Japan. J. Breed. 35 : 109～117(1985)

Varietal Comparison on the Responses of Photosynthetic Rate and Leaf Water Balance at Different Soil Moisture Tensions in Rice

Mario Thukasha FUKOSHIMA[1], Kokichi HINATA and Shigesaburo TSUNODA[2]
Faculty of Agriculture, Tohoku University, Sendai, 〒 980

Differences in the photosynthetic activity and related leaf water balance were studied in eight rice varieties subjected to various levels of soil moisture tensions, i. e. flooded condition, values of 10, 20, 40 cbar and values at which leaf rolling began (50-62 cbar depending on the variety). The materials consisted of two lowland (IR 8 and Bosque), three tropical upland (Moroberekan, IAC 1246 and Batatais), two Japanese upland (Sensho and Rikuto Norin 24) and one dwarf mutant (Daikoku 1) varieties, respectively. The parameters observed were the photosynthetic rate (P), transpiration rate (T), leaf water potential (LWP), leaf diffusive conductance ($1/r_l$) and leaf water content (W). The P decreased with the decrease in soil moisture with a concomitant decrease of T, LWP, $1/r_l$ and W, suggesting that the leaf water balance directly affects the P. Based on the responses of these parameters to soil-water stress, the material varieties were differentiated into four types. The lowland varieties performed high P and good leaf-water balance under flooded condition. But they were very sensitive to the changes of the soil moisture, showing remarkable decreases of these parameters under moderate and severe drought. The tropical upland varieties showed rather low P under flooded condition, but they kept relatively good performance of P and leaf-water balance under moderate and severe drought conditions. The Japanese upland varieties showed intermediate values between the formers under flooded and moderate levels of the soil moisture tension (10-20 cbar), but under severe drought they showed sharp decrease of the values of these parameters as the lowland varieties did. The dwarf mutant Daikoku 1 performed comparatively high values of these parameters at every level of the soil moisture tension. The characteristics of these four types were discussed in view of their adaptation and plant-types.

KEY WORDS : *Oryza sativa* L., rice, drought resistance, photosynthesis, leaf water balance, soil moisture tension.

Introduction

Cultivation of rice (*Oryza sativa* L.) is spreading from irrigated paddy to rainfed upland fields and from tropical to temperate regions world-wide resulting in the differentiation of varieties adapted to lowland and upland conditions. Since rice is particularly well suited to irrigated cultivation, varietal improvement for high resistance to drought has received a great deal of attention.

In spite of the recent interest in the physiological basis of drought resistance in rice (IRRI 1975, O'TOOLE and MOYA 1978, O'TOOLE and CRUZ 1980, SINGH and SASAHARA 1981), more data on the varietal differences in the response to drought are needed for developing a program aimed at the breeding of varieties highly tolerant to water stress.

The present studies were undertaken to analyse the differences in the photosynthetic activity and related leaf water balance among upland, lowland and dwarf mutant varieties under various soil moisture tensions ranging from flooded condition to severe drought causing leaf rolling (wilting).

Received October 20, 1984.

[1] Home Address : *Fundacção Instituto Agronômico bo Paraná,* Caixa Postal 1331, 86.100-Londrina, Paraná, Brazil.

[2] Professor Emeritus of Tohoku University.

Materials and Methods

Eight rice varieties were selected for the investigations, i. e. five upland varieties consisting of Sensho and Rikuto Norin 24 from Japan, Batatais and IAC 1246 from Brazil and Moroberekan from Africa, two lowland varieties, namely IR 8 from the Philippines and Bosque from Brazil and one dwarf mutant, Daikoku 1 from Japan. The seeds were treated with Benlate 1/1000 for 12 hrs followed by pregermination at 32°C. They were sown at a rate of 5 per Wagner pot 1/5000 a containing river clay silt under glasshouse condition. The seedlings grown with daily irrigation were thinned to one plant in each pot at the three leaf stage. Fertilizer was supplied at the sowing time at the rate of 0.5 g each for N, P and K, and topdressing with 7 m*l* per pot of a nutrient solution (47 g ammonium sulphate, 10 g sodium phosphate dibasic and 12 g potassium chloride per liter) was performed twice 50 and 60 days after the sowing. Five sets of pots were prepared for each variety. One set of pots was maintained under flooded condition. The other four sets were used for the water stress treatment consisting of the interruption of irrigation 62 days after seeding. The soil moisture tension of each pot was monitored with a tensiometer installed at 10 cm depth.

Photosynthetic rate (P), transpiration rate (T) and leaf water content (W) were measured on the second expanded leaf from the top of the main stem, and leaf diffusive conductance ($1/r_1$) and leaf water potential (LWP) were measured on the second expanded leaf on the secondary stem of the same plant. When the soil moisture tension of a pot reached a given value, the plant was transferred to the laboratory adjacent to the glasshouse for the measurements. The leaf was placed in an acrylic air-sealed chamber (5 mm inner thickness and 25 mm width) and P and T were estimated under a radiation flux of (4.5 J. cm^{-2}. min^{-1}), an air flow rate of 1.5 liter per minute, and at an air temperature of 29±1°C by reading the differences in CO_2 and H_2O concentrations between the incoming and outgoing air of the leaf chamber with an infrared gas analyser (Hitachi-Horiba, model ASSA-2) and two sets of dry and wet bulb thermometers. The relative humidity of the air entering the leaf chamber was about 72%. The aeration and illumination of the leaf were maintained for about 30 minutes to reach the maximum P value and allow for the simultaneous reading of T. Immediately after the measurements, the leaf was cut off from the stem for determining the fresh weight and leaf area. Thereafter, it was oven-dried for estimation of the leaf water content. Leaf diffusive conductance was determined with an autoporometer (Lambda, model LI-65) equipped with a sensor (Lambda, model LI-20 S, aperture size 3.5×20 mm) on the adaxial and abaxial leaf surfaces, and the averaged value was used. Leaf water potential was estimated with a pressure chamber (PMS Instruments).

The measurements for the water stressed plants were performed when the soil moisture tension of each pot reached 10±1, 20±1, and 40±1 cbar, and when leaf rolling began. The measurements for the flooded plants were carried out during the time when the water stressed plants were examined. It took about one week from the initial measurement up to the end for the latest variety.

Experiments under the same design were replicated four times for the materials that had been sown each week. The averaged value of the replication was considered in the present report.

Results

Under flooded condition the lowland varieties IR 8, Bosque and the dwarf mutant Daikoku 1 showed a higher P than the other varieties (Fig. 1). At 10 cbar of soil moisture tension, a remarkable decrease of P was observed in the lowland varieties, and a less conspicuous one in the upland varieties. However, the varietal differences in the P values were not significant except in the dwarf mutant. A moisture tension of 20 cbar caused a significant decrease of P in the lowland varieties, resulting in the differentiation of upland and lowland varieties while P remained high in Daikoku 1. When the soil moisture tension reached 40 cbar or higher values, the P of the lowland and Japanese upland varieties decreased significantly, while the P of the tropical upland and Daikoku 1 varieties was higher than that of the other varieties. Thus the varieties examined could be divided into four types. The lowland varieties had a higher P under

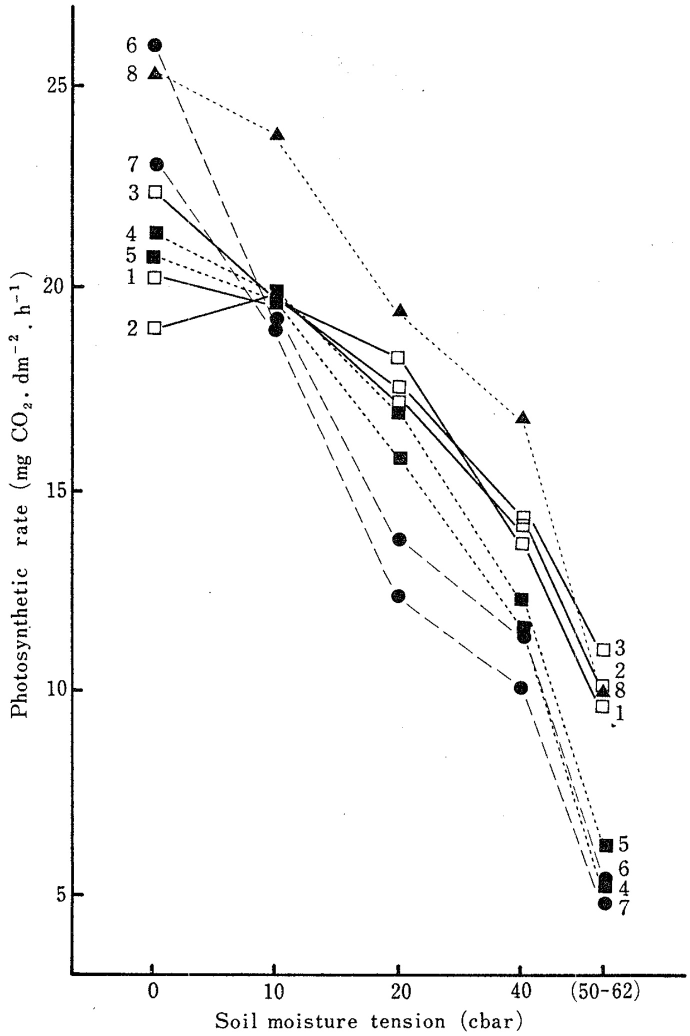

Fig. 1. Photosynthetic rate at different levels of moisture tension in the tropical upland varieties (□ : 1, Moroberekan ; 2, IAC 1246 ; 3, Batatais), Japanese upland varieties (■ : 4, Sensho; 5, R. Norin 24), lowland varieties (● : 6, IR 8 ; 7, Bosque), and dwarf mutant variety (▲ : 8, Daikoku 1).

flooded condition but their P decreased sharply in case of moderate and severe drought. The tropical upland varieties had a low to intermediate P under flooded condition, but the decrease of P was lower under moderate and severe drought conditions. The Japanese upland varieties were intermediate between the formers at moderate levels of moisture tension but their P decreased greatly by severe drought. The dwarf mutant, Daikoku 1 maintained a comparatively high P value regardless of the level of the soil moisture tension.

Rolling of leaves (wilting) occurred at different levels of soil moisture tension depending

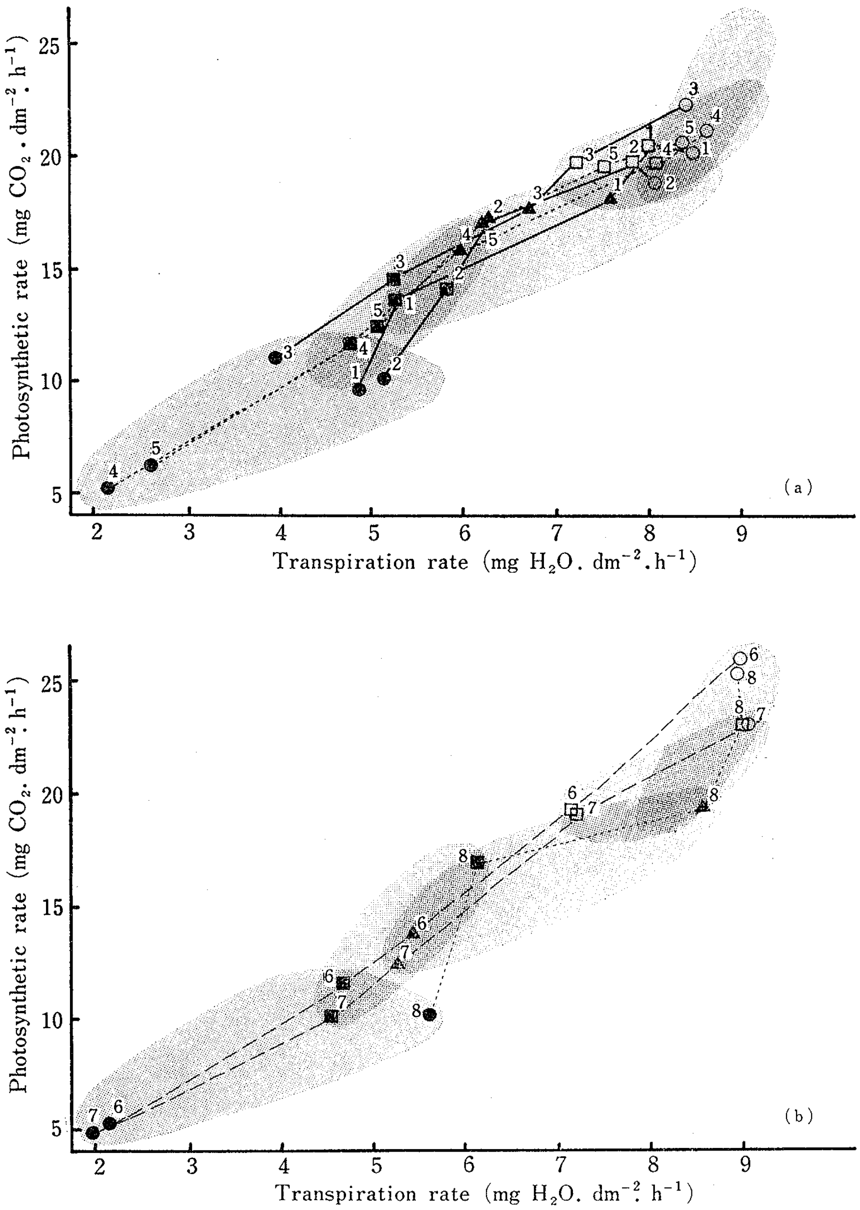

Fig. 2. Relationship between photosynthetic and transpiration rates in eight rice varieties at different levels of soil moisture tension : flooded condition (○), 10 cbar (□), 20 cbar (▲), 40 cbar (■), value causing leaf rolling (●).

(a) for varieties : 1, Moroberekan ; 2, IAC 1246 ; 3, Batatais ; 4, Sensho ; 5, R. Norin 24, and (b) for varieties : 6, IR 8 ; 7, Bosque ; and 8, Daikoku 1.

on the varieties. The values of the soil moisture tension were 50, 53, 56 and 62 cbars for the lowland, the Japanese upland, the tropical upland and the dwarf mutant varieties, respectively. The time interval between the beginning of the treatment and the occurrence of leaf rolling also varied with the varieties. These intervals were 9.6, 10.5, 10.8 and 12.8 days for the lowland, the Japanese upland, the tropical upland and the dwarf mutant varieties, respectively.

Fig. 2 shows the relationship between P and the transpiration rate (T) at different soil moisture levels. P and T as a rule showed a highly positive correlation. In the lowland varieties, both parameters were high under flooded condition and they decreased

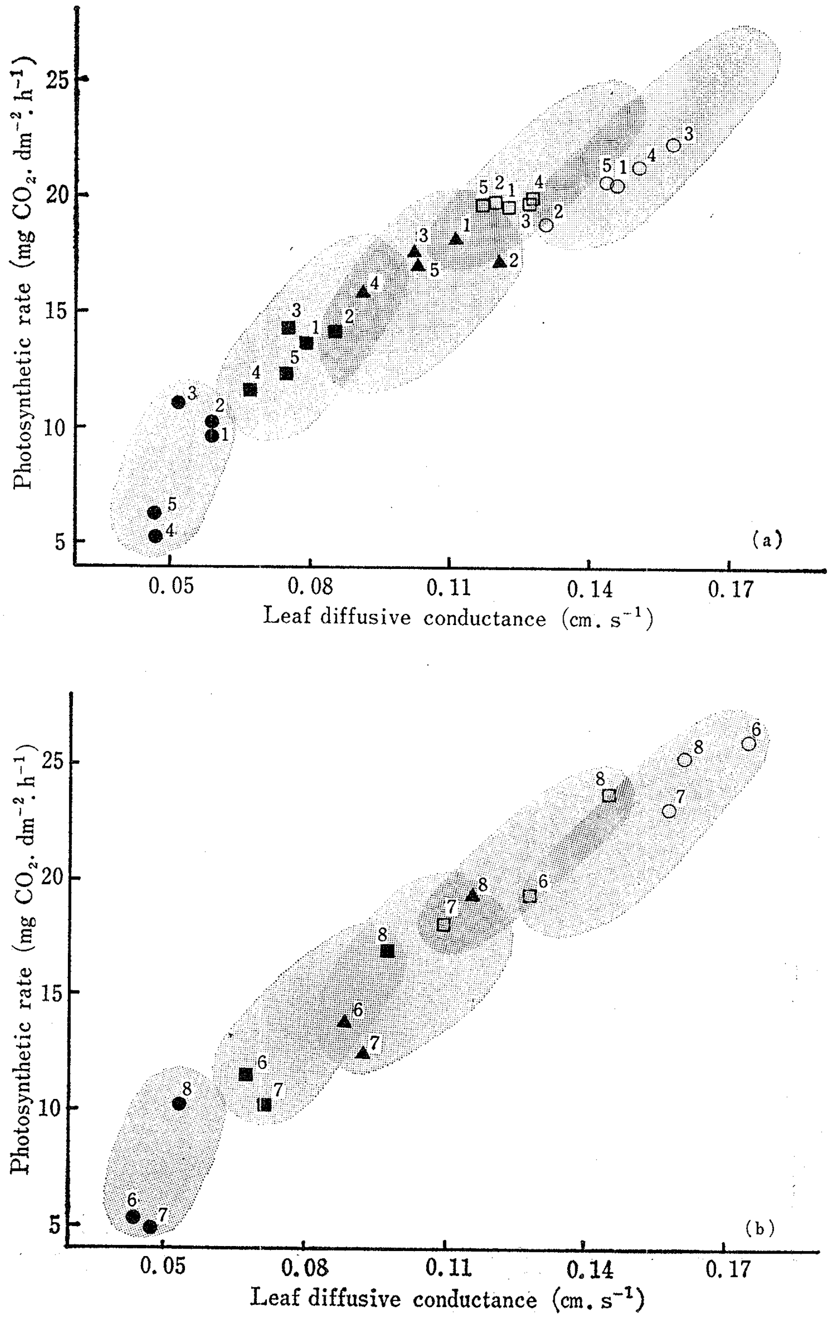

Fig. 3. Relationship between photosynthetic rate and leaf diffusive conductance in eight rice varieties at different levels of soil moisture tension. Symbols are the same as in Fig. 2.

linearly with the decrease of the soil moisture level (Fig. 2 b, 6, 7). As compared with these lowland varieties, the values of P and T in the upland varieties were not very high under flooded condition (Fig. 2 a). Under severe drought conditions, both parameters decreased markedly in the Japanese upland varieties (4, 5) as in the lowland varieties, but the tropical upland varieties showed comparatively high T values (1, 2, 3). The response of the dwarf mutant (8) was peculiar and resembled that of the lowland

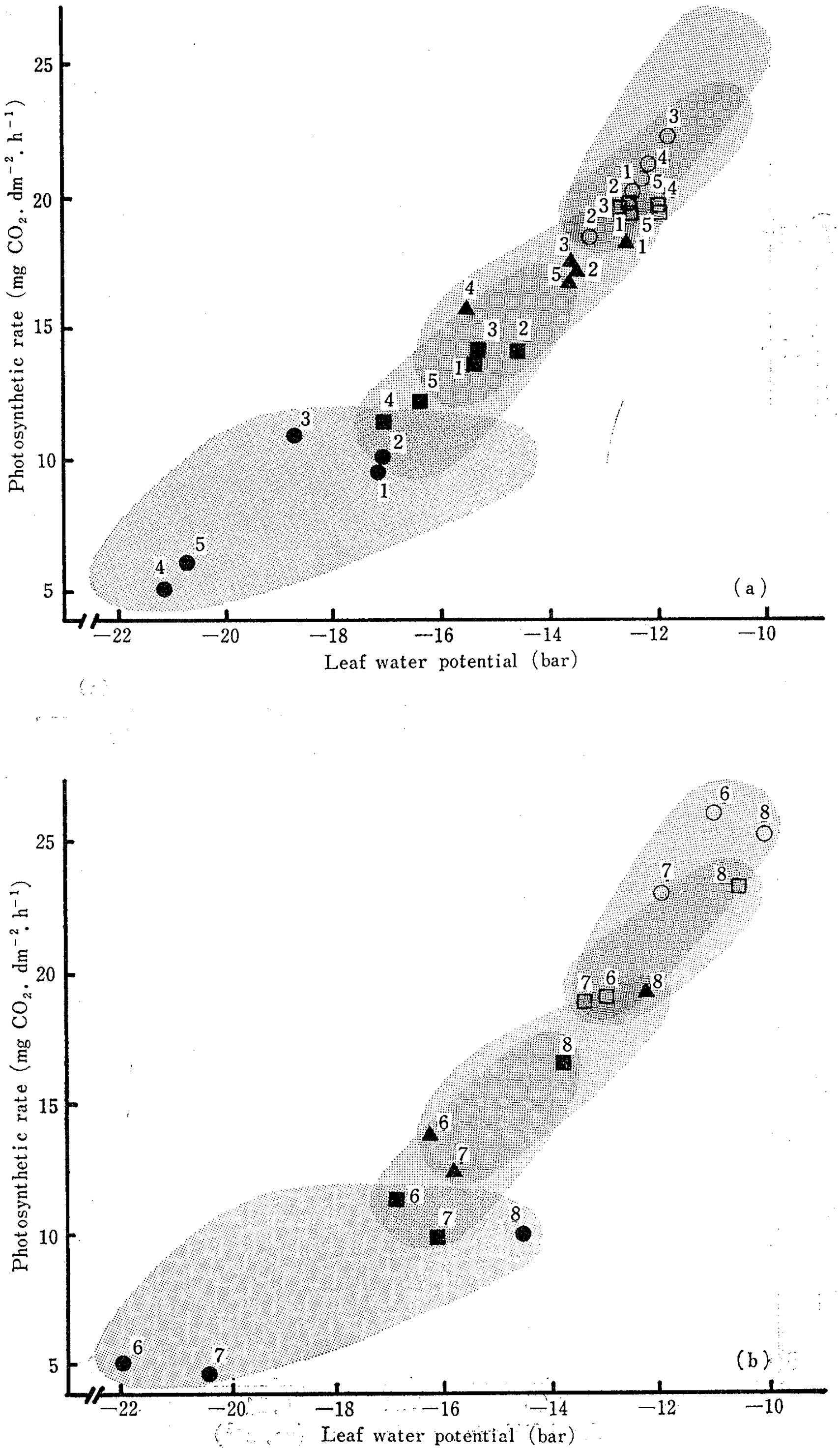

Fig. 4. Relationship between photosynthetic rate and leaf water potential in eight rice varieties at different levels of soil moisture tension. Symbols are the same as in Fig. 2.

varieties under flooded condition and that of tropical upland varieties under drought conditions. The photosynthetic activity was directly affected by the water balance of leaves.

Figs. 3 and 4 show the relationships between P and leaf diffusive conductance ($1/r_1$) and between P and leaf water potential (LWP), respectively. Under flooded condition, where the water supply was abundant, $1/r_1$ and LWP of the lowland (6, 7) and dwarf mutant (8) varieties were remarkably higher than those of upland varieties (1–5). Under severe drought conditions, these parameters decreased in all varieties, and LWP differentiated clearly the types of varieties, i. e., tropical upland (1–3) and dwarf mutant (8) types from Japanese upland (4, 5) and lowland ones (6, 7). Leaf water content that was also measured in the present experiment, differentiated these types similarly but not so clearly as LWP did.

Discussion

In the survey of the performance of rice varieties under severe drought conditions, O'Toole and Moya (1978) observed a high correlation between the leaf rolling score and leaf water potential. Further linear relationship was found between the leaf water potential and leaf diffusion resistance (O'Toole and Cruz 1980). In the present study, P decreased with concomitant decreases of T, W, LWP and $1/r_1$, as the soil moisture tensions increased. The changes in the leaf water balance influenced by soil water deficit directly affected the photosynthetic activity. It was found that based on the changes of these parameters with different soil moisture levels, lowland, tropical upland, Japanese upland and dwarf mutant varieties, could be characterized as follows.

Under flooded condition, the lowland varieties (IR 8 and Bosque) showed a high P, and were characterized by a high leaf water potential and leaf diffusive conductance. With the increase of the soil moisture tension, however, their leaf water potential and leaf diffusive conductance decreased very sharply with concomitant decreases of T and P. These varieties lost water most quickly and the leaves started to roll at higher moisture levels presumably due partly to a larger number of stomata (Yoshida and Ono 1978, Terao and Yamashita 1983, and Tsunoda and Fukoshima 1985). In this type of varieties the variations in the leaf water balance with the soil moisture conditions were the most pronounced.

The tropical upland varieties (Moroberekan, IAC 1246 and Batatais) had a comparatively low photosynthetic rate under flooded condition, presumably due to their low transpiration rate and leaf diffusive conductance. Under severe drought conditions, they were able to maintain a comparatively high leaf water potential in spite of the relatively low values of the diffusive conductance. The leaves remained unrolled at rather high levels of soil moisture tension presumably due to the development of the vessels associated with the preservation of the water balance in these varieties, as discussed by Tsunoda and Fukoshima (1985). The leaf water balance varied comparatively less with the changes in the soil moisture tension. Thus, P and T could remain comparatively high under drought conditions. Such characteristics may be the result of selection associated with dry farming under high temperature conditions.

In the Japanese upland varieties (Sensho and R. Norin 24) the values of these parameters were relatively high under moderate drought conditions, but they decreased sharply under severe drought conditions to values close to those recorded in the lowland varieties. Decrease of the leaf diffusive conductance and the leaf water potential caused a decrease of P and T. This varietal type can be considered as being intermediate between the lowland and the tropical upland varieties. They have became adapted to weather conditions characterized by frequent rainfall and mild temperature as in Japan, but have not undergone a process of selection under severe drought conditions.

Daikoku 1 showed the highest values for the parameters regardless of the soil moisture tension levels. This variety has smaller and thicker leaves with a dark green color compared with the other varieties. It is possible to consider that such properties of leaves and character combinations make it possible for this variety to maintain a good water balance, resulting in a high P. In addition, this variety has a lower tillering ability as in the case of the upland varieties (ONO 1971 and IRRI 1975). The period from the beginning of the stress treatment to the onset of leaf rolling was the longest in this mutant, among the varieties, indicating a slow consumption of water. This mutant appears to be superior physiologically as well as in its ability to avoid drought, as will be discussed in more detail in another paper (FUKOSHIMA *et al.* 1985).

Acknowledgements

The authors thank the Ministry of Agriculture, Forestry and Fisheries for providing the seeds of rice and the Ministry of Education of Japan for awarding a fellowship to the first author.

Literature Cited

FUKOSHIMA, M. T., K. HINATA and S. TSUNODA 1985. Effects of defoliation on the photosynthetic parameters and yield components under flooded and drought conditions in rice varieties. Japan. J. Breed. (in submittance).

IRRI 1975. Major Research in Upland Rice. International Rice Research Institute, Philippines. 255.

ONO, S. 1971. Upland rice breeding in Japan. JARQ **6** : 68–72.

O'TOOLE, J. C. and T. B. MOYA 1978. Genotypic variation in maintenance of leaf water potential in rice. Crop Sci. **18** : 873–876.

——— and R. T. CRUZ 1980. Response of leaf water potential, stomatal resistance and leaf rolling to water stress. Plant Physiol. **65** : 428–432.

SINGH, M. K. and T. SASAHARA 1981. Photosynthesis and transpiration in rice as influenced by soil moisture and air humidity. Ann. Bot. **48** : 513–517.

TERAO, T. and A. YAMASHITA 1983. Physiological differentiation of crop cultivars in photosynthetic activity. 2. Principal component analysis of photosynthetic rate and its related leaf characters of semi-dwarf rice cultivars. Japan. J. Breed. **33** (Suppl. 1) : 94–95.

TSUNODA, S. and M. T. FUKOSHIMA 1985. Leaf properties related to the photosynthetic response to drought in upland and lowland rice varieties. Ann. Bot. (in submittance).

YOSHIDA, T. and T. ONO 1978. Environmental differences in leaf stomatal frequency of rice. Japan. Jour. Crop Sci. **47** : 506–514.

異なった土壌水分条件における光合成速度および葉水分バランスのイネ品種間差異

Mario Thukasha FUKOSHIMA・日向康吉・角田重三郎
（東北大学農学部，仙台市，〒 980）

水・陸稲8品種を使用し，光合成速度（P），蒸散速度，水ポテンシャル，拡散伝導度，水分含量を各種土壌湿度条件下で測定した．土壌湿度は，湛水，10，20，40 cbar および捲葉点（50〜62 cbar）とした．湛水状態では水稲（IR 8 および Bosque）および矮性突然変異体（大黒1号）が高いP値を示した．10 cbar では水稲品種のPが大幅に低下したが，陸稲品種（熱帯陸稲，Moroberekan，IAC 1246，Batatais；日本陸稲，戦捷，陸稲農林24号）の P の低下は少なかった．そして大黒1号以外の品種の P 値は近似した．20 cbar に土壌湿度を下げると陸稲品種のP値が高く，大幅にP値を低下した水稲品種とに差が見られるようになった．土壌水分が 40 cbar 以上になると，水稲品種および日本陸稲の P 値が大幅に低下し，熱帯陸稲と大黒1号は比較的高い P 値を示した．以上の結果から乾燥に対する反応によって，供試品種を，水稲，熱帯陸稲，日本陸稲，大黒1号の4型に分類した．

ある土壌水分で品種を比較した時も，またある品種について各種の土壌水分条件で比較した時も，P の値と葉水分バランスに関与するパラメーターとの間には常に相関が認められ，品種の反応には差があること，また，葉水分バランスが P 値に強い影響を与えていることがわかった．水稲品種は土壌湿度の変化に応じて，水分バランスを大幅に変化させるが，熱帯陸稲品種の水分バランスの変化は少ない．日本陸稲の湛水下での水分バランスは熱帯陸稲に似ているが，強乾燥条件下における日本陸稲は水稲と同様水分パラメータを極度に低下させる．一方大黒1号は，湛水下で水稲品種同様の良好な水分バランスを示し，また，いずれの条件下でも水分含量が高く，水ポテンシャルも高い値を示した．

捲葉を示す土壌湿度も品種によって異なり，水稲では 50 cbar，日本陸稲 53 cbar，熱帯陸稲 56 cbar，大黒1号 62 cbar であった．また灌水停止時から捲葉が認められる迄の日数も品種によって異なり，水稲 9.6 日，日本陸稲 10.5 日，熱帯陸稲 10.8 日，大黒1号 12.8 日であった．

水稲は土壌の乾燥に従って葉水分ポテンシャル，葉水分伝導度を急速に低下させるが，この特質は，恐らくその高い気孔密度などの葉形質と関連しているものと考えた．一方熱帯陸稲の乾燥下における高い葉水分ポテンシャルは，発達した維管束系と関連しているものと思われる．熱帯陸稲は高温下の乾地農業による選抜を受けているのであろう．一方日本陸稲は，比較的低温多湿の条件で栽培されているために，それ程の耐旱性を得ていないものと考えることができよう．大黒1号は，いずれの土壌湿度条件でも高い葉水分ポテンシャルを示したが，これは本品種が短小で厚い葉を有し，分げつが少ない特性と関連しているものと思われる．