CHAPTER 2

LITERATURE REVIEW

2.1 Rainfed lowland rice ecosystem characteristics

Rainfed lowland rice is grown in a wide diversity of environments, most of which are located in South and Southeast Asia (Wade *et al.,* 1999a). From the responses of crop nutrition and rice productivity, the main distinguishing characteristics of the rainfed lowlands are lack of irrigation water and intermittent submergence of the soil during crop season. There are two significant and closely linked constraints: variable rainfall and lack of soil nutrients. Intermittent draining and submerging of soils depresses availability of some nutrients especially nitrogen and phosphorus (Bell *et al.,* 2001). Moreover, extreme fluctuations in soil-water levels may impair root activity, further restricting nutrient uptake. Rainfed lowland rice often experienced such conditions within a growing season and from year-to-year.

About 20% of rainfed lowland rice grows in favorable environments where only minor events of drought or submergence limit rice production. These areas are relatively more prevalent in Indonesia, Philippines, Vietnam, Laos and Myanmar (Wade *et al.,* 1999a). In contrast, more than half of the rainfed lowlands of India and Thailand occur in drought-prone environments.

Yields in rainfed lowlands are typically half those in irrigated rice ecosystems (Wade *et al.*, 1999a), it averages only 2.3 t ha^{-1} (IRRI, 1993). In addition, small to medium topographic differences cause considerable short range variability in water availability (Huke *et al.,* 1997; Huke, 1982). The amount and timing of rainfall is considered as the major constraint to rice productivity, followed by low soil fertility, as represented by a range of limiting factors, including salinity, alkalinity, Fe toxicity, sulfide toxicity, and N, P deficiency (Bell *et al.,* 2001). The lack of soil fertility is exacerbated by the effects of a changing soil-water regime on nutrient forms and their availability in the soil. The combinations of these constraints during growing period continue limiting rice production in farmers' fields.

In general, the rainfall pattern in main rice growing regions of Southeast Asia is such that there is insufficient water to submerge the soil and keep at least 15-20 centimetres of standing water in the field as required for wetland rice for the first one or two month of the growing season. Traditionally the rice is sown in seed beds in a small area that can be kept flooded. The seedlings are transplanted out when the main fields are expected to be flooded, e.g. about August in Thailand and about September in Central Vietnam. In Central Vietnam, the summer season is often from June to August and followed by the main rainy season in September to December. Transplanting is often delayed until there is sufficient rainfall at the start of the main rainy season for submergence of the soil to occur. After transplanting the rice plants may still be growing in unsubmerged soil for a period in areas of unreliable rainfall or in years with dry spells. Furthermore, early growth in aerobic soils is also common in areas with direct seeding, which is becoming more common as labour cost rises. It is therefore important for rainfed rice production in Southeast Asia to understand how rice plants adapt to aerated soils in its early growth and then anaerobic condition when the soil becomes submerged, especially in soils that are low in the main limiting nutrients, nitrogen and phosphorus.

2.2 Aerobic and waterlogged (anaerobic) soils

2.2.1 Aerobic soil

In rainfed lowland rice, the soils may be unsaturated and topsoil is often low in moisture content when it has not rained for a long time. The most obvious differences between aerobic and anaerobic (waterlogged) soils are the presence of a layer of standing water and oxygen diffusion in soil bulk (Ponnamperuma, 1975). Rice grown in aerobic condition is better for oxygen supply by diffusing and interchanging O_2 between soil space and the atmosphere. Roots of rice in such conditions normally have long maximum length to facilitate water and nutrients acquisition (Colmer, 2003).

However, nutrients are less available in the soil when moisture content is low or soil has no standing water. Many nutrients are soluble in water particularly of phosphorus; their availability is thus much smaller in aerobic soil (Ponnamperuma, 1975). Therefore, delivery of nutrients to rice roots by both mass-flow and diffusion is decreased (Parish, 1971). A decrease in soil water also influences the uptake indirectly: it reduces contact between the roots and soil solution and affects the redox state of the soil, converting nutrients into unavailable forms (Matsuo *et al.*, 1995). The phosphate ions in soil solution (native soil-P or added-P fertilizer) may either precipitate with the precipitating cations (Fe^{3+} and Al^{3+} hydroxides in acid soils, and $CaCO_3$ in calcareous soils), or become sorbed on the clay minerals and oxy-hydroxides, which can decrease P availability (Willett *et al.*, 1978).

Rice growing in rainfed lowlands experience nitrogen deficiency almost everywhere unless nitrogen is supplied as a fertilizer. The nitrogen regime in aerobic soils is quite different from that in anaerobic soils. Under aerobic soil, the principal form of nitrogen taken up by rice plant is NO_3^-, even in strongly acid soils (Kirk *et al.*, 1998) while in anaerobic soil N is often present as ammonium (Yoshida, 1979). Aerobic soils, on the other hand, unlike waterlogged soils are not able to adjust their pH levels to favorable range of 6.5 to 7. This means that manganese and aluminium toxicities can occur in strongly acid soils, and iron deficiency in alkaline soils (Ponnamperuma, 1975).

2.2.2 Waterlogged (anaerobic) soil

Rainfed lowland rice soils are usually submerged if rainfall is high and persistent, or bunds retain water during the crop season. Ponnamperuma (1972) pointed that a submerged soil has mostly beneficial effects on nutrient availability and uptake by rice plants. Increase in the availability of P and decreased level of soluble Al are particularly significant benefits of submergence on rice growth and nutrient uptake on sandy, acidic low fertility rainfed lowland soils (Ponnamperuma, 1972; Bell *et al.,* 2001). During soil submergence, the concentration of Fe^{2+} in the solution stabilizes, but the level of acid-soluble Fe^{2+} continues to increase (Willett, 1986). The precipitation of ferrosis hydroxides $Fe_3(OH)_8$ on prolonged submerged increases the soil capacity to adsorb P from the soil solution, which causes a decline in P concentration in soil solution (Willett and Higgins, 1978; Sanyal *et al.,* 1991). However, sorbed P may be still acid-extractable, and it may contribute to the labile P pools, and thus remain available to rice plants (Sanyal *et al.,* 1991).

Submergence also has possible negative consequences, including increased levels of Fe^{2+} in some soils, loss of nitrogen (type NO_3^-), sulfide toxicity, organic acid toxicity and Zn deficiency. The availability of N under submerged conditions is different from that on oxidized soils. Under submerged conditions, NO_3^- is subject to losses by leaching, except if an impermeable hardpan exists, and by denitrification in the reduced layers of waterlogged soils. Thus, NO_3^- present in soils at submergence may be lost, whereas nitrogen (type NH_4^+) supplied and incorporated into the waterlogged soil or released by mineralization of organic matter is relatively stable (Bell *et al.,* 2000).

However, when a soil is submerged, oxygen is displaced by water and rapidly depleted (Kennedy *et al.,* 1992). The limiting of oxygen diffusion in the bulk soil becomes a main adverse factor for rice roots growth because they need oxygen for respiration and nutrient uptake (Vlamis *et al.,* 1943 *cited by* Ponnamperuma, 1975).

2.2.3 Changes between aerobic and waterlogged soil conditions

Compared with rice plants growing in waterlogged soils, the rice plants growing in aerobic soils are better supplied with O_2 but more limited in supply of nutrients. The supply of nutrients in aerobic soils is controlled by solubility of the nutrient compounds and the flow rate to the root surface. The compounds of plant nutrients are more soluble with higher water contents, so most nutrients will be less available in aerobic soils than when there is standing water (Fukai *et al.,* 1999).

On the other hand, one important chemical characteristics of soils that is related to soil aeration is the reduction and oxidation states (redox potential) of chemical elements in these soils (Brady, 1974). In aerobic soils, oxidized states such as that of ferric iron (Fe^{3+}), nitrate (NO_3^-), and sulfate (SO_4^{2-}) dominate. In submerged soils (anaeration), the reduced forms of such elements are found, ferrous iron (Fe^{2+}), ammonium (NH_4^+), and sulfides (S^{2-}) (Ponnamperuma, 1972). Thus, the availability of nutrient elements in a soil is per se that influenced by redox potential reactions of that soil (Ponnamperuma, 1972; Brady, 1974). However, the fact that the redox potential stages of a soil most depending on that soil aeration, which related to soil moisture content (soil-water regimes) (Brady, 1974).

After submergence, soil microorganisms rapidly deplete the O_2 in the soil, because the rate of O_2 diffusion is about 10^4 times slower in water-filled than in air-filled soil pores (Ponnamperuma, 1984). Ponnamperuma (1972) also reported that many rice soils experience an increase in soil solution or extractable P form during the first few weeks of flooding or around the time of cultivation. In Northeast Thailand exhibit an increase in available P soon after soil flooding, but the effect is short-lived, and P deficiency is still widespread in these rice growing areas (White *et al.,* 1997a; Seng, 2000). The behavior of P in waterlogged soils is markedly different from that in dry soils. Submergence of a dry soil in general increases the P concentration in the soil solution (Patnaik, 1978), because of the release of absorbed and co-precipitated P following the reduction of Fe^{3+} compounds. Willett (1991) also pointed out that in anaerobic soil, a flush of easily-extractable soil P in first few days follows soil submergence for rice growth as a result of chemical reduction processes.

In addition, within a few days of submergence, NO_3^- is reduced and lost as N_2 and N_2O, while NH_4^+ tends to accumulate as a result of N mineralization. NH_4^+ is nitrified to NO_3^- in the thin oxidized surface layer and the rice rhizosphere (Dobermann *et al.,* 2000). Nitrate is highly mobile, however, and may leach or diffuse into the reduced soil layer, where it is quickly lost due to denitrification (as gaseous N_2 and NO_2) or leaching (in course texture soils). Some of the NH_4^+ diffusing towards rice roots from the bulk soil is probably oxidized to NO_3^- in the rhizophere of rice and absorbed by roots in the NO_3-N form (Dobermann *et al.,* 2000).

Generally, the effects of change aeration and anaeration of soils on nutrient transformations particularly P, and subsequent effects on crop growth are of importance in the rainfed lowland rice ecosystem, which frequently experience losses of soil-water saturation caused by erratic rainfall. However, the practical implications of the intermittent loss of soil-water saturation in the rainfed lowland system for N and P nutrition of rice have not been fully investigated (Seng *et al.,* 1999).

2.3 Adaptation of rice to aerobic and anaerobic conditions

In rainfed lowland environments, rice plants may experience extremely variable water-soil regimes during growth. After transplanting, the plants may still be growing in unsaturated soil for a period in areas of unreliable rainfall or in years with dry status. However, subsequently soils may be submerged when rainfall is sufficient to keep standing water in the fields. Therefore, the process of acclimation of the rice roots in aerobic soils is very different from that in anaerobic soils. In aerobic soils, the roots do not have any problem of oxygen supply for respiration. The essential constraints in aerobic soils are water and nutrients availability. Under aerobic condition, rice roots are modified morphologically to facilitate water and nutrients uptake. Colmer (2003) found that roots formed in aerobic condition are longer than that in anaerobic condition, but had fewer adventitious roots. The aerobic rice roots are more elongated for water uptake at deep layer in soils.

In waterlogged or anaerobic soil, oxygen becomes the limiting factor for root function and growth. Root of rice is essentially an aerobic organ; it can be damaged in anaerobic conditions by reduced aerobic respiration. Root growth into waterlogged soils therefore depends upon an internal supply of oxygen, which moves from the atmosphere through aerenchyma in the plant to the root apex (Armstrong, 1979). The adaptation of plants to anaerobic soils is the production aerenchyma that are mostly formed in adventitious roots (Justin and Armstrong, 1987; Visser *et al.,* 1996). Oxygen is transported from the shoot to the roots via aerenchyma (Armstrong, 1979). Oxygen in aerenchymatous roots may be consumed by respiration or be lost to the rhizosphere via radial diffusion from the root (Kirk and Du, 1997). In addition, in order to reduce the radial oxygen loss, roots may induce a barrier (Colmer *et al.,* 1998). However, one possible drawback of the barrier may be inhibition of nutrient absorption by anaerobic roots (Colmer and Bloom, 1998). While the axial root with aerenchyma is inefficient for nutrient uptake, new fine lateral roots are induced for nutrient absorption (Kirk and Du, 1997). A critical question is how the rice plant under intermittent aerobic and anaerobic conditions balances between its aerenchymatous roots for O_2 supply and the fine lateral roots for nutrient uptake.

2.4 Adaptations of rice to low phosphorus

Phosphorus deficiency is widespread in many rainfed lowland rice ecosystems and is a major growth limiting factor for rice plants (Mackill *et al.,* 1996). The cause of limiting P supply for rice crops may be low total P content and/or a high P sorption capacity of the soil. Phosphorus is mobile within the plant and promotes tillering, root development, early flowering, and ripening (Dobermann *et al.,* 2000). The addition of mineral P is required fertilizer when the rice plant's root system is not yet fully developed and the native soil P supply is small (Yoshida, 1979; Dobermann *et al.,* 2000). Rice plants absorb most of their P requirements at the initial growth stages and relative uptake decreases as the plant ages (De Datta, 1981; Yoshida, 1981). In P-sufficient plants, P absorbed by roots is transported through the xylem to the younger leaves. In addition, there is significant re-translocation of P in the phloem from older leaves to the growing shoots and from the shoots to the roots. In P-deficient plants, the limited supply of P to the shoots from the roots via the xylem means that both the younger leaves and growing shoots are heavily dependent on mobilization and re-translocation of P from the older leaves (Schachtman *et al.,* 1998).

In general, in aerobic soils three main factors contributing to P uptake efficiency: root geometry effects, mycorrhizal effects, and solubilization effects (Kirk *et al.,* 1998). Simple geometrical considerations indicated that long fine roots provide a greater absorbing surface per unit mass than short thick ones. Thus, a system of long fine roots is likely to be the best for P capture, and increases in surface area caused by increased root length conserve root mass more effectively than increases in root radius. Some plants are able to increase the length and fineness of their roots when subjected to low P conditions (Foeshe and Jungk, 1983). Kirk and Du (1997) also reported that P deficiency rice plants are an increase in roots elongation, lateral roots number, root dry mass and root surface area but reduces plant dry mass. Thus, P-deficient plants typically have higher root:shoot ratios than P-sufficient plants (Gutschick, 1993; Nielsen *et al.,* 2001; Kirk *et al.,* 1998). Furthermore, upland rice can have rooting depths between 70 and 80 cm (Morita and Abe, 1996). Roots of upland rice are usually deeper and longer in length in order to facilitate for nutrient uptake at depth soil layers.

In contrast, rice roots growing in anaerobic soils tend to be less hairy than those in aerobic soils (Ladha *et al.,* 1998). Plants are also able to concentrate their roots in P enriched soils. The rate of development of the root system in zones containing P is also important, particularly in rainfed lowland environments where root growth must be rapid at the onset of rains so that subsequent dry periods can be survived (Kirk *et al.,* 1995). In addition, lowland rice has an unusually shallow root system. Generally, 70% or more of the roots are in the 0-10 cm layer, 90% in the 0-20 cm layer, and very few roots penetrate below 40 cm (Sharma *et al.,* 1994).

2.5 Simulation of aerobic and waterlogged soils by using nutrient solutions

Rainfed lowland rice encounters an unfavorable environment during the same growing season. It is therefore experiences hydrologic conditions changing from unsaturation or no standing water to submergence of soil surface of the paddies field (Wade *et al.,* 1998; Singh *et al.,* 1999; Bell *et al.,* 2001). Such changes have marked effects on soil conditions and the availability of nutrients, especially P availability. In addition, a change of soil-water condition will result in change of O_2 concentration in the bulk soil, inducing hypoxia (low O_2) or anoxia (zero O_2) around the rice rhizosphere (Kennedy *et al.,* 1992). Growing under different O_2 concentration rice plants have to adapt themselves by responses to change in both morphological and physiological characteristics in order to survive and grow (Kirk *et al.,* 1997; Colmer *et al.,* 1998; Wiengweera *et al.,* 1997).

In fact, a study on morphological and/or physiological responses of rice to nutrient applications with changing O_2 concentration is quite difficult to conduct in soil cultures because of above causes. Moreover, the change of rainfed lowlands from aerobic to anaerobic condition is often occurred, but rice plants particularly rice root systems are being grown in such environment can not be easily transferred as examining expectation. To use nutrient solutions as simulative aerobic or anaerobic condition will facilitate not only the control in nutrient supply but also the transitions. Rubinigg *et al.* (2002) have pointed out that using the nutrient solution cultures for study on plant root adaptations and uptake efficiency, which grown in aerated and then transferred to stagnant solution or vice versa is very favorable. Therefore, the study on responses of rice to nutrient supply under changing between aerobic and waterlogged soils is instead of using nutrient solutions.

Aerobic soil is imposed by utilizing nutrient solution with supply oxygen by continuously bubbling air. In contrast, anaerobic soil (waterlogged) is simulated by utilizing stagnant nutrient solution contained 0.1% (w/v) of agar to prevent mixing of atmospheric O_2 into the nutrient solution by convection as well as slow diffusion of O_2 (Wiengweera *et al.*, 1997).

In rainfed lowland systems, rice is often affected by change in aerobic and anaerobic soils that combined with P deficiency. On the other hand, the acclimation processes of rainfed lowland rice are very different and complex under unfavorable environments of cultivated soils. Consequently, this work will investigate how rice plants adapt to change from aerobic to anaerobic condition, especially when external supply of nutrient P is low.