GROWTH AND ASSIMILATE PARTITIONING IN RICE CULTIVARS OF DIFFERENT MATURITY GROUPS

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INTRODUCTION

The growth duration of a rice cultivar is highly specific to location and season. In photoperiod-insensitive cultivars it is strongly affected by air temperature. Very-short-season cultivars have been important in US rice production for many years. Those cultivars fit into intensified cropping systems, provide a second (ratoon) crop if the crop season is long enough, lower irrigation cost, and have high water use efficiency. They also give flexibility to seeding dates, avoiding low temperature damage at the beginning or the end of the season, and result in high production per day and in high harvest index.

The increase in total dry matter during grain filling usually shows close correlation with grain yield. At anthesis and grain filling, crop growth rate is generally higher in short-season cultivars, and if it is high enough, it may compensate for a short growth duration. Traits related to sink size have moderately high heritability and can be modified by genetic manipulation. Sink size may have an important effect on short-season cultivars, affecting their high growth rates during grain filling.

Carbohydrate storage contributes 20 to 40% of grain carbohydrates, acting as a buffer to prevent grain abortion during periods of cloudy weather and high sink demand. Preheading storage is higher with a long-season cultivar, while short-season cultivars produce a great amount of carbohydrates during their flowering and ripening phases. The amount of carbohydrates translocated to the grain was reported to be lower in the short-season cultivars, resulting in higher growth efficiency during grain filling. However, preheading storage is believed to play an important role in yield for modern cultivars.

Transplanting, or seeding at wide spacings, where tillering is critical, may affect very-short-season cultivars, and their yield has been considered to be limited in tropical environments. A vegetative growth duration of 45 days, or total growth duration of 90 to 100 days, is not limiting for high yield in some modern rice cultivars, if the cultural practices are properly timed. We may have approached the limit, and further attempts to shorten growth duration may reduce yield potential.

With the advent of some new very-short-season breeding lines and cultivars in the Arkansas breeding program, there is a need for more information about the yield physiology of this material. It is necessary to determine if yield potential is reduced and, if so, which yield components are affected, and to establish differences in assimilate storage and partitioning. The understanding of these relationships is important in setting breeding objectives.

The purpose of this work was to compare phenology, growth, assimilate partitioning, and yield components of some US rice cultivars, from extremely-short- to long-season (from 90 to 145 days to maturity), under two seeding dates.

The objectives of the research were 1) to determine the phenology of the cultivars; 2) to analyze growth and dry matter partitioning, using growth analysis techniques for the calculation of growth rates, net assimilation rate, and leaf area index; 3) to study total nonstructural carbohydrate storage and partitioning in vegetative organs; and 4) to determine yield and yield components.

CHAPTER I

LITERATURE REVIEW

A.- GROWTH AND GROWTH PHASES OF RICE PLANTS

Growth includes dry matter production (quantitative aspect) and phasal development during ontogenesis (qualitative aspect). The ontogenesis of the rice plant is generally considered to consist of three phases, vegetative, reproductive, and ripening or grain filling (Tanaka, 1976). The vegetative phase is from germination to the panicle-primordia initiation stage and the reproductive phase is from panicle initiation to the end of flowering.

Tanaka (1976) classified rice growth curves into several types. Type I has a vigorous growth at early stages followed by a weak growth at later stages and, sometimes, a decrease of weight. This type is observed in traditional, tall cultivars and is associated with a large total dry matter production, small harvest index, and low grain yield. Type II, considered to be normal, has a continuous moderate growth rate followed by a slight decrease at the end. It is generally associated with a moderate total dry matter production, large harvest index, and good grain yield. Type III, with a slow growth at early stages, followed by a high growth rate until maturity, is frequently observed where the temperature is low in spring. Total dry matter production is small, and yield is moderate to low, depending on harvest index. Type V has moderate or high growth rate during early stages, followed by a high growth rate during later stages. It is possible only with abundant solar radiation and good plant type. Yield may be extremely high due to large values of total dry matter production and harvest index.

Tanaka (1976) also classified three types of growth patterns from the standpoint of phasal development. In Type A (vegetative phase-reproductive phase) the panicle is initiated soon after the maximum tiller number stage, considered to be normal. The growth curve is generally Type II or V. In Type B (vegetative phase-reproductive phase overlapped with vegetative phase), tillering continues after the panicle initiation and may be caused by low temperatures, excess nitrogen, or the use of very short-season cultivars. Number of spikelets per panicle is small because of the competition between the panicle and the newly developing tillers after panicle initiation and is frequently associated with the growth curve of Type III and low grain yields. In Type C (vegetative phase-vegetative lag phase-reproductive phase) tillering discontinues long before the panicle initiation stage. This type occurs when the vegetative phase is extremely long, the number of panicles per unit of field area tends to be small due to a high percentage of ineffective tillers, the number of spikelets is frequently small due to insufficient supply of nitrogen during the reproductive phase, and the grain yield is often low. The growth curve is generally Type I.

Types II and V curves indicate a good balance between vegetative growth and reproductive growth, Type I curve shows an excessive vegetative growth, and the Type III curve indicates a weak vegetative growth relative to reproductive growth (Tanaka, 1976).

Mean crop growth rates (CGR), obtained by dividing total dry matter production by the number of days from transplanting to maturity, are reported to be as high as 14.08 g m^{-2} s^{-1} in Japan (Murata, 1976). Long-term CGR of an erect-leaved cultivar, such as 'IR8', can reach 22.9 g m^{-2} day^{-1} (160 g of carbohydrates m^{-2} $week^{-1}$). Maximum short-term CGR recorded for rice is reported to be 36 g m^{-2} day^{-1} (Yoshida, 1981). Dry matter production is generally higher in the late-maturing cultivars than in the early-maturing ones, while the situation is the reverse as to mean CGR (Murata, 1976).

The total leaf area or leaf area index (LAI) increases rapidly for some time after the maximum tiller number stage, but the rate of increase becomes smaller until the plant attains its maximum leaf area at around heading time. Leaf area decreases thereafter as the plant matures, due to death of the lower leaves. A fast increase in LAI at early growth phases is frequently associated with a low CGR during later growth stages, whereas a rather slow growth at early stages is associated with a high CGR during later growth stages (Tanaka and Vergara, 1967, cited by Tanaka, 1976).

Net assimilation rate (NAR), defined as the dry matter production per square meter of leaf per unit of time, allows the estimation of the net photosynthetic ability, not the actual value. NAR is affected by solar radiation, LAI, and age or the physiological state of leaves. Temperatures lower than 18 C may reduce NAR at early growth phases but have no effect at later phases (Murata, 1976). Monteith (discussion of paper by Murata, 1976) supports the idea that the concepts of NAR and relative growth rate (RGR) were derived initially for spaced plants, and for crops in a closed canopy, the growth rate of the stand becomes limited by available light energy and not by the size of the photosynthetic system. He suggests that NAR and RGR should not be calculated for crop stands, and that CGR is the quantity that matters, and nothing is gained by dividing it by either LAI or plant weight, but Murata believes that NAR is an important factor for dry matter production even with closed canopy stands.

B.- VARIABILITY IN GROWTH DURATION

There is an important variability in growth duration among rice cultivars. The maturity period is generally controlled by polygenes, so transgressive segregation is common for both earliness and lateness. The very early maturity of US varieties 'Belle Patna' and 'Bluebelle' appears to be controlled by a single dominant gene, making them important sources of earliness (Jennings et al., 1979).

Growth duration of a given rice cultivar is strongly influenced by photoperiod and temperature. Photoperiod-insensitive cultivars are characteristic of progressive agriculture where cultural practices, such as irrigation, are controlled, and they make planning for rice cultivation more flexible and more suitable to multiple cropping systems (Yoshida, 1981). Photoperiod sensitivity is a useful characteristic of rainfed lowland or floating rice cultivars, where irrigation is not controlled.

1.- Effect of temperature on growth

Maturity or growth duration of photoperiod-insensitive cultivars is strongly affected by air temperature. In the tropics, very short-season cultivars are those that mature in less than 105 days. In the southern US, very-short-season cultivars such as 'Tebonnet' and 'Labelle', mature in 110 to 115 days in Louisiana and less than 120 days in Arkansas. 'Bluebelle', an old US cultivar that matures in 110 days in Texas, has a growth duration of 130 to 150 days in Uruguay.

The rate of plant development depends upon the amount of heat expressed in terms of degree-days or heat units to which the plant is subjected during its growth period. The degree-day is the direct summation of daily mean temperatures above a certain threshold value and a constant accumulation is required to reach a specific development stage of the plant (Keisling et al., 1984; Kanyeka, 1982). When air temperature drops to a certain level, growth and development may stop, and the temperatures below this threshold are considered ineffective. The estimated threshold temperatures for some rice varieties range from 9 to 18 C. (Yoshida, 1981; Dua and Garrity, 1988). In Arkansas, for a particular rice cultivar, the phenological stages have been shown to be predictable with a thermal time base of 10 C (50 F) through the DD50 degree-day program (Keisling et al., 1984; Kanyeka, 1982).

2.- Duration of growth phases

a) VEGETATIVE PHASE. Tillering is increased, the leafing interval is shorter and each leaf is larger when the temperature is higher. A rise in temperature increases the rate at which leaves emerge, and the number of developed leaves on the main stem before heading is fairly constant, so that the main effect of temperature is its influence on the period from seeding to panicle initiation that accounts for much of the variability in the growth duration of rice cultivars (Yoshida, 1981; Tanaka, 1976; Stansel, 1975a). Muchow and Carberry (1990) reported that leaf initiation in sorghum is a function of photoperiod and thermal time and leaf appearance is a function of thermal time.

b) PANICLE DEVELOPMENT. The period from panicle initiation to heading is often mentioned as fairly constant, but it varies with cultivar and weather and ranges from 27 to 46 days. The duration of panicle development is shorter in early-maturing cultivars than in late-maturing cultivars but, in most situations, is about 30 days. The extension of the time for panicle development is one possibility to increase yield capacity. In general, total growth duration and the length of the period from panicle initiation to heading are positively correlated. The extension of this period, independent of total growth duration, may improve yield potential of very-short-season cultivars (Yoshida, 1981). According to Tanaka (1976) this phase may be somewhat shorter when temperature is higher. During this phase the panicle-primordia develops, three internodes at the top of each stem elongate, and the three top leaves which were differentiated in the previous phase develop.

c) GRAIN FILLING. The grain filling period (GF) of rice cultivars is largely determined by varietal characteristics and temperature. A rise in the temperature increases the rate of grain filling after flowering; that period ranges from 40 to 60 days in temperate areas and 25 to 30 days in the tropics (Jennings et al., 1979; Chang and Vergara, 1972; Tanaka, 1976).

A long grain-filling period has repeatedly been observed to be associated with increased grain yields (Jennings et al., 1979; Murata and Matsushima, 1975). Jennings et al. (1979) believe that this extension in the grain-filling period is mainly an effect of temperature and that the known variability among rice cultivars is low. Studies at IRRI (1977) suggested that small-grained cultivars took 12 days for completing grain filling, and large-grained cultivars took 15 to 25 days. Further, the large-grained cultivars had higher grain growth rate and more efficient starch accumulation than the small-grained cultivars. Venkateswarlu et al.

(1981) did not find this trend in a similar study dealing with a smaller group of rice cultivars.

Slowly senescing genotypes of temperate origin often have a longer ripening period. Chang and Vergara (1972) reported that slow leaf senescence may be an indirect selection index for extended grain maturation. These scientists believe that the extension of the reproductive and grain ripening phases, independent of the vegetative growth period, may result in an increase in supply of assimilation products, or storage capacity, or both.

As the grain filling period is generally considered a constant for each rice growing area and varietal differences are reported to be low, the classification of growth duration may be based on the duration from seeding to heading. In Arkansas, maturity groups are defined according to days from seeding to 50% heading as: mid-season 100 to 110 days, short-season 90 to 100 days, very-short-season 80 to 90 days, and extremely short-season less than 80 days.

C. YIELD COMPONENTS AND SINK SIZE

Grain yield of rice (t ha^{-1}) can be expressed with the formula: Panicles m^{-2} x spikelets per panicle x grain weight (mg) x % filled grain x 10^{-5} (IRRI, 1977). According to Tanaka (1976) the production of dry matter during the grain filling period is determined by the potential ability of the population to photosynthesize (source) and by the capacity of spikelets to accept the photosynthates (sink). The sink is composed of (a) the panicle number per unit of land area, (b) the spikelet number per panicle, (c) the filled grain percentage, and (d) the size of individual spikelets or the grain weight. Panicle number is determined predominantly during the vegetative period, spikelets per panicle and the size of the spikelets during the reproductive phase or panicle development, and the filled grain percentage during panicle development and anthesis (Tanaka, 1976). The sink size is determined at and before flowering and the relative importance of climatic influence before and after flowering depends up on whether sink size is limiting to grain yield or not (Yoshida and Parao, 1976).

The sink size or yield capacity of the rice plants depends up on the total number of spikelets per square meter and the average size of individual spikelets, but some scientists believe that it is largely determined by the spikelet number per square meter (Murata, 1976; Yoshida and Parao, 1976). There are often negative correlations between panicle number and spikelet number per panicle, or between spikelet number per land area and filled grain percentage or grain weight, due to compensation effects. So it is necessary to reach the optimum balance among these yield components within the potential of the source (Tanaka, 1976). Whether weather conditions before or after flowering have a greater effect on yield is location- or season-specific (Yoshida and Parao, 1976).

1.- Panicles per square meter

Tillering is reported to increase with a rise in temperature, within a range up to 31 C. In a temperate climate, solar radiation during the vegetative phase has a favorable effect on spikelet number per square meter through an increase in panicles per square meter (Murata, 1976; Stansel, 1975b), but neither solar radiation nor temperature during vegetative growth affected spikelet number per square meter at IRRI (Yoshida and Parao, 1976).

2.- Spikelets per panicle

Mean temperature and solar radiation during panicle development affect the number of spikelets per panicle (Murata, 1976; Yoshida and Parao, 1976). Within a moderate range (24 to 29 C), low temperature during the reproductive stage appears to favor increasing spikelet number and Yoshida and Parao (1976) reported a negative linear correlation between spikelet number per plant and daily mean temperature. Solar radiation during the reproductive phase is positively correlated to spikelet number per panicle and per square meter (Murata, 1976; Yoshida and Parao, 1976; Stansel, 1975b). Spikelet number is also positively and linearly correlated with dry matter production during the reproductive phase and seems to be linked with photosynthetic production during that phase of growth. The competition for assimilates during the later stages of panicle growth may affect the degeneration of already differentiated spikelets and the final size of the hull. Such competition may become critical in determining the final spikelet number when the level of solar radiation is relatively low (IRRI, 1977).

3.- Sterility percentage

The term sterility percentage usually is not strictly used and refers to percentage of unfertile grains plus partially filled grains. Crops shaded during the ripening period had a low percentage of filled grains, not because of increased sterility but because of increased partially filled grains. However, extremely low temperatures during panicle development, at the meiotic stage of pollen mother cells, cause a sharp increase in sterility. Solar radiation appears to affect grain filling and filled-grain percentage mainly by controlling source activity, while temperature, within a moderate range, appears to affect this component by controlling the capability of grains to accept carbohydrates or the length of the ripening period. The tendency for filled grain percentage to decrease with increasing spikelet number seems to be an internal varietal character (Yoshida and Parao, 1976).

4.- Grain weight

Variability in grain weight, within the same cultivar, is reported to be restricted. Constant grain weight for a given rice cultivar may come from the size of the rigid hull, determined during reproductive growth. Thus, according to Yoshida and Parao (1976), when the assimilate supply is adequate (from current photosynthesis or stored assimilates) most grains ripen, and a surplus remains in the straw. When there is shortage of carbohydrate, some grains ripen at the expense of other grains (i.e. unfilled grains) thereby attaining almost constant weight. However, Murata (1976) reported that the higher the temperature during the most active grain filling period, the smaller the grain weight.

The concurrent variations in yield components are complex and often correlated, but rice cultivars differ markedly in 1000-grain weight and this component has a higher heritability than others. Chang and Vergara (1972) reported that grain weight can be readily compensated for by more spikelets on the panicle or by more panicles, but cultivars that have low grain weight usually have a lower yield ceiling than heavy-grained types under the most favorable cultural system. Akita et al. (1990) indicated that lower grain weight of American semidwarf rice cultivars was one of the causes for their lower yields, compared to Asian semidwarfs. Early studies conducted at IRRI (1977) have indicated an optimum grain size for higher yield potential. In view of the compensatory relationship observed between grain size and grain number, the computed yield showed a positive relationship up to 39 g and later decreased. However, Venkateswarlu et al. (1981) reported a negative association of grain size (ranging from 15 to 30 g/1000 grains) with number of grains and with yield in long-season cultivars. This negative association of grain size and grain number appeared around 20 to 22 g per 1000-grain weight (Venkateswarlu et al., 1981).

There is variability in grain weight within the same panicle. High density (HD) grains (specific gravity > 1.2) are found mostly on primary branches of rice panicles. Heritability of HD grains was estimated at 80%. Thus, selection for more high density grains may be effective in early segregating generations such as F3 or F4 (Mallik et al., 1988a). Increasing the percentage of HD grains by decreasing the number of secondary branches in the panicle can increase grain yield. The number of HD grains may also improve with better delivery system of the assimilates, such as more vascular bundles and thicker stems. Panicles with more primary branches and fewer secondary branches can be obtained without reducing total spikelets per panicle (Mallik et al., 1988b).

Recently, Venkateswarlu et al. (1987) concluded that it should be possible to combine the character of a high number of high density grains (high quality grade) with any vegetative growth duration. Rao (1987) found similar results relating to grain grade.

D. SINK:SOURCE RELATIONSHIPS

Sources are organs that export photosynthates and sinks are regions that import photosynthates. Source strength or capacity is expressed as the product of the state variable source size (leaf area) and the rate variable source activity (rate of photosynthesis), and sink capacity as *sink size times sink activity (Wilson, 1972, cited by Lafitte and Travis,* 1984).

Crop growth rates from steps in calculation of potential yields of rice are close to maximum recorded growth rates, but actual grain yields are substantially below those estimated, suggesting that storage capacity may limit grain yield in rice (Evans, 1972). Since leaf photosynthetic rates can reflect the demand for assimilates, varietal differences in photosynthetic rate or leaf area duration (LAD), which parallel differences in yield, may do so, not because the supply of assimilates limits yield, but because higher storage rates elicit higher photosynthetic rates (Evans, 1972). Yield capacity may have an important effect in very-short-season cultivars, increasing LAD and allowing a more efficient use of high photosynthetic rates.

Cock and Yoshida (1973) studied the effects of CO_2 enrichment, before and after heading, on grain yield. Enrichment before heading increased grain yield 29%, and after heading, 21%. The yield increase from CO_2 enrichment before heading was caused by increased grain number and grain weight. Enrichment after heading did not change grain number but increased grain weight and filled grain percentage. In the Philippines, Yoshida (1981) concluded that, if total spikelet number per unit of land area, or yield capacity, can be increased, neither photosynthetic capacity, nor light, nor CO_2 concentration after flowering is likely to limit grain filling.

However, Venkateswarlu (1976) and Venkateswarlu and Visperas (1987) believe that source appears to be the major limitation to higher yields in rice in tropical and subtropical climates because of the wide gap between the number of spikelets and the number of filled grains. In temperate climates, and particularly with japonicas, those scientists support the theory that the sink is the limiting factor, as nearly all spikelets are filled, but this high percentage of filled grains may be a varietal character of japonicas related to an effective pollination during anthesis.

Lafitte and Travis (1984) reported that increased rates of carbon exchange were associated with increased ratios of sink to source size only when these were achieved by reductions in leaf area and concomitant increases in specific leaf weight. They did not find increased carbon exchange ratios in genotypes where the sink to source ratio was raised by selection for increased seed number or seed size; however, some of these lines showed the highest yields, with LAI from 4.4 to 6.5, under wide spacing (10.8 plants m^{-2}). Those scientists did not report measurements of the length of the grain-filling period.

In modern cultivars under contemporary cultural practices, frequently more than 85% of the grains are filled, but appreciable levels of nonstructural carbohydrates remain in the leaves or stems, suggesting that sink size is inadequate (Murata and Matsushima, 1975). A related parameter which reflects the degree to which sink activity is matched by source supply is the extent of carbohydrate remobilization from vegetative sinks during ripening (Yoshida, 1981, cited by Lafitte and Travis, 1984).

Instead of large physical dimensions of the source, greater and more stable functional efficiency at moderate source size are more advantageous to realize the potential sink size under field conditions. Sink capacity is also governed by certain enzymes, like phosphorylases and amylases, besides the endogenous hormonal level about which little is known (Venkateswarlu and Visperas, 1987).

The extension of the time for panicle development is mentioned as another possibility to increase yield capacity. Evans (1972) reported that the extent of vascular differentiation and the capacity for translocation are, by some means, coupled with the extent of spikelet differentiation in wheat.

Recently, Choi (1985), cited by Venkateswarlu and Visperas (1987), found that all sink characters except grain yield are regulated mainly by additive genetic components. Potential kernel size and sink capacity per panicle also showed significant dominance effects and non-allelic genic interaction for sink capacity per tiller. High density grains (specific gravity > 1.2) were found mostly on primary branches of rice panicles, and the heritability of the trait was estimated at 80%. Increasing the percentage of HD grains by decreasing the number of secondary branches in the panicle can increase grain yield. Panicles with more primary branches and fewer secondary branches can be obtained without reducing total spikelets per panicle (Mallik et al., 1988b).

Venkateswarlu and Visperas (1987) believe that these promising plant capabilities indicate possible manipulations for furthering yield potentials through the source-sink concept and that the source-sink system deserves priority in research pursuits in crop plants. Lafitte and Travis (1984) concluded that sink:source ratios can be altered genetically and that these manipulations affect plant yield, as complete yield component compensation does not occur. Yoshida and Parao (1976) indicated that the next major breakthrough in grain yield would come from a substantial increase in spikelet number per square meter by genetic manipulation.

E. YIELD POTENTIAL AND MATURITY GROUP

Yield potential of very-short-season cultivars has been believed to be limited, especially in tropical environments. Varieties that mature in about 110 to 135 days were reported to yield more than those that mature earlier or later (Jennings et al., 1979). A difficult breeding objective, in tropical breeding programs, is the recombination of very early maturity with heavy tillering, which is one of the morphological characters associated with high yields under a transplanted cropping system. The proportion of fertile tillers has also been reported to be higher in lines with a longer vegetative period (Chang and Vergara, 1972). If the panicle differentiates by 30 days before flowering and the period from flowering to harvest takes 30 days, a very-short-season cultivar has 45 to 50 days of vegetative growth before panicle initiation (Jennings et al., 1979; Yoshida, 1981). Since 20 days are required in the seedbed, only 25 days are left for active vegetative growth. About 100 days is the shortest duration for achieving reasonably high yields with transplanted rice, according to Yoshida (1981). He believes that attempts to shorten growth duration are approaching the limit for the shortest possible growth duration with high yielding potential.

However, in experiments using closer spacings, as 10 x 10 cm, along with 25 x 25 and 50 x 50 cm, under transplanted conditions, the highest yields were obtained at 10 x 10 cm spacing, and at this planting density, increased growth duration did not result in increased yield. When planted at 10 x 10 cm, short-season cultivars (less than 100 days of growth duration) outyielded mid-season and long-season cultivars planted at 25 x 25 cm (Vergara et al., 1966).

In a recent study, Venkateswarlu et al. (1987) concluded that a vegetative growth duration of 45 days (total growth duration of 91 days) is not limiting for high yield potential. Grain yield was higher with 45 and 65 days of vegetative period and gradually decreased with increased growth duration. The higher grain yield at 45 and 65 days was due mainly to high panicle numbers, fertility percentage and total grain number per hill.

Under direct seeding, tillering capacity does not affect yield because close spacings are used with populations of about 200 to 350 plants per square meter. To some extent, increasing the planting density in direct-seeded rice supplements or complements early vigor and increases leaf area and yield in very-short-season cultivars. If growth rate of very short-season cultivars is high enough to compensate for a short duration, the plant can produce a large amount of growth within a limited time and an adequate LAI at heading.

The extension of the time for panicle development is one possibility to increase yield capacity. In general, total growth duration and the length of the period from panicle initiation to heading are positively correlated. The extension of this period, independent of total growth duration, may improve yield potential of very-short-season cultivars (Yoshida, 1981).

Cooler temperatures in temperate climates cause extended grain-filling periods and are reported to increase the yield potential of very short-season cultivars. The increase in total dry matter and carbohydrates during the grain-filling period usually shows a close correlation with grain yield (Matsushima and Wada, 1959, and Murata and Togari, 1972; both cited by Murata and Matsushima, 1975). At late growth stages the photosynthetic rate falls due to ageing, especially in long-season cultivars, with a result that, at anthesis and grain filling, the photosynthetic rate is generally higher in short-season cultivars (Murata, 1957 and 1961; cited by Murata and Matsushima, 1975). Chang and Vergara (1972) reported that early-maturing lines tend to have a higher growth rate at heading, which was correlated with the increase of dry matter after heading.

F.- CHARACTERISTICS OF RICE PHOTOSYNTHESIS

Rice has the C3 photosynthetic pathway; however, one report suggests the operation of both C3 and C4 pathways in a salt tolerant indica cultivar (Hedge and Joshi, 1974, cited by Yoshida, 1981). Recently, Imaizumi et al. (1990) found high levels of activity of enzymes involved in C4 photosynthesis in spikelets, and indicated the possible existence of C3-C4 intermediate photosynthesis or C4-like photosynthesis in rice lemmas and paleas. Compared to other C3 species, rice has a relatively higher net photosynthetic rate per unit of leaf area. The CO_2 assimilation rate (CA) typical of rice was considered to be of about 1.3 mg CO_2 m^{-2} s^{-1} (Sinclair and Horie, 1989). Some papers indicate a rate of 40 to 50 mg CO_2 dm^{-2} h^{-1} (1.11 to 1.39 mg CO_2 m^{-2} s^{-1}) (Yoshida, 1981). Lafitte and Travis (1984) reported maximal rates of leaf apparent photosynthesis of 0.75 mg CO_2 m^{-2} s^{-1}, while Imaizumi et al. (1990) found a similar rate in flag leaves (0.85 mg CO_2 m^{-2} s^{-1}). Canopy net photosynthesis reaches a maximum at about the time of full canopy closure and remains relatively constant across the growing season, beginning to decline after flowering, at the onset of canopy senescence (Baker et al., 1990).

Mean crop growth rates over the season, from transplanting to maturity, are reported to reach 14.08 g m^{-2} s^{-1} in Japan (Murata, 1976). The CGR rates of an erect-leaved cultivar, as IR8, can reach 160 g of carbohydrates m^{-2} $week^{-1}$ (22.9 g m^{-2} day^{-1}) but are even higher in high-yielding very-short-season cultivars. Maximum short term CGR recorded for rice is reported to be 36 g m^{-2} day^{-1} (Yoshida, 1981).

Light compensation point was established in 400 to 1000 lx, saturation in 45 to 60 Klx, and carbon dioxide compensation point in 55 ppm. The photorespiration rate increases with increasing light intensity, but the rate of photorespiration relative to the rate of CO_2 fixation is higher at lower light intensities. At light intensities lower than 10 Klx, photorespiration accounts for 70 to 90% of CO_2 fixation. At 40 Klx, it accounts for 40% (Ishii et al. 1977, cited by Yoshida, 1981).

The net photosynthesis of single leaves reaches maximum at about 40 to 60 Klx, about one half of full sunlight. Photosynthesis of a well-developed canopy, however, increases with increasing light intensity up to full sunlight, without indication of light saturation (Murata, 1961, cited by Yoshida, 1981). Net photosynthesis of single leaves is zero at light intensity of about 400 lx (light compensation point), and it increases with increasing light intensity up to about 50 Klx. Photosynthetic efficiency, when it is defined as photosynthesis per unit of light energy, is higher at lower light intensities. When the amount of daily incident solar radiation is constant, the intensity of light energy per unit of time weakens as the day length increases. Consequently, as the days lengthen, daily photosynthesis increases, and this effect is considered an advantage of the temperate climate over the tropical (Yoshida, 1981).

A large leaf area index (LAI) is necessary to intercept the incident solar radiation, but the size of LAI needed to give maximum crop photosynthesis depends on leaf orientation of the canopy. The erect-leaved canopy requires a greater LAI than does the droopy-leaved canopy and receives weaker sunlight per unit of leaf area, resulting in greater canopy photosynthesis. Erect leaves receive a lower light intensity per unit of leaf surface but for a larger leaf area. In general, a LAI of 4 to 8 is needed for good rice photosynthesis (Yoshida, 1981).

Photosynthetic rates averaged over the season do not correlate well with total dry weight accumulation. The rates measured at the time of panicle initiation and/or during ripening are correlated with yield (Lafitte and Travis, 1984). At later growth stages the photosynthetic rate falls due to ageing, especially in long-season cultivars, with a result that, at anthesis and grain filling, the photosynthetic rate is generally higher in short-season cultivars (Murata, 1957 and 1961; cited by Murata and Matsushima, 1975).

1.- Photosynthesis of different parts of the rice plant

Yoshida (1981) reported that the potential net photosynthesis of the leaves was 94% of the total. The top 3 leaves of rice plants export assimilates to the panicle, and lower leaves send their assimilates to the roots. The top 3 leaves of plants in a IR8 crop made up 74% of the total leaf area when LAI was 5.5 at heading. The net photosynthesis of the leaf sheath and panicle was indicated as extremely small. However, Imaizumi et al. (1990) reported that the contribution of panicle photosynthesis to grain filling increases as the ripening process proceeds. In their experiment, the gross amount of CO_2 assimilated in an entire panicle was about 30% of that in the flag leaf. The spikelets have high ability to photosynthesize in terms of their content of chlorophyll, and the affinity for CO_2, through a carboxylation reaction, is higher in lemmas and paleae than in the flag leaf. Photosynthesis in spikelets seems to be oxygen-insensitive, and their contribution to grain filling increases under moderate water stress.

2.- Effect of leaf nitrogen content

Rice photosynthetic rate per unit of leaf area (PLA) is positively related to nitrogen content per unit leaf area (NLA) at high light intensities (Tsunoda, 1972; Sinclair and Horie, 1989; Lafitte and Travis, 1984). The differences in NLA may be due to environment or genotype and may also be observed among different leaves of one strain. Leaf nitrogen content of rice ranges from 1.1 to 2.1 g m^{-2} and, according to Tsunoda (1972), even at the highest N content observed among rice cultivars, the PLA had not reached its ceiling rate. However, some quadratic equations describing the relationship between CO_2 assimilation rate per unit area and NLA show a strong linear component below 1.6 g N m^{-2} and a curvilinear component at greater NLA (Sinclair and Horie, 1989).

Tsunoda (1972) believes that a further increase in NLA due to plant breeding may produce a higher PLA, under high light intensities; but Sinclair and Horie (1989) support the theory that increases above current assimilation rates will not have a large effect on radiation use efficiency (RUE). At the leaf CO_2 assimilation rates (CA) typical of a species, the RUE was predicted to be about 1.2 g MJ^{-1} for soybean, 1.4 g MJ^{-1} for rice (which corresponds to a CA of about 1.3 mg CO_2 m^{-2} s^{-1}), and 1.7 g MJ^{-1} for maize (Sinclair and Horie, 1989). Hayashi (1967), cited by Sinclair and Horie (1989), found the mean RUE for eight rice cultivars during vegetative growth to be 1.55 g MJ^{-1}. The large advantage in CA of a C4 crop is greatly diminished when the biomass accumulation rates of whole crops are compared. A RUE of 1.4 g MJ^{-1} for rice compares favorably with a RUE of 1.7 g MJ^{-1} for maize (Sinclair and Horie, 1989). Sun elevation and LAI had little effect on RUE, but CA had a strong effect. At relatively low CA, RUE was especially sensitive to changes in CA. Important differences exist among species in RUE response to NLA. The RUE response to NLA in rice is intermediate between that of maize and soybeans (Sinclair and Horie, 1989).

Among rice cultivars, nitrogen content is reported to be closely associated with chlorophyll content and positively related to absorption rate and negatively to reflection and transmission rate (Tsunoda, 1972). Short-season cultivars have a higher nitrogen content than the long-season cultivars, even at harvest (Vergara et al., 1966). In leaves of C3 plants, RuBP carboxylase enzyme alone accounts for up to 50% of the soluble protein. In C4 leaves it accounts for 10 to 25% while PEP carboxylase enzyme alone accounts for another 10% (Sinclair and Horie, 1989). If the source capacity of the plant is described on the basis of leaf protein, the efficacy of carboxylation can be estimated.

Changes in the density of leaves or the nitrogen content per unit leaf area seem to have an effect similar to that resulting from changes in leaf inclination, and in a rice canopy, the effect of an increase in leaf angle can complement the NLA content to some extent (Tsunoda, 1972).

Reddy et al. (1989) assayed leaf nitrate reductase activity (NRA) in rice flag leaves at different growth stages. The NRA activity was higher in the tillering stage, followed by activity at panicle initiation, but it was lower at flowering stage.

3.- Influence of leaf structure and density

Lafitte and Travis (1984) reported that increased rates of carbon exchange were associated with increased ratios of sink to source size only when these were achieved by reductions in leaf area and concomitant increases in specific leaf weight. Under low population densities, no analogous increase occurred in those cases where the sink:source ratio was raised by selection for increased seed number or seed size. In their study, the small-leaved rice lines showed higher apparent photosynthesis, had higher specific leaf weights (SLW), and more nitrogen per unit leaf area. An increased demand for assimilates was placed on each unit of leaf area in the small leaf lines, and the increase in demand was associated with greater source activity per unit leaf area.

Tu et al. (1988) studied US and Chinese cultivars under controlled conditions. In preliminary studies, US cultivars had much higher light saturation for photosynthesis than a popular Chinese cultivar. They proposed that rice cultivars may be differentiated into sun and shaded ecotypes. Early cultivars 'Bellemont' and 'Lemont', from bright light habitats of Texas, have some properties of sun plants, while the Chinese cultivar 'Gui-Chao 2', selected under low light conditions, has many characteristics of a shade plant. Leaf thickness of US cultivars increased in response to increased illumination during growth (1000 umol photons m^{-2} s^{-1}), and photosynthesis and quantum yields remained high. Bellemont and Lemont also had higher carboxylase enzyme activities than the Chinese variety for both RuBP and PEP carboxylase. Ability to acclimate to bright light in US rice cultivars correlates with increased leaf thickness and photosynthetic rate observed in other sun ecotypes. The inability of Gui-Chao 2 to acclimate and its lower quantum yield in bright light imply sensitivity to photoinhibition normally associated with a shade plant, according to Tu et al. (1988).

Modern japonica cultivars are reported to have more compact structure than indica cultivars (Tsunoda, 1972). The number of large vascular bundles in the first internode from the top was 20.9 for indica type and 10.1 for japonica type. This difference between both types may relate to evolution and to nutrient transport (Huang, 1988). Tsunoda (1972) cited a positive correlation between the ratio of xylem area to leaf area and photosynthesis per leaf area (PLA) among 14 rice cultivars. Xylem area was measured as a total cross-sectional area of all xylems at the base of leaf blade. The cultivar Bluebelle showed the highest PLA with the highest ratio (Tsunoda, 1972).

The development of vascular bundles, in particular of xylem systems, and the arrangements of photosynthetic cells close to the bundles may be important for maintaining the water balance with a lower gas exchange resistance. Tsunoda (1972) reported that, with leaf structures combined with a high NLA (thick, compact mesophile tissues), a high PLA as well as a high transpiration rate can be achieved. The cultivar Bluebelle had also been reported to have a good drought tolerance. Tsunoda established that the compactness of mesophile tissues might have a bearing on cold tolerance, in addition to drought resistance and nitrogen response. Application of an analogue of abscisic acid increased chilling tolerance in rice seedlings, and this effect may be due to the action on stomatal closure that prevented water loss through transpiration (Flores and Dorffling, 1988).

In rice, a decrease in PLA due to a low temperature preconditioning of 17 C was most remarkable in indica varieties, while 'Calrose', adapted to cold temperatures, showed the highest tolerance. Tsunoda (1972) also established that size of sinks and photorespiration at low temperature might have a bearing. Under low temperatures, inadequate available sugars for translocation to the developing grains contribute to spikelet sterility (Carnahan et al., 1972).

G.- CHARACTERISTICS OF RICE RESPIRATION

Crop respiration is closely related to gross photosynthesis and is reported to be approximately 40% of gross photosynthesis over a wide range of values for LAI and leaf area ratio, until 2 weeks after flowering.

Maximum values reported for IR8 and 'Peta' were about 120 g CH_2O m^{-2} wk^{-1}, at LAI's higher than 8 (Yoshida, 1981; Cock and Yoshida, 1973). Tsunoda (1972) reported that dark respiration rate tended to be higher in leaves with high nitrogen content than in leaves with low content. Mean dark respiration was estimated at about 0.128 mg CO_2 mg^{-1} leaf nitrogen h^{-1} at 30 C.

New organs formed during growth are synthesized from intermediates and energy supplied by respiration (R). Growth efficiency (GE) is expressed as:

$$GE = GR/GR+R$$

GR+R represents the total amount of substrate consumed to produce new organs (GR) (Tanaka, 1972; Yoshida, 1981). Growth efficiency indicates how much of the substrate is converted into the constituents of new tissues.

The growth rate is strongly affected by temperature, but growth efficiency is reported to be about 60%. The concept may be applied to growing plants until maturity and to the growth of individual organs such as leaves or panicles. When active vegetative growth is taking place, growth efficiency is high (60 to 65%). Growth efficiency drops sharply after the milk stage of ripening, but the growth efficiency of the panicle is high (65 to 75%) (Yoshida, 1981).

Respiration may be divided into respiration necessary for growth (Rg) and that for maintenance (Rm). Growth respiration appears to be the same for different species and is not affected by temperature. On the other hand, maintenance respiration varies with plant species and is a temperature-dependent process (Yoshida, 1981). At early growth stages, the growth efficiency is reported to remain at about 0.6; it starts to decrease after panicle initiation and continues to decrease until the end of growth (Tanaka, 1972). When active grain filling slows down toward maturity, Rg decreases and Rm increases, so the proportion of Rg to total respiration decreases, as well as the growth efficiency (Yoshida, 1981).

The high growth efficiency value of the panicle during ripening occurs because the substance produced is mostly starch. Formation of starch from sucrose, which is the major substance translocating into the grain, requires less energy, while retranslocation of substances from decomposing old organs to growing new organs causes a decrease of growth efficiency. The re-use of substances in vegetative organs for grain development is indicated as one reason for the low growth efficiency of the whole plant after flowering. During this period the growth efficiency of the reproductive organs themselves is high, but the growth efficiency of the whole plant is small because of the re-use of substances in vegetative organs, respiration of elongated internodes, and limited storage capacity (Tanaka, 1972). Remobilization is not so important in short-season cultivars (Vergara et al., 1966) and may be one of the reasons contributing to higher growth rates during grain filling in these cultivars.

Tanaka (1972) estimated maintenance respiration to be 25% of the total respiration. He considered that improvement of the efficiency of respiration may be approached through the plant type concept and from the source-sink theory. He believed that the second approach may have promise for raising grain yield beyond the level achieved through the plant type approach.

The most important maintenance processes are protein turnover and active transport processes. Maintenance respiration cost was estimated at 15 to 25 mg glucose g^{-1} dry matter d^{-1}, and important differences are reported among species (Yoshida, 1981).

A high content of sugars occurs in the stem at flowering in tropical rice, especially in the wet season. The carbohydrates that accumulate in the stem have been reported to be mostly starch in temperate rice. With accumulation of sugars there may be more chance for respiration leakage than with accumulation of starch (Tanaka, 1972). In short-season cultivars, almost no carbohydrates (starch and sugars) were accumulated during the vegetative and reproductive phases (Vergara et al., 1966). Senescence of rachilla is reported to cause a weakening of the sink, especially in long-season cultivars, resulting in a decrease in photosynthetic rate and growth efficiency. Extension of the ripening period is one important way to increase grain yield, but senescence of the sink may be a major problem in extending the duration (Tanaka, 1972; Murata and Matsushima, 1975).

H.- BALANCE BETWEEN PHOTOSYNTHESIS AND RESPIRATION CRITICAL AND OPTIMUM LAI CONCEPTS

In early models for canopy production, respiration was assumed to increase linearly with increasing LAI and an optimum LAI was expected (Yoshida, 1981). The use of photosynthetic products by the respiration of the lower culm and roots was considered to be one reason for the existence of optimum LAI. But it was demonstrated that the loss of carbon by respiration from shaded lower leaves is rather limited (Tanaka, 1972).

Optimum LAI has been repeatedly observed in populations of leafy rice cultivars, while no optimum LAI was reported in populations with good plant type. Rather there is a ceiling LAI, and no change in dry matter production occurs as LAI increases above the ceiling LAI (Tanaka, 1972).

Cock and Yoshida (1973) studied photosynthesis and crop growth of tall and short rice cultivars under different spacing. There was no optimum LAI value for CGR in both plant types, and respiration was not a linear function of LAI. The relation between CGR and LAI was similar in both cultivars (IR8 and Peta), but the plateau value of CGR was 20 g m^{-2} wk^{-1} greater in the improved plant type. Leaf angle of the traditional cultivar decreased with increasing LAI. Respiration increased curvilinearly with increasing LAI, and both cultivars reached maximum CGR at a LAI of about 6 (IR8) to 4 (Peta), beyond which it remained the same despite further increases in LAI (critical LAI). Crop respiration was estimated to be 40% of gross photosynthesis over a wide range of values for LAI until 2 weeks after flowering in several experiments including other cultivars (Cock and Yoshida, 1972).

Yoshida (1981) reported that, agronomically, there is an optimum growth size for maximum yield, but this optimum size is related to the lodging resistance of a cultivar and is not related to the balance between photosynthesis and respiration. When LAI is varied by changing nitrogen levels rather than changing spacing, the resulting droopiness at high LAI values may be greater than that observed in the reported spacing experiments. Gross photosynthesis, thus, may be decreased sufficiently to produce an optimum LAI value, but it is not due to an imbalance between photosynthesis and respiration (Cock and Yoshida, 1973).

I.- CARBOHYDRATE PARTITIONING

Preheading storage plays a large role in yield for modern high-yielding rice cultivars under standard field conditions (Park et al., 1988). Carbohydrates such as sugars and starch begin to accumulate sharply about 2 weeks before heading, and the plant's vegetative parts, mainly the leaf sheath and stem, reach a maximum content at around heading (Yoshida, 1981). The concentration begins to decrease as ripening proceeds and may rise again slightly near maturity (Yoshida, 1981; Lafitte and Travis, 1984; Turner and Jund, 1990; Murayama et al., 1955). A high content of sugars occurs in the stem at flowering in tropical rice, especially in the wet season, but in temperate rice, the carbohydrates that accumulate in the stem have been reported to be mostly starch (Tanaka, 1972).

Total nonstructural carbohydrate (TNC) levels in stems and leaves of the rice cultivars 'Labelle', 'Gulfmont', 'Skybonnet', and 'Mars' decreased to minimum levels (0 to 9%) during grain filling, and then increased at harvest to levels of 4 to 17% (Turner and Jund, 1990). The fluctuation of starch content in the stem is nearly the same as in the leaf sheath, but the maximum value of the former is higher than that of the latter (Yoshida, 1981).

Lafitte and Travis (1984) studied carbohydrate concentration after heading in closely related rice genotypes differing in sink to source ratios. Carbohydrate content of storage organs (internodes and leaf sheaths) decreased rapidly after heading, and in most of the lines the nonstructural carbohydrate content decreased to less than 1% of the dry weight of the tissue by one month after anthesis. Starch concentration of one of the lines studied (large leaves, large seeds) increased in the two weeks following anthesis and declined later. There were no significant differences among lines in the sugar contents of leaf lamina or panicles, although these values did change over time. The starch content of the panicles increased rapidly in all cultivars during the first month after anthesis. The genotypes with greater sink to source ratios had the lowest concentrations of TNC in the vegetative tissues, indicating that sink activity was relatively high.

In the same experiment, no starch buildup occurred in the leaves of any of the lines studied. High apparent photosynthesis was correlated with low concentrations of nonstructural carbohydrates in the vegetative storage tissues (stems), but no depression of apparent photosynthesis occurred because of elevated carbohydrate levels in those tissues.

Concentrations of TNC also show diurnal variation, and Lafitte and Travis (1984) sampled rice plants at a fixed time of the day to avoid this fluctuation. In soybean, TNC and starch concentration of leaflet blades increased during the day, and most of the increase was between 0900 and 1500 EST (Allen et al., 1988). However, reducing sugars, sucrose, and total soluble sugars remained relatively constant throughout the day compared with starch. Almost all of the diurnal pattern of TNC was due to changes in starch concentration.

Preheading storage may contribute 20 to 40% of the starch that is stored in the grain at harvest and acts as a biological buffer to prevent grain abortion during periods of maximal sink demand (Park et al., 1988). In an experiment reported by Cock and Yoshida (1972), 68% of the accumulated carbohydrate was translocated into the grains, 20% was respired during the ripening period, and 12% remained in the vegetative parts. The amount of the carbohydrate translocated was equal to about 26% of the grain carbohydrate, so 74% of grain carbohydrate at maturity was produced by photosynthesis after flowering. In general, according to Yoshida (1981), photosynthesis during ripening contributes to grain carbohydrates by 60 to 100%. The extent of carbohydrate remobilization from vegetative sinks during ripening may reflect the degree to which sink activity is matched by source supply (Yoshida, 1981, cited by Lafitte and Travis, 1984).

Preheading storage is higher with a long-season cultivar (Murata and Matsushima, 1975). It was reported that short-season cultivars produced a great amount of carbohydrates during their flowering and ripening phases, but the long-season varieties produced a greater percentage before flowering. At flowering, short-season cultivars had 10 to 20% of the total carbohydrates that they would accumulate by harvest, and long-season cultivars had 40 to 80% (Vergara et al., 1966).

Moderately high temperature after heading affects grain filling through acceleration of the translocation of carbohydrates and other substances. The dry weight decrease of leaf sheaths and stems during grain filling due to translocation of carbohydrates (and partly to transpiration loss), as well as the speed of dry weight increase of ears, were greater at a mean temperature of 25.5 C than at 21.3 C (Murata, 1976).

Carbohydrate storage is reported to influence ratoon rice yields, inducing regeneration of ratoon tillers. According to Turner and Jund (1990), much of the variability in ratoon crop yields may be attributed to TNC levels in leaf and stem at main crop harvest. Main crop plants with elevated TNC levels produced ratoon yields 33 to 48% higher than those from plants with normal TNC concentration. Palchamy et al. (1990) reported that rice cultivars having thicker stems and higher carbohydrate content had higher ratoon crop grain yield.

J.- YIELD POTENTIAL OF VERY-SHORT-SEASON CULTIVARS IN SOME TEMPERATE AREAS

In Arkansas, Tebonnet has a yield index superior to that of 'Newbonnet' and slightly lower than that of Lemont. The very-short-season cultivar L202 had the highest yield index among long-grain types with heavy kernel weight and an extended grain-filling period (Huey and Moldenhauer, 1988). The recently released cultivar 'Alan' has a yield potential similar to that of L202 and is 4 days earlier. Skybonnet is the earliest long-grain cultivar recommended in Louisiana, but its grain yield potential is lower than that of Lemont (Louisiana State University, 1987).

Some very-short-season breeding lines selected in Uruguay, from crosses of Bluebelle and other cultivars showed high yield potential. 'EEE-L370' has had an average grain yield of 10.1 t ha^{-1} in replicated trials during 2 years, while Bluebelle, the control cultivar, averaged 9.4 t ha^{-1}. In the 1988-89 crop season, some of those lines (from the cross EEE-L58/Bluebelle) were tested in different seeding dates ranging from early to extremely late. Yield was over 7 t ha^{-1} when seeded extremely late (by the end of December) and more than 10 t ha^{-1} with the normal seeding date. Growth cycle, from seeding to heading, ranged from 74 to 94 days (Est. Exp. del Este, 1989). With seeding dates ranging from October 11 to

December 6, in 1988, EEE-L370 produced 79.5 kg of rough rice per day of growth, while Bluebelle produced 66.2 kg day^{-1}. In the 1988/89 crop season, some short and very short-season breeding lines yielded 11 to 12 t ha^{-1}, with a total maturity period 7 to 10 days shorter than that of Bluebelle. These lines produced 91.5 to 96.8 kg of rough rice per hectare per day of growth cycle.

These very-short-season lines have improved plant type with a height of 80 to 85 cm. Leaves are erect and thick and have dark green color. Panicles are heavy with large grains (26 to 27 g per 1000 grains), resulting in a high sink to source ratio. EEE-L370 reaches the flowering stage 10 to 15 days earlier than Bluebelle, but the period from heading to maturity is similar in both cultivars (41 to 42 days). This material was selected under high cold pressure during the reproductive phase and high light intensity that is prevalent in Uruguay. Growth rate and efficiency of these lines are high, and the threshold temperature seems to be low (Est. Exp. del Este, 1989).

K.- REFERENCES

Akita, S., C.N. Bollich, and B.D. Webb. 1990. Eco-physiological analysis of energy partitioning among organs for lodging resistance in rice (Oryza sativa L.). p. 38. In Proc. XXIII Rice Technical Working Group. Biloxi. Mississippi.

Allen Jr., L.H., J.C.V. Vu, R.R. Valle, K.J. Boote, and P.H. Jones. 1988. Nonstructural carbohydrates and nitrogen of soybean grown under carbon dioxide enrichment. Crop Sci. 28:84-94.

Baker, J.T., L.H. Allen Jr., and K.J. Boote. 1990. Effects of atmospheric carbon dioxide concentration and air temperature on development, growth, and yield of paddy rice. p.118-119. In Proc. XXIII Rice Technical Working Group. Biloxi. Mississippi.

-----, L.H. Allen Jr., K.J. Boote, P. Jones, and J.W. Jones. 1990. Rice photosynthesis and evapotranspiration in subambient, ambient, and superambient carbon dioxide concentrations. Agron. J. 82:834-840.

Carnahan, H.L., J.R. Ericson, and J.J. Mastenbrock. 1972. Tolerance of rice to cool temperatures-USA. p.535-540. In Rice Breeding. IRRI. Los Banos. Philippines.

Chang, T.T., and B.S. Vergara. 1971. Ecological and genetic aspects of photoperiod sensitivity and thermo sensitivity in relation to the regional adaptability of rice varieties. Int. Rice Comm. Newslett. 20(2):1-10.

-----, and -----. 1972. Ecological and genetic information on adaptability and yielding ability in tropical rice varieties. p.431-453. In Rice Breeding. IRRI. Los Banos. Philippines.

Cock, J.H., and S. Yoshida. 1972. Accumulation of 14C-labelled carbohydrate before flowering and the subsequent redistribution and respiration in the rice plant. Proc. Crop Sci. Soc. Jpn. 41:226-234.

-----, and -----. 1973. Photosynthesis, crop growth, and respiration of tall and short rice varieties. Soil Sci. Plant Nutr. (Tokio) 19:53-59.

Dua, A.B., and D.P. Garrity. 1988. Models for predicting rice flowering. Int. Rice Res. Newslett. 13(2):7-8.

Estacion Experimental del Este. 1989. Arroz. Resultados Experimentales. Centro de Investigaciones Agricolas "Alberto Boerger". Min. Gan. Agric. y Pesca. T. y Tres. Uruguay.

Evans, L.T. 1972. Storage capacity as a limitation on grain yield. p.499-511. In Rice Breeding. IRRI. Los Banos. Philippines.

Flores, A.A., and K. Dorffling. 1988. Influence of new terpenoid analogue of abscisic acid on chilling resistance of rice seedlings. Int. Rice Res. Newslett. 13(6):29.

Gardner, F.P., R.B. Pearce, and R.L. Mitchell. 1985. Physiology of crop plants. Iowa State University Press. Ames. Iowa.

Huang, H. 1988. Japonica and indica differences in large vascular bundles in cult. Int. Rice Res. Newslett. 13(1):7.

Huey, B., and K. Moldenhauer. 1988. Choosing a profitable variety. p.11-13. In Rice Production Handbook. MP 192. Cooperative Ext. Center, Univ. of Arkansas, USDA.

Imaizumi, N., H. Usuda, H. Nakamoto, and K. Ishihara. 1990. Change in the rate of photosynthesis during grain filling and the enzymatic activities associated with the photosynthetic carbon metabolism in rice panicles. Plant Cell Physiol. 31(6):835-843.

Int. Rice Res. Inst. 1977. Growth duration, plant height, and yield. p. 21-25. In Annual Report for 1976. IRRI. Los Banos. Philippines.

Jennings, P.R., W.R. Coffman, and H.E. Kauffman. 1979. Rice improvement. IRRI. Los Banos. Philippines.

Kanyeka, Z.L. 1982. Use of temperature data to estimate development stages of rice varieties. M.S. Thesis. Univ. of Arkansas, Fayetteville.

Keisling, T.C., B.R. Wells, and G.L. Davis. 1984. Rice management decision aids based upon thermal time base 50 F. Extension Computer Technical Bulletin No. 1. Cooperative Ext. Service, Univ. of Arkansas, USDA.

Lafitte, H.R., and R.L. Travis. 1984. Photosynthesis and assimilate partitioning in closely related lines of rice exhibiting different sink:source relationships. Crop Sci. 24:447-452.

Louisiana State University. 1987. Rice. Production Handbook. Agricultural Center.

Mallik, S., A.M. Aguilar, and B.S. Vergara. 1988a. Inheritance of high density grain in rice. Int. Rice Res. Newslett. 13(6):8-9.

-----, -----, and -----. 1988b. Rice panicle characteristics. Int. Rice Res. Newslett. 13(5):7-8.

Muchow, R.C., and P.S. Carberry. 1990. Phenology and leaf-area development in a tropical grain sorghum. Field Crops Res. 23:221-237.

Murata, Y., and S. Matsushima. 1975. Rice. p.73-99. In Crop Physiology. Some case histories. L.T. Evans ed. Cambridge University Press. London.

-----. 1976. Productivity of rice in different climatic regions of Japan. p. 449-470. In Climate and rice. IRRI. Los Banos. Philippines.

Murayama, N., M. Yoshino, M. Oshima, S. Tsukahara, and U. Kawarasaki. 1955. Studies on the accumulation process of carbohydrates associated with growth of rice. Bull. Natl. Inst. Agric. Sci. (Tokio), B, 4:123-166. Jpn. Eng. Summ.

Palchamy, A., S. Purushothaman, and A. Rajagopal. 1990. Effect of stem thickness and carbohydrate content on ratoon rice yield. Int. Rice Res. Newslett. 15(2):10.

Park, W.D., D.L. Andrews, C.N. Bollich, and B.D. Webb. 1988. Role of preheading storage in rice yield. p.26. In Proc. XXII Rice Technical Working Group. Davis. California.

Rajewski, J.F., C.A. Francis, and J.D. Eastin. 1991. Differential responses to defoliation of grain sorghum yield components and yield-related traits. Crop Sci. 31:561-567.

Rao, S.P. 1987. High density grain index among primary and secondary tillers of short and long-duration rices. Int. Rice Res. Newslett. 12(4):12.

Reddy, A.T., D.V.R. Reddy, V.S. Rao, T.V. Kumar, R.N. Pillai, and I.V. Subba. 1988. Effect of N forms on leaf nitrate reductase activity, yield and protein content of rice. Int. Rice Res. Newslett. 13(5):23.

Sinclair, T.R., and T. Horie. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. Crop Sci. 29:90-98.

Smith, D. 1981. Removing and analyzing total nonstructural carbohydrates from plant tissue. R2107. Research Division, College of Agricultural and Life Sciences. University of Wisconsin-Madison.

Stansel, J.W. 1975a. The rice plant- Its development and yield. p.9-21. In Six decades of rice research in Texas. Res. Monogr. #4. Texas Agric. Exp. Stn. and US Dep. Agric., College Station, TX.

-----. 1975b. Effective utilization of sunlight. p.43-50. In Six decades of rice research in Texas. Res. Monogr. #4. Texas Agric. Exp. Stn. and US Dep. Agric., College Station, TX.

Tanaka, A. 1972. Efficiency of respiration. p.438-498. In Rice breeding. IRRI. Los Banos. Philippines.

-----. 1976. Comparisons of rice growth in different environments. p 429-448. In Climate and rice. IRRI. Los Banos. Philippines.

Tsunoda, S. 1972. Photosynthetic efficiency in rice and wheat. p.471-482. In Rice breeding. IRRI. Los Banos. Philippines.

Tu, Z.P., X.Z. Lin, Q.M. Huang, W.I. Cai, H.Y. Feng, and L.Y. Ye. 1988. Photosynthetic characterization of rice varieties in relation to growth irradiance. Aust. J. Plant Physiol. 15:277-286.

Turner, F.T., and M.F. Jund. 1990. Main-crop N and stem carbohydrate influence on ratoon rice yields. p.116-117. In Proc. XXIII Rice Technical Working Group. Biloxi. Mississippi.

Venkateswarlu, B. 1976. Source-sink interrelationships in lowland rice. Plant Soil 44:575-586.

-----, G.S.V. Prasad, and A.S.R. Prasad. 1981. Studies on the nature of relationships between grain size, spikelet number, grain yield and spikelet filling in late duration varieties of rice (Oryza sativa L.). Plant Soil 60:123-130.

-----, and R.M. Visperas. 1987. Source-sink relationships in crop plants. IRRI Res. Paper Series No. 125. Los Banos. Philippines.

-----, B.S. Vergara, and R.M. Visperas. 1987. Influence of vegetative growth duration on grain grade. Int. Rice Res. Newslett. 12(1):4-5.

Vergara, B.S., A. Tanaka, R. Lilis, and S. Puranabhavung. 1966. Relationships between growth duration and grain yield of rice plants. Soil Sci. Plant Nutr. 12(1):31-39.

Yoshida, S. 1981. Fundamentals of rice crop science. IRRI. Los Banos. Philippines.

-----, D.A. Forno, J.H. Cock, and K.A. Gomez. 1976. Laboratory Manual for Physiological Studies of Rice. IRRI. Los Banos. Philippines.

-----, F.T. Parao. 1976. Climatic influence on yield and yield components of lowland rice in the tropics. p. 471-494. In Climate and rice. IRRI. Los Banos. Philippines.

CHAPTER 2

PHENOLOGY AND YIELD COMPONENTS IN RICE CULTIVARS OF DIFFERENT MATURITY GROUPS

ABSTRACT

The extremely short growth duration of some rice (Oryza sativa L.) lines being tested in Arkansas may affect their yield potential. This study compared the phenology, yield and yield components of cultivars from different maturity groups. The line RU9101001 and cultivars 'Alan', 'L202, 'Newbonnet' and 'Starbonnet', with maturity periods ranging from extremely-short- to long-season, were evaluated at two seeding dates, April 24 and May 25, 1990, at Stuttgart, AR. The duration of development phases was established in calendar and thermal time, based on the DD50 degree-day program. Total growth duration of cultivars ranged from 101 to 136 days, and from 83 to 126 days, for the first and second seeding date, respectively. The shorter vegetative and panicle development phases for short-season cultivars determined most of the observed differences in total growth duration. Panicle development required 16 and 32 days for RU9101001 and Starbonnet, respectively. Most of the reduction in growth duration from the first to second seeding date was due to a shorter vegetative phase. Short-season cultivars had more, smaller panicles and showed less compensation among yield components than mid- and long-season cultivars. Grain yield of the mid-season cultivar Newbonnet (9.13 to 7.94 t/ha) was not significantly higher than that of the extremely-short-season line RU9101001 (8.55 to 7.52 t/ha) for either seeding date. Yield reduction of RU9101001 from the first to second experiment was due to smaller panicles, and that of mid- and long-season cultivars was due to an increase in unfilled grains. For the first seeding date there was not a clear relationship between yield and growth duration. In the second

seeding date, the very-short-season cultivars Alan and L202 had significantly higher yields, 8.86 and 9.07 t/ha, respectively, compared to the other cultivars.

INTRODUCTION

The maturity of photoperiod insensitive cultivars is strongly affected by air temperature. The rate of plant development depends upon the amount of heat expressed in terms of degree days, or heat units over a threshold value, to which the plant is subjected during its growing period (Keisling et al., 1984; Kanyeka, 1982; Yoshida, 1981; Dua and Garrity, 1988). In Arkansas, for a particular rice cultivar, the phenological stages have been shown to be predictable with a thermal time base of 10 C (50 F) through the DD50 degree-day program (Keisling et al., 1984; Kanyeka, 1982).

The ontogeny of the rice plant is generally considered to consist of three phases, vegetative, reproductive, and ripening or grain filling. The main effect of temperature is on the vegetative period, from seeding to panicle initiation. This phase accounts for much of the variability in the growth duration of rice cultivars. A rise in temperature during the vegetative phase increases both the rate at which leaves emerge and the leaf size (Yoshida, 1981; Tanaka, 1976; Baker et al.,1990). The period from panicle initiation to heading is usually considered to be fairly constant, but it may be shorter when temperature is higher (Tanaka, 1976; Stansel, 1975a). The duration of panicle development (PD) varies from 25 to 46 days, being shorter in early-maturing cultivars, but in most situations it is about 30 days (Yoshida, 1981).

The grain-filling period (GF) of rice cultivars is generally considered as a constant for a given rice growing area, and cultivar differences are reported to be minimal. A rise in temperature increases the rate of grain filling (Jennings et al., 1979; Chang and Vergara, 1972; Tanaka, 1976). However, among 14,128 accessions from the IRRI world collection, small-grain cultivars tended to have a shorter GF period than large-grain cultivars (IRRI, 1977).

Rice yield may be expressed as the product of (a) the panicle number per unit of land area, (b) the spikelet number per panicle, (c) the filled grain percentage, and (d) the size of individual spikelets or the grain weight. Those yield components define sink size, and are determined at and before flowering (Tanaka, 1976; Yoshida and Parao, 1976).

The potential sink size or yield capacity of rice depends on the total number of spikelets per square meter and the average size of individual spikelets (Murata, 1976; Yoshida and Parao, 1976). There are often negative correlations among some yield components (Tanaka, 1976), but the tendency for filled-grain percentage to decrease with increasing spikelet number seems to be an internal varietal character (Yoshida and Parao, 1976).

In a temperate climate, solar radiation during the vegetative phase is reported to have a favorable effect on spikelet number per square meter through an increase in panicle population (Murata, 1976; Stansel, 1975b). Within a limited temperature range (24 to 29 C), there is a negative linear correlation between spikelet number per plant and daily mean temperature during the PD phase. Solar radiation during the same phase is positively correlated to spikelet number per panicle and per square meter (Murata, 1976; Yoshida and Parao, 1976; Stansel, 1975b). Spikelet number is also positively and linearly correlated with dry matter production during the reproductive phase and seems to be linked with photosynthetic production during that phase of development (Yoshida and Parao, 1976).

Grain weight does not vary substantially within a given cultivar. This constant grain weight may be determined by the size of the hull, specified during reproductive growth. Rice cultivars differ markedly in grain weight and this component has a higher heritability than the other yield components. Cultivars having low grain weight were reported to have a lower yield ceiling and lower grain growth rate than heavy-grained types (Chang and Vergara, 1972; IRRI, 1977; Akita et al., 1990). Rajewski et al. (1991) reported similar results relative to grain growth rates in sorghum, but Venkateswarlu et al. (1981) did not find this trend in a similar study dealing with a smaller group of rice cultivars.

Evans (1972) suggested that storage capacity may limit grain yield in rice, and that higher photosynthetic rates may be the result of higher storage rates. In modern cultivars under contemporary cultural practices, more than 85% of the grains are frequently filled, while appreciable levels of nonstructural carbohydrates remain in the leaves or stems, suggesting that sink size is inadequate (Murata and Matsushima, 1975). From CO_2 enrichment studies, it was concluded that, if yield capacity can be increased by varietal improvement, source activity after flowering is not likely to limit grain filling in a tropical environment (Cock and Yoshida, 1973; Yoshida, 1981). However, Venkateswarlu and Visperas (1987) and Venkateswarlu (1976) believe that this condition is valid only in a temperate climate.

All sink characters are regulated mainly by additive genetic components, indicating the promising potential of increasing yield by increasing sink size through genetic manipulations (Yoshida and Parao, 1976; Venkateswarlu and Visperas, 1987). Panicles with more primary branches and a higher percentage of high density grains can be obtained for short-, medium-, or long-season cultivars, without reducing total spikelets per panicle, resulting in an increase in grain yield (Mallik et al., 1988a, 1988b; Venkateswarlu et al., 1987: Rao, 1987).

Yield potential of very-short-season cultivars may be limited by transplanting or seeding at wide spacings, where tillering is critical (Jennings et al., 1979; Chang and Vergara, 1972; Vergara et al., 1966; IRRI, 1977). A vegetative growth duration of 45 days (total growth duration of 91 days) was not limiting for high yield potential (Venkateswarlu et al., 1987). Some scientists believe the limit has been approached and that further attempts to shorten growth duration will reduce the yield potential. With the advent of some new very-short-season breeding lines and cultivars in the Arkansas breeding program, it is necessary to determine if yield potential has been reduced and, if so, which yield components have been affected. Understanding these relationships is important in setting breeding objectives. The purpose of this work is to compare the phenology, yield and yield components of cultivars from different maturity groups.

MATERIALS AND METHODS

Plant culture. This study was conducted at the University of Arkansas Rice Research and Extension Center, Stuttgart, on a Crowley silt loam soil (Typic Albaqualfs), during the 1990 crop season. Five long-grain rice cultivars were included, with maturity periods ranging from extremely short- to long-season (92 to 131 d):

-'Starbonnet' (CI9584) is a tall (1.17 m), long-season cultivar that requires 103 days from seeding to heading. It has moderate yield potential and is susceptible to lodging. Kernel weight 16 mg (Huey and Moldenhauer, 1988).

-'Newbonnet' (PI474580) is a mid-season cultivar, requiring 95 days from seeding to heading. It has good yield potential, straw strength and lodging resistance with an average height of 1.01 m. Kernel weight is 17.5 mg.

-'L202' (PI483097) is a very-short-season, high yielding cultivar that requires 81 days to 50% heading. L202 has narrow and erect leaves with an average plant height of 0.91 m. Grains are large with a kernel weight of 20 mg, the highest among the very-short-season cultivars.

-'Alan' (PI538253) is a very-short-season high-yielding cultivar released in 1990. It is one of the earliest maturing commercial cultivars available, with 77 days to 50% heading and an average plant height of 1.04 m. Kernel weight of Alan is 15.7 mg, the lightest kernel weight among very-short-season cultivars.

-RU9101001 is an extremely-short-season line, originated from the cross BN73/9837//PI265116/3/V6DW/STTD//L 201. The line requires 68 days to 50% flowering. It has heavy kernels (22 mg) and plant height is about 0.85 m.

The cultivars were evaluated at two seeding dates with four replications. The first experiment was seeded April 24 and emerged May 5, the second experiment was seeded May 25 and emerged May 31. The rice was drill seeded at a rate of 134 kg ha^{-1}. Each plot consisted of six rows 4.6 m in length, spaced at 0.19 m. Plots were fertilized with a total of 165 kg N ha^{-1}, as urea, in a 3-way split application with 87 kg applied prior to flooding, 39 kg at internode elongation (IE), and 39 kg at booting.

Determinations. Phenological events including date of panicle initiation, beginning of anthesis, end of anthesis, and physiological maturity were recorded as a mean value for each cultivar for the four replications. Panicle initiation was estimated as the beginning of internode elongation by dissecting several tillers per plot. Degree-day accumulations were based on the DD50 Program, with a base temperature of 10 C, assigning upper limits of 34.4 and 21.1 C for daily high and low temperatures, respectively (Keisling et al., 1984).

Yield was calculated by harvesting 3.66 m of the two central rows of each plot and expressed in kg ha^{-1}, [at 120 g H_2O kg^{-1} (12% moisture)]. Yield components were determined from a sample taken before harvest at physiological maturity. The sample size was 1 m of row taken from one of the inner four rows of each plot (rows 2 or 5). The procedure consisted of counting the number of panicles in each sample (P), threshing grains from a subsample of 15 panicles, separating unfilled grains from filled grains with a seed separator, counting the number of filled grains (F) and the number of unfilled grains (U), and weighing the filled grains (W).

The four basic yield components estimated were:

- Panicles per m^2= P/sample area in m^2
- Spikelets per panicle= U+F/P
- Percentage of unfilled grains= 100 x U/F+U
- Grain weight (mg)= 1000 x W(g)/F

These basic yield components were used to calculate: spikelets per square meter, potential yield or sink size at heading, and sink to source ratio. Sink size at heading was estimated as:

Panicles per m^2 x spikelets per panicle x grain weight

Sink:source ratio was calculated by three different procedures:

a) Potential yield (g of grain)/ LAI (m^2 leaf) at flowering (IRRI, 1977).

b) Actual yield (g of grain)/ LAI (m^2 leaf) at flowering (Lafitte and Travis, 1984).

c) Actual yield (g of grain)/ LAI (m^2 leaf) at early grain filling.

Harvest index (HI) was calculated using total dry matter (Chap. 3) from the growth analysis, as well as LAI at flowering, used to calculate the sink: source ratio. LAI was obtained by measuring all leaves of a subsample of 15 tillers (Delta-T Devices), and these results were used to calculate the LAI for the whole sample by using a modification of a method proposed by Yoshida et al. (1976):

$$\text{LAI} = \frac{\text{tot. leaf area of sub-sample tillers x dry wt. of all sample tillers}}{\text{dry weight of measured sub-sample tillers}}$$

Experimental design. Each seeding date was arranged as a randomized complete block design (RCBD) with four replications. Both experiments were analyzed together as a RCBD two-factor factorial with split combined over seeding dates, testing the effects of seeding date (S), cultivars (C) and the interaction seeding date x cultivar (SxC). The least significant differences (LSD) at P=0.05 are reported for cultivars means, and for the two comparisons within the interaction SxC, cultivar means within the same seeding date, and seeding date means within the same cultivar. Phenological events were not statistically analyzed, since data did not show variability within replications for a given cultivar.

RESULTS

Phenology. The first seeding date experiment (4/24) emerged in 11 days and the second (5/25) emerged in 6 days. Growth duration of the cultivars in the first seeding experiment, as days from emergence to maturity, ranged from 101 to 136 days. In the second experiment all cultivars reduced their growth duration, reaching maturity in an interval from 83 to 126 days from emergence (Table 2a.1).

The length of the vegetative and panicle development phases were shorter in short-season cultivars. The differences in these phases generally determined the observed differences in total growth duration (Fig. 2.1). Vegetative growth of RU9101001 lasted for 48 and 34 days in the first and second seeding, respectively, and that of Starbonnet lasted 66 and 55 days. There were also large differences in the reproductive phase. RU9101001 panicles developed 18 days sooner than those of Starbonnet in the first seeding, and 15 days sooner in the second. Duration of panicle development accounted for most of the difference in days to heading between the very-short-season cultivar Alan and the extremely-short-season line RU9101001, especially in the second seeding.

Thermal time accumulations (base temperature = 10 C) for the growth phases followed the same pattern as that of calendar time. The important differences among cultivars were observed in the vegetative and panicle development phases. The very-short-season cultivar Alan required about 100 degree days more than the line RU9101001 to complete panicle development (Fig. 2.1) (Fig. 2a.1, Table 2a.1).

The vegetative growth period accounted for most of the reduction in growth duration from the first to the second seeding dates, but panicle development and anthesis did not show an appreciable difference. The extremely short-season line RU9101001 required a total of 101 and 83 days to reach maturity in the first and second seeding, respectively (Fig. 2.1).

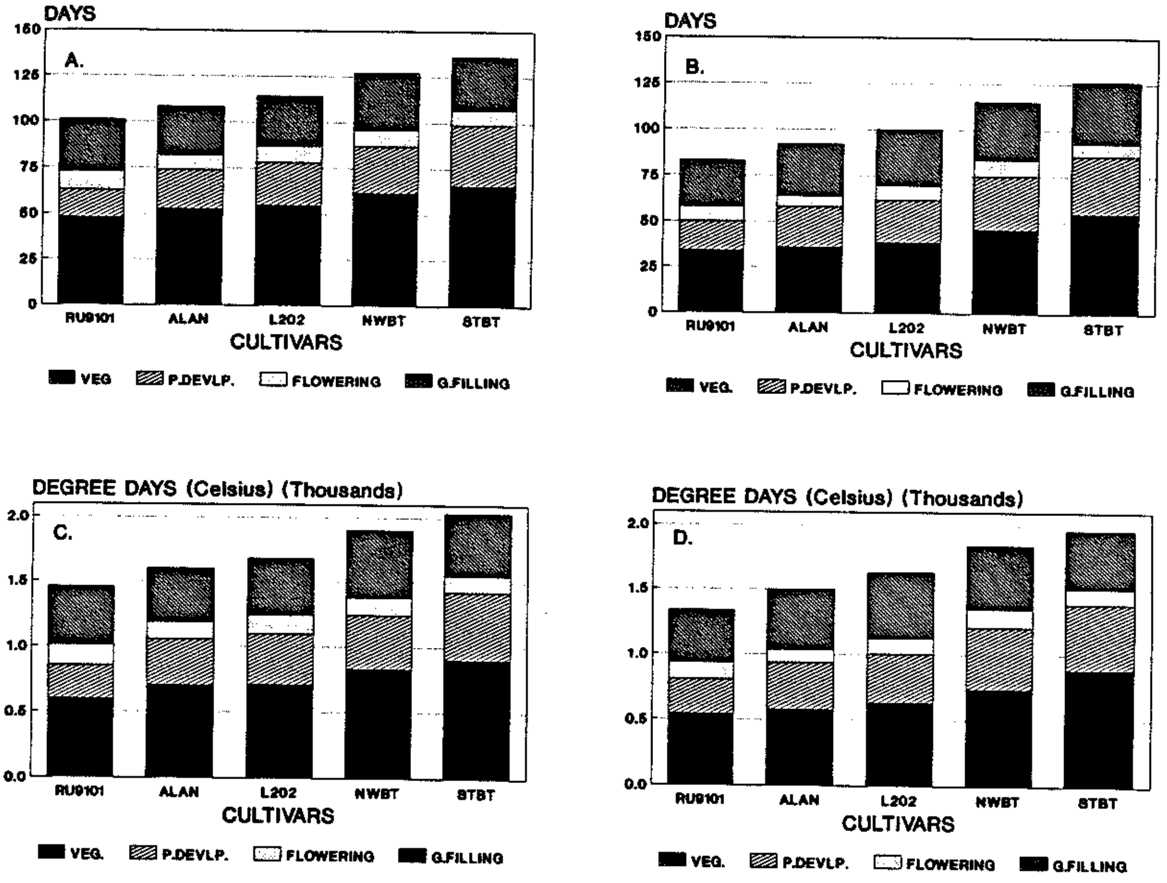


Fig. 2.1. Duration of growth phases in calendar time (days), and thermal time (degree-days) base 10 °C, for rice cultivars of different maturity groups. Calendar time for (A) first seeding and (B) second seeding date. Thermal time for (C) first seeding and (D) second seeding date. Vegetative phase: from crop emergence to internode elongation.

Degree days accumulated during the vegetative phase were reduced from the first to the second seeding by 2 to 18%, but this reduction was not as important as that observed in calendar time. Starbonnet showed the smallest reduction in degree days for the vegetative phase and Alan the largest. In this study, the DD50 accumulations for panicle development were affected only by seeding date for the cultivar Newbonnet, which tended to have a longer panicle development duration in the second seeding (Fig. 2a.1).

Table 2.1. Mean squares from the combined analysis of variance of yield components of five rice cultivars (C) grown at two seeding dates (S).

		Yield components					
Source	df	Panicles m^{-2} no.	Spklt.per panicle no.	Unfill. spklt. %	Grain weight mg	Spklt. m^{-2} no.	Filled grains m^{-2} no.
S	1	50979.6**	1311.0**	469.9**	3.08*	209869353**	327248
R(S)	6	1146.1	17.4	4.3	0.29	12556521	10385605
C	4	24004.6**	8887.4**	242.6**	86.23**	89606304**	291014174**
S x C	4	11731.3**	718.3**	125.0**	1.78*	44158628	44388840*
Error	24	2489.1	48.7	7.7	0.15	20576908	14637992
CV%		11.0	6.6	18.0	1.9	9.8	9.9

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Yield components. Cultivars, seeding dates, and the interaction of both factors had significant effects on the four basic yield components (Table 2.1). The short-season cultivars RU9101001, Alan, and L202 had more panicles per square meter than mid- and long-season cultivars in the first seeding and overall (Fig. 2.2) (Table 2a.2). Alan, Newbonnet, and Starbonnet exhibited a significant increase in panicle density from the first to the second seeding date, but the short-statured cultivars L202 and RU9101001 maintained a similar panicle number in both experiments.

The mid- and long-season cultivars Newbonnet and Starbonnet had the largest panicles overall, but showed a significant reduction in the number of spikelets per panicle in the second seeding date (Fig. 2.2). RU9101001 and L202 had smaller panicles, and although the former tended to reduce spikelet number, the latter was the only cultivar that increased panicle size in the second experiment.

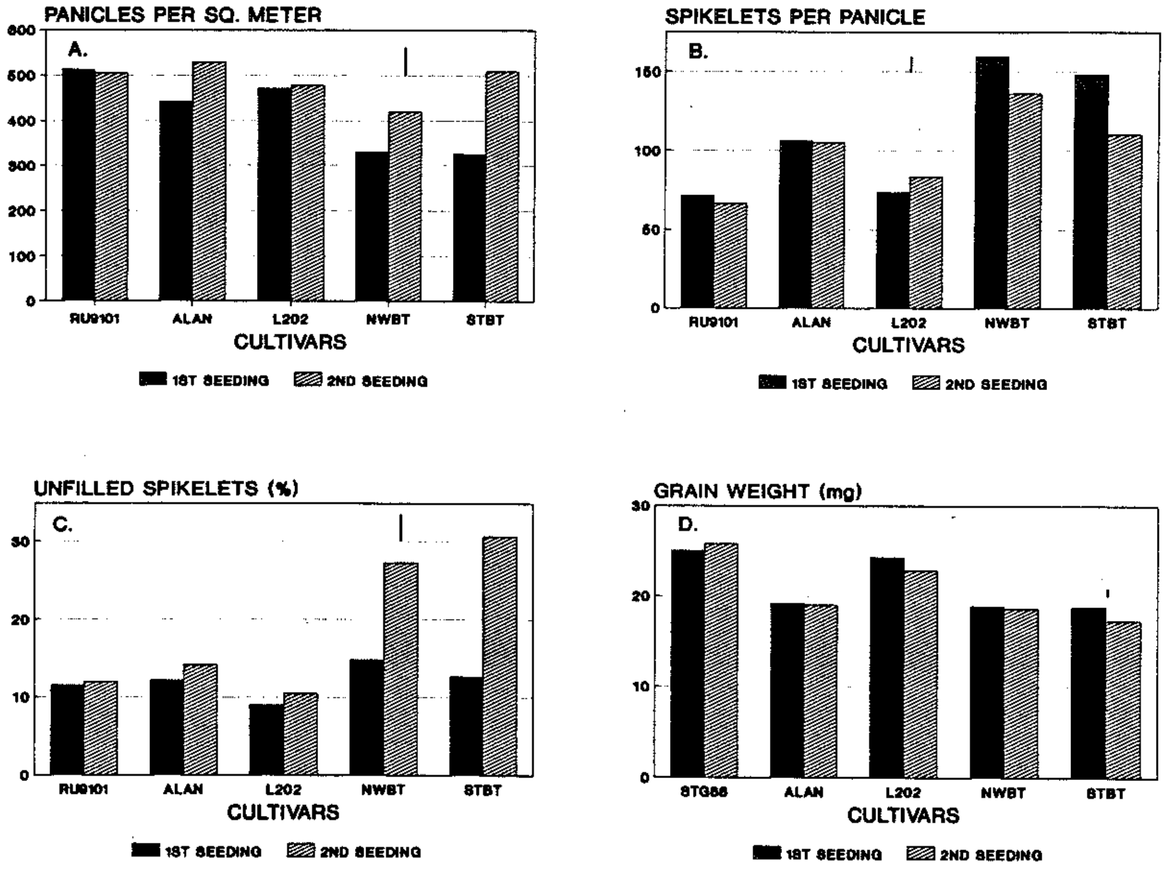


Fig. 2.2. Yield components of rice cultivars of different maturity groups grown at two seeding dates: (A) panicles m^{-2}, (B) spikelets per panicle, (C) unfilled spikelet percentage, and (D) grain weight. The bars indicate the LSD at P=0.05.

There were no important differences among cultivars for unfilled grain percentage in the first seeding date; however, Newbonnet and Starbonnet had sharp increases in unfilled grains in the second date (Fig. 2.2). Starbonnet lodged before maturity, and Newbonnet showed an early senescence of the leaves during the last half of ripening due to a stem rot (Sclerotium spp.) infection, resulting in the lowest number of active leaves at harvest. For these reasons, grain filling could have been disturbed in both cultivars.

RU9101001 had the heaviest grains, followed by L202. The former increased grain weight from the first to the second seeding date, but the latter and Starbonnet decreased grain weight (Fig. 2.2).

Sink size or potential yield at heading. Alan, Starbonnet, and Newbonnet had more spikelets per square meter than RU9101001 and L202 in both experiments. All cultivars, except the extremely short-season line RU9101001, showed a trend to increase the number of spikelets per ground area from the first to the second seeding date (Fig. 2.3). This increase in spikelets per m^2 was significant for Alan and Starbonnet. However, as a result of the high percentage of unfilled grains in the mid- and long-season cultivars Newbonnet and Starbonnet, only Alan had significantly more filled grains per square meter at the second seeding date. L202 showed the same trend but the difference was not significant (Fig. 2.3).

An estimation of the sink size or potential yield of each cultivar at heading was obtained by combining the total number of spikelets per square meter and the grain weight (IRRI, 1977). In the first trial, yield potentials of all cultivars, except L202, were higher than 900 g per square meter (9 t ha^{-1}). The heavier grains of RU9101001 compensated for the lower number of grains per unit ground area, and its yield potential was not significantly different from that of Newbonnet. In the second date, however, RU9101001 had a significantly lower yield potential at heading than that of Newbonnet or Alan (Fig. 2.3, Table 2.2).

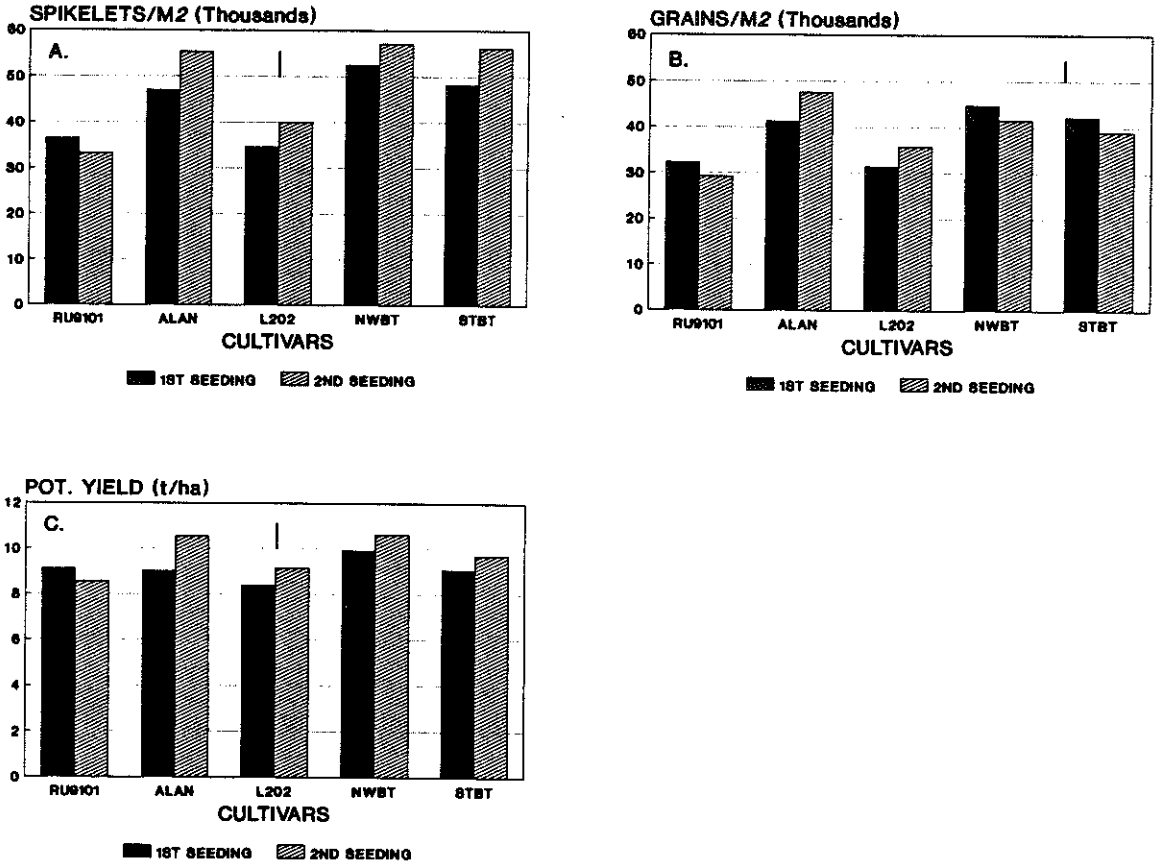


Fig. 2.3. Effect of seeding date on (A) total number of spikelets, (B) filled spikelets or grains per square meter and (C) sink size or potential yield developed at flowering by rice cultivars of different maturity groups. The bars indicate the LSD at P=0.05.

Table 2.2. Mean squares from the combined analysis of variance of sink size, yield, harvest index and sink:source ratio of five rice cultivars (C) grown at two seeding dates (S).

					Sink:source		
Source	df	Potent. Yield(1) g m^{-2}	Yield t ha^{-1}	Harvest Index	Potent./ LAIf(2)	Actual/ LAIf(3)	Actual/ LAIgf(4)
					------ g grain m^{-2} leaf ------		
S	1	35700.1*	2.316#	0.008**	2839.2	10903.2**	10595.0*
R(S)	6	4966.8	0.469	0.0002	1631.9	791.8	967.7
C	4	32552.0*	2.067**	0.020**	7984.4**	11689.8**	11703.3**
S x C	4	11264.8	1.523**	0.004**	747.1	1337.3#	2115.8
Error	24	9492.4	0.175	0.0002	1227.7	534.4	1282.9
CV%		0.4	5.0	2.9	17.8	13.1	16.0

(1) Potential yield= (total spikelets m^{-2}) x (grain weight). Not accounting for sterility.
(2) Potential yield / LAI at flowering.
(3) Actual yield / LAI at flowering.
(4) Actual yield / LAI at grain filling.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
Significant at the 0.10 probability level.

Yield. Newbonnet produced the highest yield in the first seeding date experiment, 9.131 t ha^{-1}. This was not significantly different from that of L202 and RU9101001, which were 8.632 and 8.546 t ha^{-1}, respectively. In the second date, RU9101001, Newbonnet and Starbonnet had significant yield reductions, while yields of Alan and L202 tended to increase (Table 2.2, Fig. 2.4). The differences observed between the potential yield and the actual yield are due to unfilled grains and the sampling error of yield components.

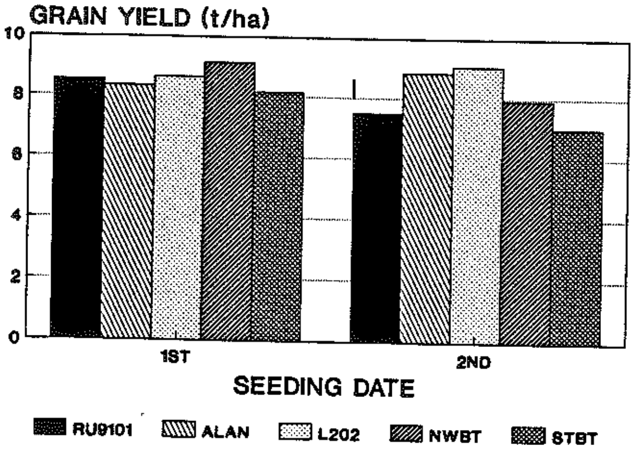


Fig. 2.4. Grain yield of rice cultivars of different maturity groups at two seeding dates. The bar indicates the LSD at P= 0.05 for cultivar means within seeding date.

Sink to source ratios. In the first seeding date, the cultivars developed an adequate sink size or yield potential despite the lower LAI at heading (3.84 to 5.62). In the second seeding date, relative high LAI's, as those of Newbonnet, Alan, and Starbonnet, of 5.52, 6.16, and 7.12, respectively, were associated with larger sink size at heading, but this was not reflected in the observed yield, since L202 and Alan had the highest production with LAI's as different as 4.28 and 6.16 (Table 2a.3).

Sink to source ratios are expressed in grams of grain per square meter of leaf. When potential yield was used in the calculations, with LAI at flowering, there were no significant effects for seeding date and for the interaction with cultivar. Alan and Starbonnet maintained a low ratio for both seeding dates, while RU9101001, Newbonnet, and L202 had the highest sink:source ratios, from 227 to 212 g m^{-2} (Table 2a.3) (Fig. 2.5). When actual yield (from harvested plots) was used to describe the ratio, the overall sink:source ratio of the first seeding date was higher than that of the second. In that experiment, RU9101001, L202, and Newbonnet had the highest ratios, but only L202 maintained the same value in the second seeding date. RU9101001 and L202 had mean ratios of 206 and 218 g of grain m^{-2} of leaf, Starbonnet had the lowest (123 g m^{-2}), and Newbonnet and Alan were intermediate.

As LAI decreased, from flowering to maturity (Chap. 3) (Table 2a.3), at different rates in each cultivar, LAI at early grain filling (12 days after 50% heading) may be more appropriate to represent the average LAI during that period of growth. When this value of LAI was used with actual yield, L202 (264 g m^{-2}), RU9101001 (246 g m^{-2}), and Newbonnet (232 g m^{-2}) had the highest sink:source ratios overall (Fig. 2.5) (Table 2a.3).

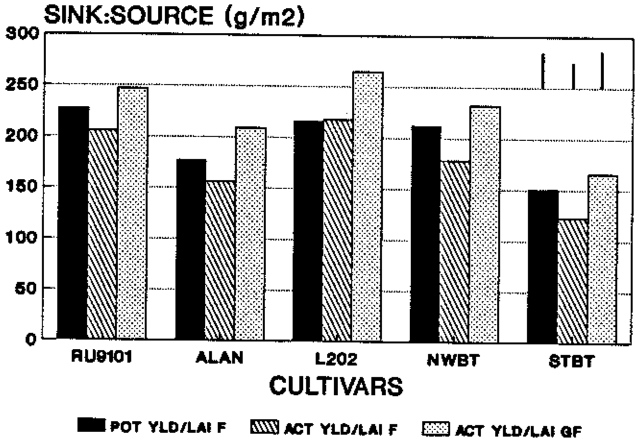


Fig. 2.5. Different estimations of sink:source ratio (g grain m^{-2} leaf) for rice cultivars: sink size or potential yield at flowering/ LAI at flowering, actual yield/ LAI at flowering, and actual yield/ LAI at early grain filling. The bars indicate the LSD at P= 0.05 for each estimation. Each value is the mean of two seeding dates and four replications.

Harvest index. HI was generally higher in the short-season cultivars, especially in RU9101001 and L202. The extremely short-season line showed the highest value (0.54) in the first seeding date. The mid- and long-season cultivars, Newbonnet and Starbonnet, reduced their HI in the second seeding due to the increased percentage of unfilled grains (Table 2a.3).

DISCUSSION

Phenology. Variation in the length of the vegetative and reproductive phases were responsible for most of the differences in total growth duration among cultivars. Varietal differences in the length of the panicle development phase (15 to 33 days) were more important than those reported in the literature (Tanaka, 1976; Yoshida, 1981), especially among short-season cultivars. The duration of this phase was not affected by seeding date.

The very-short-season cultivar Alan had a total growth duration which was 19 days shorter (330 degree days) than that of the mid-season cultivar Newbonnet, when seeded at the optimal date, as defined by the University of Arkansas Cooperative Extension Service. This shorter growth duration was accomplished without a dramatic difference in the length of the panicle development period, 21 and 25 days for Alan and Newbonnet (348 and 408 degree-days), respectively. However, a large part of the difference in total growth duration between Alan and the extremely-short-season line RU9101001 was due to the shorter reproductive phase of the line (15 days or 252 degree days).

Yoshida (1981) and Murata and Matsushima (1975) indicated that, if the panicle development period can be extended independently of the vegetative phase, yield potential of very-short-season cultivars may be increased. A further study of several extremely-short-season breeding lines may show variability for the length of the panicle development phase within the maturity group. For the cultivars included in the present report, a short reproductive phase was important to determine the reduction in total growth duration from the short-season to the extremely short-season maturity group.

Most of the reduction in growth duration from the first to the second seeding was caused by a shorter vegetative period. The reduction in the length of the vegetative phase ranged from 17 to 32% in calendar time, but was less pronounced in thermal time, i.e. 2 to 18%, indicating that the most important factor involved was the higher temperature during the vegetative phase of the second seeding. The smaller degree-day accumulations for the vegetative phase of the very-short-season cultivars in the second seeding suggest that a day-length effect may also be present in the induction of panicle initiation or that the present temperature limiters built into the DD50 program are not accurate for these cultivars (B. R. Wells, personal communication). Alan had the largest reduction, 18%, in the degree-days required to reach the reproductive phase, resulting in a vegetative period similar to that of RU9101001, while Starbonnet showed almost no reduction. Lack of response to day length may be desirable in extremely-short-season cultivars, to avoid a sharp reduction in the vegetative growth when seeded late in the season.

Yield components. Despite the shorter vegetative periods and reduced time for tillering, the extremely-short-season line RU9101001 and the very-short-season cultivars Alan and L202 showed a greater number of panicles per square meter than Newbonnet and Starbonnet. Venkateswarlu et al. (1987) reported similar results for lines having vegetative periods of 45 days.

Most of the cultivars included in the study had an increase in sink size, defined as the number of spikelets per square meter x grain weight, in the second seeding date. This increase was achieved by the cultivars through different means. Newbonnet (mid-season), and Starbonnet (long-season) had intermediate to tall plant height, low number of panicles per ground area (375 to 418), large panicles (148 to 129 spikelets) and small grain weight (18.7 to 18.1 mg). Alan (very-short-season) had more (485) but smaller panicles (106 spikelets) than Newbonnet, and slightly heavier grains (19.1 mg). Average temperature during the vegetative phase was about 3 C higher in the second seeding, and these three cultivars had an important increase in panicles per square meter, mainly because of a higher retention of tillers (Chap. 3).

Newbonnet and Starbonnet showed the expected negative association between panicle number and spikelets per panicle, with a reduction in panicle size from the first to the second seeding date. Starbonnet also showed a reduction in grain weight that was not observed in Newbonnet. However, the balance of these components resulted in an increase in sink size or potential yield at heading. Alan did not follow this trend, breaking this negative association among yield components. The increased yield capacity of this cultivar, in the second trial, was due to more panicles, without any change in panicle size or grain weight. This higher yield potential was not realized in the mid- and long-season cultivars because of an increase in the percentage of unfilled grains. As this problem was not important in Alan, grain yield tended to increase (Fig. 2.3 and 2.4).

RU9101001 (extremely-short-season) and L202 (short-season) had moderate to short plant height, high number of panicles per ground area (509 to 474), small panicles (69 to 79 spikelets), and heavy grains (25.4 to 23.5 mg). In L202, panicle number and spikelet number were not negatively associated, and the increase in sink size in the second seeding came from larger panicles without changes in panicle number. Grain weight for L202 did show a negative relation to spikelets per square meter and was lower in the second date, but there was still an increase in potential yield. This was noted in actual yield because the unfilled grain percentage was the lowest in L202, increasing the yield in the second trial (Fig. 2.3 and 2.4).

RU9101001 tended to reduce its yield in the second seeding. With higher temperatures during the vegetative phase of the second seeding date, the extremely-short-season line developed a larger LAI in a shorter time. The smaller number of grains per panicle were not compensated for by further increases in grain weight. This may be the result of competition for assimilates with the elongating internodes and upper leaves during the development of the panicle or a reduction in sunlight rather than a temperature effect (Yoshida and Parao, 1976), because temperature during the reproductive period of both experiments was about the same. The extremely-short-season line did not show a reproductive phase overlapped with vegetative phase (Growth Pattern Type B, Tanaka, 1976), since tiller number decreased after panicle initiation (Chap. 3).

A vegetative period of 48 days and a panicle development phase of 15 days in the first seeding date were not limiting for a reasonable yield in RU9101001 (8.55 t ha^{-1}), since it was not significantly different from that of the high-yielding mid-season cultivar Newbonnet (Fig. 2.4). Under these circumstances RU9101001 showed a high sink:source ratio. An even shorter vegetative period, as that of the second seeding date (34 days), did not seem to limit the number of panicles, but panicle size was limited by some of the factors already mentioned, and yield potential and the sink:source ratio were reduced (Fig. 2.3). If the sink size could be increased in this line, source activity should not be limiting, since concentration of storage carbohydrates increased during late grain filling of the second seeding date (Chap. 4).

A very short period for panicle development, 15 days compared to 25 days, coupled with a short vegetative growth, may make a cultivar relatively more susceptible to a period of cloudy weather. An increase in the yield component grain weight, which is less sensitive to environmental influences or to competition for assimilates during the reproductive phase, may be an important factor for achieving a reasonable and stable yield potential in extremely-short-season cultivars having a short period for panicle growth.

REFERENCES

Akita, S., C.N. Bollich, and B.D. Webb. 1990. Physiological analysis of energy partitioning among organs for lodging resistance in rice (Oryza sativa L.). Proc. of the XXIII Rice Technical Working Group. Biloxi. Mississippi.

Baker, J.T., L.H. Allen Jr., and K.J. Boote. 1990. Effects of atmospheric carbon dioxide concentration and air temperature on development, growth, and yield of paddy rice. Proc. of the XXIII Rice Technical Working Group. Biloxi. Mississippi.

Chang, T.T., and B.S. Vergara. 1972. Ecological and genetic information on adaptability and yielding ability in tropical rice varieties. p.431-453. In Rice breeding. IRRI. Los Banos. Philippines.

Cock, J.H., and S. Yoshida. 1972. Accumulation of 14C-labelled carbohydrate before flowering and the subsequent redistribution and respiration in the rice plant. Proc. Crop Sci. Soc. Jpn. 41:226-234.

Dua, A.B., and D.P. Garrity. 1988. Models for predicting rice flowering. Int. Rice Res. Newslett. 13(2):7-8.

Evans, L.T. 1972. Storage capacity as a limitation on grain yield. p.499-511. In Rice breeding. IRRI. Los Banos. Philippines.

Huey, B., and K. Moldenhauer. 1988. Choosing a profitable variety. p.11-13. In Rice production handbook. MP 192. Cooperative Ext. Center, Univ. of Arkansas and US Dep. Agric.

Int. Rice Res. Inst. 1977. Growth duration, plant height, and yield. p. 21-25. In Annual report for 1976. IRRI. Los Banos. Philippines.

Jennings,P.R., W.R. Coffman, and H.E. Kauffman. 1979. Rice improvement. IRRI. Los Banos. Philippines.

Kanyeka, Z.L. 1982. Use of temperature data to estimate development stages of rice varieties. M.S. Thesis. Univ. of Arkansas, Fayetteville.

Keisling, T.C., B.R. Wells, and G.L. Davis. 1984. Rice management decision aids based upon thermal time base 50 F. Extension Computer Technical Bulletin No. 1. Cooperative Ext. Service, Univ. of Arkansas, US Dep. Agric.

Lafitte, H.R., and R.L. Travis. 1984. Photosynthesis and assimilate partitioning in closely related lines of rice exhibiting different sink:source relationships. Crop Sci. 24:447-452.

Mallik, S., A.M. Aguilar, and B.S. Vergara. 1988a. Inheritance of high density grain in rice. Int. Rice Res. Newslett. 13(6):8-9.

-----, -----, and -----. 1988b. Rice panicle characteristics. Int. Rice Res. Newslett. 13(5):7-8.

Murata, Y., and S. Matsushima. 1975. Rice. p.73-99. In Crop physiology. Some case histories. L.T. Evans. Cambridge University Press. London.

-----. 1976. Productivity of rice in different climatic regions of Japan. p. 449-470. In Climate and rice. IRRI. Los Banos. Philippines.

Rajewski, J.F., C.A. Francis, and J.D. Eastin. 1991. Differential responses to defoliation of grain sorghum yield components and yield-related traits. Crop Sci. 31:561-567.

Rao, S.P. 1987. High density grain index among primary and secondary tillers of short and long-duration rices. Int. Rice Res. Newslett. 12(4):12.

Stansel, J.W. 1975a. The rice plant- Its development and yield. p.9-21. In Six decades of rice research in Texas. Res. Monogr. #4. Texas Agric. Exp. Stn. and US Dep. Agric., College Station, TX.

-----. 1975b. Effective utilization of sunlight. p.43-50. In Six decades of rice research in Texas. Res. Monogr. #4. Texas Agric. Exp. Stn. and US Dep. Agric., College Station, TX.

Tanaka, A. 1976. Comparisons of rice growth in different environments. p. 429-448. In Climate and rice. IRRI. Los Banos. Philippines.

Venkateswarlu, B. 1976. Source-sink interrelationships in lowland rice. Plant Soil 44:575-586.

-----, G.S.V. Prasad, and A.S.R. Prasad. 1981. Studies on the nature of relationships between grain size, spikelet number, grain yield and spikelet filling in late duration varieties of rice (*Oryza sativa* L.). Plant Soil 60:123-130.

-----, and R.M. Visperas. 1987. Source-sink relationships in crop plants. IRRI Res. Paper Series No. 125. IRRI. Los Banos. Philippines.

-----, B.S. Vergara, and R.M. Visperas. 1987. Influence of vegetative growth duration on grain grade. Int. Rice Res. Newslett. 12(1):4-5.

Vergara, B.S., A. Tanaka, R. Lilis, and S. Puranabhavung. 1966. Relationships between growth duration and grain yield of rice plants. Soil Sci. Plant Nutr. 12(1):31-39.

Yoshida, S. 1981. Fundamentals of rice crop science. IRRI. Los Banos. Philippines.

-----, D.A. Forno, J.H. Cock, and K.A. Gomez. 1976. Laboratory manual for physiological studies of rice. IRRI. Los Banos. Philippines.

-----, and F.T. Parao. 1976. Climatic influence on yield and yield components of lowland rice in the tropics. p. 471-494. In Climate and rice. IRRI. Los Banos. Philippines.

APPENDIX

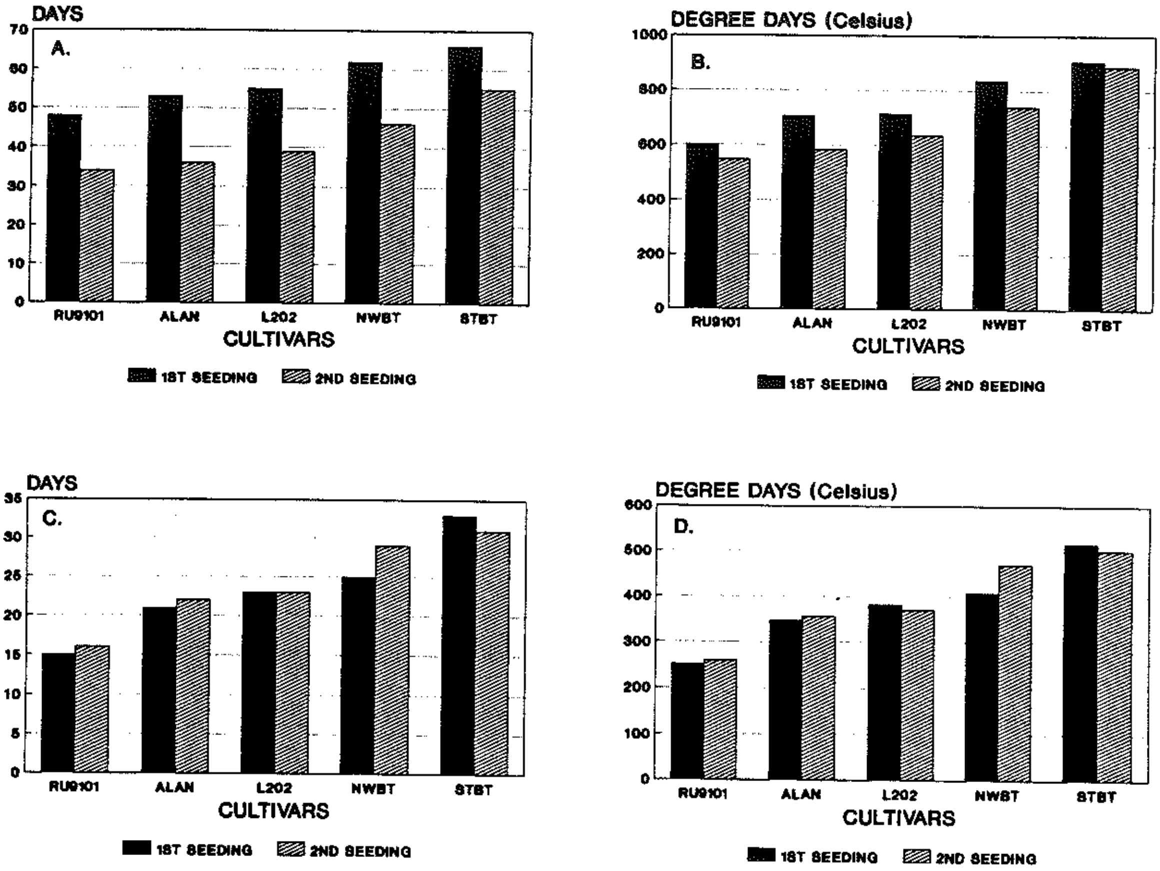


Fig. 2a.1. Effect of seeding date on duration of vegetative (A, B) and panicle development (C, D) phases, expressed in calendar time (days) and thermal time, base 10 °C (degree-days), in rice cultivars of different maturity groups: (A) vegetative phase, calendar time, (B) vegetative phase, thermal time, (C) panicle development phase, calendar time, and (D) panicle development phase, thermal time.

Table 2a.1. Length of different growth phases in calendar time (days) and thermal time (degree days) for five rice cultivars grown at two seeding dates. Degree day accumulations are based on the DD50 program, with a base temperature of 10 C.

Growth phase	RU9101001	Alan	L202	Newbonnet	Starbonnet
	Calendar time (days)				
	1st seeding				
Vegetative (1)	48	53	55	62	66
Panicle development	15	21	23	25	33
Anthesis	10	8	9	9	8
Grain filling	28	26	27	31	29
Total (1)	101	108	114	127	136
	2nd seeding				
Vegetative (1)	34	36	39	46	55
Panicle development	16	22	23	29	31
Anthesis	8	6	8	9	7
Grain filling	25	28	30	31	33
Total (1)	83	92	100	115	126
	Thermal time (degree days, °C)				
	1st seeding				
Vegetative (1)	602	706	713	836	907
Panicle development	252	348	382	408	516
Anthesis	157	132	149	136	131
Grain filling	444	414	434	521	481
Total (1)	1454	1572	1678	1901	2034
	2nd seeding				
Vegetative (1)	546	582	635	739	887
Panicle development	259	356	370	469	501
Anthesis	132	99	121	145	123
Grain filling	398	458	507	489	448
Total (1)	1335	1494	1632	1841	1958

(1): from crop emergence to panicle initiation.

Table 2a.2. Cultivar means for yield components, sink size at heading, and yield at each seeding date and overall.

	Yield components							
Cultivar	Panic. m^{-2} no.	Spklt. per panic. no.	Unfill. spklt. %	Grain wt. mg	Spklt. m^{-2} no.	Filled spklt. m^{-2} no.	Pot.(1) yield $g\ m^{-2}$	Yield $t\ ha^{-1}$
				1st seeding				
RU9101001	514	71	11.5	25.0	36447	32242	912.3	8.546
Alan	442	107	12.2	19.2	47048	41251	902.5	8.349
L202	471	74	9.0	24.3	34635	31491	838.0	8.632
Newbonnet	330	160	14.8	18.9	52559	44805	991.5	9.131
Starbonnet	327	148	12.7	18.8	48241	42180	908.0	8.149
Mean	417	112	12.0	21.2	43786	38394	910.5	8.561
				2nd seeding				
RU9101001	505	66	12.0	25.8	33147	29151	853.8	7.520
Alan	529	105	14.1	19.0	55395	47556	1052.8	8.858
L202	478	84	10.5	22.8	39995	35745	913.5	9.068
Newbonnet	420	136	27.3	18.6	57098	41529	1061.5	7.939
Starbonnet	509	111	30.7	17.3	56200	38893	969.5	7.016
Mean	488	100	18.9	20.7	48367	38575	970.2	8.080
				Mean of 2 seeding dates				
RU9101001	509	69	11.7	25.4	34797	30696	883.0	8.033
Alan	485	106	13.2	19.1	51221	44403	977.6	8.603
L202	474	79	9.7	23.5	37315	33618	875.8	8.850
Newbonnet	375	148	21.0	18.7	54828	43167	1026.5	8.535
Starbonnet	418	129	21.7	18.1	52221	40537	938.8	7.583
LSD P=0.05:								
Cult.(C)	51.48	7.20	2.87	0.40	4681.1	3948.2	100.54	0.43
S x C(a)	72.81	10.18	4.06	0.57	-	5583.6	-	0.61
(b)	70.09	9.65	3.96	0.65	-	5570.7	-	0.76

(1) Potential yield= (total spikelets m^{-2}) x (grain weight). Not accounting for sterility.
a: Cultivar means within the same seeding date.
b: Seeding date means within the same cultivar.

Table 2a.3. Cultivar means for harvest index, LAI at flowering (LAIf), LAI at grain filling (LAIgf), and sink:source ratio at each seeding date and overall.

Cultivar	Harvest Index	LAIf	LAIgf	Sink:source		
				Pot./ LAIf(1)	Actual/ LAIf(2)	Actual/ LAIgf(3)
				----- g grain m^{-2} leaf ------		
			1st seeding			
RU9101001	0.54	3.84	3.48	244	224	253
Alan	0.49	5.09	3.99	178	164	210
L202	0.51	4.00	3.24	212	217	271
Newbonnet	0.52	4.39	3.48	229	211	271
Starbonnet	0.44	5.62	4.28	163	146	194
Mean	0.50	4.59	3.69	205	193	240
			2nd seeding			
RU9101001	0.51	4.14	3.21	210	187	240
Alan	0.50	6.16	4.31	177	148	208
L202	0.53	4.28	3.53	220	218	258
Newbonnet	0.44	5.52	4.15	195	145	194
Starbonnet	0.37	7.12	5.21	139	100	137
Mean	0.47	5.45	4.08	188	160	207
			Mean of 2 seeding dates			
RU9101001	0.52	3.99	3.34	227	206	246
Alan	0.49	5.62	4.15	177	156	209
L202	0.52	4.14	3.39	216	218	264
Newbonnet	0.48	4.96	3.81	212	178	232
Starbonnet	0.40	6.37	4.74	151	123	166
LSD P=0.05:						
Cult.(C)	0.015			36.159	23.855	36.962
S x C (a)	0.021			-	33.735	-
(b)	0.022			-	-	-

(1) Potential yield / LAI at flowering.
(2) Actual yield / LAI at flowering.
(3) Actual yield / LAI at grain filling.
a: Cultivar means within the same seeding date.
b: Seeding date means within the same cultivar.

CHAPTER 3

GROWTH AND DRY MATTER PARTITIONING OF RICE CULTIVARS OF DIFFERENT MATURITY GROUPS

ABSTRACT

Higher growth rates of extremely-short-season rice (Oryza sativa L.) cultivars, especially during reproductive and ripening phases, may compensate for a short period of growth. This research studied dry matter partitioning and growth patterns of rice cultivars from different maturity groups, using growth analysis techniques. The line RU9101001 and cultivars 'Alan', 'L202', 'Newbonnet' and 'Starbonnet', with maturity periods ranging from extremely-short- to long-season, were evaluated at two seeding dates, April 24 and May 25, 1990, at Stuttgart, AR. Cultivars were sampled at internode elongation, 50% flowering, 12 days after flowering, and maturity. Leaf area and dry weight were used to calculate leaf area index (LAI), crop growth rate (CGR), net assimilation rate (NAR), panicle growth rate, and specific leaf weight. The cultivars did not overlap vegetative and reproductive phases. Tiller number decreased from internode elongation to maturity and tiller retention was higher in short-season cultivars. The very-short-season cultivar Alan produced similar or higher LAI at flowering than did Newbonnet. The longer the growth duration of the cultivar, the smaller the dry weight accumulation observed from flowering to maturity. For the mean of both seeding dates, this increase ranged from 66 to 18% for RU9101001 and Starbonnet, respectively. Mean CGR and NAR were inversely related to maturity group. Mean CGR of RU9101001 for the whole season, in the second experiment, was 17.9 g m^{-2} d^{-1}. RU9101001 and Alan had higher CGR during the reproductive and late grain-filling phases, with rates of 30 g m^{-2} d^{-1} during panicle development. Both cultivars maintained high NAR during late grain filling. The high CGR and NAR of the

earliest-maturing cultivars resulted in yields similar or higher than those observed in the high-yielding mid-season cultivar Newbonnet.

INTRODUCTION

Rice cultivars have different dry matter accumulation patterns. Tanaka (1976) classified rice growth curves into several types. The normal growth curve has a continuous moderate growth rate followed by a slight decrease at the end, is generally associated with a moderate total dry matter production, and large harvest index (Type II). Traditional, tall cultivars have a vigorous growth at early stages followed by a weak growth at later stages and, sometimes, a decrease in weight (Type I), and this is associated with a large total dry matter production and small harvest index. With abundant solar radiation and good plant type, some cultivars may show a moderate or high growth rate during early stages followed by a high growth rate during later stages (Type V). Yield may be extremely high due to large values of total dry matter production and harvest index (Tanaka, 1976).

Mean crop growth rates (CGR), obtained by dividing total dry matter production by the number of days from transplanting to maturity, are reported to be as high as 14.08 g m^{-2} d^{-1} (Murata, 1976), while the long-term CGR of an erect-leaved cultivar can reach 22.9 g m^{-2} day^{-1}. Maximum short-term CGR recorded for rice is reported to be 36 g m^{-2} day^{-1} (Yoshida, 1981). Dry matter production is generally higher in late-maturing cultivars than in early-maturing ones, while the situation is the reverse for mean CGR (Murata, 1976).

Leaf area index (LAI) of plants increases rapidly for some time after the maximum tiller number stage. The plant attains its maximum LAI near heading time. Leaf area then decreases as the rice plant matures due to the death of lower leaves. No optimum LAI is observed in populations with good plant type. Rather, there is a ceiling or critical LAI (Tanaka, 1972; Yoshida, 1981). A fast increase in LAI at early growth phases is frequently associated with a low CGR during later growth stages, whereas a rather slow growth at early stages is associated with a high CGR late in the season. Panicle initiation generally occurs after the maximum tiller number, but in some very-short-season cultivars, tillering continues after panicle initiation, resulting in a reduced yield potential (Tanaka, 1976).

The increase in total dry matter and carbohydrates during grain filling and the photosynthetic rate measured during the same period usually show a close correlation with grain yield. At anthesis and grain filling, the leaf nitrogen content, photosynthetic rate, and CGR are generally higher in short-season cultivars (Vergara et al., 1966; Murata and Matsushima, 1975; Chang and Vergara, 1972). Remobilization of stored carbohydrates for grain development may be one of the reasons for low growth efficiency of the whole plant after flowering, but it is not as important in short-season cultivars, and this may contribute to higher growth rates during grain filling in these cultivars (Vergara et al., 1966; Tanaka, 1972; Yoshida, 1981).

Compared to other C3 species, rice has a relatively higher net photosynthetic rate per unit of leaf area. The CO_2 assimilation rate typical of rice is considered to be about 1.3 mg CO_2 m^{-2} s^{-1} (Sinclair and Horie, 1989). Some papers indicate a rate of 1.11 to 1.39 mg CO_2 m^{-2} s^{-1} (Yoshida, 1981). Leaf apparent photosynthesis is reported to be 0.75 to 0.85 mg CO_2 m^{-2} s^{-1} (Lafitte and Travis, 1984; Imaizumi et al., 1990). Canopy net photosynthesis reaches a maximum at the time of canopy closure and begins to decline after flowering (Baker et al., 1990). Recently, Imaizumi et al. (1990) found high levels of activity of enzymes involved in C4 photosynthesis in spikelets, and indicated the possible existence of C3-C4 intermediate photosynthesis or C4-like photosynthesis in rice lemmas and paleas. Crop respiration is closely related to gross photosynthesis (40%) over a wide range of values of LAI until 2 weeks after flowering (Tanaka, 1972; Yoshida, 1981).

Some very-short-season cultivars have been released by the Arkansas rice breeding program, and extremely-short-season breeding lines are being tested. Some of these lines may be approaching the limit of the shortest possible growth duration without a reduction in yield potential; however, their higher growth rates may compensate for a reduced period of growth. The purpose of this work is to study dry matter partitioning and growth patterns of rice cultivars of different maturity groups, using growth analysis techniques.

MATERIALS AND METHODS

Plant culture. The study was conducted at the University of Arkansas Rice Research and Extension Center, Stuttgart, on a Crowley silt loam soil (Typic Albaqualfs) during the 1990 crop season. Five long-grain cultivars were included with maturity periods ranging from extremely short- to long-season:

-Starbonnet is a tall (1.17 m), long-season cultivar that requires 103 days from seeding to heading, is susceptible to lodging, and has a good seedling vigor.

-Newbonnet is a mid-season high yielding cultivar, requiring 93 days from seeding to heading, with an average height of 1.01 m.

-L202 is a short-season, high yielding cultivar that requires 81 days to 50% heading. L202 has narrow and erect leaves with an average plant height of 0.91 m.

-Alan is a very-short-season, high-yielding cultivar that was released in 1990. It is one of the earliest maturing commercial cultivars available with 77 days to 50% heading and with an average plant height of 1.04 m.

-RU9101001 is an extremely-short-season line with large kernels and a plant height of about 0.85 m. The line requires 68 days to 50% flowering.

The cultivars were evaluated at two seeding dates with four replications. The first experiment was seeded April 24 and emerged May 5, the second was seeded May 25 and emerged May 31. The rice was drill seeded at a rate of 134 kg ha^{-1}. Each plot consisted of six rows of 4.6 m in length, spaced at 0.19 m. Plots were fertilized with a total of 165 kg N ha^{-1}, as urea, in a three-way split application with 87 kg applied prior to flooding, 39 kg at internode elongation, and 39 kg at booting.

Sampling and Growth Analysis. Each cultivar was sampled at four growth stages: 1) internode elongation (IE), 2) 50% flowering (F), 3) 12 days after 50% flowering (F+12), and 4) physiological maturity (MAT). Results for most of the variables are reported as mean values for each growth stage. Some variables, as crop growth rate (CGR), net assimilation rate (NAR), relative growth rate (RGR), and panicle growth rate (PGR), are reported as mean values for the growth phases between samples (emergence to 1, 1 to 2, 2 to 3, 3 to 4). These growth phases are defined as: vegetative (VG), panicle development (PD), early grain filling (EGF), and late grain filling (LGF), respectively. The NAR, RGR, and PGR were calculated only for the last three phases.

Sample size was 1 m of row, taken from one of the inner four rows of the plot (rows 2 or 5). A sub-sample of 15 tillers was divided into leaf, sheath, stem, and panicle components, for the calculation of dry matter and leaf area. After measuring leaf area (Delta-T Devices), the samples were dried at 85 C for 2 h, and then at 65 to 70 C for 3 days. Dry matter and leaf area determinations were used to calculate LAI, specific leaf weight (SLW), CGR, PGR, RGR, and NAR. The LAI and SLW were calculated at each growth stage, and CGR, PGR, RGR, and NAR were calculated as mean values for time intervals between sampling times, according to formulas reported by Gardner et al. (1985):

$\mathrm{SLW} = \mathrm{LW}/\mathrm{LA} = \mathrm{g\ m^{-2}}$

$\mathrm{CGR} = (1/\mathrm{GA})\ (\mathrm{W2}-\mathrm{W1})/(\mathrm{T2}-\mathrm{T1}) = \mathrm{g\ m^{-2}\ d^{-1}}$

$\mathrm{PGR} = (1/\mathrm{GA})\ (\mathrm{PW2}-\mathrm{PW1})/(\mathrm{T2}-\mathrm{T1}) = \mathrm{g\ m^{-2}\ d^{-1}}$

$\mathrm{RGR} = (\mathrm{Ln\ W2}-\mathrm{Ln\ W1})/(\mathrm{T2}-\mathrm{T1}) = \mathrm{g\ g^{-1}\ d^{-1}}$

$\mathrm{NAR} = (\mathrm{W2}-\mathrm{W1})/(\mathrm{T2}-\mathrm{T1})\ (\mathrm{Ln\ LA2}-\mathrm{Ln\ LA1})/(\mathrm{LA2}-\mathrm{LA1}) = \mathrm{g\ m^{-2}\ d^{-1}}$

In the formulas, LA=leaf area, LW= leaf weight, GA= ground area, T= time, W= above ground weight, and PW= panicle weight.

The LAI was calculated by measuring all leaves of the subsample of 15 tillers, and results were extended to the whole sample by using a modification of a method proposed by Yoshida et al. (1976):

$$\mathrm{LAI} = \frac{\text{total LA of sub-sample tillers x dry wt. of all sample tillers}}{\text{dry wt. of measured subsample tillers}}$$

The NAR allows the estimation of net photosynthetic efficiency (Murata, 1976). As the concepts of NAR and RGR were derived initially for spaced plants, some scientists (Monteith, discussion of paper by Murata, 1976) suggested that NAR and RGR should not be calculated for closed canopy stands, and that CGR is the most important determination.

Experimental Design. Each seeding time was arranged as a randomized complete block design (RCBD), with growth stage as a split-plot in cultivar, with four replications. Both experiments were analyzed together as a RCBD two factor factorial with split combined over locations, testing the effects of seeding date (S), cultivars (C), growth stage (G), and the interactions S x C, S x G, C x G, and S x C x G. Least significant differences (LSD), at P=0.05, were calculated for the pertinent main effects and for some of the different comparisons within the interactions, as for the comparison of growth stage means within the same cultivar and of cultivar means within the same growth stage.

RESULTS

Tillers per square meter. Table 3.1 contains the results of the analysis of variance for variables calculated at the four growth stages. Tiller number per land area decreased from internode elongation to maturity in all cultivars. Reduction in tiller number generally proceeded at a slower rate in the second seeding date, resulting in a higher mean tiller density in this trial, as well as in more tillers at harvest (Appendix, Fig. 3a. 1). However, in the second seeding date, RU9101001 had a sharp reduction in tiller number during the reproductive phase, and a lower mean tiller density. The line had fewer tillers at IE rather than fewer tillers at harvest (Appendix, Table 3a.2).

Table 3.1. Mean squares from the combined analysis of variance for variables calculated at four growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

				Dry Matter				
Source (1)	df	Tillers m^{-2}	LAI	Total	Leaf	Sheath	Stem	Panicle
		no.		t ha^{-1}				
S	1	46820**	10.9**	21.57**	4.42**	1.40**	0.14#	0.96#
R(P)	6	4140	1.1*	1.12	0.18	0.11	0.03	0.08
C	4	58936**	12.5**	90.51**	11.95**	12.36**	3.51**	0.97*
SxC	4	40373**	2.9**	1.03	0.47**	0.20#	0.06	0.40
Error	24	4606	0.4	1.36	0.09	0.09	0.05	0.28
G	3	434179**	9.2**	837.02**	7.42**	16.96**	52.64**	506.31**
SxG	3	6576#	1.8**	1.45	0.14	0.19	1.00**	1.31**
CxG	12	15325**	3.3**	3.75**	0.21**	0.67**	0.60**	0.67**
SxCxG	12	4633	0.5*	2.00*	0.10	0.22*	0.08#	0.98**
Error	90	2903	0.3	1.06	0.07	0.09	0.05	0.19
CV%		9.6	15.2	9.5	10.8	10.2	12.3	12.2

(1) S= seeding date, C= cultivar, G= growth stage.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
Significant at the 0.10 probability level.

Most of the decrease in tillers occurred from internode elongation to anthesis, and this was more pronounced in Starbonnet, Newbonnet and L202. Starbonnet had a great reduction in tiller number from IE to heading with no further decrease after flowering. The other cultivars showed a reduction until early grain filling, this reduction being at a slower rate in RU9101001. This extremely-short-season line had the lowest number of tillers at IE but the highest number at harvest. Alan had a significant decrease even at late grain filling (Fig. 3.1).

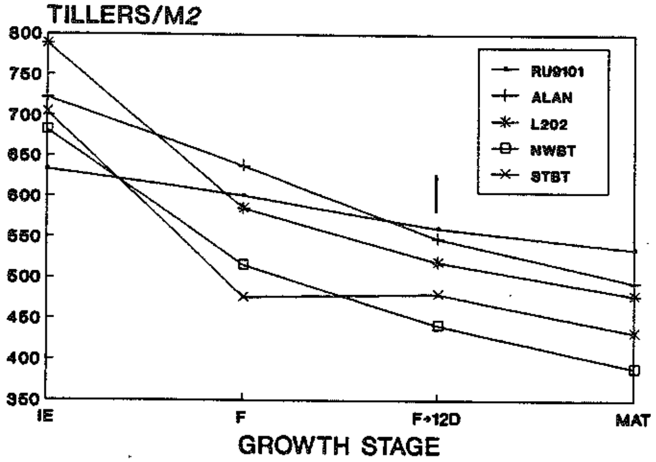


Fig. 3.1. Tiller density at internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT) for five rice cultivars. Each point is the mean of two seeding dates and four replications. The bar indicates the LSD at P= 0.05 for G means within the same C.

<u>Leaf area index</u>. The LAI showed significant differences for all main effects and interactions (Table 3.1). Mid- and long-season cultivars produced larger LAI during the vegetative and panicle development phases of the second seeding date, resulting in a larger mean LAI during the whole period of growth for that trial. Alan had similar LAI at IE in both experiments, but LAI developed at heading was larger in the second seeding. The short-statured lines RU9101001 and L202 showed a similar trend, but the differences were not statistically significant (Appendix, Table 3a.3).

All cultivars increased LAI from IE to flowering and decreased it thereafter (Fig. 3.2). The mean LAI at harvest was lower than the one at IE. In the second seeding date, with higher temperatures during the vegetative phase, there were important differences among rice cultivars in

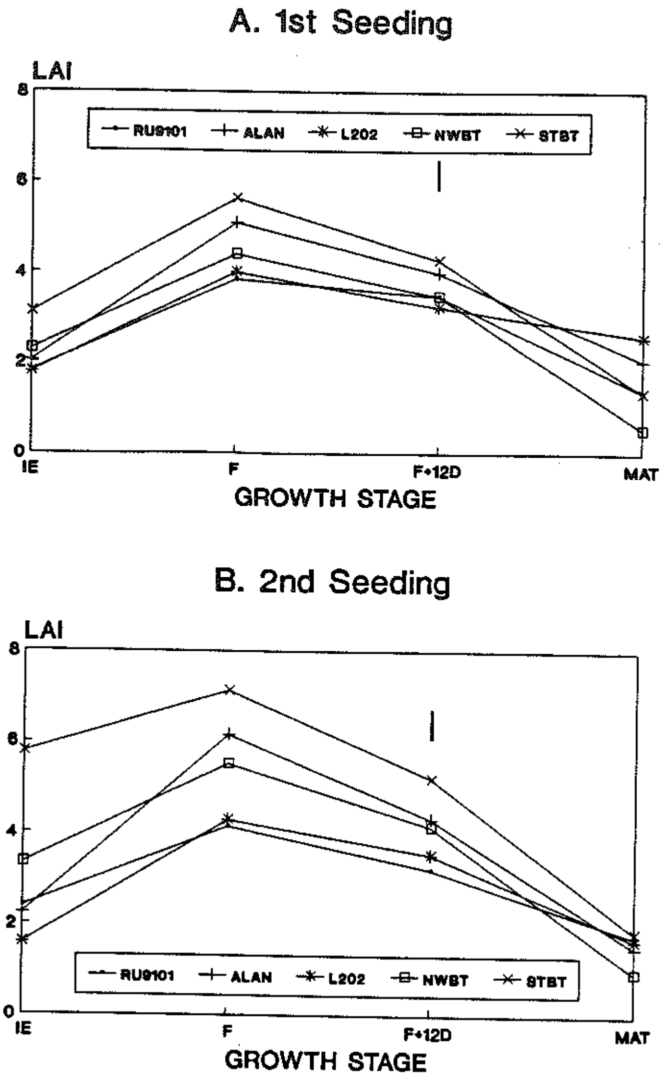


Fig. 3.2. Leaf Area Index (LAI) at each growth stage for five rice cultivars at (A) first seeding date and (B) second seeding date. Points are the mean of four replications. Bars indicate LSD at P= 0.05 for G means within C. Growth stages are internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

LAI at IE, and the long-season cultivar Starbonnet had a LAI of 5.78 at IE, and a maximum of 7.12 at flowering. The very-short-season cultivar Alan tended to produce a larger LAI at heading and early grain filling than the mid-season cultivar Newbonnet. The LAI at harvest varied widely among cultivars in the first seeding date, where L202 showed the slowest decrease (Fig. 3.2). In the second trial, however, senescence was more pronounced and all cultivars reached harvest with similar low LAI. The important decrease in LAI observed in Newbonnet, during grain filling of both experiments, was enhanced by a late infection of stem rot.

Dry matter production. Total dry matter production was significantly greater in the second seeding date. With the exception of the semidwarf cultivar L202, dry matter production was inversely associated with maturity group. For the second seeding date, RU9101001 produced 14.0 t ha^{-1} at harvest in 83 days from emergence, and the long-season cultivar Starbonnet produced 17.2 t ha^{-1} in 126 days (Appendix, Table 3a.4).

All short-season cultivars had a significant increase in dry matter production from early grain filling to physiological maturity, in both seeding dates. However, mid- and long-season cultivars did not show a consistent trend through both experiments, and dry weight increase from early to late grain filling was not significant for Starbonnet in the first seeding, Newbonnet in the second (Appendix, Table 3a.4), or either cultivar for the mean of both trials (Fig. 3.3). The very-short-season cultivar Alan produced the same amount of dry weight at harvest (about 15 t ha^{-1}) as Newbonnet, with a mean difference in total growth duration of 338 degree days, or 19 to 23 days. The longer the growth duration of the cultivar, the smaller the dry weight accumulation observed from flowering to maturity. The increase in dry matter in this period for the mean of both seeding dates was 66, 42, 39, 27, and 18% for RU9101001, Alan, L202, Newbonnet, and Starbonnet, respectively.

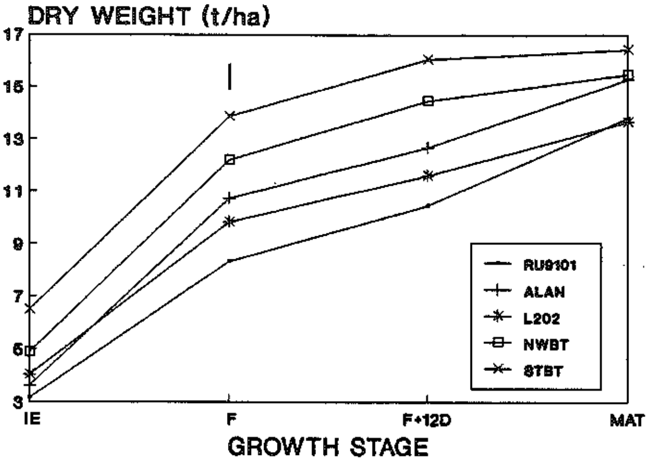


Fig. 3.3. Dry matter production at internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT) for five rice cultivars. Each point is the mean of two seeding dates and four replications. The bar indicates the LSD at P= 0.05 for G means within the same C.

Dry matter partitioning. The analysis of variance for leaf weight showed highly significant effects of seeding date, cultivars, and the interaction of both factors (Table 3.1). Mean leaf dry weights per hectare of the taller cultivars, Alan, Newbonnet, and Starbonnet, were higher in the second seeding date, but were constant for RU9101001 and L202 (Appendix, Table 3a.5). Except for L202, the longer the growth duration of the cultivars, the larger the leaf dry matter production (Fig. 3.4). Dry weight of leaves increased from IE to flowering and decreased thereafter. Mid- and long-season cultivars had an important decrease in leaf dry weight late in the season, however, this decrease was not significant in RU9101001 and Alan. Short-season cultivars had similar leaf dry matter at IE, but important differences were established during panicle development and maintained during ripening (Fig. 3.4) (Appendix, Fig. 3a.2).

Sheath dry matter reached a maximum at heading in all cultivars, and was larger in the second trial. Newbonnet and Starbonnet decreased sheath dry weight significantly during early and late grain filling for both seeding dates. The reduction was not so pronounced in Alan and RU9101001, especially during late grain filling. RU9101001 tended to increase sheath dry matter in the second trial (Fig. 3.4) (Appendix, Fig. 3a.2).

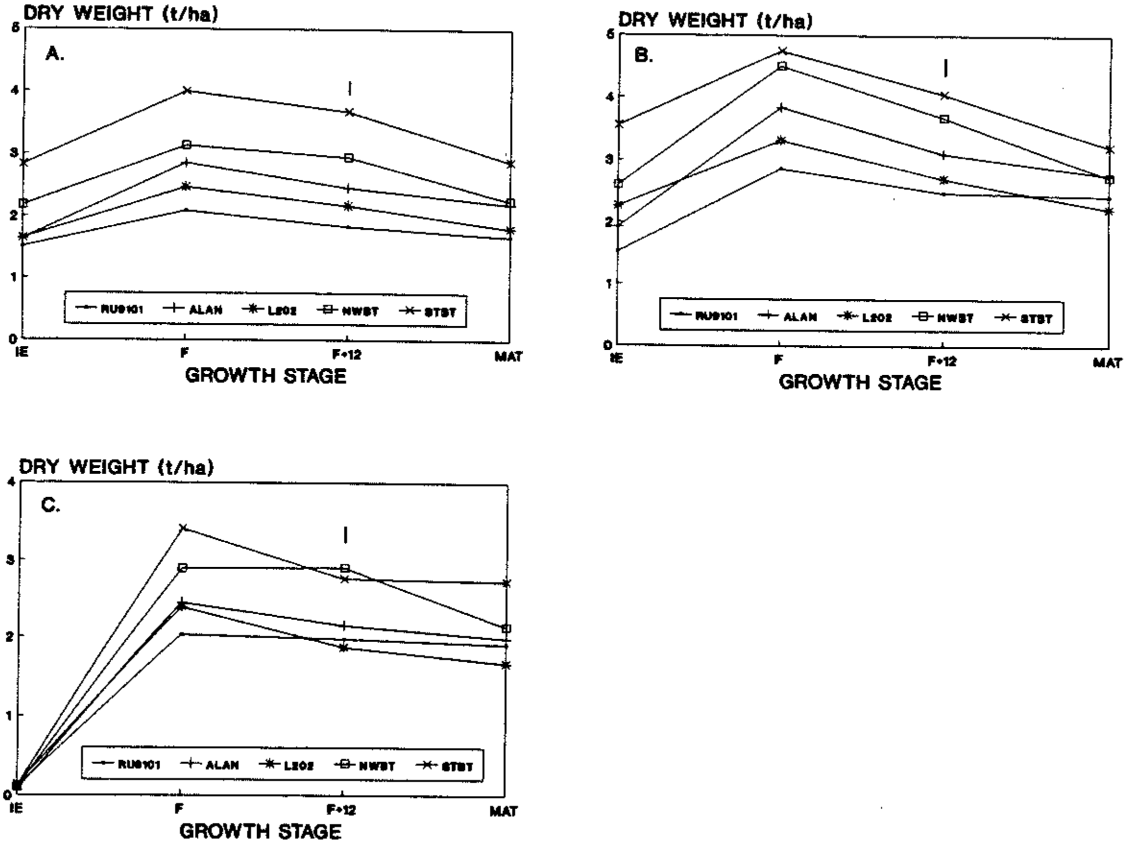


Fig. 3.4. Dry matter production of (A) leaf blades, (B) leaf sheaths, and (C) stems at internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT) for five rice cultivars. Each point is the mean of two seeding dates and four replications. Bars indicate the LSD at P= 0.05 for G means within the same C.

Stem dry matter production was not significantly higher in the second seeding date, and the differences among cultivars were not as important as those observed for leaf and sheath dry matter. The interaction of cultivar x growth stage was highly significant (Table 3.1). RU9101001 maintained constant stem weight from flowering to maturity for the average of both seeding dates, Newbonnet had a significant decrease in stem weight during the second half of grain filling, and the rest of the cultivars showed a reduction only during the first half (Fig. 3.4).

There was an important seeding date x growth stage interaction for stem dry weight (Table 3.1). In the first seeding date, there was no decrease in mean dry weight during the first part of grain filling (Appendix, Table 3a.7, Fig. 3a.3), and RU9101001 and Newbonnet even increased stem weight significantly, reaching a maximum weight 12 days after heading (Appendix, Fig. 3a.2). In the second seeding date, however, there was a significant reduction in stem weight during early grain filling, and weight tended to increase during the second half of ripening, especially in RU9101001 and Starbonnet, but the increase was not significant (Appendix, Fig. 3a.2 and 3a.3).

Panicle dry matter was not significantly different for both seeding dates (Table 3.1). Grain filling proceeded at a faster rate in the second experiment, since panicle weight 12 days after flowering was significantly higher in the second seeding date than in the first (Appendix, Table 3a.8, and Fig. 3a.2). For the mean of both seeding dates, dry weight accumulation in the panicles of RU9101001 at early grain filling was only 53% of the dry weight accumulation at harvest, while this value was approximately 60% in Alan and L202, and 73% in Starbonnet (Appendix, Table

3a.8).

Specific leaf weight. Specific leaf weight (SLW) was evaluated only in the first two sampling, IE and F, to avoid errors caused by differential senescence of the leaves observed in the cultivars during ripening. The SLW was higher at IE, decreasing significantly during panicle development (Table 3.2) (Appendix, Table 3a.9, Fig. 3a.4). Short-season cultivars maintained or increased SLW from first to second seeding, but mid- and long-season cultivars decreased it significantly. L202 and Newbonnet had the highest SLW in the first seeding date; however, while L202 increased SLW in the second trial, Newbonnet reduced it. L202 had the highest values overall, 79 g m^{-2} leaf, and a maximum of 110 g m^{-2} at IE in the second seeding. RU9101001 and Alan had lower overall SLW (62 to 64 g m^{-2}) than L202 and Newbonnet.

Growth and assimilation rates. Crop growth rates (CGR) showed high variability and only some main effects, such as cultivar and growth stage were significant (Table 3.2). Mean CGR was inversely related to maturity group. RU9101001 and Alan had greater CGR than other cultivars over the whole season, especially during PD and LGF (Fig. 3.5) (Appendix, Table 3a.10), with peak values from IE to F of 30 g m^{-2} d^{-1} in the first and second experiment, respectively. Among cultivars, CGR's were similar during vegetative growth and EGF, but tended to be different during PD, and were significantly different during LGF. RU9101001 and Alan maintained similar CGR at EGF and LGF, while CGR of mid- and long- season cultivars was significantly reduced from the first to the second half of grain filling.

Table 3.2. Mean squares from the combined analysis of variance for CGR, PGR, NAR, RGR, and SLW. CGR was calculated for the growth phases VG, PD, EGF, and LGF, while PGR, NAR, and RGR were calculated for the last three phases. SLW was analyzed at the first two growth stages (IE and F).

	-- 4 G phases --		--------- 3 G phases -------------				-2 G stages-	
Source	df	CGR	df	PGR	NAR	RGR (1)	df	SLW
		g m^{-2} d^{-1}		--- g m^{-2} d^{-1} ---		g g^{-1} d^{-1}		g m^{-2}
S	1	4.56	1	2.49	30.44*	0.388**	1	108.8*
R(S)	6	6.33	6	0.49	1.88	0.004	6	85.8**
C	4	147.17*	4	14.94	75.73**	1.004**	4	805.8**
SxC	4	5.13	4	4.89	2.30	0.033	4	473.2**
Error	24	36.61	24	7.62	4.63	0.029	24	19.5
G	2	2239.87**	2	4563.68**	173.29**	10.000**	1	10444.7**
SxG	2	136.17	2	195.66**	1.62	0.065	1	16.7
SxG	8	101.93	8	113.14**	12.69	0.272**	4	497.9**
SxCxG	8	117.76	8	73.08**	14.82#	0.152	4	299.8**
Error	60	101.89	60	16.59	8.35	0.092	30	24.9
CV%		68.1		25.8	59.2	48.8		7.4

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.
Significant at the 0.10 probability level.
(1): Values reported should be multiplied by 10^{-03}

Relative growth rate (RGR) was larger for the first seeding date. There were also significant effects for cultivar, growth stage and their interaction (Table 3.2). The RGR was inversely related to growth duration and was larger in the very-short-season cultivars with a mean value of 0.029 g g^{-1} d^{-1} in RU9101001 for the average of both experiments (Appendix, Table 3a.11). All cultivars had larger RGR during PD, when the largest differences were observed, with a maximum of 0.054 g g^{-1} d^{-1} in RU9101001 for the average of both seeding dates. Rates decreased significantly during EGF, except in Starbonnet, and were maintained during

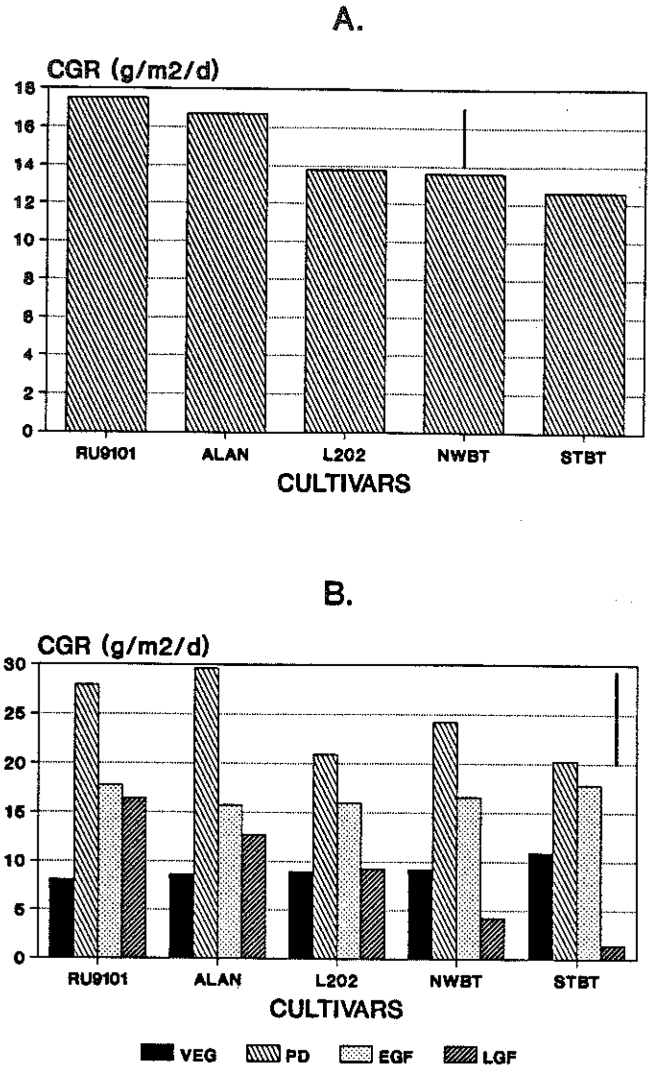


Fig. 3.5. Crop Growth Rate (CGR) for five rice cultivars. (A) Mean CGR for the whole season. Each value is the mean of two seeding dates, four replications, and four growth phases. The bar indicates the LSD at P=0.05. (B) CGR during the vegetative (VG), panicle development (PD), early grain filling (EGF), and late grain filling (LGF) phases. Each value is the mean of two seeding dates and four replications. The bar indicates the LSD at P=0.05 for growth stage means within the same cultivar.

LGF (Appendix, Fig. 3a.5). The cultivars had similar rates during the first half of ripening, but in the second half, RU9101001 and Alan had larger RGR.

Along with CGR, net assimilation rate (NAR) showed high variability, and the analysis detected significant differences only for the main effects. The NAR was higher for the first seeding date and in the short-season cultivars. RU9101001 had the highest long-term NAR over all (7.33 g m^{-2} d^{-1}), while Alan and L202 were intermediate (5.46 and 5.17 g m^{-2} d^{-1}) (Fig. 3.6) (Appendix, Fig. 3a.6). The maximum NAR was obtained for RU9101001 during reproductive growth of first seeding date (11.21 g m^{-2} d^{-1}) (Appendix, Table 3a.12). The rates decreased significantly during EGF and were maintained during LGF, except in Starbonnet. The very-short-season cultivars showed a trend to increase NAR from the first to the second half of ripening, especially for the second seeding date. Although the C x G interaction was not significant, RU9101001 had similar NAR during PD and LGF, for the mean of both experiments (Fig. 3.6).

Panicle growth rate (PGR) showed significant effects for growth stage and for all the interactions with this factor (Table 3.2). The PGR was generally maximum at EGF, and there was an important interaction S x G. The PGR during EGF were larger in the second seeding date, but were lower during LGF (Fig. 3.7). The long-season cultivar Starbonnet showed the highest PGR during EGF for the mean of both experiments and the lowest rate during the last part of ripening, but the very-short-season cultivars maintained high PGR late in the season (Fig. 3.7) (Appendix, Table 3a.13).

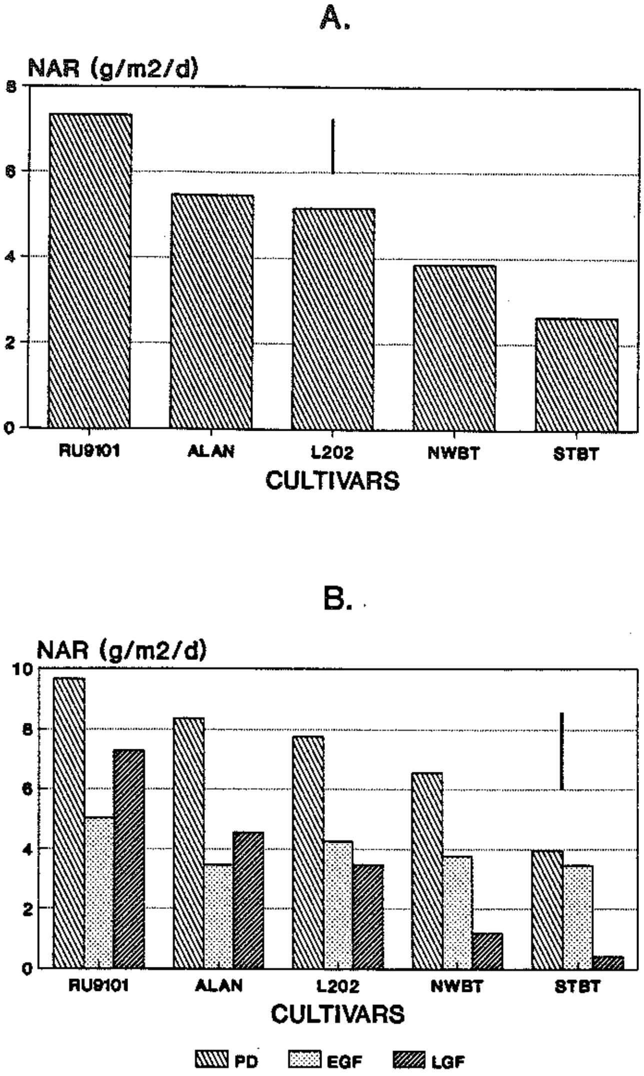


Fig. 3.6. Net assimilation rate (NAR) during growth for five rice cultivars. (A) Mean NAR for the whole season. Each value is the mean of two seeding dates, four replications, and three growth phases. The bar indicates the LSD at P= 0.05 for C means. (B) NAR during panicle development (PD), early grain filling (EGF), and late grain filling (LGF). Each point is the mean of two seeding dates and four replications. The bar indicates the LSD at P=0.05 for G means within C.

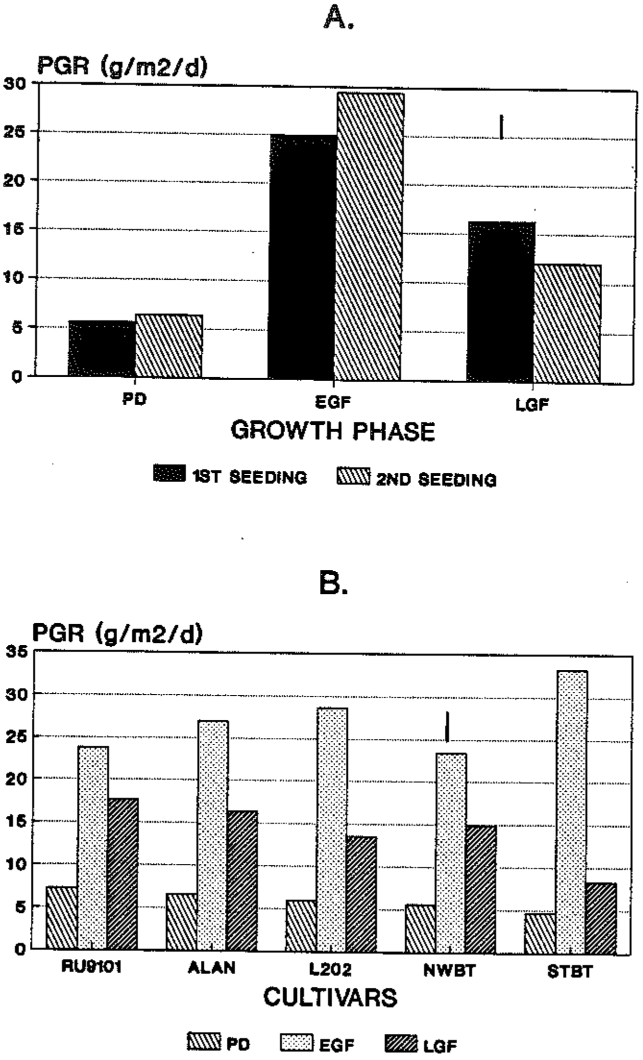


Fig. 3.7. Panicle growth rate (PGR) during the panicle development (PD), early (EGF), and late grain filling (LGF) phases. (A) PGR for two seeding dates. Each value is the mean of five cultivars and four replications. The bar indicates the LSD at P=0.05. (B) PGR for five rice cultivars. Each value is the mean of two seeding dates and four replications. The bars indicates the LSD at P=0.05.

DISCUSSION

The cultivars included in the study did not show a reproductive phase overlapped with the vegetative phase that is reported to be common in very-short-season cultivars (Tanaka, 1976). Even the extremely-short-season line RU9101001 tended to decrease tiller number after IE. This line had fewer tillers at the end of the vegetative phase, but the decline in tiller number was less pronounced, resulting in the highest tiller or panicle density at maturity. Mid- and long-season cultivars had an important decline in tiller number during the reproductive phase. The considerable decrease in tiller number of RU9101001 during the panicle development phase of the second seeding date may indicate that the competition between the developing tillers and panicles was the cause for the reduced sink size of the line in that experiment (Chap. II).

Short-season cultivars accumulated more dry matter from heading to maturity than mid- and long-season cultivars, in accordance to previous reports (Chang and Vergara, 1972). The increase in total dry weight during grain filling ranged from 66% in RU9101001, to 18% in Starbonnet, for the average of both trials.

RU9101001 and Alan had moderate CGR during the vegetative phase, and high CGR during PD and late in the season, with growth curves that may be considered Type V in the Tanaka (1976) classification. This growth pattern is possible only with abundant solar radiation, and some US cultivars were classified as sun-rice ecotypes, because of their ability to acclimate to high solar radiation, with high light saturation (Tu et al., 1988). Both cultivars had high harvest index (Chap. II), and Alan had high total dry matter production. The CGR of the very-short-season cultivars were as high as 30 g m^{-2} d^{-1} for the whole period of PD, which is close to the maximum short-term growth rate reported for rice, according to Yoshida (1981). Mean CGR of RU9101001 for the season for the second seeding date (17.9 g m^{-2} d^{-1}) was larger than values reported by Tanaka (1976) from transplant to maturity.

Very-short-season cultivars also showed a slight decline in dry weight of vegetative organs after flowering. This result may indicate less remobilization of stored assimilates, as was reported by Vergara et al., 1966; Tanaka, 1972; Yoshida, 1981. A long-season cultivar, such as Starbonnet, achieved high PGR during EGF through the mobilization of large amounts of stored carbohydrates, as indicated by a sharp decrease in dry weight of vegetative organs during this period. As growth duration decreased, PGR during EGF decreased, the decline in vegetative dry weight was less important, and PGR during LGF increased.

In the second seeding date, the cultivars developed higher LAI and dry matter during the vegetative and panicle development phases, but LAI at harvest was similar in both experiments. Increase in dry matter from first to second seeding was due to leaf and sheath components, with no change in stem and panicle dry weights. The increases in LAI, tillering and dry matter of vegetative parts for the second seeding date caused a decrease in RGR and NAR. Conditions during EGF of the second seeding apparently enhanced translocation of stored assimilates, as indicated by the faster decline in stem dry weight during that period of the second trial, and a higher PGR. Murata (1976) obtained similar results when temperatures after heading were relatively high.

Lafitte and Travis (1984) reported that small-leaved rice lines showed higher apparent photosynthesis, had higher SLW, and more nitrogen per unit leaf area. Apparent photosynthesis was not measured in the present experiment, but a larger SLW in the small-leaved cultivar L202 did not result in larger NAR. RU9101001, with lower SLW and leaf area similar to that of L202, had a significantly higher NAR, averaging 7.33 g m^{-2} d^{-1} for the whole season and both seeding dates. Mean NAR of the cultivars was inversely related to growth duration.

The extremely-short-season line RU9101001 and the very-short-season cultivar Alan showed a trend to increase NAR from EGF to LGF. Dry weight accumulation late in the season continued at a high rate in these cultivars, despite the reduction in LAI due to senescence and resulting in a high assimilation rate per unit of active leaf area. Assimilation during this phase of growth was high enough to maintain a good dry weight accumulation in the panicles and to maintain sheath and stem weight or even increase it.

Imaizumi et al. (1990) indicated that contribution of panicle photosynthesis increased during grain filling, and they reported that the gross amount of CO_2 assimilated in an entire panicle was about 30% of that in the flag leaf. A higher contribution of panicle photosynthesis may be one of the factors involved in the high NAR observed during LGF in very-short-season cultivars. Both Alan and, especially, RU9101001 showed good ratoon-ability, and the regrowth was initiated even before harvest. The regrowth buds, developing in the basal nodes, may have stimulated photosynthetic activity in the remaining leaves, favoring assimilate storage in the stems that is transported to the regrowth after harvest.

The increase in stem weight observed in RU9101001 late in the season, was achieved with a high NAR and PGR during LGF. A high demand for assimilates was placed on a reduced leaf area, as indicated by Lafitte and Travis (1984), and source activity remained high until harvest. Starbonnet also tended to increase stem weight in the second seeding, but showed low source activity and low PGR during LGF, suggesting that sink size may be limiting in this cultivar.

V.-REFERENCES

Baker, J.T., L.H. Allen Jr., K.J. Boote, P. Jones, and J.W. Jones. 1990. Rice photosynthesis and evapotranspiration in subambient, ambient, and superambient carbon dioxide concentrations. Agron. J. 82:834-840.

Chang, T.T., and B.S. Vergara. 1972. Ecological and genetic information on adaptability and yielding ability in tropical rice varieties. p.431-453. In Rice Breeding. IRRI. Los Banos. Philippines.

Gardner, F.P., R.B. Pearce, and R.L. Mitchell. 1985. Physiology of crop plants. Iowa State University Press. Ames, Iowa.

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

Lafitte, H.R., and R.L. Travis. 1984. Photosynthesis and assimilate partitioning in closely related lines of rice exhibiting different sink:source relationships. Crop Sci. 24:447-452.

Murata, Y., and S. Matsushima. 1975. Rice. p.73-99. In Crop physiology. Some case histories. L.T. Evans. Cambridge University Press. London.

-----. 1976. Productivity of rice in different climatic regions of Japan. p. 449-470. In Climate and rice. IRRI. Los Banos. Philippines.

Sinclair, T.R., and T. Horie. 1989. Leaf nitrogen, photosynthesis, and crop radiation use efficiency: A review. Crop Sci. 29:90-98.

Tanaka, A. 1972. Efficiency of respiration. p.438-498. In Rice breeding. IRRI. Los Banos. Philippines.

-----. 1976. Comparisons of rice growth in different environments. p 429-448. In Climate and rice. IRRI. Los Banos. Philippines.

Tu, Z.P., X.Z. Lin, Q.M. Huang, W.I. Cai, H.Y. Feng, and L.Y. Ye. 1988. Photosynthetic characterization of rice varieties in relation to growth irradiance. Aust. J. Plant Physiol. 15:277-286.

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

Yoshida, S. 1981. Fundamentals of rice crop science. IRRI. Los Banos. Philippines.

-----, D.A. Forno, J.H. Cock, and K.A. Gomez. 1976. Laboratory manual for physiological studies of rice. IRRI. Los Banos. Philippines.

APPENDIX

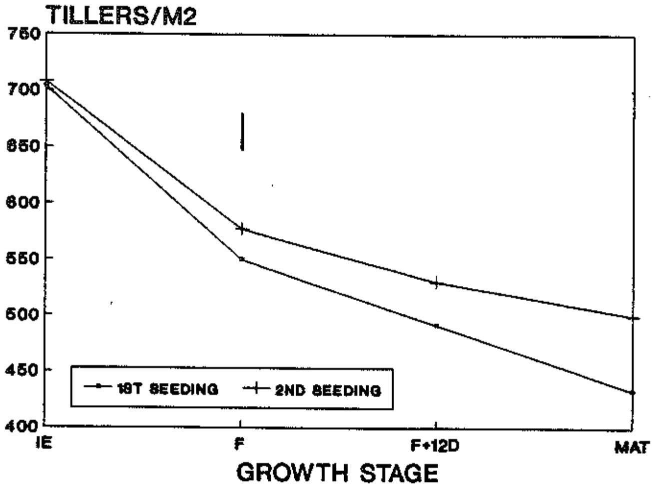
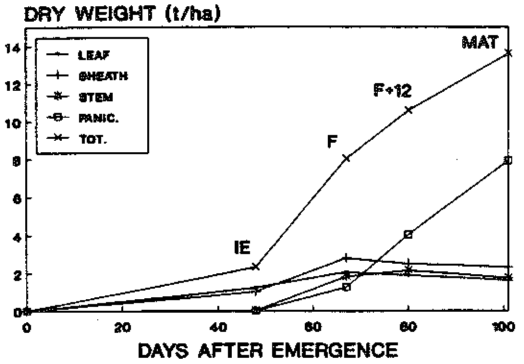
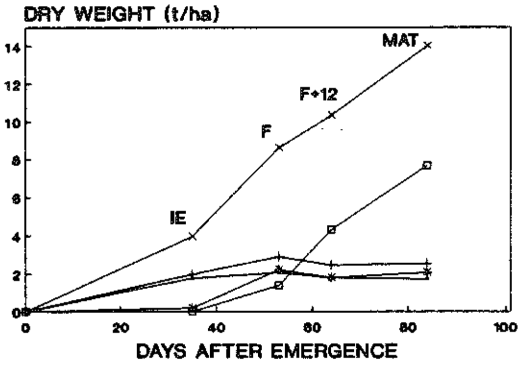


Fig. 3a.1. Tiller population at internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT) for two seeding dates. Each point is the mean of five cultivars and four replications.

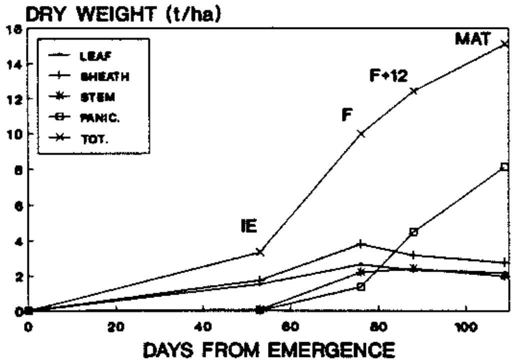
RU9101001. 1st Seeding



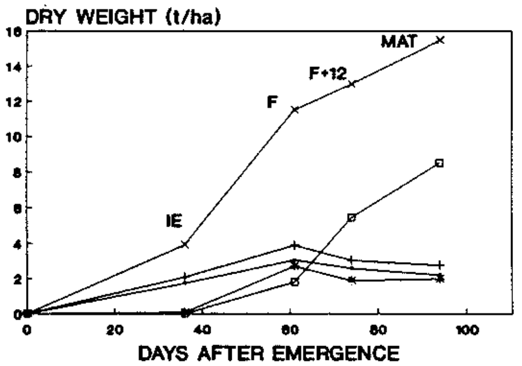
RU9101001. 2nd Seeding



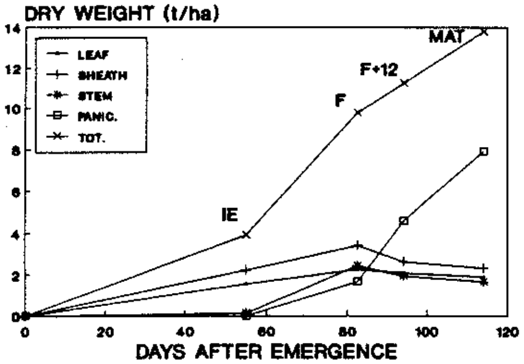
Alan. 1st Seeding



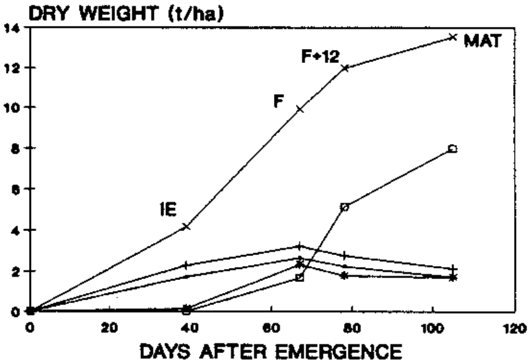
Alan. 2nd Seeding



L202. 1st Seeding



L202. 2nd Seeding



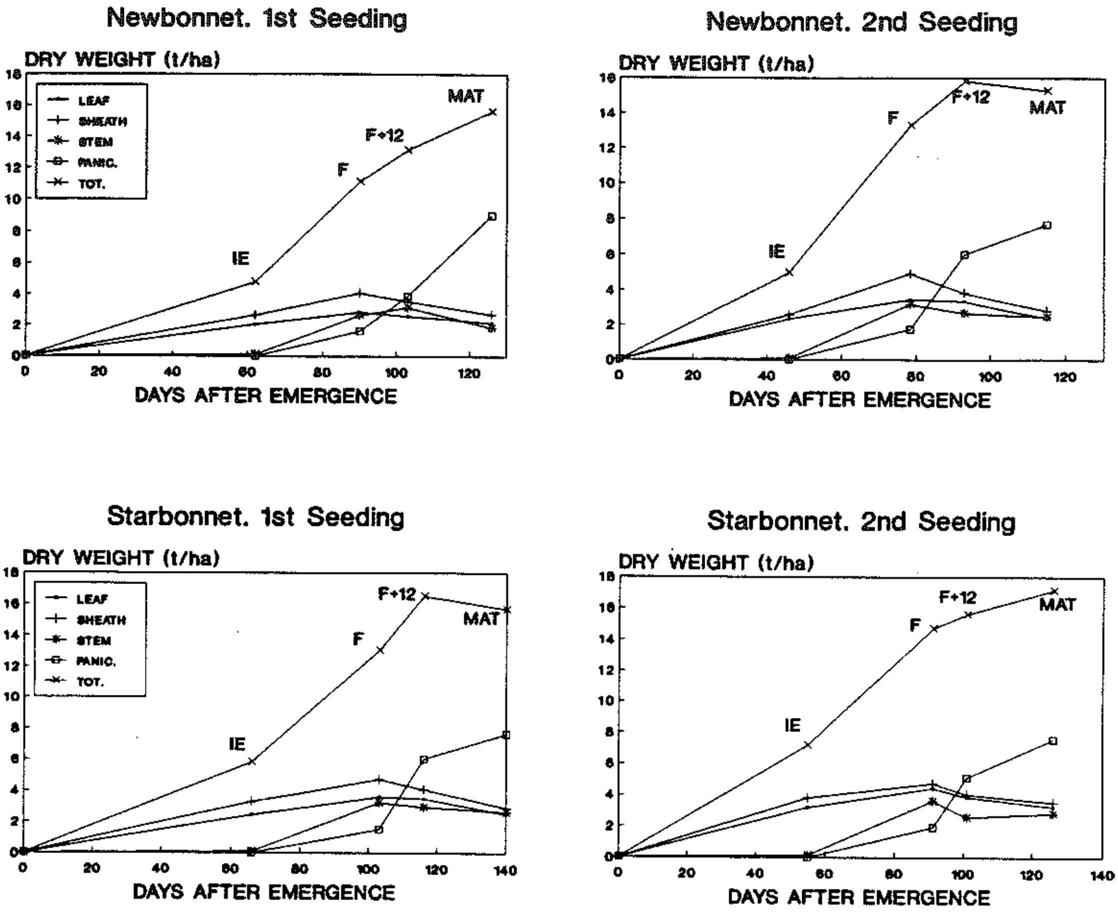


Fig. 3a.2. Dry matter production and partitioning at four growth stages (IE, F, F+12, MAT) and two seeding dates for five rice cultivars. Each point is the mean of four replications. Note the different scale for each cultivar.

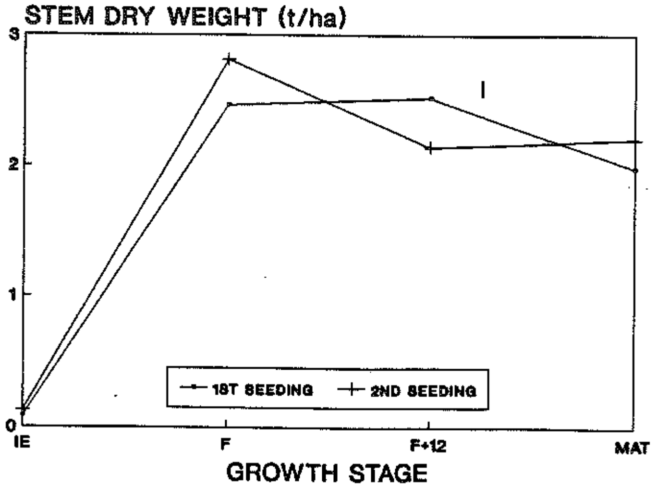


Fig. 3a.3. Dry weight of stems at internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT) for two seeding dates. Each point is the mean of five rice cultivars and four replications. The bars indicates the LSD at P=0.05 for G means within seeding. Note the different scale for both graphs.

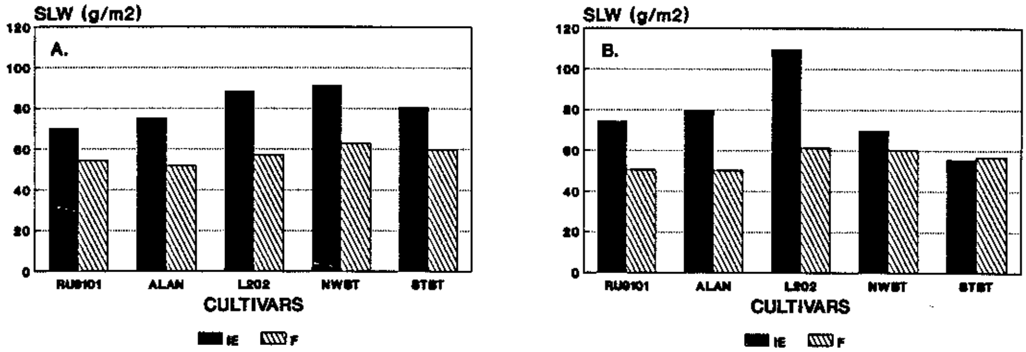


Fig. 3a.4. Specific leaf weight (SLW) at internode elongation (IE), and flowering (F) for five rice cultivars at (A) first seeding date and (B) second seeding date. Each value is the mean of four replications.

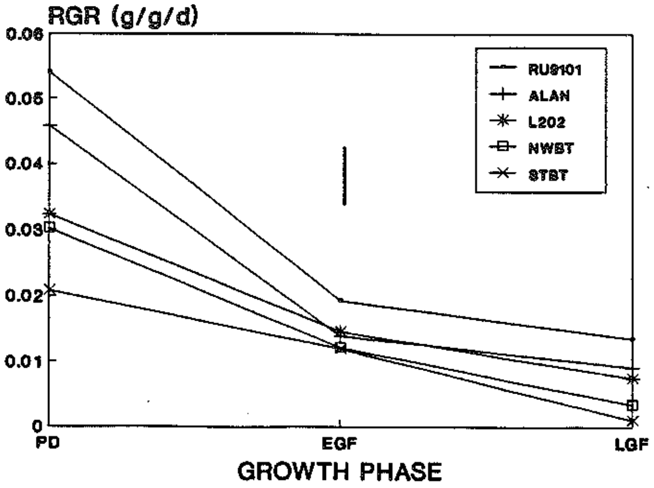


Fig. 3a.5. Relative growth rate (RGR) during panicle development (PD), early (EGF) and late grain filling (LGF) phases for five rice cultivars. Each point is the mean of two seeding dates and four replications.

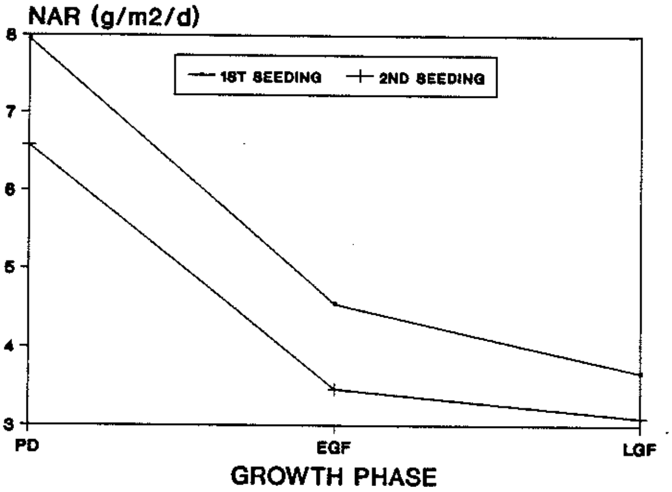


Fig. 3a.6. Net assimilation rate (NAR) during panicle development (PD), early (EGF) and late grain filling (LGF) for two seeding dates. Each point is the mean of five cultivars and four replications.

Table 3a.1. Plant height (m) at four growth stages and two seeding dates for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

Growth Stage	Plant height					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	m					
			1st seeding			
IE	0.57	0.62	0.55	0.60	0.69	0.60
F	0.92	1.00	0.89	1.03	1.19	1.01
F+12	0.93	0.99	0.91	1.08	1.20	1.02
MAT	0.93	1.00	0.92	1.07	1.20	1.02
			2nd seeding			
IE	0.63	0.62	0.52	0.64	0.82	0.65
F	0.92	1.01	0.91	1.10	1.22	1.03
F+12	0.94	1.00	0.91	1.10	1.20	1.03
MAT	0.90	0.98	0.93	1.09	1.21	1.02
			Mean of 2 seeding dates			
IE	0.60	0.62	0.53	0.62	0.75	0.63
F	0.92	1.00	0.90	1.06	1.21	1.02
F+12	0.94	0.99	0.91	1.09	1.20	1.03
MAT	0.91	0.99	0.93	1.08	1.20	1.02

LSD P=0.05:
G means= 0.0082
G means within the same S= 0.0116
G means within the same C for the average of S= 0.0184
G means within the same combination of C and S= 0.0260
C means within the same combination of G and S= 0.0334

Table 3a.2. Tillers per square meter at four growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

	Tillers					
Growth Stage	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	no. m^{-2}					
	1st seeding					
IE	661	680	779	707	691	703
F	668	618	565	499	399	550
F+12	594	545	498	415	404	491
MAT	544	458	479	347	337	433
Mean	617	575	580	492	458	544
	2nd seeding					
IE	607	763	796	658	716	708
F	534	658	607	533	554	577
F+12	528	553	541	470	557	530
MAT	526	531	479	431	529	499
Mean	549	626	606	523	589	578
	Mean of 2 seeding dates					
IE	634	722	788	682	704	706
F	601	638	586	516	476	563
F+12	561	549	519	442	480	510
MAT	535	495	479	389	433	466
Mean	583	601	593	507	523	

LSD P=0.05:
C means= 35.02
C means within the same S= 49.52
G means= 23.94
G means within the same S= 33.85
G means within the same C for the average of S= 53.53

Table 3a.3. Leaf area index (LAI) at four growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

Growth Stage	Leaf area index					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
			1st seeding			
IE	1.80	2.03	1.78	2.28	3.10	2.20
F	3.84	5.09	4.00	4.39	5.62	4.59
F+12	3.48	3.99	3.24	3.48	4.28	3.69
MAT	1.36	2.05	2.58	0.53	1.34	1.57
Mean	2.62	3.29	2.90	2.67	3.59	3.01
			2nd seeding			
IE	2.39	2.23	1.58	3.33	5.78	3.06
F	4.14	6.16	4.28	5.52	7.12	5.45
F+12	3.21	4.31	3.53	4.15	5.21	4.08
MAT	1.74	1.52	1.68	0.96	1.85	1.55
Mean	2.87	3.55	2.77	3.49	4.99	3.53
			Mean of 2 seeding dates			
IE	2.10	2.13	1.68	2.81	4.44	2.63
F	3.99	5.62	4.14	4.96	6.37	5.02
F+12	3.34	4.15	3.39	3.81	4.74	3.89
MAT	1.55	1.78	2.13	0.74	1.60	1.56
Mean	2.74	3.42	2.83	3.08	4.29	

LSD P=0.05:
C means= 0.33
C means within the same S= 0.46
G means= 0.22
G means within the same S= 0.31
G means within the same C for the average of S= 0.49
G means within the same combination of C and S= 0.70
C means within the same combination of G and P= 0.76

Table 3a.4. Total dry matter production at four growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

Growth Stage	Dry matter					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	k ha^{-1}					
	1st seeding					
IE	2323	3315	3908	4777	5808	4026
F	8011	9972	9771	11131	13035	10384
F+12	10572	12390	11244	13119	16514	12768
MAT	13590	15097	13794	15648	15710	14768
	2nd seeding					
IE	3950	3914	4153	4971	7176	4833
F	8617	11501	9904	13297	14714	11606
F+12	10354	12970	11978	15842	15608	13350
MAT	14029	15472	13522	15285	17159	15093
	Mean of 2 seeding dates					
IE	3136	3614	4031	4874	6492	4429
F	8314	10737	9837	12214	13874	10995
F+12	10463	12680	11611	14480	16061	13059
MAT	13810	15284	13658	15466	16434	14931

LSD P=0.05
G means= 456.6
G means within the same C for the average of S= 1021.1
G means within the same combination of C and S= 1444.0
C means within the same combination of G and S= 1511.6

Table 3a.5. Leaf dry matter at four growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

Growth Stage	Leaf dry matter					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	----------------------- k ha^{-1} -----------------------------					
			1st seeding			
IE	1242	1519	1560	2047	2446	1763
F	2088	2636	2272	2819	3579	2679
F+12	1886	2328	2097	2566	3477	2471
MAT	1624	2189	1905	2141	2517	2075
Mean	1710	2168	1958	2393	3004	2247
			2nd seeding			
IE	1772	1745	1728	2305	3208	2151
F	2079	3071	2662	3443	4429	3137
F+12	1791	2584	2254	3333	3887	2770
MAT	1730	2218	1727	2370	3248	2259
Mean	1843	2404	2093	2863	3693	2579
			Mean of 2 seeding dates			
IE	1507	1632	1644	2176	2827	1957
F	2084	2853	2467	3131	4004	2908
F+12	1838	2456	2175	2950	3682	2620
MAT	1677	2203	1816	2255	2883	2167
Mean	1777	2286	2026	2628	3349	

LSD P=0.05:
C means= 156.1
C means within the same S= 220.7
G means= 115.8
G means within the same C for the average of S= 258.9

Table 3a.6. Sheath dry matter at four growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

Growth Stage	Sheath dry matter					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	k ha^{-1}					
			1st seeding			
IE	1051	1749	2225	2622	3268	2183
F	2816	3798	3407	4073	4732	3765
F+12	2508	3165	2623	3549	4075	3184
MAT	2309	2771	2328	2679	2917	2601
Mean	2171	2870	2645	3231	3748	2933
			2nd seeding			
IE	1992	2090	2290	2575	3831	2555
F	2907	3895	3225	4934	4757	3944
F+12	2454	3038	2781	3825	4039	3227
MAT	2552	2760	2136	2795	3525	2753
Mean	2476	2946	2608	3532	4038	3120
			Mean of 2 seeding dates			
IE	1521	1920	2257	2598	3549	2369
F	2862	3846	3316	4503	4744	3854
F+12	2481	3101	2702	3687	4057	3206
MAT	2431	2765	2232	2737	3221	2677
Mean	2324	2908	2627	3381	3893	

LSD P=0.05:
C means= 153.4
C means within the same S= 217.0
G means= 136.8
G means within the same C for the average of S= 305.9
G means within the same combination of C and S= 432.7
C means within the same combination of G and S= 434.8

Table 3a.7. Stem dry matter at four growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

Growth Stage	Stem dry matter					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	----------------------		k ha^{-1}	----------------------		
			1st seeding			
IE	30	47	124	108	95	81
F	1838	2188	2443	2620	3212	2460
F+12	2151	2421	1948	3144	2954	2523
MAT	1753	2000	1655	1851	2646	1981
Mean	1443	1664	1542	1931	2227	1761
			2nd seeding			
IE	186	79	135	92	137	126
F	2228	2711	2337	3173	3606	2811
F+12	1804	1892	1790	2670	2578	2147
MAT	2068	1984	1688	2439	2830	2202
Mean	1572	1666	1487	2093	2288	1821
			Mean of 2 seeding dates			
IE	108	63	130	100	116	103
F	2033	2450	2390	2897	3409	2636
F+12	1978	2156	1869	2907	2766	2335
MAT	1911	1992	1671	2145	2738	2091
Mean	1507	1665	1515	2012	2257	

LSD P=0.05:
C means= 115.6
G means= 97.8
G means within the same S= 138.3
G means within the same C for the average of S= 218.6
G means within the same combination of C and S= 309.2
C means within the same combination of G and S= 313.6

Table 3a.8. Panicle dry matter at four growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE), flowering (F), 12 days after flowering (F+12), and maturity (MAT).

Growth Stage	Panicle dry matter					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	k ha^{-1}					
			1st seeding			
IE	-	-	-	-	-	-
F	1269	1350	1649	1620	1514	1480
F+12	4027	4477	4577	3861	6007	4590
MAT	7904	8138	7907	8978	7631	8111
			2nd seeding			
IE	-	-	-	-	-	-
F	1402	1824	1680	1748	1921	1715
F+12	4305	5456	5153	6015	5105	5207
MAT	7679	8510	7972	7682	7556	7880
			Mean of 2 seeding dates			
IE	-	-	-	-	-	-
F	1335	1587	1665	1684	1717	1598
F+12	4166	4967	4865	4938	5556	4898
MAT	7791	8324	7939	8330	7593	7996

LSD P=0.05:
G means= 195.5
G means within the same S= 276.4
G means within the same C for the average of S= 437.1
G means within the same combination of C and S= 618.1
C means within the same combination of G and S= 659.9

Table 3a.9. Specific leaf weight (SLW) at two growth stages and two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth stages: internode elongation (IE) and flowering (F).

Growth Stage	Specific leaf weight					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	$g\ m^{-2}$					
			1st seeding			
IE	70.2	75.3	88.3	91.1	80.4	81.0
F	54.5	51.9	57.2	62.9	59.8	57.3
Mean	62.3	63.6	72.8	77.0	70.1	69.1
			2nd seeding			
IE	74.1	79.6	109.7	69.7	55.8	77.8
F	50.8	50.2	61.3	60.2	56.8	55.8
Mean	62.5	64.9	85.5	65.0	56.3	66.8
			Mean of 2 seeding dates			
IE	72.1	77.4	99.0	80.4	68.1	79.4
F	52.6	51.0	59.2	61.6	58.3	56.6
Mean	62.4	64.2	79.1	70.1	63.2	

Table 3a.10. Crop growth rate (CGR) during four growth phases and at two seeding dates for five rice cultivars. Values at each seeding date are the mean of four replications. Growth phases: vegetative (VG), panicle development (PD), early grain filling (EGF) and late grain filling (LGF).

Growth Phase	Crop growth rate					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	g m^{-2} d^{-1}					
			1st seeding			
VG #	4.8	6.3	7.1	7.7	8.8	6.9
PD	30.0	29.0	21.3	22.7	19.6	24.5
EGF	19.7	20.2	13.1	15.3	26.8	19.0
LGF	14.4	12.9	12.8	11.0	-3.4	9.5
Mean	17.2	17.1	13.6	14.2	12.9	15.0
			2nd seeding			
VG #	11.3	10.9	10.7	10.8	13.1	11.3
PD	26.0	30.4	20.6	25.7	20.9	24.7
EGF	15.8	11.3	18.9	17.9	9.0	14.6
LGF	18.4	12.5	5.7	-2.6	6.2	8.1
Mean	17.9	16.3	13.9	12.9	12.3	14.7
			Mean of 2 seeding dates			
VG #	8.1	8.6	8.9	9.2	10.9	9.1
PD	28.0	29.7	20.9	24.2	20.2	24.6
EGF	17.8	15.7	16.0	16.6	17.9	16.8
LGF	16.4	12.7	9.2	4.2	1.4	8.8
Mean	17.5	16.7	13.8	13.6	12.6	

LSD P=0.05:
C means= 3.12
G means= 4.48
G means within the same C for the average of S= 10.03
C means within the same G for the average of S= 8.99
#: From crop emergence

Table 3a.11. Relative growth rate (RGR) during three growth phases and at two seeding dates for five rice cultivars. Values at each seeding date are the mean of four replications. Growth phases: panicle development (PD), early grain filling (EGF) and late grain filling (LGF).

Growth Phase	Relative growth rate					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	g g^{-1} d^{-1}					
1st seeding						
VG	-	-	-	-	-	-
PD	0.065	0.049	0.034	0.030	0.022	0.040
EGF	0.022	0.018	0.012	0.012	0.018	0.016
LGF	0.012	0.010	0.010	0.008	-0.002	0.008
Mean	0.033	0.025	0.019	0.017	0.013	0.021
2nd seeding						
VG	-	-	-	-	-	-
PD	0.043	0.043	0.031	0.031	0.020	0.034
EGF	0.017	0.010	0.017	0.012	0.006	0.012
LGF	0.015	0.009	0.005	-0.001	0.004	0.006
Mean	0.025	0.021	0.018	0.014	0.010	0.017
Mean of 2 seeding dates						
VG	-	-	-	-	-	-
PD	0.054	0.046	0.032	0.030	0.021	0.037
EGF	0.019	0.014	0.015	0.012	0.012	0.014
LGF	0.014	0.009	0.008	0.003	0.001	0.007
Mean	0.029	0.023	0.018	0.015	0.011	

LSD P=0.05:
C means= 0.0032
G means= 0.0042
G means within the same C for the average of S= 0.0095
C means within the same G for the average of S= 0.0084

Table 3a.12. Net assimilation rate (NAR) during three growth phases and at two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth phases: panicle development (PD), early grain filling (EGF) and late grain filling (LGF).

Growth Phase	Net assimilation rate					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	----------	----------	$g\ m^{-2}\ d^{-1}$	----------	----------	----------
			1st seeding			
VG	-	-	-	-	-	-
PD	11.21	8.80	7.89	7.16	4.67	7.95
EGF	5.55	4.46	3.48	3.69	5.54	4.54
LGF	6.85	4.45	4.66	3.69	-1.26	3.68
Mean	7.87	5.90	5.34	4.84	2.99	5.39
			2nd seeding			
VG	-	-	-	-	-	-
PD	8.14	7.90	7.63	5.97	3.26	6.58
EGF	4.52	2.49	5.05	3.86	1.40	3.46
LGF	7.71	4.69	2.33	-1.31	2.10	3.10
Mean	6.79	5.02	5.00	2.84	2.25	4.38
			Mean of 2 seeding dates			
VG	-	-	-	-	-	-
PD	9.68	8.35	7.76	6.56	3.97	7.26
EGF	5.04	3.47	4.26	3.77	3.47	4.00
LGF	7.28	4.57	3.49	1.19	0.42	3.39
Mean	7.33	5.46	5.17	3.84	2.62	

LSD P=0.05:
C means= 1.28
G means= 1.29
G means within the same C for the average of S= 2.89
C means within the same G for the average of S= 2.685
G means within the same combination of C and S= 4.088
C means within the same combination of G and S= 3.80

Table 3a.13. Panicle growth rate (PGR) during three growth phases and at two seeding dates, for five rice cultivars. Values at each seeding date are the mean of four replications. Growth phases: panicle development (PD), early grain filling (EGF) and late grain filling (LGF).

Growth Phase	Panicle growth rate					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	$g\ m^{-2}\ d^{-1}$					
	1st seeding					
VG	-	-	-	-	-	-
PD	6.7	5.9	6.0	5.8	4.1	5.7
EGF	21.2	26.0	25.7	17.2	34.6	25.0
LGF	18.5	17.4	16.7	22.3	6.8	16.3
Mean	15.5	16.4	16.1	15.1	15.1	15.6
	2nd seeding					
VG	-	-	-	-	-	-
PD	7.8	7.3	6.0	5.4	5.4	6.4
EGF	26.4	28.0	31.6	29.5	31.8	29.5
LGF	16.9	15.3	10.5	7.6	9.8	12.0
Mean	17.0	16.8	16.0	14.2	15.7	15.9
	Mean of 2 seeding dates					
VG	-	-	-	-	-	-
PD	7.3	6.6	6.0	5.6	4.7	6.0
EGF	23.8	27.0	28.6	23.4	33.2	27.2
LGF	17.7	16.4	13.6	14.9	8.3	14.2
Mean	16.2	16.6	16.1	14.6	15.4	

LSD P=0.05:
G means= 1.82
G means within the same S= 2.58
G means within the same C for the average of S= 4.07
C means within the same G for the average of S= 3.71
G means within the same combination of C and S= 5.76
C means within the same combination of G and S= 5.25

CHAPTER IV

CARBOHYDRATE STORAGE AND PARTITIONING IN RICE CULTIVARS OF DIFFERENT MATURITY GROUPS

ABSTRACT

Preheading carbohydrate storage is considered an important contribution to grain yield in modern rice (Oryza sativa L.) cultivars, but it has been reported to be higher in long-season cultivars. The objectives of this study were to determine total nonstructural carbohydrate (TNC) concentration and absolute content in storage organs of rice cultivars from different maturity groups. The line RU9101001, and the cultivars 'Alan', 'L202', 'Newbonnet', and 'Starbonnet' with maturity periods ranging from extremely-short- to long-season, were evaluated at two seeding dates, April 24 and May 25, 1990, at Stuttgart, AR. The cultivars were sampled at internode elongation (IE), flowering, 12 days after flowering and maturity. Carbohydrate concentration was determined in leaf blades, leaf sheaths and stems. Starch was gelatinized in a boiling water bath, carbohydrates were hydrolyzed with a 0.5% takadiastase enzyme solution, and samples were analyzed for reducing power. The TNC concentration decreased after internode elongation, and absolute content was maximum at flowering. Depletion of stored carbohydrates was faster for the second seeding date. Maximum mean TNC concentration in leaf sheaths and stems was 214.3 and 279 g kg^{-1} at IE and flowering, respectively. Leaf sheath TNC concentration at maturity was low in all cultivars (27.8 g kg^{-1}), but stem concentration at harvest ranged from 171 to 91 g kg^{-1} for the mean of both experiments, and some concentrations increased during the last part of grain filling. Absolute TNC content was higher in mid- and long-season cultivars until flowering. The total carbohydrates remobilizated from vegetative tissues, from flowering to maturity, was

similar for cultivars with growth durations ranging from very-short- to long-season (1015 to 1228 kg TNC ha^{-1}), but was lower in RU9101001 (549 kg ha^{-1}). The extremely-short-season line RU9101001 maintained a high TNC concentration in the stems during grain filling. Stored carbohydrates appeared to be an important contributor to grain filling even in very-short-season cultivars like Alan and L202.

INTRODUCTION

Preheading storage plays a large role in yield of modern high-yielding rice cultivars under standard field conditions (Park et al., 1988). Carbohydrates begin to accumulate sharply about 2 weeks before heading, and the plant's vegetative parts, the leaf sheath and culm particularly, reach a maximum CH_2O content at near heading (Yoshida, 1981). The concentration begins to decrease as ripening proceeds and may rise again slightly near maturity (Yoshida, 1981; Lafitte and Travis, 1984; Turner and Jund, 1990; Murayama et al., 1955). A high content of sugars occurs in the culm at flowering in tropical rice, especially in the wet season, but in temperate rice, starch is reported to accumulate in the culm (Tanaka, 1972).

Total nonstructural carbohydrate (TNC) levels, in stems and leaves of the rice cultivars Labelle, Gulfmont, Skybonnet, and Mars, decreased to minimum levels (0 to 9%) during grain filling, and then increased at harvest to levels of 4 to 17% (Turner and Jund, 1990). The fluctuation of starch content in the culm is nearly the same as in the leaf sheath, but the maximum value in the culm is higher than that of the leaf sheath (Yoshida, 1981).

Lafitte and Travis (1984) studied carbohydrate concentration after heading in closely related rice genotypes differing in sink to source ratios. Carbohydrate content of storage organs decreased rapidly after heading, but there were no significant differences among lines in the sugar contents of leaf lamina or panicles. The genotypes with greater sink to source ratios had the lowest concentrations of TNC in the vegetative tissues, indicating that sink activity was relatively high. No starch buildup occurred in the leaves of any of the lines studied. High apparent photosynthesis was correlated with low concentrations of nonstructural carbohydrates in the vegetative storage tissues (culms), but no depression of apparent photosynthesis occurred because of elevated carbohydrate levels in those tissues.

The TNC concentration also shows diurnal variation. In soybean, TNC and starch concentration of leaflet blades increased during the day. However, reducing sugars, sucrose, and total soluble sugars remained relatively constant throughout the day compared with starch. Almost all of the diurnal pattern of TNC was due to changes in starch concentration (Allen et al., 1988).

Preheading storage may contribute 20 to 40% of the starch that is stored in the grain at harvest and acts as a biological buffer to prevent grain abortion during periods of maximal sink demand (Park et al., 1988; Cock and Yoshida, 1972). The extent of carbohydrate remobilization from vegetative sinks during ripening may reflect the degree to which sink activity is matched by source supply (Yoshida, 1981, cited by Lafitte and Travis, 1984).

Moderately high temperature after heading affects grain filling through acceleration of the translocation of carbohydrates and other substances. The dry weight decrease of leaf sheaths and culms during grain filling due to translocation of carbohydrates (and partly to transpiration loss), as well as the speed of dry weight increase of ears, were greater at a mean temperature of 25.5 C than at 21.3 C (Murata, 1976).

Preheading storage is higher with a long-season cultivar (Murata and

Matsushima, 1975). It was reported that short-season cultivars produced a great amount of carbohydrates during their flowering and ripening phases, while the long-season cultivars produced a greater percentage before flowering (Vergara et al., 1966).

Storage of TNC is reported to influence ratoon rice yields, inducing regeneration of ratoon tillers (Turner and Jund, 1990; Palchamy et al., 1990). According to Turner and Jund (1990), much of the variability in ratoon crop yields may be attributed to TNC levels in leaf and stem at main crop harvest. Main crop plants with elevated TNC levels produced ratoon yields 33 to 48% higher than those from plants with normal TNC concentration.

The purpose of this work is to determine TNC concentration and absolute content in storage organs of rice cultivars from different maturity groups grown at two seeding dates.

MATERIALS AND METHODS

Plant culture. The study was conducted at the University of Arkansas Rice Research and Extension Center, Stuttgart, on a Crowley silt loam soil (Typic Albaqualfs), during the 1990 crop season. Five long-grain cultivars were included, with maturity periods ranging from extremely short- to long-season:

-Starbonnet is a long-season cultivar that requires 103 days from seeding to heading. It is tall (1.17 m) and susceptible to lodging.

-Newbonnet is a mid-season high yielding cultivar, requiring 93 days from seeding to heading, with an average height of 1.01 m.

-L202 is a short-season high yielding cultivar that requires 81 days to 50% heading, with an average height of 0.91 m. It has narrow and erect leaves.

-Alan is a very-short-season, high-yielding cultivar that was released in 1990. Is one of the earliest maturing commercial cultivars available, with 77 days to 50% heading; with an average plant height of 1.04 m.

-RU9101001 is an extremely-short-season line, with heavy kernels and plant height of about 0.85 m. The line requires 68 days to 50% flowering.

The cultivars were evaluated at two seeding dates with three replications. The first experiment was seeded April 24 and emerged May 5, the second was seeded May 25 and emerged May 31. The rice was drill seeded at a rate of 134 kg ha^{-1}. Each plot consisted of six rows of 4.6 m in length, spaced at 19 cm. Plots were fertilized with a total of 165 kg N ha^{-1}, as urea, in a 3-way split application with 87 kg applied prior to flooding, 39 kg at internode elongation (IE), and 39 kg at booting.

<u>Sampling</u>. Each cultivar was sampled at four growth stages: 1) IE, 2) 50% flowering (F), 3) 12 days after 50% flowering (F+12D), and 4) physiological maturity (MAT). Results are reported as mean values for each growth stage. Sample size was 1 m of row, taken from one of the inner rows of the plot (rows 2 or 5). A subsample of 15 tillers was divided into leaf, sheath, stem, and panicle components. The samples and subsamples were dried at 85 C for 2 h, and then at 65 to 70 C for 3 days. Dry weight of each component and of the whole sample were recorded, and samples were stored in an air-conditioned room in sealed plastic bags.

<u>Carbohydrate analysis</u>. The TNC were determined in leaves, leaf sheaths, and stems by the procedure outlined in the Regional Rice Quality

Laboratory (B. Webb, Beaumont, TX, personal communication), adapted to the equipment availability (C. West and K. Turner, Fayetteville, AR, personal communication). The procedure is a modification of the method described by Smith (1981).

Samples were finely grounded to 40 mesh and dried at 65 C overnight to equilibrate moisture before weighing out 200 mg. Actual moisture content was determined on composite samples by drying at 130 °C for 1 h. Concentration is reported on dry weight basis.

The TNC were removed according to the modified Weinmann Method. Starch was gelatinized in a boiling water bath at 98 to 100 °C, cooled to room temperature, and hydrolyzed with 0.5% takadiastase enzyme (Clarase 40000) in a buffer solution. Samples were incubated for 44 h and filtered. A 10% neutral lead acetate was added and diluted, and the samples were decanted and centrifugated for 5 min at 3500 rpm. The supernatant was decanted into flasks containing powdered potassium oxalate and refrigerated overnight. A set of samples was also acid hydrolyzed, confirming that the enzyme was efficient in converting all sucrose to monomers and that acid hydrolysis was not necessary.

The samples were analyzed for reducing power, according to the Shaeffer-Somogyi Copper-Iodometric Titration. After filtration, 5-ml aliquots, as well as blanks and checks, containing 10 ml of reagent 50, were heated in a boiling water bath for 15 min and then cooled to room temperature. Titration was done manually with a burette and 0.02 N sodium thiosulfate solution to a pale blue end-point, with starch solution as indicator.

Experimental Design. Each seeding date was arranged as a randomized complete block design (RCBD), with growth stage as a split-plot in cultivar, and three replications. Both experiments were analyzed together as a RCBD two factor factorial with split combined over locations, testing the effects of seeding date (S), cultivars (C), growth stage (G), and the interactions of SxC, SxG, CxG, and SxCxG. The least significant differences (LSD), at P=0.05, were calculated for the pertinent main effects and for some of the different comparisons within the interactions, such as for the comparison of growth stage means within the same cultivar and cultivar means within the same growth stage.

RESULTS

TNC concentration. Table 4.1 contains the results of the analysis of variance for TNC concentration in the three fractions (leaf blades, leaf sheaths, and stems), as well as absolute TNC content of vegetative organs. All the interactions (SxG, CxG, SxCxG) were significant or highly significant for all the variables tested. Mean TNC concentration in the leaf blades was similar for both seeding dates, but concentration in the leaf sheaths and stems was higher for the first seeding.

The TNC concentration in leaf blades, leaf sheaths, and stems decreased after internode elongation for both seeding dates, but the depletion of stored carbohydrates was faster in the second experiment (Appendix, Fig. 4a.1, Tables 4a.1, 4a.2, and 4a.3).

Leaf blade TNC concentration generally decreased after IE, but some cultivars increased concentration from F+12D to maturity, as Starbonnet for the first seeding date and RU9101001 and L202 for the second seeding

(Fig. 4.1) (Appendix, Table 4a.1).

Table 4.1. Mean squares and significance for the combined analysis of variance of TNC concentration in leaves, leaf sheaths, and stems, and absolute content in the vegetative fraction.

Source of Variation	df (1)	Leaves	Leaf Sheaths	Stems	Absolute Content
		------------	(g k^{-1})	------------	(t ha^{-1})
Seeding date (S)	1	68.9	5110.4**	6296.8*	0.045
Replications R(S)	4	396.9**	1160.5*	1871.2	0.024
Cultivar (C)	4	1652.7**	3922.3**	8154.6**	0.325**
S x C	4	425.9**	1854.0**	1834.3	0.064*
Error	16	71.8	249.7	776.0	0.015
Growth stage (G)	3 (2)	15838.9**	220181.9**	204411.0**	5.804**
S x G	3 (2)	333.6*	3538.6**	22454.6**	0.354**
C x G	12 (8)	276.1**	2163.5**	6367.6**	0.202**
S x C x G	12 (8)	186.4*	838.7**	4249.0**	0.087**
Error	60 (40)	91.4	254.7	821.0	0.022
CV%		17.7	15.0	15.4	18.6

(1) Numbers in parentheses indicate degrees of freedom for stem concentration.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

For the first seeding date, all cultivars, except Starbonnet, had a gradual decrease in leaf sheath TNC concentration after IE. Starbonnet depleted carbohydrates faster, reaching a minimum concentration at early grain filling with no further decrease. For the second seeding, however, all cultivars showed this trend, with similar low concentrations at early grain filling and maturity (Fig. 4.2) (Appendix, Table 4a.2). Carbohydrate concentration at maturity, in the leaf sheaths, was very low for both experiments, with a mean of 27.8 g k^{-1}, even slightly lower than that in the leaf blades (38.2 g k^{-1}).

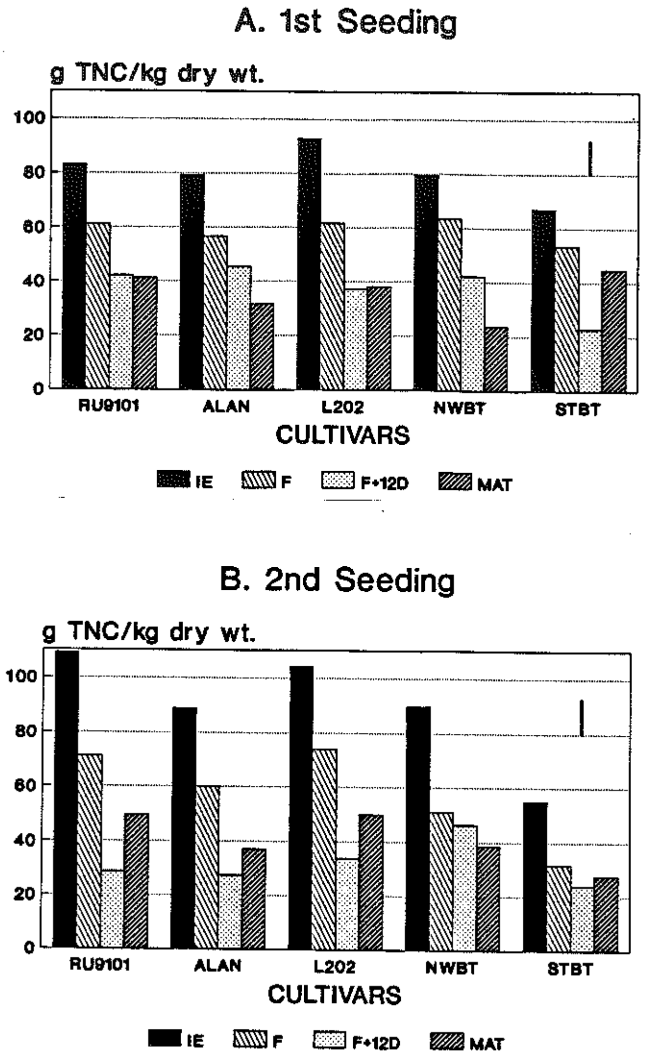
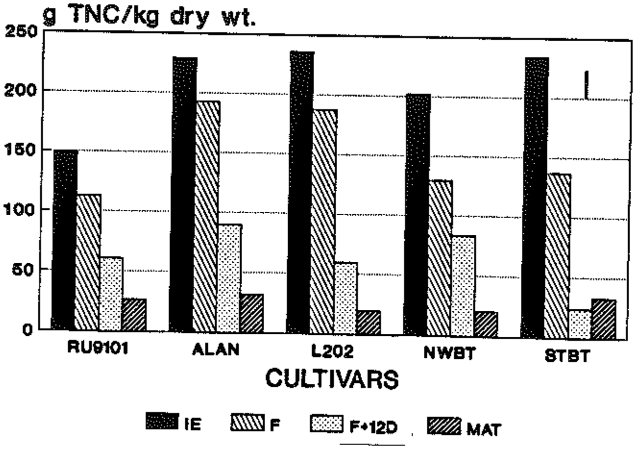


Fig. 4.1. TNC leaf blade concentration at internode elongation (IE), flowering (F), 12 days after flowering (F+12D), and maturity (MAT) for five rice cultivars at (A) first seeding date and (B) second seeding date. Each value is the mean of three replications. The bar represents the LSD at P= 0.05 for growth stage (G) means within cultivars.

A. 1st Seeding



B. 2nd Seeding

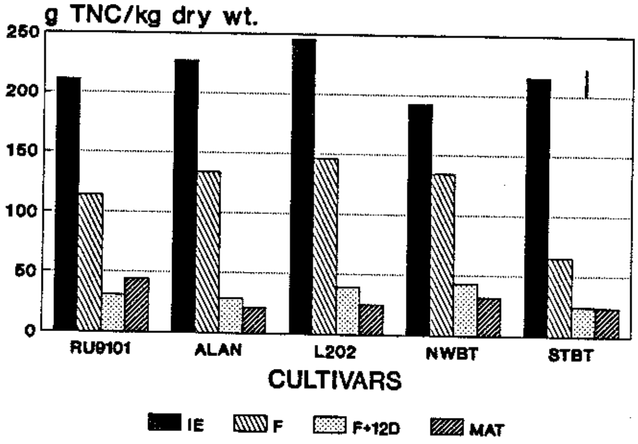


Fig. 4.2. TNC leaf sheath concentration at internode elongation (IE), flowering (F), 12 days after flowering (F+12D), and maturity (MAT) for five rice cultivars at (A) first seeding date and (B) second seeding date. Each value is the mean of three replications. The bar represents the LSD at P= 0.05 for growth stage (G) means within cultivars.

Stem TNC concentration in the first experiment decreased linearly from IE to maturity (286 to 102 g k^{-1}). For the second seeding, however, concentration at early grain filling and maturity were similar (125 and 138 g k^{-1}) (Appendix, Fig. 4a.1).

Stem TNC concentration of Starbonnet tended to increase during late grain filling for both seeding dates. RU9101001 and Newbonnet showed this non-significant trend only in the second trial (Fig. 4.3) (Appendix, Table 4a.3). As with leaf sheath concentration, stem concentration was greatly reduced during the first days of grain filling for the second seeding date. However, a considerable amount of carbohydrates remained in the stems for that seeding date, especially in the extremely-short-season line (Fig. 4.3). Newbonnet showed a slow depletion of stem carbohydrates during early grain filling for the first experiment.

Absolute TNC content. All the interactions among the factors (S, C, and G) were highly significant (Table 4.1). Due to the fast increase in dry matter from IE to flowering, absolute TNC content increased during that period of development in all cultivars despite the reduction in concentration (Fig. 4.4, and 4.5). Depletion of carbohydrates after flowering due to translocation or respiration followed the same tendency that concentration, and was faster for the second seeding date (Fig. 4.4).

Mean dry weight of carbohydrates in the vegetative organs was positively related to growth duration. Starbonnet and Newbonnet had the highest mean absolute TNC content for the whole season, 920 and 901 k ha^{-1}, respectively, while that of RU9101001 was 652 k ha^{-1} (Appendix, Table 4.4). However, RU9101001 had a low absolute TNC content at IE and flowering, but at maturity, the extremely-short-season line had similar or

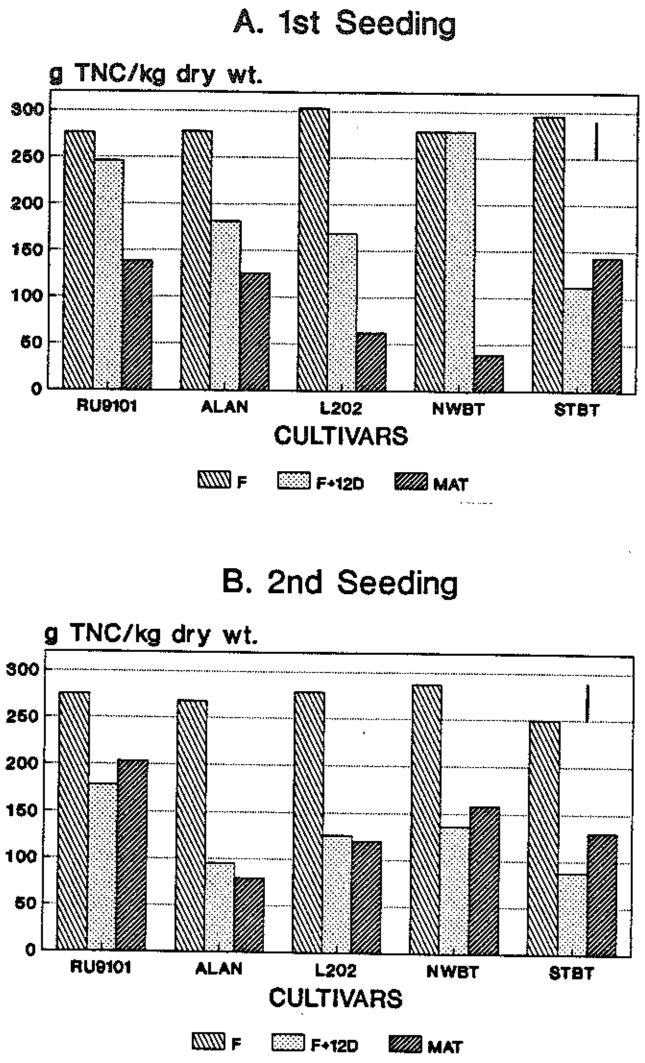


Fig. 4.3. TNC stem concentration at flowering (F), 12 days after flowering (F+12D), and maturity (MAT) for five rice cultivars at (A) first seeding date and (B) second seeding date. Each value is the mean of three replications. The bar represents the LSD at P= 0.05 for growth stage (G) means within cultivars.

higher content than the rest of the cultivars (Fig. 4.5).

For the first seeding, all cultivars, except Starbonnet, had a reduction in absolute TNC storage from 12 days after flowering to maturity. For the second seeding date, because of the faster depletion of carbohydrates, TNC storage at early grain filling was similar to that at maturity for all cultivars (Fig. 4.5). RU9101001 and Starbonnet tended to increase TNC content during late grain filling for the second experiment. The cultivars reached maturity with 413 k ha^{-1} of carbohydrates stored in the vegetative organs for the mean of both trials.

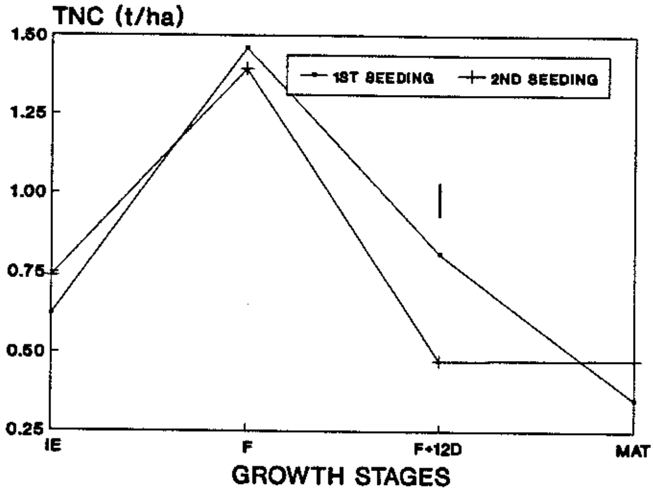
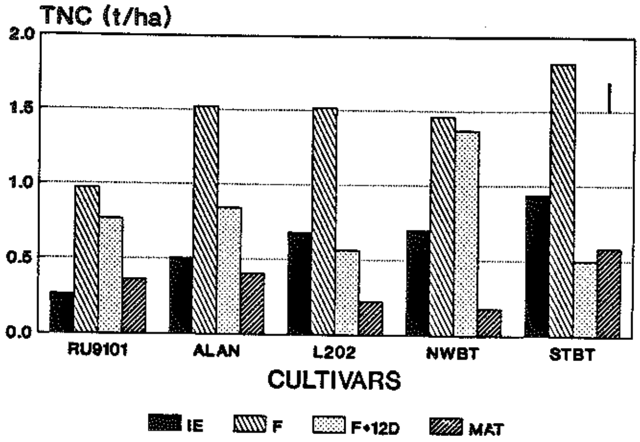


Fig. 4.4. Absolute total nonstructural carbohydrates (TNC) dry weight at internode elongation (IE), flowering (F), 12 days after flowering (F+12D), and maturity (MAT) for two seeding dates. Each point is the mean of five cultivars and three replications. The bar represents the LSD at P= 0.05 for growth stage (G) means within seeding dates.

A. 1st Seeding



B. 2nd Seeding

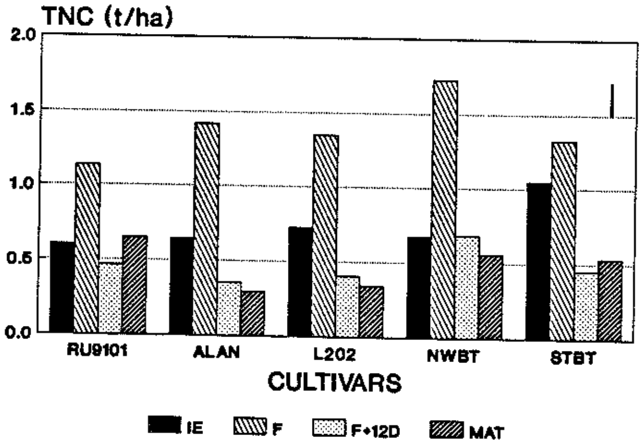


Fig. 4.5. Absolute TNC dry weight at internode elongation (IE), flowering (F), 12 days after flowering (F+12D), and maturity (MAT) for five rice cultivars at (A) first seeding date and (B) second seeding date. Each value is the mean of three replications. The bar represents the LSD at P= 0.05 for growth stage (G) means within cultivars.

DISCUSSION

Mean TNC concentration decreased from IE to maturity, but absolute TNC content obtained a maximum at flowering and then decreased during grain filling. Stored carbohydrates were depleted faster during the reproductive and grain filling phases of the second seeding date. Murata's (1976) report, that moderately high temperatures after flowering accelerated translocation, agrees with the data reported here. In the second trial the decrease in dry weight of the vegetative fraction during early grain filling and the increase in panicle weight were faster (Chap. 3).

Carbohydrate concentration in the vegetative tissue was not directly related to growth duration of the cultivars. Mean TNC concentration in the leaf blade was highest in RU9101001 and L202. Mean leaf sheath concentration was highest in the very-short-season cultivars Alan and L202. These cultivars stored a significant amount of carbohydrates in the leaf sheath compared to the stems. The extremely-short-season line, RU9101001, had the highest mean carbohydrate concentration in the stems and a low concentration in the leaf sheath (Fig. 4a.2).

The reduction of TNC concentration in the leaf sheaths and stems in this experiment did not follow the same pattern as reported by Yoshida (1981). Leaf sheath carbohydrate concentration at harvest was very low in all cultivars and for both seeding dates without any increase late in the season. Stem TNC concentration at harvest, however, showed important variability among cultivars, and some cultivars showed an increase in carbohydrate concentration during the last part of grain filling. This increase in TNC content late in the season was also reported by Yoshida (1981) and Turner and Jund (1990). The cultivars included in this study showed this trend for the leaf blade and stems for the second seeding date but not in the leaf sheaths.

Alan, Newbonnet, and Starbonnet had a larger sink size at heading for the second seeding date (Chap. 3). This increase in sink size may be associated with the lower TNC stem concentration observed at harvest in Alan, for the second trial. As Newbonnet and Starbonnet had a high incidence of unfilled grains for the second seeding date, the increase in sink size was not reflected in a lower concentration at harvest (Fig. 4.3). RU9101001 had a smaller sink size the second seeding, and the lower sink demand may determine the high TNC stem concentration for that experiment.

Source activity of RU9101001 during grain filling was high enough to meet the requirements of the panicles without translocating a great amount of carbohydrates from the stems. This high concentration during late ripening did not affect source activity, since RU9101001 maintained a high net assimilation rate during that phase of development (Chap. 3). Alan and L202 had a considerable reduction in stem TNC concentration during grain filling.

Mean absolute TNC content during the season was directly related to growth duration of the cultivars, but it was higher in mid- and long-season cultivars only until flowering. Carbohydrate content at harvest was similar in RU9101001 and Starbonnet (Fig. 4.5).

The total amount of carbohydrates remobilizated from vegetative tissues from flowering to maturity was similar for the cultivars with growth durations ranging from very short-season to long-season. Alan, L202, Newbonnet, and Starbonnet had a decrease in absolute stored TNC from flowering to maturity that varied from 1015 to 1228 kg TNC ha^{-1} for the mean of both seeding dates. The extremely-short-season line (RU9101001), however, had a decrease of 549 kg ha^{-1}. Park et al. (1988) pointed out the important role of stored carbohydrates in modern high-yielding cultivars. This storage appears to be an important contribution to grain filling even in very-short-season cultivars like Alan and L202. Carbohydrate storage in early-maturing cultivars seems to be high enough to provide a buffer action during grain filling, in case of cloudy weather.

Turner and Jund (1990) reported that carbohydrate storage influences ratoon growth of rice cultivars. The high stem TNC concentration maintained by RU9101001 at harvest, especially in the second experiment, may be determining the good ratoon growth observed in that line. The earliest-maturing cultivars included in the study, RU9101001 and Alan, showed a different pattern in carbohydrate storage and important variability in stem concentration, which may affect ratoon performance. RU9101001 stored most of the carbohydrates in the stems, and Alan also stored an important amount of carbohydrates in the leaf sheath. For the mean of both seeding dates, stem TNC concentration at harvest was 171 and 102 g k^{-1}, for RU9101001 and Alan, respectively.

REFERENCES

Allen Jr., L.H., J.C.V. Vu, R.R. Valle, K.J. Boote, and P.H. Jones. 1988. Nonstructural carbohydrates and nitrogen of soybean grown under carbon dioxide enrichment. Crop Sci. 28:84-94.

Cock, J.H., and S. Yoshida. 1972. Accumulation of 14 C-labelled carbohydrate before flowering and the subsequent redistribution and respiration in the rice plant. Proc. Crop Sci. Soc. Jpn. 41:226-234.

Lafitte, H.R., and R.L. Travis. 1984. Photosynthesis and assimilate partitioning in closely related lines of rice exhibiting different sink:source relationships. Crop Sci. 24:447-452.

Murata, Y., and S. Matsushima. 1975. Rice. p.73-99. In Crop physiology. Some case histories. L.T. Evans. Cambridge University Press. London.

-----. 1976. Productivity of rice in different climatic regions of Japan. p. 449-470. In Climate and rice. IRRI. Los Banos. Philippines.

Murayama, N., M. Yoshino, M. Oshima, S. Tsukahara, and U. Kawarasaki. 1955. Studies on the accumulation process of carbohydrates associated with growth of rice. Bull. Natl. Inst. Agric. Sci. (Tokio), B, 4:123-166. Jpn. Eng. Summ.

Palchamy, A., S. Purushothaman, and A. Rajagopal. 1990. Effect of stem thickness and carbohydrate content on ratoon rice yield. Int. Rice Res. Newslett. 15(2):10.

Park, W.D., D.L. Andrews, C.N. Bollich, and B.D. Webb. 1988. Role of preheading storage in rice yield. p.26. In Proc. XXII Rice Technical Working Group. Davis. California.

Smith, D. 1981. Removing and analyzing total nonstructural carbohydrates from plant tissue. R2107. Research Division, College of Agricultural and Life Sciences. University of Wisconsin-Madison.

Tanaka, A. 1972. Efficiency of respiration. p.438-498. In Rice breeding. IRRI. Los Banos. Philippines.

Turner, F.T., and M.F. Jund. 1990. Main-crop N and stem carbohydrate influence on ratoon rice yields. p.116-117. In Proc. XXIII Rice Technical Working Group. Biloxi. Mississippi.

Vergara, B.S., A. Tanaka, R. Lilis, and S. Puranabhavung. 1966. Relationships between growth duration and grain yield of rice plants. Soil Sci. Plant Nutr. 12(1):31-39.

Yoshida, S. 1981. Fundamentals of rice crop science. IRRI. Los Banos. Philippines.

APPENDIX

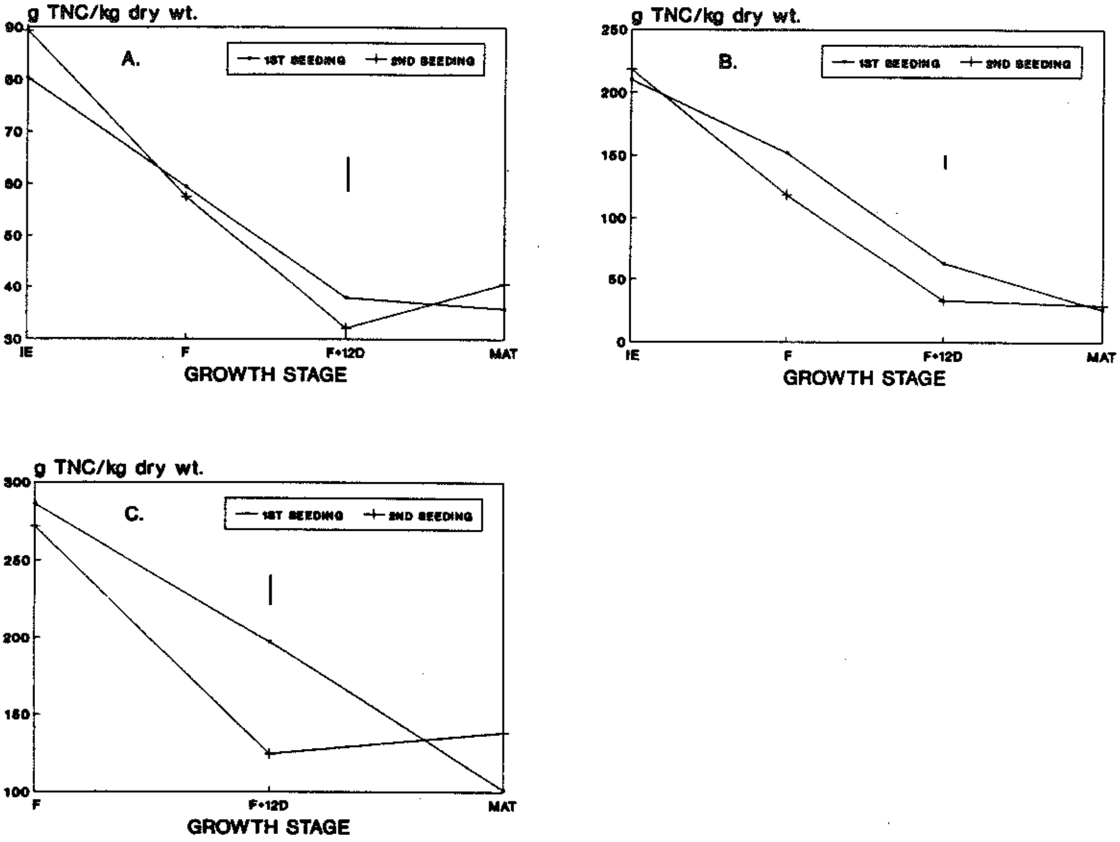


Fig. 4a.1. TNC concentration in vegetative organs at internode elongation (IE), flowering (F), 12 days after flowering (F+12D), and maturity (MAT) for two seeding dates. (A) leaf blade, (B) leaf sheath and (C) stem. Each value is the mean of five cultivars and three replications.

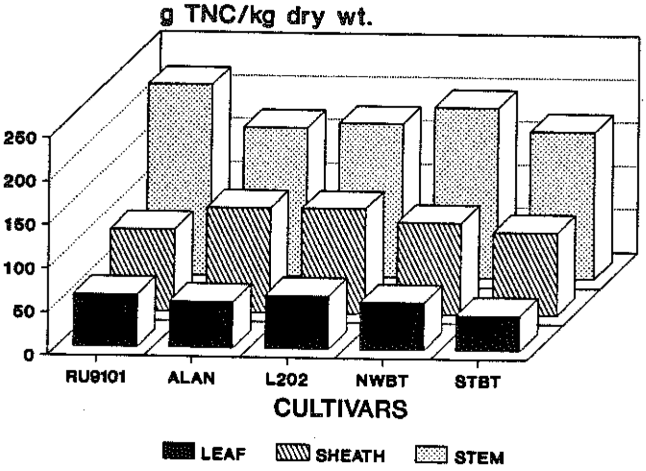


Fig. 4a.2. Mean TNC concentration in leaf blades, leaf sheaths, and stems for five rice cultivars. Each value is the mean of two seeding dates and three replications.

Table 4a.1. TNC leaf blade concentration at four growth stages and two seeding dates for five rice cultivars. Values at each seeding date are the mean of three replications.

Growth Stage (1)	Leaf blade TNC					
	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	$g\ k^{-1}$					
			1st seeding			
IE	83.0	79.2	93.0	79.3	67.2	80.4
F	61.3	56.8	61.8	63.7	53.5	59.4
F+12D	42.1	45.5	37.2	42.1	22.8	37.9
MAT	41.2	31.5	38.2	23.6	44.7	35.8
Mean	56.9	53.3	57.5	52.2	47.1	53.4
			2nd seeding			
IE	109.2	88.8	104.1	89.9	55.0	89.4
F	71.1	60.0	74.0	51.1	31.6	57.6
F+12D	28.6	27.5	33.8	46.3	24.0	32.0
MAT	49.4	37.1	50.0	38.7	27.8	40.6
Mean	64.6	53.3	65.5	56.5	34.6	54.9
			Mean of 2 seeding dates			
IE	96.1	84.0	98.5	84.6	61.1	84.9
F	66.2	58.4	67.9	57.4	42.6	58.5
F+12D	35.4	36.5	35.5	44.2	23.4	35.0
MAT	45.3	34.3	44.1	31.2	36.2	38.2
Mean	60.7	53.3	61.5	54.3	40.8	

(1) Growth stages: (IE) internode elongation, (F) 50% flowering, (F+12D) 12 days after flowering, (MAT) maturity.

LSD P=0.05:
C means= 5.19
C means within the same P= 7.33
G means= 4.94
G means within the same P= 6.98
G means within the same C for the average of P= 11.04
G means within the same combination of C and P= 15.61

Table 4a.2. TNC leaf sheath concentration at four growth stages and two seeding dates for five rice cultivars. Values at each seeding date are the mean of three replications.

	Leaf sheath TNC					
Growth Stage (1)	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	g k^{-1}					
			1st seeding			
IE	149.2	229.4	236.1	202.1	234.2	210.2
F	112.7	193.0	187.3	129.5	137.1	151.9
F+12D	60.9	89.7	60.1	83.6	23.7	63.6
MAT	26.5	31.6	19.7	20.5	33.2	26.3
Mean	87.3	135.9	125.8	108.9	107.1	113.0
			2nd seeding			
IE	211.3	227.3	246.0	192.4	215.3	218.5
F	114.2	134.0	146.0	134.2	65.2	118.7
F+12D	30.9	28.8	39.5	43.1	24.2	33.3
MAT	44.4	21.1	25.2	31.9	24.0	29.3
Mean	100.2	102.8	114.2	100.4	82.2	100.0
			Mean of 2 seeding dates			
IE	180.2	228.3	241.1	197.3	224.7	214.3
F	113.5	163.5	166.6	131.9	101.2	135.3
F+12D	45.9	59.3	49.8	63.4	24.0	48.5
MAT	35.5	26.3	22.5	26.2	28.6	27.8
Mean	93.8	119.4	120.0	104.7	94.6	

(1) Growth stages: (IE) internode elongation, (F) 50% flowering, (F+12D) 12 days after flowering, (MAT) maturity.

LSD P=0.05:
C means= 9.670
C means within the same P= 13.68
G means= 8.24
G means within the same P= 11.66
G means within the same C for the average of P= 18.43
G means within the same combination of C and P= 26.07

Table 4a.3. TNC stem concentration at three growth stages and two seeding dates for five rice cultivars. Values at each seeding date are the mean of three replications.

	Stem TNC					
Growth Stage (1)	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
	$g\ k^{-1}$					
			1st seeding			
IE (2)	-	-	-	-	-	-
F	276.5	277.8	302.8	278.2	295.5	286.2
F+12D	245.9	181.4	168.7	278.3	111.6	197.2
MAT	138.4	125.0	62.3	38.6	143.2	101.5
Mean	220.3	194.7	177.9	198.4	183.4	194.9
			2nd seeding			
IE	-	-	-	-	-	-
F	275.2	267.9	278.7	287.0	249.5	271.7
F+12D	177.9	95.0	126.3	136.3	87.7	124.6
MAT	203.7	79.5	119.9	158.6	130.1	138.4
Mean	218.9	147.5	175.0	194.0	155.8	178.2
			Mean of 2 seeding dates			
IE	-	-	-	-	-	-
F	275.9	272.9	290.8	282.6	272.5	278.9
F+12D	211.9	138.2	147.5	207.3	99.7	160.9
MAT	171.0	102.3	91.1	98.6	136.7	119.9
Mean	219.6	171.1	176.5	196.2	169.6	

(1) Growth stages: (IE) internode elongation, (F) 50% flowering, (F+12D) 12 days after flowering, (MAT) maturity.
(2) Stem concentration was not determined at IE.

LSD P=0.05:
C means= 19.69
G means= 14.95
G means within the same P= 21.15
G means within the same C for the average of P= 33.43
G means within the same combination of C and P= 47.28

Table 4a.4. Absolute TNC content (k ha) of vegetative organs (leaves, sheaths, stems) at four growth stages and two seeding dates for five rice cultivars. Values at each seeding date are the mean of three replications.

	Absolute TNC					
Growth Stage (1)	RU9101001	Alan	L202	Newbonnet	Starbonnet	Mean
			$k\ ha^{-1}$			
			1st seeding			
IE	264	504	678	703	943	618
F	972	1520	1517	1463	1820	1458
F+12D	766	841	565	1369	497	808
MAT	362	406	222	177	583	350
Mean	591	818	746	928	961	809
			2nd seeding			
IE	602	646	726	677	1048	740
F	1135	1419	1349	1729	1328	1392
F+12D	464	353	407	686	451	472
MAT	648	296	342	559	534	476
Mean	712	679	706	913	840	770
			Mean of 2 seeding dates			
IE	433	575	702	690	996	679
F	1054	1469	1433	1596	1574	1425
F+12D	615	597	486	1028	474	640
MAT	505	351	282	368	559	413
Mean	652	748	726	920	901	

(1) Growth stages: (IE) internode elongation, (F) 50% flowering, (F+12D) 12 days after flowering, (MAT) maturity.

LSD P=0.05:
C means= 74.04
C means within the same P= 104.71
G means= 75.82
G means within the same P= 107.23
G means within the same C for the average of P= 169.55
G means within the same combination of C and P= 239.77