

EFFECT OF PLANTING DENSITY ON COMMUNITY PHOTOSYNTHESIS AND ON YIELDING COMPONENTS OF RICE PLANTS^(1,2)

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Abstract

Two rice varieties Taichung 65 and Hsinchu Ai-chueh-chien were transplanted in the second crop season under three levels of spacing, 25 cm×20 cm, 20 cm×17 cm, and 20 cm×13 cm, to understand the effect of the changes and interaction of plant factors constituting canopy photosynthesis on the dry matter production.

The total dry weight, tiller number and leaf area based on unit ground area increased with increasing planting density, although values of the three characters per hill decreased with increasing planting density.

The crop growth rate increased gradually with time and reached at the maximum, and decreased gradually. The maximal value of the crop growth rate for both rice varieties was about 30 g/m² day.

If dividing growth stage into vegetative stage, reproductive stage and ripening stage, and looking for the correlation between the crop growth rate and factors constituting canopy photosynthesis, the contribution rate of each factor to the crop growth rate and their interactions for the crop growth rate became clear. The crop growth rate was mainly governed by leaf area index during vegetative growth phase. Thus, significantly positive correlation coefficient between leaf area index and crop growth rate was found at vegetative growth stage. With maintenance of higher leaf area index after heading, the unit leaf rate was significantly correlated with the crop growth rate. During the stages having large amount of leaf area, the crop extinction coefficient was positively correlated with the crop growth rate.

The grain yield was closely correlated with the crop growth rate at vegetative growth stage and with the number of spikelets per unit ground area.

The grain yield was increased with increasing planting density. The best result for grain yield was obtained with the planting density of 29 hills/m² for both rice varieties.

The grain yield was limited not only by yield capacity but also by assimilate supply after heading.

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Introduction

One critical factor causing the low yield of rice in the second crop in Taiwan is the less number of panicles per plant (Wu *et al.*, 1915). Two possibilities of increasing tiller number per unit ground area are thought, i.e. (1) to induce the differentiation and development of the tillers, and (2) to increase the planting density. However, the former seems difficult because the high temperature during the early growth stage in the second season would cause the dormancy of the tiller bud (Matsushima *et al.*, 1968). Therefore, the possible way is to increase the planting density. Several workers in Taiwan reported that grain yield of rice plants was increased by dense planting (Chang and Yang, 1964a, b; Hsieh *et al.*, 1966).

In a plant community the photosynthetic activity of a single leaf is determined by the plant factors that constitute canopy photosynthesis (Murata *et al.*, 1957). Many experiments have made to study the effect of individual factor on photosynthesis. However, few are taken to investigate the change and interaction of the plant factors with the advancement of growth stage and their relation with dry matter production and grain yield of rice plants. Two important parameters regarding the dry matter production of a plant stand are leaf area index (LAI) and unit leaf rate (ULR). In a plant community ULR often shows negative correlation with dry matter production. In fact, ULR does contribute to the growth, but it is only masked by some plant factors. Among such covering factors, the most powerful one may be the LAI and plant type which cause difference in the degree of mutual shading of the crop stand (Murata, 1975; Murata *et al.*, 1966; Murata and Togari, 1972). On the other hand, there is an existence of a closely positive correlation between dry matter production and LAI (Murata, 1975; Akiyama and Takeda, 1975).

In this paper, the experiment was attempted to study the effect of changes and interactions of the plant factors constituting canopy photosynthesis at various growth stages on dry matter production and yield of the rice plant.

Materials and Methods

Methods of Culture

The experiment was conducted at the experimental farm of the Academia Sinica at Nankang. Two rice varieties Taichung (TC 65) and Hsinchu Ai-chueh-chien (HCA) were transplanted on August 9 in the second crop season of 1975. Three levels of spacing were used, i.e. D₁: 25 cm×20 cm (20 hills/m²); D₂: 20 cm×17 cm (29 hills/m²); and D₃: 20 cm×13 cm (38 hills/m²). The amount

of fertilizers used was 120, 60 and 60 kilogram per hectare for N, P and K, respectively. The experimental lay out was a randomized block design with four replications.

The date of growth stages and the changes of climatic conditions during the experimental period are shown in Fig. 1.

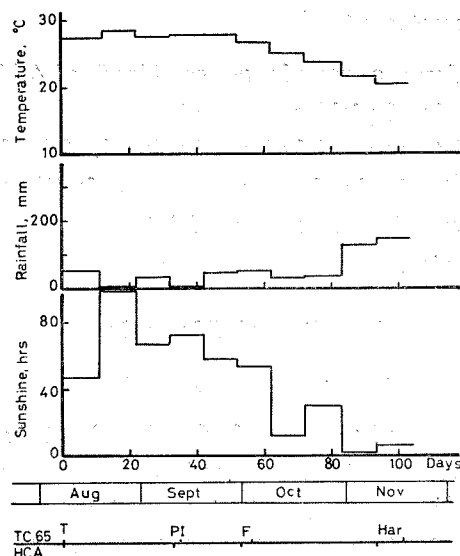


Fig. 1. Growth pattern of Taichung 65 (TC 65) and Hsinchu Ai-chueh-chien (HCA) and the changes of weather conditions. T: transplanting; PI: panicle initiation; F: heading; and Har: harvesting.

Procedure of various measurements

Beginning on the day of transplanting, 4 hills of rice plants were sampled every 10 to 11 days from each plot through the growth period until harvesting. The plant materials were washed free from soil and the number of tillers was counted. The plants were then separated into green leaf blade, withered leaf blade, leaf sheath and stem, and panicle components. The green materials were immediately dried in an oven at 100°C for one hour and then two days at 80°C. After drying the dry weight of each plant portion was weighed.

The leaf area was estimated using the blue-print method as described by Tanaka *et al.* (1966).

The above obtained data were used for growth analysis of crop growth rate (CGR), LAI and ULR as described by Shieh (1976).

The light transmission ratio (LTR) of the rice canopy was measured by measuring the incident irradiation at the top of the plant community (I₀) and

at the ground level within the canopy (I) with a Kaneko lux meter. Measurements were made at 10:30 to 11:30 a.m. on cloudy days. The obtained LTR (I/I₀) was substituted in the Monsi-Saeki's equation to obtain the crop extinction coefficient (α_L):

$$\text{LTR} = I/I_0 = \exp - (\alpha_L) \times (\text{LAI})$$

Analysis of the yield components

Thirty panicles from a sample as combined of 4 hills were sampled at random for the analysis of yield components.

The sterile spikelets were picked out by hand. The fertilized grains were weighed and counted to obtain the percentage of fertility and grain weight. The fertilized grains were further separated into un-ripened and ripened grains by wind machine selector.

Results and Discussion

Effect of planting density on the pattern of growth

In general, the stage of growth of the rice plant is arbitrarily divided into three phases, i.e. vegetative growth stage, reproductive stage and ripening stage. In this experiment, the intervening time between two successive samplings was defined as growth periods (Table 1). P_I is at the initial vegetative growth stage. P_{II} and P_{III} are at the active vegetative growth stage. P_{IV} is the vegetative lag phase. P_V and the early period of P_{VI} are the reproductive stage. P_{VI} to P_{VIII} is the ripening stage.

Table 1. *Correlations of crop growth rate (CGR) with some growth attributes of rice stand*

Elements ⁽¹⁾	Growth priod ⁽²⁾							
	P _I	P _{II}	P _{III}	P _{IV}	P _V	P _{VI}	P _{VII}	P _{VIII}
LAI-CGR	0.998** ⁽³⁾	0.963**	0.940**	0.175	-0.578	-0.116	0.498	0.982**
LAD-CGR	0.981**	0.969**	0.950**	0.296	-0.542	-0.219	0.466	0.942**
ULR-CGR	0.824*	-0.459	-0.533	-0.176	0.949**	0.969**	0.992**	0.976**
α_L -CGR	—	0.258	-0.865*	0.637	0.368	0.299	-0.666	—

(1) The abbreviations of the elements: CGR, crop growth rate; LAI, leaf area index; LAD, leaf area duration; ULR, unit leaf rate; α_L , crop extinction coefficient.

(2) P_I: 0-12; P_{II}: 12-23; P_{III}: 23-33; P_{IV}: 33-44; P_V: 44-55; P_{VI}: 55-65; P_{VII}: 65-75; P_{VIII}: 75-93, days after transplanting.

(3) *, **: Singificant at 5% and 1% level, respectively.

Fig. 2 shows that the number of tillers per plant decreased with increasing planting density. It reached the maximum at the end of P_{III} and gradually

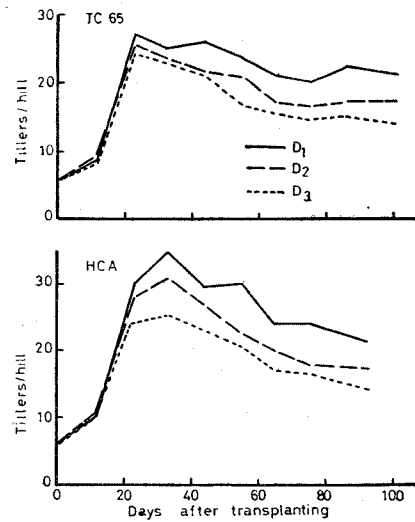


Fig. 2. Seasonal changes of the number of tillers under three levels of planting density. D₁: 20 hills/m²; D₂: 29 hills/m²; and D₃: 38 hills/m².

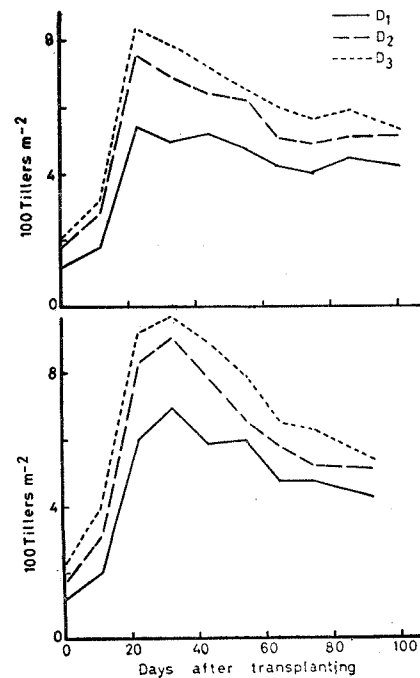


Fig. 3. Seasonal changes of the number of tillers per m². D₁, D₂ and D₃ are the same as in Fig. 2.

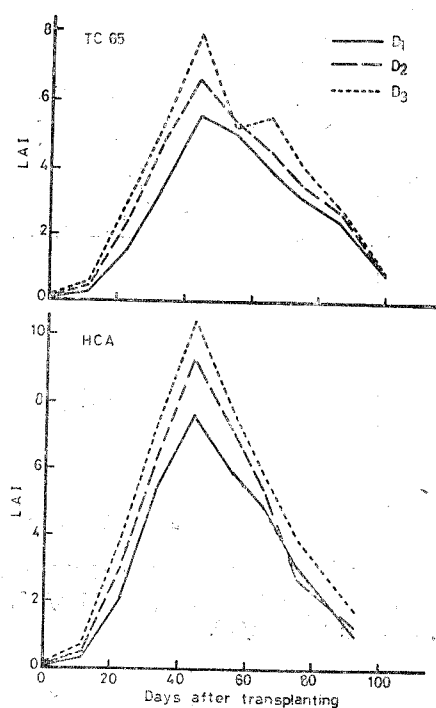


Fig. 4. Effect of planting density on the change of leaf area index (LAI). The symbols are the same as in Fig. 2.

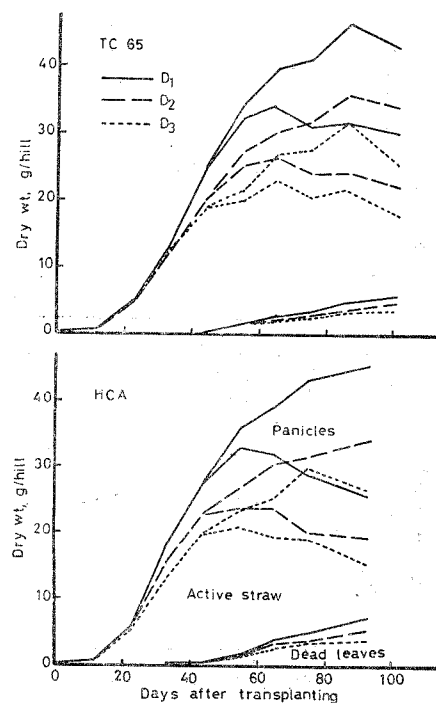


Fig. 5. Effect of planting density on the growth pattern of rice plants. The symbols are the same as in Fig. 2.

decreased to a steady level. However, the number of tillers per unit ground area is high as the planting density was increased (Fig. 3). It was found that the decline of tillers was more pronounced under dense planting.

In comparison of the tiller development between 1975 and 1974 (Shieh, 1976), the number of seedlings per hill transplanted was about the same, but the tiller number in 1975 is substantially higher than that of 1974. Yamazaki (1960) reported that the initiation of tiller primordia was free from the influence of environment, but the emergence and development are greatly influenced by such factors as nitrogen application, solar radiation and temperature. The mean temperature was similar in the two years, but solar radiation and nitrogen application are higher in 1975. These may cause the difference in the tillering ability between 1974 and 1975. On the other hand, increasing the planting density caused the decrease of tillers per seedling, but it was significantly compensated by the increase of seedlings per unit ground area.

The LAI also increased with increasing planting density and reached its maximum between period of P_{IV} and P_V (Fig. 4). It was found that the number of leaves and leaf area per tiller was not affected by varying the planting density. The time of reaching at maximal LAI was about 15 to 20 days behind the maximum tiller stage. The increase of LAI was caused by two factors; the increase in the number of tillers and in the size of successive leaves. The average size of a leaf is the largest at P_{VI} and P_V for TC 65 and HCA, respectively. The LAI was decreased before heading in both varieties.

The pattern of the changes of the dry weight of plant, active straw, withered leaves, and panicles under three planting densities is shown in Fig. 5, which shows that the change of straw weight before and after heading is more flat in dense planting.

Seasonal changes of leaf area index, unit leaf rate, crop extinction coefficient and crop growth rate

The seasonal changes of the photosynthetic factors, LAI, ULR and the crop extinction coefficient α_L , are shown in Fig. 6 and Fig. 7.

Under D_3 treatment the mean LAI reached to 6.5 for TC 65 and 8.6 for HCA, while under D_1 treatment it went 5.4 for TC 65 and 7.0 for HCA. In the ripening stage the decline of LAI was more conspicuous in heavier densities. According to a review by Yoshida (1972), many workers have reported values of 4 to 7 as the optimum LAI of rice stand. The rice variety HCA which has short and erect leaves many stand high LAI.

The extinction coefficient α_L was distinguished into two categories at the

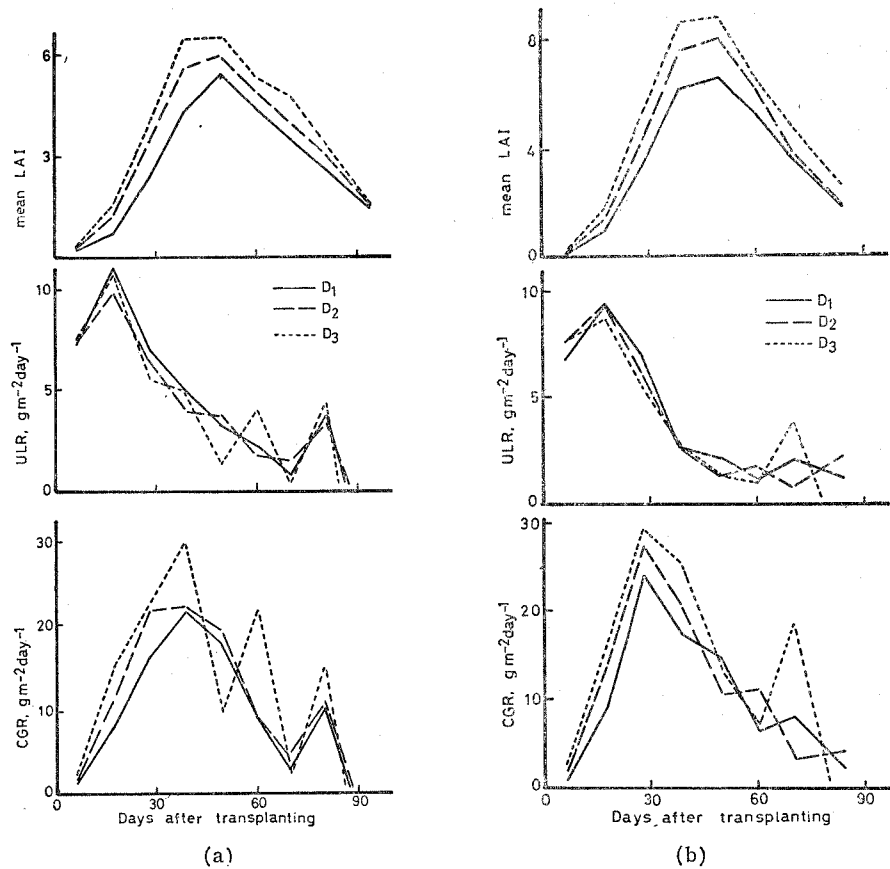


Fig. 6. Seasonal changes of mean LAI, unit leaf rate (ULR) and crop growth rate (CGR) in TC 65 (a) and HCA (b). The symbols are the same as in Fig. 2.

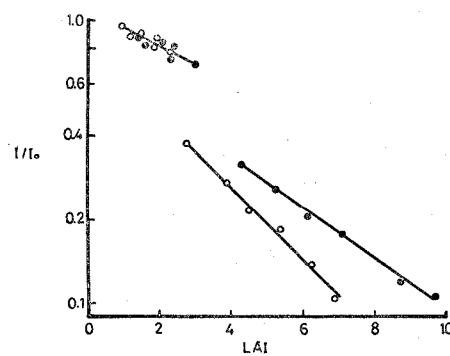


Fig. 7. The relation between light transmission ratio (LTR) and LAI in TC 65 (○) and HCA (●).

vegetative growth stage as shown by the slope of lines in Fig. 7. When the amount of leaves was small ($LAI < 2$), the α_L was small. As the LAI increased, the α_L became larger. It may indicate that the growth pattern of rice plant changed due to the appearance of tillers. There is no difference in α_L among the three levels of planting density at the vegetative growth stage from P_{II} to P_{IV} . At this period the relation between light transmission ratio (LTR) and the LAI showed linear, suggesting a well Monsi-Saeki's relationship $LTR = \exp(-\alpha_L)(LAI)$. It may imply that the distribution of light within rice stand is more even with increasing LAI during this period. After the LAI reached the maximum, the LTR went to the lowest value and was about the same and independent of the planting density, especially after booting, owing to the enlargement of leaves and the spreading of plant form. Thus, the α_L rised (Fig. 8).

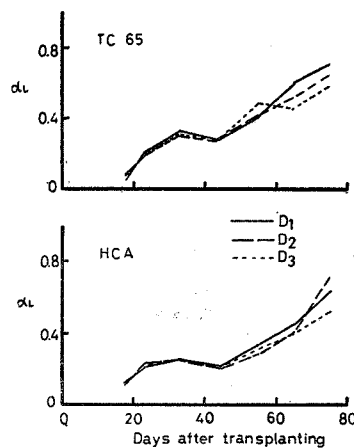


Fig. 8. Time trend of crop extinction coefficient (α_L).

The ULR rised between P_I and P_{II} (mid of Fig. 6). The promotion of ULR coincided with the increase of nitrogen content in leaf (Fig. 9). Murata (1975) have indicated the aging effect on ULR in which the nitrogen content of leaf plays a important role in ULR. After the initial rise of ULR, with increasing LAI the ULR declined gradually declined as growth advanced and rise a little at ripening stage. The rise of ULR at ripening may be due to the change of light receiving of leaves with the withering of old leaves. But the range of ULR rise was small due to the low solar radiation and the nitrogen content at this period.

The process of dry matter production, the crop growth rate (CGR), is the combination result of the changes and interactions of the photosynthetic factors. As shown in the bottom of Fig. 6, the CGR increased with increasing

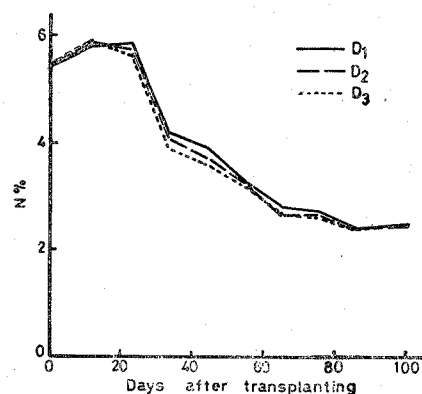


Fig. 9. Seasonal change of nitrogen content in leaf blades of TC 65. The symbols are the same as in Fig. 2.

LAI and planting density and reached its maximum before LAI reaching at maximum. It can be seen that the ULR was already decline during this period. Therefore, LAI and α_L play an important role in the dry matter production of the rice stand.

Relation of the crop growth rate with photosynthetic factors at various growth stages

The correlation of CGR with LAI, leaf area duration (LAD), ULR and α_L are shown in Table 1. The data were computed from two rice varieties and three levels of planting density, having a total of six treatments, except that α_L was not measured at early vegetative growth phase due to the difficulty of measuring in thin rice community.

As shown in Table 1 and Fig. 10, LAI and LAD were significantly correlated with CGR at vegetative growth stage from P_I to P_{III} . The earlier the growth period was, the greater the correlation coefficient was obtained. During P_V and P_{VI} with plentiful leafiness, a negative correlation was found between LAI and CGR. Then LAI and CGR showed a positive correlation with the advancement of growth. It implies that the CGR are mainly governed by LAI at the vegetative growth stage, and the maintenance of LAI at ripening stage is favour for CGR. The possible reasons for the negative correlation at mid stage may be due to: (1) the transit of growth from vegetative to reproductive phase; (2) the gross photosynthesis increases asymptotically with the increase in LAI, while respiration increases more or less linearly; and (3) mutual shading occurs. As shown in Fig. 5, indeed, the growth of straw decreased with increasing planting density during this period.

Weakly positive correlation between α_L and CGR was found at early

vegetative stage and after maximal tiller stage, indicating that less of incident light penetrates the canopy is favour for dry matter production. During the tillering stage, the correlation coefficient between α_L and CGR was significantly negative, suggesting that the plant type having more of the incident penetrating to lower depths in a stand is favour for the tiller development. At P_{III} the mean LAI of D_3 was 4.0 for TC 65 and 5.4 for HCA. It may indicate that the semidwarf variety has better light receiving in a stand.

The correlation between the dry matter production ability of a single leaf, the ULR, and CGR is shown in Fig. 11. Only at the earliest vegetative

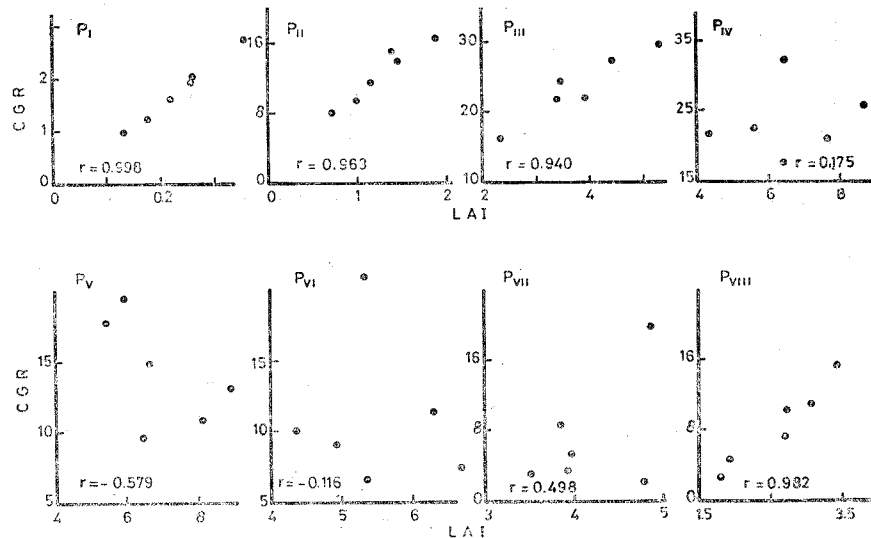


Fig. 10. The relation between CGR and LAI at various growth periods.

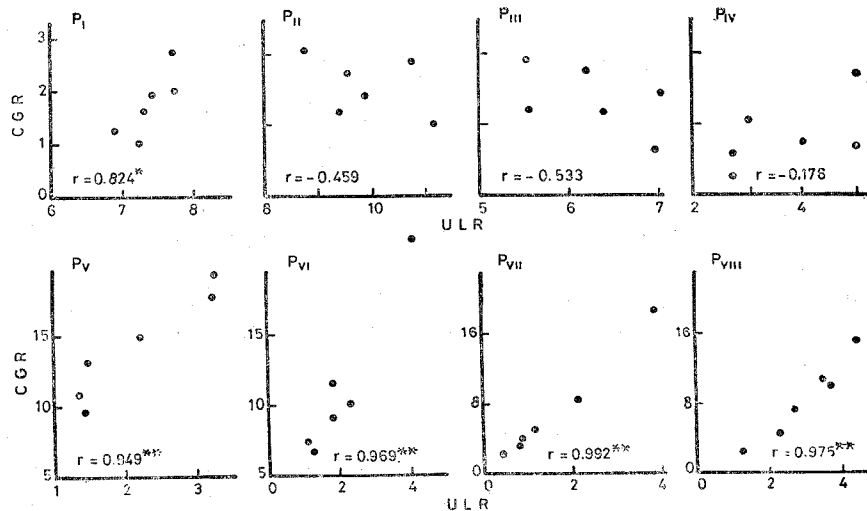


Fig. 11. The relation between CGR and ULR at various growth periods.

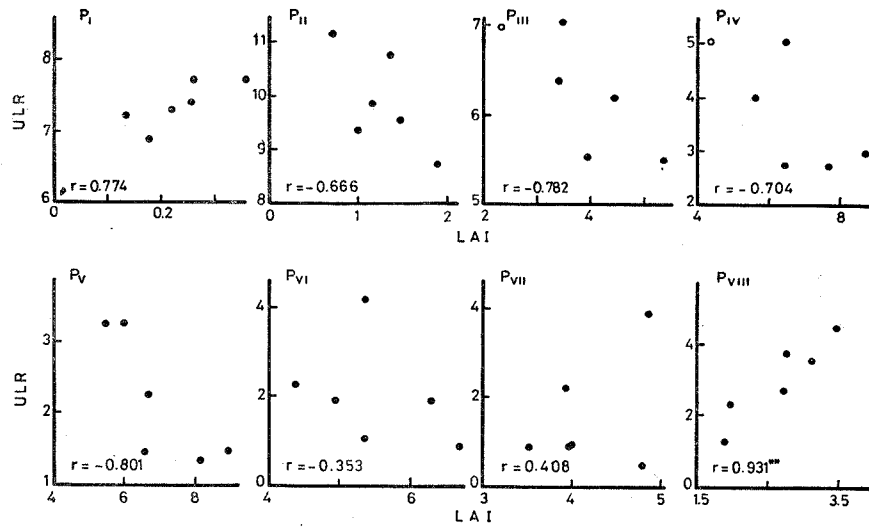


Fig. 12. The relation between ULR and LAI at various growth periods.

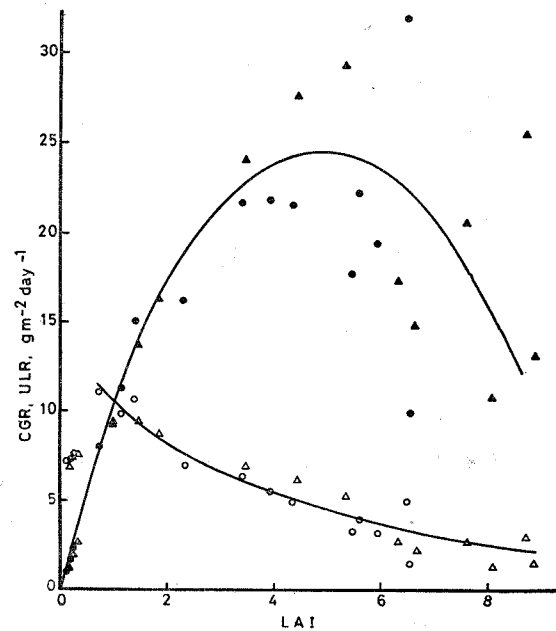


Fig. 13. The relation of LAI with CGR (closed symbols) and ULR (open symbols) in TC 65 (circles) and HCA (triangles) from transplanting to heading.

growth stage with small amount of leaf area, there was a positive correlation between ULR and CGR. At active vegetative growth stage with the attainment of plentiful leaves the ULR showed negative correlation with CGR, but was insignificantly different among planting densities. It may be suggested

the ULR was not seriously affected by increasing LAI in three levels of planting densities. After heading the ULR was significantly correlated with CGR, suggesting that the CGR was governed by ULR at ripening stage. At this growth stage the dry matter production was mainly the growth of grains (Fig. 5).

The way of constituting CGR was controlled by LAI and ULR in a rice community, i.e. $CGR = ULR \times LAI$. The changes and interactions of ULR and LAI formed the presentment of the CGR at various growth stages. Except at P_I , P_{VII} and P_{VIII} , the ULR was negatively correlated with LAI (Fig. 12).

Fig. 13 shows the relationship of LAI to ULR and CGR from transplanting to heading. The curve of CGR against LAI approaches parabola. The curve of ULR against LAI is hyperbolic, except during having a small amount of leaf area.

Yield and yield components

The effect of planting density on the total dry weight, yield, and yield components in TC 65 and HCA is summarized in Table 2. The total dry weight of D_2 was higher than that of D_1 , while the total dry weight of D_2 and D_3 made no difference in both varieties. The harvest index was similar in D_1 and D_2 , while that was smaller in D_3 . Grain yield was higher in D_2 for TC 65 and in D_2 and D_3 for HCA.

Table 2. *Relations between planting density and total dry weight, yield components and yield*

Variety	Plant ⁽¹⁾ density	Total dry weight (g/m ²)	Yield component						Grain yield (g/m ²)	Grain- straw ratio (%)
			Panicle No. per m ²	Panicle length (cm)	Panicle weight (g)	Spikelet No. per m ²	Ferti- lity (%)	Grain weight (g/1000)		
TC 65	D_1	839.6	417	17.8	0.67	22733	68.0	20.8	258.4	46.3
	D_2	988.1	505	17.5	0.66	25457	65.6	21.6	314.3	45.6
	D_3	982.9	522	17.5	0.58	25692	61.1	19.8	277.2	40.7
HCA	D_1	909.7	383	17.7	1.04	35112	79.8	17.7	391.6	76.3
	D_2	1008.1	456	17.6	0.97	37007	79.8	18.2	430.2	76.1
	D_3	1028.3	498	17.5	0.90	37698	76.9	17.7	437.0	74.8

(1) D_1 : 20 hills/m²; D_2 : 29 hills/m²; D_3 : 38 hills/m².

Fig. 14 shows that the grain weight per hill decreased with increasing planting density due to the less number of panicles and spikelets per hill. On the contrary, the grain yield was higher in dense plots. The increase of grain yield was due to the increase of panicles per unit ground area and consequently increasing in the number of spikelets per unit ground area. It

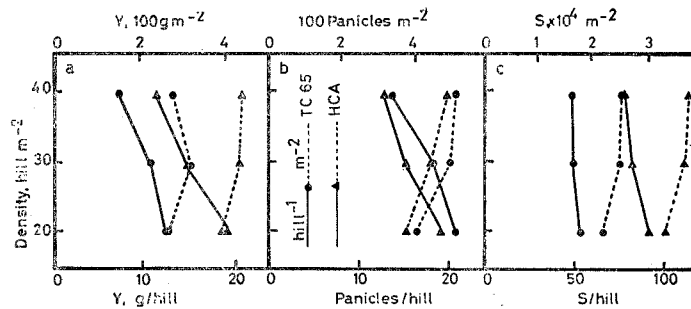


Fig. 14. Relationships of the planting density with (a) grain yield (Y), (b) the number of panicles, and (c) the number of spikelets (S).

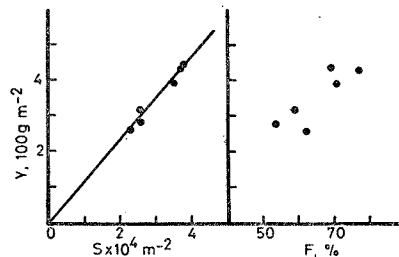


Fig. 15. Relations of grain yield (Y) to the number of spikelets (S) and the portion of ripened grains (F).

seems clear that the grain yield of rice in the second crop is limited by the yield capacity (Murata, 1969) as shown in Fig. 15, which indicates the grain yield was closely correlated with the number of spikelets per unit ground area within the range of planting densities used. The low fertility are also liable to the low yield of rice in the second crop.

The importance of yield capacity to grain yield in the second crop is also shown in Table 3, which reveals that the CGR was positively correlated

Table 3. Correlation of the crop growth rate with yield and yield components

Growth period ⁽¹⁾	Yield component		Yield
	Panicles/m ²	Spikelets/m ²	
P _I	0.675	0.604	0.781
P _{II}	0.762	0.454	0.741
P _{III}	0.217	0.926** ⁽²⁾	0.951**
P _{IV}	0.001	-0.306	0.100
P _V	-0.027	-0.444	-0.726
P _{VI}	0.539	-0.417	-0.005
P _{VII}	0.078	0.579	0.522
P _{VIII}	0.698	-0.773	-0.453

(1) Growth periods are the same as in Table 1.

(2) **: significant at 1% level.

with the number of panicles and spikelets per unit ground area at early growth stage.

The grain growth was mainly contributed by the photosynthetic supply as shown by the positive correlation between ULR and CGR during grain filling (Fig. 11). However, analysis of the correlation of ULR and the grain yield did not show a positive correlation coefficient during ripening. It is, therefore, presumed that the photosynthesis activity alone is insufficient to supply necessary material for grain filling and the grain growth may depend on the translocation of the pre-heading storage of assimilate. The assumption may be true because it was found that the grain yield was well correlated with the total dry weight per unit ground area at heading (correlation coefficient $r=0.956$, significant at 1% level). Thus, it indicates that the assimilate supply after heading was limiting to grain yield.

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栽植密度對水稻羣落光合作用構成因子與 產量構成因素的影響

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本試驗於1975年在南港中央研究院試驗田進行。以水稻品種臺中65號新竹矮腳尖兩品種在第二期作以三種栽植密度，即 $25\text{ cm} \times 20\text{ cm}$ ， $20\text{ cm} \times 17\text{ cm}$ 及 $20\text{ cm} \times 13\text{ cm}$ 。目的在探討水稻羣落之光合成能力構成因子在生育期間之變化及其互相作用對水稻乾物質生產形成過程的影響。結果獲致以下數點結論：

1. 增加栽植密度，增加單位面積之分蘗數，全乾物重及葉面積指數。
2. 若將水稻生育期分成生育前期，生育中期及生育後期等三期就光合成因子對 CGR 的作用，發現 CGR 在生育前期受 LAI 之支配，兩者呈顯著的正相關。抽穗以後，保持較高的 LAI 時單葉之光合作用能力 ULR 和 CGR 有極高的正相關。
3. 水稻的產量和單位面積的穎花數有密切關係。
4. 水稻的產量不僅受限於產量能力 (Yield capacity) 而且受抽穗後，同化物質供給的限制。
5. 產量隨栽植密度的增加而增進。其產量的提高仍得自單位面積穗數及穎花數的增加。而品種的栽植密度以每平方公尺30株左右最宜。矮化的新竹矮腳尖較適於密植。