. A further paper on this subject by the same worker appears in the present Proceedings. Four types of mosaic are clearly described and defined. Not only do they produce recognizable differences in symptoms, but preliminary trials suggest that one strain is perhaps unable to infect two varieties of cane which are susceptible to the other three strains. Here again we meet with the concept of physiologic forms! The possible origin of these strains is discussed and the explanations which are considered to be most probable are that either the strains are the result of fractionation through vectors and hosts of a complex virus or else that they are variants or mutants of what had previously been a single entity.

Variability in Varietal Resistance.

Red Rot: Other things being equal varietal resistance to this disease will depend upon the physiologic form of the pathogen which happens to be present. Thus the relatively resistant variety Co 281 is quite susceptible to at least one form [1, p. 559].

Pythium Root Rot: Here also varietal resistance depends partly upon the physiologic form of the fungus [17].

Leaf-scald: According to Shepherd [18, p. 4] Malabar (White Tanna) is more susceptible and less tolerant to leaf-scald in Mauritius than in Australia. Martin, Carpenter, and Weller [14, pp. 190-191] give lists obtained from
different countries of varieties arranged in order of resistance or susceptibility to this disease. According to this list Wilbrink classes varieties in Java as "very sensitive," "sensitive," and slightly "sensitive" while Bell classifies Queensland varieties into six classes ranging from "highly resistant" down to "very susceptible"; it is of interest to note that the variety E.K. 28 is placed by Wilbrink in her middle class whereas it stands alone in Bell’s "very susceptible" class. In Australia Badila has been found to suffer more from leaf-scall in North Queensland than in New South Wales.

**Red Stripe:** Bolle [4, p. 1217] considers that P.O.J. 2878 is not sufficiently susceptible to this disease to warrant the adoption of control measures. Shepherd [18, p. 7], reporting on a visit to Java, goes further and states that "In Java red stripe is of very minor importance at present owing to the high resistance shown by P.O.J. 2878." In Queensland the same variety is classed as "very susceptible" and death of harvestable stalks to the extent of considerably over 40 per cent. as a result of this disease is not uncommon in the tropical belt. Badila is reported as being resistant to red stripe in Hawaii [12], in Queensland it is quite susceptible.

**Mottled Stripe:** Christopher and Edgerton [7] class Badila as being resistant to mottled stripe in Louisiana; in Queensland it is one of the most commonly affected varieties.

**Mosaic:** As has already been pointed out, work in Louisiana suggests that certain canes may vary in susceptibility to different "strains" of mosaic. Martin, in a personal note, points out that whereas P.O.J. 36 in Hawaii is highly resistant, it has proved quite susceptible in Louisiana.

**Discussion.**

Sufficient examples have been given to convince the most sceptical that no plant pathogen can be considered a single clearly defined entity whether it be fungus, bacterium, or virus. In every case variability has been found to exist within a species if searched for carefully enough. At one end of the scale variations consist of recognized physiologic forms whose reactions to given varieties or host are known and can be predicted. At the other end we find simple cultural changes, as for example with *B. albilineans*, whose true significance we do not understand. Between these two limits occur variations of all types and intensities. The occurrence of variants has been shown to be influenced very largely, in some cases, by environment. Their origin has been attributed to hybridization, mutation, dissociation, saltation, etc., according to the nature of the organism, and perhaps sometimes of the authors. But their principal significance to us is that they do exist. If the leaf-scall organism is capable of producing strains which differ from the normal in appearance, it is equally possible, or better probable, that it can produce strains which will differ in pathogenicity. If a certain kind of medium will encourage the appearance of new forms with varying virulence it is not feasible that some
varieties may have a similar influence and that a variety which now is resistant to, say gumming, might no longer be so in ten or twenty years' time or even sooner? The history of plant pathology is filled with instances of the kind which are sometimes difficult to explain.

It may be argued that many of the variations observed which cannot be attributed to hybridization are really but part of the make-up of the species; that what we consider to be a new form has been latent and has only appeared because its environment has been favourable. But such an explanation is far from reassuring; rather the reverse since, if correct, each disease agent may have in ambush hordes of virulent forms awaiting a favourable opportunity to pounce upon our most dependable resistant varieties. It is simpler not to worry too much about causes and explanations but to accept it as a fact that each species does contain a number of more or less well differentiated strains and that new genotypic forms do arise from time to time in pathogens of all types. Such an article of faith should be included in every sugar pathologist's creed. After all, our quarrel is not with the taxonomist nor with the geneticist but with the pathogens themselves, and such a belief has the merit of prudence and has also a very good chance of being correct.

Some examples have been given which suggest that varietal resistance sometimes varies from country to country. These differences may of course be due entirely to differences in vectors, changes in the varieties themselves, differences in soil and climatic conditions, etc., but we cannot afford to overlook the possibility of their being due to differences in the pathogens, especially since these are already known to exhibit certain other differences. Perhaps there exist physiologic forms or geographic races of our disease bacteria just as forms of Puccinia graminis tritici occurring in Sweden and in South Africa are able to attack some of the most rust-resistant wheats of the United States. The red rot and root rot fungi have been shown to contain physiologic forms, and it seems that something of the kind may exist in mosaic.

In conclusion the practical importance to the sugar pathologist of a true appreciation of the factor of variability in plant pathogens will be pointed out. This will perhaps seem unnecessary but may be useful in encouraging a full discussion at the Conference:

(1) It is evident that no laxity can be allowed in quarantine regulations, even in a country such as Australia which is a trysting place for most of the cane diseases known to science, since it is not only imperative that new diseases be kept out but the entry of fresh strains of diseases already present must also be prevented.

(2) The factor of variability must be taken into consideration in disease resistance trials. The inoculum used for such trials should be obtained from a number of districts and varieties and should, if possible, contain infective material obtained
directly from diseased canes since growth on culture media may eliminate some virulent strains; it is, for instance, a well known fact that the leaf-sclad bacterium tends to lose its virulence in culture though the reason for this is not known. Where resistance trials are not isolated they should be carried out in several districts in order that geographic forms, if they exist, may be located. Furthermore it should be made a practice always to include varieties of different parentage which are known to be resistant in order that the pathogen may be given every opportunity to segregate, or mutate, or saltate, in the direction of increased virulence since it is better for this to happen if possible under observation than in the fields. These principles are already largely followed in our Sugar Experiment Station trials.

(3) At least in the case of fungus diseases the advisability of rotation of varieties, as recommended to the Louisiana growers by Brandes, Rands, Abbott, and Summers [6], in order to discourage the accumulation of any physiologic form, should receive serious consideration.

REFERENCES.


Discussion.

Mr. Bell referred to the fact that Hansen and Smith, in California, had shown that variant morphological strains of single cell cultures of Botrytis can arise by anastomoses of adjacent hyphae and redistribution of nuclei. He stressed the importance of the possibility of resistant varieties being attacked by a new strain.

Dr. Matz asked what was the degree of resistance to mosaic shown by P.O.J. 36 in Hawaii.

Mr. Bell thought it had never been seen in that variety.

Dr. Matz said that in Louisiana, this variety was one of the easiest to inoculate artificially.

Mr. Bell stated that in Queensland there were two strains of alleged P.O.J. 36; one of which was very susceptible, while the other was not.

Dr. Brandes remarked that observations made in different years may lead to different conclusions. In Louisiana, P.O.J. 213 was once very highly susceptible. Subsequently, whole fields recovered, and the variety had been free from mosaic for several years.

Mr. Bell asked him if he thought the predominating strain of mosaic had undergone some change in the interim.

Dr. Brandes said there was no reason for any change.
Dr. Matz suggested that it may be a quantitative rather than a qualitative change in the virus. A virus taken from cane which had apparently recovered was just as virulent as that taken from an obviously diseased cane, which pointed to a change in the resistance of the host rather than a change in the virulence of the virus, causing the plants to recover.

Mr. Bell, referring to red stripe disease mentioned by Mr. Dormer, said that in Queensland, in the variety P.O.J. 2878 there may be 40 per cent. death from top rot, and this would be exceeded if cane were planted as closely as it is in Java.

Dr. Bolle stated that in Java this variety was not susceptible, but top rot had been severe in P.O.J. 2722. Top rot was rare in Java now; however, P.O.J. 2878 was susceptible to pokkah boeng. She thought that differences in susceptibility were due to various strains, but this could not be tested owing to the danger of importing new strains. They could, perhaps, be compared in some isolated place.

Mr. Dormer said that changes may occur in culture.

Mr. North stated that differences in environment may cause varieties to give different reactions.

Mr. Bell said that with P.O.J. 2714 and gumming disease, the results of one Queensland trial differed from those in New South Wales, but when another trial was laid out in a different locality in Queensland the results were similar to those obtained by Mr. North. There was as yet no evidence of strains of gumming disease.

Dr. Brandes read the paper, "Strains of the Sugar-cane Mosaic Virus in Louisiana," by Eaton M. Summers.

Paper.

Strains of the Sugar-Cane Mosaic Virus in Louisiana.

by

EATON M. SUMMERS.*

Division of Sugar Plant Investigations, Bureau of Plant Industry, United States Department of Agriculture.

The mosaic of sugar cane and related grasses to which it is readily communicated has in general been attributed to a single virus, although Brandes and Klaphaak [2] suggested the possible existence of more than one type of the disease among the numerous wild representatives of the family. On sugar cane alone many variations in symptoms among the diverse assortment of varieties are described in the literature, but these have always been explained

* The writer is indebted to Dr. R. D. Rands for suggestions in the course of the work and assistance in preparation of the manuscript.