PROCEEDINGS

OF THE

CARIBBEAN FOOD CROPS SOCIETY

TENTH ANNUAL MEETING
PUERTO RICO

1972

VOLUME X

PLANT RESPONSES TO TROPICAL CONDITIONS

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INTRODUCTION

Almost three years ago I had the honour of addressing a seminar sponsored by the World Meteorological organization and in preparing material for that lecture I became acutely aware of how lacking we are in knowledge about the responses of crop plants to tropical climates. Most of us were, I suppose brought up on plant physiology worked out for temperate conditions; most of us have learned in practice that we have to modify our ideas quite a lot when we work in the tropics, and most of us have suffered, no doubt, from experts from northern countries who do not appreciate that plants can react in quite peculiar ways to tropical climates.

I think it is important to recognize some of these differences and to appreciate that our knowledge of plant responses is often lacking in important respects. I should like to set the keynote of this paper with two quotations. First, L.P. Smith in the foreword to Professor J.Y. Wang's book Agricultural Meteorology (1) says: "Much can be done by the application of existing knowledge; much more could be done if we knew a little more." The second is from Hudson (2) who says "We should continue to spend money on deepening our knowledge of the relationship between the weather, which we cannot choose, and the plants about which we know so little."

Here in the Caribbean we are trying to apply existing knowledge; many of us concerned with food production have not the resources to seek new fundamental principles; we have neither the time nor the money to go in for basic plant physiology nor can we set about plant breeding. Fortunately, there is a small amount of such work going on, but for the most part we have to be content with selecting crop varieties suitable for our use and we try to adapt existing knowledge for our particular climatic circumstances. We know full well, however, that if we knew more we might be able to achieve more - for example, we might be able to smooth out the sharp variations in seasonality which, as Samuels (3) pointed out a few years ago, are so striking a feature of many of our crops, for no very clearly understood reasons. This paper is intended to outline a few instances where our knowledge is lacking, or at the best, incomplete.

LIGHT

There is abundant literature about the utilization of light by plants in photosynthesis, and the relationship between the total radiation received and the growth of the plant or crop, and it was generally believed that the more the solar radiation the greater the rate of photosynthesis. While this is normally the case under temperate light intensities it was shown in the 1920s, "30s and '40s, by a number of workers, that under strong tropical sunlight the rate of photosynthesis in certain plants fell off or even completely stopped. Maclean (4) found it for coconut, Nutman (5) for coffee, Murray (6) for cocoa and Gooding (7) for sugar cane. In one or two instances this seemed to be associated with stomatal closure, presumably due to water stress, and Hudson (8) has recently confirmed this for sugar cane. However, the matter can be far more complex. For example Murray (9) and others have shown that nutrient status has an effect on the behaviour of cocoa towards strong insolation, while Hersey and Miller (10) point out that different plants have different saturation light intensities, quoting *Zea mays* as 10,000 foot-candles and *Acer saccharinum* (the sugar maple) and Philodendron (a forest climber) as less than 1,200 foot candles. They also quote Behnung and Burnside as giving saturation light intensities as 2,000 to 2,500 foot candles for cotton, tomatoes, tobacco and castor oil. As the midday intensity of the tropical sun is in the order of 10,000 foot candles the implication is that many of our crop plants might do a great deal better under some form of shade. Even so, differences like these leave quite unanswered the question as to why they should exist.

DAY LENGTH

Day length follows logically any considerations of light. It is, of course, of profound importance in several crops.

Onions

Most onions require long days to set bulbs, but fairly recently a number of short day cultivars have been produced, and it is only the appearance of these that has enabled this crop to become a commercial proposition in the tropics. In actual fact the response of some of these short day onions is critical and Eavis and Jeffers (11) have shown that Granex F-1 Hybrid and Texas Early Grano will not initiate bulbs when the length of day is less than 11 1/2 hours, but with days of 12 to 12 1/2 hours bulbing starts very early and small bulbs result. Thus, in Barbados we find the best results are obtained with plants sown in October and November which grow until the end of January before bulb initiation, and will be well grown plants when bulbing does commence and will, therefore, produce large bulbs. Of course, extensive screening of other cultivars, is under way to find some which will perform satisfactorily at other seasons of the year.

It is an unfortunate fact that the most successful short day onions we have so far tried are also relatively poor in storage, being liable to quick rotting and sometimes early sprouting. Recent work by Bleasdale and his team (12) in Britain has suggested that there is a photoperiodic component which hastens early sprouting. They postulate a sprout inhibitor which is formed in the leaves at the time of die-back of the tops, and which is formed much less under short day conditions than under long days. In other words, absence of this inhibitor will permit rapid sprouting in onions grown under short day length.

Maize

Maize is highly sensitive to day length; the hybrid maizes of the United States that give yields of up to 200 bushels per acre have all been bred for long-day conditions. When they are brought to the tropics, without exception the results are miserable. Only in the past few years has short day-length been deliverately bred into high-yielding strains of maize, notably in Mexico, Colombia and Jamaica, and so we are beginning to get better strains for tropical use.

Irish Potatoes

Burton (13) says that long day conditions lead to greater and more prolonged growth. The total length of life of the plant is reduced under short dey conditions and the time of tuber initiation is earlier. Thus the effects of short days are opposing: on the one hand they cause early production of tubers, a desirable characteristics, but on the other they limit the growth and life of the haulms which have to supply metabolites to the developing tubers. The net results are disadvantageous, though another factor, that of temperature which I shall discuss shortly, also has an effect.

Pigeon Peas

I should at this point draw your attention to the recent work by Spence (Crop Science Jan. 1972) which I saw only after this paper was prepared, in which he has used the well known short day nature of Pigeon Pea (Cajanus cajan), by sowing dwarf cultivars in December so that flower inducing conditions prevail from germination and the plants grow to only about 1 metre in height end fruit within 4 months, so giving an "out of season crop" in April.

TEMPERATURE

The effect of temperature on plants is an interesting and challenging phenomenon. Some plants have almost World Wide distribution, e.g. Devil's Grass, Cynodon dactylon, grows from the tropics to as far north as England, though indeed there may be different strains. Others have very limited distribution; most of our tropical trees for example, will grow only in warm latitudes. Among crops in which we are interested and which we know are affected by temperature are:

Maize

Yields of even the best short day cultivars of maize are never anywhere as high es those of the long day varieties grown in temperate climates. Seghal (15) attributes this, at least partly, to a combination of short day length, which limits the total amount of radiation received by the crop, and high night temperature which leads to a relatively high rate of respiration, thus respiring away the carbohydrate that would otherwise be going into the grain. More rapid maturing at the higher temperatures of the tropics, and thus shorter life of the plant, is also a contributory factor.

Irish Potato

Burton (13) states that the optimum temperature for maximum yield is 15-20°C, and at temperatures in the order of 30°C complete inhibition of tuberisation has been found. With short day length the adverse response to high temperature is reduced. It has been shown that the rate of photosynthesis at 30°C is only about half that at 20°C, possibly associated with more rapid ageing of the leaves at the higher temperature, and possibly with the fundamental chemistry of the photosynthetic system. In passing, however, I may note that a leading authority on potatoes, Dr. N. W. Simmonds, Director of the Scottish Plant Breeding Station, firmly believes that potatoes will be developed suitable for the lowland tropics (16).

Went (17) demonstrated that night temperatures have a profund effect on potato tuberisation, and said that 20°C (68°F) was the upper limit; he postulated a tuber-forming hormone which was produced only when the temperature fell below this level. Although breeding may raise this upper level of temperature dependence we are still left wondering whether we shall ever be able to grow this crop commercially in the lowland tropics.

Tomatoes

Charles (18) thinks that night temperatures are a major cause of poor yields in Trinidad and our observations in Barbados have tended to support this. Samuels (3) in Puerto Rico has stated categorically that no fruit set is possible with night temperatures above 72°F (22°C), while Went (17) states that "at high night temperatures flowers remain small and often are abscissed before fertilization has occurred" but that once the fruit has set, even with night temperatures as high as 26°C, they will grow and ripen.

Recent work at the Glasshouse Crops Research Institute at Littlehampton, England, has shown that for the cultivars tested, night temperatures of 18°C and day temperatures of 20°C gave the best results; tomatoes grown at a continuous temperature of 30°C did not even set flowers, let alone fruit (19). The consensus of opinion at that Institute is very much the same as that formulated in 1957 by Went (17), that the reason for poor flower and fruit formation at high night temperatures was due to competition for carbohydrates between the vegetative and productive parts of the plant, with the vegetative parts "gaining the upper hand" at higher temperatures. What we would now dearly like to know is something of the chemistry controlling these phenomena.

But this is not the end of the story of the effects of temperature on tomatoes. It has been suggested that pollination fails at high temperatures. For example Howlett (20) has shown that carbohydrate deficiency - as when carbohydrates are being preferentially diverted to the growing vegetative parts - resulted in the suppression of anthers and/or spermatogenesis, leading to pollen deficiency. Walker (21) has suggested that at high temperatures the style grows rapidly and pushes the stigma outside the anther tube before the pollen is shed.

In passing it may be noted that the natural habitat of the tomato, is a narrow coastal strip extending from southern Ecuador, along the Pacific border of Peru, to northern Chile. Here for six months of the year there is virtually no rain, but constant sea mist with day temperatures 17° - 24°C and night 11° - 18°C (note the similarity of these temperatures with those previously quoted as ideal for greenhouses in the U.K.). In fact, in the lowland tropics we are trying to grow tomatoes so far outside their normal temperature range that it is not at all surprising that most varieties perform badly, and only a few with special built-in heat tolerance can be expected to perform at all adequately. We are so near the limits of climatic tolerance that the small differences between our hot and cool seasons can have a very great influence on the performance of the plant.

I have quoted that effects of temperature on some or the crop plants with which we are concerned in the tropics. There are some, of course, which we know we cannot even attempt to grow at low levels - e.g. wheat, peas (Pisum sativum), and many others. We have only the most sketchy knowledge of the fundamental differences between plants which thrive in the tropics and those which thrive in cooler climates. For example, Hirsey and Miller (10) point out that there are distinct ecological races with different tolerance to temperature; different species show maximum rates of photosynthesis at different temperatures; e.g. Cynodon dactylon shows its peak at 35°C while barley and perennial rye grass (temperate plants) peak at 10° - 15°C. Wareing and Tryhane (23) also point to such temperature differences, stating that Paspalum (a tropical grass) shows maximum photosynthetic activity at 40°C and Lolium (temperate) at 20°C. Tomatoes have particularly high photorespiration rates suggesting, in passing, that if it were practicable, CO_2 enrichment could be valuable. Whittingham (24) has pointed out that Hatch and Slack have been able to distinguish between certain temperate and tropical plants on the basis of biochemical characteristics of their photosynthetic systems, one of these being excess of aspartate in the mesophyll of tropical grasses, while Langridge (25) states that in tropical plants the photosynthetic pathway has a C-4-dicarboxylic acid intermediate while in temperate plants the usual C-3 (Calvin) cycle operates. The C-4 pathway is associated with special photosynthetic cells around the bundle sheath.

Langridge and Criffing (26) and Langridge (27) showed that "at certain temperatures plant growth is depressed by the inactivation of a few specially sensitive reactions and that such growth depression may be prevented by providing the plant with the normal products of the inhibited reactions." Much of their work was done with micro-organisms. When growth ceased at temperatures slightly above optimum it could be restored by the addition of a single substance; glutamic acid, biotin or thiamine were the most frequently required metabolites. In extensive experiments using 43 races of Arabidopsis thaliana they found that sensitivity to high temperature was polygenically determined; and that for two races, biotin completely overcame high temperature sensitivity while for a third, cytidine was partially effective. Bonner (28) and Ketellapper (29) describe several examples of hormonal imbalance, resulting from high temperatures, but again showed that these effects could be mitigated by applying certain essential metabolites to the plants concerned. The nature of the metabolite depended upon the plant species and the temperature. For example, ascorbic acid stimulated the growth of broad bean at elevated temperatures (23-30°C), a mixture of B vitamins that of Lupins, and sucrose or ascorbic acid permitted peas (Pisum sativum) to grow satisfactorily at 17-23°C. Langridge (27) suggested that possible causes of poor performance at higher temperatures might include: (a) decreased availability of gases; (b) rate imbalance including a decrease in coordination of interrelated syntheses; (c) accelerated breakdown of metabolites; (d) the onset of various types of inhibition; (e) increase in velocity of destructive as opposed to constructive reactions; (f) non formation of some enzymes; (g) reversible and irreversible heat inactivation of some enzymes. Bonner (30) discussing mutant strains of bacteria which will grow only at low temperatures, states "it is clear that the mutant makes a particular altered enzyme which is unstable at high temperature and stable at low temperature. It is my surmise that the same is true of the higher plants - that plants cannot produce at too high a temperature, or do not do so, because they have some enzyme which is unstable at that temperature."

WATER

The effects of water on plants are better understood than those of day length or temperature, but even so there are areas where our basic knowledge is still lacking and where a fuller understanding might well lead to practical results. Many workers have shown that even when the soil is saturated the plant can lose water faster than it is replaced by the roots (e.g. Weatherley (31), Gooding (32), Hudson (33). Weatherley has postulated local dry zones developing in the soil around the absorbing roots. Whatever the reason for the development of water stress in plants, this condition leads to decreased growth. Further, it is well known that shortage of water (e.g.) drought, especially under conditions of high light intensity, lead to xeromorphism (e.g. Henckel (34)), among the features of which is high lignin content in herbaccous plants. I believe that the normal water stress of plants growing in such climates as that of the lower levels in the Caribbean territories is such as to induce some measure of xermomophism. Some unpublished experiments in Barbados have suggested that even with irrigation - and much more so without irrigation - pangola grass develops a high fibre (i.e. lignin) content. I suggest that this combination of water stress and strong insolation may be a major reason why, in general, grasses grown in the tropics are low in digestibility and inferior as cattle feed when compared with temperate spring swards.

I might add that plants differ quite widely in their ability to control water loss by stomatal movement. For example, Glover in East Africa has shown that sorghums have a much higher degree of stomatal control than does maize, and Hudson (33) has found differences in stomatal control between different varieties of sugarcane used for breeding. The importance of this is, of course, obvious.

Salter and Goode (35) have collated practical information of the requirements of a large number of crops for water; and have noted at what time its application is most effective. For example, adequate water is important for maize just before tasselling; for cotton before and during flowering to prevent shedding of bolls; for tomatoes at the start of fruit set; for Irish potatoes, throughout their life both to increase the number of tubers and to increase the size of the tubers. Conversely, a short period of drought is required for flower initiation to take place in citrus and mangoes, though after fruit set abundant water is necessary.

CONCLUSION

I have tried to outline some of the effects of climatic factors with particular reference to tropical conditions, on the behaviour of crop plants. This has necessarily been a very incomplete exercise, but I think I have said enough to indicate that the "temperate" botany we learned in our youth is by no means always applicable; that complex physiological and biochemical systems are involved, and that could we but gain more knowledge, we should have a good chance of being able to improve the performance of our crops, certainly by appropriate breeding for physiological characteristics, perhaps by chemical sprays, by appropriate shading, and by suitable patterns of irrigation.

We have a challenge to knowledge and a lead or two. The small agricultural research units and Ministries of Agriculture in our region - indeed in most of the tropics - have neither the time nor the facilities to undertake the fundamental research needed to solve these problems. But we do have an ever-increasing chain of universities encircling the tropical world, universities anxious to pursue projects of intrinsic and basic science.

Surely the kind of problems I have been outlining, especially in connection with photosynthesis and temperature, are ideal for tropical universities. Fundamental biochemistry of a high order of complexity, pure science indeed, but with a real possibility of useful application when the problems are solved. Some attention must be paid to these problems.

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