REVIEW OF LITERATURE
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I. Characteristics of water-logged soils

   (i) Paucity of oxygen

   In a flooded soil, aeration is greatly impeded, and oxygen entry virtually occluded, because of the presence of a water table on the soil. Oxygen can enter the soil only by molecular diffusion in still water but, as the ratio of diffusion coefficient of oxygen in water/air is of the magnitude of 10^{-4} this process is rather slow. The result is, the concentration of oxygen in the soil is heavily restricted. Thus, Evans and Scott (1955) found all of the oxygen added to an air-dry soil by flooding it with distilled water disappeared within 10 hr. Takai et al. (1956) found in three soils the dissolved oxygen being consumed within a day. Yamane (1958), while studying muck and alluvial fields, found that in the former the oxygen concentration fell from 1.61 to 0.15 per cent and in the latter from 2.68 to 1.15 per cent within about a month.

   To explain the capacity of the rice plant to grow under depleted oxygen conditions, many investigators have proposed various physiological mechanisms. Erygin (1936) attributed this to a well developed anaerobic respiratory system in the rice plant. He found the
respiratory coefficients \((\text{CO}_2/\text{O}_2)\) for barley, upland rice and low land rice to be respectively 1.40, 3.86 and 4.50. Taylor (1942) was also of a similar view. He compared the respiratory activity of rice with that of wheat over a range of partial pressures of oxygen. He attributed the superiority of rice over wheat in germination and growth at low oxygen concentrations to its possession of a very efficient fermentation system and suggested that rice is more tolerant of ethyl alcohol, the end product of carbohydrate fermentation. Okajima and Kimura (1952) also were of a similar view. Harrison and Aiyer (1913), however, were of the view that at the soil surface methane is utilized by bacteria and oxidised to carbon dioxide, which in turn is used by algae in this layer in the assimilation process by which oxygen is liberated. This oxygen is made use of by the plant. However, Vlamis and Davis (1944) criticised this hypothesis, as rice plants thrived well in culture solutions through which a stream of nitrogen was bubbling. They concluded that oxygen must, of necessity, pass downwards through the plant itself. That the rice plant can indeed supply the roots with oxygen in this way was clearly demonstrated by Raalte (1944) who analysed the oxygen content in the air channels of the root cortex. The percentage of oxygen was the same whether the roots were in a normal
or reduced medium, but in the latter the oxygen concentration dropped immediately when the shoots were cut off and the stumps sealed with wax. That oxygen necessary for the roots is transported through the plant itself by means of large air spaces from leaf has since been confirmed by several workers (Lin, 1946; Aimi, 1960).

By means of $^{15}$ tracing, rapid internal diffusion of oxygen from the foliage to the roots has been directly demonstrated in rice by Barber et al. (1962).

Arikado (1959) observed that the volume of air transported from the aerial parts to the roots increased with the progress of plant growth till differentiation of ear primordia. In other words, the ventilating pressure decreased with increase in age up to ear initiation. Towards maturity, however, there was a decline in the oxygen transport, owing to the decrease in the number of green leaves. He further observed that the ventilating system of upland rice was inferior to that of low land rice.

Alberda (1953) found a further adaptation. According to him, the rice plant possesses special types of roots which are able to take up oxygen and transport it to other parts of the root system. These special respiration roots start to develop at the end of tillering stage and remain active until the ripening of seed. These roots are thinner and more abundantly branched than normal roots and grow either horizontally or
vertically upwards into the air. Thus, both morphologically and physiologically, they differ from the normal roots. Mitsui et al. (1962) proposed a mechanism of oxygen secretion through the glycolic acid respiratory pathway.

Not only adequate supplies of oxygen reach the respiring root tissues from the foliage, but also appreciable surplus quantities of the gas diffuse from the root apices and counteract the anaerobiosis in the rhizosphere. That rice roots exude oxygen has been demonstrated by Raalte (1941, 1944) and Mitsui (1955). Oxidative power of rice, therefore, is an important character for adaptation to water-logged conditions where reductive conditions exist. Thus, ferrous iron in the soil is oxidised at the root surface and deposited there as ferric compounds allowing little iron to enter the plant (Nagai and Matano, 1961). Thus, susceptibility to iron toxicity is related to oxidizing power of the roots (Baba, 1955). Doi (1952) reported that roots of paddy rice have stronger oxidising power than other crops. Okajima (1964) found that the oxidative power of young rice roots was superior to that of old ones. The young ones which had a sufficient nutritional status of nitrogen, particularly showed the highest oxidative power (Okajima, 1960). The oxidative power of rice roots
was at its peak at tillering stage, then it declined with growth corresponding to the increase in the number of old roots. At about heading stage, it was at its nadir (Mitsui and Tensho, 1952; Alberda, 1953; Okajima, 1960).

Armstrong (1969) contended that oxygen flux by polarography gives a more reliable estimate of at least one aspect of oxidizing activity than do measurements involving dye systems. He found in Norin varieties, the greater the oxygen flux from the root, the more resistant they were to the effects of waterlogging. However, it is not known whether the differences in the oxygen flux rates between varieties are caused by differences in the anatomy of roots and leaves or differences in the respiratory rate.

Since soil aeration is ruled out under flooding, and plant aeration becomes the dominant pathway for oxygen, the phenomenon of root porosity gains significance. Root porosity may be defined as the volume of gas space per unit volume of roots. Because the rate of oxygen supply by internal aeration is dependent upon root air porosity, Peter et al. (1969) found plant’s tolerance to excess water to be related to root porosity and root length. The maximum values of root porosity were 26-30 per cent for rice and 7-11 per cent for maize (Jensen et al., 1969; Luxmoore et al., 1970). A linear increase
In porosity from the root tip seemed to occur for the first 6 cm for both rice and maize; further along the root, the porosity was more or less constant, though, for rice, the data were very variable (Luxmoore et al., 1970).

(ii) Increase in carbon dioxide and other gases

Even as the entry of oxygen is restrained by the existence of a perched water table, the exit of gases produced in the soil is also drastically impeded. The main gases liberated in a flooded soil are nitrogen, methane, carbon dioxide and hydrogen (Harrison and Aiyer, 1913). The nature of gas is dependent upon the period of submergence. Thus, Takai et al. (1956) found that after obliteration of oxygen within a day, occurrence of hydrogen was first evident. This was followed by an increase in carbon dioxide which, after reaching its maximum, began to decrease slowly with another spurt later. Coincident with the decrease in carbon dioxide was an increase in methane suggesting that methane may be produced at the expense of carbon dioxide.

The liberation of carbon dioxide is governed by both temperature and organic content. Carbon dioxide production was maximum at 40°C in the studied range of 15-60°C. Again, it was more in a muck than in an alluvial soil after 28 days of submergence (Yamano and
A rapid decrease in permeability to water, causing sudden wilting, ascribable more to excess of carbondioxide than to lack of oxygen, was demonstrated in tobacco under flooding by Kramer and Jackson (1951). Chang and Loomis (1945) also reported reduced water absorption under increased carbondioxide in the rhizosphere. Leonard and Pinckard (1946) found retardation of shoot and roots under high concentrations (60%) of carbondioxide in cotton causing wilting and even death of the plant. Concentration up to 15 per cent resulted in the production of long slender roots; 35-45 per cent resulted in the formation of somewhat short thick roots; 60 per cent and higher prevented growth either in length or thickness of the root. Vlamis and Davis (1944) also reported similar poor development of shoot and root in presence of hyper-concentrations of carbondioxide. Takijima (1963) found restricted root development under increased carbondioxide content. An interference in the absorption of five elements tested, viz., K, N, P, Ca and Mg was reported by Chang and Loomis (1945). The per cent absorption of these elements respectively was 4.5, 33.1, 44.4, 52.9 and 63.9, the absorption of K being much affected. Saito and Takahashi (1954) also observed vitiation in the uptake of NH$_4$ ions, K, Mg, Ca, P and Si by rice plants. Tanaka and Navasero (1967) reported decrease in plant weight.
and element content of rice plant especially that of K and Mn when carbon dioxide was bubbled through the culture solution.

However, Grable (1966) was of the opinion that it is not known whether excessive carbon dioxide or oxygen deficiency, or both are responsible for poor plant growth in waterlogged soils. Russell (1962) in his review concluded that carbon dioxide rarely accumulates to toxic proportions in soils, a view shared by many other investigators (Tackett and Pearson, 1964; Unger and Danielsen, 1965; Kanwar et al., 1966).

(iii) Soil reduction

When oxygen supply is cut off as a result of flooding, the aerobic soil organisms become extinct and the anaerobes begin to assert themselves. Takai et al. (1956) showed that the number of anaerobes reached a peak 5 days after flooding. Oxidised soil constituents like nitrate, manganic oxides, ferric oxides, sulphates and phosphates are utilized by these anaerobes as electron acceptors in their respiration which results in the reduction of the soil.

(a) Denitrification: Nitrate in an anaerobic medium is lost by its reduction to oxides of nitrogen or nitrogen. Broadbent and Stajanovic (1952) found that the amount of nitrogen lost from the soil system was inversely related to oxygen content of the soil air.
Concerning the fate of nitrate added to the soil they concluded that a part is rapidly converted to microbial protein, some is lost through denitrification, a very small quantity may be reduced to ammonia and some remains unchanged. The relative importance of these different processes depends on the kind and amount of available energy material present in the soil and on partial pressure of oxygen in the soil environment.

Bremner and Shaw (1958) reported that denitrification occurred when the oxygen supply to soil micro-organisms was restrained. The rate of denitrification was proportional to the increase in pH, temperature, nitrate and organic content.

Wiljer and Delwiche (1954) following denitrification quantitatively with KNO3 as tracer, found three products, nitrous oxide, nitrogen and nitric oxide. Nitrous oxide was found to be the major product of denitrification under most soil conditions. Reduction of nitrate to ammonia was feeble.

(b) Ammonia accumulation: Because of the lack of oxygen, the mineralization of organic nitrogen stops at the ammonia stage in submerged soils. Ammonification is controlled by several factors like temperature, organic matter and predisposition of soil. Yamane and Sato (1961a) reported that with increase in the temperature up to 60 °C, ammonia production also registered an increase in a muck
and an alluvial soil. Mitsui (1955) recorded that air
drying of the soil prior to submergence almost doubled
the ammonia content. According to Ponnampерuma (1964),
however, the nature and content of organic matter existent
in the soil is of prime importance in deciding the
release of ammonia, higher the organic matter, more
being the ammonia. Lopez and Galvez (1958) also observed
a close association between organic matter and ammonia
released.

(c) Increase in manganese: Contemporaneous
with the denitrification, the oxides of manganese are
also reduced in flooded soils (Ponnampерuma, 1964) and
thus the solubility of Mn is considerably increased.
Clark and Resnicky (1956) in their study on mineral
element levels in the soil solution of a submerged soil
found that Mn and Fe increased by a hundredfold, Ca and
Mg increased tenfold but K, Cu and B were not markedly
affected. However, whether the increased solubility is
detrimental or beneficial to rice crop is still being
debated.

Aiyer (1946) contended that rice needs more
of Mn than of other trace elements. According to Koba-
yashi (1958) barley and wheat require 100-200 g of Mn
per hectare, but rice requires ten times as much.
Clark et al. (1957) observed that tissues of rice plant
sometimes contain as much as 4000 ppm Mn and that under-
flooded conditions, Mn uptake is very high and he attributed higher yields under flooded than under unflooded conditions to higher Mn uptake in the former. Tewari et al. (1969) reported increase in dry matter and yield in rice when available Mn in the culture solution was increased. Weeraratna (1969) also reported higher dry matter and higher absorbed Mn in flooded than in unflooded conditions. Enyi (1969) found grain yields of an upland and a swamp rice varieties to be both significantly reduced with flooding, and the flooded plants to have the lowest concentration of Mn especially during tillering. Singh (1966) also reported low yields due to low concentration of Mn. He further observed that of the two elements, Fe and Mn, rice had greater requirements for the latter. However, Senewiratne and Mikkelsen (1961) associated poor tillering, depressed leaf growth, low moisture content and foliar chlorosis of plants grown under unflooded conditions with high Mn content in the plants. Manganese toxicity in tissues containing 2000 ppm Mn has been reported by Soshagiri Rao and Krishna Rao (1958) and Perumal (1961). Under water culture conditions, 10 ppm Mn was reported to be the upper critical level in the culture solution for maintaining normal rice growth; at this level, the straw contained 1000 ppm Mn (Ishizuka et al., 1961). Toxicity symptoms developed at 60 ppm Mn in the
culture solution (Patnaik and Bhadrachalam, 1965). Tokuoka and Gyo (1940) showed that the addition of 300 ppm Mn increased the height of the stem and 600 ppm reduced it. Addition up to 1000 ppm accelerated tillering. Tanaka and Navasero (1966a) observed that in culture solution, 25 ppm and 50 ppm Mn to be the critical levels at pH 6 and 4 respectively, above which toxicity symptoms developed.

(d) Increase in iron solubility: The iron concentration in the soil solution increases when a soil is submerged, more so if the soil has low pH, high organic matter content, low active iron or reducible manganese (Ponnamperuma, 1964; Tanaka and Yoshida, 1970). In a clayey latosolic soil, within 30 days of submergence, soluble iron may increase up to 10000-15000 ppm (Ponnamperuma, 1964).

As rice has a greater requirement for iron than other plants, this enhanced solubility may be beneficial (Lin, 1946). But, an excess may prove toxic (Ponnamperuma et al., 1956; Takahashi, 1960). The poor yield of paddy grain in flooded soil was attributed to excess Fe in the soil (Obordo, 1969). Excessive soluble iron may also induce potassium and phosphate deficiency as shown by Yamada (1959a). The excessive iron absorbed by the plant forms an insoluble product FePO₄ with
phosphate and thus the phosphorus deficiency is caused. Baba and Tajima (1960) recorded that in the presence of excessive ferrous iron, nutrient absorption was inhibited in the order $P_2O_5 > K_2O > Sio_2 > NH_4^+ > NO_3^-$, $CaO$. Tanaka et al. (1966b) also observed that at high levels of iron in the soil, the uptake of $P$, $K$ and $Mn$ was adversely affected though uptake of $N$ was not impaired. Respiratory rate and cytochrome oxidase activity of root were retarded. Content of protein $N$ of leaf and total sugars and starch in shoot decreased.

However, the reported critical limit in the growth medium beyond which toxicity symptoms might develop varies widely. It has been variously assessed as 10 ppm (Ishizuka et al., 1961), 40 ppm (Patnaik and Bhadrachalam, 1965), 50 ppm (Aiyer, 1946) and 75 ppm (Tanaka et al., 1966b).

A ratio of 1.5 to 2.5 of $Fe$ to $Mn$ in plants is required for normal growth (Shive, 1941). Iron and Mn appear to have antagonistic relations; at a higher Mn level in the culture medium the Fe content of plants is lower than at low levels of Mn (Somers and Shive, 1942). Excess Mn hinders the translocation of Fe by causing the iron in the plant to be converted into an insoluble form (Me Harguo, 1945). Manganese in the rice plant decreases as iron supply increases (Senewiratne and Mikkelsen, 1961; Ishizuka et al., 1961; Tanaka and
Navasero, 1966b). With a low level of Mn in the plant, iron is in the ferrous form and may cause iron toxicity while at high Mn level, iron may be in the ferric form and iron deficiency may occur (Somers and Shive, 1942).

When the ratio between available Fe and Mn was decreased by adding Mn, dry matter, yield and Mn content of plants increased, giving support to the concept that it is the ratio between available Fe and Mn, rather than the absolute amounts that determines plant growth (Tewari et al., 1969).

(e) Accumulation of hydrogen sulphide: Concentration of sulphide also increases when a soil is submerged. The time taken for the production of sulphide from flooding, however, depends on the nature of the soil. But addition of sulphate increases sulphide production (Yamane and Sato, 1961b).

Sulphide is reported to inhibit the respiration and the oxidative power of the roots, thus retarding the uptake of various elements (Mitsui et al., 1951; Baba et al., 1952; Mitsui et al., 1953; Baba, 1958; Baba and Tajima, 1962). Sometimes, it enters the plant and disturbs metabolic processes even in the shoot (Takagi and Okajima, 1953, 1954). The sulphide in the soil solution injures the roots, ushers in imbalance and retarded nutrient uptake, and eventually causes disturbed
growth (Shioiri, 1945; Mitsui, 1949a, b; Baba and Harada, 1954; Shioiri and Tanaka, 1954; Shiga, 1962). Mitsui (1964) placed the nutrient elements affected by hydrogen sulphide, a well known inhibitor of terminal oxidases of the TCA cycle, in four groups, the inhibition decreasing in the order: potassium, phosphorus > silica, bromide > manganese, ammonia, water > magnesium, calcium. Hydrogen sulphide injury decreases number of ear-bearing tillers, yield of grain and straw, ratio of grain to chaff and resistance to Halmithosphorium leaf spot disease (Nair and Subramoney, 1969).

There is a contradiction in the fact that a submerged soil abounds in both hydrogen sulphide and ferrous iron. For, in the presence of the latter the former should be precipitated as insoluble FeS, minimising the severity of hydrogen sulphide. But Tanaka et al. (1968) observed that even in the presence of ferrous iron, sulphide lowered root respiration and increased the iron content of shoot.

(f) Accumulation of organic acids: In submerged soils, especially, those possessing readily decomposable organic matter, organic acids such as acetate and butyrate accumulate (Onodera, 1929; Wada and Iida, 1933; Takai, 1958; Mitsui et al., 1959a, b; Yamane and Sato, 1967). The organic acids are toxic to rice roots and impede nutrient uptake (Mitsui et al., 1959a, b;
Takijima, 1963, 1964b; Yamane and Sato, 1967). The inhibitory effect on seedling root elongation of the organic acids studied was in the order butyric > propionic > acetic, formic > oxalic acid. Stronger reduction in nutrient uptake by the treated plants was found in the elements of \( \text{P}_2\text{O}_5 \), \( \text{K}_2\text{O} \) and \( \text{SiO}_2 \) (Takijima, 1964b). Organic acid addition to the culture medium caused withering of the seedlings, fading of leaf colour, sloughing off of the root epidermis (Mitsui et al., 1953; Baba et al., 1954; Yamada and Ota, 1953c). Tanaka and Yoshida (1970), however, doubt whether organic acids accumulate in concentrations high enough to injure the roots.

II. Growth analysis

(i) Tillering in relation to mineral nutrition

The number of tillers on a rice plant is strongly influenced by both heredity and environment. That genetic variability exists in tillering capacity is a well-known fact. Workers at IRRI have adequately brought out this using panicle number per hill as the index of inherent tillering capacity (IRRI, 1966, 1968). Among the environmental factors, nutrition, temperature, light intensity and cultural practices are important.
Regarding nitrogen nutrition in relation to tillering, two schools of thought have been current. One is that nitrogen content nor so influences tillering; the other is that it is the nitrogen uptake that is responsible for tillering. Thus Kuno (1943) and Kumura (1956) demonstrated a strong correlation between nitrogen content of leaf blade during tillering with tiller number. Tanaka (1957) and Ishizuka and Tanaka (1963) reported that tillering stops when N content of leaf blade becomes less than 2.5 per cent. Tanaka et al. (1964) stated that tillering stopped when the N content of straw dropped below 1.7 per cent and at the maximum tiller number stage N per cent in straw varied from 1.5-2.0 per cent. Takahashi et al. (1956) indicated that tillering is more closely related with nitrogen content of the culm than that of the whole straw. However, Oshima (1962b) contended that tillering is more closely related to soluble nitrogen in the culm than to the protein nitrogen. Tanaka and Garcia (1965) gave a conciliatory statement, so to say, that total nitrogen content of the culm or the total nitrogen content of the straw or the soluble nitrogen content of the culm are all more or less equally associated with tillering so that any one of these values can be used. They further observed that tillering increased when the N content of the culm is above 2 per cent and at about
0.8 per cent the death of weak tillers begins. Yoshida and Hayakawa (1970) extended the statement of Tanaka and Garcia (1965) further to encompass the nitrogen per cent in the leaf blade also and stated that for diagnostic purpose, the whole straw, the culm or the leaf blade can be used. They found that tiller number increased when the N content of leaf blade was over 2 per cent and tillering stopped when the same dropped below 2 per cent. On the other hand, Kiuchi and Ishizaka (1960) were of the opinion that tillering is more favourably influenced by the absorption rate of nitrogen than by the N content in the plant during tillering period.

Kiuchi et al. (1961) found that N uptake of 1 mg per day per gram of dry weight is necessary for maintaining tiller development. IRRI (1968) reported tillering to be governed by the nitrogen supply in the soil, greater the nitrogen content of the substrate, greater being the tillers per plant. Matsuura (1962) said that an optimum concentration of 30-40 ppm in culture solution is needed for emergence of tillers, lowest critical being 3 ppm. Two mg of N per 100 g of dry soil was the lowest limit for developing tillers (Kiuchi et al., 1961).

These apart, there are several reports of the influence of other major and minor elements either in conjunction with or without nitrogen on tillering behaviour.
Thus Sekiya (1963a, b) found N and P deficiency to cause repression of tillering, the former more so. Yoshida and Hayakawa (1970) reported that 5 per cent nitrogen, 0.2 per cent phosphorus and 1.5 per cent potassium in the leaf blade were required for maximum tillering rate. If the nutrient contents are reduced respectively to 2, 0.03 and 0.5 per cent tillering rate became nil. Below these rates tiller number starts to decrease. Honya (1961) reported 0.25 per cent of phosphorus and Kiuchi and Ishizaka (1961) stated 1.5 per cent potassium to be the critical requirement for increase in tillering. Silicon deficiency during vegetative growth phase to be instrumental in decreasing the ear number has been reported by Okuda and Takahashi (1964).

(ii) Growth parameters like RGR, MAR, LAR, LVR and LALR

The increase in dry weight was regarded as following a compound interest law, the increment in any interval adding to the capital for growth in subsequent periods. Gregory (1917) suggested the use of net assimilation rate in the analysis of growth. Briggs et al. (1920) introduced the term unit leaf rate which is the same as MAR of Gregory.

Variations in MAR may be determined by the following factors either independently or in combinations: heredity, age or time, climatic factors, either
light intensity, temperature or solar radiation and edaphic conditions.

That MAR varies between and within species has been adequately demonstrated by various workers (Watson, 1947; Goodall, 1950; Watson and Witts, 1959; Wilson and Cooper, 1969). In rice, this has been recorded by Hayashi (1963).

Evidence on the effect of age or plant size on MAR, however, is conflicting. Many workers have indicated that there were no significant trends in MAR with time during vegetative phase (Crowther, 1934; Heath, 1937; Hammond and Krikham, 1949; Blackman and Wilson, 1951). However, a significant decline in MAR during vegetative phase was reported for tobacco, sudan grass and oats (Ballard and Petrie, 1936; Williams, 1937), sugarbeet, potato and barley (Thorne, 1960, 1961), cotton (Crowther, 1944), sugarcane (Asana, 1950) and Dactylis glomerata (Eagles, 1969, 1971).

That MAR declines with a decrease in light intensity has been reported by many workers (Crowther, 1937; Milthorpe, 1945; Blackman and Rutter, 1948; Blackman and Wilson, 1951; Watson, 1958; Blackman and Black, 1959). In rice, Hayashi (1968) found similar results. Eighteen medium and late rice varieties covering a wide range of types grown in single plot stand
in field were subjected to 20%, 40% or full natural sunlight. With decrease in light intensity MAR decreased. McKee, G.W. (1962) also showed this to be true in birdsfoot trefoil.

Watson (1947) stated that changes in MAR are attributable to environmental factors. Ikenaga et al. (1968) found that in a rice variety Fijimorin, the MAR altered favourably in proportion to increase in solar radiation and air temperature. Lian (1963) also attributed the lesser MAR (in the Taiwanese variety, Chianan-8) during the second crop to the low solar radiation, when compared with the first crop. Voldeng and Slackman (1973) found that in Zea mays, MAR was positively dependent upon solar radiation. Dependence of MAR in corn on solar radiation has also been reported by Denmead and Shaw (1962). Enyi (1962a) while studying the growth of swamp rice and upland rice under tropical glass house conditions in Trinidad found MAR greater in swamp rice.

Relative growth rate is a measure of the weight increase per unit of plant weight present per unit of time (g/g/day). Since it is based upon initial weight, differences due to seedling size are nullified. Thus growth rates of seedlings of dissimilar size become relative. Like MAR, RGR is also dependent upon, heredity, age, light intensity and solar radiation. Thus signifi-
cant variations in RGR between alfalfa and birdsfoot trefoil has been reported by Cooper (1967). It also registers a fall with time as has been shown by Cooper (1966) in alfalfa and birdsfoot trefoil and by Eagles (1969, 1971) in Dactylis glomerata, with decrease in light intensity as evidenced by Cooper (1967) in alfalfa and birdsfoot trefoil seedlings and is positively related to solar radiation as recorded by Voldeng and Blackman (1973) in Zea mays.

III. Nutrient uptake at different growth stages

Nutrient uptake is a function of the age of the plant, its genetic make-up, climate, edaphic factors, quantum of fertilizer input and cultural practices. Studies on nutrient uptake in rice were initiated as far back as in 1918, when Aso published a book on the nutrient uptake of the plant at different growth stages.

Ishizaka and Tanaka (1952) divided the major nutrients into three groups. Nitrogen, phosphorus and sulphur comprising group-I were absorbed vigorously during growth and attained maximal values by flowering, after which their rate of absorption was low. More than 70 per cent of these elements moved to the ear after flowering. Potassium and calcium, making up the second group, were absorbed up to dough stage. Translocation of potassium from leaves to panicle was limited.
Magnesium, constituting group-III, showed a slow rate of absorption till flower primordia formation, after which it became high.

Ishizuka (1932), Osugi et al. (1933) and Kasugai (1939) gave a qualitative expression of N requirement at different growth stages in relation to grain yield. Ishizuka (1932) reported that N starvation ten weeks after germination did not impair yield. Osugi et al. (1933) also reported that N starvation at later stages did not affect yield. Kasugai (1939) found that N starvation two months following planting scarcely affected yield, but earlier starvation adversely affected yield.

Matsushima (1964) found that nitrogen absorbed just after establishment of the plant determined the tillering capacity of the plant, which in turn, determined the ear bearing tillers. Nitrogen absorbed during reproductive phase decided the number of spikelets per panicle and that at full heading influenced the percentage of ripened grains and 1000 grain weight.

Takahashi et al. (1955) found a rapid absorption of N, P and K during the tillering stage. During the elongation period, there was a decrease in N and K absorption while that of P and Mn increased remarkably. Seshagiri Rao and Krishna Rao (1961) reported from their studies on the medium duration varieties HR10 and HR104.
absorption curves for N and P to be sigmoidal, with two absorption peaks, one at vegetative and the other at reproductive stages. A major proportion of the absorbed N and P moved to the grain. Tanaka (1964a) observed that during early stages of growth, the N uptake was rapid in Peta than in Tainan-3; further, while it ceased at some stage in Peta, uptake continued up to maturity in Tainan-3. In BPI.76 the uptake was vigorous during active vegetative phase, slowed down during active lag phase, spurted again after ear initiation and after reaching a peak, decreased. Tanaka (1957) also reported variations in the nutrient uptake of 3 varieties, Pth.10, T.141 and BA1.2 belonging to early, medium and late maturing varieties. Mikkelsen (1970) observed nitrogen absorption to be slow at first, rapid during vegetative stage and then to decline rapidly after flowering; but phosphorus uptake was observed to be continuous during the entire growing season, by the time of heading two-third of the total phosphorus, to have already accumulated. He further noted that potassium accumulation occurred a little faster than either nitrogen or phosphorus, about three-fourths of the total requirement having been absorbed by booting. Potassium did not accumulate in grain as did nitrogen and phosphorus. Ali and Morachan (1973) while studying nutrient uptake in IR.8 and IR.20
found more nitrogen and phosphorus content at early stages; potassium content was high at harvest. Mehrotra et al. (1963) also reported nitrogen and phosphorus to be high at tillering. Feng (1963) reported that potassium was absorbed throughout the growth period but Reyes et al. (1962) and Sadanandan et al. (1969) found potassium absorption to be more at tillering and flowering and to decline towards maturity.

Nathuswaray et al. (1973) while studying nutrient uptake at different growth stages in cultivars, Karuna, Kavari and Kanchi at five fertility levels found highest uptake of N, P and K in Kanchi followed by Karuna at all growth stages. Uptake of nitrogen was slow up to panicle initiation, rapid between panicle initiation and flowering and considerably slow after flowering. The uptake of P and K was highest between primordial initiation and flowering stages.

Patnaik and Mania (1969) concluded from their studies on four high yielding varieties that nitrogen and phosphorus were vigorously absorbed from planting up to flowering; potassium was absorbed from planting up to dough stage and a major proportion of absorbed nitrogen and phosphorus translocated from shoot to panicle, while the magnitude of translocation of potassium was comparatively less.
IV. Response to nitrogen

About four decades of field experiments in India have shown that more often than not, higher doses of over 44.8 kg/ha of nitrogen were detrimental to crop yield (Ghose et al., 1960). Usually, rice varieties in the *japonica* group show higher yield responses than those in the *indica* group (De Geus, 1957; Beachell and Evatt, 1961).

The relation of morphological traits to nitrogen responsiveness drew attention ever since the pioneering work of Tsunoda (1959a, b, 1964b). Probably, height of the plant is more important in deciding the nitrogen responsiveness. Tall, weak-strawed varieties lodge early and easily under high N supply (Usali et al., 1966; Basak et al., 1962; Singh and Takahashi, 1962; Chang, 1964; Jennings and Sornchai, 1964; Mukherji et al., 1962; Chandler, 1969b). Lodging-susceptible varieties are characterised by an elongation of the two basal internodes beyond 4 cm when grown at high fertility levels (Chang, 1967). Lodging reduces the cross-sectional area of vascular bundles, which interferes with the translocation of assimilates and nutrients. Added to this is the change in the leaf display causing increased shading (Hitaka, 1968). A shorter culm is usually associated with erect leaves (Hayashi and Ito, 1962;
Tanaka et al., 1966a). Respiration loss in the culm is also considerably abridged by a short stature (Tanaka et al., 1966a). All the same, for light penetration tallness shall be more conducive (Murata, 1961).

Erect leaf habit is related with nitrogen response (Yoshida, 1972). Baba (1961) summarised that varieties less adaptable to heavy fertilization show increase in leaf area and leaf weight, an abundance of lignin and cellulose and feeble amount of straw carbohydrates under high N application. Root length is curtailed under higher N level and the decrease in root development caused by increase in N level is marked in low-response varieties than in high response varieties (Tanaka et al., 1958).

Low nitrogen response varieties absorb nitrogen more actively than do high nitrogen response varieties at the early stages of growth (Matsuo, 1952; Takahashi et al., 1969). In indica varieties, sterility was closely correlated with the degree of N response. Ota and Yamada (1965) reported that heavy doses of N fertilizer greatly increased percentage of sterility. A similar phenomenon was also observed by Togari and Kashiwakura (1953).

V. Photosynthesis, translocation, source and sink relationship

Yield in a crop plant is related to both total assimilation during a growing season and partition of
the acquired material between harvestable storage structures and the rest of the plant (harvest index).

In a plant population, photosynthetic production increases linearly with increase in the size of foliage area per ground area (leaf area index). However, this increase is not indefinite but is limited by competitive canopy, whereby the mean photosynthetic production per unit leaf area (net assimilation rate) is reduced. However, the existence of an optimal LAI has been a much debated subject. There is considerable disagreement as to whether photosynthetic production reaches a zenith value at an optimum LAI or whether this value is attained asymptotically with increasing LAI.

The existence of an optimum leaf area for a rice community was established theoretically by Monsi and Saeki (1953) and experimentally by Yin et al. (1960), Murata (1961), Takeda (1961), Hayashi and Ito (1962), Kanda and Sato (1963), Tanaka et al. (1966a) and Tanaka and Kawano (1966). But other investigators, notably Wang and Wei (1964) and Yoshida et al. (1972), could not, in general, confirm the presence of an optimum LAI.

A reduction in net photosynthetic production beyond an optimal LAI is likely because respiration will be unaffected by mutual shading and shall proceed at a constant value for all leaves. Further, the shaded lower leaves drain photosynthetic products from the photosynthe-
sising organs (Havasero and Tanaka, 1966). This conten­
tion, however, is being questioned. Ludwig et al. (1965) 
and King and Evans (1967) have shown that dark respira­
tion rates of lower leaves in a canopy are lower than 
in the apical leaves. Loomis et al. (1967) have also 
shown that leaves below light compensation (shaded 
leaves) do not represent a major sink importing sugars 
from the upper leaves.

(1) Changes in photosynthesis

Varial variations in photosynthetic efficiency 
in rice have been reported (Murata, 1957; Osada, 1966; 
Chandler, 1969a; Murty and Nayak, 1970; Murty et al., 1973).
It is considered that the rates of photosynthesis recorded 
experimentally may not represent the true inherent 
values characteristic of the species (Stoy, 1969). Even 
if plants are exposed to identical extrinsic factors, 
the behaviour of the plant may be considerably altered 
by intrinsic factors. Thus, a significant reduction in 
photosynthesis has been shown to occur when the storage 
capacity or sink is removed for aν., ear in wheat 
(King et al., 1967), fruits from tomato (Moss, 1962) and 
tubers of a potato (Burt, 1964). Similarly, removal of 
the source has resulted in increased photosynthetic 
rates. Thus, removal of a portion of leaves in rice 
(Lizandr and Drovtsyna, 1964) resulted in a remarkable
increase in photosynthetic rates of the rest of the leaves.

It is now well established that foliage below the flag leaf makes little contribution to grain yield in rice. The flag leaf carbohydrate contribution is about 60 per cent and in combination with the second leaf 90 per cent (IRRI, 1972). The efficiency of lower leaves below the second leaf is inferior to the top leaves (Murata, 1963). Compared to leaf blade, the efficiency of ear and leaf sheath is negligible (Yoshida, 1972).

There is immense data to show the role of nitrogen in promoting photosynthetic activity (Mitsui and Ishii, 1938, 1939; Osada, 1964, 1966; Osada and Murata, 1965; Murata et al., 1966; Tanaka et al., 1966a; Rao, 1972). All the same, Murata (1961) reported that nitrogen supply, sometimes, by promoting leaf growth, reduces the nitrogen content of leaf relatively less compared to other nutrients. Under such conditions photosynthetic activity is lowered. Photosynthetic activity was proportional to nitrogen content of leaf (Fujiwara, 1964; Murata et al., 1966). Photosynthetic activity is also associated with thickness of the leaf (Murata, 1961; Tsunoda, 1964b).

(ii) Translocation

A major proportion of the photosynthetic products is exported out and only a very small fraction is retained at the site of production (leaves). A
juvenile leaf drains photosynthetic products from other parts of the plant, but soon becomes self-sustaining and begins to expatriate assimilates (Jones et al., 1959).

There is also a division of labour among the leaves. The apical leaves supply the growing part of the shoot and the lower leaves deliver their goods to the roots (Tanaka, 1953a, 1961b).

Sieve tubes of the phloem being the main conduit of the assimilates, its size and longevity greatly tell upon the translocatory volume and velocity. Murata (1969) presumed that nitrogen can influence translocation through its effect on the development or longevity of the conducting tissue. When all tillers, barring the main culm were excised the cross-sectional area of the conducting tissue was found to be larger by Matsushima (1957).

(iii) Source-sink relationship

Two or rather three hypotheses have been advanced to explain the source-sink relationship. The first concept is that the source activity is dependent upon the sink demand or size. Removal of the sink promotes accumulation of assimilates in the source which, in turn, impairs photosynthesis (Tsuno and Fujise, 1965; Tanaka and Fujita, 1971). The second theory assumes that the source activity is governed by certain hormones effluxed from the sink. Disturbance
of any kind in the sink reduces the hormonal supply which is reflected in a reduced photosynthesis (Sweet and Wareing, 1966; Bidwell and Turner, 1966). A third, which is a compromise between the two, states that the efflux of assimilates from the source is prodded by hormones produced in the sink, preventing thus the accumulation of assimilates in the source (Seth and Wareing, 1967; Hew et al., 1967). However, it is not known whether hormonal influence on photosynthesis is direct or indirect through enhanced translocation rates. Direct influence gains buttress from the finding by Treharne and Stoddart (1963) in clover, of a close correlation between photosynthetic rate and gibberellin content of leaves.

VI. Plant submergence and its effects

(i) Survival of seedlings under submergence

Initial height of the seedlings is no index of their capacity to tolerate submersion. However, older seedlings are more tolerant than the younger ones (Ramiah, 1953). But Palada and Vergara (1972) report that tall Petä was significantly more resistant than short Petä. The percentage of survival was significantly higher in plants grown at lower nitrogen level than at the higher level (Palada and Vergara, 1972).
Yamada (1959b) also reported that nitrogen top-dressing before flooding caused a large decrease in resistance against submergence. Again survival was poorer in turbid water than in clear water (Kondo and Okamura, 1934; Oka and Kubota, 1961; Palada and Vergara, 1972). While Palada and Vergara (1972) attributed this phenomenon to decreased light transmittance in turbid water, Kondo and Okamura (1934) explained it to be due to the mud that adhered to the plant even after recession of submergence. Survival was better under lower water temperature than at higher temperature due to presence of more green leaves in the former (Kondo and Okamura, 1932; Palada and Vergara, 1972). Survival rate decreased with depth of water and increased with light intensity (Palada and Vergara, 1972).

Tolerance to submersion bears a high positive correlation with total carbohydrates or starch content; no significant correlation exists between resistance and sugar or insoluble nitrogen content (Yamada and Ota, 1956). Palada and Vergara (1972) also stated that seedlings with more initial carbohydrates survive better. Resistance to submersion has a negative relationship with the respiratory rate (Yamada and Ota, 1957).

(ii) Morphological changes

One of the primary effects of submergence is the reduction in the number of tillers (Ghosh, 1945,
Increase in height is also a natural concomitant of submersion (Basak, 1957; Koyama et al., 1962; Basak et al., 1962; Vamadevan, 1971; Roy, 1972).

(iii) **Anatomical changes**

Submergence also brings about changes in the anatomy of the rice plant. Thus Parija (1941) observed development of sclerenchymatous tissues in the leaf sheath of plants subjected to prolonged submersion. Roy (1972) observed in the culm restriction in the number of vascular bundles, reduction in the number of parenchyma layers and development of prominent air cavities under submergence.

(iv) **Physiological changes**

The submerged rice plants show reduced respiratory and photosynthetic rates of leaves compared to the control plants. At the end of three days of submergence, the respiratory rate was around only 30 per cent of the control; and the photosynthetic rate about 50 per cent (Yamada and Ota, 1951). When submerged, reducing sugars and sucrose were consumed rapidly, while acid hydrolysable polysaccharides including starch and hemicellulose were also decreased to some extent. Protein hydrolysis was observed to be inhibited by deficiency of oxygen. Soluble nitrogenous fraction increased soon after flooding.
reaching a peak and then decreased (Yamada et al., 1951, 1955). Reduction of starch observed under submergence was greater at low than at high submergence level (Palada and Vergara, 1972).

Kawase (1974) reported in sunflower the accumulation of ethylene in roots and the immersed portions of stem when the plants were partially submerged and stated that the increase in ethylene concentration was largely, if not exclusively, responsible for such flooding damage symptoms observed as hypertrophy of hypocotyls, new root formation from hypocotyls, leaf epinasty (drooping) and chlorosis. Accumulation of ethylene under submergence which may account partially for the degeneration of roots has also been indicated in rice (Sircar, personal communication).

(v) Critical stage of submergence

Yamada (1963) reported that rice plants at the active tillering stage (during 10-20 days after planting) and flowering suffer the most serious damage from submergence. Workers at IRRI showed that yield loss was high when the crop was submerged at the seedling or panicle initiation stage (Anonymous, 1971). They further observed that a crop that was submerged at the seedling stage bore few panicles and those submerged at panicle initiation less spikelet number/panicle and grain weight.
VII. Low light intensity and its repercussions on plant behaviour

Rice yields are directly related to light intensity (Stansel, 1966). There are two stages at which low light intensity has a critical effect on grain yield. It depresses grain yield either by increasing the number of degenerated spikelets at the reduction division stage or by impairing grain filling (Matsushina, 1957). Ample evidence indicates a close positive correlation of rice yield and the amount of solar radiation during the period from reproductive stage to maturity. Thus, solar radiation received from 10-15 days prior to flowering up to harvest (Murata, 1964; De Datta and Zarate, 1970), or during the ripening period (Moomaw et al., 1967; Munakata et al., 1967) is associated with grain yield.

Though, photosynthesis of single rice leaves does not increase beyond light intensity of 50 k lux (Murata, 1961), that of a rice community has a linear relationship with light intensity up to about 70-90 k lux (Togari et al., 1956; Murata, 1961; Takeda, 1961; Tanaka et al., 1966a; 1969).

The low rice yields during kharif or rainy season when compared with rabi or summer season, may, thus be ascribed to weak light intensity during the wet season.
A favourable yield response to high levels of nitrogen accrues only under high light levels (Tanaka et al., 1964; Stansel et al., 1965; Stansel, 1966).

Light is not necessarily a limiting factor of yield early in the growth of the rice plant. However, as the plants grow in stature and put forth more leaves, light levels become progressively more critical, primarily due to mutual shading of one plant by others and of lower leaves by upper leaves (Stansel, 1966). The ratio of soluble to total nitrogen was larger in the shaded than in the exposed leaves; the shaded leaves lacked starch and contained less sugars and phosphorus (Navasero and Tanaka, 1966). Under limited light, leaf protein was degraded into amino acids, amides and ammonia, and these were prone to leaching by rain or dew (Tanaka and Navasero, 1964).

Thus high light is indispensable for high photosynthetic activity, formation of more spikelets, better grain filling and greater nitrogen response (Yoshida, 1972).

VIII. Role of nitrate reductase, RuDP carboxylase and phenols in plant metabolism

(i) Nitrate reductase

Nitrogen constitutes approximately 2 per cent and carbon approximately 40 per cent of the dry weight of plants. Species having a symbiotic relation with
nitrogen-fixing bacteria apart, the bulk of the plant nitrogen comes through the reduction of nitrate taken up from the soil (Beevers and Hageman, 1969). The incorporation of the inorganic nitrogen into organic nitrogen requires the reduction of nitrate to the valence level of NH$_3$, and the first step of reduction of nitrate to nitrite is catalysed by the enzyme, nitrate reductase (Conn and Stumpf, 1971). There is a preponderance of evidence that nitrate reductase from leaves of most plant species has a specific requirement for reduced nicotinamide adenine dinucleotide (NADH) as electron donor (Beevers et al., 1964; Sanderson and Cocking, 1964; Maretski and Dela Cruz, 1967). However, the question of the source of NADH has been an enigma. Observations of Sanderson and Cocking (1964), Maretski and Dela Cruz (1967) and Miflin (1967) suggest the respiratory metabolism to be the source of the electron donor. But those of Beevers and Hageman (1969) and Klepper (1969) imply photosynthetic cycle to be the source, generation of the reductant to emanate from the carbon products formed during carbon dioxide fixation.

Though the presence of the enzyme can be demonstrated in all plant tissues, the activity in leaves appears to be always in excess of that in roots in crop plants. Thus, Candela et al. (1957), Hageman and Flesher (1960a) and Maretski and Dela Cruz (1967).
reported low levels of nitrato reductase in extracts of roots from cauliflower, corn and sugarcane respectively. Similar results were reported in peas by Wallace and Pate (1965) and in barley by Miflin (1967).

The enzyme is characterised by its susceptibility to a wide spectrum of environmental conditions. It has been established that mineral nutrition, light, drought, temperature, plant age, and genetic composition—all influence the capacity of nitrate reduction.

Evidence that nitrate reductase is inducible by nitrate has been provided by several workers (Canclina et al., 1957; Tang and Wu, 1957; Hewitt and Afridi, 1959; Hageman and Flesher, 1960a, b; Afridi and Hewitt, 1962, 1964; Morris and Syrett, 1963; Beevers et al., 1965). A feature of these observations is that different levels of nitrate are required for optimum induction in different species. These differences point to differences in nitrogen uptake because with a given species the level of enzyme is dependent upon the concentration and rate of supply of nitrate to the tissue (Beevers et al., 1965). However, Bowerman and Goodman (1971) found no correlation between nitrate uptake or concentration with enzyme activity in Lolium.

The induction of the enzyme in response to inducer is related to age (Afridi and Hewitt, 1964; Kannangara and Woolhouse, 1967). Increasing maturity
is associated with decreased enzyme inductibility and this may be either due to decreased protein synthesis or accumulation of soluble nitrogenous products, that repress synthesis of the enzyme (Bevers and Hageman, 1969).

Molybdenum has also been reported to induce the enzyme activity (Candela et al., 1967; Hewitt and Afridi, 1969; Afridi and Hewitt, 1964).

Nitrate reductase level varies diurnally (Hageman et al., 1961; Roth Bejerano and Lips, 1970; Bowerman and Goodman, 1971), and is influenced by intensity of illumination (Bevers et al., 1967; Hageman et al., 1961; Sanderson and Cocking, 1968; Kannangara and Woolhouse, 1967; Bevers and Hageman, 1969; Chen and Ries, 1969; Travis et al., 1969, 1970). However, the role of light is difficult to delineate and is being elucidated variously by various investigators. It is not clear whether the mode of operation of light vests in its effect on the enzyme nor aq (Hageman and Flesher, 1960a), availability of nitrate (Bevers et al., 1967), generation of reductant (Evans and Mason, 1953), enzyme cofactors (Bowerman and Goodman, 1971) or protein synthesis (Travis et al., 1970; Glyan’ko, 1973).

Supra-Optimal temperatures and moisture deficits also result in a relatively rapid decrease in nitrate reducing ability in corn (Mattas and Pauli, 1965).
Younis et al., 1965; Schrader et al., 1963), in barley (Onwueme et al., 1971) and in wheat (Plaut, 1974). Plaut (1974) also reported inhibition of the enzyme activity as a result of NaCl application. Bardzik et al., (1971) and Maranville and Paulsen (1972) found a distinct drop in enzyme activity of maize seedlings when relative water content of leaves was reduced by 10 to 20 per cent as a result of withholding irrigation. Plaut (1973) noted a significant decrease in enzyme activity of wheat seedlings when relative water content was reduced by only 7 per cent.

It is, however, not known whether with changes in environment the enzyme is only inactivated, completely destroyed or synthesised poorly (Seevers and Hageman, 1969).

(ii) RuDP carboxylase

Ribulose 1,5-diphosphate carboxylase, also known as carboxydismutase, catalyses the reaction of carbon dioxide with ribulose 1,5-diphosphate, the first step in the Calvin's cycle, and is probably the enzyme responsible for the bulk of carbon dioxide fixation in most green plants.

Wildman and Bonner (1947) found that a major fraction of the total soluble protein in leaves is fraction-I protein, the principal component of which is carboxydismutase (Gibbs, 1967). That RuDP carboxylase is identical with fraction-I protein has also been
recorded by many other workers (Weissbach et al., 1956; Lyttleton and T'so, 1958; Irown, 1965).

There is a plethora of evidence that indicates a close relationship between RuDP carboxylase and photosynthetic capacity. In investigations on the development of enzymes after etiolated plants were exposed to light, changes in carboxydismutase activity and photosynthetic capacity were found to be almost parallel (Lascelles, 1960; Hudock and Levine, 1964; Hudock et al., 1964; Levine and Togasaki, 1965). Chlamydomonas muscicena grown autotrophically was capable of photosynthetic carbon dioxide fixation, but cells grown heterotrophically were unable to fix carbon dioxide, ascribable partly to low activity of carboxydismutase (Russell and Gibbs, 1966). During leaf development in bean, Smillie (1962) found that carboxydismutase activity roughly paralleled the rate of light saturated carbon dioxide fixation.

Carboxydismutase is housed entirely in the chloroplasts (Heber et al., 1963; Smillie, 1963; Slack and Hatch, 1967; Latzko and Gibbs, 1968). Synthesis and activation of this enzyme are connected with the structural differentiation of chloroplasts (Kannangara, 1968) because of the existence of a close association between accumulation of chlorophyll and the enzyme activity. However, Nagy et al. (1971) found the enzyme activity to be independent of chlorophyll content of the leaves.
They, however, contended that a common mechanism reigning the synthesis of both RuDP carboxylase and chlorophyll cannot however be ruled out. Huffaker et al. (1970) were of the opinion that initial induction of carboxylase and chlorophyll may be related, but after induction, the carboxylase was not linearly correlated with chlorophyll and had a different temperature optimum.

Synthesis of the enzyme takes place upon illumination (Chen et al., 1967; Margulies, 1964, 1966). In dark the enzyme does not perform its function (Siggins and Park, 1966; Margulies, 1966). Bjorkman (1968) also reported that the enzyme is more in sun-adapted than in shade-adapted plants. Huffaker et al. (1970) reported the synthesis of carboxylase activity to be effectively blocked at 10°C.

(iii) Phenols

Phenolics make up a vast class of compounds comprising anthocyanins, leucoanthocyanins, anthoxanths, hydroxybenzoic acid and coumarin derivatives.

Two possibilities for the synthesis of phenolics from carbohydrates have been demonstrated in higher plants, the shikimate and the acetate pathways. The most important of the two is the former leading to the biosynthesis of aromatic amino acids. The phosphoenol pyruvic acid derived from the glycolytic pathway, and the
erythrose phosphate from the pentose phosphate respiratory cycle combine to form shikimic acid through various intermediaries, like deoxyheptulosonate phosphate, dehydroquinic acid and dehydroshikimic acid. The shikimic acid formed thus, is converted again, through various intermediaries (phosphoshikimic acid, enol-pyruvyl-shikimate phosphate, chorismic acid) gives rise to prephenic acid, which serves as a branching point in this route, being converted to either phenylalanine or tyrosine. The intermediaries of phenylalanine and tyrosine pools serve as precursors of various aromatic compounds. Thus through deamination of phenylalanine by phenylalanine deaminase, cinnamic acid is formed and its hydroxylation leads to the formation of other phenolic cinnamic acids such as p-coumaric, caffeic acid and ferulic acids. Reduction of phenolic cinnamic acids to the cinnamyl alcohol, followed by oxidative polymerisation of the alcohols plays an important role in the formation of lignin (Goodman et al., 1967).

There seems to be a connection between protein metabolism and the phenol-phenolase system. Some oxidised phenol compounds with amino acids, peptides and simple proteins, called 'adducts', act as catalysts for the oxidative deamination of amino acids (Hess, 1958). Complex phenolics of high molecular weight and their oxidation products have also been found to be effective
inhibitors of pectic enzymes, thereby influencing cell wall metabolism (Williams, 1963).

Phenols inhibit the peroxidase catalysed oxidation of IAA by acting as antioxidants (Stonier et al., 1968) and thus IAA is preserved in their presence. However, the role of phenolic compounds in IAA oxidation is both voluminous and confounding. That polyhydroxyphenols inhibit the oxidation of IAA has been reported by a plethora of workers and for a complete list of them one is referred to Stonier et al. (1970b). However, not all phenols inhibit the oxidation. Goldacre et al. (1963) were among the first to demonstrate that IAA oxidation is usually accelerated by monophenols and impeded by diphenols, an observation since supported by numerous workers. This distinction resides in the electron donating or accepting tendencies of the compounds involved. Thus Gaspar (1966) reported that m-diphenols act as activators of IAA oxidation, whereas p-diphenols, and especially the o-diphenols serve as inhibitors. But in vivo studies of Mitsch and Mitsch (1962) present a totally different picture. They found that m-diphenol inhibited the elongation of oat mesocotyl segments while o-diphenol augmented it; p-diphenol which should have promoted elongation actually proscribed it.

Sondheimor and Griffin (1960) showed that addition of coumaric and chlorogenic acids accelerates
or decelerates IAA oxidation, depending upon the relative concentration employed. That phenolics stimulate or inhibit IAA oxidase activity has also been reported by Gottinor and Kent (1953), Varga and Koves (1962) and Mare (1964). The phenolic compounds, in turn, are under the regulation of polyphenol oxidase, which is able to convert monophenols to o-diphenols and o-quinones. Under certain circumstances, the phenolics also accelerate the oxidation of NADH (Stoner et al., 1970a). Because of their dual role of both encouraging and discouraging oxidation, they may be looked upon as metabolic poisons or regulators of redox potential.

Phenolics are generally relegated to the juvenile regions in plants, like growing apices (Yoneda and Stonier, 1967). They are also associated with mature stem tissue responding to injury (Stoner, 1960). Further, they exist along a gradient from young to old tissue, their concentration being greater at the apex of the shoot, with a bipotential decline. Secondly, the IAA oxidase activity displays an inverse gradient, it increasing towards the base (Yoneda and Stonier, 1966, 1967; Stonier et al., 1970b).

Does the review of literature pertain to waterlogging condition?