

AN ABSTRACT OF THE THESIS OF

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Title: An Evaluation of Weed Interference in Rice Grown on Hydromorphic
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Field, screenhouse, and laboratory experiments were conducted to study weed interference in rice grown on hydromorphic soils at the International Institute of Tropical Agriculture (IITA) at Ibadan, Nigeria.

Rice and weeds emerged at the same time, 1 week after planting. Weed dry weight was significantly reduced when the crop was kept weed-free for at least 4 weeks after emergence. Initial weeding for 2 weeks was not effective, because weeds reappeared and competed actively with rice plants. Season-long weed competition reduced rice grain yield by 73%.

Weed competition reduced the number of tillers and panicles of rice. The detrimental effect of early weed interference was not offset by keeping the crop weed-free later in the growing season. At 6 weeks after emergence, most of the weed species had reached flowering stage when rice was still producing tillers. Handweeding at 2 and 6 weeks was effective enough to reduce weed pressure. Rice seems to be most sensitive to weed interference during this period from the second to the sixth week.

AN EVALUATION OF WEED INTERFERENCE IN RICE GROWN ON
HYDROMORPHIC SOILS IN WEST AFRICA

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AN EVALUATION OF WEED INTERFERENCE IN RICE GROWN ON HYDROMORPHIC SOILS IN WEST AFRICA

Chapter I.

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Cereals are the world's most important food crops. Cereals provide three-quarters of the energy needs of humans and more than one half of their protein needs. Wheat and rice together provide 60% of the world's carbohydrate for human energy (Gallagher, 1984). Rice has become an increasingly important crop in many countries in tropical Africa. In 1985 paddy rice production in Africa was 9.5 million tons, of which 3.9 million tons (41%) were from West Africa (FAO, 1986).

In the last 15 years, drought has contributed to a reduction in the total land area for crop production in Africa. Rice is one of the crops that has been most affected. The unfavorable weather has complicated further the food deficit problem already resulting from low productivity, pests, and high human population pressure. Consequently, African countries import more rice than other countries of the world. African countries in 1984 imported 3.1 million tons of milled rice, which constitutes 27.2% of the world's imports of that commodity (FAO, 1987).

West African countries spend over 378 million dollars on rice importation. This expenditure is obviously a major drain on the scarce foreign exchange reserves. It is, therefore, important to increase rice production efforts in African countries. Rice is grown under widely diverse

hydrological conditions. Rice lands have been classified on the basis of natural water supply into pluvial, phreatic, and fluxial soils (Moormann and Veldkamp, 1978). Pluvial soils receive water from rainfall only. They are generally well-drained. Phreatic soils receive water from both rainfall and subterranean water supplies. Fluxial soils rely mainly on surface water. Rice ecologies in which fluxial soils occur include swamp, deep water, and mangrove. The pluvial and phreatic soils also are known as 'dryland' and 'hydromorphic' soils, respectively.

Hydromorphic soils are poorly drained, often water-logged, tropical soils that are high in organic matter. Such soils are often fertile when drained (IITA, 1980). These soils occur in the forest, forest-savanna, and savanna ecological zones of West Africa. They are found over a wide range of land forms such as inland depressions, river valleys, and flood plains.

Hydromorphic soils are among the untapped natural resources of West Africa. Water-logging associated with poor drainage, iron toxicity, and weed infestation are among the major constraints to agronomic use of these soils. Improved water management practices and introduction of iron-tolerant rice cultivars will contribute to rice production in hydromorphic soils. Both drainage and flood control are important. Although rice is the major annual food crop which thrives on land that is water-saturated or inundated during part or all of its growth cycle, its production in hydromorphic soils can be adversely affected by uncontrolled floodings (Moormann and Veldkamp, 1978). These workers recommend drainage of the land and interception of the interflow water by deep drainage ditches across the line of flow as a means of reducing damage to rice by uncontrolled flooding.

Reports from several countries indicate that weed problems in rice are more serious on hydromorphic soils than in paddy fields (Bertrand, 1973; De Datta, 1974; Akobundu and Fagade, 1978; Crauford and Lembela, 1978; Schwaar, 1983 ; Akobundu and Ahissou, 1983). Both dryland weeds and weeds adapted to water-logged conditions are problems on hydromorphic soils (Akobundu and Fagade, 1978). Weed growth in such an environment is favored by the presence of ample supply of water, while weed control is difficult. Herbicides that provide good weed control in paddy fields and dryland rice cultures do not persist long enough to provide satisfactory weed control in hydromorphic soils (IITA, 1976). Poor weed control in hydromorphic soils could be attributed to flooding which is not always predictable and occurs at varying times after planting. Without adequate flood control, both preemergence and postemergence herbicide applications are unreliable. Schwaar (1983) reported that successful application of postemergence herbicides to rice in many parts of West Africa was difficult and often impossible because flooding often occurs shortly after planting. While some progress has been made through breeding and use of improved crop husbandry practices to alleviate rice production constraints such as iron toxicity and inherent low productivity of rice, weed infestation in hydromorphic rice has remained a difficult problem for most rice growers, particularly smallholder farmers.

The objectives of this research were to:

1. determine if a critical period of weed competition with rice grown on hydromorphic soils exists.
2. evaluate the competitive ability of rice and selected weed species.

3. assess the effects of weed species on growth and development of rice.
4. understand the nature of weed interference in rice culture.

LITERATURE REVIEW

Crop-weed interactions

Organisms that exist within sufficient proximity often interact. In plant communities, interaction is used to refer to all mutual influences of one plant on another (Trenbath, 1976). This is true in a weed-crop association.

According to Silvertown (1982), plant interactions may be asymmetrical (affecting only one species) or symmetrical (affecting both species). The symmetry of an interaction between species obviously will affect the outcome of plant-plant association.

In an environment where individuals are small in size or far apart, interaction may not take place until they experience a conflict of interest, which can be, for example, a result of limitation in resources. When plant species are in association, the effects of their interactions can be positive, neutral, or negative. Burkholder (1952) described different types of plant interaction. These include mutualism, commensalism, competition, amensalism, and parasitism. Examples of positive interactions are commensalism and mutualism, while those of negative interaction are competition and amensalism. Crops are often selected for yield or harvest attributes rather than competitiveness and this selection is done in weed-free growth conditions. Although weeds may also be affected by neighboring plants, crop yields are in most cases reduced. However, weed growth also is often reduced by crop presence.

Interference: Allelopathy and Competition

Harper (1961) defined interference as 'any interaction that may occur among plant species in mixtures which causes a reduction in plastic growth or survival of one or both species'. The consideration of the term 'space' as embracing all resources, makes it possible to examine the outcome of interference in the context of proximity to neighboring individuals without actual determination of the kind or amount of resources for which the interaction occurs. Therefore, the factors that affect the outcome of interference between plants should not be limited to environmental resources.

Weeds may interfere with crops not only through competition but also through allelopathy. Trenbath and Harper (1973) suggested that lower crop yields in the presence of weeds may be due to competition for environmental resources, allelopathic effect, or presence of neighbors promoting disease incidence or lodging in the associated crop. Types of interference covered in my studies are competition and allelopathy. The latter is an example of amensalism, a type of interaction in which growth of one of the organism (plants) is depressed while the other is unaffected (Akobundu, 1987). Although effects of weed-crop interference have traditionally been attributed to competition for environmental resources, Barnes and Putnam (1986) pointed out that the ability of plant to chemically interfere also may be important.

Allelopathy

Allelopathy is any direct or indirect harmful effect of one plant on another through production of chemicals that escape into the environment

(Rice, 1974). The fact that extracts of a plant are inhibitory to other plants does not always indicate that the donor plant has allelopathic action against other plants (Rice, 1979). Rather, allelopathy occurs when a chemical released by a donor plant causes injury to another plant in the same habitat. An inhibitory effect can result from direct action of such chemicals or from an interaction between chemicals and soil microorganisms. The effect of an allelochemical may be inhibitory or stimulatory to neighboring plants depending on its concentration in the surrounding medium (Rice, 1979; Weston and Putnam, 1986; Barnes and Putnam, 1986). Toxic substances that inhibit growth of some species at some concentrations may stimulate growth of the same or different species at other (lower) concentrations. In addition to the living leaves and roots of a donor plant, the dead and decaying plant parts could be a source of allelochemicals.

Whether annual weed species have allelopathic effects on crops is debatable. Perennial weeds such as quackgrass (*Agropyron repens*), nutsedge (*Cyperus rotundus*) and johnsongrass (*Sorghum halepense*) often have been implicated as being allelopathic (Schrieber and Williams, 1967; Bhowmik and Doll, 1984). The amount of corn root growing in soil containing residues of giant foxtail (*Setaria faberii*), crabgrass (*Digitaria sanguinalis*), or yellow foxtail (*Setaria glauca*) were less than in soil without plant residues (Schreiber and Williams, 1967). Although this observation does not prove that toxins are present, it suggests this possibility.

In recent years annual weeds have shown allelopathic potential. When allelopathic potential of weed residues (shoot materials) was evaluated on corn and soybeans, common lambsquarters (*Chenopodium album*) extract reduced coleoptile growth of corn (Bhowmik and Doll,

1982). In greenhouse studies, they also found that residues of lambsquarters, redroot pigweed (*Amaranthus retroflexus*), and yellow foxtail had allelopathic activity on corn and soybeans.

Few studies clearly assess the effects of weed residues on growth inhibition and nutrient uptake in crops. Bhowmik and Doll (1984) reported that, regardless of nutrient level, all plant residues used except those of common ragweed inhibited corn height, leaf area, and total dry weight. Weed residues generally reduced N uptake in corn and soybeans. Growth inhibition caused by weed residues could be due to interference with growth processes in plants or other causes such as altered pH, nutrient availability or carbohydrate : nitrogen ratios.

Allelopathic influence of weeds upon crops include reduction in seed germination, root and shoot growth, stand density, yield, resistance to pathogens, nodulation, and nitrogen fixation (Rice, 1974). Plant growth is affected mainly through the effects of toxic chemicals on cell division, mineral uptake, and photosynthesis (Einhellig, 1986). Specific effects of allelopathy on plant growth has seldom been studied in the field, because of difficulties in separating effects of allelopathy from those of competition. Putnam (1978) reviewed extraction and bioassay techniques used for allelopathic studies. The most difficult process is the isolation and extraction of toxic substances from plant materials in the form they exert their effects in nature. Extraction using ground plant material in aqueous solvents are subject to criticism, since cell constituents may interfere with substances suspected to be toxic. In addition, problems arise when it is uncertain if an effective concentration of the chemicals can be released into the environment (Akobundu, 1987).

Several techniques have been proposed for the study of allelopathy. In addition to the methods for toxin isolation followed by simple

bioassay, a stair-step system has been proposed (Bell and Koeppel, 1972). In this system, donor plants and recipient plants are grown separately in pots filled with sand solution and alternated in a stair-step fashion so that any liberated chemical substance from the weed will leach down and come into contact with the roots of the crop.

Recently, questions have arisen concerning of allelopathy as the inhibitory effect from a living donor or the effect from dead plant materials. In case of the latter, any plant material could exert an inhibitory effect on neighboring plants. In this context, the suggestion by Akobundu (1987) that the term allelopathy be limited to the detrimental effects of chemical substances released by living plants into their environment, seems to minimize confusion especially on demonstration of allelopathic potential of given species. In plant extracts or litter there is a variety of organic compounds which may be in different in forms when they are naturally released through leachates, root extracts, or decomposition of litter.

Demonstration of allelopathic potential of selected weed species is not a major objective of my thesis work. However, since weed interference is being evaluated, I have made attempts to account for any chemical interaction, bearing in mind that the ability of weeds to interfere with the crop may not be wholly due to their competition for environmental resources.

Competition

Competition is another mechanism of plant interference and can be distinguished from allelopathy since it does not involve the release of allelochemicals. Grime (1977) defined competition as the tendency of neighboring plants to utilize the same quantum of light, ion of mineral nutrient, molecule of water, or volume of space. However, for competition

to occur, an environmental resource must be limiting. In other words, two plants do not compete with each other while environmental resources satisfy their needs.

Plants respond to density stress in different ways and the populations are regulated via density-dependent processes of plasticity and mortality. At low density, individual plants contribute their expected yield to the total yield per unit area (Harper, 1977). With increasing density, plants have the ability to alter their size, biomass, and number. At high densities, plants may respond to one another by altering their growth form, by allocating environmental resources to different parts, or by altering the impact on fecundity. This response to density has been referred to as plasticity (Radosevich and Holt, 1984). Each of these responses is an expression of competition. Silvertown (1982), noted that competition among plant species does not distinguish between plastic growth and mortality.

It must be remembered, however, that two types of competition (intraspecific and interspecific) can take place in mixed plant populations. This separation is important to understand interactions that occur among plants in associations. Competition among individuals of the same species is known as intraspecific competition (Antonovics and Levin, 1980; Radosevich and Holt, 1984). Negative interaction among plants of different species is interspecific competition.

The competitive ability of plants is determined by the space a species is able to occupy at the beginning of the growing season, the relative rate at which a plant can expand into unoccupied space, and the access of the plants to factors limiting growth (Spitters and van den Bergh 1982). Competitive advantage of some species is largely associated with rapid emergence and rapid root and shoot growth during the early stages.

Black *et al.*, (1969) suggest that competitive ability depends on the net capacity of a plant to assimilate carbon dioxide and use the photosynthates to extend its foliage, or increase its size. For example at high temperatures and light intensity, plants which have the C₄ cycle should have a photosynthetic advantage over plants that do not. The outcome of interference also is influenced by factors such as crop density and onset and duration of interactions among plants.

In a crop-weed association, density of both weeds and crop have an impact on the resulting interactions. At low total density, individual plants may not share the same space, consequently, interference does not occur. Studies on effects of weed density on crop yield show little yield reduction at low weed densities (Smith, 1968; Zimdahl, 1980; Bhan, 1983). As weed density increases, the proximity of neighboring plants increases and competition ultimately occurs. Thereafter, individual plants react to the presence of each other and the abundance of space or environmental resources. Antonovics and Levin (1980) have demonstrated that density-dependent processes affect natural plant populations. They referred to the 'ecologically effective distance' as the interplant distance beyond which effects of density are absent. Consequently, the space each plant preempts is proportional to its size. At high densities, there is an overlapping of the area occupied by individual plant species and resources are more likely to become limiting.

There is an optimum weed density for a given level of resources beyond which significant mortality occurs. This phenomenon is termed selfthinning (Antonovics and Levin, 1980). Radosevich (1987) noted that increasing the amount of a limited resource such as water or fertility when plant density is already high usually enhances mortality. This form of mortality is frequently a consequence of increased population density

and differences in sizes of individuals (Sagar and Harper, 1961). One hypothesis for this phenomenon is that as density increases and resources become limiting, bigger plants grow bigger and suppress smaller plants.

In plant competition studies, influences of proportion of each species in a mixed community often have been confounded with influences of total plant density. Each species will respond mainly to interspecific interactions. These relationships are influenced by the increase in number of any component of the mixture (Radosevich and Holt, 1984). Such increase in number would lead to a more intense intraspecific competition.

Growth and development of cereals and other crops is sensitive to competition from weeds. Many studies on weed competition with rice have been reported in the literature (Boerema, 1963; Smith, 1968 and 1984; Swain, 1973; Swain *et al.*, 1975; Moody, 1978; Dominicata and Alcala, 1983; Utomo, 1981; Singh and Ram, 1984).

Rice-weed competition studies have focused on effects of water (Okafor and De Datta, 1976; Cruz *et al.*, 1983; Munger *et al.*, 1987), mineral nutrients (Pande and Bhan, 1966; Kleinig and Noble, 1968; De Datta *et al.*, 1969; Sahai and Bhan, 1984;), and light (Okafor and De Datta, 1976; Donald, 1958). Sahai and Bhan (1984) found that weeds removed high quantities of nitrogen up to 60 days after seeding, and barnyardgrass (*E. colona*) was the most competitive weed species. The degree and pattern of damage to rice plants caused by weed competition depends also on the weed species. The onset and duration of competition is also a determining factor for the outcome of crop-weed interactions. Barnyardgrass, one of the most common weeds that infests rice, has been used for competition studies in many parts of the world. Noda *et al.*, (1969) reported that high densities of barnyardgrass increased rice height,

significantly reduced tillering and panicle number, and delayed heading. In later studies, Noda (1973) observed that barnyardgrass at densities of more than 80 plants per m² lowered the assimilatory activity of rice. The fact that rice has a water requirement nearly twice that of most other tropical grasses (Black *et al.*, 1969) may explain the adverse effect of barnyardgrass on the crop. Smith (1968) reported that rice and barnyardgrass growing together under irrigated conditions competed primarily for nutrients because the two species produced overlapping fibrous root systems. The yield of irrigated rice was reduced by 82% from barnyardgrass competition at a density of 100 weed plants per unit area (Andrade, 1983).

Competition studies have been performed with weeds other than barnyardgrass. At the International Rice Research Institute (IRRI, 1983) crop failure was reported when irrigated rice was grown under season-long competition from *Scirpus maritimus*. Panicle weight of the crop was more affected than panicle number. When *Cyperus difformis* grew with rice, Swain *et al.*, (1975) found that the number of panicles was affected the most. They also noted that weed removal prior to tillering led to significantly higher grain yields than when weeds were removed late. The number of rice tillers was positively correlated with the number of rice panicles. On the other hand, Smith (1984) did not observe any significant reduction in stand of drilled paddy rice due to competition from dayflower (*Commelina diffusa*) for up to 80 days after seeding.

Critical period of weed competition

In a crop-weed association, delayed emergence of one species may markedly influence its contribution to the total output of the interaction. Determination of the of the period during which crops are more sensitive to

weed competition is necessary for development of integrated weed management programs. This information is useful in formulating guidelines for herbicide use and in determining if and when other control measures are necessary to minimize yield reduction due to weed competition. Dawson (1970), Schreiber (1982), and Lolas (1986) pointed out the importance of determining critical periods of competition when setting up weed management programs. The knowledge of these periods guides the farmer in deciding when weeding should be done or how long the crop can tolerate weed competition. It is known that a period exists during which most crops can tolerate competition without yield reductions. This is usually when crop and weed plants are small. The optimum period for weed control for a given crop is determined on the basis of the critical period when that crop is sensitive to weed competition (Spitters and van den Bergh, 1982).

The duration of weed interference affects competitive relationships of weeds and crops. Weed competition in direct-seeded or transplanted rice during the early growth stages of rice reduced grain yields more severely than when competition occurred after rice plants became well developed. According to Noda (1973), barnyardgrass competition during early crop growth stages reduced the number of rice panicles, while later competition reduced grain weight. Singh and Ram (1984) concluded that the first 45 days after sowing rice were most important for weed removal in order to obtain higher yields of direct-seeded rice. Dominicata and Alcala (1983) reported that the critical period of weed competition for transplanted irrigated rice was from 2 to 6 weeks after transplanting. The critical period of weed competition is affected by differences in environmental conditions, weed species composition, and plant density and size.

Plants vary in their plasticity and interactions with the environment. Studies on critical periods of competition do not, therefore, provide enough insight for determining the level of weed control necessary to achieve biologically or economically optimal crop production. The determination of critical period of weed competition in terms of time period does not allow adjustment for the different environmental factors which may affect crop and weed growth. Therefore, reference to the growth stage, physiological, and morphological states of the crop are important in understanding competition and determining critical periods of weed control. The critical periods of competition may involve complex interactions as well as different mechanisms and phenomena that occur in a discontinuous manner.

Effects of weed competition on crop yield

Many studies on the effect of weed infestation on field crops show that weed competition reduces crop yield (Smith, 1968; Utomo, 1981; Andrade, 1983; Bhan, 1983; Tisdell *et al.*, 1984). It is now evident that merely showing that weeds reduce crop yield is not enough. Many researchers have advocated additional information such as time of weed seedling emergence in relation to competition, duration of weed-crop association, effects of weed species and density on crops, effects of crops on weeds, impact of environmental factors, etc (Dawson, 1970; IRRI, 1983; Dominicata and Alcala, 1983).

Bowden and Friesen (1967) studied the effect of wild oat density and stage of growth at the time of weed removal on yield of both spring sown wheat and flax. Their studies showed that wild oat significantly reduced yield of wheat and flax at densities of 48 plants m^{-2} and 12 plants m^{-2} , respectively, and that competition with the crop started before wild oat

reached the 1-2 leaf stage of growth. Dawson (1970) studied the time and duration of weed infestation in relation to weed-crop competition and concluded that there was a physiological similarity between weeds and crop with respect to their needs for growth factors. It should, however, be recognized that plant species differ in their requirements for levels of environmental resources. The stages of crop growth during which competition with weeds occurs is important (Dawson, 1964; Wilson and Cole, 1966).

The extent of crop loss caused by weeds depends on several factors that include species of weeds present, density of weeds and crop, duration of weed-crop association, and growth and distribution of weeds (Hill and Santelmann, 1969; Noda, 1973; Williams *et al.*, 1984; Chubb and Friesen, 1985). Since weeds vary in their competitive ability with crops, the differences between species and also within species in different competitive situations should be known in order to determine when substantial crop losses are likely to occur (Wells, 1979). Competition studies have been carried out with different crops grown in association with different weed species. Buchanan and Burns (1970) conducted a series of experiments to study the period of weed-free maintenance after cotton emergence and found that the crop requires a weed-free period of approximately 8 weeks to produce maximum yields in Alabama. If herbicides are used for initial weed control, the herbicide must have sufficient residual effects for the duration of this critical period.

Zimdahl (1980) reviewed several works demonstrating the detrimental effects of weeds on various crops. These studies describe the extent of yield or economic loss that occurs at various weed densities and under different conditions. Smith (1968) found that barnyardgrass competition with dry-seeded rice reduced grain yields from 8 to 79%

when competition began at crop emergence and lasted for periods ranging from 15 days to maturity. Andrade (1983) examined the effects of barnyardgrass density on yield of irrigated rice and found that grain yield decreased by 16% with 5 plants m^{-2} and by up to 80% with 80-100 plants m^{-2} . The effect of weed density was significantly influenced by nitrogen levels (Kleinig and Noble, 1968). A low population of weed seedlings can become a serious problem in rice under high soil fertility conditions.

Type of rice cultivars also affects weed competition. De Datta (1972), Smith (1974; 1984), and Moody (1978) showed that rice cultivars grown in paddy fields differ in their ability to compete with weed. Effects of cultivar differences in relation to weed competition have also been reported under hydromorphic conditions (Akobundu and Ahissou, 1985). In the latter study, plots with a profusely tillering cultivar, Adny-11, had a significantly lower weed weight than plots with cultivars that tiller moderately.

Methods for studying weed competition

Different methods have been used to evaluate weed-crop interactions. These are additive, substitutive, systematic, and neighborhood approaches.

Additive method

The additive method was commonly used in earlier studies of interference. The additive method of competition study involves growing weeds at varying densities in association with a constant population of a crop plant. This experimental approach is widely used because of its relevance to actual field situations, where one or more weed species infest

an area already occupied by a crop. It has also an advantage because it permits the assessment of effects of weeds on yield and cost to the farmer under current management constraints (Dekker *et al.*, 1983).

In spite of its practicality, this approach has received considerable criticism because of its failure to control adequately the interferences associated with proximity factors especially density and proportion, on plant responses (yield). In the additive approach, the total density of plants varies and the proportion among species also changes simultaneously with density. Thus, two of the major components of competition (density and proportion) vary, making it difficult to interpret the relative effect of either factor. This complication has been demonstrated by numerous workers (Harper, 1977; Zimdahl, 1980; Carlson and Hill, 1985). To reduce the impact of two simultaneously changing variables, Carlson and Hill (1985), studying wild oat competition with spring wheat, expressed the response of wheat (yield) as a function of the ratio of wild oat density to total stand density.

Substitutive method

The substitutive or replacement series design (de Wit, 1960) is commonly used to study interactions between component species in a mixture. In this approach, a range of mixtures is generated by starting with a monoculture of species A, and then progressively replacing plants of species A with those of species B until a monoculture of species B is obtained. This type of design requires that all stands have the same density and that the two species occur in varying proportions. Each species is grown alone to assess intraspecific competition. The outcome of competition can be represented in different models. From the resulting graphs it is possible to determine whether competition has occurred and if

so, which of the species is the most successful components of the mixture. The relative yield total (RYT) has been used for comparisons between mixtures and monocultures (de Wit and van den Bergh, 1965) while the regression analysis approach has been used to examine the density dependent effects of the associated species (Hill, 1973). Utomo (1981) used the space occupation and replacement series concept developed from de Wit's (1960) model to describe the complex of environmental factors that affect plant growth and interaction between weed species and upland rice. He found that maximum yield was obtained when the available space is completely occupied by the population of the crop plants. To determine the competition effects between plants, therefore, environmental factors contributing to the growth of plants should be considered.

Connolly (1986) evaluated different indices proposed for analysis and interpretation of results obtained from replacement series experiments. He indicated that the assessment of species aggressiveness is influenced by the replacement lines selected, and indices, generally, varied significantly. The relative yield total (RYT) was the most stable of all indices tested. Difficulties associated with the replacement series approach also include the confounding effects of intra- and interspecific competition (Harper, 1977; Connolly, 1986; Radosevich, 1986), because, in most of the studies, the total density is held constant and this prevents the assessment of the density dependence of RYT. For better interpretation of data obtained from substitutive or replacement series experiments, it is necessary to have a range of total densities of mixtures and monocultures of each species. In many of these studies, yield is frequently the only parameter assessed (Jolliffe *et al.*, 1984). However, the basis of yield variations in monocultures and mixtures could be better understood if

observations on other plant characteristics such as leaf area and dry matter partitioning are made. When species of different individual sizes are involved in mixtures and the yield measured in terms of biomass other than seed production, the use of indices such as relative crowding coefficient, aggressivity, or competitive ratios, tends to favor the larger species (Connolly, 1986).

Interpretation of data obtained from replacement series is difficult when species of different strategies or growth forms are involved. In this case, Radosevich (1987) suggested that proportions expressed as ratios of biomass may be more appropriate than ratios based on plant density.

Systematic method

The concept of systematic design was developed by Nelder (1962) for spacing studies involving single species. This design is important for competition studies focusing on proximity factors (density, proportion, and spatial arrangement). It is useful for competition studies in row crops such as soybean, corn, cassava, or vegetables. The advantage of this design is that it can be used to provide a wide range of plant densities without changing the pattern of arrangement (Bleasdale, 1961). This type of arrangement can account for spatial relationship among plants and it is also possible to consider density and proportion of the species under study. This technique is widely used in studies on effects of intraspecific competition on crop yields. Spitters (1983) has criticized this design, pointing out that plant arrangements in this design are not consistent with practical weed situations, and that the influence of total density is not adequately addressed.

Spitters (1983) introduced another systematic method known as the addition series. In the addition series approach to competition studies, the

densities of the two species under study vary in two directions, generating a wide range of species proportions. The response of each species to density and proportion of the components of the mixtures is influenced by intra- and interspecific competition. These competition effects can be estimated with the addition series experiments. The model suggested by Spitters (1983), was derived from the yield-density models originally developed by Shinosaki and Kira (1956), Willey and Heath (1969), and Watkinson (1980). It is a simple model to quantify the competition effect and estimate the degree of intraspecific and interspecific competition.

This approach suggested by Spitters (1983) uses the reciprocal yield law to describe plant interactions. This law can be expressed by the following equation:

$$1/W = A + BN \quad (1)$$

where: $1/W$ is the reciprocal of individual plant weight,

A is a constant equal to the reciprocal of the theoretical maximum plant size,

B is the slope of the line reflecting the relationship between individual plant weight (W) and density (N).

The equation predicts that individual plant weight, size or yield decreases as density increases. According to Radosevich (1987), this principle is important in understanding interactions between neighboring plants. With the assumption that the effects from intraspecific and interspecific competition are additive, Spitters (1983) suggests that it can be expanded to a two- or multispecies reciprocal yield equation:

$$1/W_1 = A_1 + B_{1.1}N_1 + B_{1.2}N_2 \quad (2)$$

where: $B_{1.1}$ and $B_{1.2}$ are regression coefficients which quantify the effects of intra- and interspecific competition, respectively. This equation also can be used to predict the competitive ability of one species, based on the total and relative density of all other species in the mixture (Radosevich 1987). This model does not account for spatial arrangement. Radosevich (1987) believes that there may be valid statistical arguments for more randomization, since the treatments are arranged according to direction or orientation.

Spitters (1983) defined the relative competition ability of each species as the ratio of regression coefficients. The relative competitive ability of species 1 in association with species 2 is defined by the ratio $B_{1.1}/B_{1.2}$, and intraspecific and interspecific competitive effects are quantified by these coefficients, $B_{1.1}$ and $B_{1.2}$, respectively.

Neighborhood method

Most of the previously discussed designs used density to measure the outcome of competitive relationships. Weiner (1982) pointed out that, while density has been a basis for description of plant populations, plasticity and spatial arrangement limit its use in describing and predicting the behavior of plant populations. He proposed the use of a neighborhood approach for describing the behavior of individual plants as well as those of plant populations. For example, seed production of individual annual plants within a population is a function of the number of individuals within each of several concentric neighborhoods. When several plant species share the available space, seed production of

individual plants can be ultimately affected by the presence of neighbors.

Mack and Harper (1977) reported that the seedling growth of individual grasses was a function of the biological space available to each of the individual seedlings. This biological space was defined not only by the position but also by the stage of growth of neighbors. However, different types of neighbor effect might be achieved by a variety of character combinations in response to their associated species and environments (Sano *et al.*, 1984). The increased proximity of neighbors may lead to a lower growth rate and dry matter production of an individual plant. Weiner (1982) used a neighborhood model to show that the effect of increasing competition was to reduce seed production in a hyperbolic fashion, and that the contribution of each individual to this effect was inversely proportional to the square of its distance from the test individual.

The importance of spatial arrangement in interference studies has been reported by several workers (Fisher and Miles, 1973; Radosevich and Holt, 1984). Fisher and Miles (1973) developed several theoretical models for interference between crop plants arranged at points of a rectangular lattice and randomly located weeds. Their assumption regarding interspecific interactions is that a plant grows from emergence until it meets another plant.

Ultimately, each plant establishes its own zone of exploitation and the field is occupied by many non-overlapping weed and crop domains. Goldberg and Weiner (1983) described the effect of neighboring plants on a target species using the slope of a regression model relating the performance of target individuals with the amount of neighbors. The major advantage of their design is that it measures competition on the basis of individual plant biomass. Different measures of amount of neighbors can suggest the mechanisms of competition. The general theory of plant

growth analysis can provide information which may help explain plant responses to the environment, competition relationship between different species, and the allocation and partitioning of dry matter.

Analysis of plant growth

Observations of plant characteristics (e.g. leaf area and dry matter partitioning) are important factors to explain the yield variations in monocultures and mixtures (Jolliffe *et al.*, 1984). Growth analysis experiments satisfactorily complement field studies where the interactions among species are not readily detectable. The technique of mathematical growth analysis provides a convenient means of examining the process of total dry matter production and leaf area expansion that are important in determining a plant's vegetative growth and potential competitiveness under a variety of environmental conditions (Patterson, 1982). The relative growth rate has been proposed as a means of integrating physiological attributes of a species (Evans, 1972; Grime and Hunt, 1975). Roush and Radosovich (1985) indicated that integrative growth rates (such as relative growth rate) and growth responses that are partitioned into more tightly defined physiological and morphological parameters could prove valuable in characterizing aggressiveness among weed species.

As Ralph (1976) has proposed, analysis of growth data to estimate growth rates is always desirable. However, he believes that the estimation of growth rates often presents some problems because while growth is continuous, measurements are, for practical reasons, made only at intervals and errors arising from the measurement as a result of imperfect control of growing conditions or from sampling procedures are always present. According to Grime and Hunt (1975), the relative growth rate

exerts a major influence upon dry matter production. In the studies of Gilmour (1985), a pattern emerged which indicated that dry matter produced during vegetative growth could be used as a prediction of final grain yield of rice.

Potter and Jones (1977) suggested that partitioning of photosynthate into new leaf area is an important component of growth. A great portion of the dry weight of higher plants is derived from CO₂ assimilated through photosynthesis. In an earlier competition study (Welbank, 1961), the use of dry weight and leaf area provided evidence of the factors involved in root competition between *Impatiens parviflora* and *Agropyron repens*. Simultaneous growth analysis under controlled conditions is a useful tool in assessing the competitive ability of each species when grown in mixtures.

Chapter II.

WEED INTERFERENCE WITH RICE

INTRODUCTION

Weeds interfere with crops in three ways: through competitive interference, allelopathy (chemical interference), or directly through changes in physical or biological environment that affect plant growth. Although my thesis research dealt with the first two, which are the direct causes of interference, emphasis will be on competition.

The wide range of dryland and wetland weed species that interfere with crops in hydromorphic soils makes weed control in rice more difficult than in upland or lowland rice. The outcome of weed competition depends on factors such as duration and onset of crop-weed association, density, proportion, and architecture of weeds and crop, and the competitive ability of specific weeds competing with the crop.

The other component of interference is allelopathy, which involves inhibitory effects of chemicals released by a donor plant. Fuerst and Putnam (1983) pointed out that few studies, if any, have definitively separated the components of weed interference because of the complexity of this phenomenon. Nevertheless, attempts have been made in this thesis research to investigate the possible involvement of competition and chemical interference in rice-weeds association on hydromorphic soils.

Specific objectives are to:

1. determine the critical period of weed interference.
2. assess the effects of weed density on rice growth.
3. evaluate the allelopathic potential of selected weed species.

MATERIALS AND METHODS

Field and screenhouse experiments were conducted from June 1986 to November 1987 at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria (7°29'N, 3°45'E), a location with subhumid tropical climate. Fields were irrigated whenever necessary during the dry season to supplement residual soil moisture in the hydromorphic soils. Weed seeds used for these studies were collected periodically from plants occurring on hydromorphic soils at IITA.

Land preparation was accomplished by rotovating the field twice before seeding rice. In each of the field experiments, a compound fertilizer (15-15-15) was applied at the rate of 30 kg ha⁻¹ each of N, P and K at rice planting. Additional nitrogen was applied as urea at 4 and 8 weeks (30 kg N ha⁻¹) each time after sowing rice.

All the screenhouse experiments were conducted using plastic pots (perforated at the base) filled with sieved greenhouse soil. Full strength Hoagland's nutrient solution (Hoagland and Arnon, 1950) was provided as needed. Pots were kept moist throughout the experiment by sub-irrigation. Specific details of each experiment follow.

Experiment 2.1. Critical period of weed interference.

Two experiments were conducted to determine the critical period for weed control in rice (*Oryza sativa* L.). The first experiment was established during the 1986 rainy season. The field had been in a short-duration fallow prior to the experiment. The field was first sprayed with glyphosate (N-phosphonomethyl glycine) at the rate of 2.8 kg ha⁻¹ to suppress perennial weeds. Tillage followed 3 weeks after spraying.

Rice seeds (var. ITA 306) were drilled by hand at the rate of 50 kg ha⁻¹ with 25cm spacing between rows. Two weeks after emergence rice seedlings were thinned to maintain approximately 20 cm spacing within rows. Two sets of weeding treatments were used (Dawson, 1970):

- a) Maintaining weed-free periods for 0, 2, 4, 6, or 8 weeks after rice emergence (WAE), followed by not weeding each of these treatments until harvest.
- b) Allowing natural weed population to grow for 0, 2, 4, 6, or 8 WAE followed by keeping the plots weed-free until harvest.

Two additional hand weeding treatments included in this study were weeding twice 2 and 6 WAE and at 4 and 8 WAE. Weeding was done by frequent hand pullings.

The experiment was conducted as a randomized complete block design with four replications. Plot size was 3 by 5 m. Rice in these plots was sprayed two times at 15-day intervals with benomyl [methyl-(butylcarbamoyl)-2-benzimidazole carbamate] at 1.0 kg a.i. ha⁻¹ to control rice blast. The experiment was repeated in the dry season of 1987 (January-April) on another hydromorphic soil. A few modifications to the 1986 experiment included replacing the ITA 306 rice variety with ITA 222 which is blast tolerant. The two hand weeding treatments were substituted with keeping one plot weed-free for 1 WAE, and keeping another plot unweeded for 1 WAE. This field had only a few perennial weeds present at the time of land preparation and was not sprayed with a preplant herbicide.

Data collection and analyses.

Time of emergence and growth stages of the crop and weeds were recorded at the beginning of the growing season. Rice plant height, tiller

number, and panicle number were recorded at harvest. Mature rice was hand harvested from a 2 by 3 m center quadrat in each plot and the grain was threshed for yield determination based on grain weight adjusted to 14% moisture.

Weeds were counted and dry weight determined 10 weeks after rice emergence (WAE) and at crop harvest. Data were obtained from two 25 by 50 cm quadrats per plot taken from an area outside that from which yield data were to be collected. The above-ground portion of weeds within the same quadrats, were clipped, oven dried at 80°C for 48 h, separated by species, and weighed for dry weight determination.

Analysis of variance was conducted on the different parameters measured on each evaluation date. Mean separation was performed where applicable using Duncan's Multiple Range Test (DMRT) at 5% probability level. The two sets of treatments (weed-free maintenance and unweeded periods) were subjected separately to regression analysis.

Experiment 2.2. Growth analysis.

Rice, jungle rice [*Echinochloa colona* (Linn.) Link], and wild poinsettia (*Euphorbia heterophylla* Linn.) were grown in pots in the screenhouse to study their growth and development. Six rice seeds (var. ITA 222) and 10 seeds of each weed species were planted in plastic pots which had a diameter of 17.8 cm. Five days after emergence, the plants were thinned to 1 plant of each species per pot. The pots were replicated 20 times and arranged in a randomized complete block design.

Data collection and analyses.

Destructive samples were taken four times from each of the four

replicates at 2, 4, 6, and 8 weeks after emergence (WAE). The fifth set of four replicates was maintained for the last harvest at weed maturity. During growth measurements, plants were ranked from smallest to largest.

Plant height was measured at each sampling date. The number of tillers and branches was also recorded. Shoots were removed at soil level and washed. Leaf area per plant was determined at each harvest using a Licor leaf area meter, model LI-3000. Dry weight data were collected as described in the previous experiment. The biomass of roots was measured only during the first two samplings, because separation of roots from the soil was difficult in later samplings. Soil was washed from the roots of each plant before separating shoots from roots.

Growth analysis formulas were used to derive parameters such as absolute growth (G) for a given time period, relative growth rate (RGR), leaf area ratio (LAR), net assimilation rate (NAR), and root/shoot ratio (R/S). These parameters were calculated with the instantaneous values from growth analysis formulas of Radford (1967) and Patterson (1982). Absolute growth was expressed as weight (W) increase over time (t) (Radford, 1967):

$$G = (W_2 - W_1) / (t_2 - t_1) \quad (3)$$

The relative growth rate was calculated from the natural log of weight increase over time using the following equation (Patterson, 1982):

$$RGR = (\ln W_2 - \ln W_1) / (t_2 - t_1) \quad (4)$$

where W_1 , W_2 are the dry weight at beginning and at end of harvest

interval; t_1, t_2 are time of harvest (days). This equation determines the weight increase relative to the size already attained (W_1). The leaf area ratio (LAR) which is a component of RGR was calculated on the basis of the leaf area per unit dry matter produced. The net assimilation rate (NAR) characterizing the efficiency of production of new material per unit leaf area that is present, was calculated from the following formula (Patterson, 1982):

$$NAR = (W_2 - W_1 / T_2 - T_1) (\ln A_2 - \ln A_1 / A_2 - A_1) \quad (5)$$

where A_1, A_2 are leaf area at beginning and end of harvest interval. Root/shoot ratio was calculated as the ratio of below-ground to above-ground biomass produced. Dry matter production for each species was determined from the above-ground portion of the plants at final harvest. Analysis of variance of the growth parameters was conducted at each sampling date. Means were separated by DMRT, at 5% probability level.

Experiment 2.3. Competitive influence of monospecific weed density on rice.

This experiment was conducted to assess the influence of two weed species, jungle rice and wild poinsettia, on rice (var. ITA 306) using an additive approach (Harper, 1977). The experiment was established outdoors. About 10 seeds of each plant species were planted in 25.4 cm diameter plastic pots. Seedlings were thinned to desired densities (Figure 2.1) at one week after emergence. Weed densities were two, four, and six plants per pot, which are equivalent to 40, 80, and 120 plants m^{-2} ,

respectively, under field conditions. The treatments consisted of an individual rice plant grown alone or in association with two, four, or six plants of jungle rice or wild pinsettia (Figure 2.1). The experimental design was a randomized complete block design with 10 replications.

Data collection and analyses.

Destructive sampling was done at the tillering stage, 6 weeks after emergence (WAE), with one set of five replicates. Number of tillers, leaf area, and dry weight of shoots were determined. The plants were cut at soil level and oven dried as stated earlier. Another set of five replicates was left to grow until 12 WAE. Dry weight of each species was determined. Analysis of variance was performed with two binary associations (rice-jungle rice) and (rice-wild poinsettia), and dry weight of individual rice plants were related to density of each weed species using regression analysis.

Experiment 2.4. Allelopathic potential of selected weed species.

An experiment was conducted in a screenhouse to assess allelopathic potential of selected weed species that grew with rice on hydromorphic soils using 11.4 cm diameter plastic pots. Top soil used for this study was collected to a depth of 15 cm from each of the sites on which uniform stands of the following weeds grew in monoculture: *Echinochloa colona*, *Euphorbia heterophylla*, *Cyperus difformis* and *Fimbritylis littoralis*. Soils from each weed site were used to fill four plastic pots (diameter 11.4 cm), one for each soil collection. Another set of four pots were filled with greenhouse soil (top soil taken from a tropical forest) and used as a control treatment. Fifteen rice seeds (var.ITA 222) were planted in each pot. There

were five treatments (including the control) in this study and these were arranged in a randomized complete block design with four replications. Height of all rice seedlings in a pot was measured at 3 WAE before seedlings were thinned to five plants of uniform stage of growth.

In a related study, concentrations of leaf aqueous extracts of the same species were also tested for effect on germination, shoot and radicle length of rice and cowpea (a species sensitive to growth inhibitors) grown in petri dishes. The dried materials (20g of each weed species) were soaked in 200 ml distilled water for 2 hrs and filtered using Whatman No.1 filter paper to obtain an aqueous extract concentration that is described here as full strength. Different concentrations of the various weed leaf extracts were diluted to obtain additional concentrations of 1/20 and 1/40 by adding 10-ml extracts to 200 and 400ml of distilled water, respectively. Seeds/test solutions (8 ml/petri dish) were incubated in a germinator chamber with a light/dark (12/12 hrs) cycle and temperature regime (25°C) optimum for germination. Distilled water was used for moistening seeds of control treatments.

Data collection and analyses.

Rice germination was monitored at 3, 5, and 7 days after sowing (DAS) in the screenhouse. Plant height measurements (five plants per pot) were done at 4 WAP and harvested to determine the fresh weight of shoots and the data were analysed statistically. Percent germination, and radicle and shoot length of rice and cowpea were recorded at 3 days and 1 WAP and data obtained were analysed statistically.

RESULTS AND DISCUSSION

Experiment 2.1. Critical period of weed interference

Rice and weeds emerged at about the same time, 1 week after planting (WAP). Two weeks after emergence (WAE), weeds were at 4-6 leaf stage, while rice had 6 leaves. The major weed species in this field were *Fimbristylis littoralis* Gaudet, *Cyperus iria* Linn., *C. difformis* Linn., *Echinochloa colona* (Linn.) Link., *Leptochloa caerulescens* Steud., *Eleusine indica* Gaertn., *Ageratum conyzoides* Linn., and *Pentodon pentandrus* (Schum & Thonn.) Vatke. Although recently developed lands are said to be relatively free of jungle rice (Swain, 1973), this plant occurred frequently on the experimental site. However, its frequency was less than that of *L. caerulescens* and sedges, especially at harvest, mainly because of its shorter life cycle. The observation on frequency of each species was based on the number of individuals of each weed species in the different plots, before the weeds were pooled together for total weed density and dry weight. Tillering started in jungle rice at 2 WAE and at 3 WAE for rice.

Weed growth was significantly influenced by the treatments (Table 2.1a). At 10 WAE, weed growth was significantly reduced in plots kept weed-free for at least 4 weeks as compared to weed growth in unweeded plots. Extending weed-free periods beyond the 4th week did not reduced weed growth significantly. Weed density and dry weight of the 2-week growth period (from the 8th to the 10th WAE) were similar to when weeds were allowed to grow for 6 weeks (from the 4th to the 10th WAE). At harvest, weed growth was reduced only in plots kept weed-free for 6 WAE. This suggests that when the weed-free period was shorter, weeds

reappeared and grew actively until harvest. This is why initial weeding for 2 weeks was not effective in preventing yield loss since weed competition begins early enough to damage the crop. The frequent soil disturbance during weeding operations may have favored germination of more weed seeds that were allowed to germinate and the plants to grow for a longer period.

Weed species in the dry season experiment were similar to those in the previous trial, except that *Ludwigia octovalvis* (Jacq.) P. Raven was present instead of *Leptochloa caerulescens*. *Fimbristylis littoralis* and rice plants emerged at the same time (4 days after planting). At 6 WAE, most weed species had reached flowering stage, while rice had produced 4 to 6 tillers. In this experiment weed population was much higher (Table 2.2a) than in the previous experiment (Table 2.1a), which did not receive any rainfall from planting to early tillering stage. The dry season experiment was irrigated and therefore had adequate moisture for good crop establishment. At 6 WAE, weed pressure was lowest in plots kept weed-free until the 4th week. As in the previous trial, extending the weed-free period beyond the 6th WAE did not reduce the number, and dry weight of weeds.

Rice grain yield was significantly increased when rice was kept weed-free for the first 2 WAE in the wet season (Table 2.1b), and the first 6 weeks in the dry season (Table 2.2b). Despite the higher weed density and biomass, rice yields were much higher in the dry than in the wet season study. This is probably because a higher solar radiation occurs in the lowland tropics during the dry season than during the wet season. The negative role of low solar radiation on rice yield during the rainy season in West Africa has previously been reported by many workers (Posner, 1978;

Lawson, 1980; IITA, 1982). Late weeding, after the 6th WAE did not reduce significantly the detrimental effects of weeds on rice grain yield and yield components. This observation was probably because rice plants could not recover from the negative effect of early weed interference. Most of the weed species had reached the flowering stage (6 WAE) when rice was still tillering. There was a tendency for the rice plants to produce as many panicles as tillers in plots kept weed-free for different periods. Uncontrolled weed growth reduced rice grain yield by 72.5% in 1986 and 58.2% in 1987 (Tables 2.1b and 2.2b). Weeds significantly reduced tillering and number of panicles in rice. Keeping rice crop weed-free for 6 WAE was necessary to minimize weed-related grain yield loss and reduction in yield components. When rice was weeded at 2 and 6 WAE, grain yield was similar to yield from plots kept weed-free until harvest. These results suggest that most intensive weed growth occurred between the 4th and 6th weeks after crop emergence.

Regression analysis on rice grain yield, and weed density and biomass indicates that the rate of change in rice grain yield is better described by the equation with weed biomass as the independent variable (Figure 2.2). The linear relationship was described with a coefficient of determination of 0.77. There are two possible explanations to the low value (0.22) of this coefficient between yield and weed density. Either the assumption of linearity is incorrect or there are some factors other than density affecting grain yield. Several others (Hill and Santelmann, 1969; Noda, 1973; Chubb and Friesen, 1985) have pointed out that the extent of crop loss due to weeds depends on factors that include not only density but also species, duration of weed competition and growth, size, and distribution of weeds. Rice grain yields were related to the duration of weed

competition (Figure 2.3). The variations in grain yield were best described by a second and third degree polynomials for plots left unweeded and weed-free for a certain period of time, respectively. Weed-free for only 1 or 2 WAE was not sufficient enough to improve yields. To obtain high yields, it was necessary to remove the weeds from the 2nd to 6th WAE, thereafter, no yield increase was observed. Substantial yield reductions occurred when weeds were allowed to compete with rice during the first 4 weeks after crop emergence.

The detrimental effect of early weed presence is not offset by keeping the crop weed-free later in the season, especially if the weed-crop association, occurs when the crop is sensitive to weed competition. Weed removal later in the growing season does not benefit the crop. In both experiments, extending the period of weed removal beyond the 6th week did not increase significantly rice yields in this study. These results suggest an existence of a critical period (2-6 WAE) of weed interference with rice grown on hydromorphic soils which may vary with seasons and environmental conditions. It is during this period that rice plants produce majority of tillers that later leads to optimal crop productivity. Swain *et al.*, (1975) reported that rice yield reduction due to weeds was more pronounced when competition took place during the pre-tillering and tillering stages of its growth. Results of this study are consistent with these observations.

✕ Experiment 2.2. Growth Analysis

Both weed species emerged 3 to 5 days before rice. Wild poinsettia (*Euphorbia heterophylla*) emerged 3 days after planting, while jungle rice,

also called jungle rice (*Echinochloa colona*), emerged 2 days later. Rice plants were taller than the two weed species initially, but neither grass species was significantly taller than wild poinsettia for the first 2 WAE (Figure 2.4). Jungle rice and rice grew taller than wild poinsettia 4 WAE, suggesting that competition for light may not be critical in a rice/jungle rice association during this early growth period. From the 4th WAE the sharpest increase in plant height was observed with jungle rice and wild poinsettia. At 8 WAE, rice plants were significantly shorter than either of the weed species. Root/shoot ratios of the three plant species were not significantly different from one another. In a related experiment (Experiment 3.1), the root biomass of individual plants of rice and jungle rice were similarly greater than that of wild poinsettia (Figure 2.7). This observation suggests that, when these species are grown together, below-ground competition for water and nutrients could be more intensive in mixtures of rice and jungle rice than rice and wild poinsettia.

Jungle rice produced more tillers than rice when both were grown separately in pots under identical conditions. Although shoot length was the same in both jungle rice and wild poinsettia, the latter, because of its upright growth habit, had greater canopy development than jungle rice which has decumbent tillers. Consequently, jungle rice plants could influence rice growth if both are grown in close proximity.

The efficient use of environmental resources by rice plants at the beginning of the growing season is reflected in its high NAR (Table 2.3). At this period, rice plants required the least amount of leaf area to produce a unit of dry matter. This observation is supported by the negative correlation found between leafiness and competitiveness for four species in the Central Valley of California, a region of high temperature and light intensity

(Roush and Radosevich, 1985). The LAR of wild poinsettia was not significantly different from that of jungle rice. Variations in NAR values occurred only between the second and fourth weeks after emergence. Rice and jungle rice were the most efficient producers of new plant materials per unit leaf area. Significant differences in NAR were observed between the second and the fourth WAE. This period falls in the critical period of weed control noted in the previous experiment 2.1.

The increase in absolute growth was similar in both weed species (Figure 2.5). Their response curves were sigmoidal over an 8-week growth period while that of rice had not reached equilibrium at 8 WAE. Between the 2nd and 6th weeks, both weeds had a sharp increase in their absolute growth before leveling at 8 WAE. Rice grew fastest between the second and the fourth week, while jungle rice had an absolute growth (G) that was significantly greater than those of rice and wild poinsettia in the period between 4 and 6 WAE (Table 2.4). This indicates that both weeds grew rapidly at a period (4 to 6 WAE) when rice seedling growth was slow. Thus, each of the weed species could be more competitive with rice if the crop and weeds were associated at that stage of rice development. The two weed species apparently can utilize environmental resources before the period of rapid growth is reached by rice plants.

Experiment 2.3. Competitive influence of monospecific weed density on rice.

At a population as low as 2 weed plants/pot, jungle rice suppressed the growth of rice (Table 2.5). At 6 WAE and at harvest, jungle rice caused significant reductions in all parameters of rice growth. Under field conditions, this density of 2 plants per pot corresponds approximately

to 40 plants m^{-2} . At this density, competition from jungle rice can result in 73, 63, and 76% reduction of leaf area, rice tillers, and dry weight of individual plants, respectively (Table 2.5). At harvest, similar trends were observed but the effects were more pronounced. The tiller number and dry weight of rice were reduced by 73-84% and 54-87%, respectively. Increase in density of jungle rice from 2 to 6 plants per pot did not cause significant reduction in rice growth.

Rice was not significantly affected at 6 WAE by wild poinsettia at densities of 2, 4, and 6 plants/pot (Table 2.6). The leaf area, number of tillers, and dry weight of rice varied slightly with increased density of wild poinsettia as compared to the rice plant grown alone. The presence of wild poinsettia caused only 24-33% reductions in tiller number and 18-35% in dry weight at harvest. The weed-free rice produced more tillers and dry matter than with either weed species at any density.

These observations indicate that rice performance is influenced when grown in association with either weed species. Although competition from 2 plants of wild poinsettia caused significant reductions of the number of rice tillers (Table 2.6), the dry weight of rice was significantly affected only when its density was 6 plants m^{-2} . The effect of wild poinsettia was less pronounced than jungle rice (Figure 2.6). The rate of decrease in dry weight of individual rice plants was greater in the rice-barnyardgrass (-17.8, $R^2=.988$, $p=0.006$) than in rice-wild poinsettia association (-6.2, $R^2=.919$, $p=0.04$).

These results suggest that jungle rice may have subjected rice to greater below-ground competition than wild poinsettia which did not produce enough roots to compete with rice early in the growing season (Figure 2.7). However, this species could allocate resources for the

production of a canopy that could have affected rice growth later in the season.

The results support the observations under field conditions, where jungle rice showed greater competitiveness than wild poinsettia when associated with rice plants. Tiller number, leaf area, and dry weight of weeds were negatively correlated with the rice dry weight. The effect of the tiller number of jungle rice was the greatest ($r=-0.685$).

There was a highly negative correlation of tiller or branch number and dry weight of weeds with tillers and dry weight of rice. The number of tillers was most affected (86.7 and 64.0% for jungle rice and 50 and 64% for wild poinsettia). Because of its rapid growth, jungle rice had the ability to use available resources more efficiently and produced a large number of tillers, thus preventing rice from doing so.

In the rice-wild poinsettia association, competition took place at a later stage and because more resources (space, water, and nutrients) were available early, rice formed large number of tillers before wild poinsettia produced branches. The below-ground competition had taken place earliest in the rice-barnyardgrass association because both species have the ability to produce voluminous root system as compared to wild poinsettia.

There was an indication that jungle rice competition affected rice yield through the reduction of tiller production (Table 2.5). In the other experiments (Chapter III), jungle rice had started to produce tillers 2 weeks before rice. Wild poinsettia may have been affected by intraspecific competition. However, it is difficult to separate the confounded effects of intra- and interspecific competition in this experiment. Further increase in density of both weed species did not significantly affect rice growth (Tables

2.5 and 2.6). The confounded effects not only affects the outcome of competition, but also influences the interpretation of the results (Harper, 1977; Radosevich, 1987), especially if conclusions on the competitiveness of rice against each weed species are made. Nevertheless, there is an indication that increasing the density of jungle rice had a detrimental effect on rice growth at 6 WAE and at harvest. Wild poinsettia had a significant effect on rice only at harvest. Results from the growth analysis experiment suggest that jungle rice had a significantly greater absolute growth (Figure 2.5) and relative growth rate (Table 2.4) than rice during the period of 4 to 6 weeks after crop emergence. These data indicate that jungle rice should not be allowed to compete with rice from the seedling stage to tillering. Provided that water and nutrients are not limiting, rice overcame the effects of competition from wild poinsettia at densities as high as 40 plants m^{-2} .

Experiment 2.4. Allelopathic potential of selected weed species.

None of the weed species tested for allelopathic properties affected the germination of rice. The addition of nutrient solution may have excluded the effects that could have resulted from competition for the essential element and water, although hydromorphic soils are fertile by nature. Under such conditions, the concentration of inhibitory compounds may not be high enough to affect germination of rice seeds. Rice (1984) pointed out that drought and nutrient deficiency had a synergistic effect on the concentration of chlorogenic and isochlorogenic acids. Such factors increase concentrations of inhibitors.

The observations on seedling growth revealed a possible allelopathic effect of *Fimbritylis littoralis*. (Table 2.7). At 3 weeks after planting (WAP), plant height was significantly lower when rice was grown

on soil where this species was growing alone. The other weed species had less pronounced effects. The fresh weight of shoots at 4 WAP followed a similar pattern. The other species had a slight effect on both parameters measured. Although the differences were significant compared to the control when rice was grown on greenhouse soil, this may not necessarily be an effect of allelopathic substances that would be released under natural conditions. As mentioned by Rice (1979), any plant extract may have an effect on plant growth, depending on its concentration. Einhellig (1986) indicated that the concentration of phytotoxins also is affected by age of the plants and the persistence of the chemical compound once released into the environment, since they can be subject to inactivation and chemical or microbial degradation.

The laboratory experiment on germination, shoot, and radicle length of rice and cowpea showed the greatest effect on the latter. All plant aqueous extracts used, inhibited shoot length of cowpea 1 week after planting at the high concentration (10%) (Table 2.8). Shoot growth of rice was reduced by extracts from wild poinsettia and *C. difformis*. The lowest concentration of extracts did not have an effect on shoot length of rice. However, a more pronounced stimulatory effect was observed on the shoot length of cowpea that received the different extracts. At low concentration, these extracts stimulated shoot growth of both test species, which means that they may have acted as auxin compounds and, therefore, may inhibit growth at much higher concentrations. This growth-stimulating property of sublethal doses (hormesis) of auxin-type compounds on plants has been reported by Wiedman and Appleby (1972), Ries (1976), Einhellig (1986), and Putnam and Tang (1986).

These observations suggest that there must be some phytotoxins present in the different extracts used. Less effects were observed on radicle

length of the two test species (Table 2.9). Cowpea was not significantly affected by any of the plant extracts. The greatest inhibition of rice was caused by the highest concentration of the extracts obtained from wild poinsettia. Lower concentrations of the different extracts also stimulated the radicle length of both rice and cowpea.

A certain level of interference of the selected weed species with rice through chemical means is obvious. However, more research is needed for a better understanding of the nature of weed interference in rice grown on hydromorphic soils. Higher concentration of the extracts will be required to show clearly the allelopathic potential of each of the weed species. For these results to be conclusive, toxic substances must be isolated from the suspected species and prove to cause symptoms similar to those previously diagnosed. Fuerst and Putnam (1983) pointed out that the isolation of a toxic substance is the first step in obtaining direct evidence that the interference which such plant species is due to a chemical. However, the isolation of toxic substances in the form they exert their action in nature is a very difficult process.

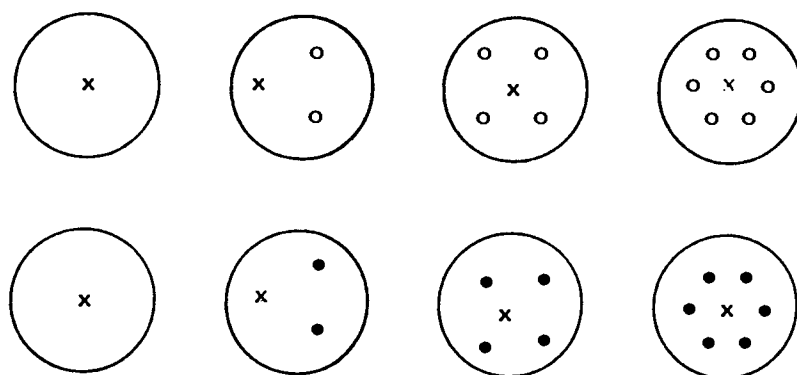


Figure 2.1. Planting design of an additive scheme with rice (x), jungle rice (o), and wild poinsettia (•)

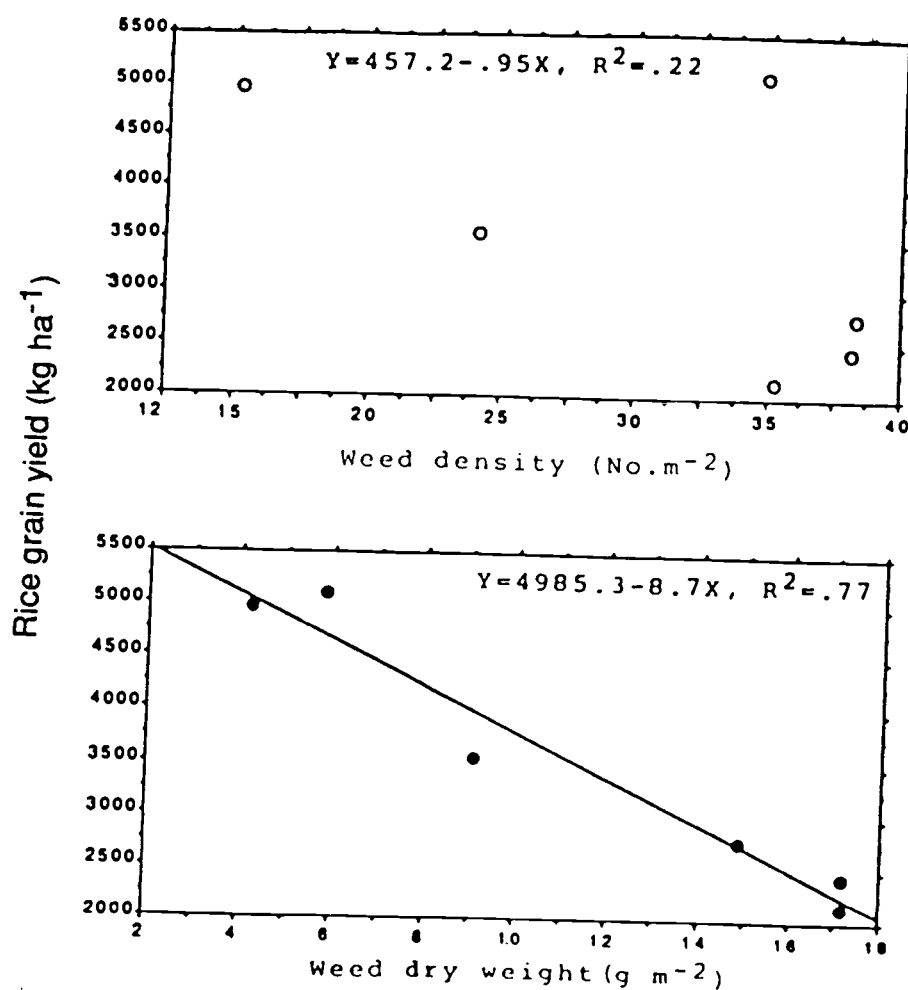


Figure 2.2. Linear relationships between rice grain yield and weed density; rice grain yield and weed dry weight at harvest.

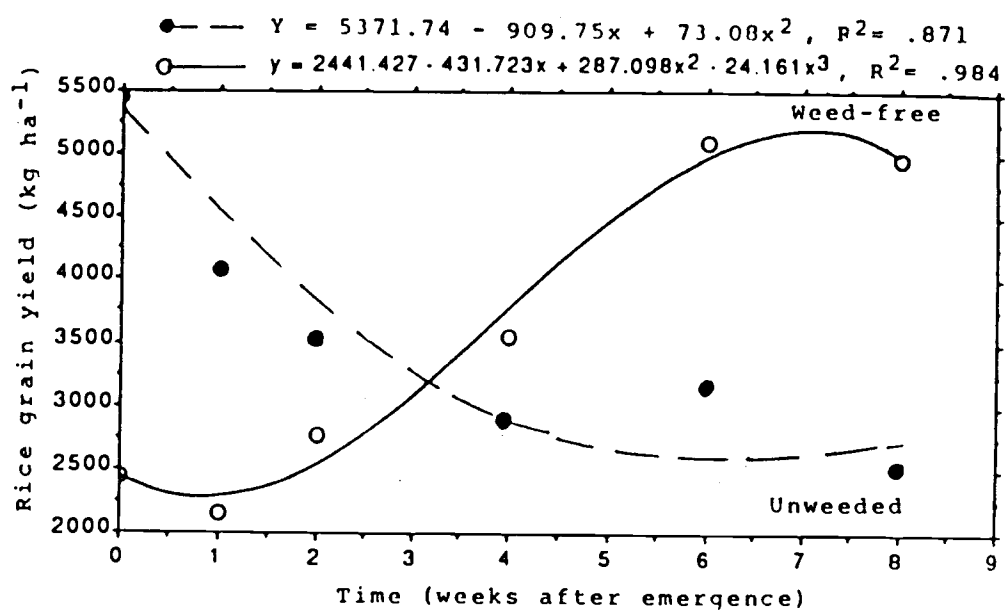


Figure 2.3. Relationships between duration of weed competition and rice grain yield. IITA, 1987 (dry season).

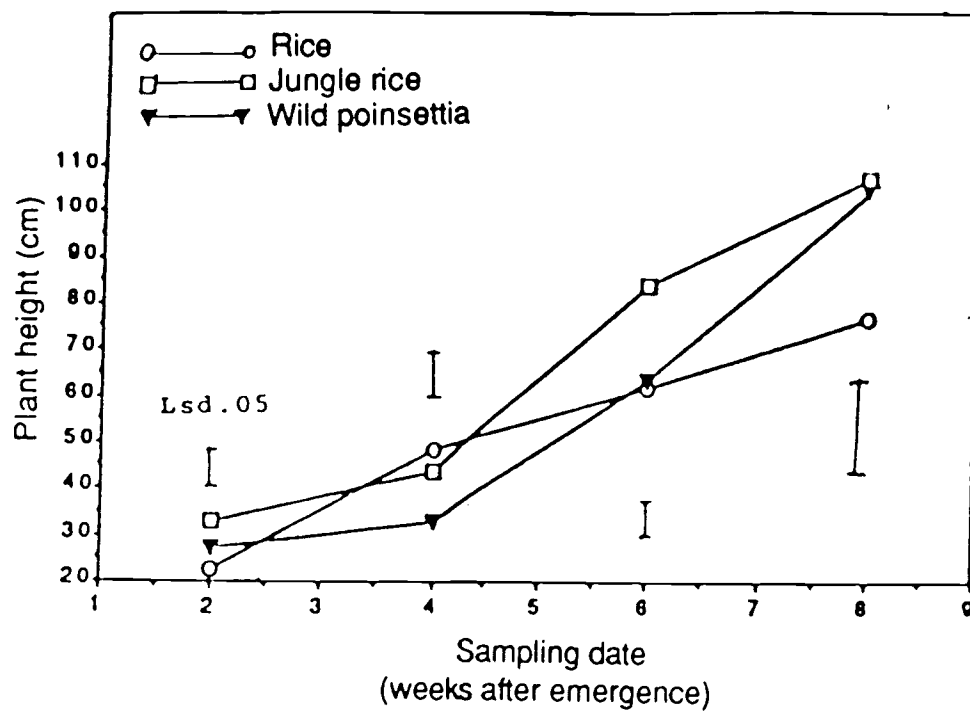


Figure 2.4. Plant height at different sampling dates.

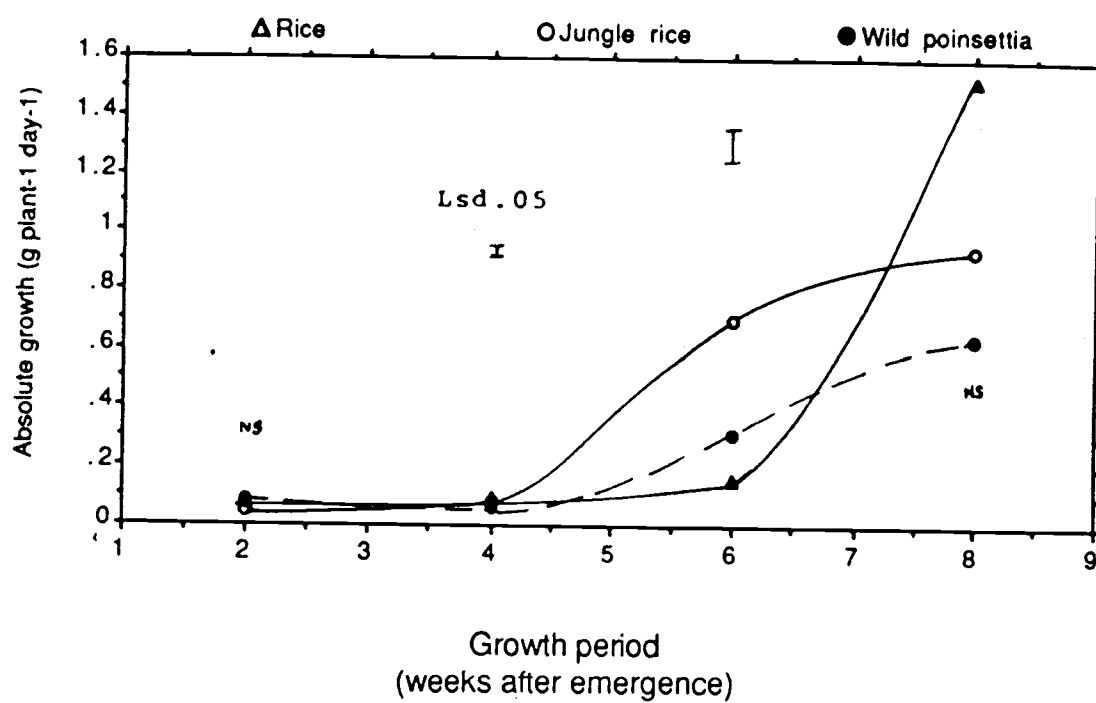


Figure 2.5. Absolute growth of rice, jungle rice, and wild poinsettia at different growth periods.

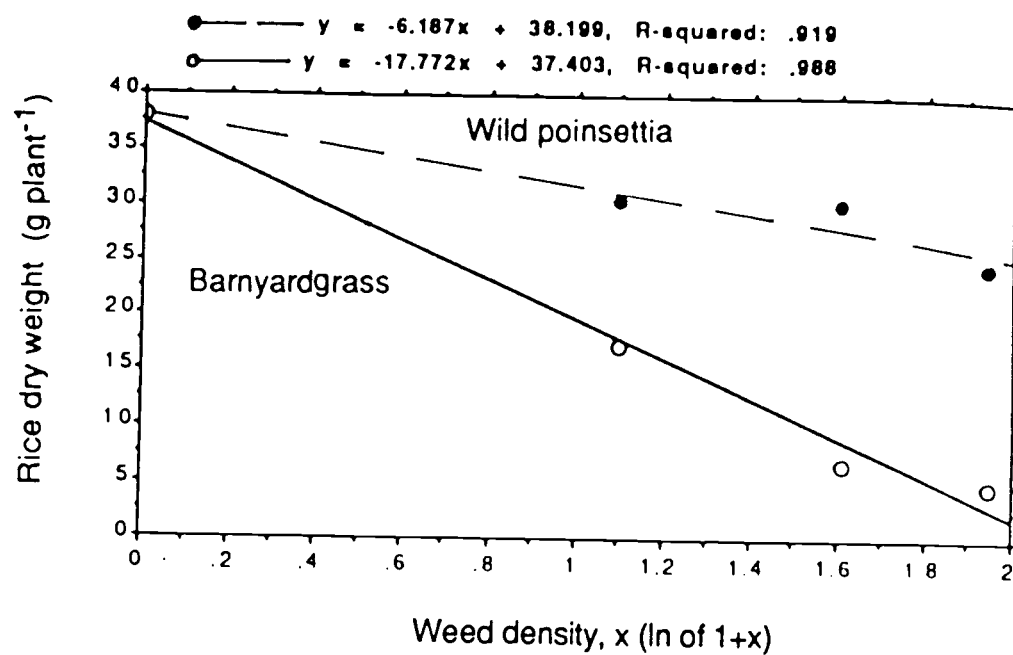
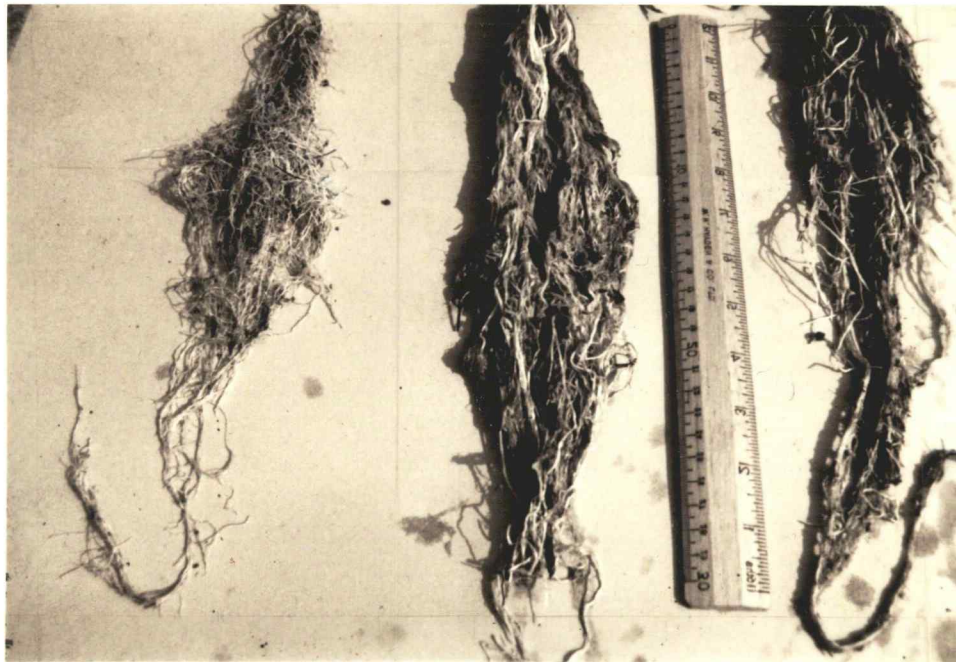


Figure 2.6. Rice dry weight as influenced by density of jungle rice or wild poinsettia at harvest.



Wild poinsettia

Jungle rice

Rice

Figure 2.7. Root growth of wild poinsettia, jungle rice, and rice at 4 weeks after emergence.

Table 2.1a. Effect of weeding on weed growth at 10 weeks after emergence (WAE) and at harvest. IITA, 1986 (rainyseason).

Weeks after rice emergence	10 WAE		At harvest	
	Weed density (No.m ⁻²)	Weed dry weight (g m ⁻²)	Weed density (No.m ⁻²)	weed dry weight (g m ⁻²)
Weed-free ¹				
0	29.6 a ²	23.1 a	15.9 a b	7.7 a b
2	25.8 a b	15.8 a	18.1 a	8.6 a
4	18.4 b c	3.3 b	11.0 b c	4.2 b c
6	11.3 c d	1.3 b	7.5 c	1.8 c
8	9.6 c d	1.3 b	8.7 c	2.2 c
2 and 6	12.3 c d	2.3 b	9.8 b c	2.0 c
4 and 8	6.9 d	1.4 b	8.0 c	2.8 c
cv%	41.6	51.4	38.7	57.8
P-value	< .001	< .0001	.01	< .01

¹ Plots maintained weed-free for a certain period of time (weeks after emergence) and then left unweeded until harvest.

² Means (square root transformations) in each column followed by the same letter (s) are not significantly different by the Duncan Multiple Range Test (DMRT).

Table 2.1b. Rice yield components as affected by weeding. IITA, 1986 (rainy season).

Weeks ¹ after rice emergence	Grain yield, kg ha ⁻¹		Tillers, no.plant ⁻¹		Panicles, no.plant ⁻¹	
	weed-free	unweeded	weed-free	unweeded	weed-free	unweeded
0	514 a ²	1873 a	4 a	9 b	4 a	8 a
2	1226 b	1771 a	6 a b	8 b	6 a b	7 a b
4	1315 b	1665 a b	8 c	9 b	8 c	8 a
6	1503 b	2180 a	9 c	8 b	9 c	8 a
8	1729 b	1308 b	8 c	7 a	8 c	6 b
2 and 6	1679 b	1679 a b	9 c	9 b	9 c	9 a
4 and 8	1471 b	1471 b	9 c	9 b	9 c	9 a
cv%	23.3	19.1	16.8	11.6	15.9	14.3
P-value	< .001	.05	< .001	.01	< .001	.01

¹ Plots maintained weed-free or unweeded for a certain period of time (weeks after emergence) and then left unweeded or weed-free until harvest.

² Means in each column followed by the same letter (s) are not significantly different by the Duncan Multiple Range Test (DMRT).

Table 2.2a. Effect of weeding on weed growth at 6 weeks after emergence (WAE) and at harvest. IITA, 1987 (dry season).

Weeks after rice emergence	6 WAE		At harvest	
	Weed density (No.m ⁻²)	Weed dry weight (g m ⁻²)	Weed density (No.m ⁻²)	weed dry weight (g m ⁻²)
Weed-free ¹				
0	55.2 a ²	20.3 a	38.2 ab	17.2 a
1	46.0 ab	13.6 ab	35.3 a	17.2 a
2	49.2 a	12.0 b	38.4 a	14.9 a
4	34.8 b	7.5 b	24.2 ab	9.1 b
6	-	-	34.8 ab	5.8 b
8	-	-	15.3 b	4.2 b
cv%	13.2	29.4	34.9	27.6
P-value	.03	.03	.1	<.001

¹ Plots maintained weed-free for a certain period of time (weeks after emergence) and then left unweeded until harvest.

² Means (square root transformations) in each column followed by the same letter (s) are not significantly different by the Duncan Multiple Range Test (DMRT).

Table 2.2b. Rice yield components as affected by weeding. IITA, 1987 (dry season).

Weeks ¹ after rice emergence	Grain yield, kg ha ⁻¹		Tillers (No./L. meter) ²		Panicles	
	weed-free	unweeded	weed-free	unweeded	weed-free	unweeded
0	2446 bc ³	5856 a	62 b	86 a	49 c	81 a
1	2161 c	4078 b	61 b	80 ab	57 bc	75 ab
2	2759 bc	3541 bc	73 ab	81 ab	67 abc	75 ab
4	3545 b	2907 bc	77 ab	73 ab	75 ab	73 ab
6	5096 a	3108 bc	82 ab	64 b	78 ab	59 b
8	4961 a	2479 c	89 a	61 b	81 a	54 b
cv%	23.3	19.1	16.8	11.6	15.9	14.3
P-value	< .001	.05	< .001	.01	< .001	.01

¹ Plots maintained weed-free or unweeded for a certain period of time (weeks after emergence) and then left unweeded or weed-free until harvest.

² Number per linear meter row.

³ Means in each column followed by the same letter (s) are not significantly different by DMRT.

Table 2.3 Mean values of LAR and NAR for rice, jungle rice, and wild poinsettia. IITA January 1987.

Species	Leaf area ratio (LAR) (cm ² g ⁻²)			Net assimilation rate (NAR) (g cm ⁻² day ⁻¹)		
	2-4WAE ¹	4-6WAE	6-8WAE	2-4WAE	4-6WAE	6-8WAE
Rice	281.6	200.3 a ²	133.0 a	69.5 a	218.4	437.7
Jungle rice	532.8	130.5 b	81.8 b	50.6 ab	334.6	425.7
Wild poinsettia	356.9	155.0 b	91.0 b	40.8 b	253.7	386.9
CV%	48.0	11.3	23.1	20.8	30.4	26.8
P-value	ns	.004	.04	.02	ns	ns

¹ WAE = weeks after emergence.

² Means in a column followed by the same letter (s) are not significantly different by DMRT.

Table 2.4. Relative growth rate of rice, jungle rice, and wild poinsettia at different growth periods. IITA, January 1987.

Species	Growth period		
	2-4	4-6	6-8
Rice	.056	.050	.123
Jungle rice	.052	.122	.052
Wild poinsettia	.049	.078	.062
CV%	18.2	15.8	29.0
P-value	.001	.001	.01
Lsd .05	.006	.02	.05

Table 2.5. Rice growth as influenced by jungle rice density. IITA, 1987.

Weed density (plants/pot)	Rice leaf area (cm ² plant ⁻¹)	Rice tillers (no. plant ⁻¹)		Rice dry weight (g plant ⁻¹)	
		6 WAE ¹	Harvest	6 WAE	Harvest
0	589.0 a ²	16 a	30 a	5.9 a	38.0 a
2	177.5 b	6 b	8b	1.4 b	17.3b
4	133.8 b	6 b	7b	1.9 b	6.8b
6	121.9 b	5 b	5b	1.1 b	4.8b
CV%	27.3	15.1	19.4	40.3	25.2
P-value	<. 0001	< .0001	< .0001	<.01	< .001

¹ WAE= Weeks after emergence.

² Means in a column followed by the same letter (s) are not significant by DMRT.

Table 2.6. Rice growth as influenced by wild poinsettia density. IITA, 1987.

Weed density (plants/pot)	Rice leaf area (cm ² plant ⁻¹)	Rice tillers (no. plant ⁻¹)		Rice dry weight (g plant ⁻¹)	
		6 WAE ¹	Harvest	6 WAE	Harvest
0	589.0	16	30 a	3.9	38.0 a
2	635.8	16	23 b	4.4	31.0 ab
4	623.0	15	22 b	4.5	30.4 ab
6	594.3	15	20 b	4.1	24.6 b
Cv%	35.8	7.5	18.5	22.1	25.2
P-value	ns	ns	< .001	ns	.002

¹ WAE = Weeks after emergence.

² Means in a column followed by the same letter (s) are not significant by DMRT.

Table 2.7. Allelopathic effect of selected weed species on plant growth. IITA, August 1987.

Soil sample from monocultures of weeds	Rice plant height, cm	Rice fresh weight, g/5plants
<i>E. colona</i>	17.0	1.3
<i>E. heterophylla</i>	18.1	1.8
<i>C. difformis</i>	19.9	1.7
<i>F. littoralis</i>	11.5	0.5
Greenhouse soil (control)	22.2	3.0
CV%	9.4	9.4
Lsd .05	2.5	.7

Table 2.8. Effect of plant aqueous extracts on shoot length (cm) of rice and cowpea. IITA, August 1987.

Treatment	Rice		Cowpea	
	Concentration			
	1/10	1/40	1/10	1/40
<i>E. colona</i>	4.4 ab ¹	5.4	3.3 b	9.0 ab
<i>E. hetrophylla</i>	3.5 b	5.4	2.3 b	10.3 ab
<i>C. difformis</i>	3.6 b	5.1	3.2 b	11.1 a
<i>F. litoralis</i>	3.9 ab	5.1	3.5 b	6.1 b
Distilled water	4.8 a	5.1	8.1 a	9.4 ab
CV%	17.1	4.8	28.1	26.2
P-value	< .1	ns	< .01	< 1

¹ Means in a column followed by the same letter (s) are not significantly different by DMRT.

Table 2.9. Effect of plant aqueous extracts on radicle length (cm) of rice and cowpea. IITA, August 1987.

Treatment	Rice		Cowpea	
	Concentration			
	1/10	1/40	1/10	1/40
<i>E.colona</i>	6.4 a ¹	7.6 ab	3.8	6.8
<i>E. heterophylla</i>	4.3 b	8.5 a	3.3	6.2
<i>C. difformis</i>	6.2 a	6.8 b	4.7	6.6
<i>F. littoralis</i>	5.7 ab	7.2 b	5.1	7.6
Distilled water	7.0 a	6.9 b	5.4	5.6
CV%	18.2	7.9	36.6	28.7
P-value	< .1	< .1	ns	ns

¹ Means in a column followed by the same letter (s) are not significantly different by DMRT.

Chapter III.

GROWTH AND COMPETITIVE RELATIONSHIPS OF RICE,
JUNGLE RICE, AND WILD POINSETTIA AS INFLUENCED
BY PLANT DENSITY AND PROPORTION

INTRODUCTION

In plant communities, competition occurs both between plants of different species, and between individuals of the same species. In competition studies the effects of intraspecific and interspecific competition are often confounded, and this makes the interpretation of the relative effects of both types of competition difficult (Harper, 1977; Zimdahl, 1980; Spitters, 1983; Jolliffe *et al.*, 1984; Connolly, 1986). To separate these effects it is necessary to grow a range of densities of each of the species involved, in monocultures and in mixtures as well (Jolliffe *et al.*, 1984; Connolly, 1986).

The relative competitive ability of weeds in crops may be influenced by crop density. Thurston (1962) and Carlson and Hill (1985) demonstrated that increasing crop density decreased weed growth and yield losses due to weed competition. The following experiments were carried out to examine in greater detail the competitive relationships described in chapter II between rice and associated weeds.

MATERIALS AND METHODS

Experiment 3.1. Influence of plant proportion and density on competitive relationships between rice, jungle rice, and wild poinsettia (Diallel experiment).

An experiment was conducted to obtain information on the nature of intraspecific and interspecific interference when rice, jungle rice (also called barnyardgrass), (*Echinochloa colona*), and wild poinsettia (*Euphorbia heterophylla*) are grown as separate species (Figure 3.1) and in mixtures (Table 3.1) at densities of one to four plants per pot. Plants were grown outdoors, in pots as in the experiment 2.3. Treatments were replicated four times. Plants were sampled at 12 WAE for weeds and at crop maturity (17 WAE) for rice.

Data collection and analyses.

Data collection included tiller number and dry weight. The yield-density model, $1/W = A + BN$ (equation 1, chapter I), describing the relationship of individual plant biomass (Spitters, 1983) was used to estimate the effect of intraspecific competition on each species grown in monocultures. Data collected at 4 WAE included tiller number, leaf area, and dry weight for weeds at 12 WAE and for rice at maturity. The response of each species to intraspecific competition was assessed by comparing the regression coefficients (slopes of the estimated linear regression) depicting the rate of change of individual plant weight as density increases. In mixtures, the relative competitive ability of the species was estimated from the regression coefficients of the expanded model (Spitters, 1983) for two-species mixtures. The relative competitive ability of rice against each of the weed species was calculated as the ratio of the regression coefficients that characterize intra- and interspecific competition.

Experiment 3.2. Effects of intraspecific and interspecific competition on growth of rice, jungle rice, and wild poinsettia (Addition series).

Two addition series described by Spitters (1983) were used in this study, varying the densities of rice in two binary associations with each of the selected weed species. This provided a means of assessing the effect of crop density on the competitive ability of jungle rice and wild poinsettia against rice. Plot size was 1 by 1 m. The experimental design was a randomized complete block with six replications.

Jungle rice and wild poinsettia seeds were broadcast uniformly and slightly raked into the soil. The densities of weeds were 0, 10, 20, 40, and 80 plants m^{-2} while rice seeds were drilled by hand to obtain 0, 20, 40, 60, and 80 plants m^{-2} (Figure 3.2). Rice variety ITA 222 was used for this study. Two weeks after emergence, plants were thinned to desired densities. Seedlings that did not emerge by that time were replaced with seedlings from a nursery plot. Weeds other than the planted jungle rice and wild poinsettia were removed by handweeding. A compound fertilizer (15-15-15) was applied at the rate of 30 kg ha^{-1} each of N, P, and K at 3 and 6 weeks after emergence.

Data collection and analyses.

One set of three replications was used for destructive sampling at 6 WAE to determine the number of tillers, leaf area, and dry weight of the aboveground parts of plants (rice and weeds). The other set of three replications was harvested 12 WAE as the weeds started to senesce. Analysis of variance and mean separation by DMRT at 5% probability level were performed for the growth parameters measured. Linear regression analysis was done with the data on individual plant weight and density as proposed by Spitters (1983) to assess the effects of intra- and interspecific

competition:

$$1/W_R = A + B_{RR}N_R + B_{REc}N_{Ec} \quad (6)$$

$$1/W_R = A + B_{RR}N_R + B_{REh}N_{Eh} \quad (7)$$

where $1/W$ is the reciprocal weight of individual rice plants.

A is the theoretical reciprocal weight of individual rice plants growing in the absence of competition.

B_{RR} is the coefficient of intraspecific competition among individual rice plants resulting from the increase in rice density.

B_{REc} and B_{REh} are coefficients of interspecific competition in the rice-jungle rice and rice-wild poinsettia associations, respectively.

N_R , N_{Ec} , and N_{Eh} are densities of rice, jungle rice, and wild poinsettia, respectively.

The relative competitive ability of rice against each of the weed species was estimated from the regression coefficients of the expanded models describing the yield-density relationships.

Experiment 3.3. Effects of plant density and proportion on competitiveness of jungle rice and wild poinsettia in different rice background densities (Modified replacement series).

A replacement series design was used to assess the competitive ability of the two weed species in association with rice (var. ITA 222) at different densities under field conditions. The experiment was established in the 1987 rainy season. Rice seeds were drilled by hand and seeds of jungle rice and wild poinsettia were broadcast uniformly as described in

experiment 3.2. Replacement series of the two weed species were subjected to different background densities of rice. Weed species at ratios of 100:0, 75:25, 50:50, 25:75, and 0:100 of jungle rice and wild poinsettia, respectively, were grown in association with rice densities of 0, 20, 40, 60, and 80 plants m^{-2} (Figure 3.3).

Seedlings of the two weed species were thinned to desired densities of each species to make up each weed proportion. Seedlings of other weeds were removed by frequent hand weeding. Total plant densities (rice plus weeds) varied from 80 to 160 plants m^{-2} . Plant growth in these mixtures should be influenced by intraspecific and interspecific competition. To isolate the intraspecific effect, each species also was grown in a monoculture at the following densities: 10, 20, 40, and 80 plants m^{-2} . Plot size was 1 by 1 m and each treatment was replicated six times in a randomized complete block design.

Data collection and analyses.

Weeds and rice were sampled from a 0.5 by 0.5 m quadrat placed at the center of each plot. Plants were sampled at harvest (12 WAE) and actual densities and dry weight of the above-ground portions of each species were determined. Measurements were made prior to the rice harvest to minimize loss in weed dry matter during senescence. The data were analyzed by calculating the relative yields and relative yield total for the two weed species in each rice stand. Replacement series diagrams were used to qualitatively assess the competitiveness of each weed species at different rice densities.

Intraspecific competition was assessed from monoculture densities using the reciprocal of individual plant weight and plant density, method described by Shinozaki and Kira (1956) and Spitters (1983) and the double reciprocal of total biomass and plant density suggested by Jolliffe *et al.*,

(1984). In the latter, monoculture yields (biomass) of each species (Y_m) were compared to their projected yields (Y_p), and the linear regression coefficients of the reciprocal yield and reciprocal density were used to estimate the maximum yields (Y_{max}) and the density (K_n) at which yield reaches 50% of Y_{max} :

$$1/Y = 1/Y_{max} + (K_n/Y_{max})(1/N) \quad (8)$$

The projected yields (expected yield in the absence of intraspecific and interspecific competition) were calculated as:

$$Y_p = (Y_{max}/K_n) * N \quad (9)$$

The species monoculture responses (SMR) and their relative values (RSMR) were calculated using the following formulas:

$$SMR = Y_p - Y_m \quad (10)$$

$$RSMR = (Y_p - Y_m) / Y_p \quad (11)$$

Log transformations of individual plant weight and density also were performed. The sensitivity of these different analytical methods of assessing intraspecific competition was evaluated based on the coefficients of determination.

The quantitative relationships between weed proportion, crop density, and biomass of jungle rice and wild poinsettia were assessed using the expanded yield-density model of Spitters (1983):

$$1/W_{Ec} = A + B_{Ec.Ec}N_{Ec} + B_{Ec.Eh}N_{Eh} + B_{Ec.R}N_R \quad (12)$$

$$1/W_{Eh} = A + B_{Eh.Eh}N_{Eh} + B_{Ec.Eh}N_{Eh} + B_{Eh.R}N_R \quad (13)$$

where $1/W_{Ec}$ and $1/W_{Eh}$ are the reciprocal weight of jungle rice and wild poinsettia, respectively.

A is their theoretical reciprocal weight of individual plants in the absence of competition.

B_{EcEc} and B_{EhEh} are coefficients of intraspecific competition among jungle rice and wild poinsettia plants, respectively.

B_{EcEh} , B_{EhEc} , B_{EcR} , and B_{EhR} are coefficients of interspecific competition between jungle rice-wild poinsettia, wild poinsettia-jungle rice, jungle rice-rice, and wild poinsettia-rice, respectively.

N_{Ec} , N_{Eh} , and N_R are densities of jungle rice, wild poinsettia, and rice, respectively.

RESULTS AND DISCUSSION

Experiment 3.1. Influence of plant proportion and density on competitive relationships between rice, jungle rice and wild poinsettia (Diallel experiment).

Pure stands of rice were more productive than those of either weed species (Figure 3.4). Rice produced twice the amount of jungle rice dry weight as did either of the weed species. The least amount of dry matter was produced by the stands of wild poinsettia. For all the species, the dry weight per plant was significantly affected at densities of 2 plants/pot and above.

The response of each species to intraspecific competition was described by the yield-density model ($1/W = A + B N$) presented in Figure 3.5. In this model, the intercept A is the theoretical reciprocal weight of an individual plant growing in the absence of competition, and the regression coefficient B describes the degree of intraspecific competition resulting from the increase in density. The steepness of the slope of this model indicates the relative sensitivity of the species to intraspecific competition. Wild poinsettia was most responsive to intraspecific competition, i.e. 3 times greater than jungle rice and more than 6 times than rice.

In the rice-weed mixtures, more detrimental effect to the crop plants was caused by the presence of jungle rice as a neighbor than wild poinsettia (Table 3.2). jungle rice plants produced large numbers of tillers at the detriment of rice plants. The number of rice tillers was not significantly affected by its density, when it was grown alone. When single rice plants were grown with jungle rice at different densities, two jungle rice plants were needed to significantly reduce rice tillers. However, dry weight

was significantly reduced when only one jungle rice plant competed with rice compared to a single rice stand. At a rice density of two plants/pot, one jungle rice plant was competitive enough to significantly affect tiller production of rice. In addition to the interspecific competition, individual rice plants competed for the space available in the pots. In the absence of the weeds, doubling the density of rice reduced dry weight per plant by 48 %. There was no significant variation in rice tillers and dry weight due to the presence of either one or two jungle rice plants.

Wild poinsettia competition (one plant per pot) reduced tiller production in a rice stand of two plants (Table 3.2). At this highest rice density of 2 plants per pot, increasing the density of the two weed species did not cause further significant reduction in tiller and dry matter production of rice. When rice density was increased to 2 plants/pot, the rice plants suffered from intraspecific competition as well. The effect of jungle rice was more detrimental to the growth and development of rice than that of wild poinsettia.

The reciprocal yield models expanded to two-species mixtures (Spitters, 1983), describe the relationships of mean biomass of individual rice plants and densities of each species in the rice-barnyardgrass or rice-wild poinsettia associations (Table 3.3). The variations in the reciprocal mean weight of individual rice plants due to density were accounted for 56 and 75% with jungle rice and wild poinsettia, respectively, as competitors. In both models, rice density had the greatest influence on the outcome of interactions among plants in the two binary mixtures. Although jungle rice densities significantly influenced the response of rice plants ($p = .01$), wild poinsettia density had no significant effect ($p = 0.3$) on the biomass of individual rice plants. The relative competitive ability for rice associated with jungle rice was directly calculated from the equations

(Table 3.3) as the ratios of regression coefficients characterizing intraspecific and interspecific competition. This ratio was 2.6, indicating that rice was more competitive than either weed species.

Similarly, rice density had the greater influence on its tiller production (Table 3.4). The effect of jungle rice on rice tillers was significant ($p = .09$). The effect of wild poinsettia was not significant ($p = .30$). The coefficients of rice density were consistently greater in both associations for both growth parameters measured (.009 and .018 for dry weight and tillers, respectively). Therefore, crop density, should be a cultural practice to consider when manipulating plant populations to improve crop production or for describing competitive relationships.

Experiment 3.2. Effects of intraspecific and interspecific competition on growth of rice, jungle rice, and wild poinsettia (Addition series).

All three species were significantly reduced in tiller number or branches per plant as a response to crowding at 6 WAE. Significant variations in number of branches, leaf area, and dry weight of wild poinsettia was observed in response to density (Table 3.5).

Jungle rice (Table 3.6) responded to crowding at high densities (40 plants m^{-2}). Increasing density decreased the number of tillers, leaf area, and dry matter production of individual plants. jungle rice produced the highest dry matter at all densities and greater number of tillers than rice. This was due to less effect of intraspecific competition on its tillering ability than that of rice (Table 3.7).

Rice response to crowding was similar to that of jungle rice although the latter had more tillers and dry matter production (Table 3.6

and 3.7). The leaf area of these two species was almost identical, suggesting a comparable ability to capture light. Rice tiller production and leaf area per individual plants also were influenced by density. However, the dry matter was reduced at densities as low as 40 plants m^{-2} (Table 3.7). Rice tiller number and leaf area were only affected when its density reached 60 plants m^{-2} .

The density response of each species was described by the reciprocal yield model ($1/W = A + BN$) that characterize the effect of intraspecific competition on biomass yield of individual plant species at 12 WAE (Figure 3.6). Increased density affected wild poinsettia the most. The effect of density on the average individual plant weight of wild poinsettia was more than twice that of density on jungle rice. Rice was the least affected by increasing species density. Similar trends were observed in the leaf area produced (Figure 3.7).

Two-species reciprocal-yield models (Spitters, 1983) (equations 6 and 7) for rice and jungle rice or wild poinsettia, in the modified addition series experiment, are presented in Table 3.8. These models describe 77 to 83 percent of the variations in reciprocal mean weight of individual rice plants as additive and linear functions of the densities in the binary weed systems (rice-barnyardgrass and rice-wild poinsettia). In both models, rice density had the greatest influence on its own biomass response and jungle rice had the greater influence on the biomass response of individual rice plants than wild poinsettia, based on the regression coefficients that characterize interspecific competition. Relative competitive ability of rice was calculated from the reciprocal-yield models (Table 3.8) as the ratios of regression coefficients characterizing intra- and interspecific competition. Rice was more competitive than either weed species. In agricultural terms, this means that the effect of adding 1 rice plant was approximately

equivalent to the presence of 5 jungle rice plants. The variations in weight of individual rice plants were better explained by the model that describes the relationships of reciprocal yield of rice in the association with jungle rice ($R^2 = .83$; $p = .0001$) than with wild poinsettia. Densities of both rice and barnyard-grass had a significant effect on the dry weight of individual rice plants. These relationships were reasonably well described by the model of rice-wild poinsettia association ($R^2 = .77$; $p = .0001$). Although, the effect of wild poinsettia density on rice dry weight was not significant ($p = 0.23$). The reason may be that the effect of wild poinsettia on rice was not noticeable at the time of sampling (12 WAE). In experiment 3, Chapter II, where each of the weed species was associated with rice grown in plastic pots, competition between rice and jungle rice plants began at a earlier stage than with wild poinsettia. The density effect of the latter on rice tillers and dry weight was only significant at harvest. The response of rice to its own density was , as in experiment 1 (Table 3.4), similar in both associations (rice-barnyardgrass and rice-wild poinsettia), judging from the parameter estimates for rice density (Tables 3.4 and 3.8). These results suggest that varying seeding rate may have improved the competitive ability of rice against both weed species.

Experiment 3.3. Effects of plant density and proportion on competitiveness of jungle rice and wild poinsettia in different rice background densities (Modified replacement series).

Qualitative comparisons of the replacement series diagrams suggest that interference among jungle rice and wild poinsettia was more intense as rice density increased and as proportion of jungle rice increased than in the absence of rice (Figure 3.8). In the absence of rice, a relative yield total (RYT) greater than 1 indicates an overyielding of the mixtures. At

a ratio of 50:50, the RYT was equal to 1.7, suggesting that the two species partitioned resources such that both performed better than in a similar density monocultures. As rice was added the RYT dropped below unity, indicating that competition occurred when total density increased. Wild poinsettia responded to the presence of rice at lower densities of rice than did jungle rice. In the absence of rice, both weed species produced dry weight similar or more than their expected yield. As rice plants were added at a density of 40 plants m^{-2} to the weed mixture, wild poinsettia dry weight was reduced by more than 50% when it was associated with jungle rice in a 1:1 ratio. jungle rice biomass was reduced when rice density was 80 plants m^{-2} . The positive response of jungle rice in association with wild poinsettia was reduced as more rice was added to the mixture. Overall, jungle rice was in advantage over wild poinsettia.

Results from previous experiments (Figure 3.5, 3.6, and 3.7) showed that wild poinsettia was more sensitive to intraspecific competition than jungle rice. Although conventional methods of interpretation of data from replacement series experiment do not include information on the species response to intraspecific competition, the performance of each species in monocultures does provide a means to evaluate the separated effects of intraspecific competition. The regression analysis of individual plant weight on density provided equations that describe the relationship of biomass yields to density of each of the weed species:

$$1/W_{Ec} = .063 + .001N_{Ec}, \quad R^2 = .78 \quad (14)$$

$$1/W_{Eh} = .518 + .007N_{Eh}, \quad R^2 = .78 \quad (15)$$

where W_{Ec} and W_{Eh} are the individual plant biomass yield of jungle rice and wild poinsettia, respectively, and N_{Ec} and N_{Eh} are their respective

densities. The overall interpretation of the models are similar to those from the addition series: wild poinsettia is more sensitive to intraspecific competition than jungle rice. The effect of density on biomass of individual wild poinsettia plants was seven times more than the effect of density on jungle rice biomass (Figure 3.9), judging from the regression coefficients characterizing intraspecific competition.

The same data were analyzed using the double reciprocal of total biomass ($1/Y$) and density ($1/N$) proposed by Jolliffe *et al.*, (1984). The yield-density relationship was described most precisely for jungle rice by the linear equation:

$$\text{Jungle rice: } 1/Y = .0014 + .05 \, 1/N, \quad R^2 = .90 \quad (16)$$

$$\text{Wild poinsettia: } 1/Y = .011 + .178 \, 1/N, \quad R^2 = .63 \quad (17)$$

where Y and N are the total weight of the plant stand and density of jungle rice, respectively. In the case of wild poinsettia, this relationship was described with an R^2 of 0.63 (Figure 3.10). According to the analysis suggested by Spitters (1983), 78% of the variations in the biomass of the two species was accounted in both jungle rice and wild poinsettia. However, the analytical method suggested by Jolliffe *et al.*, (1984) provided a more detailed interpretation of plant response to density by comparing the actual yield with the projected yield of each species.

Maximum yield of wild poinsettia was $90.9 \, \text{g m}^{-2}$ (Figure 3.11). This species required a lower density ($16 \, \text{plants m}^{-2}$) to reach 50% of its constant final yield. These results are consistent with the interpretation that wild poinsettia was more sensitive to intraspecific competition than jungle rice. Constant final yield of jungle rice was only approached at the highest density used in this study. Greater number of monoculture densities (> 80

plants m^{-2}) should have been included for better fitting of the maximum yield of jungle rice. Field observations at the experimental site indicated that this species could occur at populations as high as 180 plants m^{-2} .

Monoculture response of each weed species, characterizing the differences between the projected yield per unit area and the actual monoculture yield (Jolliffe *et al.*, 1984) varied significantly with increase in density (Table 3.9). Wild poinsettia responded significantly ($p < .001$) at density of 20 plants m^{-2} , while jungle rice was influenced by higher densities. Considering the differences in plant size of the two species, intraspecific competition effects also were assessed on a relative basis. Both species showed similar responses compared to the results obtained with absolute values of their monoculture responses. Wild poinsettia responded to the addition of plants of the same species to the monocultures more than did jungle rice. These results support the observations in earlier experiments (3.1 and 3.2).

The response of wild poinsettia to density was most precisely described by a log transformation of both biomass and density, and using a regression model ($R^2 = .82$, Figure 3.12). The individual plant weight of wild poinsettia reached a minimum value before its highest density in this study. This supports that wild poinsettia was very sensitive to intraspecific competition. The large differences in yield potentials (projected yields) of the two species can account partly for the greater advantage of jungle rice. At 6 WAE, jungle rice produced twice as many tillers as rice (Tables 3.6 and 3.7), while wild poinsettia only had 2 to 5 branches (Table 3.5). The rapid growth and shorter life cycle enable jungle rice to efficiently use the available resources early in the growing season to the detriment of the rice plants. When the species are growing together in mixtures, the contribution of intraspecific competition may have a large influence on the mixture

response of wild poinsettia (Grime and Hunt, 1975).

Methods of analysis and interpretation such as the conventional replacement series approach that consider the relative yield of both species were appropriate for describing the general competitive relationships between jungle rice and wild poinsettia. More definitive interpretations (that include quantitative assessments) could have been obtained if the two species were grown in several sets of replacement series at different total densities as suggested by Connolly (1987). For this purpose, the same data were analyzed using the expanded model (Spitters, 1983) of yield-density relationships involving the three species: rice, jungle rice, and wild poinsettia. This model described 72% ($p = .0001$) of the variations in the reciprocal mean weight of individual jungle rice plants (Table 3.10). Density of both rice and jungle rice had a significant influence on jungle rice biomass. The degree of competition between rice and jungle rice plants may have been so high that the effect of increasing density of wild poinsettia was not significant. In addition to the interspecific competition, more sensitive to intraspecific competition than either of the other species (experiments 2.2, 3.1 and 3.2). This could be the reason why the biomass of wild poinsettia was poorly described by the model ($R^2 = 0.13$). The poor relationships between densities of each species with the reciprocal biomass of wild poinsettia plants may also be due to the distribution of this species in the field, or there may have been some factors other than density, that affected its growth. Predicting the biomass yield of wild poinsettia from the densities of all three species of the mixture is difficult.

In summary, wild poinsettia was the most sensitive species to intraspecific competition under both greenhouse and field conditions. In the binary associations, the response of the reciprocal of individual plant weight of rice was almost identical in both associations (rice-jungle rice and

rice-wild poinsettia). In the mixtures, rice density significantly influenced the competitive relationships between jungle rice and wild poinsettia. Overall, jungle rice was more competitive than wild poinsettia.

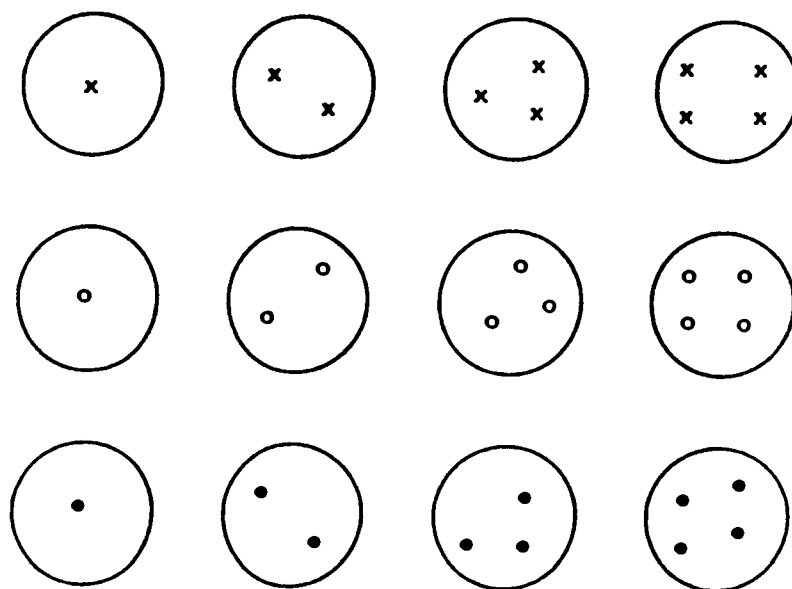


Figure 3.1. Planting scheme of monocultures of rice (x), jungle rice (o), and wild poinsettia (●).

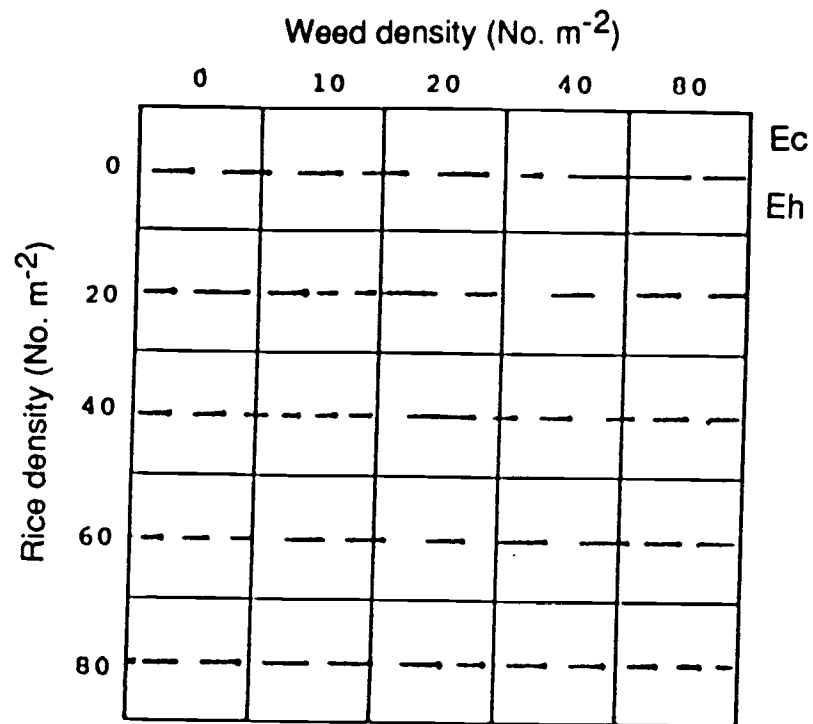


Figure 3.2. Planting scheme of rice, jungle rice (Ec), and wild poinsettia (Eh).

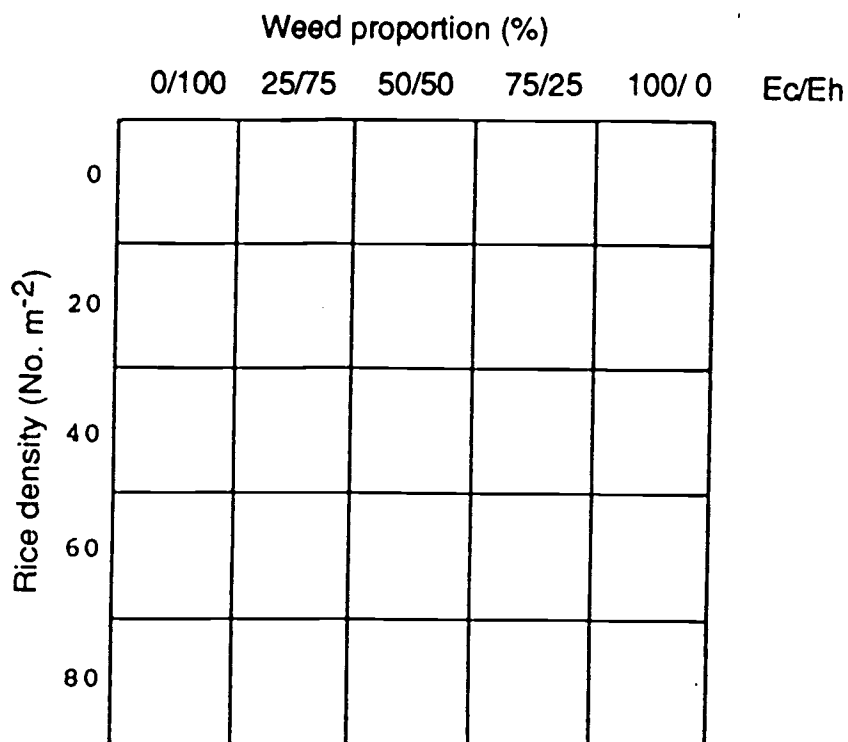


Figure 3.3. Schematic representation of a modified replacement series design with jungle rice (Ec) and wild poinsettia (Eh) planted with different rice densities.

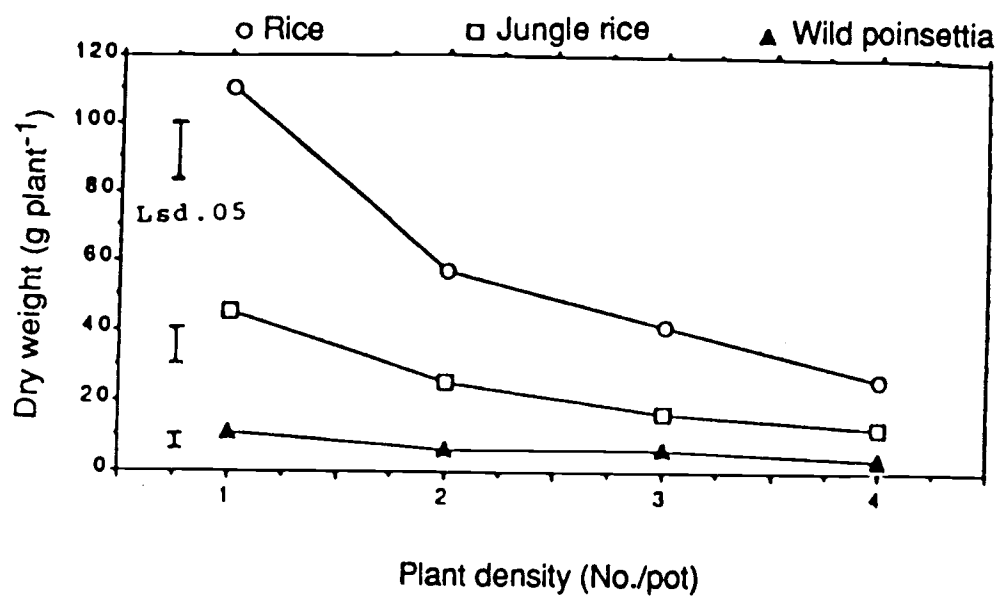


Figure 3.4. Dry weight as affected by intraspecific competition at harvest.

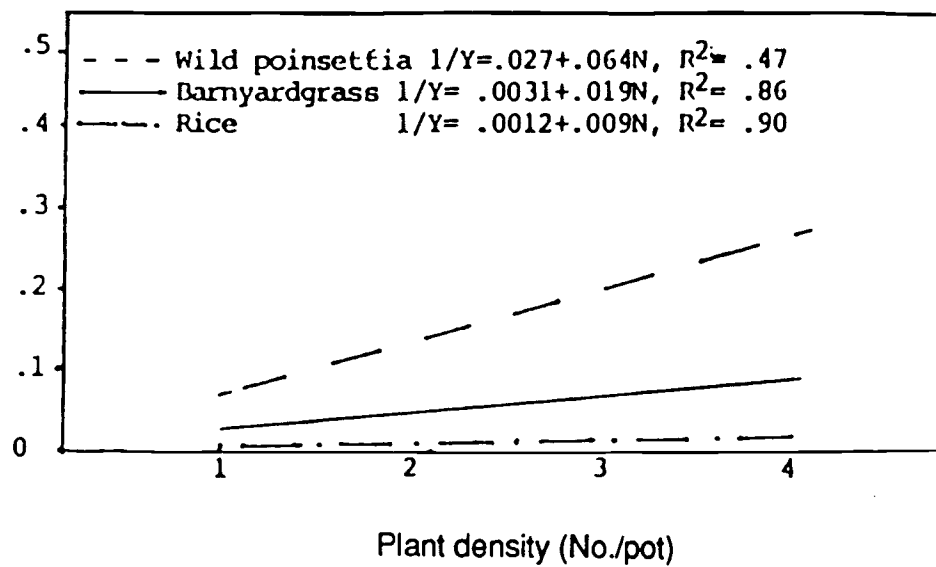


Figure 3.5. Density response: reciprocal of per plant biomass against density.

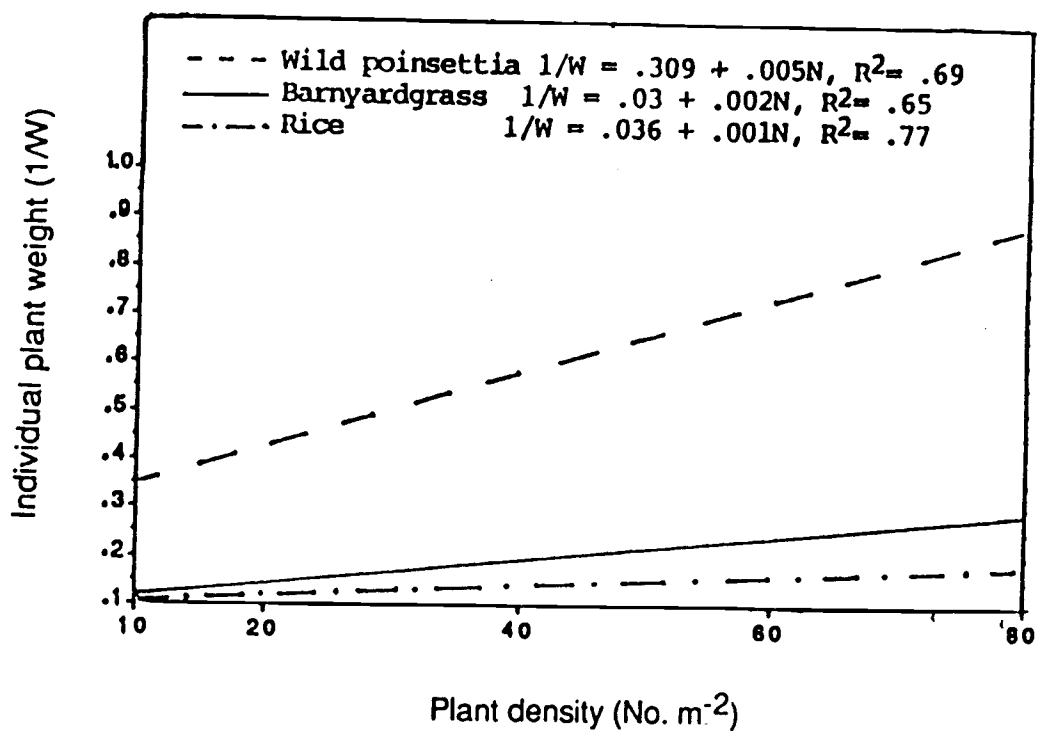


Figure 3.6. Density response of rice, jungle rice, and wild poinsettia : reciprocal of individual plant biomass at 12 weeks after emergence.

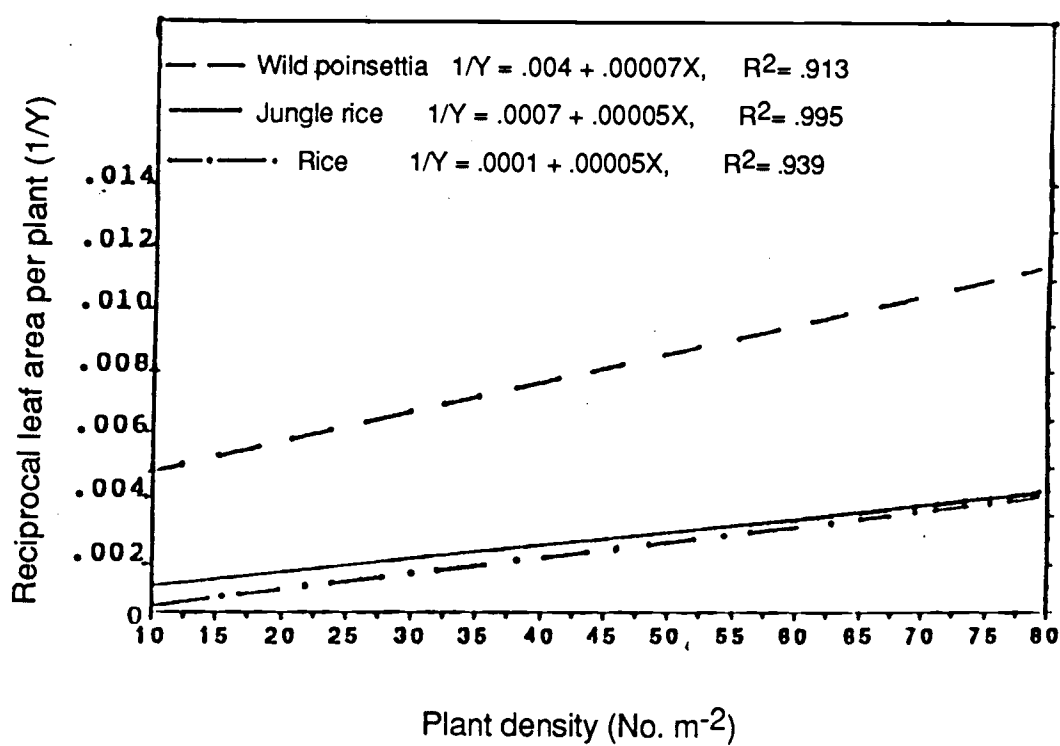
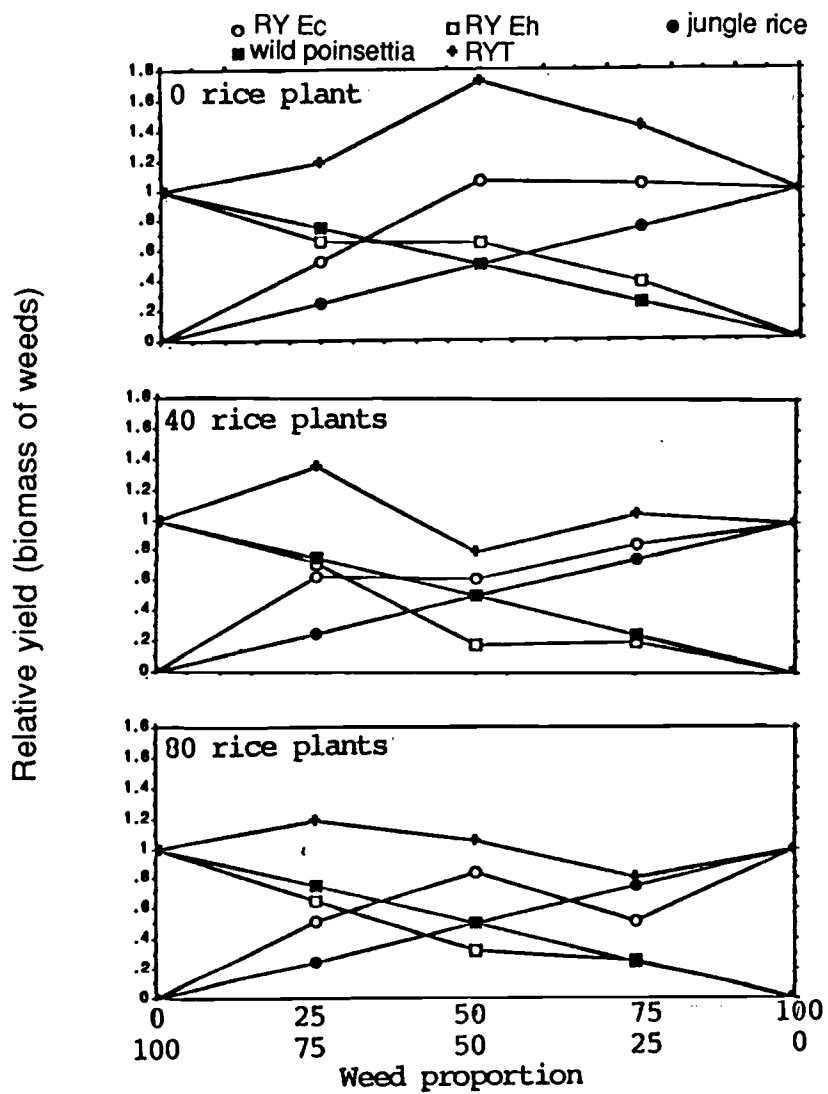


Figure 3.7. Leaf area of individual plants as influenced by density.



Jungle rice= Ec

Wild poinsettia= Eh

Figure 3.8. Replacement series diagrams, depicting the effect of weed proportion planted with different rice densities. The broken lines represent the expected relative yields of each weed species in the absence of competition; RY is the relative yield of each weed species in the mixtures; RYT is the relative yield total of barnardgrass and wild poinsettia.

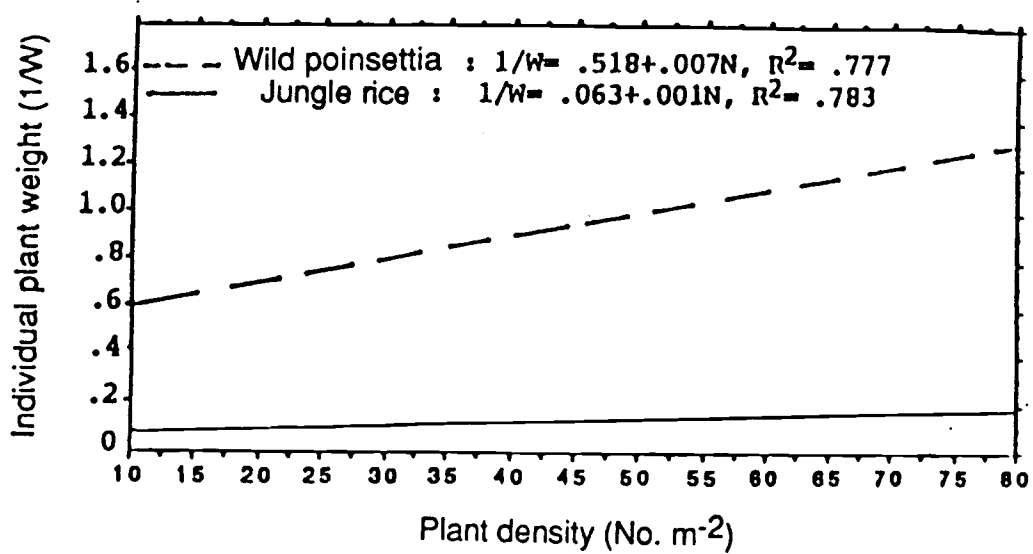


Figure 3.9. Jungle rice and wild poinsettia responses to intraspecific competition

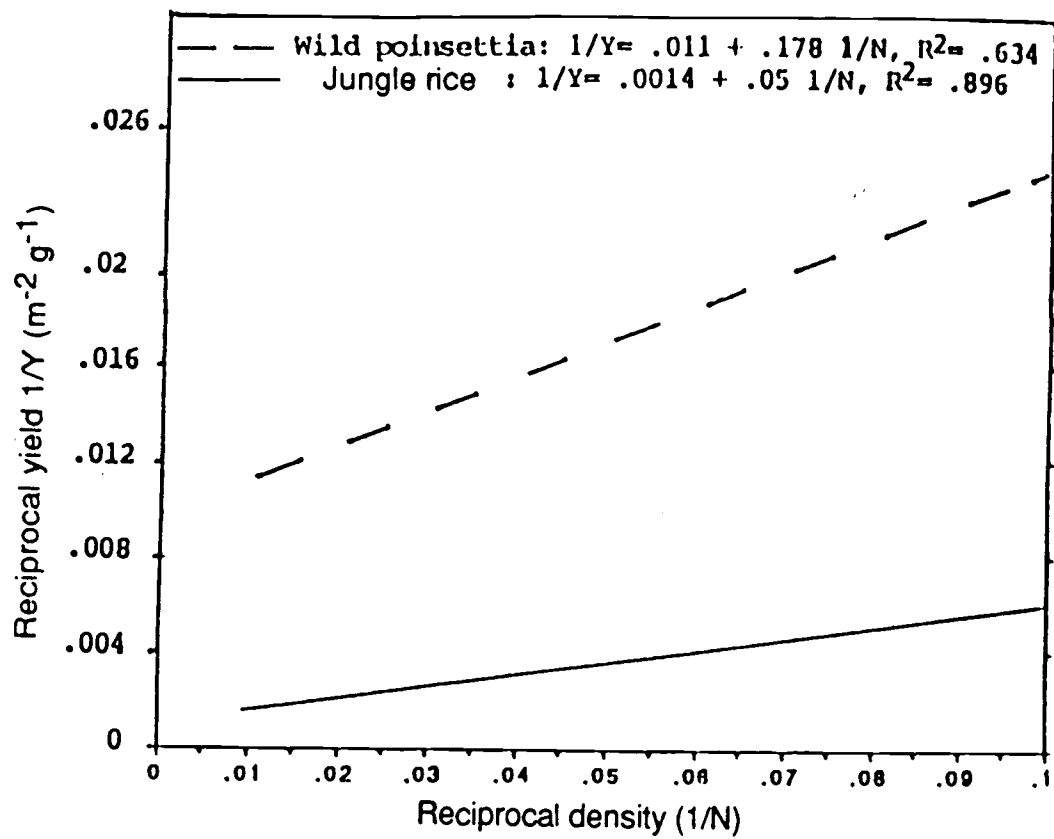


Figure 3.10. Monoculture responses of jungle rice and wild poinsettia.

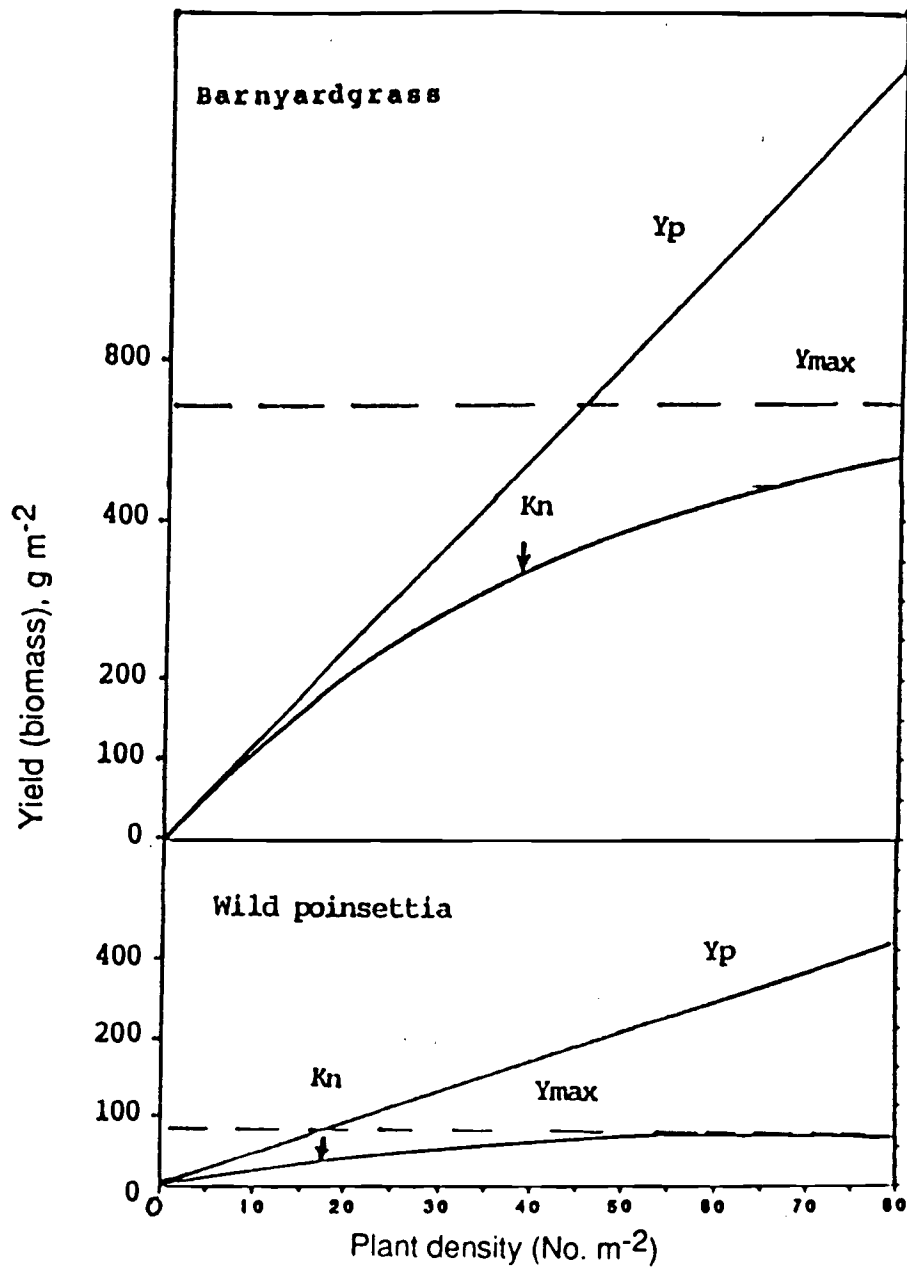


Figure 3.11. Yield response to density: Y_p = projected yield; Y_{max} = maximum yield; K_n = density at which 50% Y_{max} is reached.

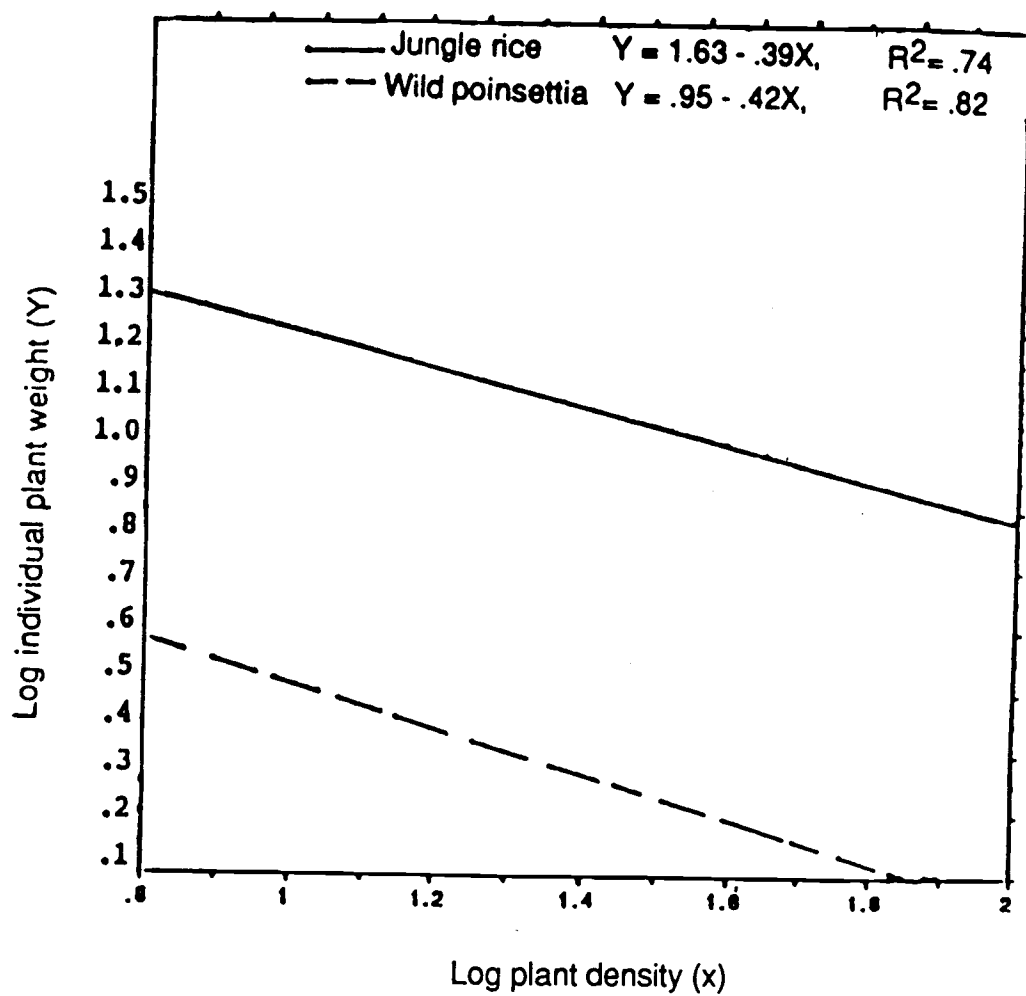


Figure 3.12. The relationship between individual plant weight and density (double log transformation).

Table 3.1. Density and proportion of rice, jungle rice, and wild poinsettia in binary associations with rice grown in pots. IITA, 1987.

Density, plants / pot	Proportions	
	Rice : jungle rice	Rice : wild poinsettia
2	1 : 1	1 : 1
3	1 : 2	1 : 2
3	2 : 1	2 : 1
4	1 : 3	1 : 3
4	3 : 1	3 : 1
4	2 : 2	2 : 2

Table 3.2. Effect of rice stand and weed density on rice growth at harvest. IITA, 1987.

Density, no.plant ⁻¹			Rice vs jungle rice		Rice vs wild poinsettia	
Rice	Weed	total	Tillers (no.plant ⁻¹)	Dry weight (g plant ⁻¹)	Tillers (no.plant ⁻¹)	Dry weight (g plant ⁻¹)
1	0	1	36	110.0	36	110.0
	1	2	32	87.1	33	108.8
	2	3	26	77.0	39	108.8
	Mean		31	91.4	36	109.2
2	0	2	30	57.0	30	57.0
	1	3	17	51.9	19	59.2
	2	4	17	41.1	19	52.2
	Mean		21	50.0	23	56.1
Lsd.05 for means at each rice density :			ns	22.9	5	15.6
Lsd.05 for means in the same rice density :			10	18.1	10	ns
Lsd.05 for Means in different rice density :			14	26.8	10	17.9

Table 3.3. Yield-density relationship between rice and jungle rice or wild poinsettia¹. IITA, 1987 (dry season).

Rice-jungle rice			
Model	$1 / W_R = -.0003 + .009 N_R + .0034 N_{Ec}$		$R^2 = .56$ $p = .0002$
Parameter	Param. est.	s.e.	p-value
Rice density	.009	.0021	.0003
Jungle rice density	.003	.0013	.01
Rice-wild poinsettia			
Model	$1 / W_R = -.004 + 0.009 N_R + .0007 N_{Eh}$		$R^2 = .75$ $p = .0001$
Parameter	Param. est.	s.e.	p-value
Rice density	.009	.001	.0001
Wild poinsettia density	.0007	.0007	.3

¹ Yield-density models (Spitters, 1983) describing the response of individual plant biomass of rice, to the densities of rice (N_R) and jungle rice (N_{Ec}) or wild poinsettia (N_{Eh}).

Table 3.4. Rice tillers per plant, as influenced by density of rice and jungle rice or wild poinsettia. IITA, 1987.

Rice - jungle rice			
Model	$1/\text{No. Tillers} = .005 + .018 N_R + .009 N_{Ec}$		$R^2 = .829$ $P = .07$
Parameter	Param. est.	s.e	p-value
Rice density	.018	.006	.06
Jungle rice density	.009	.003	.09
Rice - wild poinsettia			
Model	$1/\text{No. Tillers} = .005 + .018 N_R + .004 N_{Eh}$		$R^2 = .756$ $P = .1$
Parameter	Param. est.	s.e	P-value
Rice density	.018	.006	.06
Wild poinsettia density	.004	.003	.3

¹ Yield-density models (Spitters, 1983) describing the response of number of tillers per plant of rice to the densities of rice (N_R) and jungle rice (N_{Ec}) or wild poinsettia (N_{Eh}).

Table 3.5. Effect of intraspecific competition on wild poinsettia growth at 6 weeks after emergence. IITA, 1987 (rainy season).

Density (plants m ⁻²)	Branches (no. plant ⁻¹)	Leaf area (cm ² plant ⁻¹)	Dry weight (g plant ⁻¹)
10	5 a ²	197.2 a	1.8 a
20	4 a	178.5 a	1.4 b
40	2 b	171.4 a	1.4 b
80	2 b	96.6 b	0.9 c
CV%	10.5	8.6	9.5
P-value	< .001	< .001	< .01

¹ Density at establishment.

² Means in each column followed by the same letter (s) are not significantly different by DMRT.

Table 3.6. Effect of intraspecific competition on jungle rice growth at 6 weeks after emergence. IITA, 1987 (rainy season).

Density ¹ (plants m ⁻²)	Tillers (no. plant ⁻¹)	Leaf area (cm ² plant ⁻¹)	Dry weight (g plant ⁻¹)
10	25 a ²	773.3 a	12.5 a
20	18 a	658.1 a	11.6 a
40	11 b	379.4 b	8.2 b
80	10 b	222.2 b	5.8 b
CV%	9.2	4.5	16.0
P-value	< .0001	< .0001	< .01

¹ Density at establishment.

² Means in each column followed by the same letter (s) are not significantly different by DMRT.

Table 3.7. Effect of intraspecific competition on rice growth at 6 weeks after emergence. IITA, 1987 (rainy season).

Density ¹ (plants m ⁻²)	Tillers (no. plant ⁻¹)	Leaf area (cm ² plant ⁻¹)	Dry weight (g plant ⁻¹)
20	12 a ²	782.9 a	8.4 a
40	12 a	649.6 a	5.0 b
60	6 b	316.8 b	3.8 b
80	4 c	228.0 b	3.2 b
CV%	8.5	13.4	23.9
P-value	< .001	< .0001	< .01

¹ Density at establishment

² Means in each column followed by the same letter (s) are not significantly different by DMRT at 5% probability level.

Table 3.8. Yield-density relationship between rice and jungle rice or wild poinsettia¹. IITA, 1987 (rainy season).

Rice-jungle rice			
Model	$1 / W_R = -.023 + .0015 N_R + .0003 N_{Ec}$		$R^2 = .83$ $p = .0001$
Parameter	Param. est.	s.e.	p-value
Rice density	.0015	.0001	.0001
Jungle rice density	.0003	.00008	.0027
Rice-wild poinsettia			
Model	$1 / W_R = -.026 + .0012 N_R + .0001 N_{Eh}$		$R^2 = .77$ $p = .0001$
Parameter	Param. est.	s.e.	p-value
Rice density	.0012	.0001	.0001
Wild poinsettia density	.0001	.00008	.23

¹ Yield-density models (Spitters, 1983) describing the response of individual plant biomass of rice, to the densities of rice (N_R) and jungle rice (N_{Ec}) or wild poinsettia (N_{Eh}).

Table 3.9. Monoculture response of jungle rice and wild poinsettia to density. IITA, 1987 (rainy season).

Plant density (plants m ⁻²) ¹	Monoculture response		Relative monoculture response	
	Jungle rice	Wild poinsettia	Jungle rice	Wild poinsettia
10	46.3 a ²	17.5 a	.23 a	.31 a
20	92.0 a	71.8 b	.23 a	.64 b
40	372.0 b	159.2 c	.47 b	.71 b
80	1161.2 b	345.8 d	.73 b	.77 b
CV%	22.0	5.0	24.3	10.8
P-value	< .0001	< .0001	.002	< .001

¹ Density at establishment.

² Means in each column followed by the same letter (s) are not significantly different by DMRT.

Table 3.10. Yield-density relationship between jungle rice and wild poinsettia grown at different proportions with different rice densities. IITA, 1987 (rainy season).

Jungle rice			
Model	$1/W_{Ec} = .003 + .002 N_{Ec} - .0006 N_{Eh} + .002 N_R$		$R^2 = .72$ $p = .0001$
Parameter	Param. est.	s.e.	P-value
Jungle rice density	.002	.0007	.01
Wild poinsettia density	.0006	.0007	.4
Rice density	.002	.0004	.0001
Wild poinsettia			
Model	$1/W_{Eh} = .26 + .007 N_{Eh} + .006 N_{Ec} + .0002 N_R$		$R^2 = .13$ $p = .41$
Parameter	Param. est.	s.e.	P-value
Wild poinsettia density	.007	.0004	.14
Jungle rice density	.006	.0004	.19
Rice density	.0002	.0002	.9

¹ Expanded yield-density model (Spitters, 1983) describing the response of individual plant biomass of jungle rice ($1/W_{Ec}$) and wild poinsettia ($1/W_{Eh}$) to densities of jungle rice (N_{Ec}), rice (N_R), and wild poinsettia (N_{Eh}).

Chapter IV.

GENERAL DISCUSSION AND CONCLUSIONS

GENERAL DISCUSSION

In West Africa, efforts to increase total crop production are pushing old land uses toward radical changes and encouraging investigation of the enormous resources that have not been used. One of the approaches is to focus on genes for resistance to different diseases and pests, and recently, to tolerance to different problems (e.g. iron toxicity) and adaptation to different moisture conditions (e.g. drought, deep water etc.). Obviously, the genetic approach cannot solve all problems, and weeds remain a major constraint to improving rice production in hydromorphic soils.

I believe that, before research programs are developed, information must be gathered to characterize the ecosystems of various areas of rice cultivation for maximum use of their potential for improved crop production. At the International Institute of Tropical Agriculture (IITA), Resource Management research (RMR) is one component of the Resource and Crop Management Program (RCMP). One of the activities of this component is land characterization. My research work fits this aspect of the program.

Realistic management solutions cannot be developed without proper characterization and understanding of different crop-pest interactions. Untimely weed control is a common practice of farmers in West Africa. The critical period of weed interference has been established in different rice cultures. Previous works have been criticized, because little or no information was obtained in terms of phenological, morphological, or physiological states of the crop. These states change in time, season, and by location. The results of my research indicated that,

when rice and weeds emerge at the same time, the crop is more sensitive to weed interference during the early stages of growth, prior to tillering.

Consequently, its tiller production is primarily affected by competition from weeds such as jungle rice, which produces twice as many tillers as does rice. Proper weed control should aim to minimize crop-weed interference during this period in order to reduce yield losses. The efficient use of environmental resources by weeds is reflected in their biomass, which had an inverse linear relationship with rice grain yield, suggesting that weed dry weight is a better parameter reflecting competitive ability than density (Figure 2.2, Chapter II). This is because of the nonuniformity of natural weed populations and growth plasticity of plant species. Few weed plants may produce dry weight per unit area that equates that produced by a more dense population, because of the plastic response of plants.

However, it could have been interesting to look at the effect of proportion of selected weed species on the critical period. This could have been done by establishing proportions of two major weed species, but the area required would be much greater than when rice is associated with natural weed populations. The experiment, therefore, may become too large to conduct efficiently. It is tedious to prevent interference from weeds other than the selected species because weeds grow in profusion in warm and moist hydromorphic soils.

In newly developed hydromorphic lands, sedges are the predominant weed species, followed by grasses. A wide range of weeds, including broadleaved species, interfere with rice grown on hydromorphic soils because of the warm temperatures and the fluctuation of water table. In my studies, jungle rice and wild poinsettia were selected because they present different morphological characters, germinate readily, and their biology is better understood than that of sedges. Efforts should be made,

however, toward more biological studies on sedges to enable their consideration as potential competitors, and for a better understanding of weed interference in this rice culture.

Jungle rice and wild poinsettia were different in their interaction with rice. Early interference is expected from jungle rice, whose below-ground competition is greater than that of wild poinsettia, judging from the volume of roots each species produced in the first 4 WAE (Figure 2.7). Jungle rice also has the ability to produce tillers faster than rice. In the growth analysis experiment (experiment 2.2), plants were not grown until maturity and data on seed production were not obtained for a complete picture of plant potentials for competition. Observations of when rice and jungle rice produce maximum numbers of tillers would be helpful in determining why tiller production of rice is affected by the presence of weeds during the critical period of interference. Jungle rice started tillering one week before rice; consequently, the production of large number of decumbent tillers by jungle rice, left less space available for the crop at its tillering stage.

Wild poinsettia seemed to have greater potential to compete with rice for light, because of its upright growth habit. In a crowding situation, wild poinsettia plants tend to grow tall, and to produce fewer branches (experiment 3.2). As a result, the individual plant biomass was reduced with increasing density. Jungle rice did not seem to reach a yield plateau with the densities used. In preliminary studies where jungle rice density per m^2 varied from 50 to 200, a yield plateau was reached by both jungle rice and wild poinsettia, which made the interpretation of density effects on intra- or interspecific competition difficult. Therefore, it was a good decision to consider low densities (10, 20, 40, and 80 plants m^{-2} , but the range should have been greater to include 120 and 160 plants per m^2 .

Jungle rice was more competitive than wild poinsettia in binary

mixtures with rice, as well as in their associations in different densities of rice background (experiments 3.2 and 3.3). Since intraspecific competition had an impact on the outcome of competition, additional sets of replacement series mixtures at different total densities would have allowed better interpretation. In my study, competition was assessed between plants grown both in the field (experiments 2.1, 3.2, and 3.3) and in pots (experiments 2.2, 2.3, and 3.1). Under both conditions, wild poinsettia showed the the greatest sensitivity to intraspecific competition and jungle rice was more competitive than wild poinsettia when grown in mixtures. The high productivity of jungle rice (twice the number of tillers as produced by rice at 6 WAE when individual plants were grown at low densities in experiment 3.2, Tables 3.6 and 3.7), could explain its greater competitive ability than wild poinsettia in mixtures with rice. Sahai and Bhan (1984) have found that barndyardgrass was the most competitive among several weeds for nitrogen applied to drilled rice. This species is able to establish and grow fast and efficiently make use of the available resources to produce large number of tillers and seeds before it completes its short growth cycle. On the other hand, wild poinsettia apparently had a shading effect on rice plants later in the growing period. Its density effects on rice were only perceived at harvest (experiment 2.3, Table 2.5). The physiological and morphological attributes of the two weed species confer the ability to compete with rice in different ways and at different periods during the crop growing season. This makes development of a weed management program difficult in rice growing on hydromorphic soils, where both jungle rice and wild poinsettia can cause serious problems.

The sensitivity of the models varied with the species and with the experimental conditions. The models described 56 to 83 % the variation in individual plant biomass. In plants grown in pots , another competition

factor (space) may have had an influence on the outcome of plant interactions.

In the growth analysis experiment, because competition for light between rice and wild poinsettia is suspected, plants should have been grown in larger pots or in 1 by 1 m-square wooden containers with 50 cm height, filled with greenhouse soil, in order to monitor the leaf area index. This would, eventually, provide more information on when and why competition for light becomes important.

As earlier mentioned, the outcome of competition depends not only on density and proportion of weed species, but also on the crop attributes. Therefore, different varieties would have shown different responses to weed interference. It could be interesting to study the interference between two weed systems and some promising rice varieties, suitable for hydromorphic soils. Increasing crop density proved to increase the competitive ability of rice. One aspect of future research on crop-weed competition could be oriented towards the manipulation of plant population to improve the competitive ability of our crops against major weeds, to improve weed control and save money to low-income African farmers. Traits of individuals that contribute to rapid growth proved (Chapter II and Roush and Radosevich, 1985) to have a positive influence on the competitive ability of plant species in mixtures. This calls on plant breeders, crop physiologists, ecologists, and weed scientists for close collaborations in the task of developing successful and ecologically sound weed management strategies.

At present, handweeding twice is a practical option to keep weed pressure at a low level. However, this practice does not give satisfactory results when rice fields are infested by perennial weeds. The use of herbicides has been disappointing because most of the recommended

compounds are exposed to rapid breakdown in the warm and moist conditions of hydromorphic soils. Mechanical weeding is also unsuccessful because of a lack of water control. Land preparation twice, at the end of the cropping season and prior to the onset of rains, in combination with postemergence herbicides or handweeding, could be a good weed control package for improved rice production in hydromorphic soils.

Although allelopathy is difficult to prove, I tried, using a simple bioassay technique, to look for involvement of this phenomenon in weed interference with rice grown on hydromorphic soils. The results suggest a level of toxic substances in some of the weed species that affect the growth of rice seedlings. Soils on which uniform stands of the weeds grew and leaf aqueous extracts were used, because, under field conditions, the released substances may not be available in the root zone. They can be broken down by microorganisms, transformed to a more toxic form, tied up by soil particles, or lost through evaporation or leaching. The presence of a toxic substance in leaf extract of a given species is not necessarily allelopathic, unless it accumulates in a sufficient amount to exert an inhibitory effect. Another difficulty is to simulate natural environmental conditions in the laboratory or greenhouse. For conclusive evidence, one should be able to devise a method based on Koch's postulates as applied to identification of a previously unknown disease. The toxic substance must be isolated, identified, and applied to a test species to reproduce symptoms similar to those originally observed, although avoiding contamination in the isolation process is not always easy.

CONCLUSIONS

1. On hydromorphic soils, direct-seeded rice and weeds emerge at the same time. Consequently, weed interference occurs soon after planting.
2. The critical period of weed interference in direct-seeded rice grown on hydromorphic soils in subhumid tropics starts from the second week until the sixth week after crop emergence.
3. In addition to grain yield, rice tiller and panicle numbers appeared to be good indicators of crop response to weed interference.
4. Jungle rice was more competitive than wild poinsettia. It caused the greatest damage to rice plants at densities as low as 40 plants m^{-2} . Intraspecific competition among plants of the crop and weeds, had an impact on the outcome of weed interference.
5. Based on growth analysis and plant form, jungle rice is a potential competitor for water and nutrients, while wild poinsettia has a greater potential to compete for light when associated with rice.
6. Data from competition studies, where species of different life forms are involved, should be interpreted with caution. In such situation, assessment of the outcome of competition based on relative, rather than absolute, values would be more suitable.

7. Methods of analysis also should include both qualitative and quantitative assessments of the competitive relationships. Perhaps, the use of the expanded yield-density model is an alternative for interpretation of data obtained from replacement series experiments.
8. The outcome of weed interference was mainly due to weed competition for limited resources, because there was only little evidence for chemical inhibition of the crop growth. However, chemical interaction seemed to occur in rice associations with wild poinsettia and *F. littoralis*.

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APPENDIX

Table A.1. Rice tillers (No. plant⁻¹) and yield (Kg ha⁻¹), weed density (No. m⁻²), and weed dry weight (g m⁻²) as influenced by time of weeding: weed-free (WF) or unweeded (UNW) for a certain period of time (weeks after emergence) and then left unweeded or weed-free until harvest.

Replication	Time	Yield		Tillers		Weed-free	
		WF	UNW	WF	UNW	density	dry weight
1	0	266.4	1977.6	5	11	248	131.9
1	2	1188.6	1783.0	5	9	1060	177.4
1	4	1875.2	1799.4	8	9	160	18.7
1	6	2029.0	2260.4	10	9	100	5.8
1	8	2033.0	1578.0	8	7	192	14.1
1	2+6	1797.4	1797.4	9	9	432	21.3
1	4+8	1291.2	1291.2	10	10	56	5.4
2	0	862.8	1600.8	4	10	460	15.8
2	2	1788.0	2557.2	7	7	268	112.6
2	4	1164.2	1496.8	7	8	204	63.1
2	6	1465.6	1611.2	9	8	92	5.0
2	8	1968.8	1788.0	7	7	76	3.5
2	2+6	1927.2	1927.2	9	9	36	.7
2	4+8	1964.6	1964.6	9	9	200	50.5
3	0	215.6	2128.6	3	8	228	94.7
3	2	1224.4	1764.4	8	10	108	9.4
3	4	768.2	1883.8	10	9	24	1.7
3	6	1360.4	1733.1	10	8	8	.6
3	8	1172.0	722.8	10	7	20	1.2
3	2+6	1295.6	1295.6	9	9	12	.4
3	4+8	1412.8	1412.8	12	12	8	.4
4	0	711.6	1785.4	6	7	128	32.1
4	2	701.2	1731.4	5	8	172	54.9
4	4	1450.4	1479.8	8	8	148	9.7
4	6	1157.4	2162.0	6	9	56	2.6
4	8	1743.4	1144.8	4	5	60	4.5
4	2+6	1695.4	1695.4	9	9	80	4.1
4	4+8	1214.0	1214.0	8	8	60	1.7

Table A.2. Rice yield (Kg ha^{-1}) and tillers (No. per linear meter) as influenced by time of weeding: weed-free (WF) or unweeded (UNW) for a certain period of time (weeks after emergence) and then left unweeded or weed-free until harvest.

Replication	Time	Yield		Tillers	
		WF	UNW	WF	UNW
1	0	2192.6	4502.1	78	74
1	1	1283.4	3647.6	47	80
1	2	1679.4	3453.5	57	72
1	4	3778.8	2729.0	79	76
1	6	4568.5	3046.8	93	70
1	8	4041.9	2117.1	82	51
2	0	2269.4	7422.5	50	78
2	1	1833.9	4442.8	76	94
2	2	3393.3	2943.0	75	94
2	4	2475.4	3334.9	63	79
2	6	5299.3	3641.9	62	63
2	8	5334.0	2386.3	96	72
3	0	2875.8	5643.0	59	96
3	1	3364.8	4143.8	60	57
3	2	3204.5	4225.8	87	87
3	4	4380.6	2658.4	78	72
3	6	5421.6	2636.4	71	59
3	8	5507.4	2932.0	70	60

Table A.3. Weed density (No.m⁻²) and dry weight (g m⁻²) as influenced by time of weeding: weed-free (WF) or unweeded (UNW) for a certain period of time (weeks after emergence) and then left unweeded or weed-free until harvest.

Replication	Time	Density		Dry weight	
		WF	UNW	WF	UNW
1	0	4224	0	451.5	0
1	1	2352	0	103.6	0
1	2	3120	0	80.1	0
1	4	1888	0	45.6	0
1	6	0	2416	0	91.8
1	8	0	3273	0	79.2
2	0	4072	0	209.4	0
2	1	4656	0	255.3	0
2	2	3120	0	45.2	0
2	4	2440	0	43.2	0
2	6	0	4936	0	361.5
2	8	0	2720	0	367.2
3	0	1352	0	632.8	0
3	1	448	0	212.8	0
3	2	1080	0	413.6	0
3	4	136	0	82.4	0
3	6	0	776	0	436.0
3	8	0	568	0	451.5

Table A.4. Growth of rice (R), *E. colona* (Ec), and *E. heterophylla* (Eh): Absolute growth (G), leaf area ratio (LAR), and net assimilation rate (NAR) at different growth periods (2, 4, 6, and 8 weeks after emergence).

Replication	Species	2	Growth period		
			4	6	8
Absolute growth					
1	R	1.1	2.3	4.1	25.3
1	Ec	1.1	2.2	11.4	24.7
1	Eh	1.1	2.2	6.5	16.1
2	R	1.1	2.1	4.7	26.0
2	Ec	1.0	2.0	12.0	25.3
2	Eh	1.0	2.0	6.1	14.0
3	R	1.0	2.2	4.5	26.7
3	Ec	1.0	2.1	11.9	25.1
3	Eh	1.0	2.1	5.9	15.1
4	R	1.0	2.2	4.7	26.0
4	Ec	1.0	2.2	12.2	25.1
4	Eh	1.0	2.1	6.8	15.0
LAR					
1	R	756.5	269.7	183.9	123.7
1	Ec	726.0	366.2	132.7	59.4
1	Eh	333.2	550.7	154.4	84.1
2	R	430.0	257.9	191.8	117.6
2	Ec	760.0	266.7	141.5	64.4
2	Eh	310.0	240.0	150.4	115.3
3	R	385.0	322.9	224.5	144.7
3	Ec	690.5	578.3	113.6	134.9
3	Eh	230.7	296.0	134.6	91.4
4	R	484.0	266.4	201.0	146.0
4	Ec	850.0	920.0	134.0	68.4
4	Eh	335.8	341.3	180.8	73.3

Table A.4. cont.

Replication	species	2	Growth period		
			4	6	8
NAR					
1	R	67.8	79.8	362.0	566.4
1	Ec	55.1	75.3	452.4	339.3
1	Eh	60.4	75.9	224.5	302.4
2	R	59.3	71.3	223.0	389.4
2	Ec	24.8	38.9	410.2	348.8
2	Eh	18.1	32.5	245.8	409.0
3	R	58.4	69.1	188.1	460.9
3	Ec	20.9	33.7	222.5	544.9
3	Eh	15.8	28.6	275.2	602.0
4	R	48.9	57.9	100.3	334.1
4	Ec	46.7	54.6	253.4	469.7
4	Eh	13.9	26.3	269.2	234.2

Table A.5. Plant height (cm) and fresh weight (g /5 plants) of rice grown on soils collected from sites where *E. colona* (Ec), *E. heterophylla* (Eh), *C. difformis* (Cd), and *F. littoralis* (Fl) were growing in monocultures, and on greenhouse soil (Gh), with and without nutrient solution.

Replication	Treatment	Plant height		Fresh weight	
		With nutrient	Without	With nutrient	Without
1	Ec	17.4	17.5	1.28	1.31
1	Eh	15.9	15.0	1.00	1.09
1	Cd	18.2	20.0	2.10	1.34
1	Fl	10.9	11.4	.50	.30
1	Gh	20.9	21.0	2.78	2.46
2	Ec	16.2	20.9	.90	2.50
2	Eh	20.6	21.6	2.06	2.17
2	Cd	20.6	19.0	1.85	1.41
2	Fl	11.5	10.5	.40	.36
2	Gh	23.1	21.7	2.77	3.30
3	Ec	19.6	17.2	2.12	1.61
3	Eh	17.2	19.6	1.75	3.06
3	Cd	17.4	17.9	1.07	1.42
3	Fl	10.2	9.7	.41	.28
3	Gh	21.5	21.9	2.78	3.67
4	Ec	14.7	16.7	1.04	1.54
4	Eh	18.7	17.8	2.40	1.06
4	Cd	19.5	15.3	1.94	1.55
4	Fl	13.5	10.0	.58	.36
4	Gh	23.4	20.7	3.74	4.78

Table A.6. Different concentrations of aqueous extracts: 1/10, 1/20, and 1/40 (g/ml distilled water) of plant materials of selected weed species on shoot and radicle length (cm) of rice and cowpea. *E. colona* (Ec), *E. heterophylla* (Eh), *C. difformis* (Cd), and *F. littoralis* (Fl). Distilled water (Dw) was used as control.

Replication	Treatment	Rice				Cowpea	
		1/10	1/20	Cocentrarion 1/40	1/10	1/20	1/40
Shoot length							
1	Ec	4.2	4.9	5.1	4.0	6.5	10.0
1	Eh	4.1	4.9	5.6	0	6.5	14.0
1	Cd	3.8	5.4	4.4	0	6.6	10.5
1	Fl	3.6	5.1	4.4	5.4	10.5	3.8
1	Dw	4.5	5.3	5.1	9.5	6.8	9.8
2	Ec	4.4	5.0	4.8	2.8	7.5	7.4
2	Eh	2.7	4.8	4.8	0	11.0	11.0
2	Cd	3.2	5.0	5.2	0	7.2	0
2	Fl	3.8	5.5	5.3	2.9	12.5	5.5
2	Dw	6.3	4.9	4.7	10.1	5.8	8.3
3	Ec	4.0	5.8	6.0	3.6	8.3	10.7
3	Eh	0	5.3	5.4	1.5	0	0
3	Cd	4.1	4.8	5.6	2.4	4.2	0
3	Fl	4.2	5.0	5.7	2.5	5.8	8.8
3	Dw	4.6	5.6	5.5	6.4	7.7	9.6
4	Ec	4.9	5.5	5.8	2.8	8.6	8.0
4	Eh	3.5	5.7	4.9	0	0	0
4	Cd	3.3	6.2	4.9	0	8.9	12.5
4	Fl	3.8	4.9	5.6	3.0	3.8	0
4	Dw	3.9	4.7	5.0	6.5	0	10.0
Radicle length							
1	Ec	5.6	6.2	6.7	3.4	5.0	6.5
1	Eh	3.4	8.7	9.5	0	4.6	6.0
1	Cd	6.4	6.8	6.4	0	5.8	8.2
1	Fl	5.2	5.8	7.2	7.7	6.0	4.4
1	Dw	4.5	5.3	5.1	9.5	6.8	9.8

Table A.6. cont.

Replication	Treatment	Rice			Cowpea		
		1/10	1/20	1/40	1/10	1/20	1/40
2	Ec	6.9	7.5	7.2	3.8	5.0	6.1
2	Eh	4.6	8.0	7.0	0	6.5	4.3
2	Cd	5.3	7.5	5.8	0	5.1	0
2	Fl	5.5	8.5	6.6	3.6	6.0	5.6
2	Dw	9.2	9.2	6.3	7.3	7.5	4.4
3	Ec	6.4	7.0	7.8	3.9	5.7	8.5
3	Eh	0	8.6	8.0	3.1	0	0
3	Cd	7.3	6.0	7.5	4.5	3.2	7.5
3	Fl	6.6	6.7	7.4	4.2	7.0	13.3
3	Dw	6.0	8.2	7.2	5.6	5.9	7.4
4	Ec	6.6	7.3	8.7	4.1	5.2	6.2
4	Eh	4.6	9.3	9.4	0	0	0
4	Cd	5.8	8.7	7.7	0	7.4	5.5
4	Fl	5.5	6.6	7.7	5.0	3.1	0
4	Dw	5.2	8.8	0	3.5	0	6.0

Table A.7. Tillers (No plant⁻¹) and dry weight (g plant⁻¹) of rice (R) and *E. colona* (Ec), and branches of *E. heterophylla* (Eh) grown in pots: monoculture data at harvest. Densities: 1, 2, 3, and 4 plants per pot.

Replication	Density	Species	Tillers	Branches	Dry weight
1	1	R	39	-	133.6
1	1	Ec	61	-	31.9
1	1	Eh	-	13	14.7
1	2	R	20	-	65.5
1	2	Ec	21	-	24.9
1	2	Eh	-	8	7.8
1	3	R	24	-	48.6
1	3	Ec	17	-	18.8
1	3	Eh	-	7	7.2
1	4	R	11	-	29.4
1	4	Ec	13	-	13.1
1	4	Eh	-	7	5.6
2	1	R	30	-	97.8
2	1	Ec	43	-	48.1
2	1	Eh	-	5	8.4
2	2	R	19	-	55.9
2	2	Ec	22	-	23.9
2	2	Eh	-	7	8.5
2	3	R	14	-	38.0
2	3	Ec	19	-	17.3
2	3	Eh	-	7	7.6
2	4	R	10	-	28.3
2	4	Ec	12	-	11.1
2	4	Eh	-	3	2.1
3	1	R	37	-	94.5
3	1	Ec	45	-	48.4
3	1	Eh	-	11	12.9
3	2	R	35	-	51.0
3	2	Ec	29	-	30.2
3	2	Eh	-	8	4.1
3	3	R	13	-	37.2
3	3	Ec	22	-	18.3
3	3	Eh	-	5	4.2

Table A.7. cont.

Replication	Density	Species	Tillers	Branches	Dry weight
3	4	R	12	-	25.7
3	4	Ec	20	-	12.6
3	4	Eh	-	5	2.8
4	1	R	39	-	114.3
4	1	Ec	63	-	52.3
4	1	Eh	-	9	8.6
4	2	R	46	-	55.6
4	2	Ec	33	-	23.4
4	2	Eh	-	8	4.7
4	3	R	15	-	43.2
4	3	Ec	21	-	11.5
4	3	Eh	-	3	6.6
4	4	R	10	-	21.5
4	4	Ec	22	-	14.1
4	4	Eh	-	6	4.2

Table A.8. Individual plant weight (g plant⁻¹) of *E. colona* and *E. heterophylla* in each plot. Data obtained from monocultures of the addition series experiment at densities of 10, 20, 40, and 80 plants m⁻².

Replication	Density	<i>E. colona</i>	<i>E. heterophylla</i>
1	10	14.7	3.3
1	20	15.2	2.7
1	40	13.9	1.6
1	80	6.0	1.6
2	10	15.7	4.1
2	20	15.8	2.3
2	40	11.0	1.7
2	80	7.4	1.6
3	10	15.7	4.1
3	20	15.2	1.8
3	40	7.5	1.9
3	80	7.9	1.5

Table A.9. Reciprocal weight of individual rice plant in the rice-jungle rice(R vs Ec) and rice-wild poinsettia (R vs Eh) associations. Weeds were planted at densities of 10, 20, 40, and 80 plants m⁻², and rice at 20, 40, 60, and 80 plants m⁻².

Replication	Rice density	Weed density	R vs Ec	R vs Eh
1	20	10	.074	.062
1	20	20	.076	.066
1	20	40	.083	.054
1	20	80	.086	.079
1	40	10	.060	.064
1	40	20	.060	.062
1	40	40	.077	.076
1	40	80	.079	.077
1	60	10	.122	.089
1	60	20	.123	.081
1	60	40	.141	.075
1	60	80	.143	.086
1	80	10	.133	.119
1	80	20	.143	.143
1	80	40	.145	.141
1	80	80	.179	.104
2	20	10	.059	.072
2	20	20	.054	.077
2	20	40	.062	.083
2	20	80	.076	.082
2	40	10	.062	.063
2	40	20	.062	.066
2	40	40	.074	.076
2	40	80	.076	.083
2	60	10	.088	.132
2	60	20	.090	.125
2	60	40	.102	.125
2	60	80	.086	.139
2	80	10	.123	.127
2	80	20	.139	.167
2	80	40	.147	.169
2	80	80	.137	.172

Table A9. cont.

Replication	rice density	Weed density	R vs Ec	R vs Eh
3	20	10	.060	.071
3	20	20	.058	.043
3	20	40	.083	.071
3	20	80	.084	.072
3	40	10	.077	.076
3	40	20	.060	.068
3	40	40	.078	.072
3	40	80	.082	.075
3	60	10	.128	.093
3	60	20	.139	.099
3	60	40	.123	.100
3	60	80	.141	.103
3	80	10	.143	.139
3	80	20	.172	.167
3	80	40	.145	.145
3	80	80	.164	.164

Tasble A.10. Dry weight of individual plant of *E. colona* (Ec) and *E. heterophylla* (Eh) planted in different proportions (total density of 80 plants m⁻²) in different rice background (0, 20, 40, 60, and 80 plants m⁻²).

Density			Dry weight	
Ec	Eh	Rice	Ec	Eh
80	0	0	7.1	0
40	0	0	10.8	0
20	0	0	15.4	0
10	0	0	15.4	0
0	80	0	0	1.6
0	40	0	0	1.7
0	20	0	0	2.3
0	10	0	0	3.8
80	0	0	4.9	0
60	20	0	6.8	2.3
40	40	0	10.5	2.0
20	60	0	10.3	1.4
0	80	0	0	1.5
80	0	20	4.7	0
60	20	20	4.5	2.3
40	40	20	9.2	.6
20	60	20	13.3	.6
0	80	20	0	.9
80	0	40	4.5	0
60	20	40	5.1	1.5
40	40	40	5.5	.7
20	60	40	11.5	1.9
0	80	40	0	2.0
80	0	60	3.6	0
60	20	60	2.6	1.6
40	40	60	5.3	1.1
20	60	60	7.7	1.7
0	80	60	0	1.7
80	0	80	3.1	0
60	20	80	2.1	1.5
40	40	80	5.3	.9
20	60	80	6.4	1.2
0	80	80	0	1.4