DISCUSSION 1

Prof. Harland :

The meeting is now open for discussion on these three papers. Now if anybody wishes to take part will they give their names so that we can have this recorded.

Dr. Magoon :

Dr. Martin has indicated both the polyploid nature as well as the existence of homology amongst the genomes in sweet potato based only on the evidence of the occurrence of secondary pairing of chromosomes at meiosis. Likewise, secondary association of chromosomes at meiotic metaphase has also been used as a tool by some workers for postulating the genomic constitution and the relationship amongst these genomes in sweet potato, in spite of the fact that the exact significance of this phenomenon has been a matter of considerable controversy. As you know, secondary association is the term applied by Darlington (1937) to the close justaposition of bivalents, or higher association in metaphase I, or of split chromosomes in metaphase II; the occurrence of secondary association has been believed to be the result of a residual affinity between chromosomes which are phylogenetically or ancestrally related. Such secondary pairing is not accompanied by the formation of chiasmata. This phenomenon, first observed by Kuwada (1910) in **Oryza sativa**, has been extensively discussed by Lawrence (1931). According to the last author, secondary association may occur from pro-metaphase to second anaphase, but cannot be detected at the diakinetic stage because of inter-bivalent repulsion, unlike the associations resulting from primary pairing which are held together even at diakinesis. This phenomenon is more easily recognizable in organisms with short chromosomes than in those with long chromosomes.

He pointed out that the quality of fixation is of great importance in connection with studies on secondary association and suggested that three criteria, viz. (1) the association must be shown to be constant in the best fixation, (2) the average number of chromosomes per association and the frequency for each kind of association should be characteristic for a given species but may vary from species to species and (3) at first metaphase associated bivalents should be shown to be of similar size and configuration, should be satisfied before such secondary grouping in any one case is accepted as a real phenomenon and not an artefact. Several workers, subsequently accepted the views of Lawrence (1931) regarding the nature of secondary pairing and utilized the data of secondary groupings as an evidence in deciding the level of ploidy of any taxon or group of taxa. As I have already indicated, differences of opinion, however, exist regarding the real significance of secondary pairing of chromosomes. Factors, other than ancestral homology, have been implicated as being responsible for this phenomenon by a number of workers based on their work in different crop plants. Their observations on secondary associations have shown marked heterogeneity, even where the same species were analyzed. The lack of suitable techniques and the small size of the chromosomes, as well as, the lack of suitable morphological markers on the chromosomes, prevented very accurate analysis of bodies which take part in such associations. Further, it is liable to be greatly modified by segmental interchange, duplication of chromosome segments and other phenomena, not at all related to polyploidy. It is, therefore, not an entirely reliable index of the exact basic haploid number possessed by the original ancestors of a group. It would, therefore, appear, in my opinion that a very cautious approach is necessary in using this evidence alone to derive genomic constitution and their relationships, polyploid origin and basic chromosome number of the genus.

Dr. Martin :

I agree with your comments on the cautious use of secondary association. It is indeed a very weak form of evidence. However, in the sweet potato at the present time we do not have any good evidence of the kind of crosses to allow us to test genomic relationships. Dr. Alfred Jones of Tifton, Georgia, has been working on this and is trying to develop plants that will cross with the sweet potato by hybridizing and developing new ploypoids, but so far he has not had any luck in developing such types of analysis. It is something that we need but, something which, because of the strong barriers between species, we have not succeeded in doing so. With

respect to my own comments, I was trying to develop this as a theory and I would not put too much emphasis myself on secondary pairing.

Dr. Yen :

I would just like to comment on the cytological aspect that has been arraigned mainly because in the work we did with the Pacific sweet potato collection, we also had to do cytological work. The first specimen we worked on was a New Guinea one, and thought then we could use this as a quantitative character, similar to a morphological character to try to characterise our collection from all over the Pacific. However, it was not very long before we struck from Thailand, Fiji, and Peru what could not be secondary association but since they were so close, other workers in other parts would call these things multivalents. Now we thought that perhaps we were taking too much of a flight of fancy about this so we subjected our material to Dr. John Hare, a cytologist. His answer was immediately that we had multivalency. The second thing was to try to get some of the correlations that Dr. Martin and others had tried to get from this kind of chromosome behaviour. I can only report here that we had all sorts of abnormalities occurring in our cytological material, such as counting of nuclei and so forth, but we could not correlate it with sterility at all, as Dr. Martin has pointed out to us.

Mr. Williams :

I would like to say that, with relevance to the comments by Dr. Yen and Dr. Martin, the theory for the origination of sweet potato, which we have proposed in our paper, permits the possibility that the sweet potato could be an auto-hexaploid. If the progenitor species were self-incompatible and self-pollination with an unreduced male gamete occurred, then, because of the possible opportunity for the action of competitive interaction between heterogenic alleles in one pollen grain, it is conceivable that a triploid offspring could be formed. This, followed by doubling, could result in the generation of an auto-hexaploid.

Dr. Magoon :

What evidence do you have in proposing a theory that sweet potato could be an auto-hexaploid ?

Mr. Williams :

I did not say that I was proposing a theory that the sweet potato was not a hexaploid. I said that the theory of a possible method of origin of this species permits this possibility — the theory of the supply of unreduced gametes. But even if it did in fact originate in such a manner, there could have been, in the revolutionary history of this plant, a lot of opportunity for segmental differentiation of some of the genomes and selection for meiotic stability so that you could get a high frequency of bivalent pairing in the present-day species.

Dr. Cope :

I would like to ask Dr. Martin whether he has found evidence of homozygosity for incompatibility alleles in Ipomoea species. He mentions the segregation of parental types in that one plant as evidence for sporophytic control. Has he also found homozygosity ?

Dr. Martin :

Well I did not mention sporophytic control of self-incompatibility and, in fact, I am a little reluctant to say very much about the incompatibility system until we complete our own analysis of it, although I do have my own opinions on it. But now, as far as the possibility of homozygous alleles in the sweet potato, I think the possibility is very high because we run into these exceptional cases of crossing in which there is a unilateral incompatibility between two different plants. In other words, the cross can take place in one direction but not in the other, and in such a case we might expect that one of the alleles was in a homozygous state. This unilateral incompatibility does not seem to be the regular case. It has only been recorded on very much of a scale by one investigator, although other investigators have found

unusual plants that did not fit into their schemes. Finally, I would like to say that with the Ipomoea species that I have been working with, where the incompatibility is not confused with sterility, all of the crosses are mutually compatible or mutually incompatible. There is none of this unilateral incompatibility, which makes it look as if there is a sort of a breakdown in the sweet potato, a partial incompatibility permitting the fixation of S-genes once in a while.

Mr. Gooding :

I would like to ask Dr. Hernandez one or two questions. As one who is interested in food processing as well as in agriculture, I am rather interested in those correlations between baking quality and various other characteristics, some of which seem extraordinarily unlikely, e.g. baking quality and colour. It seems strange, that there should be such a high positive correlation. And baking quality and moistness, I am not quite sure what you meant by moistness — whether it is directly related to water content or to solid content or what. Could you expand a little bit on these please ?

Dr. Hernandez :

I shall be glad. Let me say, in baking quality, we do not consider the baking index to be composed of a mean of all the characters indicated viz. sweetness, moistness and so forth. Now, I am referring to a moist fleshed sweet potato as opposed to a dry fleshed type. Now there appears to be somewhat of a linkage between many of these characters and colour which I am talking about, so that a high quality sweet potato to us, is a sweet potato that will bake sweet, soft, moist and of course, has a high carotenoid pigment content. And it seems that we have had difficulty in obtaining a high dry matter with a high carotenoid pigment content in seedlings. In our selection programme throughout the years we aimed at reaching a point of homozygosity with most of these characters. So far, we have recovered many seedlings which combine most of these desirable horticultural characters.

Mr. Gooding :

Thank you, I was making a mistake in assuming that baking quality has been a rather isolated factor particularly related to the texture of the finished product, rather than taking the other things into consideration as well.

Prof. Skelding :

I would like to ask Dr. Martin whether in his list of causes of incompatibility he has any evidence of incompatibility between endosperm and embryo coming into the picture at all.

Dr. Martin :

Really, I do not think that I have analysed that factor sufficiently to eliminate the possibility that there is some endosperm-embryo incompatibility in the non-viable seeds of the sweet potato. Of course, there is very little endosperm in these and it is my opinion, at least at this time, that failure of germination is not a matter of incompatibility but due to the fact that the endosperm is not fully formed or not sufficiently large to support the embryo.

Dr. Milthorpe :

I would just like to ask one small question. If one uses the trick which the breeders of Irish potato use of removing the tubers during the early stage of development, could this influence the proportion of seed which develop ?

Dr. Hernandez :

Well in our case we have not had any difficulty in obtaining progress. Tuber removal as far as we are concerned, does not have any direct bearing on seed maturation — as long as the plant blooms of course. I think the previous speaker had not mentioned the effect of environment on seed set which plays a very important role i.e. temperature, humidity and so forth. We observed however, that tuber removal increased flowering intensity and seed set.

Dr. Martin :

I agree with M. Hernandez that environment does have a strong influence on the amount of seed set in the sweet potato. Yet, when one compares the maximum seed set that can be had in a cross with the minimum set under the most unfavourable circumstances, the amount of seed set is still rather small in comparison with the reproductive potential of the species. This is why I personally have not emphasised these environmental factors. Furthermore, a very large range of environmental factors have been studied by some investigators and in all cases, although there are some changes in percentage seed set, these changes have been small compared to the total sterility picture.

Prof. Harland :

I think that since there are no more contributions from the floor I would like to philosophize for a moment. First of all, I think we might accept provisionally Mr. Williams' theory that the sweet potato is the result of the crossing of two diploid species, probably one contributing an unreduced gamete followed by doubling of the chromosomes to produce a hexaploid. Now in this case, both of the contributing species, I think, must have contributed a self-incompatibility mechanism, and if one of the species was contributing an unreduced gamete, you get two sets of incompatibility mechanisms in one of the components and a single one in the other. Actually, it seems to be reasonable to suppose that you can get inter-incompatible and compatible groups and it therefore seems likely that one of the self-incompatibility mechanisms from one of the species has made a take-over bid, taking over the mechanism. Now this would mean that mutation could occur in the other self-incompatibility mechanisms leading to their almost but not quite total reduction. Now the whole situation is of course complicated by sterility. I think if we philosophize again, the impairment of the reproductive mechanisms is of course common to all or most vegetatively reproduced plants. Once you go over mainly to vegetative reproduction — as in the case of the sweet potato — the normal reproductive mechanism is no longer required to operate at 100% efficiency and, as in the case of organisms which are confined to caves, over geological times, you get in these organisms a complete breakdown of the eye mechanisms so that the organisms becomes blind. In this case, when the reproductive mechanism is not essential for the perpetuation of the species, you get genetical breakdown, mutation in the reproductive complex which is unopposed by selection and I venture to think that the sweet potato has gone pretty far along that path. Now this process, whereby unwanted or unnecessary genic complexes mutate unopposed by selection, is called genetical erosion and you can find numerous instances in the plant kingdom where this process has taken place.