

RELATIONSHIPS BETWEEN TRANSPIRATION AND PHOTOSYNTHESIS DURING A WATER STRESS.

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Abstract

Rice plants were grown in a controlled environment and transpiration and photosynthesis observed during a drying and rewatering sequence. The response of different upland rice and lowland rice were compared during vegetative growth.

Plants were grown in soil containers in a sealed growth chamber inserted in an open circuit air flow controlled for temperature and humidity. Water and CO₂ concentrations were measured by infra-red analyser in order to calculate H₂O and CO₂ exchanges between the aerial part of plant and the atmosphere. The water stress was obtained by stopping irrigation. Soil matric potential was measured with tensiometers connected to pressure cells.

Plant water deficits led to a decrease in gas exchanges, due to stomatal closure and leaf rolling. The stomatal response progressively took place at a soil water potential threshold, lower for upland rice varieties (about -700 mbar) than irrigated ones (about -450 mbar). Transpiration was more influenced than photosynthesis at the beginning of drying period. Irrigation induced a rapid resumption of transpiration and photosynthesis, simultaneously with the leaf unrolling and progressive stomatal opening. The relationship between photosynthesis and transpiration showed hysteresis from drying to rewatering for some rice varieties. The hysteresis subsists when the plant suffers other water stresses.

1. Introduction

Stomatal regulation of transpiration is one of the strategies used by the plant to delay the occurrence of plant water stress due to soil water shortage. The reduction in transpiration occurs to the detriment of the photosynthesis since the stomata are the common path way for water vapor and CO₂ exchange.

For rice (*Oriza sativa* L.) few studies deal with the incidence of water stress on gaseous exchange with atmosphere ; this is due to the aquatic mode of rice cultivation (Yoshida and Shioya, 1976). But in Western Africa, rice is much cultivated on non-saturated soil (rain-water cultivation). The water supply then becomes the yield limiting

factor and the problem of the sensitivity of rice to the water stress has to be considered.

This paper compares photosynthesis and transpiration changes, at the whole plant level, during a drying/rewatering sequence in relation to stomatal functioning and associated effects on the gaseous exchange for an upland variety and a lowland variety.

2. Material and methods

The seedlings were cultivated on soil under controlled conditions. The continuous measurement of gaseous exchanges was made with an experimental device similar to that referred to by Picard & al. (1981). It concerned an open-circuit plant chamber mainly consisting of a double-wall glass recipient tightly connected to a soil container. The chamber was supplied with air at a humidity of 60 % and a temperature of 25°C which was sampled by two infra-red differential analyzers measuring the water and CO₂ content respectively. Comparing the inlet air and outlet air allowed the plant water and CO₂ exchange by the leaves to be measured. The soil water potential was obtained by tensiometers coupled with a pressure transducer. Illumination was provided by a 600 $\mu\text{Em}^{-2}\text{s}^{-1}$ (PAR) light level over a 12-hour photoperiod.

The seedlings were put in the chamber, at the vegetative stage, when tillering was beginning (30 to 40 days after sowing). The water stress was created by an irrigation shortage and the exhaustion of soil water reserves was continued until the leaves were completely rolled. One or several "drying/rewatering" sequences separated by a few-day recovery period were monitored. The use of soil containers of various capacities (2 or 7 kg of soil) allowed the drying speed to be varied. Two varieties have been studied, one an upland type (IRAT 13) and the other a lowland type (IR 5).

3. Results

The water deficit shows a reduction of the gaseous exchange and a modification of its nycthemeral cycle (Picard et al., 1981 ; Bois et al., 1984).

During the drying phase, the relationship between the instantaneous transpiration expressed as relative value - with respect to the maximum reached before the water stress - with the mean soil water potential at a given time, shows a threshold response (Figure 1). The transpiration remains independant of water potential up to a critical value ; then decreases as the potential drops. The critical value was less for IRAT 13 (-650 mbar) than for IR 5 (-450 mbar).

Figure 2 illustrates the relationship between relative transpiration and the leaf rolling score, on the scale of O'Toole and Cruz (1980). With IR 5, variation in transpiration was not directly linked to leaf rolling, with stomatal control occurring when leaves were still at index 1. For IRAT 13, trends for stomatal control and leaf rolling were parallel.

Figure 3 shows the relationship between photosynthesis and transpiration, expressed as relative values, during the drying/rewatering sequence. In the first part of the drying phase, the slope of the curve for photosynthesis, as a function of transpiration, was less than 1 indicating that transpiration decreases more than photosynthesis. At the end of the drying phase, the slope exceeds 1. After irrigation, the drying and rewatering curves are similar for IR 5 but show significant hysteresis for IRAT 13.

With a slower drying sequence (7 days instead of 2 days), photosynthesis and transpiration were reduced in the same proportions (Figure 4). This might reflect an internal reorganization of the plant that affects photosynthetic development. However, hysteresis is still seen during recovery.

Figure 5 shows the effect of two successive stress cycles, separated by a recovery week, on IRAT 13. During the second drying out phase, the photosynthesis to transpiration curve shows equal reductions as with slow drying out. Hysteresis is present.

4. Discussion

The decrease of photosynthesis and transpiration results from two effects, stomatal closure, which increases the resistance to the gaseous interchange between the leaf and the atmosphere and leaf rolling which reduces the exchange surface. With photosynthesis, a variation of mesophyll resistance to CO_2 transfer also appears. The first two mechanisms are delayed for IR 5 where stomatal closure occurs before leaf rolling. This suggests that either IR 5 stomata are more reactive than those of IRAT 13 or that, alternatively, response to variation in leaf water potential is faster. Their reaction to a low soil water potential (Figure 1) confirms that sensitivity to the water deficit is greater than that of IRAT 13. Henson (1982) showed that stomatal control starts with a relatively high (4 to 5 bars) turgor potential whereas the leaf rolling occurs at a potential close to zero. For IRAT 13, the latter plays a greater part in transpiration control than for IR 5. It therefore constitutes an efficient adaptative mechanism. O'Toole and Cruz (1979) evaluated its contribution to the limitation of the transpirational water loss as 40 %.

The stomatal response with threshold was similar to that of Tomar and Ghildial (1973). The reaction of the plant to a small reduction in soil water potential can be explained in terms of the sensitivity of rice to water stress and of the low water reserve of the sand-clay soil used (a -1 bar soil water potential corresponds to a 10 % water by volume approximately). O'Toole and Baldia (1982) note that rice transpiration drops to -0,2/-1 bar. The lower sensitivity of the upland type compared with the irrigated type has been shown elsewhere (Bois et al. 1984). The stomatal closure critical potential is eliminated by slow drying (O'Toole and Cruz, 1980). In the field or in a high capacity soil container, the root system faces a potential gradient ; a more integrated response from the plant

results. During fast drying, the whole root system is subjected to the same water potential. This method offers the advantage to show varietal differences and allows relatively reproducible water stresses. But it should be noted that the adaptive mechanisms can be different from those obtained in the field.

At the beginning of the drying phase, photosynthesis decreases less than transpiration, due to the existence of mesophyll CO_2 resistance adding to stomatal resistance thus reducing the effect of stomata in the total resistance to CO_2 transfer (Tinus, 1974). In the case of water vapor transfer, only the stomatal resistance is significant. The closure of stomata therefore affects transpiration more than photosynthesis. At the end of the drying phase, the action of leaf rolling is dominant and impedes water and CO_2 transfers in the same way. It is also possible that an increase in mesophyll resistance occurs caused by the dehydration of tissues and affects photosynthesis. After irrigation, the recovery process is different for the two varieties. For IRAT 13, a slower recovery of photosynthesis suggests that the stomata are not the limiting factor but that the resistance of the mesophyll to CO_2 transfer or functioning of chloroplast are limiting. The important role of the leaf rolling system in recovery the transpiration (Figure 2) can also partly explain the hysteresis shown by IRAT 13. It is noted that this phenomenon still exists during successive water stresses and during slow drying. It seems to be a variety characteristic and was found in other varieties (Bois et al., 1984).

IRAT 13 is a relatively drought tolerant variety. Are this property and the difference of behavior with respect to the water stress as shown here linked? As regards the lower critical potential and the leaf rolling efficiency, the link seems obvious. The hysteresis, which results in limited recovery of photosynthesis does not seem to favour higher drought tolerance.

A better understanding of this phenomenon seems desirable; this will be the target of our future studies.

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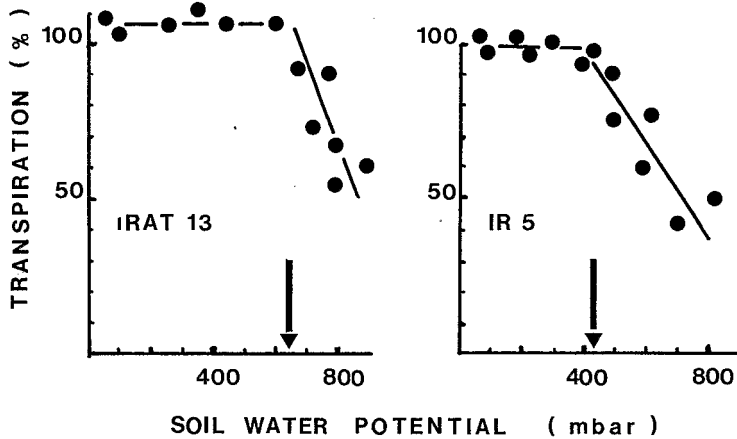


Fig. 1 - Relationship between transpiration and soil hydric potential during the drying for two rice cultivars (IRAT 13 and IR 5).

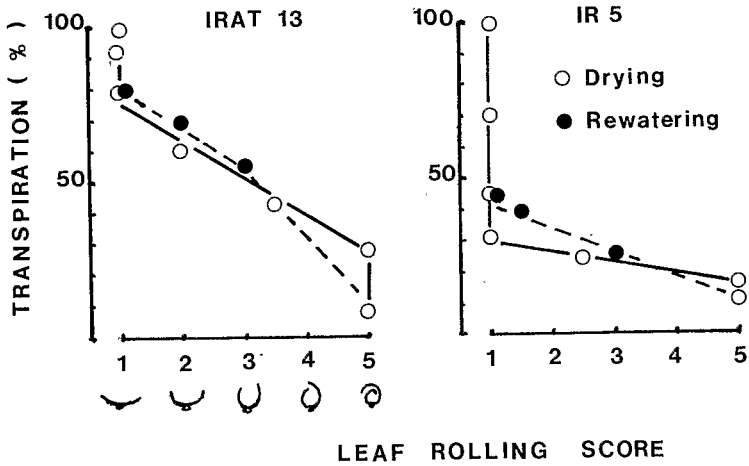


Fig. 2 - Relationship between transpiration and leaf rolling score during the drying-rewatering sequence for two rice cultivars.

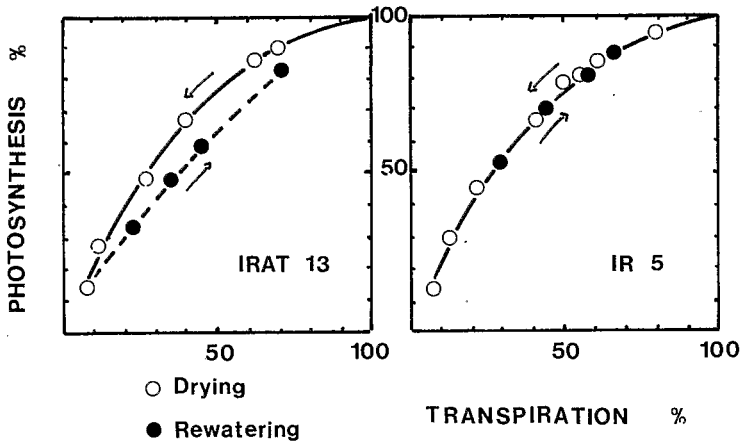


Fig. 3 - Relationship between photosynthesis and transpiration during the drying-rewatering sequence for two rice cultivars.

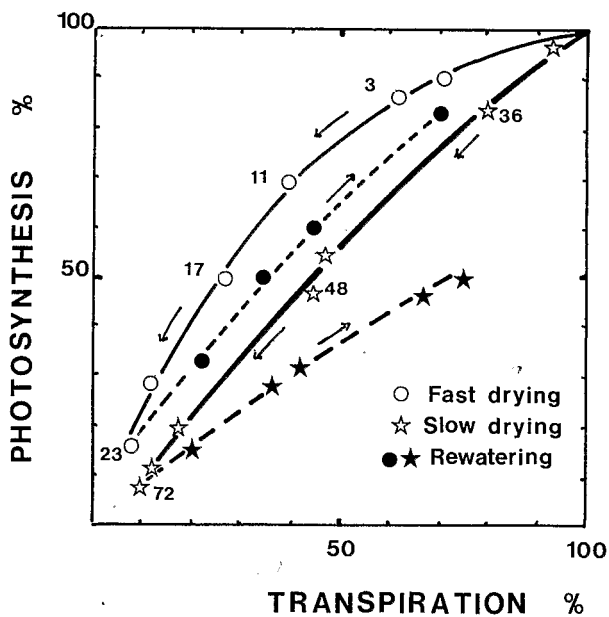


Fig. 4 - Relationship between photosynthesis and transpiration during a drying-rewatering sequence with two drying rates for one rice cultivar. Numbers indicate duration (in diurnal hours) of drying.

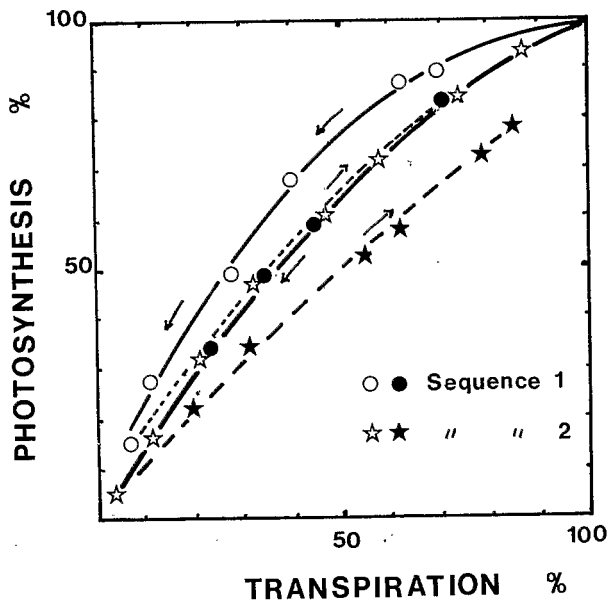


Fig. 5 - Relationship between photosynthesis and transpiration during two successive drying-rewatering sequences for one rice cultivar (IRAT 13).