Effects of Interaction Between Red Rice and Two Rice Cultivars on Morphological, Physiological and Ecological Characteristics.

Jairo Clavijo

Louisiana State University and Agricultural & Mechanical College

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EFFECTS OF INTERACTION BETWEEN RED RICE AND TWO RICE CULTIVARS ON MORPHOLOGICAL, PHYSIOLOGICAL AND ECOLOGICAL CHARACTERISTICS

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

The Department of Plant Pathology and Crop Physiology

by

Jairo Clavijo
I.A., Universidad Nacional de Colombia, 1970
M.S., Louisiana State University, 1978
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Germination, emergence, and early seedling development patterns were analyzed for red rice (Oryza sativa L.) and the rice (Oryza sativa L.) cultivars Mars, Saturn, Lemont and Bellemont. Red rice had the highest germination percentage, fastest emergence rate, and earliest development of both shoots and roots. These results suggest that the competitive ability of red rice is based on these characteristics which enable it to preempt more resources at early stages of stand development.

Interaction between red rice and Lemont or Mars was evaluated by comparing morphological and physiological characteristics of these plants when grown in pure stands and in 50:50 mixtures. Plant height, top dry weight, tiller and leaf number, leaf area index, and leaf area duration of the cultivars were reduced significantly in the presence of red rice in the mixture. The effects of the interaction were detected as early as 28 days after emergence in the cultivars, first as a reduction in leaf area index and then as reduced top dry weight. When red rice was grown in mixture it produced more tillers and leaves and greater top dry weight than when grown in monoculture. These growth attributes may also be responsible for its competitive ability.

Effects of end-of-day light quality on early growth and development of red rice, Lemont and Mars were examined in a controlled environment. Exposure of the base of the plants to red light at the end of the day promoted an increase in the number of tillers per plant. The magnitude of the increase was greater for red rice than for the
cultivars. The results support the hypothesis that tillering is controlled by a shift in spectral quality of the light reaching the bottom of the canopy.

Root interaction between red rice and Lemont or Mars reduced nitrogen and phosphorus content of shoots for Lemont and the phosphorus content of shoots for Mars. The high root cation exchange capacity exhibited by red rice could be the root property associated with its greater nutrient uptake and below ground competitive ability.
INTRODUCTION

Red rice (*Oryza sativa* L.) is one of the most important weeds of rice in many countries and has a potential for spreading to new areas where prevention is not practiced (Baker and Sonnier, 1983). Red rice is classified as a weed that causes major yield and quality losses and is economically troublesome worldwide. It can grow in lowland as well as upland rice and appears in dry- or water-seeded rice. It can also grow and produce seed in other crops such as soybeans, grain sorghum, and pastures (Smith, 1983).

In the United States, red rice is found in Louisiana, Texas, Mississippi and Arkansas. An estimated $50 million annual loss in yield and quality is attributed to red rice (Smith, 1979). However, these losses vary with the availability of red rice-free seed rice, the seeding method, the control practices and the market conditions (Baker and Sonnier, 1983).

Red rice is characterized by having a pigmented aleurone layer, a unique seed dormancy and an ease of shattering (Craigmiles, 1978). Two major biotypes are found, strawhull and blackhull, with the former being the most predominant (Constantin, 1960). Both biotypes are highly competitive when in mixture with rice cultivars and usually grow taller and tiller more profusely (Diarra et al, 1985b).

Red rice is difficult to control in rice fields because it exhibits morphological and physiological characteristics similar to those of rice cultivars. When grown together they often interact and behave differently than when grown separately. Harper (1977) stated that it would be satisfying to be able to take two species, and by analyzing
their behavior when grown together, to ascribe the success of one over
the other to a particular morphological feature, a particular pattern
of life cycle or a simple physiological trait.

This work investigates the interaction of red rice and two rice
cultivars, Lemont and Mars, by (a) analyzing their early establishment,
growth and yield components in pure stands and mixtures and (b)
dertermining the influence of light quality and nutrient uptake on
morphological and physiological characteristics. An attempt is made to
separate above and below ground competition effects.
Plant interaction. Plants in nature usually occur in association with other plants of the same or different species and when individual plants are close enough they interact with each other. Various types of interactions are included in the general term interference which is defined as the effect that the presence of a plant has upon the environment of its neighbors (Radosevich and Holt, 1984). Harper (1977) has explained interference as "changes in the environment, brought about by the proximity of individuals, which includes neighbor effects due to the consumption of resources in limited supply, the production of toxins, or changes in conditions such as protection from wind and influences on the behavior of predators".

The interaction may be positive, negative, or neutral. The interaction is positive when one or both plants are stimulated by the interaction. The interaction is negative when one or both plants are depressed by the association. The interaction is neutral when plants do not exert any influence on one another. The actual causes of interaction may include consumption of limited resources, production of stimulants or toxins, or protection (Zimdahl, 1980; Radosevich and Holt, 1984).

Competition may be defined as interaction effects of plants which utilize a resource in short supply. The factors for which competition may occur among plants are water, nutrients, light, oxygen, and carbon dioxide. There are other factors affecting growth such as temperature and humidity, but these are not commodities in finite supply and hence are not the subject of competition. Water, nutrients, and light are

Competition for space is more common in the animal kingdom and it is not usually the case with plants. When de Wit (1960) used the term "competition for space", the term space was used to include all factors or requisites such as water, nutrients, light, etc., which are homogeneously distributed over, and in the field, where the plants grow.

Interspecific competition arises when two species are grown together in a mixture. In this case, the plant of one species may utilize more than its share of the environment while the plants of the other will have less. To study interspecific competition it is important to take into account the yield of both species in monoculture and the yield of both species in a mixed population. According to Harper (1977), four basic types of response are possible when two species are grown together in mixture. First, the growth of the two species in mixture results in each contributing to the total yield in direct ratio to its proportion in the sown seed. Thus, the ability of the two species to interact with each other is exactly equivalent. Second, one species provides more than expected to the total yield, whereas the other provides less than expected. In this situation, species A can be more aggressive for a resource than species B or vice versa. Third, neither species contributes its expected share to the total yield. Such a situation would arise if each species damaged the environment of the other more than it damaged its own environment. Fourth, both species provide more to the total yield than expected.
This could indicate the escape of each species from competition with the other.

Intraspecific competition is common between plants of similar genotype, all sown at the same time, and each with closely similar environmental needs (Donald, 1963). In addition, Harper (1977) indicates that there is another class of interaction in the field besides that between plants of the same or different species. This occurs when parts of the same plant (leaves, tillers, etc) are touching or shading other parts producing intraclonal or intraplant competition.

Kawano et al. (1974) studied intraspecific-intergenotypic competition in 25 rice cultivars with different growth habits and found that the actual yield of genetically mixed rice populations was always below the yield of the better component genotype in pure populations. Thus, yield reduction in one genotype as a result of competition was not compensated by the yield increase in another.

At very low stand densities individuals do not interact and biomass production or yield of a population is proportional to the number of individuals per unit area. Once the stand density exceeds a certain level individuals will begin to interact and biomass production or yield of the population reaches a plateau which is determined by the magnitude of the resources of the environment (Harper, 1977; Radosevich and Holt, 1984).

Density stress affects growth, yield, reproduction, and mortality of individual plants in a population. Plants react to density stress by a plastic response of growth or by an altered risk of mortality. Both types of responses may occur as a consequence of either intra- or interspecific competition or other forms of interaction. Plasticity is
the ability of plants to alter their size, form, mass, or number in relation to density or other environmental stresses. At low densities, yield depends on density, but at higher densities yield becomes independent of density and dependent on the rate of availability and utilization of resources. Plants have a capacity for self-thinning as a resource becomes more and more limiting. In this situation the rate of death becomes a function of the growth rate of the survivors. Density-stressed populations tend to form a hierarchy of dominant and subordinate individuals, the later being more likely to die (Harper, 1977).

**Crop-weed interaction.** Crops and weeds have the same general requirements for growth and development and interact in several ways. One type of interaction begins when crops and weeds grow in close proximity to each other and a supply of one or more environmental factors (mainly light, water, and nutrients) falls below the demands of both. Once this occurs, the other factors necessary for plant growth cannot be used effectively even though they may be present in abundance. As a consequence, modification of the growth and development of a plant is likely (Moody, 1981).

Competition between crops and weeds is an extremely complex system and the extent of competition and subsequent effects on crop yields and quality will depend on a number of factors. In rice, the yield losses due to weed competition are influenced by the relative competitive ability of weeds and rice, species or group of weeds, weed density, duration of crop-weed competition, planting method, cultivar, fertility level, water management, spacing of the rice crop, and interactions
among these factors. Most studies have found the magnitude of rice yield reduction due to weeds to be in the 20 to 30% range (Smith, 1983).

Weed competition can cause morphological or anatomical changes or have an influence on physiological processes. As a result of physiological changes there may be quantitative or qualitative variations of the chemical composition of a species. Increases have been found in the protein content of the green parts of the superior partners in competition experiments (Glaunier and Holzner, 1982).

To study crop-weed competition the four methods most used are additive experiments, replacement series, reactive surface experiments, and dynamic simulation of competition. In additive experiments, a weed population of varying stand density is added to a population of the crop at a fixed stand density; the yield of the crop in plots with weeds is expressed in percentages of its yield in a plot without weeds. This type of experiment measures the effect of simultaneously changing stand density and proportionality of the plant population on the crop. In replacement series, a range of mixtures is generated by starting with a monoculture of species 1, progressively replacing plants of species 1 with those of species 2 until a monoculture of species 2 is obtained; as a result all stands have the same density. In this type of experiment, stand density is held constant but the proportionality varies. In reactive surface experiments, both proportionality and stand density of the two species in the mixture are varied and survival, mean yield per plant and yield per unit area for each species are estimated. The dynamic simulation of competition serves to predict the competitive relations in a mixture at any time on the basis of
parameters derived from a spacing experiment with the species grown in monoculture and harvested at intervals (De Wit, 1960; Spitters and van den Berg, 1982).

**Competition for light.** As a resource, light is continuously available to the plant community in a relatively constant quantity. Light supply usually cannot be controlled by the grower as readily as the nutrient or water supply can. Competition for light occurs whenever one plant shades another or, within a plant, when one leaf shades another leaf (Donald, 1963; Zimdahl, 1980; Glaunier and Holzner, 1982).

In the presence of an adequate water and nutrient supply and with favorable temperatures, available light energy sets the limits for plant productivity. Light supplies the energy for photosynthesis and influences the development and morphology of the plant through effects of quantity, quality and duration (Patterson, 1985; Smith, 1982).

The presence of a weed or crop canopy alters the quality or wavelength distribution, as well as, the quantity of the light energy passing through it. Understanding the ecophysiological aspects of the effects of light on weeds and crops is important because weeds compete with crops for available light energy. In fact, promoting the development of a crop canopy is a major means of cultural weed control (Patterson, 1985).

In general, under vegetation canopies there are three spectral changes which are of obvious potential physiological significance. First, the quantity of photosynthetically active radiation (PAR) is drastically reduced. Second, a marked reduction in the quantity of radiation in the blue (B) waveband may be expected to be of relevance
to the photon fluence rate dependent responses controlled through a blue light photoreceptor. The photon fluence rate refers to the number of photons falling upon a surface in an interval of time. The third spectral change which is likely to be of physiological significance is the strong depletion of the red (R) waveband and relatively weak depletion of the far-red (FR) waveband (Smith and Morgan, 1981; Holmes 1981; Holmes and Smith, 1977a).

The radiation under canopies has two components: unfiltered daylight (diffuse or direct) which has passed through holes in the canopy; and filtered, or attenuated daylight, the spectrum of which has been altered by the canopy by the processes of absorption, reflection, and transmission. Addition of transmitted and reflected light to the diffuse radiation produces the typical shadelight spectrum with troughs in the blue and red regions, where absorption by the chlorophyll of the shading canopy is most intense, a minor peak in the green, and a major peak in the far-red. Chlorophyll is transparent to far-red and the attenuation in this region is due to reflection alone (Smith and Morgan, 1981; Holmes and Smith, 1977b; Holmes, 1981).

The ratio of radiant energy of R (600-700 nm) to FR (700-800 nm) in the light (R:FR) reaching certain plants or plant parts beneath a canopy is a function of the number of leaf layers, their angle of disposition and the relative contribution of direct and diffuse radiation received (Deregibus et al., 1985). Thus, in comparison with unaltered sunlight, light under a plant canopy has a much lower R:FR. Plants respond to these light variations and have altered morphological development (Child et al., 1981; McLaren and Smith, 1978; Smith, 1982; Holmes and Smith, 1977b).
The photoreversible pigment phytochrome has been proposed as the photoreceptor which absorbs light in the R and FR regions of the spectrum and controls photomorphogenetic responses. This pigment has an inactive R-absorbing form called Pr and an active FR-absorbing form called Pfr. In broadband irradiation both Pr and Pfr will absorb photons, and so the phytochrome will cycle and come to a dynamic equilibrium called the photoequilibrium which has been expressed as the ratio of Pfr to the total amount of phytochrome in both forms (Ptot) (Morgan, 1981).

It has been stated that the function of phytochrome in the natural environment is to detect the R:FR of the incident spectrum. For green plants this may serve as an index of shade or to monitor the degree to which a plant is shaded. It may be adaptive for arable weeds which normally grow among other herbaceous plants to show a response to a reduced R:FR ratio by increasing stem elongation which elevates their leaves to the top of the shading canopy (Child et al., 1981; Morgan, 1981).

A close correlation was found between phytochrome photoequilibrium (Pfr/Ptot) and the ratio of the quantum flux in the red and the far-red wavelength bands (R:FR) in broad spectrum (400-800 nm) radiation. This relationship allows direct prediction of Pfr/Ptot from a knowledge of R:FR. Phytochrome showed greatest sensitivity to spectral changes in the range of R:FR between 0 and 1 which is the range found in the natural environment (Morgan and Smith, 1976; Holmes and Smith, 1977c; Johnson, 1981; Kendrick and Frankland, 1983).

Changes in light quality within plant canopies and effects on phytochrome in plants have been studied by several investigators.
Simulating shadelight quality by lowering R:FR has led to increase petiole length, reduced leaf area, increased stem dry weight, reduced branching, changes in chlorophyll content and changes in activity of nitrate reductase in several species. The most conspicuous developmental response to low R:FR, however, is the marked and often spectacular increase in stem elongation rate in dicots (Kasperbauer and Peaslee, 1973; Cordukes and Fisher, 1974; Leaky et al., 1978; Morgan and Smith, 1979; Morgan et al., 1980).

Another important response to altered light quality which has been reported is the branching of dicots such as Xanthium strumarium L., Lycopersicon sculentum Mill., Pisum sativum L. and Nicotiana tabacum L. (Kasperbauer, 1971; Tucker, 1975; Morgan, 1981). A similar response has been reported in grasses where tillering was altered by end-of-day red and far-red treatments or above canopy irradiations (Deregibus, Sanchez and Casal, 1983). They showed that Lolium perenne L. and L. multiflorum Lam. plants developed more tillers when illuminated with higher R:FR ratios and concluded that branching of grasses (tillering) is controlled by phytochrome activity in a way similar to that in dicot plants.

Enrichment of red light at the base of dallisgrass (Paspalum dilatatum Poir.) and smutgrass (Sporobolus indicus [L.] R.Br.) plants in a dense humid natural grassland increased tillering rates and delayed tiller death until the end of the growing season. It was concluded that light quality may play a fundamental ecological role in the adjustment of a plant population to an environment and the R:FR ratio could serve as a signal to indicate canopy cover or leaf density (Deregibus et al., 1985). In fact, studies relating plant density,
R:FR ratio and tillering have suggested that as canopy density increases the lower light interception per tiller and the photomorphogenic effect of low R:FR ratios may reduce the capacity to produce new tillers (Casal et al., 1985; Casal et al., 1986).

The influence of plant density on spectral distribution of light received by wheat (*Triticum aestivum* L.) seedlings was measured under field conditions. Close-spaced seedlings received lower R:FR ratios than wide-spaced plants because of the large amount of far-red light transmitted and reflected from green leaves of neighboring plants. The R:FR ratios in all population densities were lower in late afternoon than at noon, and the close-spaced plants developed fewer tillers. In controlled environments, wheat seedlings that received 5 minute exposures to FR at the end of the photosynthetic period developed fewer tillers. These effects were reversed by red light. It was suggested that phytochrome serves as a sensing mechanism that detects the amount of competition from other plants and regulates the development of tillers (Kasperbauer and Karlen, 1986).

Research on the effect of R:FR on morphological and physiological parameters of rice has not been reported. It has been reported that shading rice from just before to just after heading reduced rice yields more than shading at other times in the life cycle of the rice plant. On the other hand, low light intensity reduced rice yields by lowering the number of filled grains per panicle (Takeda, 1961).

Okafor and De Datta (1976) found that purple nutsedge (*Cyperus rotundus* L.) competition reduced the amount of light reaching the base of rice plants. The reduction was proportional to the increase in purple nutsedge population and greater at higher nitrogen levels.
Competition for nutrients. Competition for nutrients may constitute an important aspect of weed-crop interaction. Weeds may compete for essential nutrients and decrease crop yield even at high rates of fertilization. Weeds are reported to absorb fertilizer faster and in relatively larger amounts than crops and therefore derive greater benefit (Zimdahl, 1980).

A substantial amount of the nutrients available from the soil may be utilized by weeds. The three most commonly limiting nutrients are nitrogen, phosphorus, and potassium; with nitrogen usually being the first nutrient to become limiting as a result of crop-weed interaction (Zimdahl, 1980).

The competition for nitrogen between weeds and rice is influenced by date of fertilizer application, plant populations, ability of the weed to absorb nitrogen, crop cultivar, rainfall, rate of nitrogen, and irrigation frequency (Moody, 1981).

According to Alkamper and Do van Long (1978), *Echinochloa colona* [L.] Link, an early developing weed, was extremely competitive against rice and losses increased as the level of applied fertilizer increased. In contrast, in the case of red rice, a late developing weed, addition of nitrogen fertilizer actually reduced injury to the rice crop, although there was some competition for nutrients. At the highest level of applied nitrogen, *E. colona* reduced grain yield by 84.4% and straw yield by 69.8%. With red rice, a 3.1% increase in grain yield and a 12.9% decrease in straw yield were observed.

Chisaka (1966) found that the weight of rice at maturity decreased approximately proportional to amount of nitrogen absorbed by the weeds, irrespective of the weed species. Moody (1981) reported that the
nitrogen concentrations of weeds range from 10 mg/g dry tissue to 38 mg/g dry tissue, and was usually higher than those of crop plants. In addition, the phosphorus content of weeds is about 5 mg/g dry tissue, about the same as that in growing cereal plants.

It was shown that the addition of phosphorus to dry-seeded wetland rice increased the number of rice tillers and panicles when rice was grown alone. In the presence of *Echinochloa crus-galli* [L.] Beauv., the number of tillers and panicles was depressed when phosphorus was added (Kleinig and Noble, 1969).

Mouat and Walker (1959, cited by Zimdahl, 1980) concluded that the basis of competition for phosphorus between species could be a function of root cation exchange capacity and this could be a mechanism of competition for phosphorus.

The cation exchange capacity (CEC) of roots is believed to affect cation absorption by plants (Asher and Ozanne, 1961). Tiwari et al (1975) showed that there is a direct relationship between the CEC of the roots and the yield and nutrient uptake of rice. Highly significant correlations were observed between the CEC of the roots and the uptake and partition of P, Zn, K, Ca, Mg, and Fe by roots and shoots.

Sharma et al. (1975) working with the rice cultivar IR-8 found that the CEC of roots increased from 4.27 me/100 g at field capacity to 6.52 and 7.95 me/100 g under saturation and flooding water regimes, respectively. It appears that this property of roots bears a direct relationship to the total uptake of nutrients by the root because total content of all nutrients except Mg and Zn increased with increase in root CEC.
In general, sorghum hybrids were found to be superior to inbred lines in root CEC. Highest root CEC values were obtained with sorghum hybrids SD 441 and RS 609. It was emphasized that root CEC is a selection criteria to be taken into account when the ability of sorghum to compete with weeds is tested (Guneyli et al., 1969).

Phosphorus content in shoots of the wheat cultivar Sabarti Sonora and potassium content in shoots of the rice cultivar Jamuna were significantly correlated with the root CEC at the blossoming stage of plant growth. The CEC of rice roots was higher than that of wheat roots. The CEC of plant roots was higher at early rather than later stages of plant growth (Singh and Singh, 1981). In addition, application of nitrogen in the soil significantly increased the root CEC of wheat varieties and some varieties of rice throughout the growing season (Singh and Ram, 1976).

**Competition for water.** Competition for water usually occurs together with other forms of competition, especially for nitrogen and light, but it is by no means of parallel intensity with these other forms. Indeed, when the competition for water or nitrogen is intense, growth may be so restricted that competition for light is of reduced importance, whereas, if water and nutrients are not limiting, shading will be a major factor (Donald, 1963; Zimdahl, 1980; Glaunier and Holzner, 1982).

Water competition occurs mainly in upland rice when it is rainfed and no water control exists. Okafor and De Datta (1976) found that purple nutsedge and upland rice competed extensively for moisture. The competition was more intense with increased nitrogen fertilization.
Plant competitive ability. Competitive ability of crops and weeds changes in the course of the plant's life cycle and is influenced by the environment. Most of the studies on plant competition agree that strong, competing cultivars or weeds are characterized by fast germination and early development of both above and below ground parts. An expanded root system is of the same importance as extensive, dense shoot growth in capturing as much 'space' as quickly as possible (Harper, 1977; Zimdahl, 1980; Glaunier and Holzner, 1982).

Spitters and van den Bergh (1982) point out that the competitive ability of a species is determined by: first, the resources it is able to capture at the beginning of the growing season, in which a good starting point is achieved by a greater number of plants, early emergence, and larger seeds; second, the relative rate at which a single plant of a species is able to utilize the resources it has already captured; and third, the preemption of the limiting factor.

Certain characteristics tend to be associated with competitiveness, as point out by Clements et al. (1929) quoted by Donald (1963): "It is evident that practically all the advantages or weapons of competing species are epitomized in two words: amount and rate. Greater storage in seed or rootstock, more rapid and complete germination, earlier start, more rapid growth of roots and shoots, taller and more branching stems, deeper and more spreading roots, more tillers, larger leaves, and more numerous flowers are all the essence of success."

Larger seeds, greater storage tissues in seeds and heavier seeds are equivalent terms to indicate that the seeds should have an adequate food and mineral storage; because germination and emergence have a high
demand for energy produced by respiration of these food reserves. Thus, the heavier the seed the more vigorous the germination can be, and this is a good starting point for the seedling to expand its root system and to preempt resources rapidly (Radosevich and Holt, 1984; Gardner et al., 1985).

Before the shoots emerge from the soil considerable radicle elongation has usually occurred. In most cases, below ground competition starts earlier than above ground competition. Therefore, the success of the seedling depends on the ability of the primary root to expand and extract moisture and nutrients from increasingly lower levels in the soil profile (Radosevich and Holt, 1984; Patterson, 1985).

The ability of sorghum hybrids and inbred lines to compete with weeds was evaluated using seedling characteristics. It was found that the competitive advantage of sorghum over weeds was largely due to rapid germination, emergence, and root and shoot growth during the early stages of plant development. Particularly, the competitive ability of sorghum was highly correlated with the germination rate index (GRI) of sorghum seeds, and it was suggested that GRI would be of ecological significance for the competitive ability of other crops and weeds (Guneyli et al., 1969).

When seedling vigor was related to stand establishment in eight upland rice genotypes, it was observed that speed of germination was correlated with the three-day germination count (TDGC), and seedling vigor was significantly correlated with seedling dry weight (Chauhan et al., 1985).
Efficient photosynthesis is just one of the many features determining competitive ability, and a combination of efficient photosynthesis with other features is necessary to make a really aggressive and successful weed. Plants that fix carbon dioxide at higher rates probably secure an initial competitive advantage and develop into high yielding crops or vigorous weeds (Black et al., 1969 cited by Zimdahl, 1980).

Phenotypic and genotypic plasticity also play an important role in competition. Kawano et al. (1974), in a study with 25 rice cultivars with different growth habits, found that intraspecific competition, competition with weeds, and spacing response were highly intercorrelated with each other, suggesting that these were controlled largely by the same genetic factors through the same physiological process. Vegetative vigor, large leaf area, a high rate of nitrogen absorption in early growth stages, and plant height were the most significant characters related to competitive ability. They also found that the tall, vigorous genotypes with a long growth period were well adapted to low nitrogen levels, wide spacing and no weed control. They suggested that the development of cultivars has been accompanied by the utilization of cultural methods that compensate for the loss of competitive ability.

Jennings and Aquino (1968) postulated that competitiveness in rice is positively correlated with early growth rate and organ size. The tall and leafy plant type, by virtue of vigorous early growth followed by slow later growth, was at once competitive and low in yield. Desirable short-statured, small-leaved plant types were inevitably unsuccessful competitors but were highly productive because of slow,
early growth followed by increased growth in later developmental stages. Therefore, competition was negatively associated with yield.

**Plant growth analysis.** Growth has been defined as the irreversible increase in plant size, which is often accompanied by changes in form. The pattern of growth over a generation is described by the sigmoid curve which results from differential rates of growth during the life cycle. If plant dry matter, leaf area, or height are plotted against time, a curve fitted to the data will normally be sigmoidal (Evans, 1972; Hunt, 1978; Radosevich and Holt, 1984; Gardner et al., 1985).

According to Hunt (1978; 1982), "Plant growth analysis is a quantitative approach, using only simple basic data, for the description and interpretation of whole plants growing under natural, semi-natural or controlled environments".

Plant growth analysis is a technique which uses mathematical expressions to quantify the relationship between plant growth, dry matter production and leaf area expansion (Radosevich and Holt, 1984; Patterson, 1985). Mathematical growth analysis uses measured quantities, such as total plant dry weight, total leaf area and time, and derived quantities, such as relative growth rate, crop growth rate, and leaf area ratio, that cannot be obtained directly but must be calculated from measured quantities (Radford, 1967; Evans, 1972; Hunt, 1978).

Plant growth analysis has been approached in two different ways. First, the classic growth analysis which involved measurements made at relatively long intervals using a relatively large number of plants. Second, the functional growth analysis which involved measurements at
more frequent intervals using a smaller number of plants. The difference between the two was based on the use fitted curves (Hunt, 1978; 1982).

As pointed out before, the use of derived quantities to analyze growth is based upon calculation and formulas. The main derived quantities are: relative growth rate (RGR), leaf area ratio (LAR), net assimilation rate (NAR), specific leaf area (SLA), leaf area index (LAI), crop growth rate (CGR) and leaf area duration (LAD) (Radford, 1967; Evans, 1972; Hunt, 1978; 1982).

RGR expresses the dry weight (W) increase in a time (T) interval in relation to the initial weight. The mean RGR is calculated from measurements taken at \( T_1 \) and \( T_2 \).

\[
RGR = \frac{\ln W_2 - \ln W_1}{T_2 - T_1}
\]

RGR is a compound interest function that represents the slope of the line when \( \ln W \) is plotted against time (Evans, 1972; Hunt, 1978).

LAR is the ratio between the leaf area (LA) exposed by a plant or photosynthesizing tissue and the total respiring plant tissues or total plant biomass (W). By definition LAR is calculated as an instantaneous value.

\[
LAR = \frac{LA}{W}
\]

LAR reflects the leafiness of a plant and has two components:

\[
LAR = SLA \times LWR
\]

SLA is the mean area of leaf displayed per unit of leaf weight (LW), (LA/LW) and is a measurement of leaf density or relative thickness. Leaf weight ratio (LWR) is an index of the leafiness of the plant on a weight basis (LW/W). Of the two, SLA and LWR, the former is more sensitive to environmental conditions. Variation in light intensity
(deep shade) causes striking increases in SLA (Evans, 1972; Hunt, 1982).

NAR is a measurement of the efficiency of a plant or a population as an assimilatory system. The net gain of assimilate per unit of leaf area and time. The mean NAR is calculated as follows:

$$\text{NAR} = \frac{(W_2-W_1)}{(T_2-T_1)} * \frac{(\ln LA_2-\ln LA_1)}{(LA_2-LA_1)}$$

The equation assumes that the relationship between plant weight and leaf area is linear. This assumption may hold for early phases of development but not for later phases, as growth rate of leaf area may exceed that of dry matter or vice versa. NAR is not constant with time but shows an ontogenetic downward drift with plant age (Evans, 1972; Hunt, 1978).

LAI is the ratio of leaf surface or photosynthetic surface to the ground area (GA) occupied by the crop.

$$\text{LAI} = \frac{\text{LA}}{\text{GA}}$$

LAI varies according to leaf shape and vertical and horizontal distributions of the leaves. An optimum LAI, that is, a LAI that supports the maximum rate of dry matter increase, is found when a crop as a whole intercepts virtually all of the available photosynthetically active radiation (Evans, 1972; Hunt, 1978; Gardner et al., 1985).

CGR is the gain in weight of a community of plants on a unit of ground area in a unit of time. The mean CGR is calculated as follows:

$$\text{CGR} = \frac{(1/\text{GA}) * (W_2-W_1)}{(T_2-T_1)}$$

When total dry weight is plotted against time, the slope of the regression line of the linear phase (CGR) is usually similar for high yielding cultivars (Evans, 1972; Hunt, 1978).
LAD is an integrated value of LAI over a period of time and expresses the magnitude and persistence of leaf area or leafiness during the period of crop growth. The mean LAD is derived from the following formula:

\[ \text{LAD} = \frac{(\text{LAI}_1 + \text{LAI}_2)(T_2 - T_1)}{2} \]

LAD can be used to describe the extent and duration of the light trapping apparatus of a plant population from seedling to the period of maximum LAI (Evans, 1972; Hunt, 1978).

Several relationships between these growth parameters have arisen. The first was pointed out by Briggs, Kid and West (1920) who brought together the concepts of NAR, LAR and RGR. They postulated that

\[ \text{RGR} = \text{LAR} \times \text{NAR} \]

This equation is applied to single plants which are widely spaced, with little or no competition between individuals. However, Harper (1977) indicates that this relationship may be used to study an isolated plant, a plant in a population, a whole population, or an area of vegetation.

The second relationship was formulated by Watson (1958) and involves LAI, NAR and CGR. He proposed that

\[ \text{CGR} = \text{LAI} \times \text{NAR} \]

This equation is used to analyze plant populations or plant communities in which individual plants compete and interact between them.

A third relationship has been explained by Warren Wilson (1981) who combined the two former equations into one and postulated that

\[ \text{CGR} = \text{Biomass} \times \text{RGR} \]

He suggested that as the individual plant is a component of a plant community, so RGR is a component of CGR, the other component being the
dry weight of plants per area of ground (biomass). This type of analysis has been called integrated growth analysis and it has been applied with success in some vegetable crops to evaluate simultaneously individual and population attributes (Hunt et al., 1984; Hand et al., 1985; Warren Wilson et al., 1986).

Yet another relationship has been proposed by Warren Wilson (1981) who suggested that, since production is strongly influenced by light, CGR might usefully be analyzed as the product of incident light energy, the efficiency of light interception by the leaves and the efficiency of use of the intercepted light in dry matter production. This procedure is called light conversion analysis and provides a means of incorporating light, the primary environmental factor influencing growth (Hunt et al., 1984; Hand et al., 1985; Warren Wilson et al., 1986).

In addition to the above mentioned treatments of growth analysis, there are other mathematical models that try to increase the quantitative understanding of the growth of plants or vegetation (Hardwick, 1984). On the other hand, a modular approach to analysis of plant growth has been devised by Porter (1983a, b) who suggested that mathematical models do not take into account rates of production of plant parts, their life spans, death rates and age distribution which are better descriptors of plant form and development. His approach is based upon rates of appearance, development and death of meristems.

It has been suggested by several researchers that the selection of a particular procedure for growth analysis must depend on the objectives of the investigation and that the researcher must choose between the various available analytical schemes in terms of simplicity
or complexity of measurements and equations (Hunt, 1978; Hunt et al., 1984; Warren Wilson et al., 1986). In addition, whatever the procedure to be used, a complete growth analysis should evaluate both the individual plant and the community plant (Gardner et al., 1985).

Among the various uses of plant growth analysis, one which is gaining a lot of attention is ecophysiological evaluation. Undoubtedly, it is the amount of growth resulting from influences of biotic or abiotic factors that regulates competitive interactions among plants. A better understanding of resource limitation and its consequences could result from the analysis of growth of individual plants involved in a competitive relationship. By comparing the growth parameters of crops and weeds it may be possible to understand better the competitive nature of weeds (Radosevich and Holt, 1984; Patterson, 1985).

Plant growth analysis has been used to compare the growth and developmental characteristics of triazine-resistant and triazine-susceptible biotypes of *Senecio vulgaris* L. It was shown that the resistant biotype had lower biomass production and growth rate, and that these differences were established early in the life cycle (Holt and Radosevich, 1983).

A relationship of growth parameters and competitiveness of four annual weeds was demonstrated by Roush and Radosevich (1985). They found that except for RGR, the other growth parameters analyzed differed among the species, and that the competitive ability of the species was a function of plant size, the efficiency of production of new material (NAR) and the increase in photosynthetic material (LAR).
Patterson (1979) found that shading markedly reduced dry weight and RGR of itchgrass (*Rottboellia exaltata* L.). Increases in LAR were the result of combined increases in SLA and LWR in response to shade. Potter and Jones (1977) reported that RGR and leaf area expansion of corn, cotton, soybean and six weed species were greater at day/night temperatures of 32/21°C than 21/10°C or 38/27°C. At all three temperatures the weeds were superior to the crops. Patterson (1982) showed that shading significantly reduced height, dry matter, leaf production, leaf area expansion, branching and the partitioning of plant biomass into stems of *Crotalaria spectabilis* Roth. Eagles and Othman (1986) showed that interaction of high temperature, high light intensity and long photoperiod had an influence in the high values of NAR and low values of LAR in 10 *Trifolium repens* L. populations. These findings indicate that competitive ability in terms of physiological and morphological growth responses is influenced by the environment.

When plant species are grown together they often respond differently to environmental factors than when they are grown separately. In addition, inter- and intraspecific competition play an important role in mixed stands. Therefore, to assess the competitive ability of species involved in a mixture, they should be studied under the influence of the interaction. In this sense, Oliver et al. (1976) studied the inter- and intraspecific competitiveness of tall morningglory (*Ipomoea purpurea* [L.] Roth) in soybeans. They found that reductions in LAI, plant dry weight and CGR were the best indicators of when during the crop's cycle competition occurred. On the other hand, the competitiveness of tall morningglory depended upon a rapid increase in photosynthetic area which occurred 4 to 6 weeks after emergence.
It appears that rapid growth and greater leaf and root expansion are important characteristics of competitors (Baker, 1974; Grime, 1977). A species that grows faster and larger than its neighbors will utilize a disproportionate amount of available resources, increasing dry matter production and getting a competitive advantage (Roush and Radosevich, 1985). In this way, RGR might serve as an indicator of potential competitive ability among crop and weed species (Grime and Hunt, 1975). However, no single factor is likely to be an adequate predictor of the competitive ability of a species, and several morphological and physiological parameters must be considered (Patterson and Flint, 1983).

In a series of studies on competition in rice, a mechanism of competition among rice phenotypes was proposed. Strong and weakly competitive varieties and tall and dwarf plant types were grown in mixtures and in pure stands. Several morphological and physiological parameters were evaluated, and growth and yield component analyses were performed. It was concluded that strong competitors have more tillers, longer and more leaves, and greater LAI, height, and dry weight than weak competitors. The result of the sum of these characters is an increase in plant size. Alternatively, the same characters may be considered as a definition of greater early vigor in the development of competitive types. Therefore, the characters that increase size and early vigor are considered to be associated with competitive ability (Jennings and Herrera, 1968; Jennings and Aquino, 1968).

Diarra et al. (1985a, b), using an additive design, worked with red rice and different rice cultivars in pure stands and in mixtures in two separate experiments. They worked more with yield component
analysis than with growth analysis; however, important findings were brought out. They found that the rice cultivars, Lebonnet and Mars, were shorter, tillered less, had a lower LAI (measured once at 70 days) and produced less straw and fewer panicles/plant than red rice.

**Red rice.** The term red rice applies to weedy biotypes of *Oryza sativa*, which are important annual weeds of rice in many countries and have potential for spreading to new areas where prevention is not practiced (Baker and Sonnier, 1983). Smith (1983) classifies red rice as a weed that causes major yield and quality losses and is economically troublesome worldwide. It can grow in lowland as well as upland rice and appears in dry- or water-seeded rice.

Craigmiles (1978) defined red rice as "kernels which are distinctly red because of a red pericarp or outside bran layer". In addition to the red pericarp, red rice seeds shatter easily and may persist in the soil in a dormant condition for a long period of time. Although there are no reported differences between red rice and most of the rice cultivars at the microscopic level, particularly in seeds and leaves, there are differences on a macroscopic scale (Hoagland and Paul, 1978). Red rice plants are taller and tiller more than cultivated rice, and although it is not easy to distinguish between red and white rice in the field before heading, red rice leaves have short, stiff hairs on the upper and lower surfaces (Huey and Baldwin, 1978).

Several red rice biotypes have been reported and natural hybridization between them and cultivated rice has occurred (Constantin, 1960). However, strawhull and blackhull are the most mentioned biotypes in the United States with strawhull more prevalent
than blackhull (Smith, 1981). Both of these biotypes are able to germinate and emerge more quickly and from greater soil depths than rice cultivars (Helpert and Eastin, 1978). The blackhull biotype tillered 27% more, produced 18% more straw, and had a later maturity than the strawhull biotype (Diarra et al., 1985).

In the United States, red rice is found in Louisiana, Texas, Mississippi, and Arkansas. The rice yield and quality losses due to red rice vary with the availability of red rice-free seed rice, the seeding method, the control practices, and the market conditions (Baker and Sonnier, 1983). However, an estimate of over $50 million loss each year in the Southern states is attributed to red rice (Smith, 1979). In Latin America, red rice is a common weed of wetland and dryland rice, has moderate aggressiveness, and is difficult to control. In Colombia, red rice is a problem of wetland rice under poor management conditions (Gonzalez et al., 1983).

Red rice is difficult to control because it exhibits morphological and physiological characteristics similar to white rice. Diarra et al. (1985c) found that red rice at 5 plants/m² caused yield and quality losses in white rice and contaminated the land with shattered grains.

Most of the herbicides used in controlling rice field weeds do not control red rice, and an integrated control program has been proposed by Baker and Sonnier (1983). They state that a successful program should include crop rotation, water planting and water management, herbicide use, and other cultural and biological methods.

Effective control programs include rotation with upland crops such as sorghum or soybeans. Soybeans grown for two years using cultural and chemical methods to control red rice reduced red rice infestations
in subsequent rice crops sufficiently for satisfactory rice production (Smith, 1976). The effect of water management on red rice survival was studied by Sonnier (1978) who found that a 3- to 7-day drainage period after seeding maximized commercial rice stand establishment and minimized red rice establishment. Using laboratory and field herbicide screening tests, Baker and Bourgeois (1978) showed that molinate was the only compound giving good red rice control and rice crop tolerance.

Smith (1981) reported that preplant-incorporated molinate at rates of 4.5 and 6.7 kg/ha in a continuously flooded culture and 6.7 kg/ha in an alternately flooded and drained culture would give an estimated 87 to 93% red rice control in water-seeded rice sown with dry seed. Diarra et al. (1985) showed that rice coated with CaO₂ at 0.5% and preplant-incorporated molinate produced high yields which were associated with red rice control by molinate and good rice stands provided by O₂ supplied by the CaO₂. Finally, Baker et al. (1986) found that preplant-incorporated molinate at 4.5 kg ai/ha and a brief postseeding drainage period in water-seeded rice gave the best red rice control without a significant reduction in cultivar stand density.
MANUSCRIPT I

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Germination, Emergence and Early Seedling Development of Red Rice
*Oryza sativa* and Four Rice (*O. sativa*) Cultivars.

JAIRO CLAVIJO and JOHN B. BAKER.

Abstract. Germination, emergence and early seedling development patterns were analyzed for red rice (*Oryza sativa* L. ♂*ORYSA*) and rice (*Oryza sativa* L.) cultivars Mars, Saturn, Lemont and Bellemont. Germination was expressed as percentage and as germination rate index (GRI), which is a measure of the time taken by a population of seeds to germinate. The red rice germination percentage was significantly higher than that of Lemont, Mars and Saturn. However, when the GRI was analyzed, Saturn had the quickest germination followed by red rice. Emergence was also expressed as percentage and as emergence rate index (ERI). There were no significant differences between varietal emergence percentages, but differences in the ERI of red rice and the four cultivars were significant, indicating that red rice emerged more quickly. Radicle length at germination and length and dry weight of shoots and roots 10 days after emergence were recorded as characteristics of early seedling development. In all cases, a significant difference between red rice and the four cultivars was found with red rice showing the highest value. When the shoot:root ratio was calculated on a dry weight basis, Saturn had the highest ratio followed by red rice. These results suggest that the rapid germination and emergence and early development of both shoots and roots exhibited by red rice may contribute to its competitive ability.
by enabling it to preempt more resources at early stages of stand development.

Additional index words. Weed biology, germination rate index, emergence rate index, competitive ability, seedling vigor, ORYSA.

INTRODUCTION

Competition between crops and weeds may occur during the vegetative or reproductive stages of development, or both. In the case of competition during the vegetative stage, strong, competitive cultivars and weeds are characterized by fast germination and early development of both above and below ground parts (7, 9, 16). It has been suggested that the competitive ability of a species is determined by the
resources it is able to capture at the beginning of the growing season, the relative rate at which it is able to utilize the resources it has already captured, and the preemption of the limiting factor (15).

Certain characteristics tend to be associated with competitiveness, such as larger seeds, rapid germination and emergence, more rapid growth of roots and shoots, more tillers, larger leaves and a rapid growth through the vegetative phase to flowering. Most of these characteristics were pointed out by Clements et al. as early as 1929 and have been studied in several crop and weed species (13, 16).

The ability of sorghum hybrids and inbred lines to compete with weeds has been correlated with seedling characteristics. It was concluded that the competitive advantage of sorghum over weeds was largely due to rapid germination, emergence, and root and shoot growth during the early stages of plant development (8).

Phenotypic and genotypic plasticity also play an important role in competition. In a study with 25 rice cultivars with different growth habits it was concluded that intraspecific competition, competition with weeds, and spacing response were highly intercorrelated with each other suggesting that these were controlled largely by the same genetic factors. Vegetative vigor, large leaf area, greater plant height, and a high rate of nitrogen absorption in early growth stages were the plant characters associated with competitive ability (12).

Competition studies between rice cultivars and weeds are summarized by Zimdahl (16). Red rice has been pointed out as one of the most important annual weed of rice, and several of its morphological characteristics have been related to competitive ability (1, 4). Growth and morphological differences between red rice biotypes have
been also evaluated (5). However, few investigators have focused their attention on seedling characteristics as criteria to evaluate the competitive ability of red rice. It was the purpose of this study to analyze and compare the germination, emergence, and early seedling development of red rice and four rice cultivars to establish the morphological and physiological advantages that may be associated with the competitiveness of red rice at the seedling stages.

MATERIALS AND METHODS

Mature strawhull red rice seeds for this study were collected from fields at the South Farm of the Louisiana State University Rice Research Station at Crowley, Louisiana. Seeds harvested from individual plants were placed in plastic bags, brought into the laboratory and dried at 20°C from a harvest moisture content of 22% (fresh weight basis) to 11%. Seeds were cleaned using a seed blower to remove trash and empty florets, placed into sealed glass jars, and stored in darkness at 30°C for four weeks. This procedure gave red rice seeds which were nondormant and highly viable (3). These seeds had a mean germination percentage after this treatment of 96.

Seed of the four rice cultivars to be used in this research were obtained from stocks maintained by Dr. Kent McKenzie of the Rice Research Station. Bellemont and Lemont were selected from a group characterized by high yielding ability, resistance to lodging, short stature, and erect leaves. Mars and Saturn were selected from a group characterized by good seedling vigor, good yield potential, tall stature, and profuse tillering ability. Strawhull red rice plants are
characterized by tall stature, leafy, high tillering ability, and easy grain shattering.

All seeds were treated with Dithane FZ fungicide (Maneb 37% active ingredient) at a rate of 1.18 ml/500 g of seed. Seeds were placed in sealed glass jars and stored in a freezer at -10°C for the time that this study was carried out.

A seed index analysis was conducted to measure the seed weight of the material used in this study. One hundred seeds of each rice cultivar and the red rice were randomly selected and weighed on a Mettler Type H6 scale. A completely randomized design with two replications was used and the results were expressed in grams per 100 seeds.

Germination tests were carried out by placing 30 seeds in a square plastic petri dish (9x9 cm) on two layers of Anchor regular weight germination paper moistened with 10 ml distilled water. Seeds were covered with a double layer of tissue paper to insure uniform hydration. Petri dishes were placed slightly tilted in an incubator at 30°C and maintained for seven days in the dark. Germination, defined as seeds having one cm shoot length, was recorded every day and expressed as percentage and as germination rate index (GRI) which was a measure of the time taken by the seeds to germinate. The GRI was calculated by the following formula (6):

\[ GRI = \frac{G_1/T_1 + G_2/T_2 + \ldots + G_n/T_n}{\%G} \]

where \( G_1 \) = percentage of seeds germinated at \( T_1 \).

\( G_2 \) = percentage of seeds germinated between \( T_1 \) and \( T_2 \).

\( G_n \) = percentage of seeds germinated at the final time.

\( T_1 \) = days to the first count.
$T_2 =$ days to the second count.

$T_n =$ days to the final count.

$\%G =$ percent germination obtained.

Radicle length at the time of germination was recorded as a characteristic indicative of early seedling vigor. A completely randomized design with four replications was applied and treatment means were compared using the LSD test.

Tests on emergence and early seedling development were conducted for 10 days in a growth chamber programmed to provide 14 hours light and 10 hours dark at 30°C. Thirty seeds of each rice cultivar and red rice were planted in individual rows in sand at 2.5 cm depth with 5.0 cm spacing between rows in a 30x25x10 cm plastic boxes. Seedlings which emerged to a height of one cm were considered emerged and recorded every day. Emergence was expressed as percentage and as emergence rate index (ERI) calculated by the same procedure as GRI. A randomized complete block design with three replication was used and treatments means were compared using the LSD test.

Early development of these seedlings was determined by measuring shoot and root length, shoot and root dry weight, and by calculating the shoot:root ratio at 10 days after emergence based on dry weight. In all cases, the seedlings were washed out of the sand in the plastic boxes, taking care not to damage the seedlings, and measured, oven-dried, and weighed. A randomized complete block design with three replications was used and treatment means were compared using the LSD test.
RESULTS AND DISCUSSION

Seed index analysis. Comparison of the seed weight indexes showed that red rice seeds were the heaviest with 3.26 g/100 seeds followed by Lemont, Mars, Saturn and Bellemont seeds. The red rice and cultivar differences were significant (Table 1). Larger and heavier seed with greater energy and mineral storage are able to support germination and emergence processes which have high respiration rates. Thus, the heavier the seed the more vigorous the germination should be. This gives an opportunity for the seedling to expand its root system and to preempt the available resources as quickly as possible (14, 15).

Germination. When germination was expressed as a percentage, red rice had a significantly higher value than Lemont, Mars and Saturn. No significant differences were found between red rice and Bellemont or between the four rice cultivars as recorded in Table 1. Germination rate index (GRI) values indicated that Saturn had the most rapid germination rate, red rice had an intermediate value, and Lemont showed the slowest germination rate. No differences existed between red rice, Mars and Bellemont (Table 1). It has been stated that the amount and rate are the most appropriate parameters for analyzing a process (13). In this case, red rice showed the highest percent germination and an intermediate GRI when compared to the four rice cultivars. It has been suggested that fast germination is an attribute of competitive ability (14).

Emergence. No significant difference was found between red rice and the four rice cultivars for percentage emergence. However, when the emergence rate index (ERI) was analyzed, a significant difference was found between red rice and the cultivars. Red rice emerged more
rapidly than the cultivars (Table 1). The greatest advantage to a weed would result by combining early emergence (14) and a greater number of plants at the beginning of the growing season (15). Early plants have the opportunity to preempt a greater share of the available resources thereby using these resources to grow even larger (7).

**Early seedling development.** There was a significant difference in radicle length recorded at germination between red rice and Mars, Saturn and Bellemont (Table 1). Red rice obtained the highest value. Before the shoots emerge from the soil considerable radicle elongation usually has occurred (14). Below ground competition may start earlier than above ground competition. Therefore, the success of the seedling depends on the ability of the primary root to expand and extract moisture and nutrients from an increasingly larger portion of the soil profile (7, 9).

When the shoot and root length were measured at 10 days after emergence, a significant difference between red rice and the four rice cultivars was found. Data presented in Table 2 show that red rice had the longest shoot and root lengths while Bellemont had the shortest. Shoot and root dry weights, recorded at 10 days after emergence, also showed differences between red rice and the four rice cultivars. Red rice was significantly heavier than the rice cultivars with both parameters (Table 2). Seedling vigor has been shown to be positively correlated with seedling dry weight and rapid growth rate of above and below ground plant parts in eight upland rice cultivars (2).

The shoot:root ratio for red rice was second only to Saturn and was significantly greater than that of the other cultivars (Table 2). A high shoot:root ratio might indicate an inability of the plant to use
light efficiently in photosynthesis and to allocate assimilates to the roots, resulting in a disadvantage to the roots for below ground competition. It might also indicate an efficient root system which supplies water and minerals to support greater shoot growth, permitting capture of a greater portion of radiant energy (11).

Guneyli et al. (8) showed that the competitive ability of sorghum was highly correlated with the germination rate index of sorghum seed and concluded that GRI would be of ecological significance for the competitive ability of other crops and weeds. Strawhull red rice has been reported to germinate and emerge more quickly and from greater soil depths than several rice cultivars (5, 10). Kawano et al. (12) working with 25 rice cultivars found that plant weight at an early stage of growth was significantly related to competitive ability.

The results of this study suggest that differences in rate of germination, emergence, and early development of both shoots and roots exist between red rice and the rice cultivars. While competitive tests were not performed here, differences in germination and growth displayed trends in agreement with previously observed competitive abilities.

LITERATURE CITED


Table 1. Germination and emergence of red rice and four rice cultivars.¹

<table>
<thead>
<tr>
<th>Red rice or cultivar</th>
<th>Seed index</th>
<th>Germination rate index</th>
<th>Radicle length²</th>
<th>Emergence rate index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red rice</td>
<td>3.26a</td>
<td>100.00a</td>
<td>25.00b</td>
<td>5.85a</td>
</tr>
<tr>
<td>Lemont</td>
<td>2.76b</td>
<td>88.35b</td>
<td>22.03c</td>
<td>5.33ab</td>
</tr>
<tr>
<td>Mars</td>
<td>2.52c</td>
<td>87.50b</td>
<td>25.81b</td>
<td>4.63bc</td>
</tr>
<tr>
<td>Saturn</td>
<td>2.40d</td>
<td>81.65b</td>
<td>28.12a</td>
<td>4.25c</td>
</tr>
<tr>
<td>Bellemont</td>
<td>2.33e</td>
<td>90.83ab</td>
<td>24.39b</td>
<td>4.23c</td>
</tr>
</tbody>
</table>

¹ Means within a column followed by the same letter are not significantly different at 5% level.

² Taken at germination.
Table 2. Seedling development of red rice and four rice cultivars 10 days after emergence.

<table>
<thead>
<tr>
<th>Red rice or cultivar</th>
<th>Shoot length</th>
<th>Root length</th>
<th>Shoot dry wt.</th>
<th>Root dry wt.</th>
<th>S/R ratio²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red rice</td>
<td>13.97a</td>
<td>6.24a</td>
<td>9.83a</td>
<td>6.53a</td>
<td>1.52b</td>
</tr>
<tr>
<td>Lemont</td>
<td>8.65c</td>
<td>3.82c</td>
<td>6.78bc</td>
<td>5.45b</td>
<td>1.25c</td>
</tr>
<tr>
<td>Mars</td>
<td>10.13b</td>
<td>4.44b</td>
<td>5.85c</td>
<td>4.98bc</td>
<td>1.19c</td>
</tr>
<tr>
<td>Saturn</td>
<td>10.03b</td>
<td>4.31bc</td>
<td>7.13b</td>
<td>4.18c</td>
<td>1.71a</td>
</tr>
<tr>
<td>Bellemont</td>
<td>7.84d</td>
<td>3.23d</td>
<td>6.20bc</td>
<td>4.65bc</td>
<td>1.34c</td>
</tr>
</tbody>
</table>

¹ Means within a column followed by the same letter are not significantly different at 5% level.

² Shoot to root ratio in dry weight.
MANUSCRIPT II

To be submitted to Weed Science
Effects of the Interaction of Red Rice (*Oryza sativa*) and Two Rice (*Oryza sativa*) Cultivars on Some Morphological and Physiological Characteristics.

JAIRO CLAVIJO and JOHN B. BAKER

Abstract. Pure stands and 50:50 mixtures of red rice (*Oryza sativa* L. ORYS) with two rice (*Oryza sativa*) cultivars, Lemont and Mars, were grown outside in pots with uniformly spaced plants at a density of 100 plants/m² in order to analyze and evaluate the morphological and physiological characteristics associated with their growth. The plant height, top dry weight, tiller and leaf number, leaf area index (LAI) and leaf area duration of the cultivars grown in mixture with red rice were significantly lower than when grown in pure stand. Leaf area ratio, specific leaf area, net assimilation rate, relative growth rate and crop growth rate did not indicate intraspecific competition. Red rice affected the semidwarf cultivar Lemont more than the taller Mars. The effects of the interaction were detected as early as 28 days after emergence in the cultivars, first as a reduction in LAI and then as reduced top dry weight. Red rice when in mixture with the cultivars produced more tillers and leaves and greater top dry weight than when grown in a pure stand. These growth attributes may be responsible for its ability to capture and utilize more than its portion of environmental resources.

Additional index words. Growth analysis, yield component analysis, weed biology, competition, ORYS.
INTRODUCTION

Growth analysis is a quantitative approach to understand the growth of a plant or a population under natural or controlled environmental conditions (6, 13). It is a technique which uses mathematical expressions to quantify the relationship between plant growth, dry matter production and leaf area expansion or between these factors and a growth factor such as light (6, 26). To accomplish this, several parameters of a morphological, physiological and ecological nature are measured or calculated at frequent intervals throughout the life cycle of a plant or a crop (6, 12, 25).

Application of growth analysis in ecophysiological studies is very valuable (19, 23). The competitive interaction between plants is undoubtedly regulated by the amount and type of growth which occurs in the presence of various biotic and abiotic factors (11, 23). A better
understanding of resource limitation and its consequences should result from growth analysis of individual plants involved in a competitive situation (18, 20, 21). By comparing the growth parameters of several crops and weeds, it may be possible to get an insight into the competitive nature of weeds (17, 21, 24).

It appears that rapid growth and greater leaf and root expansion are important characteristics of plant competitors (1, 8, 11). A species that grows faster and larger than its neighbors will utilize a disproportionately greater amount of the available resources, thereby increasing dry matter production and getting a competitive advantage (24). In this way, relative growth rate and its components or crop growth rate and its components might serve as an indicator of potential competitive ability among crop and weed species (2, 9, 27). No single factor is likely to be an adequate predictor of the competitive ability of a species, and several morphological and physiological parameters should normally be considered (7, 19).

A relationship between growth parameters and the competitiveness of four annual weeds was demonstrated (24). It was found that the competitive ability of the weed species was a function of plant size, net assimilation rate, and leaf area ratio. Diarra et al. (4) worked with different red rice biotypes and concluded that plant size, profuse tillering, and a high leaf area index were important morphological characteristics of these biotypes.

It is known that when plant species are grown together they often respond differently to environmental factors than when they are grown separately (11). Both inter- and intraspecific competition are known to play an important role in mixed stands and impose different plant
interactions (17). Therefore, to assess the competitive ability of species involved in a mixture, these factors should be studied under the influence of these interactions (23).

The objective of this study was to analyze and evaluate the morphological and physiological characteristics of red rice and two rice cultivars growing either in pure stands or in mixture to determine, if possible, those which were associated with competitive ability.

MATERIALS AND METHODS

Mature strawhull red rice seeds for this study were collected from fields at the South Farm of the Louisiana State University Rice Research Station at Crowley, Louisiana. Seeds harvested from individual plants were placed in plastic bags, brought into the laboratory and dried at 20°C from a harvest moisture content of 22% (fresh weight basis) to 11%. Seeds were cleaned using a seed blower to remove trash and empty florets, placed into sealed glass jars, and stored in the dark at 30°C for four weeks. This procedure gave red rice seeds which were nondormant and highly viable (3). Seeds of the cultivars were obtained from stocks maintained by Dr. Kent MacKenzie of the Rice Research Station. All seeds were treated with Dithane FZ fungicide (Maneb 37% active ingredient) at a rate of 1.18 ml/500 g of seed.

Two rice cultivars were used in this study. Lemont was selected from a group characterized by high yielding ability, resistance to lodging, short stature, and erect leaves. Mars represented a group characterized by good seedling vigor, good yield potential, tall
stature, and profuse tillering ability. Strawhull red rice plants were characterized by tall stature, leafiness, high tillering ability, and grain shattering at or before maturity.

Pure stands and mixtures of red rice with Lemont and with Mars were grown outside using a plant density of a 100 plants/m². This density was established by planting two seeds at a spacing of 10x10 cm in 39x43x20 cm plastic containers and then thinning to a population of 16 plants per container after seedlings developed. The same population was obtained for the mixtures by placing the cultivars and red rice in a checkerboard fashion such that each cultivar was surrounded by four red rice plants and vice versa, resulting in a stand proportion of half and half.

The plastic containers were filled with Crowley silt loam soil containing 1.52% OM, 17 mg/kg P₂O₅, 83 mg/kg K₂O and a pH of 4.7. All containers were fertilized using 120 kg N/ha, 40 Kg P₂O₅/ha, 40 Kg K₂O/ha and 0.2 Kg of Zn, Fe, Cu and Mn/ha. Half of the fertilizer was applied 15 days after emergence and the other half 60 days after emergence. Fifteen days after emergence the containers were flooded and the water level was maintained until eight days before final harvest.

Treatments consisted of red rice, Lemont, and Mars in pure stands and red rice in mixtures with Lemont and Mars. Each treatment was randomly assigned to each of 15 plastic containers in three replicates which were sampled at each of 10 harvest times. A completely randomized design with sampling was used. Data were evaluated by analysis of variance and treatment means separated using the LSD test.
Changes in each parameter over time were analyzed by regression analysis.

Data were recorded by sacrificing two of the central plants in a container with a pure stand and the four central plants, two of each component, in a container with a mixture. The plants were cut at the crown level at weekly intervals for the first six weeks after emergence and then every other week until maturity. Data recorded at each harvest time included plant height, tiller number, leaf area, leaf dry weight, and shoot dry weight. Root length and root dry weight were taken for the first four weeks while it was still possible to take out the roots without causing too much damage.

Whenever dry weight of plant parts was measured, the samples were placed in paper bags, oven-dried and weighed with a Mettler H6 balance to the nearest \(10^{-2}\) mg. Plant height was measured from the stem base to the longest leaf tip and root length from the crown to the longest root tip. Leaf area (only the blades) was measured with a LI-COR LI-3000 portable area meter. Leaf area index (LAI) was calculated by dividing the leaf area of a plant by 100, and specific leaf area (SLA) by dividing leaf area by leaf dry weight. Top dry weight was the sum of leaf and shoot dry weights.

Leaf area ratio (LAR), leaf area duration (LAD), net assimilation rate (NAR), relative growth rate (RGR) and crop growth rate (CGR) were calculated according to formulas for mean values over a time interval (13, 22).

\[
\begin{align*}
LAR & = \frac{\left(\frac{LA_1}{W_1}\right) + \left(\frac{LA_2}{W_2}\right)}{2} \\
LAD & = \left(\frac{LAI_1 + LAI_2}{2}\right) \frac{T_2 - T_1}{2} \\
NAR & = \frac{W_2 - W_1}{(T_2 - T_1) \cdot \left(\ln LA_2 - \ln LA_1\right)} \cdot \frac{LA_2 - LA_1}{LA_2 - LA_1}
\end{align*}
\]
\[
RGR = \frac{\ln W_2 - \ln W_1}{(T_2 - T_1)}
\]
\[
CGR = \frac{1}{100} \left( \frac{(W_2 - W_1)}{(T_2 - T_1)} \right)
\]

Where \(W\) is dry weight per plant (excluding the roots), \(LA\) is leaf area per plant (only the blades), \(LAI\) is leaf area index, and \(T\) is time. Subscripts 1 and 2 refer to the beginning and end of a time interval, respectively.

Yield components of red rice and cultivars were determined by recording number of panicles per plant, number of florets per panicle, filled floret percentage and individual grain weight. Yield was calculated as weight of filled grain per plant. A special procedure with red rice was followed to obtain the data on filled floret percentage and individual grain weight at maturity. Three randomly selected red rice panicles per plant were bagged before grain shattering with a cloth mesh bag.

**RESULTS AND DISCUSSION**

**Plant height.** Change in plant height of cultivars in pure stands and mixtures with time is shown in Figure 1a and b. The effect of the interaction with red rice was detected 35 days after emergence for Lemont and 56 days after emergence for Mars and continued to maturity. Red rice affected Lemont more than Mars. Red rice did not show any significant difference in plant height between the pure stand and the mixtures with Lemont and Mars (Table 3). It has been reported that red rice density, of 108 plants/m\(^2\) at 60 days after seeding reduced height of rice plants (5). In the present study, red rice density of 50 plants/m\(^2\) reduced the height of both cultivars and the reduction was greater and appeared earlier in the short statured cultivar.
Top dry weight. Lemont and Mars in mixture had significantly lower top dry weights from as early as 35 days after emergence to maturity when compared with pure stands (Figure 2a and b). A significant increase in top dry weight of red rice was observed when grown in mixture with the cultivars rather than in pure stand (Table 3). The increase is greater in red rice growing with Lemont than in red rice growing with Mars. The dominant component in a mixture always shows a greater individual plant dry weight than it does in a monoculture of the same overall density. The weak component usually shows a decrease, relative to its own monoculture (16).

Number of tillers. Lemont and Mars had fewer tillers when mixed with red rice than in pure stands (Table 1 and 2). Number of tillers per plant was significantly reduced in Lemont with red rice from 35 days after emergence to maturity (Figure 3a). The reduction in tillers in the mixture of Mars with red rice started as early as 28 days after emergence, but at maturity tiller mortality in the pure stand was so great that no significant difference with the mixture was found (Figure 3b). Tiller mortality may be attributed to intense intraspecific or interspecific competition for an environmental factor such as light (11). Table 3 shows that the number of tillers per plant in red rice was greater in the mixtures than in the pure stand. No significant difference was detected between the mixtures. Researchers have reported that short-statured rice plants had fewer tillers than tall-statured rice plants when grown in mixture (14, 15) and that red rice plants tillered more than shorter rice plants (5). The results of the present study indicate that red rice plants produced more tillers in
mixture than in pure stands irrespective of the size of the partner in the mixture.

Number of leaves. The pattern of behavior for number of leaves per plant was the same as found for number of tillers per plant. It has been hypothesized that tiller number is a function of leaf number (14) and that a synchronous growth between leaves and tillers exists (28). In addition, the effect of red rice on Lemont is greater than the effect of red rice on Mars for this particular plant characteristic (Table 1 and 2). Red rice interaction reduced the number of leaves more in Lemont than in Mars when compared to their pure stands. The decrease in number of leaves appeared earlier (28 days) than the decrease in number of tillers (35 days) in the mixture of Lemont with red rice (Figure 4a). This was not true for the mixture of Mars with red rice in which the reduction in number of leaves appeared at the same time (28 days) as the reduction in number of tillers (Figure 4b). Red rice had more leaves in the mixture with Lemont than in the mixture with Mars or in a pure stand (Table 3).

Shoot dry weight. A significant decrease in shoot dry weight at 42 days after emergence was observed when Lemont was in mixture with red rice (Figure 5a). Lemont pure stand shoot dry weight responded linearly with time while the mixture with red rice was greatly inhibited. Mars in mixture with red rice showed a significant decrease in shoot dry weight starting at 35 days after emergence (Figure 5b). The reduction in shoot dry weight was greater in Lemont than in Mars, especially at maturity. Red rice shoot dry weight differed significantly with the highest value in mixture with Lemont followed by the mixture with Mars and then the pure stand (Table 3).
Leaf dry weight. Changes in leaf dry weight with time in pure stands of Lemont and Mars and in mixtures of the cultivars with red rice are presented in Figure 6 a and b. Reduction in leaf dry weight due to the interaction of red rice was detected at 35 days after emergence in Lemont and at 28 days after emergence in Mars. The decrease in leaf dry weight was greater in Lemont than in Mars probably as a reflection of the fewer number of leaves exhibited by Lemont as noted earlier. The leaf dry weight of red rice mixed with Lemont attained the greatest value and was significantly higher than when mixed with Mars or in pure stand (Table 3).

The fact that only leaf blades were weighed while the leaf sheaths remained attached to the shoots could account for the higher values of shoot dry weight over those of leaf dry weight. However, the tendency of the two parameters to vary with time and the negative effect caused by the presence of red rice in the mixtures were demonstrated (Figures 5 and 6). These two parameters were components of top dry weight which also reflected the reductions due to the presence of red rice. It has been reported that reduction in plant dry weight is an indication of competition, is a consequence of reduced assimilatory surface, and is usually detected after reductions in leaf area (17).

Root dry weight and root length. There were no significant differences between pure stands and mixtures in root dry weight or root length of red rice or the cultivars (Tables 1, 2 and 3). It has been shown that root length increases as the shoot grows (28) and that root dry weight is closely related to total dry weight of the plant (13, 28). In the present study, the fact that these types of relationships were not
detected was probably because of the way the roots were extracted from the soil. Evans (6) pointed out the difficulties involved in extracting root systems from the soil and the influences this has on root measurements and data analysis.

Yield and its components. The effects of the interaction of red rice on yield and yield components of Lemont are reported in Table 1. A significant decrease in the number of florets per panicle was found in Lemont when in mixture with red rice. Number of panicles per plant, filled floret percentage, individual grain weight, and yield of Lemont were not affected by the presence of red rice.

The effects of the interaction of red rice on yield and yield components of Mars are shown in Table 2. Number of panicles per plant, individual grain weight, and yield were significantly decreased when Mars was in mixture with red rice. No significant difference was detected between Mars in pure stand and in mixture with red rice when number of florets per panicle or filled floret percentage were recorded.

Effects of the interaction of the two cultivars on yield and yield components of red rice are presented in Table 3. A significant increase in number of florets per panicle and filled grain weight per panicle was detected in red rice when in mixture with Lemont and Mars. The number of panicles per plant, individual filled grain weight, filled grain percentage, and yield did not differ significantly between red rice in pure stand and in the mixtures.

It has been reported that short rice plants when mixed with tall plants exhibited a reduction in yield and panicle size (14, 15). A red rice density of 108 plants/m² reduced panicles/m² and panicle size in
commercial rice (5). The present study showed that red rice reduced the number of panicles per plant, individual grain weight, and yield of Mars but not for those of Lemont. Even though Lemont in pure stand grew well during the whole experiment, its yield was lower than expected. There was no clear explanation for this.

**Growth measurement.** Change in LAI over time for Lemont and Mars in pure stands and in mixture with red rice is shown in Figure 7 a and b. The negative effect of red rice on Lemont and Mars was noted as early as 28 days after emergence and was greater in Lemont than in Mars. It has been found that competitive rice types drastically reduced the LAI of the weaker competitor (14, 15) and, in morningglory, a reduction in LAI was an indicator of initiation of inter- and intraspecific competition (17). The present study showed similar responses and accounts, at least in part, for differences in the competitive ability of rice cultivars.

The reduction in LAD as a result of the interaction of red rice with Lemont and Mars is reported in Figure 8 a and b. The magnitude of the reduction was greater in Lemont than in Mars and was detected 42 days after emergence. LAD describes the extent and duration of the light-trapping apparatus of a plant population (6, 13). LAD and NAR are the components of dry matter production (20). Thus, the presence of red rice in the mixtures affected not only the duration of the leaves, but also the production of dry matter by the cultivars.

SLA, LAR, NAR, and RGR were not significantly different in pure stands and in mixtures (Table 1 and 2). NAR and LAR are components of RGR (2) and their influence on RGR is inversely related (13) and compensatory (21, 24). It has been found that RGR varies little
between winter lettuce cultivars (10) and that intraspecific differences in RGR are rarely seen (13). In addition, RGR was not found to be different among four annual weeds (24).

The components of CGR are NAR and LAI (27), and it would be expected that at similar NAR values a decrease in LAI would produce a variation in CGR. However, CGR did not vary among the pure stands and the mixtures (Table 1 and 2) and did not reflect the behavior of LAI.

None of the integrated growth parameters changed when red rice was evaluated as a pure stand or in mixture with Lemont and Mars (Table 3). This result indicated that red rice behaved in the same fashion irrespective of the partner in the mixture.

It has been stated that, even though LAI and plant dry weight are indicators of when the competition pressure was exerted, LAI reduction was detected first and was greater (17). In the present study, leaf area parameters of the cultivars reflected the effects of the interaction earlier than other growth parameters. In fact, a reduction in leaf number and LAI was observed at 28 days after emergence whereas a reduction in top dry weight and leaf dry weight was observed 35 days after emergence. Similar studies suggest that direct seeded rice could show the effects of competition earlier than 53 days (14).

The results of the present study support the hypothesis that the effects of competitive ability are better described by measuring individual physiological and morphological characteristics than by integrating growth parameters (24). In mixtures with red rice, plant height, top dry weight, tiller and leaf number, LAI and LAD of the cultivars were reduced. Lemont was affected more than Mars. SLA, LAR,
NAR, RGR, and CGR were not adequate indicators of intraspecific competition.

In general, red rice behaved equivalently irrespective of the partner type in the mixture. Top dry weight, tiller and leaf number, shoot and leaf dry weight, and floret number per panicle of the red rice were increased when red rice was grown in mixtures. These growth attributes, along with rapid germination and emergence and early development of shoots and roots (Manuscript I), may play an important role in the mechanism of competitive ability of red rice.

LITERATURE CITED


Table 1. Effects of the interaction of red rice on some morphological and physiological characteristics of Lemont.

<table>
<thead>
<tr>
<th>Plant characteristic</th>
<th>Pure stand</th>
<th>With red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height (cm)</td>
<td>64.03a</td>
<td>57.11b</td>
</tr>
<tr>
<td>Top dry weight (g/plant)</td>
<td>4.64a</td>
<td>2.51b</td>
</tr>
<tr>
<td>Number of tillers (no./plant)</td>
<td>3.98a</td>
<td>2.72b</td>
</tr>
<tr>
<td>Number of leaves (no./plant)</td>
<td>20.10a</td>
<td>13.81b</td>
</tr>
<tr>
<td>Shoot dry weight (g/plant)</td>
<td>2.59a</td>
<td>1.31b</td>
</tr>
<tr>
<td>Leaf dry weight (g/plant)</td>
<td>1.76a</td>
<td>0.91b</td>
</tr>
<tr>
<td>Root dry weight (g/plant)</td>
<td>0.27</td>
<td>0.19</td>
</tr>
<tr>
<td>Root length (cm)</td>
<td>20.44</td>
<td>18.96</td>
</tr>
<tr>
<td>Number of panicles (no./plant)</td>
<td>3.50</td>
<td>3.00</td>
</tr>
<tr>
<td>Number of florets (no./panicle)</td>
<td>86.71a</td>
<td>58.27b</td>
</tr>
<tr>
<td>Filled floret percentage</td>
<td>52.88</td>
<td>65.58</td>
</tr>
<tr>
<td>Individual grain weight (mg)</td>
<td>22.08</td>
<td>20.91</td>
</tr>
<tr>
<td>Yield (g/plant)</td>
<td>4.32</td>
<td>2.43</td>
</tr>
<tr>
<td>Specific leaf area-SLA (cm²/g)</td>
<td>292.65</td>
<td>263.93</td>
</tr>
<tr>
<td>Leaf area ratio-LAR (cm²/g)</td>
<td>129.32</td>
<td>117.54</td>
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<tr>
<td>Leaf area index-LAI</td>
<td>4.59a</td>
<td>2.13b</td>
</tr>
<tr>
<td>Leaf area duration-LAD (LAI/days)</td>
<td>54.33a</td>
<td>24.02b</td>
</tr>
<tr>
<td>Net assimilation rate-NAR (mg/cm²/day)</td>
<td>0.67</td>
<td>0.64</td>
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<tr>
<td>Relative growth rate-RGR (g/g/day)</td>
<td>0.10</td>
<td>0.09</td>
</tr>
<tr>
<td>Crop growth rate-CGR (mg/cm²/day)</td>
<td>1.28</td>
<td>0.64</td>
</tr>
</tbody>
</table>

1 Data are means over time as follows:
   From 7 to 98 days: Plant height, top dry weight.
   From 7 to 84 days: Tillers, leaves, shoot and leaf dry wt., SLA, LAR, LAI.
   From 7 to 28 days: Root length, root dry weight.
   From 14 to 84 days: LAR, LAD, NAR, RGR, CGR.
   98 days: Panicles, florets, filled floret percentage, grain weight, yield (not over time).

2 Means within a row with no letter are not significantly different at the 5% level.
Table 2. Effects of the interaction of red rice on some morphological and physiological characteristics of Mars.

<table>
<thead>
<tr>
<th>Plant characteristic</th>
<th>Pure stand</th>
<th>With red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height (cm)</td>
<td>82.29a</td>
<td>78.15b</td>
</tr>
<tr>
<td>Top dry weight (g/plant)</td>
<td>6.16a</td>
<td>3.91b</td>
</tr>
<tr>
<td>Number of tillers (no./plant)</td>
<td>4.33a</td>
<td>3.14b</td>
</tr>
<tr>
<td>Number of leaves (no./plant)</td>
<td>21.74a</td>
<td>17.06b</td>
</tr>
<tr>
<td>Shoot dry weight (g/plant)</td>
<td>3.39a</td>
<td>2.08b</td>
</tr>
<tr>
<td>Leaf dry weight (g/plant)</td>
<td>2.00a</td>
<td>1.38b</td>
</tr>
<tr>
<td>Root dry weight (g/plant)</td>
<td>0.24</td>
<td>0.28</td>
</tr>
<tr>
<td>Root length (cm)</td>
<td>21.05</td>
<td>20.95</td>
</tr>
<tr>
<td>Number of panicles (no./plant)</td>
<td>4.67a</td>
<td>3.00b</td>
</tr>
<tr>
<td>Number of florets (no./panicle)</td>
<td>134.34</td>
<td>101.50</td>
</tr>
<tr>
<td>Filled floret percentage</td>
<td>64.70</td>
<td>66.80</td>
</tr>
<tr>
<td>Individual grain weight (mg)</td>
<td>23.03a</td>
<td>20.95b</td>
</tr>
<tr>
<td>Yield (g/plant)</td>
<td>9.50a</td>
<td>4.44b</td>
</tr>
<tr>
<td>Specific leaf area-SLA (cm²/g)</td>
<td>209.87</td>
<td>203.19</td>
</tr>
<tr>
<td>Leaf area ratio-LAR (cm²/g)</td>
<td>90.78</td>
<td>88.84</td>
</tr>
<tr>
<td>Leaf area index-LAI</td>
<td>3.69a</td>
<td>2.32b</td>
</tr>
<tr>
<td>Leaf area duration-LAD (LAI/days)</td>
<td>43.47a</td>
<td>26.67b</td>
</tr>
<tr>
<td>Net assimilation rate-NAR (mg/cm²/day)</td>
<td>0.87</td>
<td>0.80</td>
</tr>
<tr>
<td>Relative growth rate-RGR (g/g/day)</td>
<td>0.10</td>
<td>0.09</td>
</tr>
<tr>
<td>Crop growth rate-CGR (mg/cm²/day)</td>
<td>1.50</td>
<td>0.99</td>
</tr>
</tbody>
</table>

1 Data are means over time as follows:
   From 7 to 98 days: Plant height, top dry weight.
   From 7 to 84 days: Tillers, leaves, shoot and leaf dry wt., SLA, LAI.
   From 7 to 28 days: Root length, root dry weight.
   From 14 to 84 days: LAR, LAD, NAR, RGR, CGR.
   98 days: Panicles, florets, filled floret percentage, grain weight, yield (not over time).

2 Means within a row with no letter are not significantly different at the 5% level.
Table 3. Effects of the interaction of two rice cultivars on some morphological and physiological characteristics of red rice.

<table>
<thead>
<tr>
<th>Plant characteristic</th>
<th>Pure stand</th>
<th>With Lemont</th>
<th>With Mars</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height (cm)</td>
<td>95.26</td>
<td>97.38</td>
<td>97.14</td>
</tr>
<tr>
<td>Top dry weight (g/plant)</td>
<td>6.83c</td>
<td>9.11a</td>
<td>7.95b</td>
</tr>
<tr>
<td>Number of tillers (no./plant)</td>
<td>5.87b</td>
<td>6.56a</td>
<td>6.05ab</td>
</tr>
<tr>
<td>Number of leaves (no./plant)</td>
<td>27.19b</td>
<td>31.04a</td>
<td>28.80b</td>
</tr>
<tr>
<td>Shoot dry weight (g/plant)</td>
<td>4.08c</td>
<td>5.44a</td>
<td>4.68b</td>
</tr>
<tr>
<td>Leaf dry weight (g/plant)</td>
<td>2.10c</td>
<td>2.67a</td>
<td>2.33b</td>
</tr>
<tr>
<td>Root dry weight (g/plant)</td>
<td>0.65</td>
<td>0.68</td>
<td>0.82</td>
</tr>
<tr>
<td>Root length (cm)</td>
<td>22.89</td>
<td>22.72</td>
<td>22.56</td>
</tr>
<tr>
<td>Number of panicles (no./plant)</td>
<td>5.83</td>
<td>7.50</td>
<td>6.50</td>
</tr>
<tr>
<td>Number of florets (no./panicle)</td>
<td>91.55b</td>
<td>114.08a</td>
<td>116.22a</td>
</tr>
<tr>
<td>Filled floret percentage</td>
<td>83.14</td>
<td>84.33</td>
<td>82.49</td>
</tr>
<tr>
<td>Individual grain weight (mg)</td>
<td>28.01</td>
<td>28.15</td>
<td>26.46</td>
</tr>
<tr>
<td>Yield (g/plant)</td>
<td>12.27</td>
<td>20.34</td>
<td>17.12</td>
</tr>
<tr>
<td>Specific leaf area—SLA (cm²/g)</td>
<td>242.24</td>
<td>224.20</td>
<td>233.20</td>
</tr>
<tr>
<td>Leaf area ratio—LAR (cm²/g)</td>
<td>107.83</td>
<td>101.28</td>
<td>99.32</td>
</tr>
<tr>
<td>Leaf area index—LAI</td>
<td>4.29</td>
<td>4.92</td>
<td>4.64</td>
</tr>
<tr>
<td>Leaf area duration—LAD (LAI days)</td>
<td>48.59</td>
<td>56.51</td>
<td>54.26</td>
</tr>
<tr>
<td>Net assimil. rate—NAR (mg/cm²/day)</td>
<td>0.67</td>
<td>0.75</td>
<td>0.75</td>
</tr>
<tr>
<td>Relative growth rate—RGR (g/g/day)</td>
<td>0.09</td>
<td>0.10</td>
<td>0.09</td>
</tr>
<tr>
<td>Crop growth rate—CGR (mg/cm²/day)</td>
<td>1.45</td>
<td>2.02</td>
<td>1.80</td>
</tr>
</tbody>
</table>

1 Data are means over time as follows:
   From 7 to 98 days: Plant height, top dry weight.
   From 7 to 84 days: Tillers, leaves, shoot and leaf dry wt., SLA, LAI.
   From 14 to 84 days: LAR, LAD, NAR, RGR, CGR.
   From 7 to 28 days: Root length, root dry weight.
   98 days: Panicles, florets, filled floret percentage, grain weight, yield (not over time).

2 Means within a row followed by the same letter or with no letter are not significantly different at the 5% level.
Figure 1. Change in plant height with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.
Figure 2. Change in top dry weight with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.
Figure 3. Change in number of tillers per plant with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.
Figure 4. Change in number of leaves per plant with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.
Figure 5. Change in shoot dry weight with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.

### Lemont
- Pure stand (L): $\hat{y} = -1.64 + 0.13x$, $r^2 = 0.79$
- Mix (L*R): $\hat{y} = -1.15 + 0.11x - 0.001x^2$, $r^2 = 0.70$

### Mars
- Pure stand (M): $\hat{y} = -2.67 + 0.21x - 0.001x^2$, $r^2 = 0.87$
- Mix (M*R): $\hat{y} = -1.60 + 0.13x - 0.001x^2$, $r^2 = 0.75$
Figure 6. Change in leaf dry weight with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.
Figure 7. Change in leaf area index with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.
Figure 8. Change in leaf area duration with time of (a) Lemont pure stand (L) and Lemont with red rice (L*R), and (b) Mars pure stand (M) and Mars with red rice (M*R). Bars at harvest intervals indicate lower and upper 95% confidence limits for the mean.
MANUSCRIPT III

To be submitted to Journal of Applied Ecology
EFFECTS OF END-OF-DAY LIGHT QUALITY ON EARLY GROWTH AND DEVELOPMENT OF RED RICE AND TWO RICE CULTIVARS

By J. CLAVIJO, J. B. BAKER and P. W. JORDAN

Plant Pathology and Crop Physiology Department, Louisiana Agricultural Experiment Station, Louisiana State University Agricultural Center, Baton Rouge, LA 70803, U.S.A.

SUMMARY

(1) Effects of end-of-day light quality on early growth and development were evaluated for pure stands of red rice (*Oryza sativa* L.) and two rice (*Oryza sativa* L.) cultivars, Lemont and Mars, in a controlled environment.

(2) Light quality treatments consisted of no supplemental irradiation, irradiation with red light, and irradiation with red and far-red light in a ratio of 1.0:0.83.

(3) Tiller number per plant was the most important characteristic affected by the light irradiations. An increase in the proportion of red light at the base of the plants promoted an increase in the number of tillers per plant. The magnitude of the increase was greater for red rice than for the cultivars.

(4) Plant height did not show significant difference, but leaf area index and top dry weight were affected as a result of the effects of end-of-day light quality on tillering.
These results support the hypothesis that tillering is controlled by a shift in spectral quality of the light reaching the bottom of the canopy.

INTRODUCTION

In the presence of adequate water and nutrients, and favorable temperatures, available light energy sets the limits for plant productivity. If competition for light is occurring between crop and weed species, then effective competitors would be those able to rapidly produce and elevate leaves in response to the presence of neighboring plants. Initiation of tiller or branch elongation is one possible component of this response (Patterson 1985).

Weed or crop canopies alter both the quantity and quality of the light passing through them. Under vegetation, light is decreased in photon fluence rate as a result of reflection and absorption by the shoot. The degree of reduction is a function of the number, size, morphology, spatial position and pigment content of leaves as well as the angle of incidence of incoming radiation. The light which does pass through the canopy has a spectral quality having a lower portion of the wavelengths which are absorbed by the canopy and a higher portion of the wavelengths which are transmitted or reflected (Child, Morgan & Smith 1981b; Kendrick & Frankland 1983). Thus, the plant canopy causes large decreases in red light because of the absorption by green leaves and increases in far-red because of transmission and reflection (Holmes & Smith 1977a; Holmes 1981; Smith 1982). This produces a decrease of the R:FR ratio (mW/m² at 660 nm:mW/m² at 730 nm) beneath the canopy which affects the ratio of the red absorbing and
far-red absorbing forms of phytochrome which may influence morphogenetic processes (Holmes & Smith 1977b; Morgan 1981).

Developmental effects of phytochrome in plants and their relation to light quality within plant canopies have been studied by several researchers (Smith 1982). Light quality affects branching of species including *Nicotiana tabacum* L. (Kasperbauer 1971) and *Lycopersicon sculentum* Mill. (Tucker 1975). Variations in phytochrome status in grasses induced by end-of-day red and far-red treatments were reported by Deregibus, Sanchez & Casal (1983). They showed that *Lolium perenne* L. and *L. multiflorum* Lam. plants developed more tillers when irradiated with high R:FR ratios and concluded that tillering in grasses is controlled by phytochrome in a way similar to branching in dicots.

The influence of plant density on spectral distribution of light has been measured under field conditions and in controlled environments for different grass species (Casal, Sanchez & Deregibus 1986; Deregibus, Sanchez, Casal & Trlica 1985). It was shown that close-spaced seedlings of *Triticum aestivum* L. received lower R:FR ratios than wide-spaced plants and developed fewer tillers, less roots and longer leaves. The same effects were found in a controlled environment when the wheat seedlings received 5 minutes of far-red at the end of the photosynthetic period. These effects were reversed by 5 minutes of red light (Kasperbauer & Karlen 1986).

It has been suggested that phytochrome may serve as a sensing mechanism that detects the presence of neighboring plants or genets and regulates the development of tillers (Kasperbauer & Karlen 1986). Extensive and early tillering of rice has been pointed out as
advantageous to the plant in order to increase yield, compensate for missing plants, and increase competitive ability (Yoshida 1981). The depression in rice cultivar yields caused by competing red rice is in part a function of a reduction in the number of panicles bearing tillers (Navarro 1984). The objective of this study was to analyze and evaluate the effects of end-of-day red light treatment on the early growth and development of red rice and two rice cultivars.

MATERIALS AND METHODS

Pure stands of red rice, Lemont, and Mars were grown in a growth chamber providing a temperature of 35°C during the 14 hour light period and 30°C during the 10 hours of darkness. Illumination was from a combination of low pressure sodium lamps and 40 W incandescent bulbs which provided a photosynthetically active irradiation of 1060 micro Einsteins/m²/s and a R:FR ratio of 1.57:1.6 at the top of the canopy.

Red rice and the rice cultivars were sown in 39x43x20 cm plastic containers which were filled with Commerce silt loam soil, fertilized with 60 kg N/ha and 20 kg P₂O₅/ha and watered twice every day to keep the soil saturated. Additional fertilization was provided weekly using 60 Kg N/ha, 20 Kg P₂O₅/ha, 20 Kg K₂O/ha, and 0.1 Kg of Zn, Fe, Cu, Mn/ha total. Each container had 16 plants spaced 10x10 cm which was equivalent to a plant density of 100 plant/m².

The basal portion of two central plants in one set of containers was exposed to red light for 10 minutes at the end of the daily light period. A second was treated in this way with a combination of red and far-red light. A third set received no supplemental irradiation at all and was used as a control. Treatments were started 10 days after
emergence and lasted for 25 days. The red light was provided by a red light emitting diode (LED) with an intensity of 1.0 mW/m² at a peak wavelength of 660 nm placed at 1.0 cm from the base of the plant. The far-red light came from a 300 W R40 reflector flood lamp filtered through 5.0 cm water and a 5.0 mm CBS far-red plastic filter and was conducted to each plant by 9 glass fiber optic light guides (1.0 m long each, 440-450 fibers/guide) with tips placed 1.0 cm from the base of the plant in the same holder as the LEDs. The intensity of the far-red light was 0.83 mW/m² at a peak wavelength of 730 nm. The R:FR ratio obtained for the combination of red and far-red treatment was 1.0:0.83.

A split plot treatment arrangement in a completely randomized design with sampling and two replications was used. The two central plants from each container were harvested at 36 days after emergence and data recorded included plant height, tiller number per plant, leaf area per plant, and dry weight of the tops (shoots plus leaves). Leaf area index (LAI) was calculated. Data were subjected to analysis of variance and means separated according to the LSD method.

In a separate experiment in which red rice, Lemont and Mars were grown outside in plastic containers with a stand density of 100 plants/m², R:FR ratios were measured at 30 days after emergence using an ISCO model SR spectroradiometer attached to an ISCO model SRR recorder-scanner. The remote probe was placed above the leaf canopy and at 5 cm above the soil level at 10:00 h solar time on a clear midsummer day. Readings at 5 cm above the soil level were taken at a point equidistant between the four central plants in each container. Each container had 16 plants with the same spacing as previously mentioned.
RESULTS AND DISCUSSION

R:FR ratios measured in direct sunlight above and below canopy of red rice and the two rice cultivars at the tillering stage on a clear midsummer day ranged between 1.1:0.9 and 1.2:0.9 and were in agreement with those reported by other researchers (Smith 1982; Kasperbauer & Karlen 1986). Red rice, Lemont and Mars canopies, on average, transmitted 9% of incident red light to the base of the plants but transmitted 30% of far-red, resulting in a decreased R:FR ratio at the soil level where tillers develop. Decreases in R:FR ratio beneath a canopy have been reported for several species under field conditions, and it has been hypothesized that this enrichment of FR light spectrum reaching the base of the plants appears to be a mechanism regulating grass morphogenesis during the tillering stage (Deregibus, Sanchez, Casal & Trlica 1985; Casal, Deregibus & Sanchez 1985).

The effects of end-of-day light quality on red rice are shown in Table 1. Tiller number per plant showed a significant difference in response to the treatments. The greatest tillering occurred when red light was applied, with a lower number of tillers being formed when both red and far-red were applied. The lowest number of tillers occurred in the absence of the end-of-day light treatment. Plant height was not affected by the light treatments but LAI and dry weight of tops showed a response which was a reflection of the effect of the treatments on the tillering process. Indeed, LAI and dry weight of tops showed no significant differences between the treatments when expressed on a per tiller basis.

Lemont and Mars responded in similar fashion to the red light treatments but with a different magnitude, particularly in the LAI and
dry weight measurements. In these two characteristics, Lemont showed significantly greater values than Mars (Tables 2 and 3). Tiller number per plant was significantly different for all the treatments. In response to the red light irradiations there was a greater increase in tiller number in Mars than in Lemont when compared to no irradiation treatment. In Mars this increment was 4.2 times while in Lemont it was 2.5 times. Plant height did not vary with the treatments, but LAI and dry weight of tops showed significant differences between irradiated and nonirradiated plants. It should be noted that the Mars rice did not grow well under these experimental conditions, the plant being obviously unhealthy.

Plant height was not affected by red light irradiation in any of the three rice plant types studied. This might be due to the fact that this plant characteristic in rice is better expressed at the reproductive stage and not early (36 days) during the vegetative stage when only gradual increases in plant height occur (Yoshida 1981). In addition, it has been hypothesized that plant height is under the influence of the photon fluence rate or irradiance in those environments where shade light conditions are not extreme (Child, Morgan & Smith 1981b). In fact, the R:FR of the environment in this study was 1.57:1.6 at the top of the canopy and the irradiance was kept fairly constant at 1060 microEinstins/m²/s.

It has been reported that low R:FR ratios tend to reduce total leaf area in Chenopodium album L. (Child, Morgan & Smith 1981a; Morgan & Smith 1981) and Rumex obtusifolius L. (McLaren & Smith 1978). Similarly it has been argued that photon fluence rate is a more important factor influencing leaf area and biomass than light quality.
(Child, Morgan & Smith 1981b; Casal, Deregibus & Sanchez 1985). In addition, end-of-day red light enrichment of the environment above the canopy of Lolium perenne L. and L. multiflorum Lam. plants did not have any effect on leaf area, leaf number, and dry biomass (Deregibus, Sanchez & Casal 1983). In the present study, the increase in LAI and top dry weight found in irradiated plants was the result of the effect of light quality on tillering rather than an increase in other characteristics which contribute to LAI and top dry weight.

In general, tiller number per plant was the most important characteristic affected by the red light treatments. The results reported here for red rice and the two rice cultivars, Lemont and Mars, show that an end-of-day irradiation of the base of the plants with red light or a R:FR mixture with a ratio of 1.0:0.83 promotes an increase in the number of tillers per plant. On the other hand, the low R:FR ratios at the bottom of the canopy found in the plants growing under direct sunlight and the lower number of tillers per plant in those plants without end-of-day irradiation suggest that tillering in rice and red rice is controlled by the spectral quality of the light reaching the base of the plants. Indeed, a low R:FR ratio is likely responsible for the decrease of tillering since irradiation of plants with a R:FR ratio of 1.0:0.83 or red light alone doubled and tripled, respectively, the number of tillers per plant (Tables 1, 2, and 3).

It has been hypothesized that a function of phytochrome in the natural environment is to detect the R:FR ratio of the incident spectrum (Holmes & Smith 1977b; Morgan & Smith 1979) and that tillering is controlled by phytochrome (Deregibus, Sanchez & Casal 1983; Kasperbauer & Karlen 1986). The results of the present study also
suggest the possibility of phytochrome involvement since nonirradiated plants produced fewer tillers than irradiated ones, low R:FR ratios were found at the bottom of the canopy, and red light end-of-day treatments increased the number of tillers per plant significantly.

REFERENCES


Table 1. Effect of end-of-day light quality on early growth and development of red rice under growth chamber conditions.¹

<table>
<thead>
<tr>
<th>Light treatment</th>
<th>Plant Height (cm)</th>
<th>Tillers per plant</th>
<th>Leaf area index</th>
<th>Dry weight of tops (g/plant)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td>94.45a</td>
<td>15.50a</td>
<td>5.00a</td>
<td>6.83a</td>
</tr>
<tr>
<td>R:FR (1.0:0.83)²</td>
<td>88.15a</td>
<td>11.75b</td>
<td>4.31a</td>
<td>5.40ab</td>
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<tr>
<td>No irradiation</td>
<td>89.32a</td>
<td>6.25c</td>
<td>2.22b</td>
<td>3.28b</td>
</tr>
</tbody>
</table>

¹ Means within a column followed by the same letter are not significantly different at 5% level.

² (mW/m² at 660 nm:mW/m² at 730 nm).
Table 2. Effect of end-of-day light quality on early growth and development of Lemont under growth chamber conditions.  

<table>
<thead>
<tr>
<th>Light treatment</th>
<th>Plant Height</th>
<th>Tillers per plant</th>
<th>Leaf area index</th>
<th>Dry weight of tops</th>
</tr>
</thead>
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<tr>
<td>R</td>
<td>76.85a</td>
<td>11.50a</td>
<td>4.09a</td>
<td>5.36a</td>
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<td>R:FR (1.0:0.83)²</td>
<td>80.75a</td>
<td>9.00b</td>
<td>3.08a</td>
<td>4.62a</td>
</tr>
<tr>
<td>No irradiation</td>
<td>68.25a</td>
<td>4.50c</td>
<td>1.47b</td>
<td>2.14b</td>
</tr>
</tbody>
</table>

¹ Means within a column followed by the same letter are not significantly different at 5% level.

² (mW/m² at 660 nm:mW/m² at 730 nm).
Table 3. Effect of end-of-day light quality on early growth and development of Mars under growth chamber conditions.¹

<table>
<thead>
<tr>
<th>Light treatment</th>
<th>Plant Height (cm)</th>
<th>Tillers per plant</th>
<th>Leaf area index</th>
<th>Dry weight of tops (g/plant)</th>
</tr>
</thead>
<tbody>
<tr>
<td>R</td>
<td>72.55a</td>
<td>11.75a</td>
<td>1.40a</td>
<td>2.59a</td>
</tr>
<tr>
<td>R:FR (1.0:0.83)²</td>
<td>77.15a</td>
<td>9.50b</td>
<td>1.62a</td>
<td>3.22a</td>
</tr>
<tr>
<td>No irradiation</td>
<td>68.28a</td>
<td>2.75c</td>
<td>0.37b</td>
<td>0.83b</td>
</tr>
</tbody>
</table>

¹ Means within a column followed by the same letter are not significantly different at 5% level.

² (mW/m² at 660 nm:mW/m² at 730 nm).
Effects of the Interaction Between Red Rice (*Oryza sativa*) and Rice (*O. sativa*) Cultivars on Some Root Functions.

By JAIRO CLAVIJO and JOHN B. BAKER

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SUMMARY

Pure stands and 50:50 mixtures of red rice (*Oryza sativa* L.) and the rice (*Oryza sativa* L.) cultivars, Lemont and Mars, were grown in the greenhouse to analyze and evaluate the effects of root interaction on nitrogen and phosphorus uptake and cation exchange capacity (CEC) of the roots. Lemont grown with its roots interacting with the roots of red rice had a lower nitrogen and phosphorus content in the shoots during the entire growing season than when there was no root interaction. The only effect on Mars was a lower phosphorus content at maturity where there was root interaction with red rice. However, a significant decrease in shoot dry weight of the cultivars when in root interaction with red rice was found at maturity. Red rice in pure stand had the highest root CEC value, but the CEC values of the cultivars grown in mixture were higher than when grown in pure stand suggesting that the root CEC increases when there is an increase in competition. This study also suggests that the higher root CEC exhibited by red rice could be the cause of its competitiveness.
INTRODUCTION

Plant species growing in proximity can interact competitively for nutrients. Weeds may compete for essential nutrients and decrease crop yield even at high rates of fertilization. Thus, competition for nutrients may play an important role in the interaction of weeds and crops (11, 18).

The three most common limiting nutrients for which weeds and crops may compete are nitrogen, phosphorus, and potassium. Usually, nitrogen is the first nutrient to become limiting as a result of competition (18). It has been shown that changes in nutrient content at various stages in the life of the rice plant are very similar in both temperate regions and the tropics, even though several environmental factors affect nutrient uptake. In addition, the nitrogen, phosphorus and sulfur contents in the vegetative parts are generally high at early growth stages and decline toward maturity (17).

The relationship of competition between weeds and rice for nitrogen may be influenced by time of fertilizer application, plant populations, relative ability of the weeds and rice to absorb nitrogen, crop cultivar, rate of nitrogen and irrigation frequency (3, 9, 10). According to Alkamper and van Long (1), addition of nitrogen fertilizer reduced the injury caused by red rice to the rice crop although there was some competition for nutrients.

Using plant analysis, Jakhro (6) showed that optimum grain yield of rice should be expected if an optimum phosphorus concentration is present in the plant tissue at panicle initiation. Addition of phosphorus to dry-seeded wetland rice increased yield when rice was
grown alone. In the presence of weeds, rice yield was reduced in spite of phosphorus fertilization (8).

In general, CEC of roots is believed to affect cation absorption by plant roots (2) and has been directly related to yield and nutrient uptake in rice (15). Total content of all nutrients, except Mg and Zn, increases with increase in root CEC (12). Phosphorus content in rice shoots was significantly correlated with the CEC of the roots at flowering stage (13, 14). It has been shown that root CEC was a selection criterion to be considered when the ability of Sorghum bicolor L. to compete with weeds was tested (5). In addition, it has been concluded that the basis of competition for phosphorus between species could be a function of root CEC and this could be a possible mechanism of competition for phosphorus (9).

The objectives of the present study were (a) to quantify and analyze the nitrogen and phosphorus uptake of Lemont and Mars when grown in mixture with red rice, and (b) to evaluate the root CEC of red rice and the cultivars when grown in pure stands and mixtures.

MATERIALS AND METHODS

Nitrogen and phosphorus uptake. Mixtures of red rice with Lemont or Mars at a stand density of 100 plants/m² were grown in the greenhouse in 70x60x40 cm wooden containers which could be subdivided with fiberglass panels into six 70x10x40 cm compartments. Each compartment was sown with a row of either red rice or a cultivar. Plants within a row were spaced 10 cm apart. Each cultivar had a red rice row on each side. In this way it was possible to isolate the roots of red rice and the cultivars while aerial competition was still occurring. Two sets
of these containers with and without the fiberglass partition were built to have root interaction and no root interaction.

The containers were filled with Crowley silt loam soil and fertilized at planting time with 120 Kg N/ha and 40 Kg P_2O_5/ha. Fifteen days after emergence the containers were flooded, and this water level was maintained until maturity.

A split plot treatment arrangement in a randomized block design with sampling and two replications was used. Half of the total number of plants in each container was harvested at 40 days after emergence and the other half at maturity. Data recorded at each harvest were dry weight of shoots (leaves plus stems) and total nitrogen and phosphorus content. Attempts to secure root harvest were nullified by the inability to separate the roots of the partners in containers in which there was root interaction.

Shoots of either red rice or the cultivars were ground in a stainless steel grinder to pass a 20 mesh sieve and oven-dried. One g of dried tissue per plant was weighed and placed in a 250 ml test tube for digestion. A mixture of 25 ml of sulfuric acid, eight g cupric sulfate and five ml of hydrogen peroxide 30% was added and the test tubes were heated for one hour. Then, total nitrogen was determined by passing a 2.5 ml aliquot through a Technicon Auto Analyzer II continuous flow analytical instrument. Another g of dried tissue was digested with a 3:1 nitric perchloric acid mixture and then analyzed for phosphorus with an inductively coupled plasma emission spectrometer.

Root CEC. Pure stands of red rice, Lemont and Mars and 50:50 mixtures of red rice and Lemont or Mars were grown in the greenhouse in 39x43x20
cm plastic containers at a plant density of 100 plants/m². This density was established by planting two seeds at a spacing of 10x10 cm and then thinning to a population of 16 plants per container. The same population was obtained for the mixtures by placing the cultivars and red rice in a checkerboard fashion such that each cultivar was surrounded by four red rice plants and vice versa.

The containers were filled with sand, watered every day with deionized water to saturation and fertilized at 5 and 20 days after emergence using the equivalent of 60 Kg N/ha, 20 Kg P₂O₅/ha, 20 Kg K₂O/ha, and 0.1 Kg of Zn, Fe, Cu, Mn/ha each time.

A randomized complete block design with three replications was used. Two of the central plants from each pure stand and mixture were harvested 30 days after emergence, washed with distilled water and excised to separate the roots from the shoots. CEC of the roots was measured by a method adapted from Wiersum and Bakema (16). About 1.5 g of fresh roots were rinsed twice in separate 100 ml aliquots of HCl solutions (pH 2.0) for 40 seconds each. Then, the roots were rinsed with demineralized water to remove excess Cl⁻ and H⁺. Following this, the roots were put into a 1 N solution of KCl (adjusted to pH 8.0 with KOH) for 2 minutes and then titrated with 0.03 N KOH so that the solution pH was restored to 8.0. Nitrogen gas was bubbled through the solutions all the time to reduce the effects of atmospheric CO₂ on the pH of the solutions. The roots were subsequently rinsed with distilled water to remove excess 1N KCl, oven-dried, and weighed. The amount of KOH used to titrate the H⁺ released was a measure of root CEC and was expressed in me/100 g root dry weight.
RESULTS AND DISCUSSION

Nitrogen uptake. The effect of red rice root interactions on nitrogen content of Lemont and Mars shoots is presented in Table 1. Lemont grown in a mixture with red rice to obtain root interactions had a significantly lower nitrogen content than when grown in a pure stand. This reduction was found 40 days after emergence and at maturity. However, since Lemont shoot dry weight was significantly lower at maturity in the mixture with root interaction than with no interaction of roots (Table 3), this decrease in nitrogen per plant may be a reflection of the smaller plant size. In the case of Mars, red rice root interaction did not influence the nitrogen content at either time. It has been reported that red rice competes for nitrogen with rice (1) and that the extent of nitrogen competition in rice is affected by cultivar (9).

Phosphorus uptake. The phosphorus content of Lemont decreased as a consequence of root interaction with red rice at 40 days after emergence and maturity (Table 2). Mars was not affected by red rice root interaction at 40 days after emergence, but it was at maturity when a significant difference was observed (Table 2). This reduction in phosphorus content of Lemont and Mars at maturity as a result of the red rice-cultivar root interaction could be influenced by the decrease in cultivar shoot dry weight (Table 3). Phosphorus has been found to increase rice yield when the rice was grown alone, but a significant decrease occurred when the rice was competing with weeds (8, 9). The addition of phosphorus has been found to increase the dry matter yield of weeds when grown alone and in mixture with rice (9). In the present study, the lack of a significant reduction in phosphorus content of
Mars at 40 days after emergence could suggest that Mars is more competitive than Lemont as far as phosphorus uptake is concerned.

The early development of red rice roots (reported elsewhere) could provide an ability to rapidly absorb nutrients and promote its own growth leading to competition for nutrients as early as 40 days after emergence. It has been found that a high rate of nitrogen absorption in the early growth stages is one of the most significant characters related to competitive ability in rice (7).

Root CEC. Table 4 shows root CEC of pure stands of red rice, Mars and Lemont and mixtures of red rice with Mars of Lemont. A suggestive difference between red rice pure stand and Lemont and Mars pure stands was observed. Red rice in pure stand attained the highest value of 2.96 me/100 g root dry weight with Lemont and Mars being statistically lower. In the mixtures the root CEC values for Lemont and Mars were numerically greater than when in pure stands suggesting that the root CEC increases when the plants are in a mixture and under competition.

In mixtures red rice CEC values were numerically lower than in pure stands. Since red rice competes with itself more than the cultivars compete with red rice, the data suggest that CEC values will be higher for plants growing under competitive stress. Thus, the lower the CEC values, the less the competitive stress to which a plant is responding.

Root CEC has been considered a function of the number of free carboxyl groups of galacturonic acids of pectin of the cell wall matrix. The production of cell wall matrix has been placed very early in the cell development and would be considered an integral part of cell growth and therefore, root growth and elongation (4).
There is a direct relationship between root CEC and the total uptake of nutrients in rice (12, 15). It has been shown that red rice has a greater ability to compete for nitrogen and phosphorus when grown in mixture with Lemont. Therefore, the higher root CEC exhibited by red rice could be the root property associated with its greater uptake of nutrients and competitive ability.

LITERATURE CITED


Table 1. Effect of red rice root interaction on nitrogen content of Lemont and Mars shoots.¹

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Lemont with red rice</th>
<th>Mars with red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>40 days² Maturity</td>
<td>40 days² Maturity</td>
</tr>
<tr>
<td>No root interaction</td>
<td>118.54a 232.24a</td>
<td>182.03a 176.30a</td>
</tr>
<tr>
<td>Root interaction</td>
<td>43.38b 53.60b</td>
<td>130.55a 93.23a</td>
</tr>
</tbody>
</table>

¹ Means within a column followed by the same letter are not significantly different at 5% level.

² Days after emergence.
Table 2. Effect of red rice root interaction on phosphorus content of Lemont and Mars shoots.  

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Lemont with red rice</th>
<th>Mars with red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>40 days² Maturity</td>
<td>40 days² Maturity</td>
</tr>
<tr>
<td>No root interaction</td>
<td>11.45a 24.94a</td>
<td>16.37a 26.23a</td>
</tr>
<tr>
<td>Root interaction</td>
<td>4.71b 4.12b</td>
<td>12.54a 7.26b</td>
</tr>
</tbody>
</table>

1 Means within a column followed by the same letter are not significantly different at 5% level.

2 Days after emergence.
Table 3. Effect of red rice root interaction on shoot dry weight of Lemont and Mars.\(^1\)

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Lemont with red rice</th>
<th>Mars with red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>40 days(^2) Maturity</td>
<td>40 days(^2) Maturity</td>
</tr>
<tr>
<td>No root interaction</td>
<td>3.89a 15.39a</td>
<td>5.77a 20.37a</td>
</tr>
<tr>
<td>Root interaction</td>
<td>2.49a 5.05b</td>
<td>4.42a 11.45b</td>
</tr>
</tbody>
</table>

\(^1\) Means within a column followed by the same letter are not significantly different at 5% level.

\(^2\) Days after emergence.
Table 4. Root cation exchange capacity of red rice and two rice cultivars grown in pure stands and in red rice-cultivar mixtures.  

<table>
<thead>
<tr>
<th>Associated plant</th>
<th>Red rice</th>
<th>Lemont</th>
<th>Mars</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Red rice</td>
<td>2.96a</td>
<td>2.19abc</td>
<td>2.71abc</td>
<td></td>
</tr>
<tr>
<td>Lemont</td>
<td>2.77ab</td>
<td>1.90bc</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Mars</td>
<td>2.13abc</td>
<td>-</td>
<td>1.76c</td>
<td></td>
</tr>
</tbody>
</table>

Means followed by the same letter are not significantly different at 10% level.
Competition for Light and Nutrients Between Red Rice (Oryza sativa) and Two Rice (O. sativa) Cultivars.

JAIRO CLAVIJO AND JOHN B. BAKER

Abstract. Effects of competition for light and nutrients between red rice (Oryza sativa L.) and the rice (O. sativa L.) cultivars, Lemont and Mars, on morphological and physiological characteristics were determined 40 days after emergence. Soil and aerial partitions produced four modes of competition: no competition, light competition, nutrient competition and full competition. In general, light competition from red rice increased plant height and decreased tillers and the specific leaf area of the cultivars.

INTRODUCTION

Red rice is one of the most important annual weeds of rice in many countries causing major yield and quality losses (1, 16). Diarra et al. (4) found that red rice at 5 plants/m² reduced cultivar panicle size 8 to 18%. Red rice plants are taller and tiller more than cultivated rice (10). Red rice seeds have a pigmented pericarp and shatter easily and may persist in the soil in a dormant condition for a long period of time (3).

Red rice is difficult to control because it exhibits morphological and physiological characteristics similar to cultivated rice and competes for the same resources (16). It has been hypothesized that plants growing together compete for resources needed for growth and
development and that this competition may occur above and below ground (5). Above ground competition is primarily for light and is a function of canopy development and shading, while below ground competition may be for water, nutrients, or both (12). In many crops and pastures competition involves more than one factor because the secondary effect of competition for a nutrient or for water is differential growth and differential stature and hence competition for light and vice versa (5, 6).

Several investigators have separated the effects of above and below ground competition with some success. Donald (5) used soil and aerial partitions to separate shoot and root competition effects in pot cultures with two plants. The technique has been modified and extended using containers of various designs and more than two plants (8, 13, 14, 17, 18) and Willey and Reddy (20) have taken the technique to the field to study intercrop interactions. Cook and Ratcliff (2) and Snaydon and Howe (19) have utilized reflective aluminium tubes and polythene tubes to separate shoots and roots, respectively, of invading grass seedlings.

In all cases, the technique provided a way to study four modes of plant competition, that is, no competition where the shoots and roots of the competing plants were isolated from each other, light competition where the roots were isolated, soil competition where the shoots were isolated and full competition where shoots and roots interacted. Thus, it should be possible to separate competition into components and to analyze the nature of competition for one or more factors (5, 7, 11).
The objective of the present study was to determine the effects of light and nutrient competition of red rice on some morphological and physiological characteristics of two rice cultivars.

MATERIALS AND METHODS

Mars and Lemont were grown in mixtures with red rice in the greenhouse using 39x43x20 cm plastic containers and a plant density of 100 plants/m² in a square grid pattern with plants 10 cm from the nearest neighbor. The containers were placed and modified in such a way that it was possible to isolate the roots of red rice and the cultivar using styrofoam soil dividers permitting light competition only. In another set of containers, isolation of the aerial parts of the plants was achieved by placing black plastic strips in the middle of the containers from the soil surface up to a height equal to the shortest plant, permitting root competition only. A third set was divided above and below ground in the ways already mentioned providing for no competition and a fourth set was left without dividers to provide full competition. These modifications gave four modes of competition: no competition, light competition, nutrient competition and full competition.

The containers were filled with Crowley silt loam soil and fertilized at 15 days after emergence with 60 Kg N/ha, 20 Kg P₂O₅/ha, 20 Kg K₂O/ha and 1.0 Kg of Zn, Fe, Cu, Mn/ha. Fifteen days after emergence the containers were flooded, and the water level was maintained until harvest.

A split plot treatment arrangement in a completely randomized design with sampling was used. Four replicates were harvested at 40
days after emergence. Data recorded were plant height, number of tillers, area and dry weight of the leaf blades and shoot dry weight. Specific leaf area (SLA) was calculated by dividing the area by the dry weight of the leaf blades, and top dry weight was the sum of leaf blade and shoot dry weight.

RESULTS AND DISCUSSION

The effects of four modes of competition between red rice and Lemont and Mars on plant height 40 days after emergence are reported in Table 1. In Mars the plant height was significantly greater when there were no partitions or only the soil partition. No significant differences were found in the plant height of Lemont in response to the various modes of competition, although the highest values were associated with the same treatments as in Mars. Increased stem extension in dicots is the result of reduced light quantity, shifts in light quality and constitutes a shade-avoidance reaction (15). Results presented here suggest that rice plant height may be similarly affected.

Any type of red rice competition reduced the number of tillers per plant in Lemont, whereas the number of tillers per plant in Mars remained statistically unaffected (Table 2). Tiller number per plant has been found to be the most important morphological characteristic of Lemont and Mars affected by light quality changes that occur under competing vegetation canopies (Manuscript III). On the other hand, tiller production in rice is a reflection of soil fertility, especially when adequate amounts of N and P are present (21). The short stature
of Lemont may have predisposed it to be more susceptible to light quality shifts than the taller Mars.

The effects of mode of competition on SLA of the cultivars was different in Lemont and Mars (Table 3). Although Lemont has greater SLA values than Mars, a significant decrease in Lemont SLA was detected when light competition is compared to no competition. Changes in light quantity and quality due to competing canopies have been shown to produce changes in leaf size and structure and are reflected in changes in SLA values (15).

Lemont top dry weight was significantly reduced by nutrient competition from red rice when compared to no competition (Table 4). However, in Mars the top dry weight was increased as a result of light competition. The fact that full competition did not shown any reduction could be due to compensating interactions between factors when more than one is involved. It has been hypothesized that competition for more than one factor involves interaction of effects instead of addition. Therefore, the result of competition for more than one factor may not necessarily be the sum of the effects which occur when each factor operates alone (5, 6, 9).

LITERATURE CITED


Table 1. Effect of four modes of competition between red rice and two rice cultivars on plant height 40 days after emergence.¹

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Lemont with red rice</th>
<th>Mars with red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil and aerial partitions</td>
<td>84.71a</td>
<td>104.54b</td>
</tr>
<tr>
<td>Soil partition</td>
<td>92.03a</td>
<td>113.84a</td>
</tr>
<tr>
<td>Aerial partition</td>
<td>87.14a</td>
<td>105.23b</td>
</tr>
<tr>
<td>No partitions</td>
<td>88.75a</td>
<td>110.15a</td>
</tr>
</tbody>
</table>

¹ Treatment means within a column followed by the same letter are not significantly different at 5% level.
Table 2. Effect of four modes of competition between red rice and two rice cultivars on tillers per plant 40 days after emergence.1

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Lemont with red rice</th>
<th>Mars with red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>no./plant</td>
<td></td>
</tr>
<tr>
<td>Soil and aerial partitions</td>
<td>4.13a</td>
<td>5.25a</td>
</tr>
<tr>
<td>Soil partition</td>
<td>2.63b</td>
<td>5.25a</td>
</tr>
<tr>
<td>Aerial partition</td>
<td>2.88b</td>
<td>4.75a</td>
</tr>
<tr>
<td>No partitions</td>
<td>3.13b</td>
<td>4.50a</td>
</tr>
</tbody>
</table>

1 Treatment means within a column followed by the same letter are not significantly different at 5% level.
Table 3. Effect of four modes of competition between red rice and two rice cultivars on specific leaf area 40 days after emergence.\(^1\)

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Lemont with red rice</th>
<th>Mars with red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil and aerial partitions</td>
<td>261.00a</td>
<td>221.30a</td>
</tr>
<tr>
<td>Soil partition</td>
<td>230.23b</td>
<td>203.77a</td>
</tr>
<tr>
<td>Aerial partition</td>
<td>254.70ab</td>
<td>215.70a</td>
</tr>
<tr>
<td>No partitions</td>
<td>235.01ab</td>
<td>197.69a</td>
</tr>
</tbody>
</table>

\(^1\) Treatment means within a column followed by the same letter are not significantly different at 5% level.
Table 4. Effect of four modes of competition between red rice and two rice cultivars on top dry weight 40 days after emergence.\(^1\)

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Lemont with red rice</th>
<th>Mars with red rice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil and aerial partitions</td>
<td>3.66a</td>
<td>4.73b</td>
</tr>
<tr>
<td>Soil partition</td>
<td>3.09ab</td>
<td>6.27a</td>
</tr>
<tr>
<td>Aerial partition</td>
<td>2.60b</td>
<td>4.75b</td>
</tr>
<tr>
<td>No partitions</td>
<td>3.41ab</td>
<td>5.00ab</td>
</tr>
</tbody>
</table>

Treatment means within a column followed by the same letter are not significantly different at 5% level.

\(^1\) Treatment means within a column followed by the same letter are not significantly different at 5% level.
LITERATURE CITED


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Jairo Clavijo was born November 11, 1948, in Bogota, Colombia, the son of Eladio Clavijo and Sara Clavijo. Educated in parochial and public schools of Bogota, he received an Ingeniero Agronomo degree from Universidad Nacional de Colombia in December, 1970. He served as assistant instructor and assistant professor in Universidad Nacional de Colombia, Facultad de Agronomia, Bogota, from February 1971 until April, 1976. In 1978, he graduated with a Master of Science degree with specialization in Weed Science and Plant Physiology from Louisiana State University. He accepted the position of associate professor in Universidad Nacional de Colombia, Facultad de Agronomia, Bogota, remaining there until April 30, 1984. In May 1984, he was awarded a graduate research assistantship in the Plant Pathology and Crop Physiology Department of Louisiana State University to begin completion of the requirements for the Doctor of Philosophy degree with a major in Plant Health and a minor in Agronomy.

Mr. Clavijo was married to the former Elizabeth Perez of Bogota, Colombia, on September 28, 1972. They have two sons, Jose Luis and Juan Carlos.
Candidate: Jairo Clavijo

Major Field: Plant Health

Title of Dissertation: Effects of interaction between red rice and two rice cultivars on morphological, physiological and ecological characteristics

Approved:

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Major Professor and Chairman

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Dean of the Graduate School

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Date of Examination:

April 9, 1987