Physiological and Agronomic Aspects of Rice Varietal Responses to Low and High Nitrogen Management
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(ABSTRACT)

Modern rice (*Oryza sativa* L.) varieties produce very high yields under high input and favorable environments. Limited work has been done to develop plant types suitable for less than optimal environments at moderate *N* management levels. The objectives of this study were: 1) to examine the relationship between the uptake of *N* and different leaf characteristics, sink size, and grain yield of three morphologically distinct rice varieties; 2) to examine the CO₂ exchange rates (CER) of rice varieties in relation to light, *N* management, water use efficiencies (WUE), and *N* use efficiency (NUE); and 3) to determine characteristics of rice varieties that are associated with productive potentials under low *N* management levels. A greenhouse experiment was conducted in 1989 at Virginia Polytechnic Institute and State University, Blacksburg, VA and a field experiment was conducted in Sri Lanka at two locations in 1990. In the greenhouse experiment three varieties (a traditional, an intermediate, and a modern variety) were grown under four *N* management (rate and time) treatments: viz 1) a 0 *N* control, 2) 200 mg N kg⁻¹ of soil split into two applications, 3) 200 mg N kg⁻¹ of soil split into three applications, and 4) 400 mg N kg⁻¹ of soil split into three applications. Competitive use of fertilizer *N* for the development of either large leaf area or high leaf *N* content per unit leaf area (LNLA) varied with the rate and timing of *N* fertilizer application and rice variety. When *N* supply was limited and early *N* applications were restricted, the intermediate variety increased LNLA in the flag leaf with little increase in total leaf area of the plant. Specific leaf weight did not differ with *N* management except for the low value of the *N* control treatment. Increased *N* applications reduced stomatal density. Total stomatal number leaf⁻¹ varied little within cultivars indicating that *N* fertilization enables the leaf to increase leaf area and thereby disperses the fixed number of stomates. Carbon dioxide exchange rates were higher in the flag leaf
than lower leaves and were directly correlated to LNLA. The modern variety had the highest CER
light saturation when N levels were high whereas the intermediate variety was superior when N
supply was low. A similar trend was observed with the NUE. High levels of N fertilizer reduced
CER of the intermediate variety whereas the reverse was true with the modern variety. High
stomatal conductance resulted in low WUE in the intermediate variety. The intermediate variety
produced higher yields than the other two varieties at low N levels while the modern variety
produced highest yields at high N levels. Yield variations in both the modern and traditional vari-
eties were mainly associated with variations in panicles plant$^{-1}$, whereas in the intermediate variety
grains panicle$^{-1}$ had the greatest influence on yield. Total N content of the flag leaf and the
penultimate leaf were positively correlated to grain yield. Yield variations due to N fertilization
were mainly associated with panicles produced on tillers rather than panicles on the main culm.
The intermediate variety was more adapted to low N environments than the other two varieties.
The low WUE could be a disadvantage in environments where water is a limiting factor. In the
field experiment three rice varieties were tested at five N management levels. Nitrogen management
treatments included a control and two N levels (45 and 90 kg N ha$^{-1}$) with each level split into
either two or three applications. Yield variation of the modern variety was correlated to panicles
m$^{-2}$ whereas in the other two varieties, grains panicle$^{-1}$ were responsible for yield variations.
Panicles m$^{-2}$ was negatively correlated to grains panicle$^{-1}$ in the traditional and intermediate va-
riety. Supply of N at late vegetative/early reproductive stages was more beneficial than applying
at early vegetative stages when N supply is low. Leaf area index from very early stages of devel-
opment (17 to 29 days after transplanting) was positively correlated to the grain yield in the modern
variety but in the intermediate variety LAI was correlated to yield only 41 days after transplanting.
Grain yield was influenced more by the size of the leaf area than light receiving efficiency of erect-
leaf plant type at low N levels. A plant with low tillering capacity, high grains panicle$^{-1}$, interme-
diate leaf length, and canopy arranged somewhat horizontally is desirable in low N situations. The
intermediate variety possessed most of these characteristics.
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Table of Contents

CHAPTER I ................................................................. 1
INTRODUCTION .......................................................... 1

CHAPTER II ............................................................... 8
LITERATURE REVIEW ................................................... 8
Introduction .............................................................. 8
Rice Breeding and Variety Development ......................... 11
Photosynthesis .......................................................... 13
Environmental Influences on Photosynthesis .................... 15
Nitrogen Nutrition ....................................................... 22
Photosynthesis and Respiration ..................................... 27
Biophysical Constraints ............................................... 28
Leaf Anatomy and Photosynthesis ................................ 30
Growth and Productivity of Rice ................................... 32

CHAPTER III ............................................................... 50
Response of Three Rice Varieties to Nitrogen Management: I. Leaf Characteristics, Sink Size, and Grain Yield .......................................................... 50

ABSTRACT ........................................................................ 50

INTRODUCTION .................................................................. 52

MATERIALS AND METHODS ............................................. 54

RESULTS AND DISCUSSION .............................................. 57

CHAPTER IV ......................................................................... 74

Response of Three Rice Varieties to Nitrogen Management: II. Leaf Photosynthesis, Light Response, and Water Use Efficiency .......................................................... 74

ABSTRACT ........................................................................ 74

INTRODUCTION .................................................................. 75

MATERIALS AND METHODS ............................................. 78

RESULTS AND DISCUSSION .............................................. 80

REFERENCES ...................................................................... 95

CHAPTER V ......................................................................... 97

Agronomic Responses of Rice Varieties to Low and High Nitrogen Management ....................... 97

ABSTRACT ........................................................................ 97

INTRODUCTION .................................................................. 98

MATERIALS AND METHODS ............................................. 100

RESULTS AND DISCUSSION .............................................. 102
List of Tables

Table 3.1. Leaf N content per unit leaf area (LNLA) of the two uppermost leaves on the main culm at maximum tillering and flag leaf stages as influenced by rice variety and N management. ................................. 58

Table 3.2. Leaf area of the two uppermost leaves on the main culm at maximum tillering and flag leaf stages of development as influenced by variety and N management. .... 60

Table 3.3. Specific leaf weight of the two uppermost leaves of the main culm at maximum tillering and flag leaf stages as influenced by rice variety and N management. ... 62

Table 3.4. Stomatal density on the upper and lower leaf surface of the uppermost leaf of the main culm at maximum tillering and flag leaf stages as influenced by the variety and N management. ................................................. 64

Table 3.5. Total stomatal number on each surface of the uppermost leaf of the main culm at maximum tillering and flag leaf stages as influenced by the variety and N management .................................................. 65

Table 3.6. Grain yield, panicles per plant, total spikelets per plant, 1000-grain weight, and percentage sterility as influenced by rice variety and N management. ................................. 67

Table 3.7. Correlation coefficients between total leaf N content of two uppermost leaves and different yield parameters of the whole plant, and panicles on the main culm and subtending tillers. ................................................................. 70

Table 4.1. Analysis of variance for CER for three rice varieties grown under four N management levels at maximum tillering and flag leaf stages of development. ........ 82

Table 4.2. Correlations between CER and N content per unit leaf area at different light levels for three rice varieties at maximum tillering and flag leaf stages of development... 86

Table 4.3. Stomatal conductance at the flag leaf stage of development for different light levels for three rice varieties and four N management levels. ................................. 89

Table 4.4. Correlations between stomatal conductance and N content per unit leaf area and stomatal conductance and CER at different light levels for 3 rice varieties at flag leaf stage. ........................................................................................................ 90

Table 4.5. Water use efficiency of three rice varieties at different light levels for the flag leaf stage development. .................................................................................. 92
Table 5.1. Grain yield of three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations. ......................................................... 104

Table 5.2. Number of panicles m$^{-2}$ for three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations. ......................................................... 106

Table 5.3. Grains panicle$^{-1}$ for three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations. ......................................................... 108

Table 5.4. One thousand grain-weight for three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations. ......................................................... 109

Table 5.5. Correlation between different yield parameters for three rice varieties at Gannoruwa (GN) and Maha Illuppallama (MI). ......................................................... 110

Table 5.6. Correlation between leaf area index at different growth stages and yield and panicles m$^{-1}$ for three rice varieties at Gannoruwa and at Maha Illuppallama locations. . 112
List of Illustrations

Figure 4.1. CER at different light levels for three rice varieties at the maximum tillering stage grown at four different N management levels. 83

Figure 4.2. CER at different light levels for three rice varieties at the flag leaf stage grown at four different N management levels. 84

Figure 4.3. Relationship between leaf N content per unit leaf area (LNLA) and maximum CER for three rice varieties at maximum tillering and flag leaf stages of development. 87
CHAPTER I

INTRODUCTION

Notable advances in research during the last three decades have resulted in significant increases in rice production in many rice producing countries. An annual increase of 1.3 million Mg of rice is needed to meet the growing rice eating population in the world (Grist, 1986). This could be achieved through increased land area and by increased yields. The possibility of increasing yields and associated problems are similar in many Asian countries, therefore, Sri Lanka was used as an example in this discussion.

Rice cultivation in Sri Lanka is primarily governed by the seasonal (bimodal) nature of rainfall that produces two distinct cropping seasons. The major or ‘maha’ (wet) season corresponds to the north-east monsoon (Sept. to Dec.). The minor or ‘yala’ (dry) season corresponds to the south-west monsoon (April to June). Based on amount of annual rainfall received, the country is divided into three broad climatic zones: a) wet zone, > 2280 mm, b) intermediate zone, 1525 to 2280 mm, and c) dry zone, < 1525 mm. Based on elevation, these zones can be further subdivided: 1) low-country, elevation < 300 m, 2) mid-country, elevation 300 to 1000 m, and 3) up-country, elevation
> 1000 m. Combining major soil groups, vegetation, temperature, and rainfall, Panabokke (1978) identified 24 agro-ecological zones in the country.

There are three major rice production systems in the country: 1) major irrigation systems; 2) minor irrigation systems; and 3) totally rainfed areas. In all three production systems, rainfall plays an important role. The crop success even in major systems depends on how efficiently the rainfall is utilized for rice cultivation. The water for major systems is from river diversion. This water is stored in tanks and distributed to paddy lands through channels. In minor projects, either water received as direct rainfall in the catchment area is stored in small tanks and distributed to paddy fields, or small natural streams are directly diverted into paddy fields. Rainfed rice is totally dependent on the direct precipitation.

Significant progress has been made during the last three decades in the development of new rice varieties and technology that has resulted in large increases in rice production. Average Sri Lankan rice yields increased from 1.8 Mg ha\(^{-1}\) in 1960 to 3.5 Mg ha\(^{-1}\) in 1985 (Herath, 1987). The total rice production increased from 0.9 to 2.5 million Mg yr\(^{-1}\) for the same period. These achievements were due to the increased land area under irrigated cultivation and also to adaptation of improved varieties and technologies. The possibility of increasing the land area for rice cultivation is now very limited. To meet the estimated rice production needs of Sri Lanka in the future, the national yields need to be increased from the present 3.5 to 4.0 Mg ha\(^{-1}\) (Herath, 1987).

The average rice yields under major irrigation projects are currently about 4.0 Mg ha\(^{-1}\); under minor irrigation and rainfed conditions yields average 3.0 and 2.6 Mg ha\(^{-1}\), respectively (Herath, 1987). Increasing the rice yields in irrigated areas plays an important role in increasing the national rice production but about 60% of the rice lands are under rainfed (35%) and minor irrigation systems. Obviously the average yields of these lands must also be increased in order to achieve Sri Lankan rice production goals in the future. The basic problems of rainfed and minor irrigation rice cultivation arise from water insufficiencies and/or excesses. Based on topography and drainage, the rice lands can be classified into well-drained, moderately-drained, and poorly-drained landscape categories (Somasiri et al., 1978). Rice grown in well-drained lands has a high risk of drought during some part of the growth cycle if supplementary irrigation is not available. Drought risk in
moderately drained land categories is somewhat less because these sites receive seepage water from the upper areas and the water table is shallow. Flooding and poor drainage is common in poorly drained rice lands. During periods of heavy rainfall, flooding and waterlogging can occur in varying degrees and frequencies in any of these land categories, especially in the wet zone. Moreover, the rice soils in the wet zone are mainly hydromorphic associates or alluvial derivatives of Ultisols (Aucults), together with Inceptisols, Entisols and Histisols. They are chemically and physically less favorable for rice cultivation than those of the dry zone (Balasuriya, 1987). The number of rainy and cloudy days in the wet zone areas is much higher than the dry zone, and therefore, the irradiance for photosynthesis is low. Because of these considerations, rainfed rice growing environments can be considered unstable. However, even under irrigated conditions the water supply is not always perfect, and drought can result in unstable production.

Unstable climatic conditions increase the risk and uncertainty of rainfed rice production, and rational farmers tend to minimize cash inputs and labor on such rice crops. The prices of inputs and rice have been reasonably stable. Thus the economic risk of growing rice is largely due to high variability in grain yields (Suraweera, 1987). The performance of modern varieties is highly dependent on the input level and environment. Their performance under high inputs and favorable environments is very encouraging. However, in low input, unstable environments, modern varieties generally do not perform as well as older varieties. A limited number of comparisons have been made on the performance of the newer varieties in unstable environments with low levels of inputs and management. The varieties and technologies adapted by the farmers in unstable, low-input environments are simply an extension of the technology developed for irrigated rice. To make rainfed rice cultivation more viable appropriate technology including adapted varieties are urgently required.

Crop productivity is a complex character and high yields result only from the proper combination of genotype, environment, and cultural practices. According to Donald (1968), most crop improvement programs are based on “defect elimination” and “selection for yield”. In defect elimination, breeders attempt to remedy readily observable defects such as susceptibility to diseases and
insects or susceptibility to lodging. In selecting for high yield, parents with good combining ability are used. However, the reasons for the high yields of new varieties are often not well understood.

The developing of optimum plant types through the use of yield components and morphological and physiological traits has been proposed for wheat (Donald, 1968), maize (Frey, 1970), and rice (Jennings, 1964; Beachell and Jennings, 1965). The ideotypes proposed so far are intended for maximum production in optimum environments with very good management. Very little work has been done to propose ideotypes for less-than optimal environments at moderate management levels. Presently we have very little control over the environment, but genotype and cultural practices can be manipulated, at least to a certain extent, to suit a specific environment and management level. Some of the processes that are well understood have been altered in many crops by plant breeders. Adequate information concerning basic plant processes and the desired plant type for different environments is needed by the plant breeders so that they can more efficiently incorporate physiological and morphological traits into cultivars for higher productivity.

Nitrogen is the most important nutrient for increasing rice productivity (Barker, 1979; Prasad and De Datta, 1979). As crop production increases on a worldwide basis, the use of fertilizer N will become increasingly influenced by the availability and price of N rather than by the recommended amounts. A great deal of work has been done to improve N utilization through fertilizer application methods and proper soil and water management (Broadbent, 1979; Prasad and De Datta, 1979; Savant and De Datta, 1982; Shoiji et al., 1986; Wada et al., 1986; Broadbent et al., 1987). The importance of high N use efficiency of rice genotypes has also been noted by some researchers (Broadbent et al., 1987; Wada and Cruz, 1987). Increased N use efficiency is achieved either through the ability for greater fertilizer recovery and/or increased efficiency of conversion of the absorbed N into yield.

Improvements in yields for any grain crop depend on increased dry matter production and/or greater partitioning of the dry matter to the spikelet. Dry matter production is closely related to the photosynthetic activity of the canopy (Tanaka et al., 1966; Yoshida, 1972). High yields have been attained with improved plant types that result from the improvement of canopy photosynthesis (Vergara, 1988). There is, however, no evidence to show that yield improvements have been as-
sociated with increases in net photosynthesis although rice varieties differ in this component (Ohno, 1976; Vergara, 1988). Many workers have tried to isolate cultivars with high photosynthetic rates, but the advantage of such varieties has yet to be demonstrated or used by plant breeders (Vergara, 1988).

Research on rice photosynthesis and its association with yield has been done to examine the possibilities of increasing the yield of rice varieties suitable for optimum environments. Little or no attention has been paid to photosynthetic rates associated with varieties suitable for marginal environments. Adequate information concerning basic plant processes and desired plant types is required for plant breeders to efficiently identify and combine physiological and morphological traits into cultivars suitable for low N input situations with improved yield and quality.

The objectives of this research are:

1. To determine the relationship of important leaf characteristics and their variability in relation to N management in three morphologically different rice varieties.
2. To examine net leaf photosynthesis of rice at two different growth stages in relation to variety, N uptake, and light and water use efficiencies.
3. To evaluate the relative importance of yield, yield components, and leaf area production under low and high N management situations and to determine what plant characteristics are important at low N situations.
REFERENCES


CHAPTER I


CHAPTER II

LITERATURE REVIEW

Introduction

Rice is considered a semi aquatic, annual plant that belongs to the genus Oryza and includes 20 species (Lu and Chang, 1980). The two common species of cultivated rice are O. sativa L. and O. glaberrima Steud. (Morishima, 1984). Almost all cultivated rice belongs to O. sativa, which originated in Asia (De Datta, 1981). O. glaberrima, which is grown mainly in some west African countries, is gradually being replaced by O. sativa (De Datta, 1981). Oryza sativa has undergone far more diversification and improvement than O. glaberrima through its spread to different climatic regions and the development of new cultivars and agronomic practices (Cook and Evans, 1983b). Oryza sativa is broadly divided into indica and japonica subspecies (Chang, 1976; Takahashi, 1984). The indica subspecies is essentially tropical, while japonica is temperate, although both are grown in subtropical areas such as Taiwan (Cook and Evans, 1983b). Some recent varieties have both indica and japonica parentage (Cook and Evans, 1983b).
Remarkable diversity exists in the crop because of a long history of cultivation and selection under diverse climatic, edaphic, and biotic environments (Lu and Chang, 1980). The two cultivated species can be grown in a wide range of soil-water regimes ranging from a prolonged period of flooding in deep water to dry lands on hilly slopes (De Datta, 1981). Some morphological and physiological changes have occurred during the process of cultivation and domestication of O. sativa (Takahashi, 1984). Large leaves, long and thick culms, and long panicles have resulted in a larger plant size (Lu and Chang, 1980). There were also increases in the number of leaves, in their rate of leaf development, number of secondary panicle branches, grain weight, rate of seedling growth, tillering capacity, synchronization of tiller development, and panicle formation (Lu and Chang, 1980; Cook and Evans, 1983b).

Except for seminal roots, which emerge at germination, all roots emerge at the stem nodes keeping a definite relationship with the emergence and development of leaves (Fujii, 1961). Tillering begins at the four to five-leaf stage. Tiller emergence is closely related to that of leaves (Katayama, 1951; Matsushima, 1970). Primary tillers emerge from leaf axes on the main culm. Secondary tillers emerge from the leaf axes of the primary tillers (Matsushima 1970). Thus, all tillers are synchronized with the development of the leaves on the main culm. Tiller initiation is free from the influence of environment, but their development is greatly influenced by factors such as N, and P availability, solar radiation, and temperature (Murata and Matsushima, 1975).

A typical rice leaf is composed of a sheath and a blade. The sheath is an elongated ribbon-shaped base of the leaf rolled into a cylinder that encloses all the young parts of the shoot (Yoshida, 1981). The leaf blade contains many large and small vascular bundles. Stomates are on both sides of the leaf surface, and large air spaces are present within the leaf. The increase in leaf area index (LAI) in rice is due to the increase in number and size of successive leaves and tiller numbers. Nitrogen availability has a marked influence on LAI, increasing both leaf number and size (Murata and Matsushima, 1975).

Rice is mainly grown under submerged conditions, which creates an unique environment for growth and nutrition (Ponnamperuma, 1972). Root growth under submerged conditions is characterized by a reducing environment where, the availability of oxygen is very low (Ponnamperuma,
1972). To avoid anoxia of roots in submerged conditions, the rice plant has developed special tissues through which air is transported to the root (Yoshida, 1981). Presence of well-developed air spaces in leaf blades, sheaths, culms, and roots facilitates air movement from aerial parts (Yoshida, 1981).

Reproductive organs of the rice plant consist of spikelets supported in a panicle (Yoshida, 1981). Spikelets are borne on pedicels, which are extensions of primary, secondary, and often tertiary panicle branches (Matsushima, 1970; Sasahara, 1984). The flower is enclosed in the lemma and palea, called the hull (De Datta, 1981). The grain develops from an ovary inside the hull. Unfilled spikelets have only the lemma and the palea with no grain and are called empty spikelets. Spikelets are arranged sparsely in rice's compound panicle in contrast to the compact arrangement of grains in wheat and barley spikes (Tsunoda, 1984).

Temperature, solar radiation, and rainfall are the major climatic factors influencing rice productivity. They do so directly by affecting the physiological processes and indirectly by influencing other factors such as diseases and insects (Yoshida, 1981). Critically low and high temperatures, normally below 20°C and above 35°C, inhibit growth and yield of rice (Yoshida, 1981). Grain yields are positively correlated to photosynthetically active radiation (PAR), and solar radiation requirements of a rice crop vary with the growth stage (Moomaw and Vergara, 1964; De Datta and Malabuyoc, 1976; Venkateswarlu, 1977). The order of priority of high solar radiation required for high productivity is ripening stage, reproductive stage, and vegetative stage (Venkateswarlu, 1977). Water stress at any growth stage can reduce yields, but the growth stage in which the rice plant is most sensitive to water stress is during anthesis which is from the meiosis stage to heading (Yoshida, 1981).

The rice plant usually takes 90 to 120 days to mature depending on the variety and the environment (Matsushima 1970). Yield capacity of a rice crop depends on genotype and environment (Yoshida, 1981). The yield achieved is dependent on the ability of the plant to fill the spikelets produced and is mainly determined during the post-heading period (Matsushima, 1976). Grain yield is a function of the amount of starch accumulated in the grains, which reflects the photosynthetic output of the rice leaf canopy after anthesis.
Rice Breeding and Variety Development

Rice breeding at the beginning of the century was based on selection among varieties grown on farms. Selection was limited to removal of "off" types in the varieties popular with farmers. Subsequently, cross pollination for combining specific traits in different varieties was attempted (De Datta, 1981). Until the early 1960s, many crosses made in tropical Asia were single crosses. In the 1960s, high-yielding, lodging-resistant, fertilizer-responsive, and photoperiod-insensitive rice varieties helped to initiate the worldwide expansion of food production called the "green revolution" (Yoshida, 1981). The modern dwarf and semi-dwarf indica cultivars have been derived from crosses between dwarf indica varieties from Taiwan and tall indica varieties from tropical Asia (Cook and Evans, 1983b). Additional improvement provided varieties with resistance to several major pests and diseases and with maturity periods of only 105 to 120 days. New production practices were designed to maximize yield potentials of these modern varieties (Vergara, 1988) and were responsible for increases in rice yields. Yields have apparently reached a plateau (Flinn et al., 1982) in terms of both the maximum yield potential of the modern varieties as well as their performance on farms. Subsequent efforts to increase yield potentials since the release of IR8 have not been successful (Vergara, 1988).

Efforts to improve yield by increased photosynthetic rates, biomass production, and harvest index have not resulted in significant gains (Vergara, 1988). In the early 1970s, the rice varieties being developed were environment specific and performed best where there was an adequate supply of water, no soil problems, and high solar radiation (De Datta, 1981). Lack of these ideal conditions was the major reason for low farm yields in many rice producing-countries in Asia (Herdt and Mandac, 1980; IRRI, 1980).
The performance of modern varieties is highly dependent on the management input level and the environment (Herdt and Mandac, 1980; De Datta, 1981). These varieties perform very well in high-input and favorable environments, however, in low-input, unstable environments, their yields are generally low and inconsistent. Most of the varieties and technology currently adopted by farmers are simply an extension of the technology developed for stable environments. To make rice production in unstable environments more viable, appropriate technologies including varieties are urgently required (Herdt and Barker, 1977; De Datta, 1981).

Environmental factors are of critical importance in explaining the gap between the yield potential of the modern rices and their average farm yields (Herdt and Barker, 1977; Herdt and Mandac, 1980). Hargrove and Cabanilla (1979) in a study of 35 rice breeders throughout Asia found that all agreed on the important limiting factors to rice production. Few of those factors such as pest and disease resistance and tolerance to adverse soil conditions, have been included in subsequent efforts to improve the yielding ability of rice, because information on other factors is lacking.

Obviously, no single variety can meet the requirements of all the different environments and management levels. Therefore, the choice of individual characteristics or their combination will vary with location, cultural practices, and level of inputs (Herdt and Barker, 1977). In such situations, recognition of benefits and the disadvantages of contrasting characteristics is important.

The importance of studies on the physiological basis of yield was noted as early as the beginning of this century (Engledow and Wadham, 1923). Since then, investigations have included morphological components, growth analysis, light interception, photosynthetic measurements, dark respiration, photorespiration and enzyme activity (Wallace et al., 1972). Wallace et al. (1972) reviewed work on this area and concluded that there is genetic variation for most if not all of the physiological components of yield. However, most of these studies have been on complex components of yield with little attention to the subcomponents associated with them. According to Schrader (1985), many physiological processes (e.g. photosynthesis) may show comparable rates within species or cultivars, but a different subcomponent (controlled by a different number of genes) may be rate limiting in each genotype. Therefore, studies of genetic differences in these processes...
will be meaningful only when the limiting subcomponents in each genotype are identified and better understood.

Low solar radiation is one of the important environmental factors that limits high grain yields in the tropics (Venkateswarlu, 1977). There is a great need to find varieties adapted to low light environments (Venkateswarlu, 1977; Vergara, 1988). Another aspect that needs consideration is the use of high levels of N fertilizer under low radiation levels. The cost of N fertilizers has increased the importance of N response studies for profitable rice production. Therefore, studies on physiological and morphological factors in relation to light environment and N management are important. Maximum use of N by the plant is impossible without a photosynthetic apparatus that operates effectively at all levels. On the other hand, photosynthates produced in this process must be effectively translocated to the grain for maximum productivity. Therefore, studies on the growth characteristics and their relationship to produce yield under the above mentioned situations are also important.

Photosynthesis

Photosynthesis is the process by which solar energy is captured and converted into chemical energy and stored in the form of carbohydrates (Lawlor, 1987). Despite the obvious importance of photosynthesis to crop production the relationship is not direct (Gifford and Evans, 1981). A crop with leaves having a high rate of photosynthesis will not necessarily have a high economic yield (Moss, 1984). On the other hand, a crop cannot yield well if it does not have adequate photosynthetic capacity.

Dry matter production is closely related to photosynthetic activity of the canopy (Tanaka et al., 1966; Yoshida, 1972). About 90-95% of the dry weight of plants is derived from photosynthetically fixed CO₂. Good correlations between photosynthetic rate per unit leaf area and economic yield have not always been found (Evans, 1975; Moss, 1976; Elmore, 1980; Good and Bell, 1980). The
conclusion that no correlation exists between these two factors has been drawn from data where instantaneous measurements were made under standardized conditions, not from seasonal measurements conducted in the field (Zelitch, 1982). Therefore, information on the variability of photosynthetic rates under diverse environmental conditions is necessary for selecting photosynthetically efficient genotypes if enhanced photosynthesis can influence yield (Zelitch, 1982).

Photosynthesis can be divided into two basic processes: 1) photochemical reactions involving the interception of the light by various pigments in chloroplasts and use of that energy for photolysis of water, and 2) reduction of CO₂ into carbohydrates (Lawlor, 1987). The capture of light requires the intimate association of many chlorophyll molecules with compounds that catalyze chemical reactions (Badel et al., 1985; Lawlor, 1987). Energy captured by the light reactions is used to reduce adenosine dinucleotide phosphate (ADP) and nicotinamide adenosine dinucleotide phosphate (NADP) to ATP and NADPH (Bassham and Calvin, 1957). In the Calvin cycle, NADPH and ATP are used to fix and reduce CO₂ to carbohydrates. The key enzyme involved in this process is ribulose 1,5-bisphosphate carboxylase-oxygenase (Rubisco).

Rice has C₃ metabolism (Loomis and Gerakis, 1975; Ishii et al., 1977b); apparent photosynthesis is inhibited by O₂ and the CO₂ compensation point is high (Akita et al., 1969; Akita and Miyasaka, 1969). Further, Nishida (1962) and Ishii et al. (1977b) reported that initial products of photosynthesis in rice are sugar phosphates including PGA and that little ¹⁴CO₂ was incorporated into malic acid. However, the rice plant is of tropical origin, and its photosynthetic rates are much higher than most other cereal crops (Tanaka et al., 1966; Tsunoda, 1984). Some have suspected C₄ photosynthesis in rice, because Hegde and Joshi (1974) observed that ¹⁴CO₂ was first incorporated into aspartic acid in two rice cultivars examined in product analysis experiments. However, no further evidence is available to confirm that rice has C₄ photosynthesis. Even though rice is a C₃ species its maximum photosynthetic rate sometimes is comparable to some C₄ species (IRRI, 1976; Murata, 1981; Tsunoda, 1984). This high photosynthetic rate in rice leaves may be related to low gas diffusive resistance of the plant (Tsunoda, 1984) and will be discussed later.

CHAPTER II
Photosynthetic activity of a leaf can be limited by biochemical, biophysical, and environmental factors (Makino et al., 1984). Among the biochemical factors, the enzyme Rubisco and substrate ribulose bisphosphate are considered to play a primary role (Farquhar and Sharkey, 1982). Biophysical factors limit gas exchange between the internal atmosphere and the chloroplasts where primary fixation occurs (Mansfield and Wilson, 1981; Ball et al., 1986). Environmental factors provide the basic requirements for photosynthesis and also affect the rate of reaction (Berry and Downton, 1982).

Environmental Influences on Photosynthesis

Several environmental factors are known to influence the rate of photosynthesis (Berry and Downton, 1982; Whittingham, 1981). These include the CO₂ partial pressure surrounding the photosynthetic cells, light, temperature, nutrient availability, and water supply (Berry and Downton, 1982). Such factors are also responsible for seasonal variations in crop productivity.

Light response

Conditions during development of the photosynthetic system modify the structure of the light harvesting, energy transduction, and enzyme systems and thereby alter the efficiency of assimilation (Lawlor, 1987). Light is obviously fundamental to photosynthesis and is a major factor limiting biomass production (Berry and Downton, 1982; Lawlor, 1987). The photochemical influence of light on photosynthesis has already been indicated, but the overall influence of light on canopy photosynthesis is complicated by several factors (Mithrobe and Moorby, 1974).

Growth in green plants is directly influenced by the intensity of light, the driving force of photosynthesis which provides all chemical energy required for plant growth (Berry and Downton, 1982). Moreover, light level (quantum flux density) is perhaps the most conspicuous environmental factor that varies seasonally, diurnally, and spatially (Bjorkman, 1981). Both the quantity and
quality of light are important for photosynthesis (Lawlor, 1987). Light response curves vary with the type of carbon fixing pathway used by the plant, with C₃ plants becoming saturated at lower light levels than C₄ plants (Müthrope and Moorby, 1974). At light saturation, the limitation to photosynthesis is other factors associated with photosynthesis (Lawlor, 1987).

About 50% of the solar radiation is in the wave band 30 to 700 nm. The photosynthetic pigments of terrestrial plants use light from the visible spectrum only (400 to 700 nm), which is also referred to as photosynthetically active radiation (PAR) (Ludlow, 1982). Part of this PAR is wasted due to the physical properties of the leaf, e.g. reflectance and transmittance, and through fundamental thermodynamic considerations that limit the conversion and storage of sunlight as chemical energy in photosynthesis (Good and Bell, 1980). Thus, the potential conversion of light into chemical energy in photosynthesis is low, but no other biological process is known to fix the sun's energy into chemical energy.

Photosynthetic rate is determined not only by the incident light on the leaf but also by effective light absorption and the efficiency of its utilization (Lawlor, 1987). Moreover, light absorption is not only determined by the total leaf area but also by orientation of the leaves with respect to the incident light (Jennings, 1964; Duncan et al., 1967). It has been shown clearly in rice that there is a good relationship between leaf orientation and yield (Jennings, 1964); however, not much advantage is gained with other crops (Whittingham, 1981). The importance of leaf area and leaf area duration has been stressed in other crops (Whittingham, 1981). When rice plants are grown under low light conditions several morphological changes occur. These changes include decreased dry matter production, photosynthetic rates, relative growth rates, net assimilation rates, and specific leaf weight (Jana and Murty, 1978). Low light also results in increased plant height and leaf area ratio.

Net photosynthesis responds asymptotically quantum flux density as light becomes less of a limiting factor (Beadle et al., 1985). Individual leaves of C₃ plants are typically light saturated at about 25 to 40% of the full sunlight; but this is not true with C₄ plants, which in general fail to saturate even at full sunlight (Long and Woolhouse, 1978). Photosynthetic activity is a function of the environmental conditions to which the plant is subjected during growth and development.
Even under similar conditions there appears to be considerable variation among species (Berry and Downton, 1982; Beadel et al., 1985). According to Bennet and Rook (1978), these apparent differences probably originate in the mesophyll, though their biochemical basis is not clear. It is also not known whether these differences within C₃ species are directly related to photochemical processes, but clearly some plants are able to utilize their supply of light to better advantage than others. This may be linked to constraints in the design of their photochemical apparatus (Woolhouse, 1978). Leverenz and Jarvis (1979) have suggested that the slope of the light response curve of a species may be related to productivity. This slope should increase when the chloroplasts are evenly illuminated, and this was observed when bilateral illumination was compared to unilaterial (Leverenz and Jarvis, 1979). Most sun species (almost all cultivated crop species belong to this group) have an ability to integrate and adjust partial processes to maximize photosynthesis using the available quantum density (Badel et al., 1985).

Leaves adapted to bright sunlight are most effective at using radiation at the top of canopies, and shade leaves use dim light in the lower canopy (Lawlor, 1987). Absorption of blue and red wavelengths by upper leaves enriches light in the lower canopy in the green and infra-red (which has photomorphogenic influences on plants) and requires changes in light absorbing characteristics of leaves (Lawlor, 1987). In low light levels, assimilation is a linear function of intensity and is at its most efficient utilization (Lawlor, 1987). Plants with large photochemical efficiency in low light will have high growth rates per given light absorption and may be most successful in competition where vegetation is dense (Lawlor, 1987).

Light-use efficiency in photosynthesis is the quantum yield (Φ), defined as the moles of CO₂ fixed per mole of quanta absorbed by a leaf (Badel et al., 1985). Since light is not limiting after light saturation, the quantum yield can be measured only at low light levels where they are proportionate (Badel et al., 1985). Quantum yield is a dimensionless constant, which has a maximum value of 0.125 for photosynthesis i.e., from the maximum quantum requirement (1/Φ = 8) (Badel et al., 1985). Reflection, absorption by substances other than photosynthetic pigments (e.g. anthocyanins), and fluorescence all reduce quantum yield (Badel et al., 1985). Ehleringer and Bjorkman (1977) observed quantum yields of 0.0733 (1/Φ = 13.6) for several C₃ species and 0.0524
(1/Φ = 19.1), respectively, for several C₄ species. These measurements were made under an atmosphere with 2% O₂, where photorespiration was very low. Lea and Muflin (1979) and Schmidt (1979) reported that the probable reason for the differences between estimated and measured efficiencies could be the demand for other light-activated processes such as N and S metabolism. However, under normal environmental conditions (O₂ at 21%), the quantum yield of C₃ plants is very low and temperature sensitive where as this is not the case with C₄ plants (Ehleringer and Bjorkman, 1977).

A high quantum efficiency for CO₂ fixation would be an important advantage in habitats where the irradiance is low. Light could also have a marked influence on photosynthesis within the canopy, because the availability within the canopy is limited. Experimental evidence available on the quantum yield is variable. Bjorkman et al. (1975) and McKee (1972) found no differences in quantum yield between C₃ and C₄ species. However, Bull (1969) measured the light dependence of photosynthesis of several C₃ and C₄ species and found that C₄ plants had markedly higher efficiencies than C₃ plants. But work of Bjorkman (1981) has shown that the quantum yields of C₃ plants vary with temperature, whereas quantum yields of C₄ species do not vary with temperature. The C₃ species have a higher quantum yield compared to C₄ plants at low temperature, and their rates decline with increased temperature. Ehleringer (1975) and Berry and Raison (1981) have suggested a crossover point of 30°C, while Beadle et al. (1985) are of the view that the crossover point is approximately 22°C.

Considering the fact that the quantum yields of C₃ plants vary depending on the O₂ environment (2% and 21% O₂), quantum yield of C₃ plants can be expected to be controlled by photorespiration. Also the quantum yield in C₃ plants varies with the temperature as well as with photorespiration. Reidy and Rama Das (1987) found maximum photosynthesis coincided with maximum sucrose accumulation at photon flux density of 1600 μmoles m⁻² sec⁻¹. They also compared the levels of sucrose and fructose 2,6- diphosphate under different light levels and found low levels of sucrose and high levels of fructose 2,6- diphosphates at low light levels. Murata and Osada (1958) reported that, at high light levels, the dry matter production of varieties is determined.
by the differences in their photosynthetic ability, but, at low light levels, differences in respiration rates play an important role.

Reduced irradiation during the rainy season is considered one of the environmental constraints for rice production in tropical countries (Venkateswarlu, 1977). It has been clearly demonstrated that, under low radiation levels, both dry matter accumulation and yield are significantly reduced (Tanaka et al., 1966; Nayak and Murty, 1980; Venkateswarlu, 1977). Tanaka et al. (1966) estimated the diurnal canopy photosynthetic rate for cloudless, cloudy, and very cloudy days. According to them, photosynthetic rates dropped significantly with increase in cloudiness. The rate of decline was higher in mature populations than in young populations. Matsushima (1970) reported that there are two stages at which low light levels have critical influence on grain yield. Low light levels decrease grain yields by increasing the number of degenerated spikelets at the meiosis stage or by decreasing the number of ripened grains after flowering. Venkateswarlu et al. (1987) found higher levels of PAR increased the density of grains. They concluded that cultivars possessing a high proportion of high density grains would be advantageous even under low light levels.

Temperature

Although light is the driving force for photosynthesis, other environmental factors modify the rate of photosynthesis and productivity. Temperature has a major influence on photosynthesis (Cooper and Tainton, 1968; Kawashima, 1980). Differences in biomass production and growth between species correlate well with response of photosynthesis to temperature (Berry and Raison, 1981). Under field conditions, growth and biomass production will be determined by diurnal and seasonal changes of temperature in concert with other limiting factors. The response curve between photosynthesis and temperature is species dependent and characterized by high and low temperature compensation points and by an optimum temperature range (Ludlow and Wilson, 1971; Nobel et al., 1978).

One biophysical limitation of adverse temperature on photosynthesis is stomatal closure. Some studies have shown that stomatal closure is not the primary cause of the decline in photosynthesis at high temperatures (Raschke, 1975; Bjorkman et al., 1980). High temperatures will result in a
rapid decrease in the affinity of Rubisco for \( \text{CO}_2 \) and will increase photorespiration (Laing et al., 1974). However, according to Berry and Bjorkman (1980), the decline in photosynthesis at very high temperatures in \( \text{C}_3 \) plants cannot be fully explained by the increase in photorespiration. In contrast, the decline in photosynthesis at suboptimal temperatures is more a function of the activity of rate limiting carboxylation reactions in both \( \text{C}_3 \) and \( \text{C}_4 \) plants (Bjorkman et al., 1980).

Temperature response curves for photosynthesis of rice have been observed by many researchers. Results of Osada (1964) and Ishii et al. (1977a and 1977b) indicate that the optimum temperature range for photosynthesis is 25 to 35\( ^\circ \) C. The optimum temperature for photosynthesis in rice is lower than corn but higher than barley (Ishii et al., 1977a; 1977b). Corn leaves have shown the highest rate of photosynthesis at 35 to 40\( ^\circ \) C (Hofstra and Heskith, 1969) and barley and wheat leaves at 15 to 25\( ^\circ \) C (Sawada and Miyachi, 1974). Variation in maximum photosynthesis has been achieved by pretreatment of rice plants at high and low temperatures. Tsunoda (1984) reviewing this aspect concluded that indica rice is photosynthetically adapted to a temperature range of 25 to 35\( ^\circ \) C, however, optimum temperature for japonica rice is in the range 19 to 33\( ^\circ \) C. This indicates the thermal adaptation of indica rice to warmer areas and also points out that the cause for low productivity of rice in the tropics cannot be totally attributed to depressed photosynthetic rates. Other factors such as high respiration and low solar radiation are probably also responsible for low rice productivity in certain tropical environments.

**Moisture availability**

Water is fundamental to photosynthesis as a reactant a solvent for biochemical reactions, and a necessary component in transpiration. Net photosynthesis declines under water stress and photosynthesis may cease completely if plants are exposed to severe water deficit (Beadel et al., 1985). The cessation of leaf area expansion because of low turgor pressure (Bjorkman, 1980), the mobilization of carbohydrate reserves to offset the loss of new photosynthates (Fisher, 1973), ascorbic acid production which inhibits phloem loading, and the diversion of photosynthetic for osmoregulation (Mansfield and Wilson, 1981) are also features of plant water deficits which de-
crease productivity. Low water potentials also reduce the capacity for ribulose 1-5, bisphosphate (RuBP) regeneration (Farquhar and Sharkey, 1982).

Water lost by transpiration and biomass production are related through the term water-use efficiency (WUE), which is defined as dry weight gained per unit mass of water transpired (Good and Bell, 1980). In general, C₄ plants have much higher WUEs than C₃ plants (Good and Bell, 1980), and this is due to the higher photosynthetic rates in C₄ plants. Even though rice is grown under submerged conditions, incipient wilting and leaf rolling symptoms can be observed on hot, sunny days. This indicates an imbalance of water economy between transpiration and water absorption. Studies on the diurnal closure of stomates in rice under field conditions have shown that stomatal aperture is reduced at midday with high temperature, radiation level, and low humidity (Ishihara et al., 1971a; 1971b).

Midday decline in the photosynthetic rates of intact leaves of rice have been observed under temperate conditions with day temperatures above 30°C (Ishihara and Saitoh, 1987). Singh et al. (1988) measured the diurnal changes in photosynthetic rates of six cultivars at the flag leaf stage under tropical conditions. The plants reached light saturation at 1200 μmol m⁻² sec⁻¹ at 10 o’clock in the morning. The photosynthetic rates then declined during the midday up to about 2 o’clock followed by a slight increase at 3 o’clock and steep decline in the evening. The results indicated that the stomata were closed to a considerable extent due to water stress even though the rice plants were growing under submerged conditions.

Ishihara and Saitoh (1987) reported that stomata of rice will close in response to lowering of leaf water potential, but photosynthesis was not significantly lowered until the leaf water potential decreased considerably. Based on this fact, they concluded that the lowering of photosynthesis after stomatal closure was due more to the decrease in internal CO₂ concentration than to low water potential. This mechanism helps rice plants conserve soil moisture under dry, hot conditions. In contrast to rice, sunflower stomata are not as sensitive to lowering of leaf water potential and thus high photosynthetic rates are maintained until leaf water potential drops to -0.8 to -1.2 MPa (Boyer, 1971). But at the same time, transpiration in sunflower will continue and result in further lowering of soil moisture. The photosynthetic rate in rice leaves begins to decrease at -0.2 MPa and becomes
almost nil at -1.3 MPa (Hirasawa and Ishihara, 1978). Thus rice and sunflower differ in their response to high evaporative demand. In rice, photosynthetic rate is decreased by stomatal closure, but, at the same time transpiration, is also reduced, so that water content in plants is not greatly reduced.

Nitrogen Nutrition

One of the most common limiting nutrients for plant growth is N (N) (Tisdale and Nelson, 1984). Nitrogen nutrition during early plant growth of rice influences grain yield by controlling of the number of spikelets formed during the reproductive stage (Murata and Matsushima, 1975). Optimum N levels at maturity increase yields by maintaining optimum leaf area index (LAI) and high photosynthetic rates for maximum spikelet fill (Yoshida, 1981). Quantitatively, N required for vegetative growth is far more than that required for reproductive development (Murata and Matsushima, 1975). A rice crop that produces average yields takes up more than 90% of the N requirement before the heading stage (Inada, 1967). However, for high yields additional N is required for reproductive development of the crop and in some situations can be as high as 30 to 40% of the total N absorbed (Matsushima et al., 1966).

High N supply during early growth stages will result in vigorous vegetative growth which in turn leads to N dilution within the plant tissue (Schnier et al., 1990). High tiller numbers are negatively correlated with leaf N concentration (Schnier et al., 1990). Nitrogen status at panicle initiation (PI) stage will affect the yield potential through the number of spikelets initially, produced and a high supply of photosynthetic may minimize spikelet degeneration during reproduction (Wada and Matsushima, 1962; Evans and De Datta, 1979).

Availability of N at appropriate times can increase yields substantially. Matsushima (1970) gives a very detailed description of the influence of rate and time of N application on yield and yield components of rice. Application of N fertilizer after the onset of internode elongation is essential
for maximum yields (Hall et al., 1968; Wells and Johnston, 1970; and IRRI, 1970). The influence of excessive application of N to rice has also been reported. High rates of N applications during early vegetative growth stage will result in lodging (De Datta, 1981). High N levels applied at the late vegetative growth stage can result in the production of excessive number of spikelets. As a result, serious competition for assimilates would take place, resulting in spikelet abortion and/or poor spikelet filling (Kumura and Takeda, 1962; Wada, 1969).

The relationship between mineral nutrition and the rate of photosynthesis is complex. However, a certain rate of photosynthesis is required to maintain the mineral element absorption by the roots, and, conversely, a certain mineral nutrient supply is necessary to maintain photosynthesis (Brouwer, 1962). Nitrogen deficiency affects the photosynthetic apparatus directly, because N is an integral part of chlorophyll molecules and photosynthetic enzymes and indirectly the structure of the leaves. Experiments conducted by Hall et al. (1984) showed that the rate of CO₂ fixation was not markedly changed by the source of N in wheat and barley, but there was an increase in the rate in corn with ammonium as a N source.

Almost all assimilated N in plants is in the form of amino acids, proteins, and enzymes (Streeter and Barta, 1984). A substantial fraction of the leaf N is associated with the photosynthetic apparatus. Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco), the enzyme that is involved in fixing CO₂ with ribulose-1,5- bisphosphate (RuBP), accounts for up to 50% of the soluble protein in C₃ plants (Lawlor, 1987) and 10 to 25% of the soluble protein in C₄ plants (Schmitt and Edwards, 1981). Brown (1978) estimated that phosphoenolpyruvate carboxylase (PEP carboxylase) accounts for another 10% of the soluble protein in C₄ plants.

A close association exists between leaf N concentration and chlorophyll concentration. According to Takano and Tsunoda (1970), some varieties of O. sativa exhibit a fairly high chlorophyll level in relation to their N concentration per unit leaf area. Therefore, leaf N concentration should have a direct relationship with the leaf photosynthetic rate. Substantial evidence is available to show a linear relationship between leaf N concentration and leaf photosynthetic rate of rice (Yoshida and Coronel, 1976; Uchida et al., 1982; Cook and Evans, 1983a; 1983b). There is also evidence to show that at very high N concentrations some genotypes may not increase the
photosynthetic rate after a certain level of leaf N (Murata, 1961; Takano and Tsunoda, 1971). Sinclair and Horie (1989) reviewed the available literature on the relationship between leaf N and leaf photosynthetic rate of rice. They concluded that the relationship is generally linear from an intercept of 0.3 g N m\(^{-2}\) of leaf area to about 1.6 g N m\(^{-2}\) of leaf area. At or about this level, photosynthetic rates will reach a maximum, and any further increase in leaf N will not increase photosynthetic rate.

Rice yields normally increase when the amount of N applied is increased (Yoshida, 1981). Information on the critical concentration of N in the rice plant is required. When concentrations are above or below critical levels deficiencies or toxicities will develop (Brandon and Wells, 1986). Okajima (1960) reported at least a minimum N concentration of 1% in rice seed is needed for root emergence. According to Ishizuka and Tanaka, (1963), a N concentration of 3.5% in leaf tissues is required for active tillering. At 2.5% N, tillering may stop, and N levels below 1.5% will result in tiller death. Tanaka and Yoshida (1970) proposed a critical deficiency level of 2.5% for leaf blades of rice. Brandon and Wells (1986) reported critical leaf N levels of 2.6 to 3.2% for cultivars in the southern United States of America. Zacharias et al. (1989) used 2.75% as the critical level of leaf N for the most recently developed rice leaves at panicle initiation stage. Although the availability of N is important throughout the life cycle of the rice plant, application of N at the time of panicle initiation has a high efficiency in terms of grain production (Matsushima, 1970; 1976; Yoshida, 1981). Nitrogen applied at this stage is generally efficiently used to increase spikelet number and hence panicle size. Another aspect of N application at this stage is that it will increase the photosynthetic rate during ripening and also result in increased leaf area and leaf area duration.

Differences in light reflection, transmission, and absorption rates of rice leaves in relation to chlorophyll and N concentrations per unit leaf area have been observed (Takano and Tsunoda, 1970). A positive correlation between leaf chlorophyll concentration and light absorption and thus a negative correlation with the light reflection and transmission rates was observed. Takano and Tsunoda (1970) examined several species and strains of oryza rice (both cultivated and their wild relatives) and found that the wild species/strains that are adapted to shady habitats had a relatively higher chlorophyll concentration per unit of N in the leaf than some cultivated species. They re-
garded this observation as an adaptation mechanism of these varieties to low light levels. Among cultivated strains tested, japonica cultivars tended to have a higher N and chlorophyll concentration per unit leaf area and higher light absorption rates than indica cultivars.

Plants will absorb both nitrate and ammonium ions depending on their availability in the soil (Tisdale and Nelson, 1984). Under submerged conditions the ammonium ion is the major form of N available for rice (Ponnamperruma, 1972; Savant and De Datta, 1982). Although relatively low concentrations of ammonium are toxic to many upland crops, rice tolerates and uses ammonium efficiently at relatively high concentrations (Yoshida, 1981).

Nitrate reduction is also essential for growth and efficient photosynthesis. If the rate of NO₃⁻ conversion to ammonium ions is slower than the potential rate of protein synthesis, then the expansion of photosynthetic surface is slowed and senescence is increased (Lawlor, 1987). The rate of nitrate reduction depends on the supply of reductant and carbon skeletons from photosynthesis (Robinson and Baysdorafer, 1985) or respiration (Suzuki et al., 1985), and on the amount and turnover of enzymes (Lawlor, 1987). Energy is required for the active uptake of nitrate and ammonia N into the roots and their incorporation into organic molecules (Breevers and Hageman, 1980). Energy is also required for the conversion of nitrates into ammonium, and therefore the theoretical energy requirement is greater when plants produce proteins from nitrates rather than from ammonium ions (Miflin, 1980). However, some of the energy for this conversion is derived from photosystem II (Lea and Miflin, 1980) and could be the reason for no significant differences in energy requirements in plants treated with different sources of N.

The increase in root N absorption at least in part has been linked to photosynthetic activity of the leaves. The initial uptake of inorganic N in the roots is often accompanied by an increase in photosynthetic rates, leaf area, and root respiratory activity (Robinson and Baysdorafer, 1985). The demand by the N absorption system for reductant and energy is transmitted to the leaf and the rate of N absorption depends on the ability of the leaf to supply the energy requirement of the root (Jenson and Seftor, 1987). Therefore, N absorption is interactive with the photosynthetic apparatus.

CHAPTER II
Studies with higher plants have shown that N assimilation is also concurrent with light-dependent reactions of photosynthesis. The energy required for N assimilation is supplied by hydrolysis of water in light and never inhibits but often stimulates photosynthesis (Robinson and Baysdorffer, 1985). Increased activity of the assimilatory enzymes such as Rubisco and fructose 1,6- bisphosphatase has been found at the onset of inorganic N assimilation within the leaves (Jensen and Seftor, 1987). According to Jensen and Seftor (1987), understanding the impact of N assimilation upon C metabolism in photosynthetic tissues is extremely important to understand photosynthetic partitioning.

Changes in diffusion resistance to CO₂ uptake induced by N deficiency has been reported in corn, cotton, and beans (Ryle and Hesketh, 1969). The inhibition of photosynthesis in these N-deficient plants was accompanied by an increase in mesophyll resistance and to a lesser extent by an increase in stomatal resistance.

There are two ways that the developing grain can obtain N: 1) soil N absorbed and reduced during the grain development period, and 2) redistribution of N assimilated during the vegetative growth period (Dalling, 1985). Uptake of N during the grain filling period can be considered to be a function of the availability of soil N and the capacity of the root to absorb and translocate N to the shoot. When the plant utilizes N from vegetative organs, organs generally senesce. Nutrient mobilization, especially N, from the vegetative organs to the seed is of economic importance. If the accumulation of N in the plant during vegetative growth can be increased, a larger source of N is available for redistribution during grain filling.

There are differences in translocation efficiency of N from different organs of the wheat plant during grain filling. Dalling (1985) found 20 to 25%, 80%, and 65% of the N in root, leaf, and stem, respectively, N present at anthesis were removed to the grain by maturity for wheat. No reason has been proposed for the low redistribution of root N to the grain in wheat. It may be simply that roots do not senesce fast enough to translocate significant quantities of N to the developing panicles. Experiments conducted at the International Rice Research Institute (IRRI, 1976) have indicated that two rice cultivars, Peta and H4, both tall indica varieties, apparently extracted and used soil and fertilizer N more efficiently than other varieties. However, under typical

CHAPTER II
farm conditions, these varieties lodge, resulting in low yields. Such responses can be considered as secondary yield losses. Appropriate rates and times of applications can possibly reduce the adverse influence of N applications on these varieties and capture benefits of their higher N use efficiency.

Photosynthesis and Respiration

Respiration is the main process other than assimilation that determines dry matter production. Plant productivity is reduced by respiratory losses throughout the period of crop growth, but respiration is essential to provide energy and substrates for all biochemical processes (Lawlor, 1987).

Loomis and Williams (1963) estimated 33% of the C fixed by photosynthesis in rice is lost by respiration. However, according to Tanaka et al. (1966) this estimate is low; they concluded that 50 to 60% of the photosynthate is lost by dark respiration in rice. The proportion of C released by respiration to that retained in the rice plant is smaller at early growth stages than at later stages (Tanaka et al., 1966). Dark respiration tends to be greater in leaves with higher N concentrations (Takano and Tsunoda, 1971). Two mechanisms of dark respiration coupled with electron transport and ATP synthesis have been identified in the plant mitochondria (Storey, 1976; Lawlor, 1987). In one pathway, normal electron transport is coupled to produce three ATPs, and in the other electrons are consumed by an alternative oxidative pathway and produce only one ATP (Lawlor, 1987). Rapid photosynthesis in the previous light period stimulates respiration and probably increases carbohydrates consumed in the alternative oxidative pathway when in excess of the normal pathway (Lawlor, 1987).

High rates of N have been shown to increase both photosynthesis and dark respiration in winter wheat. However, low respiration rates in the developing wheat ears in semi-dwarf varieties compared to older, tall varieties are a major reason for high yields with semi-dwarf winter wheat varieties (Pearman et al., 1979). Increased N application to wheat increased photosynthetic rate by 2.3 fold, but the increase in yield was only 1.8 fold (Pearman et al., 1979). This discrepancy between
photosynthesis increase and yield was not accounted for by increased retention of dry matter in the stem.

Biophysical Constraints

Photosynthetic rates are determined by changes in the rate of CO₂ diffusion into leaves through stomata and photosynthetic activity in the mesophyll cells. During photosynthesis a concentration gradient develops between CO₂ in the ambient air and the chloroplast (Zelitch, 1971). The rate of net photosynthesis is partially determined by the size of the gradient and by a series of resistances to diffusion. These resistances include leaf boundary layer resistance, stomatal resistance, and mesophyll resistance (Zelitch, 1971). The resistance to diffusion of CO₂ and water vapor between the leaf and the atmosphere is a function of stomatal frequency and stomatal aperture (Ciha and Brun, 1975). As rice is a semi-aquatic plant, some of the leaf properties have adapted to guarantee the smooth transfer of CO₂ from the ambient air to the photosynthetic sites provided the stomata are not closed due to water deficit or extreme temperatures (Tsunoda, 1984).

Boundary layer resistance arises due to a nonturbulent air layer adjacent to the leaf surface. When this layer is thick, diffusion of water vapor and CO₂ is slow and the resistance is high. Some of the leaf anatomical properties that have been observed in primitive rice varieties that reduce the boundary layer resistance are: 1) narrow and dispersed leaves that are not twisted as in barley and wheat, 2) moderate frequency of hairs on the leaf surface, and 3) shallow stomatal position, which may cause air turbulence (Tsunoda, 1984).

Gases primarily diffuse through the stomata which are microscopic pores in the leaf surface encompassed by the guard cells of the epidermis. Hence, both the number of stomates on the leaf surface and their aperture controls CO₂ diffusion into the leaf interior. Factors that control stomatal opening will be important in determining photosynthesis rate in plants. When fully
opened, stomatal pores may measure from 3 to 12 μ in width and 10 to 40 μ in length (Devlin and Witham, 1983).

A linear correlation between stomatal conductance and photosynthetic rate has been reported when irradiance levels were increased and when other factors are not limiting (Wong et al., 1978). However, when a combination of environmental factors and their interactions affects the response, it is difficult to quantify the influence of stomatal conductance. Ball et al. (1986) took a multivariate approach to study stomatal conductance and showed that under many conditions the response of stomata can be described by a set of linear relationships, which include stomatal density, stomatal aperture, and stomatal sensitivity to environmental variations.

Genetic variation exists for number, size, and time of opening and closing of stomata (Rasmussan and Hengenbach, 1984). Stomatal frequencies of upland rice varieties are lower than lowland varieties, and indica varieties have higher stomatal numbers than japonica varieties (Yoshida and Ono, 1978). Tsunoda (1984), reviewing the work of others, reported differences between rice varieties for stomatal frequency for both upper and lower surfaces. They ranged from 357 mm⁻² to 534 mm⁻² on the upper leaf surface and from 445 mm⁻² to 721 mm⁻² on the lower leaf surface. According to the review of Yoshida and Ono (1978) the frequency observed in other crops is far less than that of rice, ranging from 36 to 98 mm⁻² on the lower surface of spring wheat and 81 to 175 mm⁻² on the upper (Miskin and Rasmussan, 1970), and 242 to 345 mm⁻² on the lower surface of soybean (Cih a and Brun, 1975). Miskin and Rasmussan (1970) examined 649 cultivars from the world collection of barley and found stomatal frequencies ranging from 36 to 98 stomata mm⁻² with a mean of 64 mm⁻². Data for a wide range of plant species were listed by Lacher (1980) and Willmer (1983). These numbers indicate rice has a higher total stomatal density (upper + lower) than most other crops.

The CO₂ entering through the stomata experiences mesophyll resistance before reaching the chloroplast. This barrier is called mesophyll resistance (Zelitch, 1971). Mesophyll resistance includes the resistance through the cell wall, resistance of the plasma membrane, and resistance produced by the limitation of the enzymatic carboxylation reaction. As a molecule encounters a wet cell wall, the diffusion rate is markedly decreased (Lawlor, 1987). Another kind of mesophyll
resistance is present in the junction where respiratory CO₂ joins the main flux and represents the physical barrier that separates the CO₂ coming from the atmosphere and from respiration (Zelitch, 1971). Mesophyll resistance is the largest component of all resistance in C₃ plants and therefore, it is generally recognized as the main controlling factor for CO₂ diffusion (Nobel and Longstreth, 1981). Apart from the cellular component variations, mesophyll resistance can be affected by leaf structure and anatomical components. The anatomical component is the surface area available for CO₂ absorption under a given area of leaf surface (Nobel and Longstreth, 1981). These changes can be due to changes in the number of cell layers and the conformation of the individual cells (Nobel, 1980).

Diffusive resistance resulting from boundary layer and stomata is small in rice (Tsunoda 1984). For instance, Singh and Sashara (1981) observed minimum CO₂ diffusion conductance of 1.25 to 1.43 cm sec⁻¹ in a lowland rice variety, while Kishitani and Tsunoda (1981) reported a value of 0.25 cm sec⁻¹ for a wheat cultivar. O'Toole and Tomar (1982) studied the stomatal conductance of two lowland rice varieties and barnyard grass, a C₄ weed. During the active transpiration period, leaf conductance of rice varieties remained high (0.5 to 2.0 cm sec⁻¹ ) compared to barnyard grass (0.1 to 1.0 cm sec⁻¹ ). Data relating to the minimum stomatal CO₂ diffusion resistance for different crops have been summarized by Korner et al. (1979) and listed by Larcher (1980). Low gas diffusion resistance of leaves also promotes high rates of transpiration and may also be advantageous for tropical rice because of transpirational cooling of the leaves.

Leaf Anatomy and Photosynthesis

Differences in photosynthetic capacity among C₃ and C₄ plants have been related to leaf anatomy (Zelitch, 1971). The differences in photosynthetic rates among species and varieties of C₃ plants can also be related to the differences in their leaf anatomy (Chonan, 1978). Most mesophyll cells in graminaceous crops have protuberances called armed-palisade cells (Chonan, 1970). This
is an important characteristic related to gas exchange between the intercellular spaces and mesophyll cells. The size of isolated mesophyll cells of rice was found to be the smallest among the cereal crops that had been studied (Kariya and Tsunoda, 1980). The area of single mesophyll cells of wheat, corn, and barnyardgrass were 20, 10, and 5 times, respectively, larger than rice (Kariya and Tsunoda, 1980). The surface to volume ratio of the mesophyll cells is much higher in rice than other cereal crops including corn, barley, and wheat (Chonan, 1970; Kariya and Tsunoda 1980). This is due to the small size of rice mesophyll cells (Tsunoda, 1984) and the small diameter and length of protuberances of the mesophyll cells (Chonan, 1970).

Mesophyll cells of rice leaves are conspicuously elongated in tangential and transverse direction but not so much elongated in the longitudinal direction (Chonan, 1978). The shape of armed cells is clearly observed in leaf transection but tubular palisade cells cannot be seen clearly. The number of protuberances developed by a cell ranges from 3 to 12 (Chonan, 1978). Kariya and Tsunoda (1980) studied the size, shape, and disposition of the chloroplasts located in the mesophyll cells of five cultivated species of gramineae, including rice, and three cultivars of Brassica species. The rice chloroplasts were the smallest among gramineae species. However, in spite of the different sizes of chloroplasts among species, the ratio of long and short diameter of the isolated chloroplasts were almost the same. The chloroplast surface in contact with the cell wall seems to be important as the site of gas exchange (Kariya and Tsunoda, 1980). Further, the size of the rice chloroplasts is small and this increases the chloroplasts surface contacting the cell wall compared to wheat, barley, and corn (Kariya and Tsunoda, 1980).

Gas exchange properties such as low stomatal resistance and small messophyll cells have evolved in older varieties as a result of hot, humid, and cloudy conditions of the native environments. However, these good gas exchange properties can increase the sensitivity of rice photosynthesis to low temperatures, drought, and high light level (Tsunoda, 1984). In rice breeding programs, these properties have been altered knowingly or unknowingly to adapt varieties to cool or dry climates with high light intensities (Tsunoda, 1984).

A direct relationship between net assimilation rate (NAR) and specific leaf weight (SLW) has been found (Ohno, 1976). The SLW expresses the amount of dry matter per unit leaf area and does
not necessarily imply morphological thickness of leaves in rice (Ohno, 1976). Friend et al. (1962) however, found a close relation between SLW and leaf thickness in wheat. Specific leaf weight in rice leaves is related to the leaf N content per unit leaf area. Leaf photosynthetic rates were positively correlated with leaf N content and with SLW of 41 rice cultivars that included both Asian and African cultivars (Cook and Evans, 1983b).

**Growth and Productivity of Rice**

Crop production efficiency is the dry matter accumulation rate in terms of production input units (Eastin and Sullivan, 1984). Final grain yield is determined by complex chains of development processes which take place in a definite sequence. A change in any one of these processes, or the process sequence may influence all the following processes (Yoshida, 1972; Murata and Matsushima, 1975). Dry matter production depends on transformation of light energy into chemical energy through photosynthesis. Simple photosynthetic products are translocated to the site of utilization and are elaborated into the storage component of interest. Better understanding the physiological processes involved in grain production, such as vegetative growth, formation of storage organs and dry matter partitioning can suggest improvements to achieve increased yields under given conditions (Yoshida, 1972).

**Growth analysis**

Dry matter accumulation per unit land area per unit time is referred to as crop growth rate (CGR). Studies of CGR are important in the interpretation of yield differences among crop cultivars and cultural practices (Brown, 1984). Since crop yields may be affected by many factors during the growing season, analysis of growth throughout the growth cycle may be helpful in explaining yield differences (Brown, 1984). Other growth parameters such as relative growth rate (increase in dry matter in relation to existing dry weight - RGR) and net assimilation rate (dry
matter accumulation in relation to leaf area - NAR) can also be used to assess dry matter accumulation of plants (Brown, 1984). Measuring net photosynthetic rate on a single leaf or canopy basis can be used as a measure of potential dry matter production. Even though photosynthetic measurements can be made of a large number of cultivars or treatments in a relatively short time, it measures only the net CO₂ exchange under a given set of environmental conditions. These conditions vary both diurnally as well as seasonally and thus may not represent the whole picture. On the other hand, growth analysis has the advantage of giving an integrated measurement of net photosynthetic activity over a wide range of environmental conditions that prevail in the field throughout the growing season.

Cook and Evans (1983b) compared physiological variations in 41 rice lines representing seven oryza species involved in domestication of both Asian and African cultivars. The relative growth rate shows a tendency to be low in lines with high initial dry weight. All African species (O. glaberrima, O. stapfie, and O. bartha) and O. nivara had high RGRs, while the more advanced indicas had lower rates relative to initial plant size than the older indica cultivars. The decrease in RGR was also associated with relative leaf area ratio. Plants having highest relative growth over varieties (species) tend to accumulate most dry matter in leaf sheaths and roots. Ohno (1976) studied 301 indica rice varieties for photosynthetic efficiency and dry matter production under different climatic conditions. He found that the net assimilation rate (NAR) showed a normal frequency distribution and had not only a significant correlation between different climatic conditions but also high heritability. He also reported that NAR and SLW can be used as indexes of photosynthetic capacity among varieties of indica rice.

Synthesis, translocation, partitioning, and accumulation of the photosynthetic products within the plant are controlled genetically and are influenced by the environment (Snyder and Carlson, 1984). Monsi and Murata (1970) have indicated the importance of dry matter distribution (partitioning) in influencing growth and yield. Varietal differences in photosynthetic rates and biomass production have been observed, but attempts to increase yields through the combination of these two factors have not succeeded (Evans et al., 1984). Traditional varieties have the capability to produce high biomass; but mutual shading of leaves decreases the CGR, and their assimilate par-
tioning is poor (Jennings, 1964). Without proper partitioning, increase in biomass would lead to a higher proportion of non-photosynthesizing plant parts or increase in plant height.

**Harvest index**

The harvest index (HI) is the ratio of economic product (grain) to the above ground biomass at harvest (Snyder and Carlson, 1984). Donald and Hamblin (1976) have reviewed the development of the concept of HI and presented detailed discussion of the advantages and limitations in selecting for increased yields in cereals. Harvest index of many crops correlates positively with grain yield and negatively with biological yield (Snyder and Carlson, 1984). However, others have shown that this is not the case for all situations. Murty and Sahu (1977) reported that biological yield had no negative influence on HI of rice. They concluded that selection for grain yield alone would not increase HI and that advancement can be made by selecting for high grain yield combined with high HI. Inconsistencies have been reported in HI across years, and this probably reflects the influence of environment on partitioning and accumulation of dry matter (Snyder and Carlson, 1984).

Increase in yield potential has been achieved mainly by direct selection for ability to yield under improved management situations. Any change in individual physiological characteristics have resulted only indirectly from such selection (Gifford and Evans, 1981). There is no evidence to show that yield increases in rice or in other cereal crops have been achieved through direct or indirect selection for high photosynthetic rates per unit leaf area (Gifford and Evans, 1981). It has been shown very clearly that the yield increases in cereals in the past have been achieved through an increase in proportion of dry matter harvested as grain, i.e. harvest index (HI) and not through increases in total biomass production (IRRI, 1978; Gifford and Evans, 1981; Gifford et al., 1984; Evans et al., 1984).

Modern varieties, characterized by short stature and stiff straw, differ markedly from the tall weak-stem plant type of the traditional rice varieties. It has been generally recognized that a short stature is associated with high yielding ability and N response. The low response of traditional varieties to N is due to lodging and mutual shading (Beachel and Jennings, 1965; Chandler, 1969). Low tiller survival because of mutual shading and cessation of growth after flowering probably
contributes to the relatively low yields of tall leafy varieties. However, in order to increase rice yields, total biological yield must also be maintained at a certain level so the that plant is capable of supporting a larger panicle (Shigemura, 1966).

The HI has increased from less than 0.10 in wild relatives of rice to about 0.55 in modern varieties (IRRI, 1978; Evans et al., 1984). Further increases in HI may not be a practical approach, because less non-photosynthesizing plant parts, less straw, and decreased plant height will not support a large panicle (Vergara, 1988). Rice plants with 0.60 HI generally have not increased yields, because they are very short with small leaves, low tiller numbers, and low spikelet numbers (Vergara, 1988).

**Partitioning of photosynthate**

Partitioning of photosynthate is an important component of economic yield, operates in conjunction with other physiological processes, and is influenced by the environment. Thus maximizing the economic yield in a given environment requires that all physiological processes be operating optimally (Snyder and Carlson, 1984). The literature on sink-source relationships is extensive and often contradictory. For example, Yoshida (1972) has shown in CO₂ enrichment studies that rice yields increase with increasing CO₂ concentrations due to enhanced photosynthesis. He therefore concluded that source is limited factor for higher grain yields. Others have shown that in modern cultivars, under contemporary management conditions, frequently more than 85% of the spikelets are filled; but appreciable levels of nonstructural carbohydrates remain in the leaves or culms, suggesting that the sink size is inadequate (Murata and Matsushima, 1975). Other work suggests that, while photosynthetic rates averaged over the season do not correlate well with the total dry matter accumulation, photosynthetic rates during ripening and early maturity stages do correlate with yield (Tanaka, 1961; Murata, 1965).

Methods which have been used to establish variations in the sink - source ratios have involved either changes in CO₂ concentrations to alter source component, shading or clipping leaves to reduce source, or excising panicles to reduce the sink (Lafitte and Travis, 1982). Such methods induce rather then constitute variations in the sink-source relationships; thus, such experiments are of
limited value (Geiger, 1976). Lafitte and Travis (1982) used near-isogenic lines to evaluate variations in sink-source and showed that lines with high sink-source ratios exhibited higher rates of C exchange per unit leaf area and accumulated lower amounts of nonstructural carbohydrates (< 3%) than lines with lower sink-source ratios. They are of the view that sink to source ratios can be altered genetically and that such manipulations can affect plant yields.

Allocation of photosynthate as a response to sink demands is generally accepted but it has also been shown in several systems that the rate of photosynthesis changes with changes in sink requirements (Evans 1975; Tanaka, 1976; Frey, 1981). There are indications that photosynthetic rates are controlled by feedback signals and depend on number and capacity of metabolically active sinks (Neals and Incoll. 1968). Therefore, high photosynthetic rates of flag leaves do not necessarily mean that the sink demand is totally from the panicle but may be from other sinks such as developing tillers, leaves, and roots. When developing varieties for unstable environments, the ability to shift sink strength from one organ to another has an important role to play in dry matter partitioning. If this shift does not occur, most of the photosynthate must be shared by a number of sinks rather than by the developing ear. Tanaka (1976) has stated that in southeast Asia in the early 1960s, the source was the limiting factor in rice. Evans (1975) believed that the modern cultivars of major crops are likely to have their photosynthetic and storage capacities closely balanced and further increases in yield require that both these factors increase in a coordinated way.

Grain yield

Grain yield in rice is a function of panicles per unit land area, grains per panicle, and single grain weight (Yoshida, 1981). The number of panicles in a rice crop depends upon development processes such as tiller initiation, development, and abortion (Matsushima, 1976). Grains per panicle are dependent on spikelet differentiation, fertility level, and fertilization (Matsushima, 1976). Grain weight is primarily determined during the grain filling period (Yoshida, 1981). Increasing these three yield components is necessary to increase yields. However, they are negatively correlated to each other, especially above certain limits (Matsushima, 1976; Tanaka, 1976; Yoshida, 1981;

The genetic yield potential of a rice variety is difficult to define; but, in theory, it is only the sink size that is critical, i.e. the product of maximum number of spikelets per unit land area and the average single grain weight (Gifford et al., 1984). The realization of this potential depends not only on genetic ability but also on other factors, especially environment and management. Steady improvements in genetic yield potentials together with improved agronomic practices have contributed to increased rice yields (Tsunoda, 1984). However, there is a wide yield gap between the potential and actual farmer yields (Herdt and Mandac, 1980).

Increases in actual farm yields could be achieved from many directions such as increased genetic potential, improved agronomic practices, greater resistance to pests and diseases, adaptation to environmental conditions, and the interaction among these factors (Gifford and Evans, 1981). Much of the advantage of the semi-dwarf varieties has been attributed to their short stature (preventing lodging), superior light interception, and response to N fertilization (Jennings, 1964; Zelitch, 1982). However, the same characteristics that contribute to the high yield potential decreases the competitive ability of the cultivar. Genotypes with high HI have been found to be weak competitors because of the relatively few resources allocated to root, shoot and leaf expansion (Donald and Hamblin, 1976). Recent studies have indicated that even though HI is more important under high yield potential environments, total biological yield is more important in low yield potential environments. The growth and development pattern of a given cultivar growing in different environments is determined by its genetic characteristics. Some cultivars have capabilities to overcome some of the stress. This indicates that the "yield potential" should be expressed in relation to the growing environment. A variety which has a high yield potential in stable, high input environments may not express the same potential in unstable low input situations. In many situations they have low productivity when compared with cultivars adapted to those environments. Such observations indicate that for good, wide-range environmental adaptability, the ideal plant type for high yield potentials under stable environments and high management inputs may not be the proper varieties for unstable environments where management inputs are low.
References


CHAPTER II


CHAPTER II 42


CHAPTER II


CHAPTER II 45


CHAPTER III

Response of Three Rice Varieties to Nitrogen Management:

I. Leaf Characteristics, Sink Size, and Grain Yield.

ABSTRACT

Studying plant parameters associated with utilization of N by different rice (*Oryza sativa* L.) varieties may reveal efficient and inefficient responses. The objective was to examine the relationship between the uptake of N and different leaf characteristics, sink size, and grain yield of three morphologically distinct rice varieties. Three varieties were grown under four different N management regimes. A "traditional" (tall and low-yielding) rice variety, a "modern" (semidwarf and high-yielding) variety, and a variety showing "intermediate" characteristics were grown in pots in a greenhouse. The N management treatments were: 1) a 0 N control, 2) 200 mg N kg\(^{-1}\) of soil split into two applications, 3) 200 mg N kg\(^{-1}\) of soil split into three applications, and 4) 400 mg N kg\(^{-1}\) of soil split into three applications. Leaf N per unit leaf area (LNLA), leaf area, specific leaf weight
(SLW), and stomatal density were measured at two growth stages: 1) at time of maximum tillering, and 2) upon full expansion of the flag leaf. Sink size, yield components, and grain yield were determined separately on the main panicle and subtending tillers at maturity. Correlation coefficients for different parameters were calculated. Rate and timing of N fertilizer application and variety influenced the LNLA at both growth stages. Leaf N per unit leaf area ranged from 68 µg cm⁻² to 175 µg cm⁻². Competitive use of fertilizer N for the development of either larger leaf area or higher LNLA varied with N management and variety. The modern variety had the capability to increase both leaf area and LNLA in response to high N applications. When N supply was limited and early N applications were restricted, the intermediate variety increased flag leaf LNLA with less increase in leaf area of the plant. The traditional variety responded to N by increasing leaf area more than by increasing LNLA for all N management treatments. Specific leaf weight did not differ with N management except that it was lowest in the N control treatment. Stomatal density ranged from 201 to 515 mm⁻² depending on leaf surface, variety, N management, and growth stage. Increased N reduced stomatal density as it increased leaf area. Total stomatal number per leaf varied little within cultivars, indicating that N fertilization did not increase stomatal numbers. Results showed the importance of differential N management for different varieties for optimum yields when grown under moderate N levels (200 mg kg⁻¹). The intermediate variety produced higher yields than the other two varieties at the moderate N levels, while the modern variety produced highest yields at the high N levels. Yield variations in both the modern and traditional varieties were mainly associated with variations in panicle number per plant. In the intermediate variety, grain number per panicle was the yield component most affected. Grain yields were positively correlated to total N content of the flag leaf and the penultimate leaf. Yield variations due to N fertilization were mainly associated with panicles produced on tillers rather than panicles on the main culm.
INTRODUCTION

Nitrogen plays an important role in determining grain yields. When compared to traditional varieties, modern rice varieties generally have shorter stature, erect leaves, photoperiod insensitivity, shorter maturation periods, and more responsiveness of yield to N fertilization (Jennings, 1964; De Datta, 1981). To obtain rice yields exceeding 4 Mg ha\(^{-1}\) with new varieties in tropical Asian countries, 90 kg N ha\(^{-1}\) or more are generally needed (Barker, 1979). High fertilizer costs (Prasad and De Datta, 1979), seasonal and locational yield variations (Barker, 1979), and losses of N by volatilization, leaching, and denitrification (De Datta et al., 1968; Prasad and De Datta, 1979) all contribute to the use of less than experimental optimum rates of N. The short stature and low initial crop canopies of modern varieties make them less competitive with weeds, and increased N applications can compound weed problems (De Datta, 1981).

Reports on plant characteristics associated with efficient utilization of N fertilizer are few, even though N by cultivar interactions have been observed (Ohno, 1976; Yoshida 1972; Cook and Evans, 1983a). Broadbent et al. (1987) have discussed the importance of studying genotypic differences in plant parameters associated with N utilization. Such parameters include leaf N content, specific leaf weight (SLW), stomatal density, leaf area, dry matter production (Ohno, 1976; Cook and Evans, 1983a; 1983b), spikelet number, and effectiveness in spikelet filling (Yoshida, 1972; Matsushima, 1976). A better understanding of these characteristics may allow a systematic exploration of genetic approaches to increasing N use efficiency in rice production.

Genotypic differences in N-use efficiency in rice have been observed (Broadbent et al., 1987; Wada and Cruz, 1987). Differences could be associated with the ability for high fertilizer recovery from the soil and/or with increased conservation of N in the plant for remobilization into grain yield. It would be instructive to know the N absorption pattern of rice varieties grown under different N managements as well as the influence of absorbed N on key plant characteristics and yield components. Cook and Evans (1983b) examined several genotypes of wild and cultivated Oryza species and found leaf photosynthetic rates were positively correlated with LNLA and SLW. They
reported greater SLW for flag leaves than for lower leaves but the ranking of varieties did not change with growth stage. Ohno (1976) studied morphological characteristics of 23 rice cultivars. He concluded that SLW can be regarded as a useful primary index of selection for high net assimilation rate, because SLW is a stable character that is not influenced by environmental variations.

Information about the variation in stomatal density among cultivars and the relationship to N fertilization is needed because of the importance of stomatal density in regulating gas exchange rates both in transpiration and photosynthesis. Tsunoda (1984) reviewed the work of others and concluded that varietal differences exist in stomatal density of upper and lower leaf surfaces and in total stomates per leaf area. Stomatal densities ranged from 357 to 534 mm\(^{-2}\) on the upper surface and from 445 to 721 mm\(^{-2}\) on the lower surface. The stomatal densities observed in other crops are generally far less than those of rice (Willmer, 1983). The high stomatal density of rice is considered an adaptation to semi-aquatic environments (Tsunoda, 1984). Using stomatal density as a selection criteria to breed for water use efficiency (WUE) has been proposed for other crops (Nair and Pazourer, 1986; Tanzarella et al., 1984). However, little progress has been made in breeding lowland rice for high WUE.

Developing optimum plant types through the use of optimum yield components and morphological and physiological traits has been proposed for rice (Beachell and Jennings, 1965). Ideotypes proposed so far, however, are intended to produce maximally in high-input environments. Very little work has been done on ideotypes for suboptimal environments and moderate management levels.

The number of spikelets produced during early reproductive growth stages is an important factor in determining sink size and grain yield. Examinations of grain yield components have shown that the number of spikelets per panicle is highly sensitive to environmental variations (Cook and Evans, 1983b). Both the growing environment and management during the reproductive stage play an important role in determining the grain yield in rice. Although genotype differences in plant characteristics related to physiological processes have been widely recognized, they are often analyzed without taking into account variations due to N fertilizer. Moreover, physiological functions change with the growth stages; therefore, the plant characteristics associated with them need to be
studied at different growth stages. The experiment discussed in this paper was part of a broader study to investigate some physiological characteristics of three different rice varieties that responded differently to N management.

The objective of this study was to measure the uptake of fertilizer N by three different rice varieties when grown under different N management (rate and time) levels and to determine relationships between LNL/A, stomatal density, SLW, sink size, yield components, and grain yield.

**MATERIALS AND METHODS**

Three rice varieties with different morphological characteristics were used to represent different plant types. 'Herathbanda' which is referred to as a traditional variety, is tall, leafy, and lodging susceptible. It has a relatively high tillering capacity and is popular among rice farmers in the wet zone of Sri Lanka where modern varieties have performed poorly. 'H501', an intermediate variety, was released from the Sri Lankan national rice breeding program during late 1950s. H501 is medium to tall in height and leaves are somewhat droopy. 'Bg 34-6', a modern variety, is semidwarf with erect leaves, has a moderate tillering capacity, and has a high yield potential under stable environments with good management. Seeds for the experiment were obtained from the International Rice Research Institute, Philippines.

The experiment was conducted at Virginia Polytechnic Institute and State University, Blacksburg, VA in a greenhouse with an evaporative type cooling system. Average maximum and minimum temperatures inside the greenhouse during the experiment were 32 and 22°C. Radiation inside the greenhouse was about 40% of full sunlight.

Pre-sprouted seeds were placed in trays filled with soil on 15 June 1989. When the seedlings were 15 d old two seedlings were transplanted in to plastic pots filled with one kg of soil. The soil was a clay loam (an Ochraquult) with pH of 5.9, 12 g OM kg⁻¹, and 0.8 g total N kg⁻¹. Four N management treatments were used: 1) T₀ = a 0 N control, 2) T₁ = 200 mg N kg⁻¹ of soil split

**CHAPTER III**
into two applications of 35 mg N applied at transplanting (0 DT) and 165 mg N applied at 49 d after transplanting (49 DT), 3) $T_2 = 200$ mg N kg$^{-1}$ of soil split into three applications of 35 mg N applied at 0 DT, 80 mg N applied at 21 DT, and 85 mg N soil applied at 49 DT, and 4) $T_3 = 400$ mg N kg$^{-1}$ of soil split into three applications of 75 mg N 0 DT, 175 mg N applied at 21 DT, 150 mg N applied at 49 DT.

Treatments were arranged in a randomized complete block design with 12 treatments (three varieties x four N managements) and three replications. Each treatment was assigned to four pots per replication. All four pots in each treatment were moved together within the replicate every 7 d in order to minimize shading by tall plants. Additional plants were placed around each replicate to minimize border effects.

All pots received 100 mg of P kg$^{-1}$ of soil as monocalcium phosphate and 75 mg K kg$^{-1}$ of soil as KCl at 0 DT. An additional 75 mg K kg$^{-1}$ of soil was applied to all pots at 49 DT. To avoid photoperiod effects, the day length was limited to 11.5 hr starting 28 DT by covering the plants with black plastic in the evening and uncovering them in the morning. For submerged conditions, each pot was flooded from the date of transplanting to 7 d before harvesting. At 21 DT, the main culm of each plant was marked with a small tag for identification at later growth stages.

Measurements were taken from one or two pots of each treatment at three critical growth stages. The first was at time of maximum tillering, which was 37 DT. (The first top dressing of N, where applicable, had been applied 16 d before this sampling date, i.e. 21 DT. This 16-d period was considered an adequate time for the plants to respond to the applied N). The second sampling period was at full expansion of the flag leaf, which was 70 DT. (The second top dressing of N, where applicable, was applied 21 d before this sampling date. This period of time was considered adequate for the plants to show response to applied N). Final measurements were taken at seed harvest stage. The remaining two pots (four plants) in each treatment were used for yield component determinations.
Stomatal density

Impressions of the upper and lower epidermis were taken from the midrib area in the middle portion of the leaf (Wolf et al., 1976). Typewriter correction fluid was applied on upper and lower surfaces of the leaf. After about 1 min the leaf was pressed onto double-sided adhesive celluloid tape fixed onto a microscopic slide. Stomatal counts were made from each impression (upper and lower surfaces) on two randomly chosen microscopic fields. The area of the microscopic field was 0.0573 mm$^2$. Stomatal density is expressed as stomata mm$^{-2}$. The total number of stomata for a leaf was determined by multiplying the stomatal density by the area of the leaf.

Other plant characteristics

The two uppermost fully expanded leaves of the primary culm in both plants in a pot were separated from other leaves after taking stomatal impressions. Blade length and width were measured. Leaf area was determined by (length × width × 0.75). Leaf blades were weighed after oven drying to a constant weight at 70°C. Specific leaf weight of the upper most leaves was calculated as:

$$\text{SLW (mg cm}^{-2}\text{)} = \text{dry weight (mg) of uppermost two leaves ÷ leaf area (cm}^{-2}\text{)}$$

The same two leaves were used for leaf N determination using a micro Kjedahl method. Leaf N concentration was converted to LNLA (µg cm$^{-2}$) by multiplying the N concentration values by the SLW (mg cm$^{-2}$). The total N content of the flag leaf and the penultimate leaf (the two upper most leaves at flag leaf stage) was determined by multiplying the LNLA by the area of the two leaves. The remaining leaf blades were separated from the tillers and were oven dried at 70°C for leaf dry matter determination.

The two pots (four plants) that remained were harvested at maturity and measured for panicle length, panicle number, total number of spikelets, number of filled spikelets (grains), percentage empty spikelets (percentage sterility), and grain weights. These measurements were taken separately for the main stem and for the subtending tillers. The yield component measurements for the whole plant were the sum of main and subtending panicles. The filled spikelets in the main and subtending panicles were oven dried and weighed.
Statistical analysis

Data for all measurements were analyzed as a randomized complete block design with a factorial arrangement of treatments (three varieties and four N management levels). Analysis of variance and correlation analysis were performed for various measurements using SAS software (SAS Institute Inc., 1985). When interactions were not significant, the least significant difference (LSD) values were calculated for main effects of variety and N management means. When the treatment interactions were significant, LSD values for individual treatments were used to compare individual treatment means. All references to differences were considered significant at the 0.05 level unless otherwise stated.

RESULTS AND DISCUSSION

Nitrogen management and leaf N

No interaction for LNLA was evident between varieties and N management treatments at the maximum tillering stage. No varietal differences were observed and only N management influenced the LNLA at maximum tillering (Table 3.1). Only two treatments, T2 (35-80-85) and T3 (75-175-150), received N fertilizer at 21 DT or 16 d before this sampling date. The 0 N treatment (T0) and the 35-0-165 treatment (T1) did not receive added N before the maximum tillering growth stage. Both T0 and T1 had very low LNLA, even though T1 received a basal N application of 35 mg N kg⁻¹ of soil at planting. The treatment that received 175 mg N kg⁻¹ of soil (T3) had the highest LNLA (177 μg N cm⁻²) and was higher than the T2 treatment, which received 55 mg N kg⁻¹ of soil.

Variety × N management interactions at flag leaf stage were significant, indicating differential responses of varieties to N management. For all varieties, the control treatment had the lowest
Table 3.1. Leaf N content per unit leaf area (LNLA) of the two uppermost leaves on the main culm at maximum tillering and flag leaf stages as influenced by rice variety and N management.

<table>
<thead>
<tr>
<th>Variety</th>
<th>0</th>
<th>200</th>
<th>400</th>
<th>Mean</th>
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<tbody>
<tr>
<td></td>
<td>35-0-165†</td>
<td>35-80-85</td>
<td>75-175-150</td>
<td></td>
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<tr>
<td><strong>Maximum tillering stage</strong></td>
<td><strong>µg cm⁻²</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>68</td>
<td>75</td>
<td>146</td>
<td>178</td>
</tr>
<tr>
<td>Intermediate</td>
<td>84</td>
<td>85</td>
<td>150</td>
<td>175</td>
</tr>
<tr>
<td>Modern</td>
<td>76</td>
<td>77</td>
<td>160</td>
<td>179</td>
</tr>
<tr>
<td>Mean</td>
<td>76C*</td>
<td>79C</td>
<td>152B</td>
<td>177A</td>
</tr>
<tr>
<td><strong>Flag leaf stage</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>95g</td>
<td>177b</td>
<td>170bc</td>
<td>162cd</td>
</tr>
<tr>
<td>Intermediate</td>
<td>106f</td>
<td>215a</td>
<td>152d</td>
<td>150d</td>
</tr>
<tr>
<td>Modern</td>
<td>119e</td>
<td>208a</td>
<td>151d</td>
<td>175b</td>
</tr>
</tbody>
</table>

† Indicates mg N kg⁻¹ of soil applied: at planting - 3 wk after planting - 7 wk after planting. Treatments are referred to in text as T₀ = 0 N, T₁ = 35-0-165, T₂ = 35-80-85, and T₃ = 75-175-150.

* Values followed by the same uppercase letter across N management and variety means do not differ at the p ≤ 0.05 level. Values followed by the same lowercase letter for variety × nitrogen management treatments do not differ at the p ≤ 0.05 level. When interaction is not significant individual means are not compared.
LNLA but within this treatment the varieties differed (Table 3.1). The modern variety had highest LNLA followed by the intermediate and the traditional varieties. This variability in LNLA within the control treatment was not due to differences in leaf area for the three varieties because leaf area for varieties did not differ (Table 3.2). This indicated that the capacity for N accumulation in leaves under low N differed among varieties. Traditional varieties may have higher root mass than modern varieties and therefore absorb more N in N limited situations (Matsushima, 1970) but a larger root system confined to a small soil volume in a pot may not have the benefit of exploring a large soil volume and absorbing increased N. Therefore, results indicate only the varietal capabilities of absorbing N from the immediate vicinity and not their ability to explore a large soil mass when N is limited.

The variation in LNLA at the flag leaf stage for the traditional variety was small among different treatments that received N fertilizer (T1, T2 and T3). However, the leaf area per plant increased over two-fold with the increased N application (Table 3.2). Therefore, it is clear for this variety that even restricted N applications at early vegetative growth stages (as in the case of T1, where no N was applied at 21 DT) did not increase LNLA. Total leaf N increased but was distributed across the large leaf area. At low N levels (200 mg N kg⁻¹ of soil), both the intermediate variety and the modern variety increased LNLA when N applications were withheld until a late vegetative stage (T1). This is due to their limited leaf growth at early stages of vegetative development, while heavy N applications at late stages increased leaf area only to a limited extent.

The modern variety increased both leaf area and LNLA. At the highest N level (400 mg N kg⁻¹ of soil), this treatment received high N levels at both early and late vegetative growth stages. The traditional and intermediate varieties responded to the high N applications by increasing leaf area but not by increasing LNLA. These varietal differences may influence productivity of rice varieties under different N management regimes. When N fertilization is abundant, the modern variety is the most suitable type for high productivity. However, when the N supply is rather limited, the intermediate variety has an advantage because when N application was restricted at early growth stages and all available N was applied at late vegetative stages, the intermediate variety apparently had the ability to increase leaf N without producing additional leaf area. High LNLA in the plant.
Table 3.2. Leaf area of the two uppermost leaves on the main culm at maximum tillering and flag leaf stages of development as influenced by variety and N management.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Nitrogen rate (mg N kg(^{-1}) of soil)</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>200</td>
</tr>
<tr>
<td></td>
<td>35-0-165†</td>
<td>35-80-85</td>
</tr>
<tr>
<td>Traditional</td>
<td>159</td>
<td>338</td>
</tr>
<tr>
<td>Intermediate</td>
<td>130</td>
<td>314</td>
</tr>
<tr>
<td>Modern</td>
<td>184</td>
<td>281</td>
</tr>
<tr>
<td>Mean</td>
<td>158C*</td>
<td>311B</td>
</tr>
</tbody>
</table>

Maximum tillering stage

Flag leaf stage

<table>
<thead>
<tr>
<th>Variety</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>239</td>
<td>510</td>
<td>743</td>
<td>i406</td>
</tr>
<tr>
<td>Traditional</td>
<td>211</td>
<td>542</td>
<td>756</td>
<td>1218</td>
</tr>
<tr>
<td>Intermediate</td>
<td>285</td>
<td>633</td>
<td>904</td>
<td>1202</td>
</tr>
<tr>
<td>Modern</td>
<td>254D</td>
<td>562C</td>
<td>801B</td>
<td>1275A</td>
</tr>
</tbody>
</table>

† Indicates mg N kg\(^{-1}\) of soil applied: at planting - 3 wk after planting - 7 wk after planting. Treatments are referred to in text as \(T_0 = 0\) N, \(T_1 = 35-0-165\), \(T_2 = 35-80-85\), and \(T_3 = 75-175-150\).

* Values followed by the same uppercase letter across N management and variety means do not differ at the \(p \leq 0.05\) level. When interaction is not significant individual means are not compared.
during the reproductive growth stages is important for high photosynthetic rates and conversion of dry matter into grain yield (IRRI, 1987).

Competitive use of fertilizer N for the development either of great leaf area or of high LNLA plays an important role in situations where N supply is limited. An exponential relationship describes the absorption of N during the early growth stages but a linear relationships is seen during middle and late vegetative stages (Wada et al., 1989). The crossing point of the two curves coincides with maximum tiller number stage. The time to reach maximum tillering stage varies with the maturity group of the variety as well as factors such as plant spacing and basal N fertilizer applications (Wada et al., 1989). In early maturing varieties (105 to 120 d), maximum tiller number, panicle initiation, and internode elongation occur almost simultaneously (De Datta, 1981). In medium maturity varieties (120 to 150 d), there is a lag period between the maximum tillering and the panicle initiation stage (De Datta, 1981). This provides an opportunity to apply N after maximum tillering but before the panicle initiation stage. Therefore, when developing varieties for low input environments, breeding varieties with medium maturity is appropriate.

Specific leaf weight

Nitrogen fertilizer applications at 21 DT (T2 and T3) increased SLW over the control (T0) and the T1 treatment which received only 35 mg N pot⁻¹ at 0 DT (Table 3.3). However, there were no differences between T2 and T3 (the only two treatments that received N top dressing at 21 DT) even though T3 received twice as much N as T2. The intermediate variety had higher SLW than the modern and intermediate varieties.

The SLW of the flag leaf was higher than that of the uppermost leaves present at maximum tillering stage (Table 3.3). At the flag leaf stage, all treatments in which N was provided had higher SLW values than the control but the means across T1, T2, and T3 did not differ even though T3 received two times more N. Also the varietal response to N management did not change with the growth stage. The relative SLW rankings of the varieties at the maximum tillering stage were the same at the flag leaf stage. The lack of variation among N management treatments at both growth stages indicates that SLW is little affected by N fertilization. After a minimal N provision, the SLW
Table 3.3. Specific leaf weight of the two uppermost leaves of the main culm at maximum tillering and flag leaf stages as influenced by rice variety and N management.

<table>
<thead>
<tr>
<th>Nitrogen rate (mg N kg(^{-1}) of soil)</th>
<th>0</th>
<th>200</th>
<th>400</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variety</td>
<td></td>
<td>35-0-165 (\dagger)</td>
<td>35-80-85</td>
<td>75-175-150</td>
</tr>
<tr>
<td>----------------------------------------</td>
<td>-------</td>
<td>-------</td>
<td>-------</td>
<td>--------</td>
</tr>
<tr>
<td></td>
<td>mg cm(^{-2})</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum tillering stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>2.99</td>
<td>2.87</td>
<td>3.62</td>
<td>3.76</td>
</tr>
<tr>
<td>Intermediate</td>
<td>3.59</td>
<td>3.26</td>
<td>3.76</td>
<td>3.86</td>
</tr>
<tr>
<td>Modern</td>
<td>3.15</td>
<td>2.93</td>
<td>3.31</td>
<td>3.40</td>
</tr>
<tr>
<td>Mean</td>
<td>3.24B</td>
<td>3.02B</td>
<td>3.56A</td>
<td>3.67A</td>
</tr>
<tr>
<td>Flag leaf stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>3.94</td>
<td>4.28</td>
<td>4.81</td>
<td>4.55</td>
</tr>
<tr>
<td>Intermediate</td>
<td>4.68</td>
<td>5.22</td>
<td>4.87</td>
<td>4.73</td>
</tr>
<tr>
<td>Modern</td>
<td>4.15</td>
<td>4.55</td>
<td>4.29</td>
<td>4.55</td>
</tr>
<tr>
<td>Mean</td>
<td>4.26B</td>
<td>4.69A</td>
<td>4.65A</td>
<td>4.61A</td>
</tr>
</tbody>
</table>

\(\dagger\) Indicates mg N kg\(^{-1}\) of soil applied: at planting - 3 wk after planting - 7 wk after planting. Treatments are referred to in text as \(T_0 = 0\) N, \(T_1 = 35-0-165\), \(T_2 = 35-80-85\), and \(T_3 = 75-175-150\).

* Values followed by the same uppercase letter across N management and variety means do not differ at the p \(\leq 0.05\) level. When interaction is not significant individual means are not compared.
will not change with increased N levels. This indicates that if SLW is directly associated with other physiological processes such as leaf photosynthetic rates (Cook and Evans, 1983b), then it can be used as a selection criterion for those physiological characteristics.

Stomatal density

The stomatal densities observed in this experiment (Table 3.4) were very high compared to other crops but lower than most published values on rice (Tsunoda, 1984). At the maximum tillering stage, T₀ treatment had the highest stomatal density for both leaf surfaces. The two treatments that received N at 21 DT (T₂ and T₃) did not differ but had lower stomatal densities than T₀ and T₁. There were no consistent differences between genotypes at either growth stage, except that the modern variety had higher stomatal densities than the other two varieties at flag leaf stage. Of the different N management treatments, the control treatment resulted in the highest stomatal density for the upper leaf surface followed by T₂ treatment which received 85 mg N kg⁻¹ of soil at 49 DT. Treatments T₁ and T₃, which received higher N rates at 49 DT, had significantly lower stomatal densities for the upper than lower leaf surface and differences between T₁ and T₃ were not significant. Variety × N management interaction was significant for the lower leaf surface. The intermediate variety had lower stomatal density on the lower surface than the other two varieties in the T₃ treatment, while no differences were observed between the other two varieties. In the T₃ treatment, the modern variety had a higher stomatal density than the traditional variety. Modern and intermediate varieties did not differ. It was clear that the stomatal density of all varieties at both growth stages decreased with increasing N applications. This negative relationship indicates that the application of N could have resulted in the dispersion of existing stomata within the expanded leaf rather than an increase in total stomatal numbers per leaf.

The total number of stomata for the whole leaf was calculated to examine whether the stomatal number per leaf is a constant within a cultivar or whether it changes with N fertilization. These values for the different treatments indicated little variation in total stomatal number per leaf within a cultivar (Table 3.5). Total number of stomata at the maximum tillering stage did not differ among
Table 3.4. Stomatal density on the upper and lower leaf surface of the uppermost leaf of the main culm at maximum tillering and flag leaf stages as influenced by the variety and N management.

<table>
<thead>
<tr>
<th>Nitrogen rate (mg N kg(^{-1}) of soil)</th>
<th>0</th>
<th>200</th>
<th>400</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Variety</strong></td>
<td>35-0-165(^{†})</td>
<td>35-80-85</td>
<td>75-175-150</td>
</tr>
<tr>
<td><strong>Stomata mm(^{-2})</strong></td>
<td>Mean</td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------------------------------------</td>
<td>------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper surface</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>276</td>
<td>250</td>
<td>201</td>
<td>215</td>
</tr>
<tr>
<td>273</td>
<td>261</td>
<td>221</td>
<td>241</td>
</tr>
<tr>
<td>285</td>
<td>254</td>
<td>221</td>
<td>218</td>
</tr>
<tr>
<td>Mean</td>
<td>285A*</td>
<td>254B</td>
<td>214C</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper surface</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>311</td>
<td>285</td>
<td>227</td>
<td>253</td>
</tr>
<tr>
<td>320</td>
<td>294</td>
<td>247</td>
<td>262</td>
</tr>
<tr>
<td>346</td>
<td>294</td>
<td>233</td>
<td>253</td>
</tr>
<tr>
<td>Mean</td>
<td>326A</td>
<td>291B</td>
<td>236C</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper surface</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>352</td>
<td>268</td>
<td>311</td>
<td>314</td>
</tr>
<tr>
<td>352</td>
<td>297</td>
<td>311</td>
<td>311</td>
</tr>
<tr>
<td>413</td>
<td>291</td>
<td>358</td>
<td>369</td>
</tr>
<tr>
<td>Mean</td>
<td>372A</td>
<td>285C</td>
<td>329B</td>
</tr>
<tr>
<td>Lower surface</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>515a</td>
<td>337f</td>
<td>462b</td>
</tr>
<tr>
<td>Intermediate</td>
<td>445bc</td>
<td>407de</td>
<td>419de</td>
</tr>
<tr>
<td>Modern</td>
<td>524a</td>
<td>354f</td>
<td>451bc</td>
</tr>
</tbody>
</table>

\(^{†}\) Indicates mg N kg\(^{-1}\) of soil applied: at planting - 3 wk after planting - 7 wk after planting. Treatments are referred to in text as \(T_0 = 0\) N, \(T_1 = 35-0-165\), \(T_2 = 35-80-85\), and \(T_3 = 75-175-150\).

* Values followed by the same uppercase letter across N management and variety means do not differ at the \(p \leq 0.05\) level. Values followed by the same lowercase letter for variety \(\times\) nitrogen management treatments do not differ at the \(p \leq 0.05\) level. When interaction is not significant individual means are not compared.
Table 3.5. Total stomatal number on each surface of the uppermost leaf of the main culm at maximum tillering and flag leaf stages as influenced by the variety and N management

<table>
<thead>
<tr>
<th>Variety</th>
<th>Nitrogen rate (mg N kg⁻¹ of soil)</th>
<th>0</th>
<th>200</th>
<th>400</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>35-0-165+</td>
<td>35-80-85</td>
<td>75-175-150</td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>97</td>
<td>125</td>
<td>141</td>
<td>109</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>100</td>
<td>130</td>
<td>115</td>
<td>144</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>90</td>
<td>98</td>
<td>114</td>
<td>124</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>96B*</td>
<td>113AB</td>
<td>129A</td>
<td>126A</td>
</tr>
<tr>
<td>Upper surface</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower surface</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>109</td>
<td>142</td>
<td>160</td>
<td>129</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>109</td>
<td>129</td>
<td>142</td>
<td>155</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>109</td>
<td>113</td>
<td>120</td>
<td>144</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>109B</td>
<td>128A</td>
<td>141A</td>
<td>142A</td>
</tr>
<tr>
<td>Flag leaf stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper surface</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>92</td>
<td>73</td>
<td>82</td>
<td>140</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>100</td>
<td>109</td>
<td>85</td>
<td>154</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>112</td>
<td>138</td>
<td>158</td>
<td>146</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>102B*</td>
<td>106B</td>
<td>109B</td>
<td>147A</td>
</tr>
<tr>
<td>Lower surface</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>135</td>
<td>92</td>
<td>119</td>
<td>179</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>127</td>
<td>150</td>
<td>115</td>
<td>202</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>146</td>
<td>169</td>
<td>197</td>
<td>172</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>136B</td>
<td>137B</td>
<td>144B</td>
<td>184A</td>
</tr>
</tbody>
</table>

† Indicates mg N kg⁻¹ of soil applied: at planting - 3 wk after planting - 7 wk after planting. Treatments are referred to in text as T₀ = 0 N, T₁ = 35-0-165, T₂ = 35-80-85, and T₃ = 75-175-150.

* Values followed by the same uppercase letter across N management and variety means do not differ at the p ≤ 0.05 level. When interaction is not significant individual means are not compared.
N management treatments except for the control treatment. The control treatment had fewer total stomata per leaf. At the flag leaf stage, all treatments except T3 had a similar number of stomata. The T3 treatment had higher total stomatal numbers. For both growth stages, the stomatal number for a leaf did not vary except in extreme cases such as no N or high N levels. This suggests that total stomatal number is determined at very early stages of leaf development; increased N fertilization increases the leaf area and disperses the fixed number of stomates. Therefore, stomatal density is not a good parameter for varietal comparisons unless such factors as N fertilization are similar.

**Sink size, grain yield, and yield components**

Variety × N management interaction for the grain yield was significant and all N additions produced higher grain yield than the control (Table 3.6). Grain weights did not differ for varieties within the control treatment. When grain yields of the two 200 mg N kg\(^{-1}\) soil treatments (T1 and T2) were compared, the three splits (T2) produced higher yields than two splits for all varieties. The intermediate variety was superior to the traditional and modern varieties the two low N treatments (T1 and T2). At low N levels the intermediate variety produced higher yields than both traditional and modern varieties. However, with high levels of N, the modern variety was superior to both traditional and intermediate varieties. This indicates that there is genotypic variability in expressing yield potentials in different varieties under different N management situations.

All varieties that received N produced significantly higher panicle numbers per plant than the 0 N control (Table 3.6). There were no varietal differences within the T0 treatment. Panicle numbers for the intermediate variety did not change across T1, T2, and T3 N management treatments. The yield increase of T2 and T3 over T1 in this variety was associated with total spikelet numbers and seed size rather than panicle numbers. Panicle numbers per plant for the modern and traditional varieties varied with different N management treatments. The modern variety produced the highest number of panicles per plant (11.3) at the highest N level (T3). At the low N level, three split applications of N (T2) produced more panicles per plant for the modern variety than splitting
Table 3.6. Grain yield, panicles per plant, total spikelets per plant, 1000-grain weight, and percentage sterility as influenced by rice variety and N management.

<table>
<thead>
<tr>
<th>Variety</th>
<th>0</th>
<th>200</th>
<th>35-0-165†</th>
<th>35-80-85</th>
<th>75-175-150</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>35-0-165†</td>
<td>35-80-85</td>
<td>75-175-150</td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>2.8h</td>
<td>5.9g</td>
<td>10.8de</td>
<td>13.2b</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intermediate</td>
<td>3.0h</td>
<td>10.7e</td>
<td>12.7b</td>
<td>12.5bc</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modern</td>
<td>3.6h</td>
<td>9.6ef</td>
<td>11.7cd</td>
<td>16.9a</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---------- Grain yield plant⁻¹ (g) ----------

<table>
<thead>
<tr>
<th>Variety</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Traditional</td>
<td>1.7e</td>
<td>5.0c</td>
<td>3.7d</td>
<td>6.7b</td>
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<tr>
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<td>4.7cd</td>
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<tr>
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<td>6.7b</td>
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---------- Panicles plant⁻¹ ----------

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<td>289f</td>
<td>448e</td>
<td>670c</td>
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<td>161g</td>
<td>534d</td>
<td>633c</td>
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<td>473e</td>
<td>548d</td>
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---------- Total spikelets plant⁻¹ ----------

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<td>16</td>
<td>13</td>
<td>22</td>
<td>15B</td>
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<td>16B</td>
<td>14B</td>
<td>22A</td>
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---------- % sterility ----------

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<td>23.1bcde</td>
<td>25.6a</td>
<td>22.0def</td>
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<tr>
<td>Intermediate</td>
<td>21.7ef</td>
<td>25.0a</td>
<td>24.3abc</td>
<td>20.7f</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modern</td>
<td>24.6ab</td>
<td>24.1abc</td>
<td>24.7ab</td>
<td>22.9cde</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

† Indicates mg N kg⁻¹ of soil applied: at planting - 3 wk after planting - 7 wk after planting. Treatments are referred to in text as T₀ = 0 N, T₁ = 35-0-165, T₂ = 35-80-85, and T₃ = 75-175-150.

* Values followed by the same uppercase letter across N management and variety means do not differ at the p ≤ 0.05 level. Values followed by the same lowercase letter for variety × nitrogen management treatments do not differ at the p ≤ 0.05 level. When interaction is not significant individual means are not compared.
the same total N into two applications. In the traditional variety, the two-split treatment produced higher panicle numbers than the three-split treatment.

The total number of spikelets per plant (filled and empty spikelets) in different varieties varied with N management (Table 3.6). All N management treatments had higher spikelet numbers than the control treatment. Generally at higher levels of N, three split applications (T2 and T3) increased the total spikelet numbers in all varieties. Both the intermediate and the modern variety had higher spikelet numbers than the traditional variety at any given N management level. At low N levels (T1 and T2) the intermediate variety produced higher spikelet numbers than the modern variety. But at high N level (T3), the modern variety had more spikelets than the other two varieties. Comparison of two and three split applications at the low N level indicated three split applications produced higher spikelet numbers than two split applications for all varieties. These results suggest that spikelet numbers (potential sink size) vary both with variety and with N management. The intermediate variety had the ability to produce more spikelets per plant than the traditional and the modern varieties at low N management levels. However, at the higher N level the modern variety was superior to both traditional and the intermediate varieties.

Variations were observed in the percentage of empty spikelets in different treatments and because of this the potential benefit of higher spikelet numbers in some treatments, especially with the intermediate variety, was not realized at harvest (Table 3.6). This indicates that the varieties responded differently to N during the grain development stage. The intermediate variety had a higher percentage of empty spikelets and the traditional variety had the lowest percentage of empty spikelets.

High N levels decreased the 1000-grain weight of all varieties (Table 3.6). At low N levels, intermediate and modern varieties produced highest 1000-grain weights. Different split applications of the same N level did not influence 1000-grain weight. But in the traditional variety, application of high levels of N at an early reproductive stage reduced the 1000-grain weight.

The differential behavior of varieties to N management indicates that genotype plays an important role in optimally utilizing the available N. In situations where N fertilizer is limited and the farmer intends to apply N at late vegetative stage, a variety that requires low N for tiller production
but is has high spikelet numbers is more important than a variety that requires high N for both tiller production and tiller survival. Similarly, in situations where N is applied at comparatively high levels, N should be split and adequate amounts should be applied both at early vegetative and late vegetative stages.

Leaf N content and yield components

Total grain weight per plant was positively correlated to the total N content in the two uppermost leaves at the flag leaf stage in all varieties (Table 3.7). Similarly, panicles per plant, total spikelets per plant, and number of filled spikelets per plant were positively correlated to the total leaf N content in all three varieties. Increased total leaf N content also increased with number of empty spikelets in the traditional and intermediate varieties, however, high total leaf N contents did not increase the number of empty spikelets in the modern variety. This indicates that the modern variety had higher efficiency of spikelet filling than the other two varieties at high N levels. High total leaf N content also had a negative influence on 1000-grain weight of the traditional variety. This could be due to competition for assimilates at the high N level, where very high spikelet numbers were produced. High total leaf N content did not influence the grains per panicle yield component for any variety.

Yield component analysis for the main panicle and panicles on the subtending tillers revealed that yield variations due to N fertilization were associated mainly with the variations observed in yield of subtending panicles and not due to variations in the main panicle (Table 3.7). Grain weight of the main culm was not influenced by total leaf N, but grain weight from panicles on the subtending tillers was positively correlated with total leaf N content (Table 3.7). In the intermediate variety, the number of empty spikelets in the main panicle increased with increased total leaf N contents but other yield components were not affected. All yield components of the main panicle of the traditional variety were affected by the total leaf N content. It also had a negative influence on the 1000-grain weight. Total leaf N influenced the yield parameters of the main panicle more in the traditional variety than in the other two varieties. All yield components except 1000-grain weight in panicles borne by subtending tillers were positively correlated with total leaf N content.
Table 3.7. Correlation coefficients between total leaf N content of two uppermost leaves and different yield parameters of the whole plant, and panicles on the main culm and subtending tillers.

<table>
<thead>
<tr>
<th>Yield component</th>
<th>Variety</th>
<th></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Traditional</td>
<td>Intermediate</td>
<td>Modern</td>
<td>Pooled</td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>------------</td>
<td>----------------</td>
<td>--------</td>
<td>--------</td>
</tr>
<tr>
<td><strong>Whole plant</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total grain weight</td>
<td>0.74**</td>
<td>0.62*</td>
<td>0.75**</td>
<td>0.31**</td>
</tr>
<tr>
<td>Panicle no.</td>
<td>0.74**</td>
<td>0.63*</td>
<td>0.60*</td>
<td>0.58**</td>
</tr>
<tr>
<td>Total spikelet no.</td>
<td>0.85*</td>
<td>0.73**</td>
<td>0.72**</td>
<td>0.75**</td>
</tr>
<tr>
<td>Total filled spikelets</td>
<td>0.80**</td>
<td>0.67**</td>
<td>0.75**</td>
<td>0.75**</td>
</tr>
<tr>
<td>Empty spikelets</td>
<td>0.92**</td>
<td>0.77**</td>
<td>0.56</td>
<td>0.63**</td>
</tr>
<tr>
<td>1000-grain weight</td>
<td>-0.65*</td>
<td>-0.02</td>
<td>-0.54</td>
<td>-0.32</td>
</tr>
<tr>
<td>Grains per panicle</td>
<td>0.48</td>
<td>-0.38</td>
<td>-0.02</td>
<td>0.01</td>
</tr>
<tr>
<td><strong>Panicle on the main culm</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grain weight</td>
<td>0.39</td>
<td>0.09</td>
<td>0.05</td>
<td>0.18</td>
</tr>
<tr>
<td>Total spikelets</td>
<td>0.75**</td>
<td>0.49</td>
<td>0.20</td>
<td>0.36*</td>
</tr>
<tr>
<td>Filled spikelets</td>
<td>0.65**</td>
<td>0.31</td>
<td>0.15</td>
<td>0.28</td>
</tr>
<tr>
<td>Empty spikelets</td>
<td>0.69**</td>
<td>0.61**</td>
<td>0.31</td>
<td>0.44**</td>
</tr>
<tr>
<td>1000-grain weight</td>
<td>-0.64**</td>
<td>-0.24</td>
<td>-0.34</td>
<td>-0.31</td>
</tr>
<tr>
<td><strong>Panicles on subtending tillers</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grain weight</td>
<td>0.75**</td>
<td>0.66**</td>
<td>0.77**</td>
<td>0.73**</td>
</tr>
<tr>
<td>Total spikelets</td>
<td>0.83**</td>
<td>0.76**</td>
<td>0.74**</td>
<td>0.73**</td>
</tr>
<tr>
<td>Filled spikelets</td>
<td>0.78**</td>
<td>0.69**</td>
<td>0.77**</td>
<td>0.75**</td>
</tr>
<tr>
<td>Empty spikelets</td>
<td>0.85**</td>
<td>0.77**</td>
<td>0.57*</td>
<td>0.64**</td>
</tr>
<tr>
<td>1000-grain weight</td>
<td>0.20</td>
<td>0.61</td>
<td>0.15</td>
<td>0.37*</td>
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</table>

* and ** indicates significant at p ≤ 0.05 and p ≤ 0.01 levels, respectively.
in all varieties. In the intermediate variety, 1000-grain weight was positively correlated to total leaf N content but that was not so in the other two varieties.

These results indicate that increased N levels in the leaves influence the grain yield of all varieties but the influence varies with variety, yield component, and panicle origin, i.e. main culm or tillers. As observed earlier, the intermediate variety produced highest grain yields at low N levels by producing more grains per panicle rather than increased panicle numbers per plant, as was the case with the modern variety. This is a good character that needs to be considered in breeding for low-input environments where N supply is limited. Limited N supply in the early growth stages would have little influence on tiller production on such varieties. High spikelet numbers in the few tillers that produce panicles would compensate for low panicle numbers if N supply prior to panicle initiation is high.
REFERENCES


 CHAPTER IV

Response of Three Rice Varieties to Nitrogen Management:

II. Leaf Photosynthesis, Light Response, and Water Use Efficiency.

ABSTRACT

Solar radiation, water, and N are factors that often limit rice yields in many Asian countries. Genotypes are known to differ in their response to these factors, but limited information is available on the physiological aspects associated with these responses. The objectives of this experiment were to study the CO₂ exchange rates (CER) of three morphologically different rice varieties in relation to light, N management, water use efficiency (WUE), and N use efficiency (NUE) and to identify characteristics associated with rice plant adaptability to low input environments. Three rice varieties were tested in four N management treatments (rates and times). The three varieties included
a traditional (tall, low-yielding) variety, a modern (semidwarf, high-yielding) variety, and one with intermediate characteristics. Measurements included CER, stomatal conductance, internal CO₂ concentrations, leaf N content per unit leaf area (LNLA) and WUE. All measurements were made at the maximum tillering and flag leaf stages using light levels ranging from 0 to 1200 µmol m⁻² s⁻¹. Carbon dioxide exchange rates were higher in the flag leaf than in lower leaves and were directly correlated with LNLA. Light saturation points varied from 400 to 1000 µmol m⁻² s⁻¹ depending on variety, N management, and growth stage. The modern variety had highest light response when N levels were high, whereas the intermediate variety was superior when N supply was low. A similar trend was observed with NUE but differences in CER at similar LNLA values indicated that leaf N content alone cannot be used as a selection criterion for breeding for high CER. High levels of N fertilizer had a negative influence on the CER of the intermediate variety, while the reverse was true with the modern variety. Higher stomatal conductances were observed at the flag leaf stage than at the maximum tillering stage. The intermediate variety had very high stomatal conductance that increased with increasing light levels. High stomatal conductance resulted in low WUE in the intermediate variety. The intermediate variety was more adapted to low N environments than the other two varieties. However, the low WUE could be a disadvantage in environments where water is limiting. The modern variety was superior in high N management situations. The traditional variety had high WUE but the photosynthetic efficiency remained low in all N management situations.

INTRODUCTION

The physiological basis of increased genetic yield potentials has been studied and reviewed for many characteristics of rice (Matsushima, 1970; 1976; Yoshida, 1972). Researchers continue to look for ways to increase genetic yield potentials of modern varieties (IRRI, 1982; Venkataswarlu et al, 1987; Vergara, 1988). However, limited research has been conducted to understand the
physiological processes and plant characteristics associated with grain production in unstable and low input environments. In such situations, recognition of advantages and disadvantages of contrasting plant characteristics and their interactions is important.

Nitrogen fertilizer constitutes a major cost in production of rice. A great deal of work has been done on fertilizer application methods, rates, and timing and on water management (Prasad and De Datta, 1979; De Datta and Patrick, 1986). Selection of varieties for efficiency of conversion of N into biomass and yield is also possible. Dry matter production is closely related to photosynthetic activity of the canopy (Tanaka et al., 1966; Yoshida, 1972). Good correlations between photosynthetic rate per unit leaf area and economic yield have not always been found (Elmore, 1980; Good and Bell, 1980). The conclusion that no correlation between these two factors has been drawn from data where instantaneous C-exchange measurements were made under standardized conditions rather than from seasonal measurements conducted in the field (Zelitch, 1982). However, information on the variability of photosynthetic rate is necessary for selecting photosynthetically efficient genotypes (Zelitch, 1982), especially for low input environments.

Low solar radiation limits rice yields in the tropics (Venkateswarlu, 1977). Under low radiation levels, both dry matter accumulation and grain yield are significantly reduced (Tanaka et al., 1966; Nayak and Murty, 1980; Venkateswarlu et al., 1987). There is a great need to investigate the possibilities of finding varieties adapted to low light environments (Venkateswarlu et al., 1987; Vergara, 1988). A close association exists between leaf N content and the chlorophyll concentration and some varieties of O. sativa exhibit a fairly high chlorophyll level in relation to their N content per unit leaf area (Takano and Tsunoda, 1970). Sinclair and Horie (1989) reviewed the available literature on the relationship between leaf N content and photosynthetic rate of rice. They concluded that the relationship is generally linear from an intercept of 0.3 g N m$^{-2}$ of leaf area to about 1.6 g N m$^{-2}$ of leaf area. At or about this level, CER will reach a maximum and any further increase in leaf N will not increase photosynthetic rate. Increased N use efficiency defined as the increase in CER per unit increase in LNLA can play an important role in developing varieties for low input environments.
Increasing stomatal conductance to increase CER has been suggested for other crops (Gifford and Musgrave, 1970; Prasad et al., 1985). High stomatal conductance compared to other cereal crops has been reported for rice and this has been considered as an adaptation to submerged conditions (Tsunoda, 1984). The resistance to diffusion of CO₂ and water vapor between the leaf and the atmosphere is a function of stomatal frequency and stomatal aperture. Rice is a semi-aquatic plant. Some of the leaf properties undoubtedly facilitate transfer of CO₂ from the ambient air to the photosynthetic sites provided the stomata are not closed due to water deficit or high or low temperature (Tsunoda, 1984). A linear correlation between stomatal conductance and photosynthetic rate has been reported when irradiance levels were increased and when other factors were not limiting (Ball et al., 1986). Changes in diffusive resistance to CO₂ uptake induced by N deficiency have been reported in corn, cotton, and beans (Ryle and Hesketh, 1969). The inhibition of photosynthesis in these N-deficient plants was accompanied by an increase in mesophyll resistance and to a lesser extent by an increase in stomatal resistance. However, when a combination of environmental factors and their interactions affects the response, it is difficult to quantify the influence of stomatal conductance. Ball et al. (1986) took a multivariate approach to the study of stomatal conductance and showed that under many conditions the response of stomata can be described by a set of linear relationships. Diffusive resistance at the boundary layer and stomata appears to be small in rice (Tsunoda 1984). Low gas diffusion resistances of leaves favor photosynthesis but also promote high rates of transpiration. This may be advantageous for tropical rice because of transpirational cooling of the leaves when temperatures are high. However, high transpiration rates can induce water stress in many environments and reduce grain yields.

The majority of the rice lands in Asian countries is rainfed and subjected to moisture stress during some periods of the growth cycle if supplementary irrigation is not available. Water use efficiency (WUE) defined as the ratio of leaf photosynthesis to transpiration has received considerable scrutiny in other crops (Morgan and LeCain, 1991). Much interest has focused on identifying genotypes with high photosynthetic differences in rice, but little effort has been expended on finding genotypic differences in WUE in lowland rice. This is an important trait that needs extensive study.
because it could reduce the risk of moisture stress in many rainfed environments and also reduce irrigation costs in lowland rice production.

The objectives of this research were to measure leaf CER in relation to light, N, and water use of three morphologically different rice varieties grown under four different N management regimes and to examine characteristics that might promote adaptability to low-input environments.

**MATERIALS AND METHODS**

Three rice varieties with different morphological characteristics were used to represent different plant types. ‘Herathbanda’, which is referred to as a traditional cultivar, is tall, leafy, and lodging susceptible. It has a relatively high tillering capacity and is popular among rice farmers in the wet zone of Sri Lanka, where modern varieties have performed poorly. ‘H501’ which shall be referred to as here an intermediate variety, was released from the Sri Lankan national rice breeding program during the late 1950s. H501 is medium to tall in height, and its leaves are somewhat droopy. ‘Bg 34-6’, referred to here as a modern variety, is semidwarf with erect leaves, moderate tillering capacity, and has a high yield potential under stable environments with good management. Seeds for the experiment were obtained from the International Rice Research Institute, Philippines. The experimental procedures and the material used in this experiment were the same that were used for the previous experiment (Chapter III).

Carbon dioxide exchange rates (CER), stomatal conductance, and intercellular CO₂ concentrations were measured at several light levels at maximum tillering and flag leaf stages. The most recent fully expanded leaf of the main culm at maximum tillering stage and the fully expanded flag leaf of the main culm were used for the photosynthetic measurements in order to reduce interplant variability and compare leaves of similar physiological age. The LI-6200 portable photosynthesis system (Li-Cor, Lincoln, NE, 68504, USA) was used for all CER, stomatal conductance, and intercellular CO₂ measurements. The LI-6200 is a steady-state closed, system and consists of: 1) a
leaf chamber, within which a portion of the intact leaf was inserted for measurement of leaf temperature and humidity, 2) an infrared gas analyzer - IRGA (LI-6250), which measured CO₂ concentration and flow rate, and 3) a control console and data recorder. The net exchange of CO₂ between a leaf and the atmosphere within the leaf chamber was measured with the IRGA by enclosing a portion of an intact leaf in the closed chamber and monitoring the rate at which the CO₂ concentration in the air changed over a short time interval (15 s). The CER (μmol m⁻² s⁻¹) was calculated using this rate of change and the volume of the enclosure, leaf area, temperature, and barometric pressure. The console also calculated the stomatal conductance and intercellular CO₂ concentrations directly. The transpiration rate was calculated from the change in saturated vapor pressure and was then used with the leaf and air temperatures to calculate stomatal conductance expressed in mol m⁻² s⁻¹. The internal CO₂ concentration was estimated by using the following equation:

\[ \text{Intercellular CO}_2 \text{ (ppm)} = \text{Ca} - 1.56(A/g) \]

where Ca is the external CO₂ concentration (ppm), A is CER, and g is stomatal conductance. Water use efficiency was calculated as the ratio of photosynthesis to transpiration expressed in mmol CO₂ mol⁻¹ water.

Light for the photosynthetic measurements was provided by a 1000-W, high-intensity, phosho-coated metal, halide lamp. Light levels were varied by using neutral density filters. The photosynthetically active radiation was measured with a quantum sensor (Li-Cor). The light levels for photosynthesis were maintained within 15% of 0, 200, 400, 800 and 1200 μmol m⁻² s⁻¹ for measurements taken at the maximum tillering stage and 0, 200, 300, 400, 600, 800, and 1200 μmol m⁻² s⁻¹ at the flag leaf stage. Initial CO₂ concentration in the leaf chamber was maintained in the range 340 to 360 ppm for all measurements. The air temperature and the humidity inside the chamber was maintained at 30⁰ C ± 2 and 40%, respectively.

The two uppermost fully expanded leaves of the primary culm in both plants in a pot were used for leaf N determination using a micro Kjedahl method. Leaf N concentration was converted to LNL (μg cm⁻²) by multiplying the N concentration values by the SLW (mg cm⁻²). Maximum
CER for each treatment was plotted against the LNLA to compare the N-use efficiency (NUE), defined as the change in CER per unit change in LNLA.

**Statistical analysis**

Data for all measurements were analyzed as a randomized complete block experiment with a factorial arrangement of treatments. Analysis of variance and correlations were performed for various measurements using SAS software (SAS Institute Inc., 1985). When interactions were not significant the least significant difference (LSD) values were calculated for main effects of variety and N management means. When the treatment interactions were significant, LSD values for individual treatments were used to compare individual treatment means. All references to differences are considered significant at the 0.05 level unless otherwise stated.

**RESULTS AND DISCUSSION**

**Carbon dioxide exchange rates, light response and N management**

Mean CER for different treatments ranged from 2.5 to 11.5 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) during the maximum tillering stage and from 5.0 to 20.7 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) at the flag leaf stage. These values are lower than the maximum photosynthetic rates reported (22 to 39 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) in an experiment using a large number of genotypes grown in the field (IRRI, 1976). One possible reason could be low light levels (about 35 to 40% of full sunlight or 500 to 600 \( \mu \text{mol m}^{-2} \text{s}^{-1} \)) in the greenhouse where this experiment was conducted. Low CER have been reported for rice plants grown under low light for a long period of time (Tanaka et al., 1966). A second reason for low CER could be because the experiment was conducted over a wide range of N levels (0 to 400 mg N kg\(^{-1}\) soil). Alternatively the three varieties tested could fall within the lower range of the values reported in the IRRI (1976) experiment.
Leaf CER at the flag leaf stage were higher than the rates observed at maximum tillering stage (Fig. 4.1 and 4.2). Carbon dioxide exchange rates at maximum tillering stage at different light levels varied with the variety as well as with the N management (Table 4.1). At low light levels, there was no variety × N management interaction, but above 400 μmol m⁻² s⁻¹ light level variety × N management interactions were significant. At the flag leaf stage, the variety × N management interaction was significant at all light levels and suggested that the varietal response varied with different N management treatments (Table 4.1).

Respiration rates among varieties within N treatments did not differ at the maximum tillering stage, but respiration did vary across N management treatments. Mean respiration rates for varieties at maximum tillering stage were 0.43, 0.43, and 0.37 μmol m⁻² s⁻¹ for traditional, intermediate, and modern varieties, respectively. However, varieties differed in respiration rates at the flag leaf stage, but not with the N application. The intermediate variety had the lowest respiratory rate (0.59 μmol m⁻² s⁻¹) followed by the modern variety (0.77 μmol m⁻² s⁻¹), but the difference was not significant. The traditional variety had the highest respiratory rate (0.87 μmol m⁻² s⁻¹).

All varieties reached light saturation (light level at which maximum photosynthesis was reached) approximately between 600 and 800 μmol m⁻² s⁻¹ at the maximum tillering stage (Fig. 4.1). This was about 35% of full sun light and agrees with other reports. At the maximum tillering stage, CER declined after light saturation. Declines in CER at high light intensities during midday have been observed by others and have been attributed to decreased stomatal conductance as a result of high evaporative demand (Ishihara and Saitoh, 1987). During the maximum tillering stage, CER of the modern variety was high for any light level in the two treatments (T₁ and T₂) that received N at 21 days after transplanting (Fig. 4.1). Interestingly, the intermediate variety, which had relatively high CER at low N levels, had low CER at high N treatment (T₃).

Light saturation of the flag leaf of different varieties differed with N management (Fig. 4.2). In the control treatment the traditional variety reached light saturation at approximately 400 μmol m⁻² s⁻¹. The other two varieties had a higher light saturation point for the same treatment (600 μmol m⁻² s⁻¹). The light saturation points for the other three treatments were approximately 1000, 800, and 700 μmol m⁻² s⁻¹, for T₁, T₂, and T₃ treatments, respectively (Fig. 4.2). At the
Table 4.1. Analysis of variance for CER for three rice varieties grown under four N management levels at maximum tillering and flag leaf stages of development

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>0†</th>
<th>200</th>
<th>300</th>
<th>400</th>
<th>600</th>
<th>800</th>
<th>1200</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Light level (μmol m⁻² sec⁻¹)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum tillering stage</td>
<td></td>
<td>Mean square</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variety (V)</td>
<td>2</td>
<td>0.01</td>
<td>1.80*</td>
<td>-</td>
<td>2.63**</td>
<td>-</td>
<td>2.87**</td>
<td>0.30</td>
</tr>
<tr>
<td>Nitrogen (N)</td>
<td>3</td>
<td>0.27**</td>
<td>3.38**</td>
<td>-</td>
<td>10.66**</td>
<td>-</td>
<td>24.62**</td>
<td>27.30**</td>
</tr>
<tr>
<td>V × N</td>
<td>6</td>
<td>0.01</td>
<td>0.35</td>
<td>-</td>
<td>1.69**</td>
<td>-</td>
<td>2.19**</td>
<td>3.60**</td>
</tr>
<tr>
<td>C.V. (%)</td>
<td></td>
<td>27</td>
<td>9</td>
<td>-</td>
<td>4</td>
<td>-</td>
<td>1</td>
<td>12</td>
</tr>
<tr>
<td>Flag leaf stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variety (V)</td>
<td>2</td>
<td>0.24*</td>
<td>2.35</td>
<td>9.51**</td>
<td>12.30**</td>
<td>23.50**</td>
<td>36.40**</td>
<td>62.3**</td>
</tr>
<tr>
<td>Nitrogen (N)</td>
<td>3</td>
<td>0.13</td>
<td>6.06**</td>
<td>11.80**</td>
<td>37.60**</td>
<td>57.50**</td>
<td>81.90**</td>
<td>77.20**</td>
</tr>
<tr>
<td>V × N</td>
<td>6</td>
<td>0.04</td>
<td>2.89**</td>
<td>5.70**</td>
<td>8.60**</td>
<td>8.30**</td>
<td>6.00**</td>
<td>3.40**</td>
</tr>
<tr>
<td>C.V. (%)</td>
<td></td>
<td>30</td>
<td>13</td>
<td>12</td>
<td>10</td>
<td>8</td>
<td>7</td>
<td>5</td>
</tr>
</tbody>
</table>

* and ** indicate significance at p ≤ 0.05 and p ≤ 0.01 levels, respectively.

† Light level 0 = dark respiration.
Fig. 4.1. Carbon dioxide exchange rates (CER) at different light levels for three rice varieties at the maximum tillering stage grown at four different N management levels. (T0 = no N; T1 = 35-0-165; T2 = 35‡-80-85; and T3 = 75-175-15). ‡ indicates mg N kg⁻¹ soil applied at 0 DT, 21 DT, and 49 DT.
Fig. 4.2. Carbon dioxide exchange rates (CER) at different light levels for three rice varieties at the flag leaf stage grown at four different N management levels. (T₀ = no N; T₁ = 35&dag-0-165; T₂ = 35-80-85; and T₃ = 75-175-15). † indicates mg N kg⁻¹ soil applied at 0 DT, 21 DT, and 49 DT.
flag leaf stage, the differences in light response among varieties were very clear. Under low N situations the intermediate variety had a higher light response than the other two varieties. But once again high N levels decreased photosynthetic efficiency of the intermediate variety. High photosynthetic efficiency of the intermediate variety at low light levels at the flag leaf stage indicated that it is photosynthetically more efficient than the other at low light and N levels. Thus, leaves with a high N content may not be necessarily favorable as compared to leaves with low N when plants are grown under low light levels. Moderately high CER have been reported for wild relatives of Oryza adapted to shady habitats (Takano and Tsunoda, 1971).

The intermediate and modern varieties had higher CER than the traditional variety in the control treatment at both growth stages (Fig. 4.1 and 4.2) indicating high photosynthetic capacity of those two varieties when N availability is very low. Differences in CER for different N management treatments were associated with differences in leaf N contents. The results of the LNLA for this experiment were presented earlier (Chapter III). Positive correlations between the LNLA and photosynthetic rates were observed for all varieties at all light levels except respiration rates (Table 4.2).

The highest NUE (slope) at maximum tillering stage was observed with the traditional variety (4.1 μmol CO₂ s⁻¹ g⁻¹ leaf N) followed by the modern variety (3.0 μmol CO₂ s⁻¹ g⁻¹ leaf N) (Fig. 4.3). At this growth stage, the N response of the intermediate variety was low. The reason could be the low maximum photosynthetic rates observed for this variety at the highest N management treatment. Negative influences of high levels of N fertilization have been reported (Takano and Tsunoda, 1971). In spite of the high NUE, the traditional variety could not exceed the rates of the modern variety at high leaf N levels. With greater LNLA the photosynthetic rates of the traditional variety increased, but the magnitude of the photosynthetic rate was lower for the traditional variety than the other two varieties even at high light levels. The variety response in NUE changed with the growth stage. The NUE at the flag leaf stage of the traditional and the intermediate varieties were high (7.6 and 7.8 μmol CO₂ s⁻¹ g⁻¹ leaf N, respectively). In contrast to the maximum tillering stage, the modern variety had a low NUE (5.0 μmol CO₂ s⁻¹ mg⁻¹ leaf N) at flag leaf stage.
Table 4.2. Correlations between CER and N content per unit leaf area at different light levels for three rice varieties at maximum tillering and flag leaf stages of development.

<table>
<thead>
<tr>
<th>Light level (µmol m$^{-2}$ sec$^{-1}$)</th>
<th>Variety</th>
<th>Traditional</th>
<th>Intermediate</th>
<th>Modern</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum tillering stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1200</td>
<td>0.97**</td>
<td>0.66 †</td>
<td>0.57 *</td>
<td></td>
</tr>
<tr>
<td>800</td>
<td>0.97**</td>
<td>0.85**</td>
<td>0.93**</td>
<td></td>
</tr>
<tr>
<td>400</td>
<td>0.86**</td>
<td>0.44</td>
<td>0.84**</td>
<td></td>
</tr>
<tr>
<td>200</td>
<td>0.72**</td>
<td>0.65 *</td>
<td>0.80**</td>
<td></td>
</tr>
<tr>
<td>0 (Respiration)</td>
<td>0.50 †</td>
<td>0.67 *</td>
<td>0.71**</td>
<td></td>
</tr>
<tr>
<td>Flag leaf stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1200</td>
<td>0.91**</td>
<td>0.90**</td>
<td>0.73**</td>
<td></td>
</tr>
<tr>
<td>800</td>
<td>0.86**</td>
<td>0.87**</td>
<td>0.79**</td>
<td></td>
</tr>
<tr>
<td>600</td>
<td>0.88**</td>
<td>0.69 *</td>
<td>0.72**</td>
<td></td>
</tr>
<tr>
<td>400</td>
<td>0.90**</td>
<td>0.66 *</td>
<td>0.58**</td>
<td></td>
</tr>
<tr>
<td>300</td>
<td>0.72 *</td>
<td>0.62 *</td>
<td>0.46</td>
<td></td>
</tr>
<tr>
<td>200</td>
<td>0.69 *</td>
<td>0.56 *</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td>0 (Respiration)</td>
<td>-0.14</td>
<td>-0.08</td>
<td>0.61 *</td>
<td></td>
</tr>
</tbody>
</table>

†, *, ** indicate significant at p ≤ 0.10, p ≤ 0.05, and p ≤ 0.01 level, respectively. respectively.
Fig. 4.3. Relationship between leaf N content per unit leaf area (LNLg) and maximum carbon dioxide exchange rate (CER) for three rice varieties at maximum tillering and flag leaf stages of development.
The association of a substantial fraction of leaf N with the photosynthetic apparatus is the main reason for positive correlations between leaf N and photosynthesis (Lawlor, 1987). The positive correlations between these two factors have led to the suggestion by some to use LNLA as a selection criterion when breeding for high CER (Murayama et al., 1987). However, genotypic differences in CER at similar leaf N contents (Fig. 3) indicated that leaf N content alone does not determine the maximum photosynthetic capacity of different genotypes. Results indicated that, within genotypes, allocation of leaf N into photosynthetic apparatus is more productive in some than others. For example, genotypic differences in leaf chlorophyll concentrations at the same leaf N contents have been reported for rice (Takano and Tsunoda, 1971; Tsunoda and Singh, 1986).

Stomatal conductance and WUE

No consistent differences in stomatal conductance were observed at maximum tillering stage among treatments at any light level. The mean stomatal conductance for this growth stage was 0.44 mol m$^{-2}$ s$^{-1}$. The CER and the stomatal conductance at this growth stage were not correlated at any light level. The mean stomatal conductance for all treatments at flag leaf stage was 0.78 mol m$^{-2}$ s$^{-1}$. The increase was mainly due to very high values recorded by the intermediate variety (Table 4.3). Lowest stomatal conductance was recorded by the traditional variety at all light levels, while the modern variety recorded a moderate level of stomatal conductance. Stomatal conductance for the intermediate variety increased with increasing light level to a very high rate compared to moderate increases observed in the other two varieties (Table 4.3).

Response of stomatal conductance to N fertilization varied with genotype. There were positive correlations between LNLA and stomatal conductance for the intermediate variety at all light levels except the 200 μmol m$^{-2}$ s$^{-1}$ level (Table 4.4). Stomatal conductance and LNLA were not directly correlated in the other two varieties. This indicates that there are genotype differences in stomatal conductance in response to N for this parameter.
Table 4.3. Stomatal conductance at the flag leaf stage of development for different light levels for three rice varieties and four N management levels

<table>
<thead>
<tr>
<th>Variety</th>
<th>Nitrogen rate (mg N kg$^{-1}$ of soil)</th>
<th>Light level of 1200 μmol m$^{-2}$ s$^{-1}$</th>
<th>Light level of 800 μmol m$^{-2}$ s$^{-1}$</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>35-0-165‡</td>
<td>35-80-85</td>
<td>75-175-150</td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>0.27</td>
<td>0.67</td>
<td>0.40</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>1.37</td>
<td>2.37</td>
<td>1.90</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>0.94</td>
<td>0.72</td>
<td>0.81</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>0.86BC</td>
<td>1.25A</td>
<td>1.04B</td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>0.26</td>
<td>0.62</td>
<td>0.46</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>1.35</td>
<td>2.20</td>
<td>1.81</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>0.60</td>
<td>0.82</td>
<td>0.61</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>0.74C</td>
<td>1.21A</td>
<td>0.96B</td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>0.27</td>
<td>0.62</td>
<td>0.48</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>1.30</td>
<td>2.02</td>
<td>1.64</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>0.56</td>
<td>0.83</td>
<td>0.58</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>0.71C*</td>
<td>1.15A</td>
<td>0.90B</td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>0.29</td>
<td>0.60</td>
<td>0.48</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>1.11</td>
<td>1.33</td>
<td>1.68</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>0.58</td>
<td>0.92</td>
<td>0.54</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>0.66BC</td>
<td>1.07A</td>
<td>0.78B</td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>0.30</td>
<td>0.50</td>
<td>0.41</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>0.86</td>
<td>1.29</td>
<td>1.09</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>0.52</td>
<td>0.63</td>
<td>0.48</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>0.55BC</td>
<td>0.81A</td>
<td>0.66B</td>
</tr>
<tr>
<td>Traditional</td>
<td></td>
<td>0.29</td>
<td>0.49</td>
<td>0.34</td>
</tr>
<tr>
<td>Intermediate</td>
<td></td>
<td>0.66</td>
<td>0.96</td>
<td>0.72</td>
</tr>
<tr>
<td>Modern</td>
<td></td>
<td>0.43</td>
<td>0.55</td>
<td>0.39</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>0.46B*</td>
<td>0.67A</td>
<td>0.48B</td>
</tr>
</tbody>
</table>

‡ Indicates mg N kg$^{-1}$ of soil applied: at planting - 3 wk after planting - 7 wk after planting and treatments are referred to as T$_0$ = no N; T$_1$ = 35-0-165; T$_2$ = 35-80-85; and T$_3$ = 75-175-150.

* Values followed by the same uppercase letter across N management and variety means do not differ at the p ≤ 0.05 level. When interaction is not significant, individual means are not compared.

CHAPTER IV
Table 4.4. Correlations between stomatal conductance and N content per unit leaf area and stomatal conductance and carbon dioxide exchange rate (CER) at different light levels for 3 rice at the flag leaf stage.

<table>
<thead>
<tr>
<th>Light level</th>
<th>Variety</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Traditional</td>
<td>Intermediate</td>
<td>Modern</td>
<td></td>
</tr>
<tr>
<td>µmol m(^{-2}) sec(^{-1})</td>
<td>Coefficient (r)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1200</td>
<td>0.25</td>
<td>0.91**</td>
<td>-0.26</td>
<td></td>
</tr>
<tr>
<td>800</td>
<td>0.40</td>
<td>0.84**</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td>600</td>
<td>0.41</td>
<td>0.68**</td>
<td>0.15</td>
<td></td>
</tr>
<tr>
<td>400</td>
<td>0.39</td>
<td>0.63 *</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>300</td>
<td>0.31</td>
<td>0.61 *</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>200</td>
<td>0.25</td>
<td>0.55†</td>
<td>0.03</td>
<td></td>
</tr>
</tbody>
</table>

**Conductance vs Leaf N per unit leaf area**

**Conductance vs CER**

<table>
<thead>
<tr>
<th>Light level</th>
<th>Traditional</th>
<th>Intermediate</th>
<th>Modern</th>
</tr>
</thead>
<tbody>
<tr>
<td>1200</td>
<td>0.60 *</td>
<td>0.98**</td>
<td>0.06</td>
</tr>
<tr>
<td>800</td>
<td>0.70**</td>
<td>0.99**</td>
<td>0.44</td>
</tr>
<tr>
<td>600</td>
<td>0.73**</td>
<td>0.98**</td>
<td>0.47</td>
</tr>
<tr>
<td>400</td>
<td>0.61 *</td>
<td>0.99**</td>
<td>0.65 *</td>
</tr>
<tr>
<td>300</td>
<td>0.56 *</td>
<td>0.99**</td>
<td>0.66 *</td>
</tr>
<tr>
<td>200</td>
<td>0.56 *</td>
<td>0.99**</td>
<td>0.57 *</td>
</tr>
</tbody>
</table>

* and ** indicates significant at p ≤ 0.05 and p ≤ 0.01 level, respectively.
Positive correlations between CER and stomatal conductance were observed for all three varieties at all light levels except at high light levels for the modern variety (Table 4.4). Positive correlations between these two factors have been observed for other crops (Gifford and Musgrave, 1970; Prasad et al, 1985). Stomatal conductance is important in leaf photosynthesis because it controls the diffusion of CO₂ into the leaves and reduction in stomatal conductance limits internal CO₂ concentration which in turn reduces the photosynthetic rate. Reduction in internal CO₂ concentration, however, was apparently not a limiting factor in this experiment for any treatment at any light level because correlation coefficients between CER and internal CO₂ concentrations were not significant. Therefore, in spite of the positive correlations between CER and stomatal conductance, the variation in CER for different treatments was not due to differences in stomatal conductance. The variations in CER could be due to other factors such as high mesophyll resistance and/or biochemical limitations. The size of the mesophyll cells of rice has been shown to be the smallest among cereal crops, and their high surface to volume ratio exceeds other cereal crops (Kariya and Tsunoda, 1980). These two factors have been used to explain the low mesophyll resistances observed in lowland rice (Tsunoda, 1984). Therefore, any differences in CER observed in this experiment were probably mainly due to biochemical limitations.

A high diffusive conductance can promote high rates of transpiration and thus reduce WUE. No differences in WUE due to N management were detected at the flag leaf stage but varieties and light level did influence WUE. Traditional and modern varieties had higher WUE than the intermediate variety at all light levels and increased with increasing light levels up to light saturation (Table 4.5). No increase in WUE with increased light was observed with the intermediate variety and, in fact, there was a decreasing trend. The reason for the variation between high and low WUE of varieties was the differences in stomatal conductance of the two groups with increasing light.

Water may be a limited resource in many growing situations even though rice is grown under flooded conditions. The canopy conductance is the product of stomatal conductance and LAI and this is an important measure that determines the total canopy transpiration rates. Also N management influences transpiration rates by increasing leaf area index and stomatal conductance. Varieties with high stomatal conductance have low WUE. Such varieties are more at risk of
Table 4.5. Water use efficiency of the flag leaf of three rice varieties at different light levels for the flag leaf stage development.

<table>
<thead>
<tr>
<th>Light level</th>
<th>Variety</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Traditional</td>
<td>Intermediate</td>
<td>Modern</td>
</tr>
<tr>
<td></td>
<td>mmol CO$_2$ mol$^{-1}$ H$_2$O</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1200</td>
<td>11.3a*</td>
<td>5.2b</td>
<td>10.9a</td>
</tr>
<tr>
<td>800</td>
<td>11.6a</td>
<td>5.1b</td>
<td>11.4a</td>
</tr>
<tr>
<td>600</td>
<td>11.2a</td>
<td>5.3b</td>
<td>10.7a</td>
</tr>
<tr>
<td>400</td>
<td>9.9a</td>
<td>5.7b</td>
<td>9.3a</td>
</tr>
<tr>
<td>300</td>
<td>8.4a</td>
<td>6.0b</td>
<td>8.1a</td>
</tr>
<tr>
<td>200</td>
<td>7.6a</td>
<td>6.1b</td>
<td>7.2a</td>
</tr>
<tr>
<td>LSD (0.05)†</td>
<td>2.0</td>
<td>NS</td>
<td>1.6</td>
</tr>
</tbody>
</table>

* Values within a row followed by the same letter are not significant at p ≤ 0.05 level.

† LSD to compare means within a variety (column).
moisture stress than a variety that has low stomatal conductance. Even though the intermediate variety performed well under low N levels, low WUE is a disadvantage in terms of adaptability to environments where water could be a limiting factor during any part of the growth cycle.

Decreasing LAI to reduce transpiration rates may not be possible because in rice it had been shown that leaf area and dry matter production are directly correlated. The high CER at a relatively low stomatal conductance of the modern variety indicated that the very high conductances of the intermediate variety provided no advantage except for that possibly associated with transpirational cooling at high temperatures. Thus, varieties should be selected that have high CER and low stomatal conductance in order to maximize WUE and overall productivity.

Stomatal density, size, and aperture are traits that could exert considerable influence on leaf conductance and their combined effect can override simple relationships of individual traits. A small reduction in leaf conductance theoretically should result in increased WUE because transpiration is generally more sensitive than photosynthesis to a reduction in leaf conductance (Ehleringer, 1988). In this study stomatal density was not correlated with stomatal conductance. However, CER increased and stomatal conductance either increased or remained same with LNLA. This indicates that size and aperture of the stomata increased and compensated for the decreased density in leaves with high LNLA. Therefore, stomatal density is not a stable characteristic to use as a selection criterion for WUE in rice. But, as shown in the previous chapter, total stomatal number on a leaf basis may be used, because it is more or less constant for genotypes, and low stomatal numbers could reduce total canopy transpiration rates.

Relative sensitivity of stomata to moisture condition is also an important determining factor for high productivity in situations where water is limited and needs additional evaluation. High threshold water potential (less negative) for stomatal closure and rapid reopening after stress alleviation may be desirable, as it would influence the maintenance of soil moisture for a long period. Some studies on the diurnal closure of stomata under submerged conditions have shown reduction in stomatal conductance during high light and temperature situations (Singh et al., 1988). Identifi-
fying genotypes with low stomatal conductance and stomata sensitive to water deficits would increase the adaptability of lowland rice varieties to many environments.
REFERENCES


CHAPTER V

Agronomic Responses of Rice Varieties to Low and High Nitrogen Management

ABSTRACT

Modern rice (*Oryza sativa* L.) varieties do not produce consistent profitable yields when grown in unstable climates having low levels of nitrogen fertilization. This study was conducted to determined characteristics of rice that are associated with productivity under low N fertilization levels. A field experiment was conducted in two locations in Sri Lanka at the Central Agriculture Research Institute, Gannoruwa - on an Aquult and at the Regional Agriculture Research Institute, Maha Illuppallama - on a Tropoaqualf. Three rice varieties were used (a traditional variety, a modern variety, and a variety showing intermediate characteristics). Five N management treatments were imposed: a 0 N control and two N levels (45 and 90 kg N ha\(^{-1}\)) with each level split into two and three applications. Grain yield, yield components, and leaf area index were determined. Mean grain
yields across N management treatments were similar for intermediate and modern varieties but were superior to the traditional variety. Yield responses of the intermediate and modern varieties varied with the N level. The modern variety produced highest grain yields (7.6 to 8.2 Mg ha\(^{-1}\)) at high N levels. At low N levels, grain yields were lower than at the high level with both the traditional and intermediate varieties producing higher yields than the modern variety. Yield variation of the modern variety was correlated to panicles m\(^{-2}\). In the other two varieties, grains panicle\(^{-1}\) were responsible for yield variations. Also in traditional and intermediate varieties panicle number m\(^{-2}\) was negatively correlated with grains panicle\(^{-1}\) but not with the modern variety. This indicated a low response of intermediate and traditional varieties to N fertilizer. At low N levels, application of limited N supply at late vegetative or early reproductive stages is more beneficial than applying N at early vegetative stages. In the modern variety, LAI from very early stages of development (17 to 29 d after transplanting) was positively correlated with the grain yield. In the intermediate variety, LAI was correlated with yield only 41 days after transplanting. At low N levels, grain yield was influenced more by the size of the leaf area rather than light receiving efficiency of the erect-leaf plant type. In low N situations, a desirable plant will have low tillering capacity, higher grain numbers per panicle, intermediate leaf length, and leaves arranged more towards the horizontal plain than vertical. The intermediate variety possessed most of these characteristics.

INTRODUCTION

Progress has been made during the last two decades in the development of new rice varieties and technology that has resulted in large increases in rice production. For example, in Sri Lanka, average rice yields increased from 1.8 Mg ha\(^{-1}\) in 1960 to 3.5 Mg ha\(^{-1}\) during 1985 (Herath, 1987). These achievements were due to increased land area under irrigated cultivation and to the adoption of improved varieties and technologies. The possibility of increasing the land area for rice culti-
vation is now very limited. Therefore, to meet the estimated rice production needs in the future, the average per ha yields need to be increased.

One basic problem of rice cultivation arises from water deficiencies and/or excesses. The crop success even in irrigated lands depends on how efficiently the direct rainfall is utilized for rice cultivation. Moreover, rice soils in many areas are not well adapted chemically and physically for rice production (Balasuriya, 1987). The number of rainy and cloudy days in wet zone areas is very high and therefore, the irradiance for photosynthesis is low in many Asian countries (Venkateswarlu, 1977). Under low radiation levels, both dry matter accumulation and grain yields are reduced (Tanaka et al., 1966; Nayak and Murty, 1980). These unstable conditions increase the risk and uncertainty for rice production and rational farmers tend to minimize cash inputs and labor on the rice crop (Suraweera, 1986).

The performance of modern rice varieties is highly dependent on the input level and environment (Herdt and Mandac, 1980; De Datta, 1981). Their performance under high input environments is encouraging but they are not well-adapted to low input and unstable environments (Evans et al., 1984). These varieties and the technology adopted by the farmers are simply an extension of technology developed for stable and high input environments. In some cases farmers prefer traditional cultivars over modern varieties because they are well adapted to the environment and season to season yield variation is low. Only limited studies have been conducted to investigate the relative performance of modern varieties under low input management and their performance relative to traditional cultivars or varieties in early stages of breeding programs without the semidwarf gene. Adequate information concerning plant processes and desired plant types for low input, unstable environments is required for plant breeders to develop varieties for low input environments.

Nitrogen (N) is an essential requirement in rice cultivation with modern varieties and N constitutes a major fraction of the total cost of production. Modern varieties characterized by short stature and stiff straw differ markedly from the tall weak-stemed plant types of the traditional rice varieties (Matsushima, 1976). It has been generally recognized that shorter the stature the higher the yielding ability and N response (Yoshida, 1981). Low response of traditional rice varieties to N is due to lodging and mutual shading (Chandler, 1969; De Datta, 1981). The vigorous vegetative
characteristics of traditional varieties may be one reason they produce reasonable but not high yields without addition of much N (Tanaka et al., 1966). Some traditional varieties are more efficient in extracting soil nitrogen than others (IRRI, 1976). Increased yield potential of modern varieties has been achieved through increased harvest index (HI) (Chandler, 1969; Yoshida, 1981). Increases in HI have been achieved not by increasing the total biological yield or net photosynthetic rates but by increased redistribution and partitioning of photosynthates to the spikelets (Zelitch, 1982). Therefore, modern rice varieties have been found to be weak competitors because of the relatively fewer resources allocated to the root, shoot, and leaf expansion (Donald and Hamblin, 1976). This indicates the importance of total biological yield in low input environments.

The objective of this study was to measure the variation in grain yield, grain yield components, and other plant characteristics of three morphologically different rice varieties exposed to five different N management situations. Also plant characteristics that are important in determining grain yields under low N management situations were identified.

MATERIALS AND METHODS

A field experiment was conducted in two locations: Central Agricultural Research Institute, Gannoruwa (GN): and Regional Agricultural Research Institute, Maha Illuppallama (MI), Sri Lanka - (latitude between 6° and 10° N ) during the dry season of 1990. The soil at GN was an Aquult with a pH of 5.6, 16 g organic matter kg⁻¹, and 1.6 g total N kg⁻¹. At MI, the soil was a Tropaquality with a pH of 6.0, 27 g organic matter kg⁻¹, and 2.3 g total N kg⁻¹. Three rice varieties with different morphological characteristics were grown under five N management treatments. The varieties were: 1) Herathbanda - is tall stunted, having pale green, droopy leaves with large leaf area per leaf. It is a low yielding rice variety grown by farmers in the wet zone districts of Sri Lanka where the environment is not suitable for modern varieties and where the management level is generally low, 2) Bg 34-8 - semidwarf, having dark green, erect, short leaves. It is a high yielding, N responsive modern variety released by the national rice breeding program of Sri Lanka, and 3)
Bw 267-3 - a variety showing intermediate characteristics of the other two and having the potential of replacing Herathbanda in some environments. The maturity period for these genotypes is 110 to 120 days. For simplicity, these varieties will be referred to as traditional (Herathbanda), intermediate (Bw267-3), and modern (Bg34-5) varieties. All varieties were tested at two N levels (45 and 90 kg N ha⁻¹). Nitrogen at each level was applied in two or three splits (four N treatments). For the two-split treatments, applications were made at transplanting (0 DT) and at 49 d after transplanting (49 DT). For the three-split treatment, applications were made at 0 DT, 21 DT, and 49 DT. A control treatment with no N was included. Nitrogen was supplied as urea. All treatments received 50 kg P ha⁻¹ (as triple super phosphate) and 50 kg K ha⁻¹ (as muriate of potash) with one half applied at transplanting and one half at 49 DT.

Pregermiinated seeds were sown on seed beds on 1 and 6 April 1990 at Gannoruwa and Maha Illuppallama, respectively. Eighteen day old seedlings were transplanted at two to three seedlings per hill. Hill spacing was 0.15 m x 0.15 m. A randomized complete block design with four replicates was used. Weeds were controlled by hand to avoid any growth effect due to herbicide. Carbofuran at 1 kg ha⁻¹ (a.i.) was applied as 5% granules at transplanting as a preventative measure against insects. An area of 3 m² (2.0 m x 1.5 m) in the center of each plot was marked with wooden pegs and string was put across this area to prevent any lodging of tall varieties at high N levels.

Sequential sampling of three plants per plot to determine the leaf area was conducted approximately biweekly at early growth stages and weekly thereafter until the heading stage. Leaf blades were separated from the sheaths and a subsample was taken for leaf area determination. The length and width of all leaf blades of a subsample were measured. All samples were oven dried at 70°C and dry weights were recorded. A constant factor of 0.75 was used to convert the product of length and width into leaf area. Using the dry weights of the leaf subsample, specific leaf area (SLA) was determined. Specific leaf area multiplied by leaf weight gave leaf area index (LAI). At maturity, a three m² area was harvested and threshed for grain yield. Grain subsamples were taken before grain was cleaned. These subsample were oven dried, cleaned, and separated into filled spikelets and empty spikelets. Weight and number of filled and unfilled spikelets were determined in the grain

CHAPTER V 101
subsamples. The remaining grain was oven dried and grain yield was calculated. All grain yields were expressed at 14% moisture. The grain sterility was expressed as percentage empty spikelets.

\[ \text{Sterility (\%)} = \left| \frac{E}{(E + F)} \right| \times 100 \]

where E and F are the number of empty spikelets and filled spikelets in the subsample.

Statistical analysis

Data for all measurements were analyzed as a randomized complete block design with a factorial arrangement of three varieties and five N treatments. Analysis of variance and correlations were performed for various measurements using SAS software (SAS Institute Inc., 1985). When interactions were not significant the least significant difference (LSD) values were calculated for main effects of variety and N management means. Upper case letters were used in data tables to compare treatment means due to main effects. When the treatment interactions were significant, LSD values for individual treatments were used to compare individual treatment means. In data tables, lower case letters were used to compare individual treatment means. All references to differences were considered significant at the 0.05 level unless otherwise stated.

RESULTS AND DISCUSSION

Grain yield

The mean grain yield at Gannoruwa was 5.6 Mg ha\(^{-1}\) and at Maha Illuppallama was 5.3 Mg ha\(^{-1}\). Variety and N management interacted indicating differential response of varieties to N management (Table 5.1). All four treatments that received N exceeded yield levels of the control. In the control treatment traditional and intermediate varieties produced higher grain yields than the modern variety (Table 5.1). At Gannoruwa, the intermediate variety was superior to the traditional variety but at Maha Illuppallama the differences were not significant. These varietal differences in yield for the control treatment between locations is difficult to explain but most likely reflects the
importance of genotype environment interaction. Also indicated that growth and development pattern of a given genotype are determined by genetic characteristics. Some genotypes have capabilities to be more productive than others under these conditions.

Comparisons of grain yields for varieties across different N management treatments showed that the intermediate and modern varieties produced similar yields and were higher than the traditional variety (Table 5.1). The mean yield was the product of five N management situations. This indicated that between intermediate and modern varieties, no variety has an advantage in grain production when exposed to wide range of N management situations. More important, however, was the fact that the relative productivity of intermediate and modern varieties changed with N management. At low N levels the intermediate variety outyielded the modern variety where as at high N levels the modern variety outyielded the intermediate variety. When the N levels were high (90 kg N ha\(^{-1}\)) the modern variety produced 2.0 to 2.3 Mg ha\(^{-1}\) more than the intermediate variety and 3.9 to 3.4 Mg ha\(^{-1}\) more than the traditional variety. Comparison of different splits within the high N level (T\(_3\) and T\(_4\)) indicated that application of high N levels in three splits (i.e. at 0 DT, 21 DT, and 49 DT - T\(_3\)) is more beneficial than applying the same amount in two splits for the modern variety. Variations in split applications did not influenced the grain yield of the other two varieties at this N level at Gannoruwa but at Maha Illuppallama two applications were better than three splits for both traditional and intermediate varieties. Heavy N applications to traditional and intermediate varieties at early growth stages increased leaf area to a level that resulted in mutual shading because of their droopy leaf type.

The varietal performance at the low N management level (45 kg N ha\(^{-1}\)) was the reverse of what was observed at the high N level with the intermediate and modern varieties. Even though, the highest yield recorded at this N level was lower than what was recorded at high N level with the modern variety both traditional and intermediate varieties performed better than the modern variety at this N level (Table 5.1). Also the two splits treatment performed better than the three split applications in the intermediate and modern varieties but two split applications performed better with the traditional variety (Table 5.1). The yield variations of the traditional variety was small among N management treatments. The results indicated that when the N supply was limited a variety with
Table 5.1. Grain yield of three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Nitrogen management (Rate and time)</th>
<th>Gannoruwa</th>
<th>Maha Illuppallama</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 N 45 kg N ha(^{-1}) 90 kg N ha(^{-1})</td>
<td>5 - 22 - 18(\dagger) 15 - 0 - 30</td>
<td>10 - 44 - 36 30 - 0 - 60</td>
</tr>
<tr>
<td>Traditional</td>
<td>4.0i(\dagger) 5.8def 5.5f 5.0g 4.8gh</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intermediate</td>
<td>4.5h 6.6c 7.0b 6.0d 5.9de</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Modern</td>
<td>3.5j 4.8gh 5.6ef 8.2a 7.3b</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(\dagger\) Indicates kg N ha\(^{-1}\) applied: at planting - 21 d after transplanting - 49 d after transplanting. Treatments are referred to in text as \(T_0 = 0\) N, \(T_1 = 5-22-18\), \(T_2 = 15-0-30\), \(T_3 = 10-44-36\), and \(T_4 = 30-0-60\).

*Values followed by the same letter within a location do not differ at \(p \leq 0.05\).*
plant characteristics similar to the intermediate variety is capable of utilizing the available N better than a modern variety. Also when N supply is limited, application of higher proportion of available N at late vegetative/early reproductive stages (i.e. 49 DT) resulted in higher grain yields than applying much of the N at early vegetative stages. The importance of applying N at the reproductive stage has been reported previously. (Yanagisawa et al., 1967; Patnaik and Broadbent, 1967).

Yield components

Panicle numbers m$^{-2}$ increased with increasing N supply from zero to 45 and 90 kg N ha$^{-1}$ in all varieties (Table 5.2). The panicle number m$^{-2}$ for the modern variety at the high N level was 346 compared to 279 and 266 for the intermediate and traditional varieties, respectively. Two splits produced higher number of panicles than three splits at the high N level in all but the intermediate variety at MI. The probable reason could be the high tiller survival in the two-split treatment where application of N at late vegetative stages promoted more tillers to produce a panicle.

Panicle numbers m$^{-2}$ were reduced in all varieties at the low N level. Panicle numbers m$^{-2}$ for the modern variety were 266 m$^{-2}$ at the low N level compared to 346 panicles m$^{-2}$ at the high N level. This 35% increase in panicles m$^{-2}$ due to N application was largely responsible for the increased yields of the modern variety. However, the decrease in number of panicles of the intermediate and traditional varieties were only 19% and 21% respectively. Thus at low N levels panicles m$^{-2}$ of the modern variety were similar to the intermediate and traditional varieties. This indicated that at low N levels varieties with high tillering capacity such as modern variety would not be an advantage in terms of increasing yield through increased number of panicles. However, in spite of similar number of panicles of the intermediate variety to the modern variety, it still managed to produce higher yields than the modern variety at low N levels. The reason was the high number of grains per panicle produced by this variety.

The intermediate variety had higher grains panicle$^{-1}$ than the other two varieties (Table 5.3). At GN the variety x N management interaction was significant where as at MI the interaction was not significant. At Gn the intermediate variety had higher grains panicle$^{-1}$ than the other two varieties in the control (T0), and the two low N treatment (T1 and T2) (Table 5.3). In the two
Table 5.2. Number of panicles m$^{-2}$ for three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Nitrogen management</th>
<th>(Rate and time)</th>
<th>0 N</th>
<th>45 kg N ha$^{-1}$</th>
<th>90 kg N ha$^{-1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Rate and time</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>5 - 22 - 18†</td>
<td>15 - 0 - 30</td>
<td>10 - 44 - 36</td>
<td>30 - 0 - 60</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>no. m$^{-2}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gannoruwa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>155h*</td>
<td>203fg</td>
<td>217ef</td>
<td>249de</td>
<td>294bc</td>
</tr>
<tr>
<td>Intermediate</td>
<td>180h</td>
<td>226ef</td>
<td>235def</td>
<td>262cd</td>
<td>298b</td>
</tr>
<tr>
<td>Modern</td>
<td>148h</td>
<td>217ef</td>
<td>237def</td>
<td>312b</td>
<td>346a</td>
</tr>
<tr>
<td>Maha Illuppallama</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>171fg</td>
<td>199def</td>
<td>215ced</td>
<td>238cd</td>
<td>283b</td>
</tr>
<tr>
<td>Intermediate</td>
<td>176efg</td>
<td>218cde</td>
<td>224cd</td>
<td>298b</td>
<td>256bc</td>
</tr>
<tr>
<td>Modern</td>
<td>147g</td>
<td>217cde</td>
<td>234cd</td>
<td>347a</td>
<td>378a</td>
</tr>
</tbody>
</table>

† Indicates kg N ha$^{-1}$ applied: at planting - 21 d after transplanting - 49 d after transplanting. Treatments are referred to in text as $T_0 = 0$ N, $T_1 = 5-22-18$, $T_2 = 15-0-30$, $T_3 = 10-44-36$, and $T_4 = 30-0-60$.

*Values followed by the same letter within a location do not differ at $p \leq 0.05$. 

106
treatments with the high N level, no consistant varietal differences were found within a treatment. At MI the mean for the intermediate variety was superior to the traditional and intermediate varieties. At MI the control and the two treatments with low N level treatment produced higher number of grains panicle$^{-1}$ than the high N level. Even though the interactions were not significant for this location, high grain numbers in the low N level were mainly due to high values observed with the intermediate variety (Table 3). The 1000-grain weight of the traditional variety was higher than the other two varieties (Table 5.4). Nitrogen management did not influence the 1000-grain weight.

The influence of different yield components on grain yields varied with the variety (Table 5.5). Variations in grain yield of the modern variety was highly correlated to panicles m$^{-2}$ However, correlation coefficients between panicles m$^{-2}$ and grain yield were not significant for the other two varieties. In the traditional and intermediate variety correlation coefficients between grains panicle$^{-1}$ and grain yield were significant (Table 5.5) and therefore grain yield variations in these two varieties were more closely associated with grains panicle$^{-1}$. Also in these two varieties the correlation coefficients between panicles m$^{-2}$ and grains panicle$^{-1}$ were negative (Table 5.5). At Gn panicle m$^{-2}$ had a negative influence on the 1000-grain weight of the traditional variety. Moreover, increased panicle numbers increased the spikelet sterility in the traditional variety at GN (Table 5.5). None of these negative effects due to increased panicle numbers was observed with modern variety.

Association of yield variations of the intermediate variety to grains per panicle seems to be a beneficial factor when rice is grown under low N environments. An adequate N supply is required for any variety to produce high tiller numbers. When N supply is limited a variety which depends mainly on tiller production for high yields would not likely to perform well. Yield component analysis also indicated that varieties with high grain numbers per panicle are more adapted to low N environments than varieties that depend on increased number of panicles for higher grain yields.
Table 5.3. Grains panicle$^{-1}$ for three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Nitrogen management (Rate and time)</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No N</td>
<td>45 kg N ha$^{-1}$</td>
</tr>
<tr>
<td></td>
<td>5 - 22 - 18‡</td>
<td>15 - 0 - 30</td>
</tr>
<tr>
<td>Traditional</td>
<td>87d*</td>
<td>96bc</td>
</tr>
<tr>
<td>Intermediate</td>
<td>101b</td>
<td>130a</td>
</tr>
<tr>
<td>Modern</td>
<td>94bc</td>
<td>84c</td>
</tr>
<tr>
<td>Gannoruwa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maha Illuppallama</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>94</td>
<td>103</td>
</tr>
<tr>
<td>Intermediate</td>
<td>104</td>
<td>119</td>
</tr>
<tr>
<td>Modern</td>
<td>86</td>
<td>84</td>
</tr>
<tr>
<td>Mean</td>
<td>95AB</td>
<td>102A</td>
</tr>
</tbody>
</table>

‡ Indicates kg N ha$^{-1}$ applied: at planting - 21 d after transplanting - 49 d after transplanting. Treatments are referred to in text as $T_0 = 0$ N, $T_1 = 5-22-18$, $T_2 = 15-0-30$, $T_3 = 10-44-36$, and $T_4 = 30-0-60$.

* Values followed by the same upper case letter within variety and N management means and values followed by the same lower case letter within individual treatments do not differ at $p \leq 0.05$. 
Table 5.4. One thousand grain-weight for three rice varieties at five N management levels at Gannoruwa and Maha Illuppallama locations.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Nitrogen management</th>
<th>(Rate and time)</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No N 45 kg N ha⁻¹ 1</td>
<td>90 kg N ha⁻¹ 1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5 - 22 - 18‡</td>
<td>10 - 44 - 36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>15 - 0 - 30</td>
<td>30 - 0 - 60</td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>30.1 30.0 26.7 28.9</td>
<td>26.4A</td>
<td></td>
</tr>
<tr>
<td>Intermediate</td>
<td>24.9 24.0 24.5 24.7</td>
<td>25.5A</td>
<td></td>
</tr>
<tr>
<td>Modern</td>
<td>25.0 26.3 25.9 25.5</td>
<td>25.5A</td>
<td></td>
</tr>
<tr>
<td>Gannoruwa</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>26.7A 26.8A 25.7A 26.4A</td>
<td>25.5A</td>
<td></td>
</tr>
<tr>
<td>Maha Illuppallama</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>26.1 25.9 26.1 26.7</td>
<td>26.0A</td>
<td></td>
</tr>
<tr>
<td>Intermediate</td>
<td>22.7 23.6 22.7 23.1</td>
<td>23.1B</td>
<td></td>
</tr>
<tr>
<td>Modern</td>
<td>24.4 24.1 23.8 24.1</td>
<td>24.2B</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>24.4A 24.6A 24.2A 24.6A</td>
<td>24.5A</td>
<td></td>
</tr>
</tbody>
</table>

‡ Indicates kg N ha⁻¹ applied: at planting - 21 d after transplanting - 49 d after transplanting. Treatments are referred to in text as T₀ = 0 N, T₁ = 5-22-18, T₂ = 15-0-30, T₃ = 10-44-36, and T₄ = 30-0-60.

* Values followed by the same upper case letter within variety and N management means and values followed by the same lower case letter within individual treatments do not differ at p ≤ 0.05.
Table 5.5. Correlation between different yield parameters for three rice varieties at Gannoruwa (GN) and Maha Illuppallama locations.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Variable</th>
<th>Yield</th>
<th>Pansqm†</th>
<th>Grpan</th>
<th>Grwt</th>
<th>%Ster</th>
<th>III</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>GN</td>
<td>MI</td>
<td>GN</td>
<td>MI</td>
<td>GN</td>
<td>MI</td>
</tr>
<tr>
<td>Traditional</td>
<td>Pansqm†</td>
<td>0.17</td>
<td>0.24</td>
<td>-0.75**</td>
<td>-0.87**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Grpan</td>
<td>0.44†</td>
<td>0.18</td>
<td>-0.56*</td>
<td>0.09</td>
<td>0.17</td>
<td>-0.26</td>
</tr>
<tr>
<td></td>
<td>Grwt</td>
<td>-0.11</td>
<td>0.14</td>
<td>0.67*</td>
<td>0.63**</td>
<td>-0.36</td>
<td>-0.60*</td>
</tr>
<tr>
<td></td>
<td>%Ster</td>
<td>-0.01</td>
<td>-0.16</td>
<td>0.67*</td>
<td>0.63**</td>
<td>-0.36</td>
<td>-0.60*</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.33</td>
<td>-0.03</td>
<td>-0.34</td>
<td>-0.85**</td>
<td>0.35</td>
<td>0.82**</td>
</tr>
<tr>
<td>Intermediate</td>
<td>Pansqm</td>
<td>0.36</td>
<td>0.40</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Grpan</td>
<td>0.49†</td>
<td>0.45†</td>
<td>-0.60*</td>
<td>-0.62*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Grwt</td>
<td>-0.22</td>
<td>0.24</td>
<td>-0.15</td>
<td>0.23</td>
<td>-0.49†</td>
<td>-0.14</td>
</tr>
<tr>
<td></td>
<td>%Ster</td>
<td>-0.73**</td>
<td>-0.04</td>
<td>-0.12</td>
<td>0.60*</td>
<td>-0.50*</td>
<td>-0.66**</td>
</tr>
<tr>
<td></td>
<td>III</td>
<td>0.66**</td>
<td>-0.03</td>
<td>-0.23</td>
<td>-0.58*</td>
<td>0.75**</td>
<td>0.57*</td>
</tr>
<tr>
<td>Modern</td>
<td>Pansqm</td>
<td>0.93**</td>
<td>0.90**</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Grpan</td>
<td>0.23</td>
<td>0.01</td>
<td>-0.13</td>
<td>-0.40</td>
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<tr>
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<td>Grwt</td>
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<td>0.18</td>
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<td>-0.82**</td>
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<td>-0.60*</td>
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<tr>
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<td>III</td>
<td>0.08</td>
<td>-0.06</td>
<td>-0.02</td>
<td>-0.32</td>
<td>0.30</td>
<td>0.69**</td>
</tr>
</tbody>
</table>

† Pansqm = panicles m⁻², Grpan = grains panicle⁻¹, Grwt = 1000 grain weight, and %Ster = % sterility.

†, *, and ** indicates significant at p ≤ 0.10, p ≤ 0.05, and p≤ 0.01 levels, respectively.
Leaf area and yield

The relationship between the LAI at different growth stages, starting from the day of transplanting (0 DT) to early boot stage (68-76 DT), was examined to determine the stage at which adequate leaf area needs to be maintained for high yields for different varieties (Table 5.6). In the modern variety LAI at very early stages of development starting from 17 DT at MI and 29 DT at GN was positively correlated to the grain yield. For the intermediate variety, LAI showed positive correlations only 41 DT in both locations. The traditional variety showed positive correlations only at MI from 41 DT. Also for all varieties LAI was positively correlated to panicles m⁻² starting from 17-29 DT for modern variety and from 29-41 DT for the other two varieties (Table 5.6).

The importance of LAI to dry matter production and to grain yield has been well established (Tanaka et al., 1966; Matsushima, 1976). This indicates the importance of the area of the leaf surface that intercepts solar radiation. When the angle of the sun is high and LAI is large, a canopy with erect leaves has a larger sun-lit surface than do plants with droopy leaves, thus producing a higher rate of daily photosynthesis. High LAI due to increased tiller numbers at high N levels and erect leaves plus vertical arrangement of leaves may well explain the high grain yields in the modern variety. However, at low N levels tiller production of this variety was low and therefore light interception was low. Maintaining adequate leaf area from very early stages is essential for the modern variety to produce high yields. This is not possible in low N input situations because of low tiller production. Low LAI was also observed with the intermediate variety but the size, shape, and angle of the leaves and the more horizontally arranged leaves of this variety was capable of intercepting more light than the modern variety at low N levels.

These results indicated that dry matter production was influenced by the size of leaf area at low N management level rather than light receiving efficiency of erect-leaf plant type. In such situations photosynthetic rates of single leaves could play more important role compared to total canopy photosynthesis. Research to increase yield potentials of modern rice varieties through the incorporation of high photosynthetic rates have so far not met with much success (Evans et al., 1984). This is mainly because canopy photosynthesis is more important than single leaf photosynthesis in plants with erect leaves with adequate N levels. However, when the N supply is limited LAI is low.
Table 5.6. Correlation between leaf area index at different growth stages and yield and panicles m$^{-1}$ for three at Gannoruwa and at Maha Illuppallama locations.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Variable</th>
<th>0</th>
<th>17</th>
<th>29</th>
<th>41</th>
<th>47</th>
<th>54</th>
<th>61</th>
<th>68</th>
<th>76</th>
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<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Gannoruwa</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Traditional</td>
<td>Yield</td>
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<td>0.29</td>
<td>0.39</td>
<td>0.43</td>
<td>0.36</td>
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<td>0.38</td>
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<tr>
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<td>Pansqm</td>
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<td>0.76**</td>
<td>0.51*</td>
<td>0.76**</td>
<td>0.80**</td>
<td>0.80**</td>
<td>0.83**</td>
<td>0.92**</td>
<td>0.79**</td>
</tr>
<tr>
<td>Intermediate</td>
<td>Yield</td>
<td>0.17</td>
<td>0.06</td>
<td>0.23</td>
<td>0.51*</td>
<td>0.50*</td>
<td>0.58*</td>
<td>0.61*</td>
<td>0.17</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
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<td>0.58*</td>
<td>0.44†</td>
<td>0.74**</td>
<td>0.71**</td>
<td>0.81**</td>
<td>0.78**</td>
<td>0.73**</td>
<td>0.80*†</td>
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<tr>
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<td>Yield</td>
<td>-0.13</td>
<td>0.29</td>
<td>0.66*</td>
<td>0.90**</td>
<td>0.85**</td>
<td>0.90**</td>
<td>0.80**</td>
<td>0.89**</td>
<td>0.90**</td>
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<tr>
<td></td>
<td>Pansqm</td>
<td>-0.08</td>
<td>0.43†</td>
<td>0.62*</td>
<td>0.88**</td>
<td>0.85**</td>
<td>0.89**</td>
<td>0.84*</td>
<td>0.87**</td>
<td>0.94**</td>
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<td>Maha Illuppallama</td>
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<tr>
<td>Traditional</td>
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<td>0.25</td>
<td>0.45</td>
<td>0.41</td>
<td>0.59*</td>
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<td>0.60*</td>
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<tr>
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<td>Pansqm</td>
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<td>0.07</td>
<td>0.45†</td>
<td>0.61*</td>
<td>0.67**</td>
<td>0.69**</td>
<td>0.83**</td>
<td>0.88**</td>
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<td>Yield</td>
<td>-0.23</td>
<td>0.31</td>
<td>0.39</td>
<td>0.62* NS</td>
<td>0.69**</td>
<td>0.64**</td>
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<td>0.75**</td>
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<td>0.68**</td>
<td></td>
</tr>
<tr>
<td>Modern</td>
<td>Yield</td>
<td>-0.03</td>
<td>0.47†</td>
<td>0.83**</td>
<td>0.87**</td>
<td>0.89**</td>
<td>0.83**</td>
<td>0.96**</td>
<td>0.92**</td>
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<td></td>
<td>Pansqm</td>
<td>-0.19</td>
<td>0.41</td>
<td>0.71**</td>
<td>0.91**</td>
<td>0.78**</td>
<td>0.68**</td>
<td>0.87*</td>
<td>0.87**</td>
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</tr>
</tbody>
</table>

Pansqm = panicles m$^{-2}$.
†, *, and ** indicates significant at p ≤ 0.10, p ≤ 0.05 and p ≤ 0.01 levels, respectively.
and varieties with high photosynthetic rates have an advantage over varieties with low photosynthetic rates. These results indicated that an erect-leaf canopy was beneficial only when high LAI could be attained. In situations where N supply is low, a variety with intermediate leaf length and the canopy arranged more towards the horizontal plain than vertical is more beneficial.

Conclusion

Grain yield variations observed in this study were the result of the interaction of three morphologically different rice genotypes with different N management situations. Results confirm the importance of high N levels for high productivity of modern varieties. Also varieties with long droopy leaves and low tillering capacities are poor yielders at high N levels. Tillering was a major factor that limited yields of the modern variety. Application of a major part of N the (at low total N) during the late vegetative period may not be successful because vegetative growth would be severely restricted due to low N availability during the early growth stages. In contrast, application of no nitrogen to the intermediate variety at early vegetative growth stages would not affect vegetative growth significantly and sometimes could be beneficial in terms of decreasing lodging and mutual shading. Therefore, in low N situations the erect-leaf short-stature plant type would not be able to utilize the limited N resources efficiently. In such situations a plant with low tillering capacity, but with high grain numbers per panicle, and intermediate leaf length, and canopy arranged more horizontally than vertically is desirable. The intermediate variety possesed most of these characteristics.
REFERENCES


VITA

The author was born 14 October 1950 in Beruwela, Kalutara District, Sri Lanka. He had his primary education at Roman Catholic School, Beruwela, and attended St. Benedict’s College, Colombo where he successfully completed General Certificate of Education (Advanced Level) Examination in 1970. In February 1972 he was admitted to the University of Sri Lanka, Peradeniya Campus, and graduated in March 1976 with a B. Sc. degree in Agriculture with a Second Class Upper Division.

He joined the Department of Agriculture in Sri Lanka as a Research Officer in July 1977 and was involved in conducting research on rice. In February 1982 he received a scholarship from USAID/Sri Lanka Rice Research Project to pursue graduate studies and received his M.Sc. in Agronomy from Virginia Polytechnic Institute and State University. He continued research on rice after his masters degree for five years before enrolling for the Ph. D. degree at VPI & SU in 1989.

His wife is Charmaine and has two children, Shanika and Randika.

CHAPTER V