210 Kagoshima Univ. Res. Center S. Pac., Occasional Papers, No. 18, 210-229, 1990

Growth Responses of Upland Rice and Sorghum Plants to Soil Moisture in Mixed and Pure Stands

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Introduction

Mixed-cropping, or intercropping systems which are commom traditional practices throughout the tropics [11,19,22] are also predominant in African farming systems [3,14,25,28]. It is often suggested that not only relative advantages but also improved stability of yield is one of the major reasons why intercropping continues to be an extremely important practice in many developing areas of the world, especially those areas of greater risk [28,29]. But as yet any quantitative information on the magnitude or practical importance of this improvement has been extremely limited; indeed, in many situations there is still considerable doubt as to whether improved stability is actually achieved. REES [31] indicated that intercropping, in the drought seasons of 1982/83 and 1983/84 in Botswana, gave harmful effects on crop production, particularly in standard row at the medium plant densities. FISHER [12] also showed that mixed-cropping was disadvantageous under poor moisture supply but advantageous under good moisture supply, with a conclusion that although mixed-cropping has been regarded as the expression of African farmers' desire to minimize risks, it does not appear always to operate well at the section where the major risk is from drought, whereas it may operate as it is expected if the risk is from pest or disease. However, in the rain-fed semi-arid tropics the lack of moisture has been major causes both of low yields and of marked instability of yields from season to season. If the relative advantages, indeed, depend on water resource, poor and erratic rainfall characterizing the climate of semi-arid tropics may well make the relative advantages of mixed-cropping markedly unstable. This suggestion is considerably inconsistent with the concept of improved stability. On the other hand, LIGHTFOOT *et al.* [26] failed to ascertain greater stability of intercropping in Botswana, where the environmental conditions were harsh. RAO *et al.* [29] and BAKER [6] concluded that intercropping gave yield advantage in a wide range of environmental conditions and that intercropping should be considered more stable than sole cropping, in a sense that probability of monetary returns falling below given 'disaster levels' was less in intercropping. In addition, NATARAJAN *et al.* [27] found that intercropping-advantages of various crop combinations at a fixed total density actually increased at a time when irrigation was withheld. As mentioned above, the informations on stability are very complicated, depending on the crop combinations, population density and the kind of damage, though greater yield advantages under stress have often been suggested as a probable effect of intercropping. Because it is expected that stability of mixed-cropping may be enhanced in a case when one component compensates for the damage done to another, this study was carried out in order to examine whether such a compensation might be achieved for drought damage or excess-moisture injury in the sorghum-upland rice mixture.

Materials and Methods

The experiments were carried out inside the vinyl plastic hothouse in the Experimental Farm of Faculty of Agriculture, Kagoshima University, from 17 May to 21 June, 1988. Grains of the sorghum (*Sorghum bicolor* Moench, cv. Snow brand hybrid sorgo) and the upland rice (*Oryza sativa* L., cv. Norin 11) were sown in the 13 liter seedling culture boxes filled with a sort of uniform soil of 9.24kg of dried soil passed through a sieve of 5mm across, on 17th, May. At sowing date, three treatments were established; sole sorghum, sole upland rice and mixture treatments. In order to cause the young plants, in the early stage when the present experiment was carried out, to drastically compete for the environmental resources, seeds were sown at high seeding rate of 24 grains per pot (170 grains/m^2) in the sole cropping treatments. And, seeds were sown in grid. Because it has been pointed out that relative advantages from mixed-cropping were produced, at least partly, by the increased population pressure, the seeding rate in mixture treatment was also fixed at the respective 12 grains, setting limit at 24 grains in total to exclude its effect. And, seeds were sown alternately.

Compound fertilizer (8-8-8) was applied at the rate of 21g per pot, on 30th, May. Six soil moisture treatments, from arid condition to submerged condition, were imposed on the plants for three weeks from 31st May to 21st June. At the beginning of the treatments, the soil moisture ratio in each seedling culture box was kept in about 16%, and the relative plants were noted to be at the states of growth, as shown in Table 1. Soil moisture control was carried out by a gravimetric method, and the amount of water supplied in order to keep the soil moisture condition constant was sprinkled on the soil surface every day. However, because the soil moisture conditions changed gradually with the increases in evapotranspiration and in plant weight, the soil moisture ratio used in this paper was enforced to be an averaged value during the treatment.

On 21st, June, 24 plants with two replications were harvested from each division. Five moderate plants selected from each harvest sample were separated into leaf blades, stems (including leaf sheath) and roots, after plant height, stem length, leaf age, number of tiller, number of green leaves, and leaf length and leaf width were determined. Leaf length and leaf width determined were those of the 7th and 5th leaf blades in sorghum and upland rice, respectively. The determination of leaf width was done at the most em-

Table 1. Growth increments of sorghum and upland rice at the beginning of soil moisture treatments

Treatments	Plants	Plant height (cm)	Stem length (cm)	Leaf age	Leaf area (dm^2/pot)	Total weight (g/pot)
Mono-cropping	Sorghum	23.9	6.3	5.1	6.91	4.72
	Upland rice	16.6	5.1	3.0	1.30	1.26
Mixed-cropping	Sorghum	21.6	6.0	5.1	2.81	1.96
	Upland rice	16.0	5.0	3.0	0.61	0.62
	Total	–	–	–	3.42	2.58

inent section. Leaf area was also measured with automatic area meter. The sub-samples and the bulk samples were dried at 80°C for 72 hours in the dehydrater, and dry weights were determined.

Evapotranspiration in each plot was assessed by accumulating the total amount of water supplied during the soil moisture treatment and the increased total fresh weight.

Results

Dry matter production

Total dry weight in sole sorghum increased with the increasing in soil moisture ratio and then declined with an optimum counting around 45%. But, in sole upland rice, it continued to increase steadily with the increasing in soil moisture ratio, and no optimum could be recognized within the limits of soil moisture in this experiment (Fig. 1). The

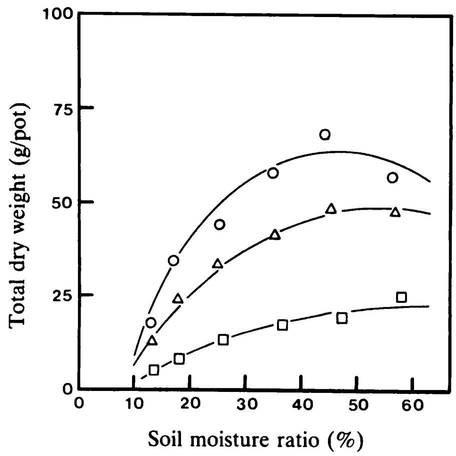

Fig. 1. Relationship between the soil moisture ratio and total dry matter weight at the time of harvest.
○ : Sole sorghum, □ : Sole upland rice, △ : Mixture

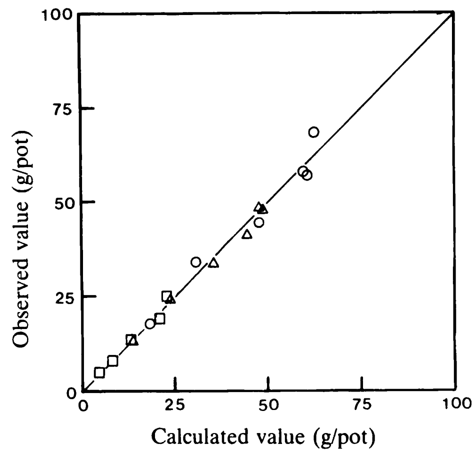

Fig. 2. Comparison of the calculated value of total dry matter weight [based on Eqs. (1), (2) and (3)] with the observed value.
Symbols are the same as those shown in Fig. 1.

effects of soil moisture upon the total dry weights of sole sorghum and sole upland rice were to be formulated by the following reciprocal equations, respectively :

Sole sorghum ; $$\frac{1}{w} = \frac{0.2625}{f - 8.0} + 0.0001917\,(f - 8.0) + 0.001667 \quad \text{Eq. (1)}$$

Sole upland rice ; $$\frac{1}{w} = \frac{0.8125}{f - 9.4} + 0.027083 \quad \text{Eq. (2)}$$

where, f and w are soil moisture ratio (%) and total dry weight (g/pot), respectively. The observed values and the calculated values based upon Eqs. (1) and (2) corresponded considerably well (Fig. 2). Eqs. (1) and (2) indicate that the soil moisture acted as optimum factor [18] and as linear factor [20] on the dry matter productions in sole sorghum and sole upland rice, respectively, and that the uppermost limit values of unavailable soil moisture (f_o) were 8.0 and 9.4% in sole sorghum and in sole upland rice, respectively. These implications bespeak that upland rice possesses larger wet endurance than sorghum and that sorghum surpasses upland rice in drought tolerance or in dehydration tolerance.

The relationship between soil moisture ratio and total dry weight in mixture was formulated satisfactorily by the following reciprocal equation (Fig. 2).

Mixture ; $$\frac{1}{w} = \frac{0.3100}{f - 8.5} + 0.000160\,(f - 8.5) + 0.0065 \quad \text{Eq. (3)}$$

Eq. (3) indicates that soil moisture acted as optimum factor on the dry matter production in mixture as well as sole sorghum, but f_o and optimum soil moisture ratio (f_{opt}) of the former were 0.5 and 7.5% higher than those of the latter, respectively. Total dry weight in mixture lay halfway between those of sole sorghum and of sole upland rice. The land equivalent ratio (*LER*), defined as a relative land area that would be required as sole crops to produce the achieved yields in the mixed-cropping, was fixed to be near-

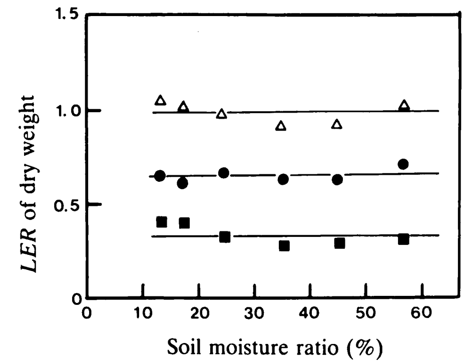

Fig. 3. Relationship between the soil moisture ratio and land equivalent ratio (*LER*) of total dry weight.
● : Sorghum *LER*, ■ : Upland rice *LER*, △ : Total *LER*

$$\text{Sorghum } LER = \frac{\text{mixed-crop sorghum dry weight}}{\text{mono-crop sorghum dry weight}}$$

$$\text{Upland rice } LER = \frac{\text{mixed-crop upland rice dry weight}}{\text{mono-crop upland rice dry weight}}$$

Total *LER* = Sorghum *LER* + Upland rice *LER*

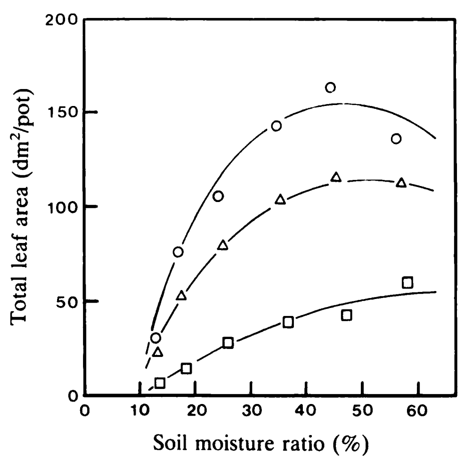

Fig. 4. Relationship between the soil moisture ratio and total leaf area at the time of harvest. Symbols are the same as those shown in Fig. 1.

ly constant, independent of soil moisture conditions (Fig. 3). *LER* of sorghum became larger than 0.5 and that of upland rice smaller than 0.5, respectively. Total *LER* was nearly equal to 1.0.

Leaf area development

Leaf area was also successfully correlated with soil moisture ratio in the same way, only the uppermost limit values of unavailable soil moisture for leaf area were 1.3-2.2% higher than those for dry weight (Fig. 4).

Sole sorghum ; $$\frac{1}{u} = \frac{0.0860}{f - 10.2} + 0.00006\,(f - 10.2) + 0.0018 \qquad \text{Eq. (4)}$$

Sole upland rice ; $$\frac{1}{u} = \frac{0.4650}{f - 10.7} + 0.0090 \qquad \text{Eq. (5)}$$

Mixture ; $$\frac{1}{u} = \frac{0.1104}{f - 10.5} + 0.000046\,(f - 10.5) + 0.0043 \qquad \text{Eq. (6)}$$

In Eqs. (4), (5) and (6), f and u indicate soil moisture ratio (%) and leaf area (dm^2/pot), respectively. The calculated values based on Eqs. (4), (5) and (6) agreed fairly well with the observed values (Fig. 5). *LER*s of leaf area were around 0.66, 0.34 and 1.0 in sorghum, upland rice, and total, respectively, independently of soil moisture ratio (Fig. 6).

The higher the soil moisture became, the more numerous the leaf number became alike in sorghum and in upland rice, but the magnitude was noted to be more conspic-

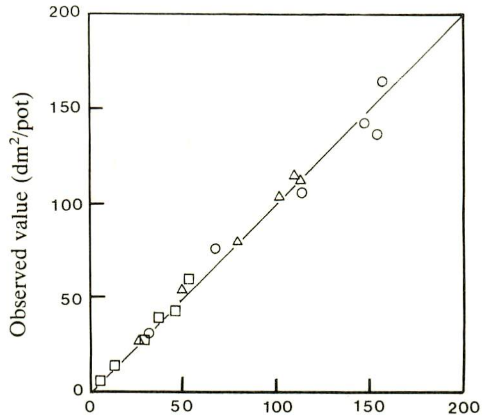

Fig. 5. Comparison of the calculated value of total leaf area [based on Eqs. (4), (5) and (6)] with the observed value.
Symbols are the same as those shown in Fig. 1

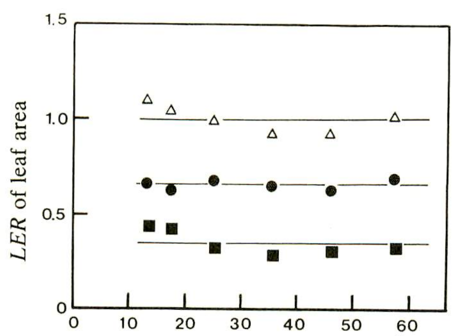

Fig. 6. Relationship between the soil moisture ratio and land equivalent ratio (*LER*) of total leaf area.
Symbols are the same as those shown in Fig. 3.

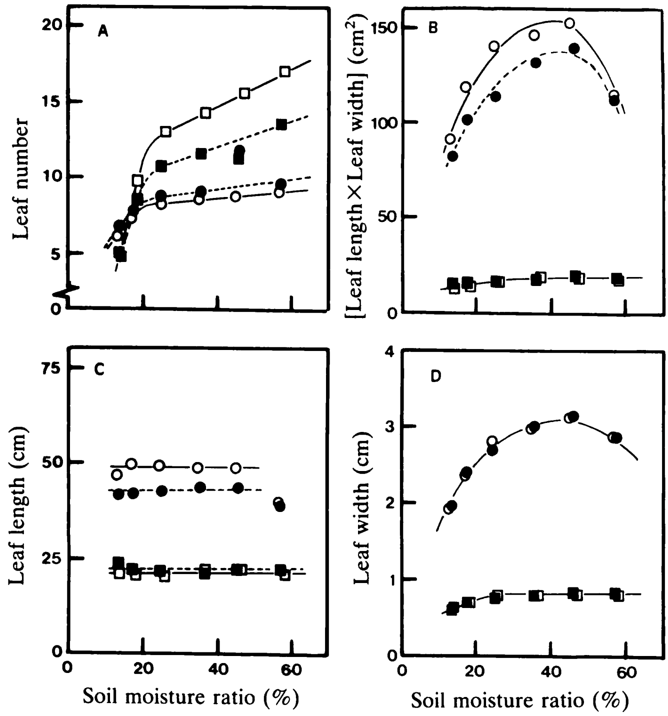

Fig. 7. Relationship between the soil moisture ratio, and leaf number (A), [leaf length × leaf width] (B), leaf length (C) and leaf width (D) at the time of harvest.
○ : Mono-crop sorghum, ● : Mixed-crop sorghum,
□ : Mono-crop upland rice, ■ : Mixed-crop upland rice
Leaf length and leaf width determined were those of the 7th and 5th leaf blades in sorghum and upland rice, respectively.

uous in upland rice than in sorghum (Fig. 7A). However, in the former, a little increasing was noted in the [leaf length × leaf width] (*LW*), which may be in proportion to leaf area per one leaf, whereas sorghum's *LW* increased rapidly due to the increase in soil moisture ratio and then declined quickly under an excess-moisture condition (Fig. 7B). These results suggest emphatically that as shown in Fig. 4, leaf areas of upland rice and sorghum were principally prescribed by the leaf number and by the leaf area per one leaf, respectively. The increases in *LW* occurred with the increasing in soil moisture were entirely correlated with an increase in the leaf width because leaf length was constant, independently of soil moisture condition, excepting an excess-moisture condition. But the abrupt decline in *LW* of sorghum under an excess-moisture condition was correlated with a rapid decreasing in leaf length rather than leaf width (Figs. 7C and 7D). The above-mentioned aspects of relationships were recognized irrespective of the sorts of cropping, namely whether in mono-cropping or in mixed-cropping, but the absolute values were, more or less, dependent on the cropping systems. In the mixed-cropping leaf number increased in sorghum and decreased in upland rice, respectively, as com-

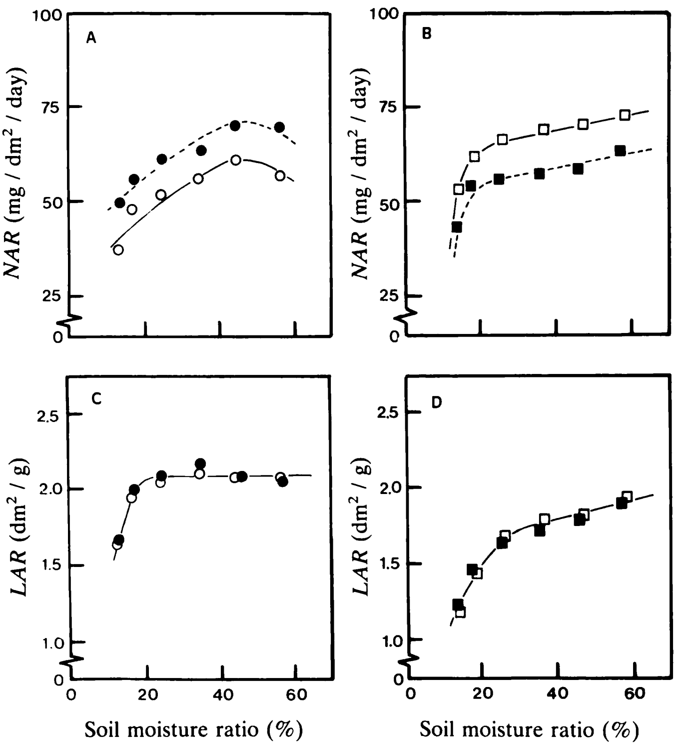

Fig. 8. Relationship between the soil moisture ratio, and net assimilation rates (*NAR*) and leaf area ratios (*LAR*) during soil moisture treatment.
(A) and (C) : Sorghum, (B) and (D) : Upland rice.
Symbols are the same as those shown in Fig. 7.

pared with those in the sole cropping. Under mixed-cropping *LW* or leaf length became slightly larger in upland rice and considerably smaller in sorghum than under mono-cropping. Fundamentally no difference was noted in the relationship between soil moisture and leaf width whether in mono-cropping or in mixed-cropping.

Growth function

The net assimilation rate (*NAR*) defined as the dry matter production rate per unit leaf area, increased continuously in upland rice together with the increasing in soil moisture ratio, whereas sorghum's *NAR* tended to decline under excess-moisture conditions more than 45% (Figs. 8A and 8B). On the whole the decline in *NAR* due to water deficit tended to be smaller in upland rice than in sorghum. The leaf area ratio (*LAR*) defined as the ratio of leaf area to the total dry weight was higher in sorghum than in upland rice under all soil moisture conditions (Figs. 8C and 8D). *LAR* declined consistently in upland rice together with the decreasing in soil moisture ratio, though soghum's *LAR* was fixed to be constant within soil moisture ratio over 20% and afterwards decreased.

*NAR*s of component crops in mixture were nearly equal to what shifted 10mg/dm^2/day above and below *NAR*s in sole sorghum and sole upland rice, respectively. In the

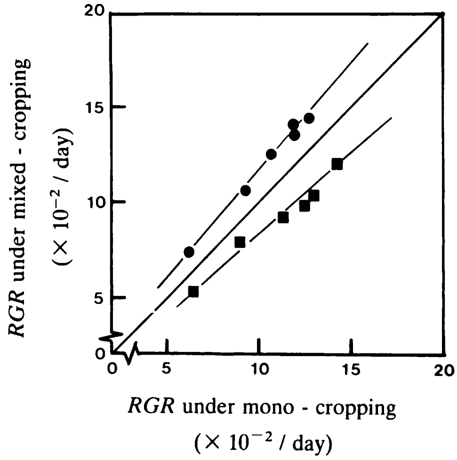

Fig. 9. Comparison of relative growth rate (*RGR*) in pure stand with one in mixed stand.
●: Sorghum, ■: Upland rice

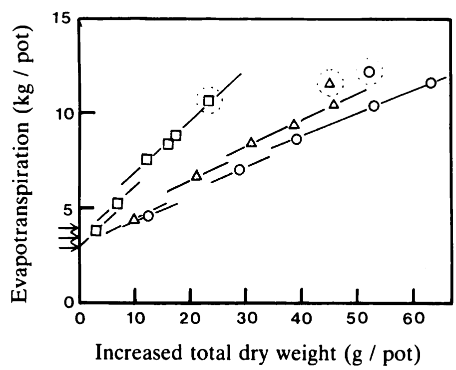

Fig. 10. Relationship between the increased total dry matter weight and evapotranspiration.
Symbols are the same as those shown in Fig. 1.
Arrows in the margin indicates 'unavailable evapotranspiration'.
◌ indicates the value under an excess-moisture condition.

result, although upland rice's *NAR* was larger than sorghum's in pure stand, the situation had been reversed in the mixed stand. On the other hand, no effect of mixed-cropping upon the relationship between soil moisture and *LAR* could be recognized at all. In mixed-cropping the relative growth rate (*RGR*), expressed as the product of *NAR* and *LAR*, became 1.16 times in sorghum and 0.84 times in upland rice as large as those in mono-cropping (Fig. 9).

Water use efficiency

When the soil moisture ratio was over 20%, evapotranspiration (*ET*) increased in proportion to the increased total dry weight, excepting sorghum and mixture under an excess moisture, though when the soil moisture ratio was less than 20%, *ET* lay below a linear equation observed above (Fig. 10). On the basis of the previous results [34,35] that the water use efficiency (*WUE*) – the reciprocal of the slope shown in Fig. 10 – was constant independently of the soil moisture ratio and fertilizer application, some straight lines passing through the observed value, as well as those having the same slope (120, 280 and 140gH_2O/g in sole sorghum, sole upland rice and sorghum-upland rice mixture, respectively) were drawn. And, on the assumption that when the increased total dry weight became zero, *ET* could be regarded as 'unavailable evapotranspiration' or 'evaporation' (*E*), the relationship between the soil moisture ratio and *E* was examined. *E* estimated in this way, increased with an increase in soil moisture ratio until it became about 4kg/pot under soil moisture conditions greater than 21.5% in all the treatments, excepting in sole sorghum and mixture treatments under an excess-moisture condition (Fig. 11). Although the estimated *E*s in sole sorghum and mixture treatments became

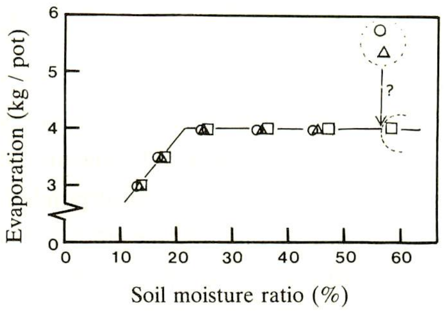

Fig. 11. Relationship between soil moisture ratio and evaporation[※1].
Symbols are the same as those shown in Fig. 10.
※1 : 'Unavailable evapotranspiration' was regarded as nearly equal evaporation.

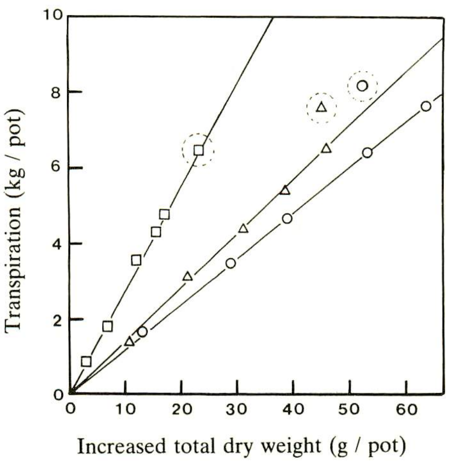

Fig. 12. Relationship between the increased total dry weight and transpiration[※2].
Symbols are the same as those shown in Fig. 10.
※2 : Transpiration was estimated by deducting unavailable evapotranspiration from evapotranspiration.

much larger than 4kg/pot under an excess-moisture condition, this was perhaps because there was a problem in the assumption that *WUE* was constant even under excess-moisture conditions rather than because *E* really increased under above-mentioned condition, for *E* in upland rice under the same condition was equal to 4kg/pot. The transpiration (*T*) assessed by deducting *E* from *ET*, increased in proportion to the increased total dry weight, though that was a natural thing to be expected (Fig. 12). *WUE*s were 8.3, 3.6 and 7.0mg/gH_2O in sole sorghum, sole upland rice and sorghum-upland rice mixture, respectively, only *WUE*s in sole sorghum and mixture fell to 6.4 and 6.0 under an excess-moisture condition, respectively.

It is very difficult to estimate *WUE*s of the components in mixture in this way. But, let it be supposed that *WUE*s of component crops would be the same as those in pure stand, then ET_M in mixture is given by the following equation :

$$ET_M = \frac{\triangle W_S}{WUE_S} + \frac{\triangle W_R}{WUE_R} + E \qquad \text{Eq. (7)}$$

where, $\triangle W_S$ and $\triangle W_R$ are the increased total dry weights of sorghum and upland rice in mixture, WUE_S and WUE_R are the water use efficiencies of sorghum and upland rice in pure stand, and *E* is an evaporation in each soil moisture condition. The calculated values based on Eq. (7) and the observed values corresponded considerably well (Fig. 13). Judging from the results shown in Fig. 13, the above-mentioned assumption that *WUE*s of component crops in mixture may be equal to *WUE*s in mono-cropping seems to be valid.

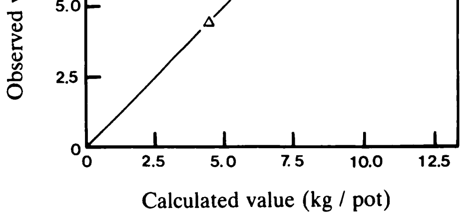

Fig. 13. Comparison of the calculated value of evapotranspiration in mixed stand [based upon Eq. (7)] with the observed value.

Discussion

Growth responses of sorghum and upland rice to soil moisture in pure stand

In Africa, rice plant was often seen grown together with maize, taro, cassava, beans, sesame etc., though it was frequently observed grown in single. Sorghum, a very important crop in the semi-arid zone, like the above crops, was seldom one of the component crops in mixture mainly composed of rice. Although it has been well known that crop combinations usually vary a great deal from one ecological zone to another [1], the percentage of rice-sorghum combination for mixed-cropping system was none too large everywhere. This may be partly because the cultural environments differ considerably between the two crops. According to the field observations in Kenya [33], it is said that sorghum culture began to be observed where the ratio of mean annual rainfall to mean annual potential evaporation (r/E_o) was only 25%, whereas it was impossible to grow rice without irrigation at any place where r/E_o was less than 80%. INTHAPAN *et al.* [21] found that the total biomass production and grain yield of rice cultivars decreased more sharply with a decrease in water supply than those of sorghum did. On the other hand, sorghum as well as the other upland field crops seen to be frail to excess-moisture. KONO *et al.* [23] divided the summer cereals into the two groups designated sorghum and upland rice which were used, in the present experiment, as the species having a large drought tolerance capacity and a large waterlogging tolerance capacity, respectively. The practice of mixed-cropping has been associated partly with an assumption of greater stability. And, it is also based on an assumption that one component crop may compensate for the damage due to drought, hail, nitrogen stress and so on to another [26,29] (although stability is enhanced when crops hinder the spread of pests and diseases, that was ignored in the present paper). The greater the growth responses of component crops to environmental conditions differ, the greater will become such a 'compensation effect'. That is why the authors dared to take up sorghum-upland rice combination in the present study, in spite of the fact that sorghum-upland rice combination isn't so much popular in Africa.

The fact that Eqs. (2) and (5) lacked a term showing inhibition effect due to the surplus of soil moisture as the reciprocal factor, as compared with Eqs. (1) and (4) perhaps answer to 'large waterlogging tolerance capacity' of upland rice pointed out by KONO *et al.* [23] . On the other hand, upland rice was in possession of the higher f_o than that of sorghum. FUKAI *et al.* [15] have attributed the sharp response of rice biomass production to water deficit, partly, to the inability to extract water thoroughly at lower depth. However, because the present study was carried out in shallow pot, it seems to be difficult to explain fully the high sensitivity of upland rice to water deficit only in their rationale. The relative importance of f_o to interspecific difference in drought tolerance is expected to be examined from a physiological point of view in the future.

Drought tolerance and excess-moisture endurance were not all the interspecific differences in the response to soil moisture. Firstly, the effects on leaf area development were expressed mainly through leaf number in upland rice and leaf area per one leaf in sorghum. Basing on the fact that leaf number in upland rice was related linearly with stem number (unshown), it was assumed that water deficit firstly forced upland rice to inhibit tillering might soften, to some extent, the direct effect of water deficit on leaf area per one leaf. On the other hand, in sorghum having no or few tillers independently of soil moisture conditions, soil moisture stress was supposed to affect directly the leaf area per one leaf. Hence the assumption that the difference in the expression of leaf area response to soil moisture is based partly on a difference in the tillering capacity between the two crops. In appearance soil moisture didn't affect the leaf length as compared with the case of leaf width. This is perhaps due to the fact that the prolongation of leaf-emergence interval under water deficit compensated the negative effect of soil moisture stress upon the leaf length, whereas in case of the leaf width no compensation was expected because it was determined prior to leaf length [37]. Under an excess-moisture condition, where the dry matter production decreased and leaf-emergence interval didn't expand as under dry condition, sorghum's leaf length abruptly got short. The result also suggests a possibility of 'compensation' due to the prolongation of leaf-emergence interval as mentioned above.

Secondly, the effects of soil moisture on *RGR* were expressed, relatively, through *LAR* in upland rice and through *NAR* in sorghum. The present result that the decline percent in *NAR* occurring with a decreasing in soil moisture ratio was larger in sorghum than in upland rice seems to be inconsistent with the indication that leaf photosynthesis is affected by the soil moisture stress more severely in rice than in sorghum [21]. When the fact that *NAR* is remotely related to leaf photosynthesis, though *NAR* and leaf photosynthesis are liable to be confused as the unit as the same, is taken into consideration together with the result that sorghum in possession of the larger *LAR* showed the smaller *NAR*, the sharper decline in sorghum's *NAR* in comparison with that of rice's, seems to be no more than a reverse of the result that sorghum's *LAR* was hard to be affected by water deficit.

Sorghum's *WUE* was about 2.3 times as large as upland rice's. It is expected that the result is to be grounded on the difference in CO_2 fixation pathway between the two crops [7,8], that is, sorghum and upland rice are C_4 and C_3 species, respectively. Sorghum's *WUE* under an excess-moisture abruptly fell to about 75% of that under other conditions. This is partly due to the fact that the dry matter production of sorghum decreased, and partly to that the transpiration increased under excess-moisture conditions. It has been generally believed that excess-moisture decreases the suction force of roots [24]. Further investigations, however, seem to be needed to clarify this inconsistency.

Growth responses of sorghum and upland rice to soil moisture in mixed stand

There are a lot of reports which have substantiated the yield advantage of mixed-cropping [1,2,3-5,11,14,19,25,30,31,36]. But, in the present study, the sorghum-upland rice combinations seemed to give no yield advantages on to mono-cropping, because both total *LER*s of dry weight and leaf area in mixture were nearly equal to 1.0 independently of soil moisture condition. According to some reports [10,12] showing that mixed-cropping has not always given yield advantage on to mono-cropping, the effect of mixed-cropping upon the yield advantage depends greatly on crop combinations. Apart from crop combination, FISHER [13] indicated an example that the yield advantage from mixed-cropping could be explained solely by the increased population pressure in the mixture. But, in this study the plant density was fixed to be constant. Those were assumed to be the major reasons why yield advantages were not given in the present study.

The responses to soil moisture, as mentioned above, differed in various points considerably between sorghum and upland rice. It is expected that in sorghum-upland rice mixture the stability to soil moisture remarkably increases when the two crops are grown together. Judging from the result that f_o and f_{opt} in mixture were lower and higher than f_o of upland rice and f_{opt} of sorghum in pure stand, respectively, mixed-cropping seems to have, somewhat, positive effect on the improved stability. However, considering that it gradually sacrificed the large tolerances to drought and excess-moisture of sorghum and upland rice, it comes to be thinkable that sorghum-upland rice mixture contributed little to the improved stability to soil moisture. The relationships between soil moisture ratio, and the total dry matter weights and leaf areas per pot of sorghum and upland rice in both pure and mixed stands are, in a lump, shown in Table 2. The calculated values agreed very well with the observed values (Fig. 14). As seen from Table 2, f_o, f_{opt} and the relative relation among *A, A'* and *B* were nearly constant independently of whether mixed- or sole- cropping, though the absolute values of *A, A'* and *B* differed between the pure and mixed stands. In addition, *WUE*s of component crops were not affected by mixed-cropping. The results show that the basic relationships between soil moisture ratio and growth increments of the two crops were not affected by mixture.

Two results, the one that the *LER*s of sorghum and upland rice in mixed stand were larger and smaller than 0.5, respectively, and another that the *RGR*s of sorghum and upland rice in the mixed stand were 1.16 and 0.84 fold of those in pure stand, indicate that sorghum conquered upland rice in the growth. Plants are conceived to be competing for the limited supplies of environmental resources necessary for growth, usually light above, and nutrients and water below, ground [9]. The general conclusion from all the experiments involving competition for light is that the component whose leaf area is higher in the canopy is at an advantage, specially if the taller component has a greater leaf area. Such an example has been found in the mixed sorghum-pigweed communities by GRAHAM *et al.* [16]. In the present study, sorghum was not only taller but had wider and longer leaves than those of upland rice, in which the number of leaves was reduced (and those of sorghum increased) when the two crops were made to be grown together. Sorghum having the taller and the greater leaf area might reduce the light penetrating into upland rice. Consequently, it is assumed that *NAR* of upland rice in mixed stand decreased because of light deficiency, whereas *NAR* of sorghum having advantage for light competition increased. According to YAMASAKI [37], shading at the occassions of

Table 2. Characteristic values of logistic growth at the time of harvest

	For mean dry weight per pot					For mean leaf area per pot				
	Sole cropping		Mixed-cropping			Sole cropping		Mixed-cropping		
	Sorghum	Rice	Total	Sorghum	Rice	Sorghum	Rice	Total	Sorghum	Rice
A	0.26250	0.81250	0.31000	0.40670	2.66670	0.08600	0.46500	0.11040	0.13030	1.36760
A'	0.00019	–	0.00016	0.00030	–	0.00006	–	0.00005	0.00009	–
B	0.00167	0.02708	0.00650	0.00258	0.08917	0.00180	0.00900	0.00430	0.00273	0.02647
τ	4.8449	3.3778	4.0882	5.2859	2.8953	4.3870	4.4482	4.2195	4.8703	4.1260
λ	0.2307	0.1608	0.1947	0.2517	0.1379	0.2089	0.2118	0.2009	0.2319	0.1965
k	3.7795	1.1889	3.1717	2.4464	0.3543	11.4833	2.1254	8.9248	7.6157	0.7194
k'	5175.4	–	6145.2	3344.3	–	16459	–	21419	10904	–
f_o	8.0	9.4	8.5	8.0	9.4	10.2	10.7	10.5	10.2	10.7
f_{opt}	45.0	–	52.5	45.0	–	48.1	–	59.5	48.1	–
w_{max}	63.1	–	48.6	40.7	–	–	–	–	–	–
u_{max}	–	–	–	–	–	157.7	–	113.5	104.0	–

Notes. 1) A, A' and B are constants when the relationship between soil moisture ratio (f), and dry weight (w) or leaf area (u) per pot were formulated by the following reciprocal equation.

$$\frac{1}{w \text{ or } u} = \frac{A}{f - f_o} + A'(f - f_o) + B \quad (A: \%/\text{g or } \%/\text{dm}^2,\ A': 1/\text{g}\cdot\% \text{ or } 1/\text{dm}^2\cdot\%,\ B: 1/\text{g or } 1/\text{dm}^2)$$

where, f_o indicates the uppermost limit value of unavailable soil moisture (f_o : %).

2) $\tau = -\ln(w_o B)$

where, w_o indicates the dry weight or leaf area at the beginnig of soil moisture treatment.

3) $$\lambda = \frac{\triangle \tau}{\triangle t} \quad (\lambda : 1/\text{day})$$

where, $\triangle t$ is the duration of soil moisture treatment (day).

4) $$k \text{ or } k' \fallingdotseq \frac{1 - e^{-\tau}}{A} \quad (k : \text{g}/\% \text{ or dm}^2/\%,\ k' : \text{g} \cdot \% \text{ or dm}^2 \cdot \%)$$

5) $$f_{opt} = \sqrt{\frac{A}{A'}} + f_o \quad (f_{opt} : \%)$$

where, f_{opt} is optimum soil moisture ratio.

6) $$w_{max} \text{ or } u_{max} = \frac{1}{2\sqrt{AA'} + B} \quad (w_{max} : \text{g/pot},\ u_{max} : \text{dm}^2/\text{pot})$$

where, w_{max} and u_{max} indicate the dry weight and leaf area in optimum soil moisture ratio.

emergence of a given leaf, increases blade length of the adjacent younger leaf. It was also found in the present experiment that leaf length of sorghum and upland rice in mixed stand became shorter and longer than those in pure stand, respectively. These results also indicate clearly that there was a keen competition for light in sorghum-upland rice mixtures.

Taking the fact that a great quantity of fertilizer application was carried out in this

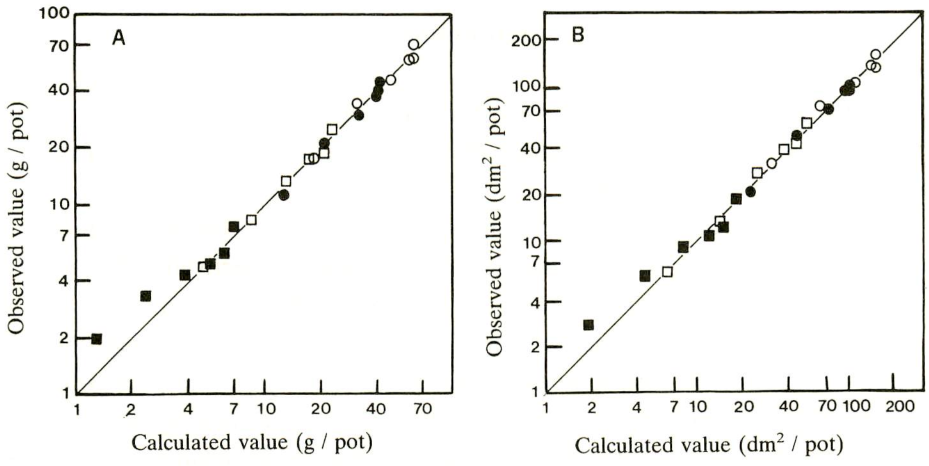

Fig. 14. Comparison of the calculated values of dry weight (A) and leaf area (B) [based upon characteristic values of logistic growth shown in Table 2] with the observed values.
Symbols are the same as those shown in Fig. 7.

study into consideration together with REMISON's result [32] that there was no competition between the crops for nitrogen or phosphorus, it is expected that there was also no or little competition for nutrients in this experiment. It was found not only that *LER*s of component crops were constant, independently of soil moisture conditions but also that the basic relationships between soil moisture ratio, and dry matter productions, leaf area developments, growth functions and *WUE*s were not affected by mixture. HAKOYAMA *et al.* [17] investigated the weed vegetation in noncultivated paddy fields and have found that the vegetation of paddy fields left off cultivation varied largely, depending on the difference of soil moisture. It, paradoxically speaking, suggests that the relative competitive power of species forming communities, varied depending on soil moisture. Although there were also some reports [12,27] showing that the relative advantages of mixed-cropping depend greatly on soil moisture conditions, the evidences showing that one component in mixture compensated for drought damage or excess-moisture injury to another, and that there was a competition for water below ground, couldn't be recognized in the present study carried out in the shallow pot at all. Therefore, if a competition for absorbing water should arise between components in mixed sorghum-upland rice communities under field condition, the relative competitive power between crops seems to be decided not by soil moisture ratio at a given layer but by the interspecific differences in the rooting habit. Consequently, if sorghum-upland rice mixture should give the stability and yield advantages, it seems to be attributed to a more efficient soil moisture extraction resulting from the complementarity of rooting depth.

Summary

Sorghum and upland rice were made to be grown in pure and mixed stands under 13 liter seedling culture boxes, respectively. The population density was fixed at 24 plants per pot in either treatment.

Soil moisture acted as linear factor and optimum factor on dry matter productions and leaf area developments of upland rice and sorghum, respectively. The uppermost limit value of unavailable soil moisture ratio (f_o) was higher in upland rice than in sorghum. From these results, it was, in general, concluded that sorghum and upland rice were in possession of the larger drought tolerance and excess-moisture endurance than upland rice and sorghum, respectively. The effect of soil moisture upon leaf area development was expressed comparatively through leaf number in upland rice and through leaf area per one leaf in sorghum. The relative growth rate (*RGR*) was affected comparatively through leaf area ratio (*LAR*) in upland rice and net assimilation rate (*NAR*) in sorghum. The water use efficiency (*WUE*) was 3.6 and 8.3 in upland rice and sorghum, independently of soil moisture conditions excepting that sorghum's *WUE* fell to 6.4 under an excess-moisture condition.

The relative advantage of mixed-cropping could not be recognized in the present experiment at all. Although f_o and optimum soil moisture ratio (f_{opt}) of total in sorghum-upland rice mixture were lower and higher than f_o of sole upland rice and f_{opt} of sole sorghum, they were higher and lower than f_o of sole sorghum and f_{opt} of sole upland rice, respectively. The basic relationships, as observed in pure stand, between soil moisture ratio, and dry matter productions, leaf area developments and growth functions weren't affected by mixture stand. *WUE* was also constant in both cropping systems. Although there were evidences that component crops were competing for a environmental resource in mixed stand, it was expected that it was not a competition for water but one for light.

From above-mentioned results, it was concluded that sorghum-upland rice mixture stand should contribute little to the improved stability to soil moisture. If sorghum-upland rice mixture should give the stability and yield advantages under field condition, it seemed to be attributable to the more efficient soil moisture extraction resulting from complementarity of the rooting depth.

Acknowledgement

The authors wish to their gratitude to Mr. N. KAJIYA, Kagoshima Prefectural Agricultural Experimental Station, for giving the seeds of upland rice.

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