ADVANCES IN TROPICAL AGRICULTURE IN THE 20TH CENTURY AND PROSPECTS FOR THE 21ST

Yield potential of rice: Past, present, and future perspectives

T.L. Setter
Agriculture Western Australia, South Perth, Western Australia

S. Peng and G.S. Khush
International Rice Research Institute, Los Baños, Philippines

M.J. Kropff
Wageningen Agricultural University, Wageningen, The Netherlands

K.G. Cassman
University of Nebraska-Lincoln, Nebraska, U.S.A.

Past: The "Green Revolution" and Development of High Yielding Semi-Dwarfs

Improvements in yield potential of rice genotypes related to leaf and canopy characteristics emerged gradually from many observations in Japan by Baba (1954, 1961) and Tsunoda (1959a, b, 1960, 1962) comparing high- and low-yielding varieties. Varieties with high yield potential at high levels of applied N had short sturdy stems to prevent lodging; leaves that were erect, short, narrow, thick, and dark green to increase photosynthesis; and plants had a high tillering capacity to compensate for missing hills in transplanted crops or thinly sown areas in direct-seeded crops (Chandler, 1972). The close association between morphological characteristics and yield potential at high N supply led to the "plant type concept" as a guide for breeding high yielding varieties (Yoshida, 1972).

Selection for semi-dwarf varieties in the late 1950s was largely motivated by attempts to reduce lodging (Yoshida, 1972, 1981; Shen, 1980; Takeda, 1984). In 1949 in Taiwan, a stiff strawed semi-dwarf indica rice from China, 'Dee-geo-woo-gen', was crossed with a tall, disease resistant variety, 'Tsai-yuan-chung'. 'Taichung Native 1' (TN1) was selected from this cross and released in 1956 (Huang *et al.*, 1972). 'Taichung Native 1' is considered the first high yielding semi-dwarf indica rice variety (Yoshida, 1981), producing

Table 1 Traits of traditional and semi-dwarf rice varieties relative to the New Plant Type under development at the International Rice Research Institute

Plant part or trait	Traditional tall variety (pre 1960s)	Semi-dwarf, modern high-yielding variety (1960s-1970s)	New Plant Type - proposed traits (1990s)
Height	>120-150 cm	90-110 cm	90-110 cm
Leaves	long, droopy	short, small, erect	thick short, small, erect
Tillers	low-tillering	upright (compact), high-tillering; 25 plant^{-1}*	none unproductive ~15 plant^{-1}*
Culm	tall and thin	short and stiff	short and stiff
Panicles	12-15 plant^{-1}	~15 plant^{-1}*	~8 plant^{-1}*
Grains panicle^{-1}	90-100	80-110	200-250
Harvest Index	0.30	0.50-0.55	0.55-0.60
Growth duration (d)	160-200	110-140	100-130
Varietal examples	Peta	Taichung Native 1, IR8, IR72	IR65598-112-2
Grain yield potential**	3-4(not N responsive)	6-10 (N responsive)	10-13 (N responsive)
Root system	-	vigorous	vigorous
Pests and diseases	variable resistance	multiple resistance	multiple resistance
Crop establishment	direct seeding or transplanted	direct seeding or transplanted	mainly direct seeding

Source: Chandler (1969, 1972); Peng *et al.* (1994); Khush (pers. commun.); Yoshida (1972,1981); IRRI (1989b); Khush (1990)
*data for IR72 and IR65598-112-2 at 20 X 20 cm spacings, single seedling hill^{-1} (Peng *et al.*, unpubl.);
** at 60-120 kg N ha^{-1}, dry season

on average 6 t ha^{-1} relative to about 3-4 t ha^{-1} for traditional varieties (Table 1). In 1956, breeders at the Guang-dong Academy of Agricultural Science in China, crossed '*Ai*-zai-zan' with 'Guang-chan' 13 to develop the semi-dwarf 'Guang-chang-ai'. This was the first semi-dwarf high-yielding variety developed in Peoples Republic of China and released in 1961 (Shen, 1980). In Japan the selections for semi-dwarf cultivars were also based on developing short culm varieties aimed at preventing lodging. Like the above breeding programmes, these selections resulted in plants with shorter leaves that tended to be more erect than the long droopy leaves of traditional varieties (Table 1). This fortuitously produced an improved canopy structure that allowed greater light penetration into the canopy and therefore more uniform light absorbance by leaves throughout the canopy (Takeda, 1984).

In 1962 in the Philippines, plant breeders at the International Rice Research Institute (IRRI) made 38 crosses, 11 of which involved the short-strawed varieties from Taiwan and tall tropical indicas. The eighth cross was between 'Dee-geo-woo-gen' and a tall vigorous variety from Indonesia, Peta. IR8-288-3, later to be called IR8, was released by IRRI from this cross in 1966, and this is considered the first high yielding modern semi-dwarf rice cultivar adapted to tropical climates (Chandler, 1992).

The above events marked the start of the "green revolution" in Asia. Compared with traditional cultivars, IR8 is a semi-dwarf with erect leaves, high tillering, short and stiff culms, a high harvest index, and N responsiveness (Table 1) at high irradiance (dry season, Figure 1). Although traditional tall varieties like Peta are also 'responsive' to N, excessive shoot growth results in severe lodging and reduced yields. In contrast, semi-dwarf varieties like IR8 had up to threefold greater yields at high N supply (Figure 1). In South, East, and southeast Asia the adoption of high yielding varieties like IR8 occurred rapidly because farmers obtained a yield advantage of 1-2 t ha^{-1} even at low fertility on irrigated land compared with traditional varieties (Chandler, 1972; Yoshida, 1981).

Early IRRI varieties such as IR8, IR20, and IR24 were extremely susceptible to bacterial blight, tungro virus, and brown planthopper, until IR36, with its wider resistance to brown planthopper, was released in 1976.

At one stage IR36 became the most widely planted rice variety in history, accounting for over 11 million hectares (Plucknett *et al.*, 1987). Greater tolerance to new or evolved pests and diseases and improvements in grain quality are several of the major factors contributing to the numerous IR varieties after IR8 (Plucknett *et al.*, 1987; Khush, 1989).

Currently used high-yielding semi-dwarf varieties include IR72 which was selected from a multiple cross made in 1981. This variety has a high milling recovery and medium-long, slender, and translucent grains.

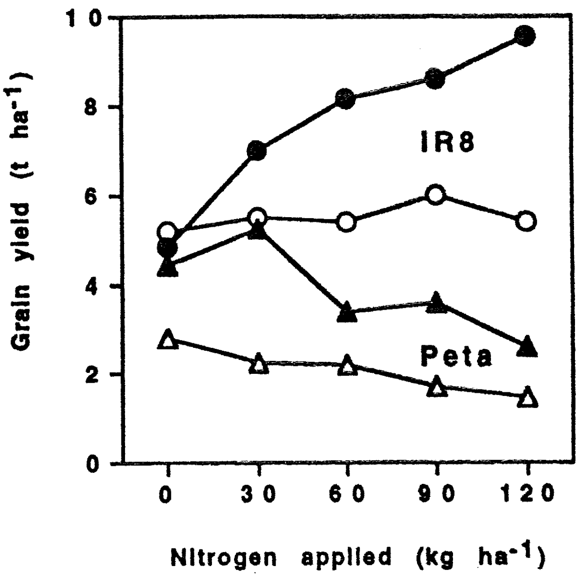

Figure 1 Effects of added fertilizer-N on grain yields of the semi-dwarf variety IR8 (O) and the traditional tall rice variety Peta (△). Data are for 1966 dry season (●) or wet season (△) (from De Datta *et al.*, 1968)

When adjusted for earlier maturity, yield potential of IR72 is 5-10% greater than IR8 on a yield-per-day basis (Kropff *et al.*, 1994a). IR72 is resistant to brown planthopper, green leaf hopper, blast, bacterial leaf blight, and grassy stunt virus, and has excellent resistance to tungro virus under field conditions (G.S. Khush, pers. commun.), while IR8 is susceptible to almost all of these pests or diseases (Plucknett *et al.*, 1987). At present about 85 million hectares of ricelands are planted to improved semi-dwarf varieties in irrigated and favourable rainfed lowland areas, and these account for about 80% of the world rice production (Khush, 1990).

The renewed focus for increasing yield potential of rice even above today's modern semi-dwarf varieties was the result of observations that human population growth was outstripping yield growth rates and this trend was predicted to worsen into the 1990s and beyond (IFPRI, 1977). In 1989, scientists at IRRI presented a plan to exceed the yield plateau of high-tillering semi-dwarf varieties by developing a rice plant with a new architecture and physiological traits that was aimed at a 20-30% yield advantage over the available varieties (IRRI, 1989a; Khush, 1990). The characteristics and progress towards development of this New Plant Type are described in the following section.

Present: A "New Plant Type" Developed from Tropical Japonicas

In the 28-year period since the development of IR8, only marginal increases have occurred in the yield potential of rice, largely due to a focus on disease and insect resistance, shortening growth duration, and improvements in grain quality (Khush, 1990). To further increase yield potential, IRRI scientists proposed modifications of the present high-yielding, semi-dwarf plant type that would support a significant increase in rice yields, particularly for direct-seeded crop establishment (Vergara, 1988; Janoria, 1989; Dingkuhn *et al.*, 1991; Penning de Vries, 1991). The traits targeted for this "New Plant Type" are described in detail by Peng *et al.* (1994; Table 1 and Figure 2) and include (i) similar leaf and canopy traits to the semi-dwarf varieties, and unique traits for (ii) reduced tillering, particularly elimination of tillers which do not produce panicles and (iii) increased panicle size and harvest index (HI). These traits and the exclusive use of the relatively obscure tropical japonica germplasm are described below.

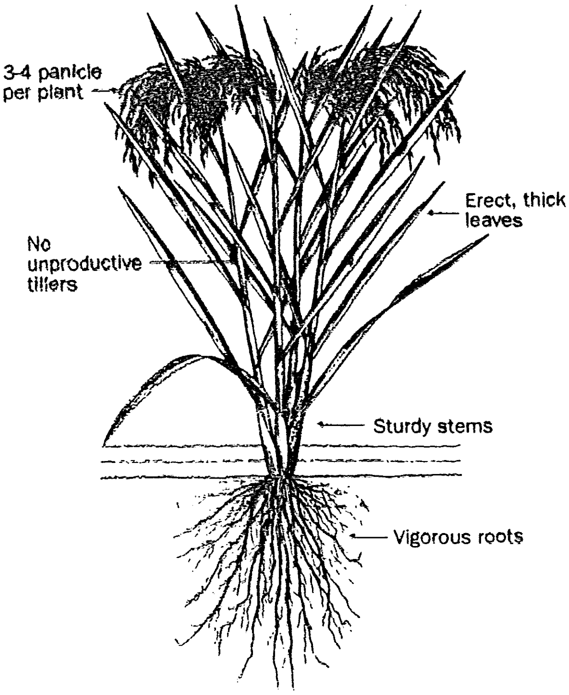

Figure 2 Drawing of the New Plant Type with traits of 3-4 panicles per plant, no unproductive tillers, sturdy stems, erect thick leaves, and vigorous roots (from IRRI, 1989a). Other traits are given in Table 1

Canopy and leaf characteristics

Canopy and leaf characteristics of the New Plant Type are similar to modern semi-dwarf varieties (Table 1), the single most important trait being erect leaves.

At high yield potential and high leaf area index (LAI) there are two key features of optimizing light distribution in a canopy with erect relative to horizontal leaves. First, light is distributed more uniformly among different leaf layers from the top to the bottom of the canopy. The absence of a uniform light distribution is one explanation for the adverse effects of lodging on yield. Lodging results in leaves with a horizontal orientation particularly in the top layers so that light is almost completely absorbed in the top few centimetres of the canopy. This results in large reductions in canopy photosynthesis at high (>3) LAI because the top leaves are light-saturated, i.e., most of the light is used ineffectively. Canopies of IR72 which were erect or lodged to 25% of their original height absorbed 4±3% and 89±5% of incident radiation respectively, at a depth of 5 cm below the top of the canopy, while net canopy photosynthesis rates were 9.8±0.7 and 1.9±0.7 μmol CO_2 m^{-2} s^{-1} respectively (at a LAI of 3.5±0.4 at 20 days after flowering; Setter *et al.*, unpubl. data).

The second feature of a canopy with erect leaves is that light is more efficiently utilized by single leaves. This was demonstrated by Tanaka (1976) who measured carbon assimilation of leaves exposed to light from different sides. Leaves exposed to light at 0.4 cal cm^{-2} min^{-1} (approx. 1250 μmol m^{-2} s^{-1} PAR; Coombs *et al.*, 1985) on only the top or the bottom side of the leaf had net photosynthesis rates equivalent to only 13.7 or 14.4 μmol CO_2 m^{-2} s^{-1} respectively, while leaves exposed to half of this light on both sides of the leaf had photosynthesis rates of 17.2 μmol CO_2 m^{-2} s^{-1}. This effect was even more pronounced at higher leaf N content and greater leaf thickness.

Droopy or horizontal leaves also increase the relative humidity and decrease the temperature inside the canopy due to reduced light penetration and reduced air movement (Akiyama and Yingchol, 1972), and such a microclimate provides a more favourable canopy environment for many diseases and some insect pests of rice (Yoshida, 1976).

There is no consistent relationship between leaf thickness and yield potential (Yoshida, 1972), however leaf thickness is positively correlated with single-leaf photosynthetic rate (Murata, 1961). This is not surprising since thicker leaves would tend to have higher N concentrations per leaf area, and there is a good relationship between leaf N on an area basis and leaf photosynthesis (r^2=0.62 for IR72, Peng, unpubl., Tsuno *et al.*, 1959; Takeda, 1961; Yoshida and Coronel, 1976; Setter *et al.*, 1994). Thick leaves are therefore thought to be a desirable trait at least at high LAI, and this trait provides a visual selection criterion for the New Plant Type. The benefits of thick leaves may break down under some circumstances. For example, at a constant dry weight, leaf area development is inversely related to leaf thickness. Therefore in situations where leaf area development may be limiting, e.g., seedling establishment, and when the crop competes with weeds, thinner leaves may provide greater leaf area, faster canopy closure, and hence a more efficient utilisation of biomass.

Reduced tillering and large panicles

Primitive corn and sorghum varieties had a large number of tillers with small cobs or heads, and increases in the yield potential of these cereals occurred mainly through increases in sink size with a reduction in tiller number (Khush, 1990). A similar strategy is adopted for the New Plant Type.

Semi-dwarf rice varieties like IR72 are high tillering with about 15-20 tillers per plant using 3-5 plants per hill at a spacing of 20 cm X 20 cm (*cf.* Table 1), however tiller number varies depending on hill spacing (Yoshida, 1981; Peng *et al.*, 1994). The major concern with the tillering traits of semi-dwarf varieties is that anywhere from 55 to 80% of the tillers are unproductive, i.e., produce no panicle (Peng *et al.*, 1994). Elimination of unproductive tillers would theoretically allow for greater light and mineral nutrients for growth of the productive tillers, assuming there are no benefits of the unproductive tillers to developing panicles on productive tillers. There is little or no published data that quantify the importance of unproductive tillers to yield. Reduced tillering is likely to be associated with more synchronous flowering and maturity and more uniform panicle size (Janoria, 1989).

Disadvantages to reduced tiller number might include reduced ability to recover from loss of tillers due to pests or from poor crop establishment. These factors were precisely the rationale for profuse tillering habit in modern semi-dwarf varieties relative to traditional varieties (Table 1; Chandler, 1969). The impact of reduced tillering needs to be evaluated under field conditions, and crop management will need to be modified to optimise spacing and fertilizer requirements of the New Plant Type which is aimed at direct seeding establishment (Peng *et al.*, 1994).

A single semi-dominant gene controls the low tillering trait in some rice genotypes, and this gene has pleiotropic effects on culm length and thickness and panicle size (Ise, 1992). Similar results were found earlier with a gene that inhibits tillering in some wheat genotypes (Richards, 1988). It is fortuitous that these other traits are associated with the low tillering gene in rice since these traits are also targeted for IRRI's New Plant Type (Table 1). The spikelet number per unit land area, or sink size, is the primary determinant of grain yield in cereal crops like wheat and maize (Fischer, 1983) and rice (Takeda, 1984) grown in high-yield environments. Therefore, to achieve increased sink size in the new plant type, reduced panicle number in low-tillering plant types is compensated by a proportionally greater increase in plants per unit area and panicle size.

Plant height, culm thickness, biomass production, and harvest index

Short plant height reduces the susceptibility to lodging and increases the HI (Tsunoda, 1962). Shorter culms also require less maintenance respiration (Tanaka *et al.*, 1966) although they could reduce the potential contribution of stem reserves to yield. The latter could be offset by thicker culms. Although grain yield can be considered as a simple product of total dry matter and HI, Vergara and Visperas (1977) demonstrated that among six rice varieties, grain yield was often but not always correlated with total dry matter, though high dry matter production was always required for high grain yield. Increased biomass production is not difficult to achieve when the rice crop is grown in a high solar radiation environment similar to the dry season conditions at IRRI, and provided with a supply of N (Akita, 1989). However, without a strong, thick culm, the increased biomass production at high N supply results in lodging, increased disease incidence, and decreased grain yield in the current semi-dwarf varieties (Vergara, 1988).

An increase in HI from 0.50-0.55 in modern semi-dwarf varieties to 0.55-0.60 in the New Plant Type (Table 1) would be partly expected from the elimination of unproductive tillers. Other contributions may come from reduced growth duration since HI increases with decreases in growth duration (Vergara *et al.*, 1966). The maximum HI in wheat was suggested as 0.62 based on a measured HI of 0.49 and assuming (i) a constant crop biomass and (ii) a 50% reduction in stem and leaf sheath dry weights with a proportional increase in chaff weight to yield (Austin *et al.*, 1980). In current semi-dwarf rice varieties with a yield potential of 10 t ha^{-1}, the HI is about 0.53; hence increasing HI to 0.62 in a New Plant Type would result in a yield potential of about 12 t ha^{-1}.

Present status of breeding and evaluations of the New Plant Type

Breeding work on the New Plant Type commenced in 1989 when 2000 entries from the IRRI germplasm bank were evaluated to identify donors for various traits (Peng *et al.*, 1994). Most of these entries were javanicas called 'bulus' from Indonesia (Table 2). This germplasm is known for long heavy panicles (Katayama and Nakagahra, 1993), low tillering, and sturdy stems (Parthasarathy, 1972). Originally, rice varieties of *Oryza sativa* L. were classified into three

Table 2 Tropical japonica donors for various traits being used for developing the New Plant Type

Trait	Donors	Country of origin
Height	MD2, Sheng-Nung 89-366	Madagascar, and China
Low tillering	Merim, Gaok, Gendjah Gempol, and Gendjah Wangkal	Indonesia
Thick culm	Sengkeu, Sipapak, and Sirah Bareh	Indonesia
Large panicles	Daringan, Djawa Serang, Ketan Gubat	Indonesia
Grain quality	Jhum Paddy, WRC4, Azucena, and Turpan 4	India and Philippines, Thailand
Pest and disease resistance:		
Bacterial blight	Ketan Lumbu, Laos Gedjah, and Tulak Bala	Indonesia
Blast	Moroberekan, Pring, Ketan Aram, Mauni	Guinea and Indonesia
Tungro	Gundil Kuning, Djawa Serut, Jimbrug, and Lembang	Indonesia
Green leafhopper	Pulut Cenrana, Pulut Senteus, and Tua Dikin	Indonesia

major groups: japonicas, indicas, and javanicas (Katayama and Nakagahra, 1993). More recently Glaszmann (1987) divided these rice varieties into six groups based on allelic constitution at 15 isozyme loci. This grouping clarified that the javanica rices, which are mainly grown in the tropics, are genetically similar to the japonicas which are grown in temperate regions. Therefore the javanicas are now referred to as "tropical japonicas".

Crosses between japonica and indica rice types have varying levels of sterility and give poor recombinant progenies due to restrictions to recombination. Crosses between (temperate) japonica and tropical japonica rice types are fertile and there are no barriers to recombination (Khush and Aquino, 1994). A decision was therefore made to limit the hybridization work for the New Plant Type within the tropical japonica and temperate japonica germplasm to avoid these problems. Tropical japonica varieties from China, India, Indonesia, Laos, Madagascar, Malaysia, Myanmar, Philippines, Thailand, and Vietnam were used for various traits and some of these varieties are listed in Table 2.

Hybridization started in 1990 and since then over 700 crosses have been made and more than 35 000 pedigree nursery rows were grown. From these, breeding lines were selected with the required traits for the New Plant Type. The first dry season field trial was conducted in 1994 by comparing 11 New Plant Type lines with IR72, and major observations from this single experiment are summarized below (S. Peng, unpubl.):

(i) The New Plant Type produced two to three times less tillers than IR72, however the productive tiller percentage of the New Plant Type was higher than IR72 (80 vs. 60%). The New Plant Type produced more tillers under high N supply and wide spacing, although the responsiveness to nitrogen and spacing was not as great as for IR72;

(ii) Spikelet number per panicle of some New Plant Type lines was two to three times greater than IR72, while panicle number per m^2 of IR72 was only two times higher than the New Plant Types. This resulted in a 15-20% larger potential sink (spikelets m^{-2}) for the New Plant Type than IR72;

(iii) In a preliminary trial, grain yields of two New Plant Type lines and IR72 were similar: the highest yields for IR72 were 8.9±0.4 t ha^{-1}, while the New Plant Type lines had yields of 8.9±0.8 t ha^{-1} (at 200 kg N ha^{-1} and 14% moisture). However during this trial there was a brown planthopper (BPH) infestation, despite attempted control with insecticides. The yield of IR72 was not affected due to its resistance to BPH, while the yields of the New Plant Type were likely reduced due to severe leaf damage; this was also indicated since almost 40% of the grains in the New Plant Type were unfilled or half filled. One interpretation of the present results is that the yield potential of the New Plant Type line was not fully expressed and may be greater than the semi-dwarf IR72. Further experiments are needed to determine whether the high percent of unfilled grains is related to BPH susceptibility or an effect of other limitations in grain filling;

(iv) Single-leaf photosynthesis per unit leaf area was 10-15% higher for some New Plant Type lines than IR72 at vegetative and early reproductive stages, and this was mainly due to the higher leaf N contents per unit leaf area of New Plant Types. This advantage did not persist to subsequent stages. Further experiments will be needed to focus on canopy photosynthesis measurements;

(v) New Plant Types had greener leaves than IR72 during the entire growing season and more erect leaves than IR72 at the vegetative stage. New Plant Types also had one to two more functional leaves per tiller at flowering than IR72;

(vi) New Plant Types had thick and sturdy stems compared with IR72, and this resulted in better lodging resistance observed in the field relative to IR72; and

(vii) Total growth duration of several New Plant Types is the same or shorter than IR72, therefore, New Plant Types will not restrict intensive double- or triple-crop systems.

Table 3 Some opportunities for future increases in yield potential of rice grown in favorable environments, i.e., without biotic and abiotic stresses

Yield potential factor
Greater Sink
Panicle size and number
High density grains
Greater Source
Greater nutrient assimilation, particularly N
Greater carbon assimilation (including heterosis)
1) Amount of storage reserves allocated to grain
stems and leaves
roots
2) Rate of net carbon assimilation during grain filling
photosynthetic carbon assimilation
light interception: leaf and canopy traits
utilisation of organic and inorganic carbon from soil
lodging tolerance
reductions in photorespiration
reductions in maintenance respiration
3) Grain filling duration
leaf "stay green"
Better partitioning (HI)

Recent reviews on these factors are given by IRRI (1989a), Khush, (1990), Penning de Vris, (1991), Cassman (1994), Kropff *et al.* (1994a), Peng *et al.* (1994) and Setter *et al.* (1994)

At present the New Plant Type is not directly selected for high density grain (Table 3) since such emphasis is considered premature until the role of source limitation governing the proportion of high density grains is clarified (Peng *et al.*, 1994). Current breeding activities on the New Plant Type lines are aimed at incorporating disease and insect-resistance and improving grain quality. Tropical japonica germplasm that have resistance to bacterial blight, blast, tungro virus, and green leafhopper have been identified (Table 2). Even though there are no donors available for resistance to brown planthopper (BPH) in the japonica germplasm, genes for brown plant hopper resistance are being transferred from indica varieties through backcrossing. Improved tropical japonicas with the proposed ideotype, resistance to diseases and insects, and acceptable grain quality should become available in next three to four years.

The basic strategy of developing the New Plant Type involves three phases. The first phase is to increase the HI from current levels of about 0.53 to 0.60 by further increasing sink size, reducing unproductive tillers, and more efficient partitioning of biomass between grain and straw. This first phase is well under way, although evaluations are continuing. The second phase is to work on improvements in tolerance to pests and diseases and grain quality. Future work beyond this will focus on a third phase targeting a grain yield potential of 15 t ha^{-1} through increases in biomass production by (i) increasing photosynthetic rate and duration using biotechnology or (ii) utilizing heterosis from japonica x indica hybrids (IRRI, 1989a, b; Khush, 1990). This future goal is to complete full development of a New Plant Type within 8-10 years with 30-50% higher yield potential than the existing semi-dwarf indica varieties in tropical environments.

Future: The "Next Generation" of Plant Types Evolving Through New Tools

Conceptualisation and development of future plant types for irrigated rice is a continually evolving process which has historically cycled from aims of increasing yield potential to enhancing tolerance of pests and diseases or improving grain quality. In future, the next generation of rice plant types will be required to increase yield potential of rice grown in tropical regions to 15 t ha^{-1} and beyond. These plants will need to have greater or more efficient light interception by the canopy, greater nitrogen and carbon assimilation by shoots and roots, and greater tolerance to lodging (Kropff *et al.*, 1994a; Setter *et al.*, 1994). Use of new research tools such as modelling and biotechnology will become increasingly important for pinpointing, evaluating, and incorporating new traits in the appropriate rice lines. Several examples of a quantitative approach to developing such future rice plant types using modelling are presented in this section, while the potential impact of biotechnology on these processes is described in other reviews (Toenniessen, 1991; Bennett *et al.*, 1994).

Plant characteristics and components of yield that determine yield potential of rice were defined by Yoshida (1981), and a simple analysis of the requirements for increased yield potential was presented by Kropff *et al.* (1993, 1994a). The driving forces in crop yield formation are well known: both a source of nitrogen and carbon as well as a sink (spikelets) are needed. This section focuses on factors related to increasing the source for yield potential, particularly carbon assimilation (Table 3), while recent reviews on the importance of sink limitations and source-sink interactions are presented by Kropff *et al.* (1994a) and Setter *et al.* (1994). Deciding the priorities and the most likely areas for success among such diverse research areas shown in Table 3 is a key challenge for rice scientists in the future.

Nitrogen requirements for future rice plants with yields of 15 t ha^{-1} can be calculated by extrapolation. At 10 t ha^{-1} grain yield and a HI of 0.5, the straw and grain biomass will contain about 1% N (Murayama, 1979) or about 200 kg N ha^{-1}. Nitrogen uptake of 300 kg ha^{-1} will therefore be required to support a yield of 15 t ha^{-1} assuming a proportional increase in biomass. The requirements of greater N uptake for tropical rice seem achievable based on yields of 15 t ha^{-1} which already occur in temperate areas like Australia (L. Lewin, pers. commun.) and China (Gaogun Yang, Yunnan Province, pers. commun.). In future, maintaining high N uptake with increasing N application will require a more intensive management strategy with multiple N applications or controlled release fertilizer which matches the available N supply with crop N demand (Cassman *et al.*, 1994).

Carbon assimilation for grain production is determined by three factors (Table 3) (i) carbon retranslocation from storage tissues, (ii) the rate of carbon assimilation during the grain filling period, and (iii) the duration of the grain filling period (Kropff *et al.*, 1994a). Each of these factors is discussed below:

Carbon retranslocation from storage tissues

Decreases in carbohydrate contents in stems of rice between flowering and maturity relative to grain yield have often been used to estimate potential contributions of stem reserves to grain filling (Yoshida, 1981). This method gives values of 0 to 40% for rice, 20% for barley, 5 to 50% for wheat and 12 to 14% for corn (Yoshida, 1972). These values may be overestimated since respiration may result in a translocation efficiency of only about 70% (for IR8, Cock and Yoshida, 1972) and the lost carbon from stems is assumed to be retranslocated only to panicles. On the other hand, values may be underestimated due to the method used, since carbohydrate contents may first decrease to low levels and then increase at maturity.

Total nonstructural carbohydrate concentrations in stems of 5 rice varieties at 0 to 4 days after flowering (DAF) ranged from 18 to 31% of dry weight, and values decreased to 0.2 to 4% by about the middle of grain filling (at 16 DAF, Figure 3). The low carbohydrate levels during mid grain-filling (Figure 3) suggest that mobilisation of available stem reserves is at a maximum level in most varieties. However, in all varieties there were increases in stem carbohydrates at maturity (25-35 DAF, Figure 3) which would have given up to threefold underestimates of carbohydrate retranslocation based on differences in concentrations between flowering and maturity relative to flowering and mid grain-filling (calculated from Figure 3). The reason for this increase in stem carbohydrates is unknown but may be related to the reduction of an effective sink with continued carbon assimilation by leaves; when panicles were excised at the middle of grain filling there was also a rapid increase in total stem carbohydrates (Setter *et al.*, unpubl.).

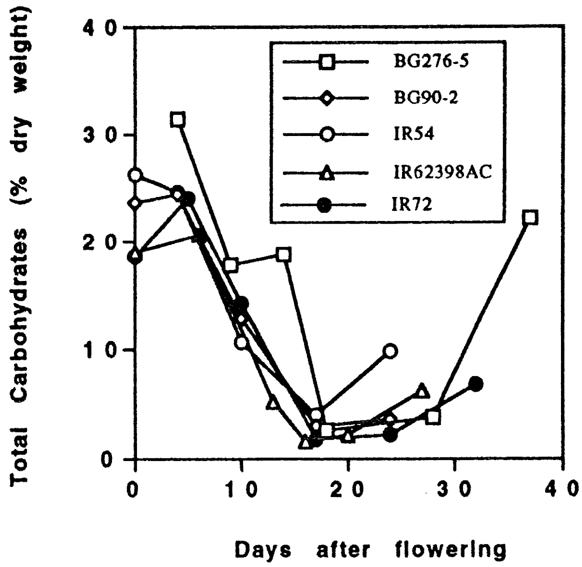

Figure 3 Carbohydrate concentrations (% dry weight) in mainstems of rice varieties during grain filling. Values are the sum of ethanol soluble (soluble sugars) and insoluble carbohydrates (starch). Plants were grown in the dry season at IRRI, Los Baños, Philippines (Setter *et al.*, unpubl.)

Measurement of ^{14}C-carbohydrate movement from stems to panicles enables a more accurate evaluation of the importance of stem carbohydrates to grain yield. Cock and Yoshida (1972) showed that for a rice crop supplied for 2 h with $^{14}CO_2$ at 10 days before flowering, the majority of assimilated ^{14}C which ended up in panicles at maturity was located in the husk plus rachis (60%) relative to the dehulled grain (40%). When only the sugar and starch fractions were considered, the loss of ^{14}C from the sheath, culm, and leaves and the increase of ^{14}C in panicles indicated that during the grain filling period, 68% of the stored carbohydrate was translocated to the grain, 20% was respired or lost to other tissues, and 12% remained in the straw. The carbohydrate that was retranslocated represented 26% of the grain yield or about 2 t of grain at a yield of 7.8 t ha^{-1}. These data were obtained from one variety (IR8) measured at one labelling time with inputs of 100 kg N ha^{-1}, hence updated measurements on current varieties as well as the New Plant Type at high N supply are a high priority.

Increasing the contribution of stem carbohydrate reserves to grain yield beyond 2.5 t ha^{-1} (14% moisture basis) seems possible but would require either (i) increased net assimilation rates in the vegetative period, (ii) changed partitioning of assimilates between leaves, roots, and stems, or (iii) a longer vegetative period. An increased CO_2 assimilation rate cannot be easily achieved without major genetic changes as the maximum rate is already achieved in well-managed crops (see below). An increased partitioning to the stems could be feasible as long as the crop could develop a maximum LAI at flowering of at least 6. The option of a longer vegetative period would possibly also lead to more stem reserves, but it would increase the total duration of the crop.

Increasing crop duration during the vegetative phase would allow greater carbon assimilation for stem reserves prior to flowering. This would also be at a time when total canopy leaf N and crop growth rates are at a maximum (see section below). Alternatively, if the crop duration has to be increased it might be more efficient to extend the grain-filling period. This is because in temperate locations where yield potentials approach 15 t ha^{-1} the grain-filling period is over 40 days (Kropff *et al.*, 1994b), and there is a substantial increase in stem carbohydrates which occurs in most varieties at maturity that might be utilised for grain filling (Figure 3). It is important to clarify that increases in grain-filling duration alone will not necessarily increase yield; this is demonstrated by comparing yield potential of rice in different temperate and tropical locations such as Australia, Japan, and the Philippines (Kropff *et al.*, 1994b). Measurements of environmental conditions, genotypic traits including crop growth rates throughout development, and the contribution of carbon and N from different tissues at high N supply will need to be evaluated in an integrated approach using modelling to evaluate these possibilities.

The importance of stem carbohydrates to grain yield increases greatly under conditions when photosynthesis during grain filling is limited due to low light (Soga and Nozaki, 1957; Wei *et al.*, 1982) or low nitrogen supply (Yoshida and Ahn, 1968). The latter is presumably related to the inverse relationship between N and carbohydrate concentrations in whole shoots; where N increased from 1 to 4% in whole shoot tissues, and starch decreased from 15 to 3% respectively (Batten and Blakeney, 1992). As suggested above, as N supply is maximised to support yields of 15 t ha^{-1} in future plant types, the preflowering carbohydrate reserves will likely reduce in importance. This means that the two key factors for carbon assimilation in future plant types will likely become rates of carbon assimilation during grain filling and the grain-filling duration.

Carbon assimilation during grain filling

The crop growth rate (CGR) requirements during grain filling can be simply calculated based on grain yields and the grain-filling duration. At yields of 10 t ha^{-1} (14% moisture content) and assuming a 25% contribution of storage-tissue reserves to grain yield (previous section), the remaining 7.5 t ha^{-1} of grain biomass would need to be produced during the 'effective (linear)' grain-filling period which is about 25 days for individual panicles in tropical ecosystems (Kropff *et al.*, 1994a). This means that the 6.45 t ha^{-1} of grain dry matter would require a net dry matter production rate of 258 kg ha^{-1} day^{-1}. This crop growth rate is not excessive since rice has maximum rates of dry matter production in the field of 300 to 360 kg ha^{-1} day^{-1} (Yoshida, 1983; Table 4), while other C-3 plants have maximum rates of 340-390 kg ha^{-1} day^{-1} (Table 4). Similar calculations for yields of 15 t ha^{-1} with 2.5 t ha from storage tissue reserves and a 25 day grain filling duration show that rates of dry matter production would have to increase to 430 kg ha^{-1} day^{-1}. This means that for yields of 15 t ha^{-1} there must be (i) increases in contributions from storage tissue reserves prior to flowering, (ii) increased rates of dry matter assimilation, or (iii) increases in grain-filling duration. The latter could be achieved by increasing grain-filling duration of individual panicles or by increasing the grain-filling duration of the entire crop via non synchronised panicle maturity.

The measured CGR in Table 4 may be underestimates of maximum CGR since none of the measurements account for root biomass which would be increasing up until about flowering, while the calculated rates of CGR from canopy CO_2 exchange rates for IR64 assume that there is no assimilation of organic or inorganic carbon by roots (Setter *et al.*, 1994). The maximum dry matter production for rice at high irradiance can be calculated from solar energy use efficiency as 450 kg ha^{-1} day^{-1} (Yoshida, 1983). These results suggest that if rice is able to maintain high

Table 4 Maximum crop growth rates (CGR) of rice relative to other plants.

Crop	CGR(kg ha^{-1} day^{-1})	Conditions	Reference
Rice			
7 varieties	210-286	field; Philippines and Japan	Yoshida and Cock (1971)
2 varieties	250-360	field; 40-60 DAS Thailand	Akiyama and Yingchol (1972)
18 varieties	229-358	field, Japan	Murata and Togari (1975)
3 varieties*	240-350	field at heading**; Philippines	Akita (1989)
3 varieties*	120-230	solution culture at heading**; Philippines	Akita (1989)
IR29723-143-3-2-1*	420-430	solution culture at 45-70 DAT; Philippines	Akita (1989)
IR64	100-380	field, Philippines; 30-105 DAS; calculated from canopy CO_2 exchange rates	Dingkhun *et al.* (1990); Schnier *et al.* (1990)
C-3 plants (including rice)	340-390	short term rates	review by Monteith (1978)
C-4 plants	510-540	short term rates	review by Monteith (1978)

*Varieties without droopy leaves; droopy leaf varieties had lower CGR rates
** approximately 85 DAT
DAS is days after sowing; DAT is days after transplanting

CGR during grain filling, a 15 t ha^{-1} grain yield could be possible but this would be the upper limit of yield potential as long as there was no carbon assimilation via roots.

The potential for maintaining high crop growth-rates during grain filling looks doubtful based on experimental evidence. There is a marked decrease in CGR for plants grown in the field from the peak of about 280-350 kg ha^{-1} day^{1} at maximum tillering to only 120 to 280 kg ha^{-1} day^{1} at flowering (Akita, 1989; Schnier *et al.*, 1990; Dingkuhn *et al.*, 1991). The explanation for this decrease is unknown but would likely be related to the loss of leaf N over this time from about 4 to 1.5% (Kropff *et al.*, 1993) that would at least partly be due to retranslocation of leaf N to the developing panicles. This loss in leaf N will have an adverse effect on CGR due to the proportional relationship between net CO_2 assimilation and leaf nitrogen (see previous section). During grain filling the CGR dropped even further to about 50 to 100 kg ha^{-1} day^{-1} at about half-way through the grain-filling period (Akita 1989; Schnier *et al.*, 1990; Dingkuhn *et al.*, 1991). These further reductions in CGR may be due to further reductions in leaf N as well as a reduced light interception by leaves in the canopy due to the absorbance of light by the developing panicles. The importance of maintaining high leaf N during the period from maximum tillering through to the mid grain filling period is discussed further below, while the possibility of improving leaf light interception, canopy photosynthesis, and tolerance to lodging during grain filling is considered in the following section.

Importance of panicle height in the canopy to leaf light interception, canopy photosynthesis, and resistance to lodging

One way to prioritize the long list of opportunities for future increases in yield potential (Table 3) is to visualise what the current semi-dwarf varieties or the present New Plant Type at 10 t ha^{-1} (Figure 2) would look like if the yield was increased by 50% or more. This clarifies two major problems that will occur with future increases in rice yield potential: (i) the majority of leaves that supply panicles with carbohydrates will be beneath the panicles and consequently at low irradiance, and (ii) plants will become very susceptible to lodging due to the high centre of gravity from panicles (Setter *et al.*, unpubl.). Both problems of light interception and lodging could be alleviated in a plant type which has a reduced panicle height in the canopy (Figure 4). This plant type would have advantages for its own sake in improving current semi-dwarf varieties in tropical as well as temperate ecosystems, in addition to enhancing future traits which would increase yield potential such as in the New Plant Type (see previous section).

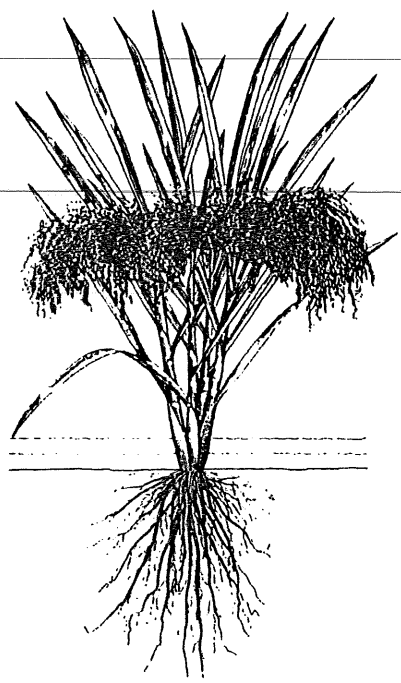

Figure 4 Drawing of a future possible rice plant type with lower panicle height in the canopy (Setter *et al.*, 1995). Plant type is based on a modified version of the New Plant Type (Figure 2) but with 50% greater yield; lower panicle heights are also applicable to current hihg-tillering semi-dwarf plant types (see text; reprinted with permission of the Australian Journal of Plant Physiology)

Based on the authors observations that panicle height in the canopy differs among varieties, the effect of panicle height on light interception by leaves was evaluated using the INTERCOM model; this is a detailed model for light competition between different plant species or tissues (IRRI, 1992; Kropff, 1993). In the 1991 wet season, the Panicle Area Index (PAI) reached values of 0.6 - 0.9 m^2 m^{-2} at a yield of about 6 t ha^{-1}, and the model predicted that panicles located in the top 10 cm of the canopy would reduce gross canopy photosynthesis by 25% at a LAI of 4. By contrast, when panicles are positioned 20 cm below the top of the flag leaves, simulations showed that gross canopy photosynthesis would be reduced by only 10% (Kropff *et al.*, 1993). These simulations were made assuming panicle photosynthesis was zero, hence experiments to evaluate the importance of panicle height on light interception and yield commenced.

In the 1994 dry season, panicle height measurements of four varieties with high yield potential (including IR72) ranged from 80 to 95% of canopy height at 14 DAF. Harvested panicle area index of IR72 and IR36 was 0.45 to 0.57 m^2 m^{-2} at a yield of about 7 t ha^{-1}, while the leaves above panicles intercepted only 4 to 12% incident radiation in these varieties at 14 DAF (Setter *et al.*, 1995). Under these conditions the potential impact of lowering panicle height in the canopy on net canopy photosynthesis was evaluated by panicle removal. When panicles were removed, the irradiance at the bottom of the panicle layer of the canopy increased by 52 to 80% in IR36 and IR72 respectively. At 11 DAF, net canopy photosynthesis of these two varieties similarly increased by 42 to 52% following removal of panicles. Increases in net canopy photosynthesis were presumably mainly due to increased light interception by leaves within the canopy since there were little or no changes in canopy dark respiration and there were no significant changes in net photosynthesis rates of single leaves at the same irradiance following panicle removal (Setter *et al.*, 1995).

The impact of panicle height in the canopy and the effect of different panicle area was simulated using the INTERCOM model with light extinction coefficients calculated from experimental measurements and assuming (i) panicles had a photosynthesis rate of 30% of flag leaves on a ground area basis (Imaizumi *et al.*, 1990; Setter *et al.*, unpubl.) and (ii) gross canopy photosynthesis was 100% at the normal panicle height which was about 90% of canopy height (Figure 5). These simulations showed that at a PAI = 1.0 (equivalent to a yield of 6.5 t ha^{-1} for IR72; calculated from Setter *et al.*, 1996), gross canopy photosynthesis would be increased more than 25% if panicles were lowered to 40% of canopy height.

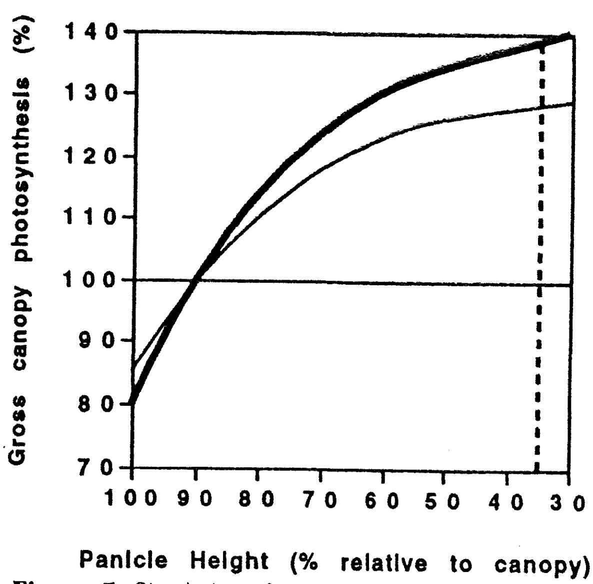

Figure 5 Simulation of canopy gross photosynthesis at different panicle heights and two levels of panicle area index (PAI). Panicle photosynthesis is assumed equivalent to 30% of leaf photosynthesis on an area basis. Simulations are made using the INTERCOM model (Kropff, 1993) using data of Setter *et al.* (unpubl.) for IR72 at PAI = 1.0 (thin lines) or 1.5 (wide lines). Vertical dashed line indicates minimum feasible peduncle height to keep panicles above water

Simulations at PAI = 1.5 indicated that canopy photosynthesis would increase by up to 40% by lowering panicles to 40% of the canopy height (Figure 5). Other simulations showed that there were relatively small effects of 50 *versus* 0% panicle photosynthesis relative to flag leaf photosynthesis, and these effects diminished at higher panicle heights in the canopy (Setter *et al.*, unpubl.). An important factor in the relationship between gross canopy photosynthesis and panicle height shown in Figure 5 is that current genotypes like IR72 have panicles at about 90% of canopy height. This is on the steepest part of the curve where, at PAI=1.0, about 1.5% gain in gross canopy photosynthesis will be achieved for each centimetre that panicles are lowered.

In the field with 15 cm water-depth and 20 cm-long panicles, the minimum feasible height of the peduncle above ground would be more like 35-40 cm to keep panicles above water. Hence future plant types should ideally have panicles at about half the height of most modern semi-dwarf varieties as shown in Figure 4. Such low panicle heights may also need to be balanced with other considerations of suitable flag leaf lengths and particularly the optimum LAI above panicles. Recent research has supported the importance of reduced panicle height to increased light interception and canopy photosynthesis as well as increased yield; these results were obtained using isogenic lines differing in panicle height (Setter *et al.*, 1996) and hormone treatments to specifically manipulate panicle height in the canopy within single genotypes.

An equally important benefit of lowering panicle height in the canopy is an increased resistance to lodging due to a lower centre of gravity. Lodging is controlled by two factors, height and strength per unit culm (Yoshida, 1976; Setter *et al.*, 1994). Lodging already limits yields even at 10 t ha^{-1} yield-potential (authors observations) and is a major constraint to maintaining optimum N supply particularly in typhoon-prone environments which are common in the tropics. Although lodging is currently not evaluated in any published model for rice yield potential, this can be estimated assuming constant culm strength based on the rotational inertia equation (Weber *et al.*, 1965),

$$I = mr^2, \text{ where}$$

I= inertia, m= biomass, and r = height of the biomass above ground. For variable mass along a radius this can be calculated as:

$$\Sigma I = m_1 r_1^2 + m_2 r_2^2 + m_3 r_3^2 \ldots m_n r_n^2.$$

There is no published data on biomass distribution in rice during grain filling so this was determined from a currently used semi-dwarf variety (IR74) grown during the 1994 dry season. The importance of lowering the panicle on ΣI is exemplified in Table 5 where shoot and panicle biomass is given over 10-cm intervals from the ground to the top of the canopy. Shoots of IR74 without panicles have a ΣI = 8.8 while shoots with panicles have a ΣI = 24.8 (Setter and Laureles, unpubl.). This ΣI increases to 32.8 with a 50% increase in grain yield per plant at equal (shoot less panicles) biomass (Table 5). Such values are difficult to relate to lodging tendency since there is no published relationship for these measurements. Further calculations help clarify the significance of these increases in ΣI. By lowering the panicle mass given in Table 5 in each level by 10 cm, a new ΣI can be calculated. Additional calculations with 20, 30, and 40 cm panicle-height reductions and at 100 or 150% yield, can then be used to determine the 2nd order polynomial relationship at each yield level as shown in Figure 6. Now it can be calculated that the increase in lodging susceptibility that would occur at a 150% yield level (Table 5) can be completely eliminated, i.e., ΣI reduced to 24.8 by lowering the mean panicle height biomass from 65 to 52 cm or less (calculated using equation in Figure 6).

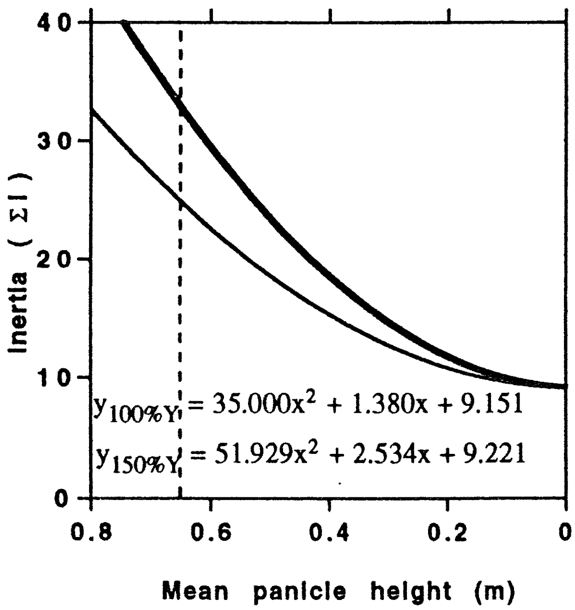

Figure 6 Relationship between the rotational inertia (ΣI; g-m^2) as an estimate of susceptibility for lodging and the mean panicle height in the canopy. Calculations for inertia at the mean panicle height of 0.65 m (vertical dashed line) are from weight distribution of the shoot at 20 DAF using values in Table 6. For other points on the curves, inertia was calculated as described in the text at 100% yield (thin line) or 150% yield (thick line)

Table 5 Biomass distribution (g fresh weight plant^{-1} ± SEM) of rice at different heights and estimate of susceptibility to lodging by calculation of rotational inertia (ΣI; g-m^2; see text). Data are for IR74 grown in the 1994 dry season at IRRI (Setter and Laureles, unpubl.); values in parentheses denote per cent weight of panicles in different layers. Predicted values for biomass and (ΣI) are also given for 150% yield; effects of different panicle heights and yield are given in Figure 6

	100% yield			150% yield
Layer (m above ground)	Shoots (less panicles)	Panicles	Shoots with panicles	Shoots with panicles
0.0-0.1	44.0±4.9	0.0	44.0±4.9	44.0
0.1-0.2	27.2±2.6	0.0	27.2±2.6	27.2
0.2-0.3	16.9±1.2	0.0	16.9±1.2	16.9
0.3-0.4	12.1±0.9	0.0	12.1±0.9	12.1
0.4-0.5	8.8±0.6	0.2±0.1 (1)	9.0±0.2	9.1
0.5-0.6	4.1±0.4	5.3±0.5 (15)	9.4±0.4	12.1
0.6-0.7	2.1±0.2	16.2±0.4 (47)	18.3±0.3	26.4
0.7-0.8	2.7±3.3	11.0±0.9 (32)	13.7±2.8	19.2
0.8-0.9	0.2±0.1	1.8±0.8(5)	2.0±0.9	2.9
0.9-1.0	0	0	0	0
Total biomass	118.1	34.5	152.6	169.9
ΣI (gm^2)	8.83	-	24.84	32.81

As with gross canopy photosynthesis, the height of panicles in the canopy of most current semi-dwarf cultivars is at the sharpest point of the curve in relation to ΣI (dashed line in Figure 6), i.e., there is the greatest potential for improving current cultivars. Further measurements of ΣI and effects of culm strength will need to be obtained throughout the grain- filling duration for different cultivars, and these values will need to be related to actual measurements of susceptibility to lodging in the field.

Reduced panicle height provides a simple selection criteria for breeding programmes in future, and at least some high-yielding genotypes may already incorporate low panicle height in the canopy as a factor contributing to their high yield potential (own observations). Nevertheless, there are several concerns for lowering panicle height in some situations due to increased susceptibility to flooding or high water levels, diseases, and rat damage. Plant types with low panicle heights may therefore have the greatest impact on irrigated rice in high-yielding environments with high inputs such as in Australia, China, Japan, and U.S.A.

Prolonged grain filling and green leaf area duration

Assuming that the contribution of stem reserves is 2.5 t ha^{-1}, and that the average crop-growth-rate is the same as in the effective grain-filling period of a 10 t ha^{-1} crop (258 kg dry matter ha^{-1} day^{-1}), it can be calculated that for a 15 t ha^{-1} grain yield the effective grain-filling period has to increase from 25 to 42 days. Similar results were obtained by the rice growth simulation model ORYZA1, which simulated an increase in grain yield from 9.3 to 14.7 t ha^{-1} with a grain-filling duration of 40 days (Kropff *et al.*, 1994a). The key assumption in these calculations is that a green leaf canopy remains active during the grain-filling period. Analysis of experimental data from temperate environments where 15 t ha^{-1} was achieved (Yanco, Australia) using simulation models, indeed showed that the higher yields were obtained as a result of environmental conditions which gave a longer grain filling duration and longer spikelet formation period (to develop a larger sink size) in combination with a high daily growth rate (Kropff *et al.*, 1994b).

Increased 'stay green' has been one of the major achievements of breeders in the past decades for several crops (Evans, 1990). In wheat, yields in Europe have increased as a result of delayed senescence which was achieved by late fertilizer-N application, and by improved crop protection against ripening diseases (Spiertz and Vos, 1985). It has been shown that increased late season N application to wheat increased concentrations of ribulose bisphosphate (RuBP) carboxylase possibly by reductions in enzyme catabolism (Wuest and Cassman, 1992). In rice, RuBP carboxylase typically represents about 30% of total leaf N (Makino *et al.*, 1984). As leaves become senescent, RuBP carboxylase levels decrease which results in a decrease in assimilation rate (Makino *et al.*, 1985). For yield levels beyond 10 t ha^{-1}, sustained carbon assimilation is needed during grain filling, and to sustain growth during grain filling, a high N content in the leaves therefore has to be maintained.

The key questions to be answered about a longer grain-filling duration are whether genetic variability exists in the length of the grain-filling period, and whether leaf senescence can be delayed for substantial periods. Senadhira and Li (1989) reported a large genetic variation in the grain-filling period of 16 to 40 days in 21 rice varieties at IRRI's experimental farm during the 1987 dry season. The relevance of these data is unclear since only main stem panicles were monitored and plants were grown at wide hill spacings and only 60 kg N ha^{-1}. In recent work at IRRI, a similar variation in grain-fill duration of mainstem panicles was found, but there was little variation in the grain-filling duration of the whole crop (Kropff and Dionora, unpubl. data).

Concluding Remarks

The most important cereal crops in developing countries are rice, wheat, and maize which in 1992 accounted for 47, 23, and 19% respectively of the total production in these countries (FAO, 1993). Over the last 25 years rice production has increased at 3% per year and this has met the population demand for rice in Asia; nearly 60% of that growth came from increases in crop yields (Hossain, 1994). Over the next 20-30 years farmers, policymakers, and scientists will be challenged to provide food at affordable prices for almost 100 million more people every year. Furthermore they will have to increase food production from more productive use of the land without further degradation of natural resources since increases in land area sown to crops is no longer a feasible option in most of the world (Pinstrup-Andersen, 1994). Some of the different approaches to present and future research on rice yield potential examined here indicate that opportunities for further yield increases in irrigated rice are strong.

While this review has focussed on opportunities for increasing yield potential of irrigated rice under high-yielding environments, much of this research is also relevant to rice grown in other ecosystems such as uplands, lowlands, or flood-prone areas. Rice yields are disappointingly low in these unfavourable rice-growing environments, typically ranging from less than 1 to about 4 t ha^{-1} due to biotic and abiotic stresses; and further research will need to focus on priorities for yield potential increases in these rice ecosystems (Hossain, 1994).

From the above information it appears that the main constraint to increased yield potential of irrigated rice is the ability to sustain the maximum dry matter accumulation rate of about 300 kg ha^{-1} day^{-1} (Table 4) between maximum tillering and mid grain-filling. An alternative view is to try and increase the maximum rates of dry matter accumulation. Earlier attempts to achieve greater maximum growth rates were unsuccessful (Gifford *et al.*, 1984). Furthermore, Evans (1990) concluded that superiority of high yielding varieties was usually associated with the duration of photosynthesis rather than its maximum rate. Small yield gains may be possible from increased storage and remobilization of carbohydrate reserves from storage tissues and a further increase in HI. Whether an increase in sink size alone will lead to an increase in yield potential remains an issue, but the existing evidence suggests it will not for the majority of rice varieties (Kropff *et al.*, 1994a), particularly in times or locations where irradiance is low during the grain filling period, e.g., the wet season in many countries.

It is useful to focus on the basic parameters that must be modified to achieve a major increase in yield potential of rice grown in tropical environments. These fundamental parameters are: (i) increased sink size, i.e., spikelets m^{-2}, (ii) a longer vegetative period for increasing stem reserves or a longer grain filling duration with a matching increase in duration of green leaf area and canopy photosynthesis, and (iii) potential for increased carbon assimilation of the crop canopy through such possibilities as increasing light interception and lodging tolerance via lowering panicle height in the canopy, increasing or maintaining maximum photosynthetic carbon assimilation, or possibly enhancing utilisation of soil organic and inorganic carbon via roots (Kropff *et al.*, 1994a; Peng *et al.*, 1994; Setter *et al.*, 1994).

Acknowledgments

The authors own unpublished data and the following researchers for use of unpublished data: E. A. Conocono, J. Dionora, J. A. Egdane, E. V. Laureles, R. Laza, D. Reano, and R. Visperas; Mr. J. Lazaro for artwork of plant types. Mr. J. Egdane and Ms. E. Fabian and E. Conocono for technical assistance in revising the manuscript.

References

Akita, S. (1989) Improving yield potential in tropical rice, in: *Progress in Irrigated Rice Research*, Proc. Intl. Rice Res. Conf. 21-25 Sept. 1987, Hangzhou, China

Akiyama, T. and Yingchol, P. (1972) Studies on response to nitrogen of rice plant as affected by difference in plant type between Thai native and improved varieties, *Proc. Crop Sci. Soc. Japan* 41 126-132

Austin, R.B., Bingham, J., Blackwell, R. D., Evans, L.T., Ford, M. A., Morgan, C.L. and Taylor, M. (1980) Genetic improvements in winter wheat yields since 1990 and associated physiological changes, *J. Agric. Sci. (Cambr.)* 94 675-689

Baba, I. (1954) Breeding of rice variety suitable for heavy manuring. Absorption and assimilation of nutrients and its relation to adaptability for heavy manuring and yield in rice variety, in: *Studies on Rice Breeding*, Society of Breeding, Faculty of Agriculture, Tokyo University, Tokyo, Vol 4, 167-184

Baba, I. (1961) Mechanism of response to heavy manuring in rice varieties, *Intl. Rice Communication Newsl.* 10 9-16

Batten, G.D. and Blakeney, A.B. (1992) Using NIR to monitor crop energy reserves, in: *Making Light Work: Advances in Near Infrared Spectroscopy*, (eds Murray, I. and Cowe, I.A.), VCH, Weinheim, pp. 303-308

Bennett, J., Brar, D.S., Khush, G.S., Huang, N. and Setter, T.L. (1994) Molecular approaches to yield potential, in: *Breaking the Yield Barrier: Proc. of a Workshop on Rice Yield Potential in Favorable Environments*, (ed. Cassman, K.G.), IRRI, Los Baños, Philippines, Ch. 5

Cassman, K.G. (1994) Report of Working Group, in: *Breaking the Yield Barrier: Proc. of a Workshop on Rice Yield Potential in Favorable Environments*, (ed. Cassman, K. G.), IRRI, Los Baños, Philippines

Cassman, K.G., De Datta, S.K., Olk, D.C., Alcantara, J., Samson, M., Descalsota, J. and Dizon, M. (1994) Yield decline and the nitrogen economy of long-term experiments on continuous, irrigated rice systems in the tropics, *Advances in Soil Science* (in press)

Chandler, R.F. Jr. (1969) Plant morphology and stand geometry in relation to nitrogen, in: *Physiological Aspects of Crop Yield*, (ed. Eastin, J.D.), ASA, Madison, Wisconsin, pp. 265-285

Chandler, R.F. Jr. (1972) The impact of the improved tropical plant type on rice yields in South and Southeast Asia, in: *Rice Breeding*, IRRI, Los Baños, Philippines, pp. 77-85

Chandler, R.F. Jr. (1992) *An Adventure in Applied Science: A History of the Intl. Rice Res. Institute*, IRRI, Los Baños, Philippines, pp. 240

Cock, J.H. and Yoshida, S. (1972) Accumulation of ^{14}C-labelled carbohydrate before flowering and the subsequent redistribution and respiration of the rice plant, *Proc. Crop Sci. Soc. Japan* 41 226-234

Coombs, J., Hall, D.O., Long, S.P. and Scurlock, J.M.O. (1985) *Techniques in Bioproductivity and Photosynthesis*, 2nd edn, Pergamon Press, Oxford, New York, Toronto, pp. 298

De Datta, S.K., Tauro, A.C. and Balaoing, S.N. (1968) Effect of plant type and nitrogen level on the growth characteristics and grain yield of indica rice in the tropics, *Agronomy J.* 60 643-647

Dingkuhn, M., Penning de Vries, F.W.T., De Datta, S.K. and van Laar, H.H. (1991) Concepts for a new plant type for direct seeded flooded tropical rice, in: *Direct Seeded Flooded Rice in the Tropics*, IRRI, Los Baños, Philippines, pp. 17-38

Evans, L.T. (1990) Raising the ceiling to yield: The key role of synergisms between agronomy and plant breeding, in: *New Frontiers in Rice Research*, Directorate of Rice Research, Hyderabad, (ed. Muralidharan, K. and Siddiq, E.A.), India, pp.103-107

FAO (1993) *The State of Food and Agriculture 1993*, Food and Agriculture Organization of the United Nations, Rome, 1993, FAO Agriculture Series No. 26

Fischer, R.A. (1983) Wheat, in: *Potential Productivity of Field Crops Under Different Environments*, IRRI, Los Baños, Philippines, pp. 129-154

Gifford, R.M., Thorne, J.H., Hitz, W.D. and Giaquinta, R.T. (1984) Crop productivity and photoassimilate partitioning, *Science* 225 801-808

Glaszmann, J.C. (1987) Isozymes and classification of Asian rice varieties, *Theor. Appl. Genet.* 74 21-30

Hossain, M. (1994) Recent development in Asian rice economy: challenges for rice research, in: *Workshop on Rice Research Prioritization in Asia*, 15-22 Feb., 1994, IRRI, Los Baños, Philippines, p. 34

Huang, C.H., Chang, W.L. and Chang, T.T. (1972) Ponlai varieties and Taichung Native 1, in: *Rice Breeding*, IRRI, Los Baños, Philippines, pp. 31-46

Imaizumi, N., Usuda, H., Nakamoto, H. and Ishihara, K. (1990) Changes in the rate of photosynthesis during grain filling and the enzymatic activities associated with the photosynthetic carbon metabolism of rice panicles, *Plant and Cell Physiology* 31 835-843

IFPRI (1977) *Food Needs of Developing Countries: Projections of Production and Consumption to 1993*, International Food Policy Research Institute, Washington, D.C. Dec., 1977, Research Report 3, p. 157

IRRI (1989a) *IRRI towards 2000 and Beyond*, IRRI, Los Baños, Philippines, p. 66

IRRI (1989b) *Implementing the Strategy: Work Plan for 1990-1994*, IRRI, Los Baños, Philippines, p. 93

IRRI (1992) *Program Report for 1992*, IRRI, Los Baños, Philippines, p. 169

Ise, K. (1992) Inheritance of a low-tillering plant type in rice, *Intl. Rice Res. Newsl.* 17 (4) 5-6

Janoria, M.P. (1989) A basic plant ideotype for rice, *Intl. Rice Res. Newsl.* 14(3)12-13

Katayama, T.C. and Nakagahra, M. (1993) Morphological and taxonomic characters of cultivated rice (*O. sativa* L.) I. Taxonomical and morphological characters of cultivars and breeding strains, Ch. 2, in: *Science of the Rice Plant, Morphology*, (eds Matsumo, T. and Hoshikawa, K.), Food and Agriculture Policy Research Centre, Tokyo, Vol.1 pp. 35-66

Khush, G.S. (1989) Multiple disease and insect resistance for increased yield stability in rice, in: *Progress in Irrigated Rice Research*, IRRI, Los Baños, Philippines

Khush, G.S. (1990) Varietal needs for different environments and breeding strategies, in: *New Frontiers in Rice Research*, (eds Muralidharan, K. and Siddiq, E.A.), Directorate of Rice Research, Hyderabad, India, pp. 68-75

Khush, G.S. and Aquino, R. (1994) Breeding tropical japonica for hybrid rice production, in: *Hybrid Rice II.*, IRRI, Los Baños, Philippines (in press)

Kropff, M.J. (1993) Mechanisms of competition for light, in: *Modeling Crop-Weed Interactions*, (eds Kropff, M. J. and van Laar, H.H.), CAB-IRRI, Ch. 4, pp. 33-61

Kropff M.J., Cassman, K.G. and van Laar, H.H. (1993) Quantitative understanding of the irrigated rice ecosystem to increase its yield plateau, in: *Proc. of the 1992 Intl. Rice Res. Conf.*, IRRI, Los Baños, Phillipines, (in press)

Kropff, M.J., Cassman, K.G., Peng, S., Matthews, R.B. and Setter, T.L. (1994a) Quantitative understanding of rice yield potential, in: *Breaking the Yield Barrier: Proc. of a Workshop on Rice Yield Potential in Favorable Environments*, (ed. Cassman, K.G.), IRRI, Los Baños, Philippines, Ch.3

Kropff, M.J., Williams, R.L., Horie, T., Angus, J.F., Singh, U., Centeno, H.G. and Cassman, K.G. (1994b) Predicting yield potential of rice in different environments, in: *Temperate Rice - Achievements and Potential*, Yanco Agricultural Research Institute, NSW, Australia, 21-24 February, 1994

Makino, A., Mae, T. and Ohira, K. (1984) Relation between nitrogen and ribulose-1,5-biphosphate carboxylase in rice leaves from emergence through senescence, *Plant and Cell* 25 429-437

Makino, A., Mae, T. and Ohira, K. (1985) Photosynthesis and ribulose-1,5-biphosphate carboxylase in rice leaves from emergence through senescence, Quantitative analysis by carboxylation/oxygenation and regeneration of ribulose-1,5-biphosphate carboxylase, *Planta* 166 414-420

Mew, T. (1991) Disease management in rice, in: *CRC Handbook of Pest Management in Agriculture*, (ed. Pimentel, D.), 2nd edn, CRC Press Inc., Boston, Vol. III, pp. 279-299

Monteith, J.L. (1978) Reassessment of maximum growth rates for C3 and C4 crops, *Experimental Agric.* 14 1-5

Murata, Y. (1961) Studies on the photosynthesis of rice plants and its cultural significance, *Bull. Nat. Inst. Agr. Sci. Jap. Ser.* D, 9 1-169

Murata, Y. and Togari, Y. (1975) Summary of data, in: *Crop Productivity and Solar Energy Utilisation in Various Climates in Japan*, Japanese Committee for the International Biological Program. (ed. Murata, Y.), 1975, Tokyo, JIBP Volume 11, pp. 9-19

Murayama, N. (1979) The importance of nitrogen for rice production, in: *Nitrogen and Rice*, IRRI, Los Baños, Philippines, pp. 5-23

Parthasarathy, N. (1972) Rice breeding in tropical Asia up to 1960, in: *Rice Breeding*, IRRI, Los Baños, Philippines, pp. 5-29

Peng, S., Khush, G.S. and Cassman, K.G. (1994) Evolution of the new plant ideotype for increased yield potential, in: *Breaking the Yield Barrier: Proc. of a Workshop on Rice Yield Potential in Favorable Environments*, (ed. Cassman, K. G.), IRRI, Los Baños, Philippines, Ch.2

Penning de Vries, F.W.T. (1991) Improving yields: designing and testing VHYVs, in: *Systems Simulation at IRRI*, (ed. Penning de Vries, F.W. T. *et al.*), IRRI, Los Baños, Philippines, IRRI Res. Paper 151, pp.13-19

Pinstrup-Andersen, P. (1994) *World Food Trends and Future Food Security*, The International Food Policy Research Institute (IFPRI), Washington, D.C. March, 1994 Food Policy Report, pp. 25

Plucknett, D.L., Smith, N.J.H., Williams, J.T. and Anishetty, N. M. (1987) A case study in rice germplasm: IR36, in: *Gene Banks and the World's Food*, Ch. 9, Princeton University Press, N.J., pp. 171-185

Richards, R.A. (1988) A tiller inhibitor gene in wheat and its effect on plant growth, *Australian J. of Agric. Res.* 39 749-57

Schnier, H.F., Dingkuhn, M., De Datta, S.K., Mewngel, K. and Faronilo, J.E. (1990) Nitrogen fertilization of direct-seeded flooded vs. transplanted rice: I. Nitrogen uptake, photosynthesis, growth and yield, *Crop Science* 30, 1276-1284

Senadhira, D. and Li, G. F. (1989) Variability in rice grain filling duration. *Intl. Rice Res. Newsl.* 14 (1) 8-9

Setter, T.L., Peng, S., Kirk, G.J.D., Virmani, S.S., Kropff, M.J. and Cassman, K.G. (1994) Physiological considerations and heterosis to increase yield potential, in: *Breaking the Yield Barrier: Proc. of a Workshop on Rice Yield Potential in Favorable Environments*, (ed. Cassman, K. G.), IRRI, Los Baños, Philippines, Ch.4

Setter, T.L., Conocono, E.A., Egdane, J.A. and Kropff, M.J. (1995). Possibility of increasing yield potential of rice by reducing panicle height in the canopy. I. Effects of panicles on light interception and canopy photosynthesis. *Aust. J. Plant Physiol.* 22 441-451 (and corrigendum p. 711)

Setter, T.L., Conocono, E.A. and Egdane, J.A. (1996). Possibility of increasing yield potential of rice by reducing panicle height in the canopy. II. Canopy photosynthesis and yield of isogenic lines. *Aust. J. Plant Physiol.* (in Press)

Shen, J.H. (1980) Rice breeding in China, in: *Rice Breeding*, IRRI, Los Baños, Philippines, pp. 9-30

Soga, Y. and Nozaki, M. (1957) Studies on the relation between seasonal changes of carbohydrates accumulated and the ripening at the stage of generative growth in rice plant, *Proc. of the Crop Sci. Soc. of Japan* 26 105-108

Spiertz, J.H.J. and Vos, J. (1985) Grain growth of wheat and its limitation by carbohydrate and nitrogen supply, in: *Wheat Growth and Modelling*, (ed. Day, W and Atkin, R. K.), NATO ASI Series, Series A: Life Sciences, Plenum Press, New York, Vol 86 pp. 129-141

Takeda, T. (1961) Studies on the photosynthesis and production of dry matter in the community of rice plants, *Japanese J. Bot.* 17 403-437

Takeda, T. (1984) Physiological and ecological characteristics of high yielding varieties of lowland rice, in: *Proc. Intl. Crop Sci. Symp.* Oct. 17-20, Fukuoka, Japan

Tanaka, T. (1976) Regulation of plant type and carbon assimilation of rice, *JARQ* 10 (4) 161-167

Tanaka, A., Kawano, K. and Yamaguchi, J. (1966) Photosynthesis, respiration, and plant type of the tropical rice plant, *Intl. Rice Res. Inst. Tech. Bull.* No. 7

Toenniessen, G.H. (1991) Potentially useful genes for rice genetic engineering, in: *Rice Biotechnology*, (eds Khush, G. S. and Toenniessen, G. H.), pp. 253-280

Tsuno, Y., Inaba, N. and Shimizu, T. (1959) Studies on yield-forecast in main crops, V. The effect of light receiving condition and nitrogen content in a plant on the dry matter production of rice plants, *Proc. Crop Sci. Soc. (Japan)* 28 188-190

Tsunoda, S. (1959a) A developmental analysis of yielding ability in varieties of field crops. I. Leaf area per plant and leaf area ratio, *Japanese J. Breed.* 9 161-168

Tsunoda, S. (1959b) A developmental analysis of yielding ability in varieties of field crops. II. The assimilation-system of plants as affected by the form, direction and arrangement of single leaves, *Japanese J. Breed.* 9 237-244

Tsunoda, S. (1960) A developmental analysis of yielding ability in varieties of field crops. III. The depth of green color and the nitrogen content of leaves, *Japanese J. Breed.* 10 107-111.

Tsunoda, S. (1962) A developmental analysis of yielding ability in varieties of field crops. IV. Quantitative and spatial development of the stem-system, *Japanese J. Breed.* 12 49-55

Vergara, B.S. (1988) Raising the yield potential of rice, *Philipp. Tech. J.* 13 3-9

Vergara, B.S. and Visperas, R. M. (1977) *Harvest Index: Criterion for Selecting Rice Plants with High Yielding Ability*, 10 Sept. IRRI Saturday Seminar, IRRI, Los Baños, Philippines

Vergara, B.S., Tanaka, A., Lilis, R. and Puranabhavung, S. (1966) Relationship between growth duration and grain yield of rice plants, *Soil Sci. Plant Nutr.* 12 31-39

Weber, R.L., Manning, K. V. and White, M. W. (1965) *College Physics*, McGrath-Hill Book Co., New York, London, Toronto. 4th edn., 710 pp.

Wei, M-L., Shen, M. C., Chen, C-S. and Liu, D-J. (1982) Physiological studies of rice tillers. I. Partition of dry matter, nitrogen and total non structural carbohydrates during grain filling *Proc. Natl. Sci. Counc. ROC (A)* 6 190-196

Wuest, S.B. and Cassman, K.G. (1992) Fertilizer-N use efficiency of irrigated wheat. II. Partitioning efficiency of preplant versus late-season applied N, *Agron. J.* 84 689-694

Yoshida, S. (1972) Physiological aspects of grain yield, *Ann. Rev. Plant Pysiol.* 23 437-464

Yoshida, S. (1976) Physiological consequences of altering plant type and maturity, in: *Proc. of the Intl. Rice Res. Conf.*, IRRI, Los Baños, Philippines

Yoshida, S. (1981) *Fundamentals of Rice Crop Science*, IRRI, Los Baños, Philippines, pp. 269

Yoshida, S. (1983) Rice, in: *Potential Productivity of Field Crops under Different Environments*. IRRI, Los Baños, Philippines, pp. 103-127

Yoshida, S. and Ahn, S.B. (1968) The accumulation process of carbohydrate in rice varieties in relation to their response to nitrogen in the tropics, *Soil Sci. and Plant Nutrition* 15 183-186

Yoshida, S. and Cock, J. H. (1971) Growth performance of an improved rice variety in the tropics, *Intl. Rice Commun. Newsl.* 20 1-15

Yoshida, S. and Coronel, V. (1976) Nitrogen nutrition, leaf resistance, and leaf photosynthetic rate of the rice plant, *Soil Sci. Plant Nutr.* 22(2) 207-211