Introduction

In rainfed lowland ecosystems, water supply comes from rainfall, the timing and amount of which can not be controlled. When it has not rained for a long time, rice soil loses water saturation until roots experience aerobic conditions. If rainfall is high and persistent, the soil remains waterlogged and the rice roots encounter anaerobic condition. Rainfed lowland rice commonly experiences intermittent anaerobic and aerobic conditions in the root zone (Zeigler and Puckridge, 1995). Root acclimation to the changing water regimes may in turn affect plant morphological features, physiological function and nutrient uptake efficiency.

In waterlogged soil, oxygen is displaced by water and rapidly depleted (Drew, 1992; Bange *et al.*, 2004). Waterlogged soil is generally anaerobic and chemically reduced (Ponnamperuma, 1972). The pH in anaerobic conditions increases in acid soil, but it decreases in sodic and calcareous soil. Hence pH tends towards neutral in waterlogged soils regardless of the initial pH. The pH value influences nutrient solubility and plant availability, especially phosphorus. Phosphate is released from aluminium phosphates as pH increases while phosphate is liberated from calcium phosphates as pH decreases (Stumm and Morgan, 1970 cited by Ponnamperuma, 1972). Therefore, oxygen deficiency and changing in nutrient availability in waterlogged soil are main effects on plant growth. Roots respiration is directly reduced by oxygen deficiency. Roots adapt waterlogged condition by increasing the internal supply of oxygen to the root tip from the atmosphere via aerenchyma (Justin

and Armstrong, 1987; Drew *et al.*, 1994; Drew, 1997). This modification of the root cortex by aerenchyma formation enhances longitudinal oxygen diffusion, but might also decrease symplastic nutrient transport across the roots to the main transport vessels in the stele (Drew and Saker, 1986; Kronzucker *et al.*, 1998). Furthermore, in order to minimize the radial oxygen loss (ROL) from the main axes of adventitious roots, rice forms a barrier (Colmer *et al.*, 1998) believed to be related to increased suberization and lignification of the exodermis (Ranathunge *et al.*, 2004). Although such a barrier might cause an inhibition of nutrient and water absorption by roots (Koncalova, 1990; Ranathunge *et al.*, 2003), direct studies of this are few, and the data available indicate that nutrient uptake might not be affected (Rubinigg *et al.*, 2002). Nevertheless, it has been proposed that the axial roots with aerenchyma are inefficient in nutrient uptake, and that new fine lateral roots are induced for nutrient absorption (Kirk and Du, 1997; Kirk, 2003). The fine lateral roots comprise the bulk of the external surface, and they are connected directly into the main water and solute transport vessels in the stele of the primary root (Matsuo and Hoshikawa, 1993). Moreover, roots of rice acclimate to growth in anaerobic condition by increasing the number of adventitious roots per plant, which presumably also contributes to waterlogging tolerance (Colmer, 2003a).

In aerobic soil, the main problems for the rice plant are water supply and nutrient availability. Lower soil moisture content reduces nutrient supply to roots in two ways. Firstly, nutrients are delivered to roots by mass flow and diffusion, and both of these mechanisms decrease with declining soil moisture content (Parish, 1971). Secondly, many nutrients are soluble in water, thus, they are less available in aerobic soil (Ponnamperuma, 1975). Rice plants grown in aerobic soils have a

different structure of roots; maximum root lengths are greater than in the anaerobic media, but plants have fewer adventitious roots and these have lower porosity and also lack a barrier against ROL (Colmer, 2003a). Deep root activity in aerobic soil is supported by oxygen uptake directly from the air-filled soil pores.

The intermittently waterlogged condition that occurs in soils of the rainfed lowland rice ecosystem is likely to have adverse effects on P nutrition of rice on low P soils, due to changes in P availability with varied water regimes (Huguenin-Elie *et al.*, 2003; Seng *et al.*, 2004) and possibly due to adverse effects of soil oxidation/reduction cycles on root function. Phosphorus deficiency depresses plant growth through a reduction in leaf expansion, leaf surface area (Fredeen *et al.*, 1989 cited by (Marschner, 1995) and number of leaves (Lynch *et al.*, 1991). The adaptations of plants for increased P acquisition include mycorrhizal symbioses, rhizosphere modification by secretion of organic acids (Gardner *et al.*, 1983; Lipton *et al.*, 1987; Lu *et al.*, 1999) and proton release (Kirk and Du, 1997). Moreover, roots also increase root surface area by root hair elongation and proliferation (Bates and Lynch, 1996; Ma *et al.*, 2001). However, these mechanisms may not operate in rainfed lowland rice. In rice at low P supply under anaerobic root condition, adventitious root elongation, lateral root development and elongation were all enhanced (Kirk and Du, 1997). Moreover, Fan *et al*. (2003) reported that in maize roots aerenchyma formation is induced by low P status, and this in turn reduced respiration and P requirement in the roots. A similar decline in respiratory costs of root growth in rice with low P may enhance its adaption to such soils. However, the adaption of rice roots in low P soils to the transitions from aerobic to anaerobic conditions and *vice versa* has not been studied. This study evaluated the responses of

morphology and physiology in rice cultivars to changes in oxygen and P supplies, and

how these in turn affect P uptake and plant growth.

Chapter 1

Literature review

1.1 Rice Production

Rice is the staple food of one-third of the world's population. Rice production occurs in temperate to subtropical to tropical climates but 90 % of rice production in the world is in Asia (2004). Outside Asia, centres of rice production include 42 African countries, Oceania, the Po Valley in Italy, several southern states (Arkansas, Louisiana, Carolinas, Texas), and California in the USA (FAO, 1998b).

Rice belongs to the genus *Oryza* consisting of 22 well-recognized wild species and two cultivated species. Most of rice species are diploid with 12 pairs of chromosomes. Some species are tetraploid containing 48 pairs of chromosomes (Chang, 2003). *Oryza sativa* is cultivated throughout the tropics and parts of temperate regions of the world, while *O. glaberrima* is endemic to the savanna of West Africa (Morishima, 1984). The two cultivated rice species are classified by distinguishing characters: *O. sativa* is essentially perennial, while *O. glaberrima* is completely annual and has shorter ligules, fewer secondary panicle branches and a thicker panicle axis (Oka, 1988).

1.1.1 Rice production in Asia

The descent of *O. sativa* is from a wild perennial (*O. rufipogon*) to a wild annual (*O. nivara*) progressing to an annual cultivar (Chang, 1985). The genotypes of

O. sativa are divided into indica and japonica sub-species which have different patterns of character association and gene combination (Chang, 1985; Oka, 1988; Second, 1991; Morishima *et al.*, 1992). Recent molecular analyses have suggested that domestication of indica and japonica rice may have occurred independently from the different ancestral *O. rufipogon* (Londo *et al.*, 2006). Historically, the rice varieties cultivated in the central plain of China before the Sung dynasty were largely of japonica types (Ting, 1949), after that the early maturing indica varieties were introduced from the south, increasing the varietal diversity. Based on variation in grain length and width, rice types are also classified into round grain (japonica) and slender grain (indica type) (Watabe, 1977). Later, Nakagahra (1978) classified *O. sativa* into three japonica, javanica and indica types, to recognize the distinctive large grain type of the tropical javanica varieties. It is still uncertain whether javanica is a sub-species, like Japonica and indica or a subgroup of the japonica type, as considered earlier by Oka (1953; 1958). However, Japonica and indica are the main types of cultivated rice genotypes in Asia, and there have been many studies comparing agronomic characters and disease resistance between them. The results of the research indicated that the indica and japanica cultivars have different genes for reaction to fungi (Morishima, 1969) and different genes for responses to cold and drought stress of rice seedling (Oka, 1953, 1958), and nitrogen uptake ability (Matsuo, 1952; Weng and Chen, 1989) etc.

Recent reports have postulated that the size of rice growing area in Asia is shrinking, under pressure from industrialization and urbanization (FAO, 1998e). Declining profit margin, the overuse of fertilizer and pesticides in rice production, and the shift in government support to facilitate fruit, vegetable and flowers production

and exports also affect rice production (Rerkasem, 2005). In China, which accounts for 34 % of rice production in Asia (IRRI, 2004) land suitable for further expansion of rice is also disappearing by water and wind erosion, estimated to affect some 400 million ha of the region's farm land, while another 47 million ha are subject to chemical and physical degradation (FAO, 1998e). The reduction of suitable rice land directly decreases rice output which in future may fail to meet the food needs of Asia's expanding population. Research is focused on increasing yield by development of hybrid rice with higher yield potential and improved disease and insect-pest resistance. Lafitte *et al.* (2006) reported that research programmes are also developing rice cultivars tailored for different rice ecosystems or specific biotic and abiotic stresses. Atlin *et al.* (2006) reported on efforts to develop superior cultivars for aerobic rice systems and to identify cultivars and germplasm types with high-yield potential under water limited conditions in Philippines and China. Likewise in northern Laos, Saito *et al.* (2006) determined the response of traditional and improved upland rice cultivars under low fertility for selection of rice cultivars which respond well to N fertilizer to increase yield.

1.1.2 Rice production in Africa

Most reports postulated that *O. glaberrima* was domesticated from *O. breviligulata* A. Chev. Et Roehr (Morishima *et al.*, 1963; Oka, 1974; Chang, 1976a; Chang, 1976b) but Richaria (1960) contend that *O. glaberrima* was introduced into Africa from Asia and *O. breviligulata* was a hybrid derivative between *O. glaberrima* and *O. longistaminata* A. Chev. Et Roehr. By contrast Nayar (1973) reported that *O. breviligulata* was a hybrid derivative between *O. glaberrima* and *O. sativa* in Africa. *O. glaberrima* has been grown in the primary area of diversity in West Africa since

1500 B.C (Chang, 2003).   Although, Africa is the home of *O. glaberrima*, the majority of rice varieties cultivated in the continent today belong to *O. sativa.* Japonica cultivars under irrigation are dominant in North Africa and indica sub-species under varying agro-ecological conditions are dominant in Sub-Saharan Africa (FAO, 1998a).   The growing area of *O. glaberrima* has declined and it has been relegated in places to the status of a weed in fields of *O. sativa* (Harlan, 1989). Plant breeders at West Africa Rice Development Association (WARDA) have developed NERICA (New Rice for Africa) cultivars that combine rice types adapted to the local ecosystems with high-yield Asian cultivars (FAO, 2005).   NERICA is drought-tolerant and produces yields 30 % higher than traditional Africa varieties.   These developed varieties for rainfed uplands are suitable in sub-Saharan Africa due to its short growing season, allowing farmers to take advantage of the short rainy season in drought-prone areas.   Further research aims to develop varieties for irrigated and lowland systems in West and Central Africa which cover 20 million ha of inland valley swamps that are well suited for rice production (FAO, 2005).

1.1.3 Rice production in other regions

The other important rice growing regions outside Asia in North and South America, Europe and Oceania.   Brazil and USA have subordinately large of rice production from Africa meaning unclear, Brazil is the most important rice producer in South America, while USA has the largest rice production in North America (FAO, 1998b; IRRI, 2004).   The American continent was almost three folds increase in rice production from 1961 to 1994 which most of the increase in rice production come mainly from improvement in productivity.   By contrast, the rice growing area in South America during 1980-1997 period has decreased result from the substantial

declining in upland rice area in Brazil and to a lesser extend in Mexico, while the rice land in USA has maintained and unchanged in the same period (FAO, 1998b). Rice in South America is grown mostly under upland and irrigated condition, both indica and japonica subspecies are grown in these region. The recent report of Pinheiro *et al*. (2006) presented the evolution of rice production in Brazil that upland rice has been used as a pioneer crop to open the Brazillian savannas "cerrados" areas for cultivation which covered more than 4.5 million ha during the 1975 and 1985. Rice cultivars used in this area were tall, japonica types with drought tolerance and bold grain type. Five years later, the shift of rice to suitable growing zone and development of a aerobic rice cultivars. From 1990 to the present, the rice production development focused on grain appearance, yield potential and blast resistance under the favourable production zones. Present, the production of rice in aerobic systems allows national demand to be met without the large investments in infrastructure and large amount of fresh water for irrigated lowland rice in Brazil (Pinheiro *et al.*, 2006). While in North America, japonica subspecies is dominant under irrigation in following states of the USA; Arkansas, California, Louisiana, Missouri, Mississippi, and Texas (FAO, 1998b).

In Europe, japonica rice is grown only under irrigation during the summer. Rice production in Europe increased rapidly during 1961 to 1988, and then it was rapidly decrease in 1997. Likewise, the rice land also three times decreased from 1989 to 1994 period and stabilized until 1997 (FAO, 1998c). Ocenian rice producing countries are Australia, Fiji, Papua New Guinea, Solomon Islands, New Caledonia, and Vanutu. Most of rice production of Ocenian comes from New South Wales in Australia, where rice was grown under irrigation (FAO, 1998d). Both of japonica and

indica sub-species are grown under varying ecology and rice yields are still low. However, Ocenia from 1961 to 1997 had the highest in the growth rate of rice production in the world from less 200,000 tons to 1,600,000 tons (FAO, 1998d).

1.2 Rice cultivation system

Rice growing systems were developed for specific environments and socioeconomic conditions of farmers. Rice cultivation systems are classified by source of water supply as rainfed or irrigated. Based on the water regime, rice lands are classified as upland (with no standing water), lowland (with 5-50 cm of standing water) and deepwater (with more than 51 cm to 5-6 meters of standing water). Globally the main rice land types are upland rice, irrigated rice, rainfed lowland rice, deepwater rice and floating rice (Fig1.1). In South and Southeast Asia, rice lands are classified into single crop irrigated, double crop irrigated, shallow rainfed, medium-deep rainfed, deepwater, floating and upland rice growing areas (Barker and Herdt, 1979). In all Asian rice growing countries, lowland rice culture is the most common system. Whereas, in Africa and Latin America, upland rice culture is the main system. For West Africa, rice culture is classified into four types and eight subtypes based on climate, soil conditions, water regime and technological level of cultivation (Buddenhagen, 1978).
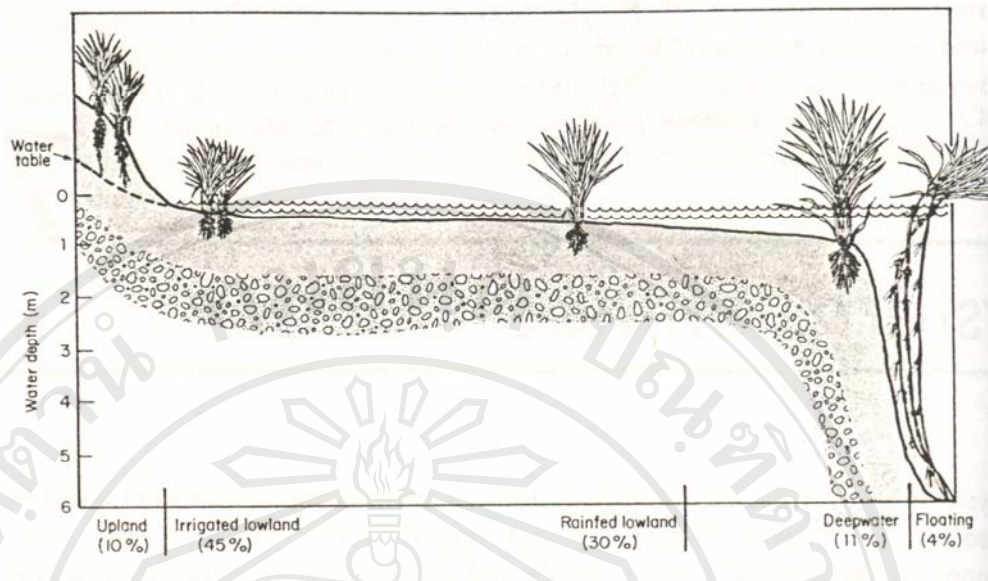
Figure 1.2.1 The rice lands classified by water regime and predominant rice type

1.2.1 Irrigated rice ecosystem

In irrigated ecosystems, rice plants are supplied with adequate water throughout the growing season. Most irrigated areas are located on alluvial river terraces which they are not normally flooded except when the river level raises to its peak. However, river water can be directed through canals and ditches to the rice paddies. The rice fields are bunded and arranged so water can flow under gravity from higher to lower paddies. In irrigated rice lands, rainfall is also an important supplement to irrigation water (FAO, 1998f). Thus, rice yield is not limited by drought. Rice is grown under irrigation during the dry season with intense radiation and insect and disease infestation. In most of irrigated rice areas, farmers have substantially adopted the modern or High Yielding Varieties (HYV) to increase rice production. Hybrid rice was developed and largely used in many countries (FAO, 2000a).

1.2.2 Rainfed rice ecosystem

Rainfed rice ecosystems cover 37 million hectares worldwide, about 25 % of the total rice area (Ingram, 1995; Mackill *et al.*, 1996). However, the rainfed ecosystem covers 50 % of rice production areas in India (DACNET, 2006), and 75 % of rice lands in Thailand (FAO, 2000b). Water supply to rice plants in this system is mainly provided by rainfall, run-off water, and under-ground water. The rainfed rice fields are bunded and transplanting is the main crop establishment method. However, direct seeding has become popular among farmer in many rainfed areas (FAO, 2000b). In general, rice fields are submerged or flooded with water depths varying from 0 to 100 cm for considerable periods during the growing season (FAO, 1998f). Rainfed rice may suffer from both submergence and drought due to the erratic amount

and duration of rainfall. The rainfed rice crop is usually based on traditional or local varieties. Varietal improvement in Asia has focused on the following biological and environmental stress in order of severity and importance (Mackill, 1986): biological stresses - stem borer, bacterial blight, blast, brown spot, and BPH; environmental stress - drought, followed by flash floods and P deficiency (Mackill, 1986). Breeders working in specific environments have developed improved germplasm with adaptation to drought (Maurya and Mall, 1986), submergence (Lamber *et al.*, 1986; Mohanty, 1986) and stagnant flooding (De Datta, 1986).

1.2.3 Deep water and floating rice ecosystem

In the deltas of large rivers such as the Mekong in Vietnam and Cambodia, the Chao Phraya in Thailand and the Ganges-Brahmaputra in Bangladesh, deepwater and floating rice are grown (FAO, 1998f). In Thailand, deepwater rice is established mostly by dry seed broadcasting (FAO, 2000b) Catling *et al*. (1988) have defined deepwater rice as rice that is usually flooded to 50 cm or more for one month or longer during the growing season. Traditional tall indica sub-species are commonly used and known as flooded rice.

1.2.4 Upland rice ecosystem

Upland rice ecosystem is important in Sub-Saharan Africa where it covers 42 % of rice cultivated area (FAO, 2000a; Pinheiro *et al.*, 2006). Upland rice is grown without impound water and no natural flooding of the land. The landscape of upland rice is usually sloping with the ground water table at 50 cm below the surface or deeper (FAO, 1998f). The upland rice is often inter-cropped with maize, cassava and other crop in shifting cultivation.

1.3 Rainfed lowland rice ecosystem

Rainfed lowland rice is the major rice ecosystem in Asia. Hydrologic conditions are the primary factor that influences crop growth and management practice. Mackill *et al.* (1996) divided the lowland rainfed rice ecosystem into 5 sub-types by their hydrologic conditions: depth of flood water in the rice field and susceptibility to drought. The sub-types are shallow, favourable; shallow, drought-prone; shallow, drought and submergence-prone; and medium-deep waterlogged. In Thailand the rainfed lowland rice areas, found in North and Northeast, are mainly of the shallow, drought-prone type. Shallow, drought-prone rice lands generally have a long rainy season, but drought of varying duration frequently occurs in the midseason. Delivery of nutrients to roots by mass flow and diffusion becomes less effective with decreasing soil moisture content (Parish, 1971). Many nutrients are soluble in water, their availability is thus much diminished in aerobic soil (Ponnamperuma, 1975). Moreover, as soil moisture declines in aerobic soil, rice growth may then be adversely affected by moisture stress.

1.3.1 Water soil conditions

The adequate water supply is one of the most important factors in rice production. In tropical Asia, rice plants encounter both too much and too little water because of variable rainfall and landscape patterns. Water affects the physical performance of the rice plant, the nutrient availability, the physical properties of the soils and the weed population.

Rice is a semi-aquatic plant, it prefers more water than other crops. The water requirement varies with the growth stage of a rice variety, type of soil and the physical features of the land. The main water losses from the rice field may be

combined into vapour losses and losses in liquid form. The vapour losses can comprise transpiration loss from the leaf surface and evaporation loss at the water or soil surface. The transpiration rate is affected by soil moisture content, plant characters and plant age. Evaporation rate is affected by solar radiation, temperature, air movement, relative humidity, plant cover and soil water regime. The liquid losses arise from percolation of free water and runoff of excess water over the field barriers. Percolation is the downward movement of free water according to gravity and hydrostatic pressure. Nutrient loss may be affected by high percolation rate. Surface run-off is a significant water loss in both irrigated or rainfed areas and most severe during the wet season. It may affect the soluble nutrient loss from the rice field.

The water requirement varies with growth stage of rice. Rice at seedling stage prefers low water supply in order to maintain oxygen supply for radicle development. Sufficient water is important in the production of tillers and roots during vegetative growth stages. Likewise, the reproductive growth period is sensitive to water stress. Insufficient water supply from panicle initiation to flowering stage increases panicle sterility. Whereas, excessive water at the reproductive stage decreases culm strength and increases lodging.

1.3.1.1 Aerobic soil or drought

Aerobic soils experience reducing nutrient supply to roots because of the lower soil moisture content. Nutrients are delivered to roots by mass flow and diffusion the rates of which decrease as the soil moisture content (Parish, 1971). Many nutrients are soluble in water and increase availability, thus they are less available in aerobic soils (Ponnamperuma, 1975). Moreover, in aerobic soil under low moisture content, rice growth is directly inhibited by moisture stress. Moisture

stress in plant tissues causes poor growth in many crops. Awkward sentence because it links cellular process with a physiological stage (Togawa and Nakagawa, 1937; Kawanara, 1944; Wade *et al.*, 1945; Nagato, 1949, cited by Yoshida, 1975).

1.3.1.2 Anaerobic soil or waterlogging

Waterlogging occurs when oxygen level in the soils is depleted. Oxygen is rapidly depleted and soil is saturated by water replacing the air in the pore spaces of saturated soil (Drew, 1992; Bange *et al.*, 2004). Oxygen diffusion rate decreases to 1/10,000 times those in aerated soil (Wild, 1981). Consequently, respiration activity of soil organisms depletes the existing soil oxygen store and produces gases (CO_2 and ethylene). Oxygen deficiency in waterlogged soil changes the soil chemistry and biochemistry to processes determined by the reduced chemical state. Soil organisms may switch to anaerobic respiration (Ponnamperuma, 1972). During waterlogging, the soil undergoes chemical reduction and pH change, making some nutrients more soluble, and increasing diffusion and mass flow to the roots (Ponnamperuma, 1972). The pH change influences nutrient availability particularly for iron, manganese, phosphate, aluminium, and silicate. Moreover, the increase in pH of acid soil is one of the benefits of waterlogged rice soils by alleviating aluminium and iron toxicity (Ponnamperuma, 1972).

Oxygen is an essential requirement for root growth. Without oxygen, roots stop growing because they lose the capacity to produce energy. Even with temporary soil waterlogging, herbaceous and woody species often slow in growth and senescence prematurely. The prolonged waterlogging produce methane gas (CH_4) as consequence of the reduction of organic compounds. These noxious gases were

believed to render the air unfit for respiration, therefore waterlogging kills the plant which lack a genetic capacity for anaerobic respiration (Atwell *et al.*, 1999).

1.3.2 Nutrient availability

Fluctuating water regimes in rainfed lowland ecosystems have a profound impact on nutrient behaviour and availability in the soil. Waterlogging can enhance the availability of important nutrients such as phosphorus and potassium in acid soils, including nitrogen as nitrate (NO_3^-) form is transformed to ammonium (NH_4^+) when the soil is flooded. In U.S. rice fields, the large amount of nutrients is applied but it has still shown the deficient in soils (Patrick *et al.*, 1985). Therefore, nutrient application should be carefully managed to support rice growth in rainfed rice cultivation.

1.3.2.1 Phosphorus

Phosphorus supports a grain yield response for rice in flooded soils, due to the positive effects of waterlogging on P availability (Bartholomew, 1931; Beacher, 1952; Place *et al.*, 1971; Ponnamperuma, 1972). However, occurrences of P deficiency in rice under rainfed conditions have led to an interest in understanding soil P transformations and availability with changing water regimes (Norman *et al.*, 2003).

Phosphorus transformation in rice soil

Phosphorus is generally present in soil solutions as a minor soil P pool and occurs in both organic and inorganic soluble forms. However, much of the soil P is present as iron (III), calcium and aluminium phosphates, phosphates adsorbed on Al^{+3}-, Fe^{+3}- and Mn^{+4}-hydrous oxides and oxyhydroxides, , and organically-bound phosphates (Ponnamperuma, 1972). The phosphorus transformation processes in waterlogged soils are extremely different from those in non-waterlogged soils. The

processes also differ with water regimes that range from continuous waterlogging (anoxic) to intermittent waterlogging (oxic-anoxic) and drained dryland condtions (oxic). In submerged and waterlogged soils, most of water-soluble P may be organic, soluble complexes of Ca, Mg, Al, and Fe, and solids which range from adsorption products to chemical compounds (Ponnamperuma, 1972; Kirk, 2004). The phosphorus status in soils is often the consequence of two opposing chemical processes that enhance availability or increase its adsorption/ precipitation. The availability of phosphorus in soil increased consistently with the decrease in redox potential (Eh) or with an increase in Fe (II), but it is not so closely related to the increase in pH (Chiang, 1963; Ponnamperuma, 1972). The important reactions involved in the changes of phosphorus availability are reduction of insoluble ferric phosphate ($FePO_4$. $2H_2O$) to ferrous phosphate ($Fe_3(PO_4)_2$. $8H_2O$), hydrolysis of aluminium and iron phosphate as soil pH rises after waterlogging, the dissolution of the apatite because of the higher soil pH that occurs in soil solution. Later work by Willett and others showed that P is re-adsorbed on Fe-oxides in flooded soils from clay and oxides of aluminium and iron (De Datta, 1981). Patrick and Mahapatra (1968) also reported that the other mechanisms of phosphorus release in waterlogged soil are release of occluded P by dissolution of hydrated ferric oxide coatings and displacement of phosphate from ferric and aluminium phosphate by organic anions. Shapiro (1958) reported that the increase in the availability of soil phosphorus with submergence is mainly due to reduction rather than hydrolysis. However, Ponnamperuma (1972) concluded that in acid soil, the concentration of water-soluble P increases following submergence from hydrolysis of Fe (III) and Al phosphates, release of P by anion exchange on clay, and reduction of Fe (III) to Fe (II) with

release of sorbed and chemically bonded P Subsequently, Davide (1960: cited by De Datta, 1981) concluded that the beneficial effects of waterlogging on phosphorus availability depend on the intensity of reduction and the iron content of the soil. By contrast, after prolonged waterlogging periods, phosphorus becomes less available, likely as a result from higher sorption (Patrick and Mahapatra, 1968).

The phosphorus sorption capacity of soils is a important factor which affects the phosphorus availability. Even though the mobility and availability of phosphorus in waterlogged soils is greater than in drained soil, the soluble phosphorus added to waterlogged soils is sorbed on the surface of Fe and Al oxides and oxyhydroxides (Chang, 1976a). The long-term fertility experiment soil samples (48 years of phosphorus application) (Lin *et al.*, 1973) demonstrated the preservation of applied phosphorus in the surface soil and subsoil. Phosphorus was fixed by aluminium, iron or calcium depending on the concentration of these cations in the soil solution. However, both aluminium and calcium phosphates transform to iron phosphate, which the transformation rate increases in the flooded water regime.

Phosphorus requirement and management for lowland rice

Phosphorus is important in the storage and transfer of energy within the plant. At a physiological level, phosphorus has been observed to increase root growth and promote early maturity, active tillering, grain development and disease resistance (Yoshida, 1979; Norman *et al.*, 2003). Hayashi *et al.* (1951) examined the productive efficiency of phosphorus for grains and found that phosphorus efficiency is higher at early growth stage because phosphorus is needed for tillering and it can be redistributed to growing organs. Although, the study of Hayashi *et al.* (1951) indicated that the total phosphorus requirement is small relative to nitrogen, rice's

need for phosphorus at early growth stages supports the need for basal P fertilizer application (Yoshida, 1979). Maximum phosphorus uptake is achieved around heading with the amount of phosphorus in the grain comprising 60-70 % of the total phosphorus uptake by the rice plant.

1.3.2.2 Nitrogen

Nitrogen is applied most frequently and in the greatest amounts in rice production. Nitrogen is subject to chemical, biochemical and microbial transformations and nitrogen loss mechanisms in waterlogged soil. Nitrogen fertilizer can be immobilized by microbes or fixed by the clay minerals or lost via leaching, denitrification and ammonia volatilization (Norman *et al.*, 2003).

In waterlogged soil, many forms of nitrogen exist in the soil, but they must transform to NH_4^+ and NO_3^- for uptake by rice plants. Ammonium (NH_4^+) moves though the soil solution to the rice roots mostly by diffusion, while nitrate (NO_3^-) moves by mass flow and diffusion (Marschner, 1995). In waterlogged soil, the lack of oxygen causes ammonium to be stable and accumulate, whereas nitrate is chemically unstable. Nitrate in anaerobic conditions is an electron acceptor for microbes instead of oxygen, which leads to loss to the atmosphere via denitrification as N_2O or N_2. Therefore, rice plants mostly use ammonium in waterlogged soil and NH_4 or NH_4-forming N fertilizers are recommended for rice.

Nitrogen uptake by rice plant follows a sigmoidal growth curve, with total nitrogen uptake parallel to total dry matter until heading stage (Fig 1.2) (Moore *et al.*, 1981; Guindo *et al.*, 1994a; Bufogle *et al.*, 1997). The amount of nitrogen needed by rice plants to reach maximum grain yield is dependent on the cultivar, climate, soil,

and location. Rice cultivars grown in the United States accumulate 150 to 200 kg
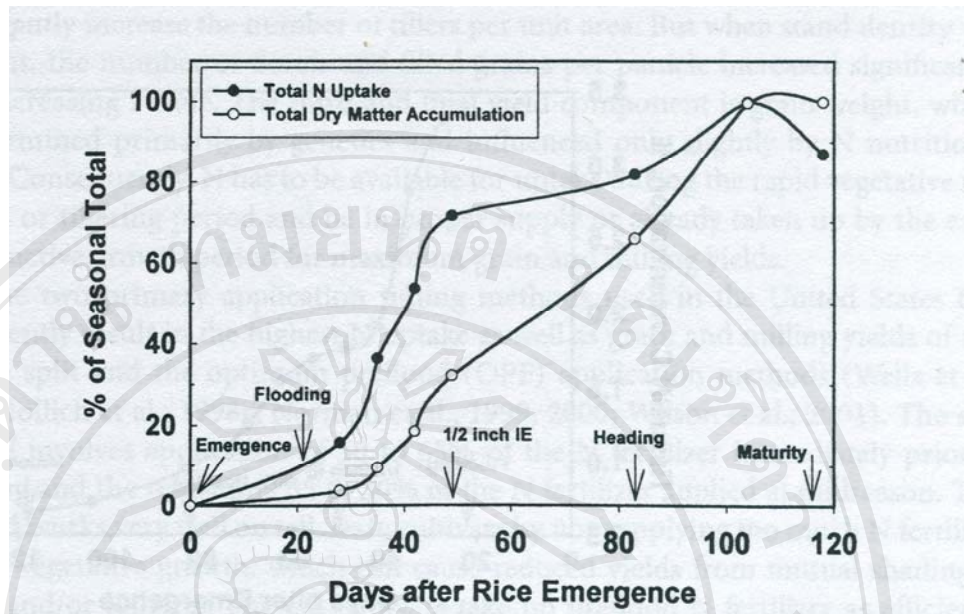N/ha to attain maximum yields (Guindo *et al.*, 1994b; Wilson *et al.*, 1998).

Figure 1.3.2.2.1 Typical seasonal total dry matter production and total nitrogen accumulation of rice plant (Guindo *et al.*, 1994a).

1.3.2.3 Potassium

Potassium occurs in four pools in the soils as solution, exchangeable, non-exchangeable (clay fixed) and in primary and secondary minerals. The potassium availability to rice increases after flooding, since exchangeable K^+ is displaced from the soil complex into the soil solution by NH^+_4, Fe^{3+} and Mn^{2+} (Patrick *et al.*, 1985). The occurrence of potassium deficiency differs among the rice growing areas, due to the differences in cropping practices and soils. In the mid-south of the United States, potassium deficiencies occur on sandy loam soil which has low cation exchange capacity (CEC) and high leaching losses (Slaton *et al.*, 1995). Norman (2003) reported that potassium deficiency in rice was also found in rotation crop system and in areas with soil salinity problems in the United States.

The potassium concentration in rice plant is the highest during the seedling stage and gradually decreases with increasing dry matter accumulation (Sims and Place, 1968). Generally, potassium uptake follows the pattern similar to the total nitrogen accumulation. Although, a report showed that approximately 50 % of the total potassium content at maturity stage is taken up by panicle differentiation, application of potassium fertilizer during late reproductive growth, has failed to increase grain yields in the field studied in Arkansas (Norman *et al.*, 2003).

1.3.2.4 Other nutrients

In flooded soils, sulfur is subject to dynamic transformations between inorganic and organic forms though mineralization-immobilization and oxidation-reduction reactions. These transformations alter the availability of sulfur to rice. The availability of SO_4 in waterlogged soils is most important and will be used as an electron acceptor by microbes which can be reduced to hydrogen sulfide (H_2S)

dissolved in the soil solution under low redox potential (Patrick *et al.*, 1985). Rice plant does not require a large amount of S for optimum growth, with minimum sulfur concentration 0.17 and 0.15 % during tillering and panicle initiation, respectively, or supplies equivalent to 27 kg SO_4-S/ha (Bell and Kovar, 2000).

Zinc (Zn), iron (Fe) and manganese (Mn) are important for plant growth and development, although they are needed in lesser amounts than for the macronutrients. Waterlogging affects the availability of each these micronutrients. Organic matter is also important for Zn availability as well as Fe and Mn availability, because the dynamics of chelation with organic compounds facilitates the solubility and transport of micronutrients in soil solution (Patrick *et al.*, 1985; Norman *et al.*, 2003).

In waterlogged or anaerobic soil conditions, $Fe(OH)_3$-Fe precipitates can cover the rice root surface as iron plaque which affects nutrient uptake by rice root. Zhang *et al*. (1999b) reported that iron plaque accumulates phosphorus and subsequently increase P concentration in shoots. Similarly Kuo (1986) suggested that phosphate is exchanged or complex with OH groups on the iron oxide surface and can be adsorbed on the specific sites with Zn, Cd and Co. Likewise, phytosiderophores were released by roots of iron deficient rice plants also enhance zinc uptake (Zhang *et al.*, 1996).

1.4 Growth and development of the rice plant

In the rainfed rice ecosystem, both oxygen and nutrient stresses may affect rice plants at any growth stage. However, the response and adaptation of rice to these stresses vary with growth stage. Rice growth comprises three distinct stages: vegetative, reproductive and ripening stages. The vegetative stage is a period from germination to the initiation of panicle primordia, the reproductive stage is from the

initiation of panicle primordia to heading, and the ripening stage is from heading to maturity. The period from germination to maturity ranges between 3-6 months, depending on the variety and the environment in which it is grown.

1.4.1 Vegetative growth stage

Rice seed consists of the brown rice (caryopsis) and hull comprising palea, lemma, sterile lemmas and rachilla. In addition, the hull of japonica rice usually includes rudimentary glumes and a portion of the pedicel which contributes to its nonshattering characteristic (Yoshida, 1981). Seed germination starts when the seed dormancy has been broken, adequate water has been imbibed and seeds exposed to a temperature ranging from 10º to 40 ºC. A short time after seed germination, the white tip of the coleoptile and radicle is appeared; seedling emerges from the soil or water surface. The radicle elongates to a maximum length about 15 cm which functions until the seventh-leaf stage. In lowland direct-sowing cultivation, seeds are covered with soil and water, but lack of oxygen results in poor seedling emergence. Yamauchi *et al*. (2000) found that the seedling of anoxia tolerant rice cultivars can be established better and faster than susceptible cultivars when grown in puddled soil by drill sowing and broadcast sowing. The coleoptile extension during anoxia could be supported by the higher soluble sugar availability, indicating that anoxia tolerant rice cultivars contain high sugar concentration and fast starch hydrolysis in seeds and coleoptiles (Huang *et al.*, 2003a). Seedling for transplanted rice with high contents of nitrogen and starch also help seedling develop new root (Yatsuyanagi, 1960).

Seedling stage takes around 30 days, then tillers are developed, depending on the variety and environment. The number of tillers and roots are affected by spacing, light, nutrient supply, and other environmental and cultural conditions.

As growth advances, the primary roots develop branched secondary roots, which develop tertiary roots, and so on. The root diameter becomes smaller as the order of branching increases. The formation of root hairs is greatly affected by soil conditions and environments around the rhizosphere. Bates and Lynch (1996) reported that root hair elongation in *Arabidopsis thaliana* are stimulated by low phosphorus availability. Likewise, root hair density also increased in response to nutrient deficiency, but strongly to low phosphorus supply (Ma *et al.*, 2001). The length of rice roots is controlled by both genetic ability and environment conditions, resulting in a maximum depth of 1 m or deeper in soft upland soil and a maximum depth of about 40 cm in flooded soils (Yoshida, 1981). One characteristic of rice roots is the presence of large air spaces (aerenchyma) in mature roots. These air spaces are connected with the culms and leaves, providing oxygen transport from shoot to root, which will be explained in more detail in the next topic (1.3.2). Age of rice root can be classified into different groups based on the appearance of rootlets and color. Young roots are without rootlets and milky white color, while the older roots become yellow, pale brown, brown, and dark brown in color (Yoshida, 1981).

1.4.2 Reproductive growth stage

The reproductive stage starts after the maximum tillering stage and is marked by the initiation of a panicle primordia in the growing shoot. Then, the spikelets become distinguishable and the panicle elongates upward inside the flag leaf sheath. During this stage, yield is adversely affected by any stress (De Datta, 1981). About 16 days after visible panicle initiation, the sheath of flag leaf swelling is called booting stage. The booting stage is followed by the heading, the emergence of the panicle out of the flag leaf sheath. Anthesis starts with panicle exsertion, spikelets at

the uppermost tip of the panicle begins to experience anthesis which the proceeds down the panicle. The complete anthesis for all spikelets on the panicle takes about 7-10 days. During anthesis, the ovary is fertilized with pollen, and after pollination is complete, the ovary develops into brown rice (De Datta, 1981; Yoshida, 1981; Moldenhauer and Gibbons, 2002).

1.4.3 Ripening and senescence stage

Ripening stage begins three weeks after fertilization which it is characterized by grain growth as increase in size and weight, changes in grain color, and senescence of leaves. At the vegetative growth and before heading, a starch and sugar accumulates in the culms and leaf sheaths. During this growth stage, root activity and nutrient uptake generally decrease, due to a decrease in carbohydrate supply to the roots. The accumulated carbohydrate is translocated to the grains with the high degree of remobilization of nutrient during this stage compared with vegetative growth (Marschner, 1995).

1.5 The adaptation of plants to aerobic and anaerobic conditions

1.5.1 Root function in aerobic soil conditions

In aerobic soil, the root is generally not limited by oxygen supply for root respiration. The key constraints in aerobic soil are water supply and nutrient availability. Under aerobic condition, rice has a structure of roots to facilitate water and nutrient uptake. Roots formed in aerobic condition have longer maximum length than in the anaerobic condition, but fewer adventitious roots (Colmer, 2003a). The

aerobic root is elongated for water uptake at depth in soils. Deep root activity is enhanced by oxygen supply from soil air by diffusion.

1.5.2 Plant in anaerobic condition

In waterlogged or anaerobic soil, roots generally suffer from oxygen deficiency. The root is essentially an aerobic organ; it can be damaged in anaerobic soils by decreased aerobic respiration. Roots of some species adapt to anaerobic conditions by increasing the internal supply of oxygen to the root tip from the atmosphere via aerenchyma (Justin and Armstrong, 1987; Drew *et al.*, 1994; Drew, 1997). Mention also anaerobic respiration of roots. This modification of root cortex with aerenchyma enhances longitudinal oxygen diffusion but may as a side effect decrease symplastic nutrient transport from the apoplast to the main transport vessels in the stele (Drew and Saker, 1986; Kronzucker *et al.*, 1998). While, oxygen is transported via aerenchyma to root tips for aerobic respiration, this oxygen can be lost to the soil by radial oxygen loss (ROL) (Kirk and Du, 1997; Rubinigg *et al.*, 2002; Colmer, 2003a; Malik *et al.*, 2003). In order to minimize the radial oxygen loss, rice induces a barrier to oxygen diffusion (Colmer and Bloom, 1998) believed to be related to increased suberization and lignification of the exodermis (Ranathunge *et al.*, 2004). The barrier may cause an inhibition of nutrient absorption by anaerobic root (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). Fine lateral roots have much less aerenchyma formation than the primary root (porosities of 1-2% compared with more than 50%) and they do not develop secondary thickenings in their walls to the same extent. The fine lateral root comprises the bulk of the external surface, and they are plumbed directly into the

main water and solute transport vessels in the stele of the primary root (Matsuo and Hoshikawa, 1993). The lateral root system is responsible for the bulk of the nutrient absorption by the root system and compensate for any impairment of nutrient absorption in the primary root due to their adaptations for internal gas transport.

1.5.3 Plant in alternate of aerobic and anaerobic conditions

In rainfed lowland environments, rice plants may experience waterlogging and lack of water supply during the same season, depending on the rainfall (Mackill *et al.*, 1996). Rice has to adapt in both physiology and morphology to survive fluctuations between aerobic and anaerobic conditions, but the mechanisms by which rice plants adapt to changing water regimes poorly understood. Diurnal changes in oxygen transfer from shoots to roots of intact rice seedlings at night was reported to cause the roots to become anaerobic and induce metabolism of ethanol, but acetaldehyde did not accumulate to harmful levels (Waters *et al.*, 1989). However, water stress in rainfed conditions is more severe and lasts longer than diurnal oxygen fluctuations.

The responses of other crops under alternate anaerobic and aerobic conditions were studied, which may be guided for the change in rice study. Under anaerobic condition, *Iris pseudacorus* and *Glyceria maxima*, enzymes are induced to protect cell metabolism of roots and switch from anaerobic to aerobic metabolism (Drew, 1997). While, soybean seedling root tips after 1-2 hour of anaerobic before exposure to air was greater injury than imposed anaerobic for 5 hours before re-aeration (Van Toai and Bolles, 1991).

1.6 Plant adaptation to phosphorus stress

Phosphorus is essential for plant growth. Phosphorus functions in plants are constituent of macromolecular structures as nucleic acid, role in energy transfer as ATP in energy metabolism in cell, and role in compartmentation and regulatory as Pi controls some key enzyme reactions (Marschner, 1995). The optimal growth of plants requires phosphorus in the range of 0.3- 0.5% of dry matter during the vegetative stage (Marschner, 1995). P deficiency depresses plant growth as reduction in leaf expansion, leaf surface area and yield (Fredeen *et al*., 1989 cited by Marschner, 1995), number of leaves (Lynch *et al.*, 1991). The adaptations of plant for increase P acquisition are mycorrhizal symbioses, rhizosphere modification by secretion of organic acids (Gardner *et al.*, 1983; Lipton *et al.*, 1987; Lu *et al.*, 1999), and proton release (Kirk and Du, 1997). Fan *et al.*, (2003) reported that in aerenchyma formation in maize roots is induced by low phosphorus availability, consequence of reducing respiration and phosphorus requirement in root metabolism. Moreover, roots also increase root surface area by root hair elongation and proliferation (Bates and Lynch, 1996; Ma *et al.*, 2001), root elongation, lateral root development and elongation in rice (Kirk and Du, 1997). However, the lateral root is a sink of nutrients and energy and for oxygen supply. The growing tip and the parts of the root actively absorbing nutrients have greater respiratory demands than mature or aerenchyma roots. The oxygen consumption and P requirement by respiration in root are covered with laterals (Fan *et al.*, 2003; Kirk, 2003).

1.7 The genotypic variation in responses to water regimes and phosphorus supply

The different of rice cultivation system, origin, history and genetic improvement of rice result in the different of rice genotypes. The genotypic variations of rice on the various conditions have been reported. The differences of rice genotype on the ability to absorb soil phosphorus, growth and yield production when grown in a phosphorus deficient acid soil in Thailand have been studied by (Koyama *et al.*, 1973). They determined rice cultivars grown in treatment of no phosphorus and phosphorus application which the cultivar Dawk Mali 3 grew better and yielded higher in no phosphorus treatment. It was indicated the varietal differences on the ability with higher phosphorus absorption (Koyama *et al.*, 1973). The authors concluded that varietal differences in the ability to grow better on a phosphorus deficient soil resulted from the differences in the ability to extract soil phosphorus. However, the varietal differences showed only in soil culture in which the level of soil P was not clear defined. The genotypic variation of rice under fluctuating soil water regimes were also reported by Banoc *et al.* (2000a; 2000b) and Kamoshita *et al*. (2000). Their study showed the different of rice cultivars on the seminal root system development under soil water fluctuations. IRAT109 (an upland japonica cultivar) had an ability to resume the seminal root elongation when grown in droughted following submergence. Dular (a traditional lowland indica cultivar) had an ability to maintain a seminal root elongation in drought plant as in well watered plant, but less plasticity response to fluctuated soil water regimes. While KDML105 (a lowland indica cultivar grown in rainfed areas of Thailand) showed a large plasticity in both seminal and lateral root development when grown in soil water

fluctuation. Honenwase (a lowland japonica cultivar) exhibits drought susceptibility with it root growth being inhibited when soil water becomes limited. These confirmed that genotypic variation found in plastic response of rice root system morphology as a key trait for the adaptation of rice plants to the fluctuation of soil water regimes. Apparently, there are a lot of studies on responses of rice to fluctuation of waterlogged and drought conditions, but little information on changing between waterlogged and aerobic conditions. In aerobic condition, rice are under non flooded, more prone to drought stress, water has to be supplied for top soil moisture reaches 25 kPa (Pinheiro *et al.*, 2006). The changing of waterlogged and aerobic soil and the responses of rice to aerobic soils is also needed to clarify, especially nutrient responsive cultivars (Bouman, 2001; lafitte *et al.*, 2002).
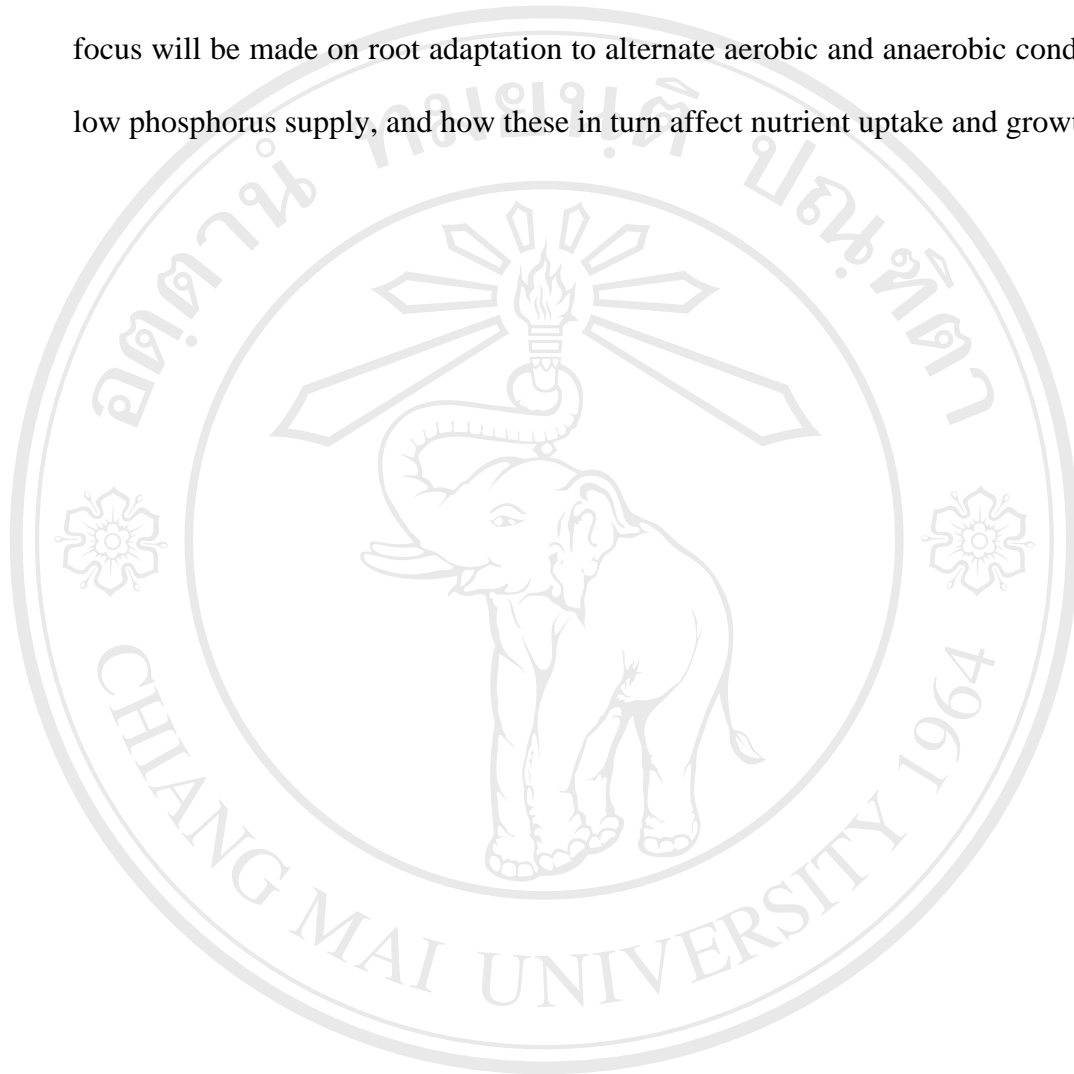
The genotypic variation study on rice root morphology was also studied under upland field of IRRI, Philippines. Eleven different genetic group and ecotypes rice varieties were variation on root development, indicating that those varieties were efficient in developing deeper root distribution with less dry matter allocated to the root (Kondo *et al.*, 2003). Moreover, the genotypic differences in nutrient uptake and utilization for grain yield production of rainfed lowland and low fertile soil were studied to identify the genetic background and extent of the specific nutritional problem in the future research (Fukai *et al.*, 1999; Inthapanya *et al.*, 2000b, a). However, information on physiological responses of rice genotypes is scant. The understanding of these performances will determine the usefulness of selection for physiological trait to breeding program of water fluctuated tolerant and high yield rice variety.

1.8 Use of nutrient solution to simulate waterlogged and aerated soils for rice culture

The study of physiological and morphological responses of roots to waterlogged and well drained soils are difficult because of there are many poorly defined chemical and biological processes in soils, especially in relation to nutrient availability. Therefore, nutrient solution culture is often used in the study of the impact on roots of variation of nutrient availability. Aerated nutrient solution cultures simulate high oxygen supply or well drained soils by continuously bubbling air. By contrast, stagnant nutrient solution cultures are created by adding 0.1 % (w/v) agar to conventional nutrient solutions to simulate lack of convection in waterlogged soils (Wiengweera *et al.*, 1997). Aerated and stagnant nutrient solution cultures are often used to simulate the effects of aerobic and anaerobic soils, respectively, on rice root morphology and physiology (Wiengweera *et al.*, 1997; Lu *et al.*, 1999; Rubinigg *et al.*, 2002; Colmer, 2003a). There is evidence for different root structure in aerated and stagnant conditions as well as in well drained and waterlogged soils. When nutrient and water supply are not limiting, rice growth in aerated solution culture is better than in stagnant culture (Colmer, 2003a). However, rice in rainfed condition is subject to fluctuation between aerobic and anaerobic condition. In Rubinigg *et al.* (2002) and Malik *et al.* (2003), solution culture was used on the study of root adaptation and uptake efficiency which grown in aerated and then transfer to stagnant condition or reverse.

P deficiency in alternate aerobic and anaerobic soils in rainfed ecosystem, rice are affected by both water and P stress. Rice has to adapt to these stresses in the same time. These adaptations may be adversely affected to nutrient uptake efficiency of

roots.   Therefore, this work will study the adaptation of rice in nutrient solution culture as aerated and stagnant nutrient solution at low P supply.   Moreover, specific focus will be made on root adaptation to alternate aerobic and anaerobic conditions at low phosphorus supply, and how these in turn affect nutrient uptake and growth.