

# THE PROBLEM OF THE BLAST DISEASE OF RICE\*

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NOTWITHSTANDING all that has been said and done in the field of blast disease of rice caused by the fungus *Piricularia oryzae* Cav. in India and abroad, mainly in Japan, much more still remains to be experimented upon and clarified regarding the pathogen itself and the biologics of its parasitism.

One need hardly go into much detail of the symptomatology of this disease as it has been recently described adequately (Suryanarayanan, 1956). The most important symptoms are the typical spindle-shaped or eye-spot lesions on the leaves and the blackening of the necks of the panicle. The latter is the most destructive since the flow of nutrients into the grains is impeded resulting in a chaffy ear-head. No critical assessment of the damage seems to have been made although it is generally agreed by many workers that it is of sufficient magnitude. The most feasible method of combating the disease has been one of breeding resistant types but, not infrequently, break-down of resistance has been noted. This is not surprising because several physiological races of the fungus have been identified and host susceptibility is determined not only by genetic factors but also, to a large extent, by a set of very critical environmental factors, particularly the nycto-temperature which influences the metabolic pattern of the host (Suryanarayanan, 1958 a). This contribution of Suryanarayanan in ascribing the incidence of the disease to low night temperatures has opened up a new field for investigation and explains many of the discrepancies noted in the disease proneness of the host in the field, in India and elsewhere. Indeed, micro-climatology in relation to the blast disease is still a matter for future investigation. Besides, our earlier investigations on the physiology of the pathogen have revealed the essentiality of Fe, Mn, Zn and possibly Cu as well as the vitamins thiamine and biotin for both growth and sporulation *in vitro*. Even though it is not possible to give an isolated consideration to these micro-nutrients *in vivo*, it is, nevertheless, plausible that these micro-nutrients as well as other macro-nutrients like amino acids, amides, sugars and the like are available on the leaf surface being exuded as guttates or reaching the cuticle by the process of exosmosis (Subba-Rao

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and Suryanarayanan, 1957). In view of the foregoing it is obvious that the problem of the blast disease of rice is one which calls for attention to the intimate host-parasite relationships for adopting any effective control measures.

In light of evidences obtained in our laboratory and elsewhere, *P. oryzae* appears to have more specialized metabolic requirements than at one time imagined. For instance, *P. oryzae* is heterotrophic to vitamins of the B group, viz., thiamine and biotin (Suryanarayanan, 1958 b). The intact thiamine molecule, however, is not needed on a sucrose-nitrate medium, the pyrimidine portion of the vitamin alone being fully effective indicating the capacity of the organism to synthesize the thiazole fraction. This ability of *P. oryzae* to grow with pyrimidine alone is evident only after 6 days, for growth in the earlier stages is apparent only when both thiazole and pyrimidine are present. Another curious feature about the biosynthesis of thiamine by *P. oryzae* is that the synthesis of the thiamine molecule by the fungus appears to depend on the type of substrate sugar (Suryanarayanan, 1958 c). Pyrimidine which is equivalent to the full molecule of thiamine when the substrate sugar is sucrose or maltose is not fully effective when the carbon source happens to be glucose. This is rather surprising since it is generally believed that a disaccharide like maltose has to be first enzymatically hydrolyzed and the products in this case would be glucose only. We, therefore, consider that pyrimidine is fully effective only when supplied with the  $\gamma$ -form of glucose which comes into existence when disaccharides are hydrolyzed, though temporarily. Further, the essentiality of Fe, Mn, Zn and to a certain extent Cu for this fungus has been established by us and that both the heavy metals and vitamins are indispensable for growth and sporulation in culture (Appa-Rao *et al.*, 1955). Higher concentrations of the vitamins and heavy metals, especially Cu and Mn, are required for sporulation than for growth (Appa-Rao, 1956 a). That sporulation of the organism is dependent on a low initial concentration of the sugar and does not occur until the medium is depleted of the carbon source has also been proved (Appa-Rao, 1956 a).

Another interesting aspect of the behaviour of the pathogen in pure culture is its ability to grow with inorganic  $\text{NO}_3$  nitrogen but not with  $\text{NH}_4$  nitrogen. This is contrary to the general belief that all nitrate users should be able to use ammonia inasmuch as  $\text{NO}_3$  is supposed to be reduced to  $\text{NH}_3$  before the primary amino acids are built up. The failure of *P. oryzae* to grow with inorganic ammoniacal sources of nitrogen as  $(\text{NH}_4)_2\text{SO}_4$  has been traced to the concomitant development of high physiological acidity con-

sequent to accumulation of anions in the medium as the ammonium ions are rapidly absorbed (Appa-Rao, 1956 *a, b*). Should such a medium be buffered with  $\text{CaCO}_3$  or if certain organic acids of the Krebs' citric acid cycle such as succinic, fumaric or citric acids are added in small amounts normal growth of the fungus is observed with ammonium nitrogen. This beneficial effect of the organic acids is considered to be two-fold. They either act directly as buffers or enter into the metabolic cycle to combine with the accumulated ammonium ions to form the primary amino acids and thereby reduce ammonia toxicity. While normal growth of *P. oryzae* with weakly ionized ammonium salts, like ammonium carbonate does, indeed, favour the former view, its favourable response to ammonium phosphate appears to be one of corroborating the latter hypothesis especially in light of our recent findings on the role of phosphorus in inorganic ammonium utilization by other fungi like *Sclerotium oryzae* Catt. and *Colletotrichum capsici* (Syd.) Butl. and Bisby.

Coming to the question of host physiology in relation to disease-resistance and susceptibility it has been our experience and of other investigators that infection often fails to develop even under optimal conditions of temperature (24–26° C.) and humidity (above 95%). The failure of the normal susceptibles to take infection not only involves considerable loss of time in evaluation of disease-resistance in various strains of rice bred for the purpose but also presents a stumbling block in the evaluation of host-parasite mechanisms. Recently we have been able to pin down this elusive problem to the effect of a low nycto-temperature (about 20° C.) on the nitrogen metabolism of the host (Suryanarayanan, 1958 *a*). The mechanism of action is the ease with which  $\text{NO}_3$  is reduced at a low nycto-temperature than at a high temperature and the subsequent shift of reactions more in favour of synthesis of soluble nitrogenous products like the amides and the amino acids. In this connection the glutamine synthesis by the rice plant under a heavy dressing of  $(\text{NH}_4)_2\text{SO}_4$  is worthy of mention. Under heavy nitrogenous manuring and low nycto-temperatures much glutamine is synthesised by the host and is actually exuded in the guttates. The guttate, when it dries over the leaf surface leaves easily identifiable macroscopic crystals mainly of glutamine (identified chromatographically) which markedly stimulates the germination of *Piricularia* spores at the infection court. This stimulation by glutamine is, however, apparent only when the atmospheric temperature is about 24–26° C., which range has been established by many workers to be the optimum for successful infection of rice by the blast fungus (Suryanarayanan, 1958 *d*).

Obviously, the pattern of nitrogen metabolism of the rice plant appears to be the most important single factor connected with its genetic constitution as well as with critical environmental factors, chiefly a low nyctotemperature. It is relevant to mention here some of our early results on the nitrogen metabolism of the host which only corroborates our recent views. Appa-Rao (1956 *a*) recorded a greater accumulation of total nitrogen in the susceptible type than in the resistant one. Nitrogenous manuring increased the total nitrogen in both types but the susceptible still showed a higher N content than the resistant one. Total carbohydrates decreased with nitrogenous manuring in either case, but the susceptible type recorded a higher carbohydrate content than the resistant one indicating, perhaps, its better photosynthetic capabilities. With nitrogenous manuring, the total carbohydrates reached a considerably lower value than in the case of the resistant types. This would again mean that the photosynthates are more efficiently used by the susceptible types to form the necessary  $\alpha$ -keto acids via the Krebs' TCA cycle to combine with the  $\text{NH}_4$  ions and to form the soluble nitrogenous substances like the amides and amino acids. Thus it is conceivable that the enzyme systems related to the assimilation of nitrogen is keyed up better in the susceptibles than in the resistant types which is probably intrinsically controlled by a gene or genes and the efficacy of which is largely determined by a critical night temperature round about  $20^\circ\text{C}$ . Even though it is not, as yet, clear in what way the resistant types differ from the susceptible types in their pathways of nitrogen utilization, we are inclined to believe from our recent studies that the former seems to have a less pronounced synthetic ability in so far as glutamine is concerned and as judged by its crystallization on the leaf surface. Much emphasis is laid here on glutamine because of its well-known occurrence as a storage reserve in plant parts and the pivotal role it plays in the nitrogen economy of plants and their well-being. It is further appropriate to mention that environmental conditions like long day stimulus and nycto-temperatures, as well as genetic factors, are involved in the biogenesis of glutamine and related compounds in plants (Steward and Pollard, 1956).

It is evident from the above discussion that many factors are involved in determining the degree of resistance/susceptibility of the host to *P. oryzae*. Apart from the genetical constitution, environment (particularly a low nyctotemperature) exerts a significant influence on host susceptibility. Low nyctotemperatures favour nitrate reduction and consequent synthesis of soluble nitrogenous substances, chiefly amino acids and amides. On the contrary, at high nycto-temperatures, nitrate reduction is possibly low as reported in tomato (Went, 1957) and the products of photosynthesis are largely diverted

into the formation of complex cell-wall material like lignin and cutin which offer resistance to mechanical puncture by the germ tubes. In considering mechanical resistance it is meet to cite the early investigations in Japan bulk of which relates to the deposition of silicon on the epidermal cells providing thereby an outermost barrier to the entry of the germ tubes. A new interpretation on the role of silicon in forming a hypothetical complex with one or more components of the cell-wall, relatively resistant to attack by the extracellular enzymes of *Piricularia*, has been offered recently by Volk *et al.* (1958). Such an assumption has been made plausible in view of the consistent inverse relationship between the silicon content of the rice plant and its susceptibility. Whatever might be the mechanisms underlying these phenomena it is logical to conclude that mechanical resistance is but a reflection of a retarded nitrogen metabolism. An entirely new facet of the problem is the recent emphasis on the function of various organic and inorganic nutrients and nutrilites available on the leaf surface through guttation or by a process of exosmosis and their role in initiating infection. The chemical stimulation of *Piricularia* spores by guttates from rice has been recently reported (Weintraub *et al.*, 1958). These authors found that while a number of sterols, steroidal saprogenins, steroidal amines and  $\alpha$ -tocopherol also stimulated germination of spores, these substances could not be identified in the guttates from rice. As has already been pointed out by our investigations, the active fraction in the guttates is mainly glutamine. It is too premature to dwell at length on the importance of cuticular excretions in initiating infection. But by our continued investigations on this question it is becoming increasingly clear that other substances like organic acids and possibly vitamins are also exuded on the rice leaf surface besides glutamine. The situation, however, is analogous to root excretions of which comparatively more is known.

Lastly, our latest finding that maleic hydrazide breaks the resistance of rice to *Piricularia* but only when grown under low nycto-temperatures (Suryanarayanan, unpublished) further strengthens our views on parasitism by the blast fungus. The mechanism of action, however, remains to be investigated, although accumulation of both carbohydrates and glutamine has been reported with other plants treated with maleic hydrazide. As far as we could visualize, the problem of the blast disease of rice should be considered not merely as a case of facultative saprophytism but only at a slightly lower level than obligate parasitism by rusts, etc., because of its exacting growth requirements and its capacity to produce toxins like pircularin and  $\alpha$ -picolinic acid (Tamari and Kaji, 1954) and the very many factors that determine host susceptibility at a physiological level. Indeed,

such an understanding of the host-parasite complex would eventually lead to better methods of combating the disease in the field.

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\* Not seen in original.