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Photosynthetic Responses of Four Legume Crops to Fluctuations of Evaporative Demand Following the Rainy Season

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Summary

In the typical climate of East Asia, summer crops develop large shoots with relatively poor root systems during the rainy season, leading to restricted photosynthetic activity in the following summer months. The objectives of the present study were 1) to determinate if there are specific differences in the photosynthetic responses of four legume crops to daily fluctuations of evaporative demand and 2) to identify physiological attributes responsible for the differences. Soybean, azuki bean, cowpea and peanut were grown in a field, and apparent leaf photosynthetic rate (AP) and gas exchange parameters as well as water potential and transpiration rate were measured at midday on three consecutive summer days. When leaf-to-air vapor pressure deficit (VPD_{la}) varied from 1.72 to 3.44 kPa during the experimental period, the four species responded differently. The AP of soybean and that of azuki bean decreased with increasing VPD_{la} over a range of 1.72 to 3.44 kPa, whereas the activities of cowpea and peanut were greatest at VPD_{la} around 2.53 kPa. The leaf water potentials of soybean, azuki bean and cowpea reached minima at VPD_{la} around 2.53 kPa, while that of peanut was fairly constant over the VPD_{la} range of 1.72 to 3.44 kPa. The transpiration rates of soybean, azuki bean and cowpea were greatest at VPD_{la} around 2.53 kPa and decreased beyond that range of VPD_{la}, while peanut transpired actively with increasing VPD_{la}. AP of soybean was correlated with leaf water potential, whereas that of cowpea and peanut was correlated with transpiration rate. With respect to water relation, peanut was most tolerant to increasing VPD_{la} among the four species tested, presumably because it maintained higher water potential and transpiration rate than the other species under the condition of high VPD_{la}.

Introduction

Under field conditions, crops may suffer water deficits because of either inadequate availability of soil water or high transpiration rates due to low atmospheric humidity. Deficits caused by the latter environmental condition are most common in East Asia, where a rainy season precedes the hot summer. Since summer crops develop relatively small root systems during the rainy season, they later often suffer from water deficits caused by high transpiration rates in summer (1).

Water stress on fine days leads to stomatal closure, ultimately resulting in a decline of photosynthetic rate at midday (2) that may amount to 26% in rice (3) and 56% in wheat (4), even if the plants are well irrigated. Soybean is particularly vulnerable to this type of water stress, and its leaves are susceptible to wilting around midday (5-10). The decline of midday photosynthesis is an important factor adversely affecting yield stability in soybean cultivars (11). Thus, a considerable amount of solar energy is wasted around midday without being utilized for dry matter production in soybean.

There have been a number of studies on the effects of soil water deficit on various physiological processes associated with growth and development of legume crops, including soybean (12-15). However, photosynthetic responses to water stress of azuki bean, which is one of the most important legume crops in East Asia, have not been characterized in detail so far. Moreover, there is little information on specific differences in the responses to contrasting atmospheric conditions of different legumes. The objectives of the present study were 1) to determine if there are specific characteristics of four legume crops regarding their photosynthetic responses to daily fluctuations of evaporative demand and 2) to identify physiological properties responsible for the differences observed.

Materials and Methods

This study was conducted under high precipitation conditions in the experimental field of Tohoku University (38°16 N, 140°50 E). The soil was a fine-textured Aquic Yellow soil (16). Soybean (*Glycine max* (L.) Merr., cv. Enrei), azuki bean (*Vigna angularis* (Willd.) Ohwi et Ohashi, cv. Dainagon), cowpea (*Vigna unguiculata* (L.) Walp., cv. Kuromidori) and peanut (*Arachis hypogaea* L., cv. Chibahandachi) were sown on June 6, 2002 at a spacing of 75 cm between rows and 20 cm between hills. Four seeds per hill were sown, and seedlings were thinned to two plants per hill after establishment. The size of each plot was 9.0 m^2 (4.5×2.0 m), with blocks arranged in a completely randomized design with three replications. Prior to sowing, fertilizer was applied at 2, 10 and 6 gm^{-2} for N, P_2O_5 and K_2O, respectively. Weeds were removed by hand, while insects were controlled by applying insecticides periodically. Measurements of apparent photosynthetic rate (AP), transpiration, leaf water potential and related parameters were carried out on Aug. 1, 2 and 3, 2002 when the climatic conditions were contrasting, as shown in Fig. 1.

The AP and transpiration rate of one fully expanded terminal leaflet of four or five plants of each plot were measured with an LI-6400 Portable Photosynthesis System (LI-COR. Inc., NE, USA) between 1,100 and 1,300 h. The rate of air flow in the leaf chamber was maintained at 500 μmol s^{-1}, and the CO_2 concentration was kept constant at 364.1±4.0 μL L^{-1}. Irradiance on the measured leaf (6 cm^2) was regulated at 1,500 μmol m^{-2} s-1 photosynthetic photon flux density (PPFD) by red-blue light-emitting diodes. The temperature of the chamber was kept at 28°C, while the relative humidity in the chamber was maintained at 61.1±5.5%. The CO_2 diffusive conductance (including stomatal and boundary layer) was calculated as described by von Caemmerer and Farquhar (17). The CO_2 conductance of the mesophyll was estimated according to the method of Gaastra (18). In this paper, these conductances are referred to as diffusive conductance and mesophyll conductance, respectively.

The water potential of the leaflets used for the measurement of photosynthesis was determined with a portable pressure chamber PMS600 (PMS Inc., OR, USA).

Meteorological data such as air temperature, relative humidity, solar radiation and wind speed were obtained from the Sendai District Meteorological Observatory, which is located 2.3 km from the experimental site. The vapor pressure difference between leaf interior and atmosphere (leaf-to-air vapor pressure deficit; VPD_{la}) was calculated from the saturation vapor pressure at leaf temperature and the ambient vapor pressure. Values of VPD_{la} between 1,100 and 1,300 h on days of measurement were 3.44±0.05 on Aug. 1, 2.53±0.05 on Aug. 2 and 1.72±0.01 kPa on Aug. 3.

Results

Climatic Conditions during the Measurements

Climatic conditions, including atmospheric evaporative demand, differed on the three days on which measurements were made (Fig. 1). Aug. 1 was clear and very hot with high evaporative demand, whereas Aug. 3 was mostly cloudy and cool with low evaporative demand. Conditions on Aug. 2 were intermediate.

Responses of Gas Exchange Parameters to Leaf-to-Air Vapor Pressure Deficit

The AP of soybean and that of azuki bean decreased with increasing VPD_{la} over a range of 1.72 to 3.44 kPa (Fig. 2). In contrast, cowpea and peanut showed maxima of AP around 2.53 kPa VPD_{la}. The diffusive conductance responded in a way similar to the response of AP in soybean and azuki bean. Response patterns of mesophyll conductance to VPD_{la} were similar to those of AP in all species.

Water Potential and Transpiration Rate and Their Relation to Gas Exchange Pparameters

The water potentials of soybean, azuki bean and cowpea decreased when VPD_{la} increased from 1.72 to 2.53 kPa, whereas that of peanut was constant over the VPD_{la} range of 1.72 to 3.44 kPa (Fig. 3). The transpiration rates of soybean, azuki bean and cowpea were greatest at VPD_{la} values of around 2.53 kPa. The transpiration rate of peanut increased beyond that range of VPD_{la}.

The relationships of leaf water potential with AP, diffusive conductance and

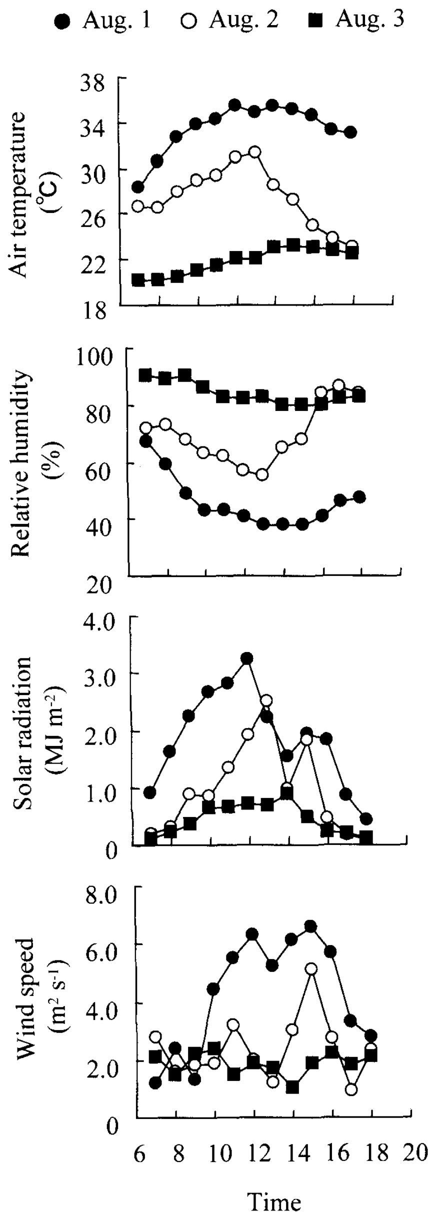

FIG. 1. Diurnal changes of air temperature, relative humidity, solar radiation and wind speed for the three consecutive days on which measurements were carried out. The data were obtained from the Sendai District Meteorological Observatory.

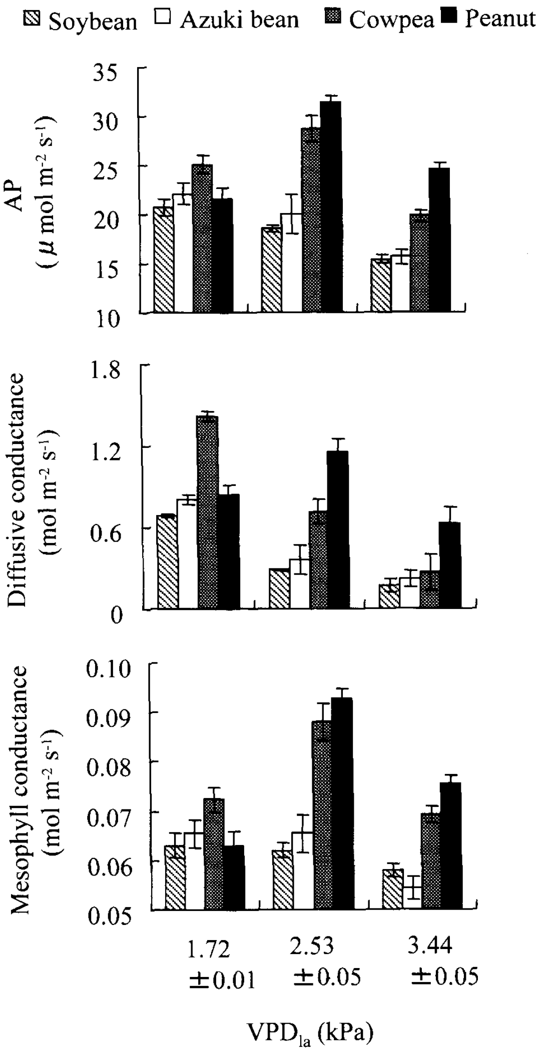

FIG. 2. Apparent photosynthetic rate (AP), diffusive conductance and mesophyll conductance as affected by leaf-to-air vapor pressure deficit (VPD_{la}) in four legume species. Each point represents the mean of four or five measurements. Vertical bars represent SE.

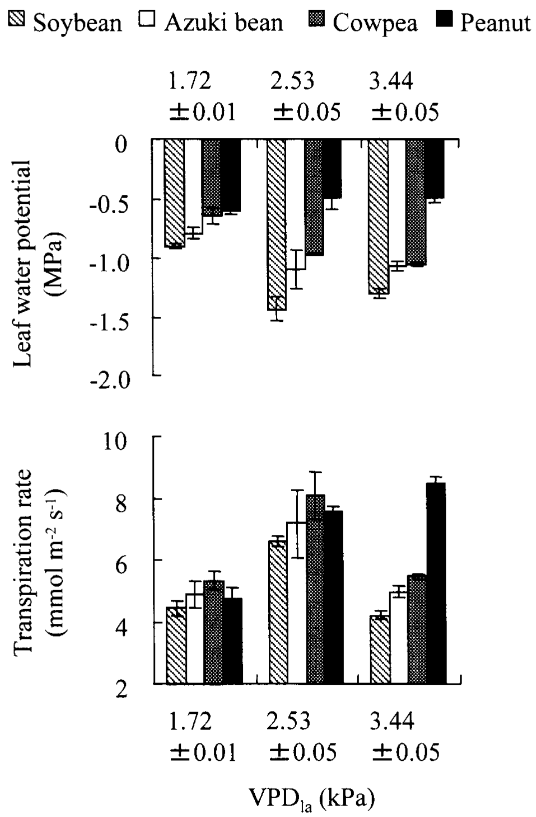

FIG. 3. Leaf water potential and transpiration rate as affected by leaf-to-air vapor pressure deficit (VPD_{la}) in four legume species. Each point represents the mean of four or five plants. Vertical bars represent SE.

mesophyll conductance varied between the species. A significant correlation of AP with leaf water potential was observed exclusively in soybean (Fig. 4). The diffusive conductance correlated with leaf water potential in soybean, azuki bean and cowpea. There was no significant correlation between mesophyll conductance and leaf water potential in any species tested. In peanut, there was no association of leaf water potential with gas exchange parameters within the range of leaf water potential considered. Transpiration rate correlated with AP and mesophyll conductance in cowpea and peanut (Fig. 5). There was no significant correlation between diffusive conductance and transpiration rate in any species tested.

Relationship between Leaf Water Potential and Transpiration

Fig. 6 illustrates the dependence of leaf water potential on transpiration rate. There were close correlations between the two parameters in soybean, azuki bean and cowpea in the VPD_{la} range of 1.72 to 2.53 kPa but not above this range. No significant correlation between the parameters in any range of VPD_{la} was found in peanut.

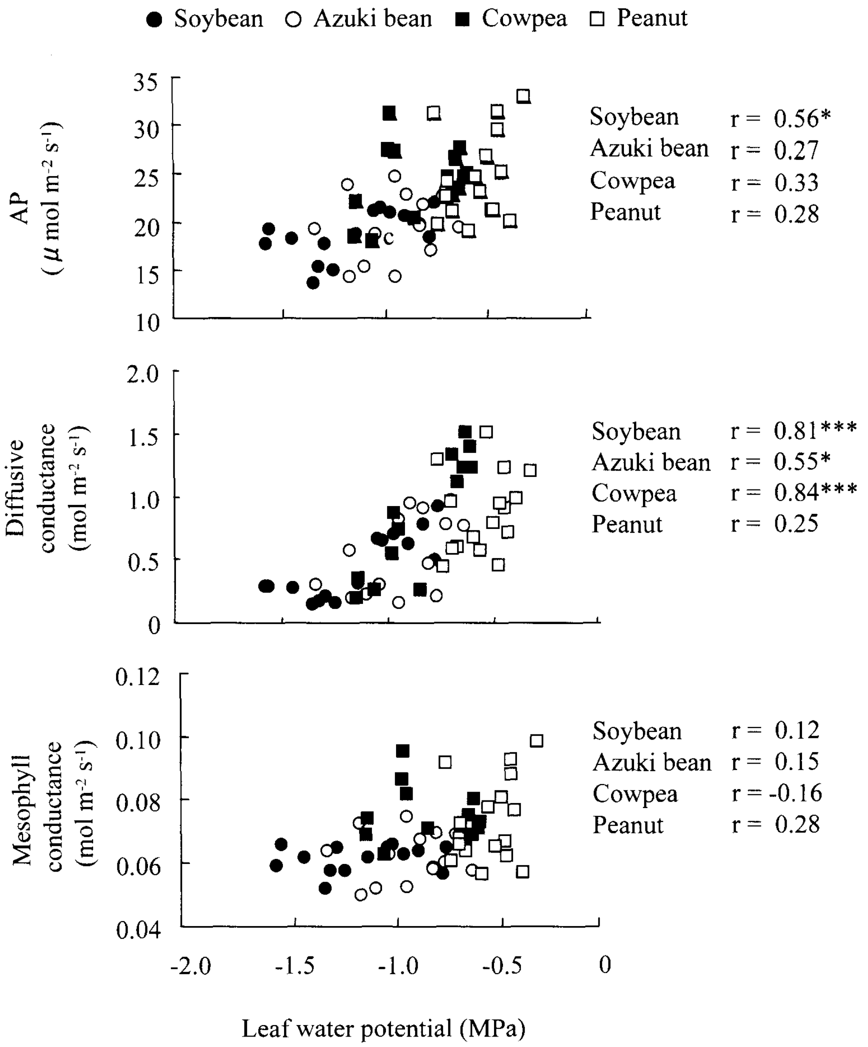

FIG. 4. Association of leaf water potential with apparent photosynthetic rate (AP), diffusive conductance and mesophyll conductance in four legume species. Each point represents one measurement from one plant; four plants of each species were used for measurements on three consecutive days and all data were plotted. *, *** indicate significant correlations at the 5% and 0.1% level, respectively.

Discussion

The four legume crops responded differently to changes in VPD_{la}. Soybean and azuki bean were photosynthetically most active at VPD_{la} around 1.72 kPa, whereas the activities of cowpea and peanut were greatest around 2.53 kPa (Fig. 2). When cowpea and peanut plants were exposed to VPD_{la} below 2.53 kPa, the photosynthetic capacity of these species appeared impaired by environmental factors such as low temperature and/or insufficient sunlight. Evidently, cowpea and peanut are capable of adapting to high evaporative demand to a greater extent than are soybean and azuki bean.

AP and diffusive conductance of soybean correlated with leaf water potential (Fig.

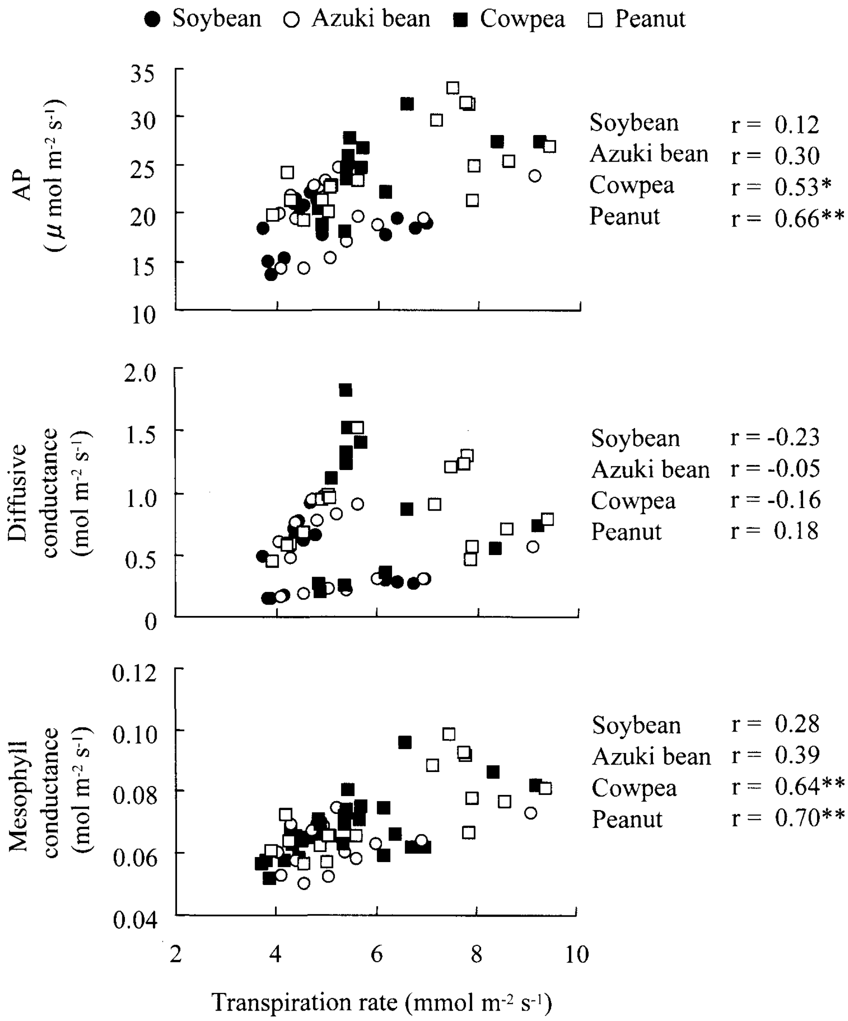

FIG. 5. Association of transpiration rate with apparent photosynthetic rate (AP), diffusive conductance and mesophyll conductance in four legume species. Each point represents one measurement from one plant; four plants of each species were used for measurements on three consecutive days and all data were plotted. *, ** indicate significant correlations at the 5% and 1% level, respectively.

4). In contrast, AP and mesophyll conductance of cowpea and peanut correlated with transpiration rate (Fig. 5). These results indicate that AP and diffusive conductance of soybean sensitively varied in response to change in leaf water status, whereas AP and mesophyll conductance of cowpea and peanut sensitively varied in response to change in passive water uptake or hydraulic conductance. In cowpea, the diffusive conductance was variable depending on leaf water potential, whereas the dependence of AP on leaf water potential was not significant (Fig. 4). Therefore, the change in stomatal aperture accompanying fluctuations of leaf water status did not appear to be responsible for the substantial depression of photosynthesis in cowpea.

In azuki bean, AP and mesophyll conductance decreased with increasing VPD_{la}, while the diffusive conductance reached minima at VPD_{la} around 2.53 kPa (Fig. 2).

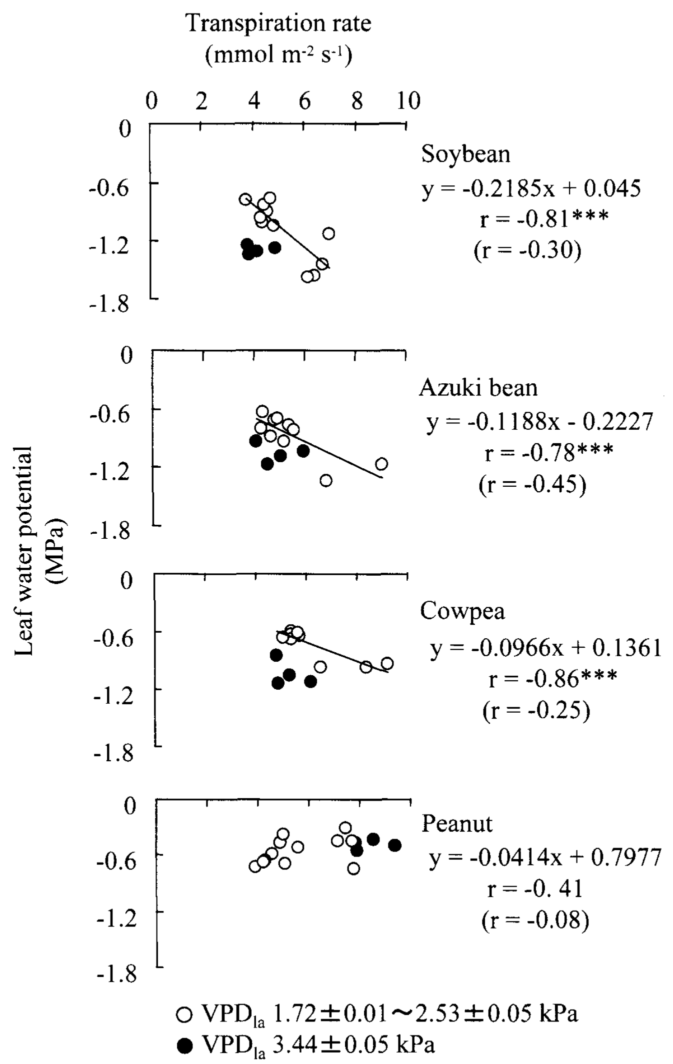

FIG. 6. Relationship between transpiration rate and leaf water potential in four legume species. Solid lines and equations indicate the linear regression in the VPD_{la} range of 1.72 to 2.53 kPa. Figures in parentheses are correlation coefficients calculated for the VPD_{la} range of 2.53 to 3.44 kPa. Four plants of each species were used for measurements on three consecutive days and all data were plotted.
*** indicates a significant correlation at the 0.1% level.

That is, decrease in mesophyll conductance in azuki bean seemed to contribute more strongly than diffusive conductance to the decrease in AP under the condition of high VPD_{la}. In rice plants with high leaf water potential under the condition of high VPD_{la}, the dominant factor responsible for the initial reduction in AP was the decrease in uptake of CO_2 via the stomata, whereas in plants with low leaf water potential under the condition of high VPD_{la}, the dominant factor was the decrease in photosynthetic activity in the mesophyll (19).

In this study, soybean, azuki bean and cowpea showed marked maxima of transpiration rate at VPD_{la} around 2.53 kPa and showed significant decreases in transpiration rate at VPD_{la} over 2.53 kPa without decrease in leaf water potential (Fig. 3). That is, the decrease in transpiration beyond that range of VPD_{la} seemed to be associated with a depression of water flow or water absorption ability, not with leaf water status ; water uptake could not catch up with intensive transpiration in these species.

As shown in Fig. 6, in soybean, azuki bean and cowpea, the relationships of leaf water potential to transpiration rate in the VPD_{la} range of 2.53 to 3.44 kPa was plotted below the regression line calculated for the VPD_{la} range of 1.72 to 2.53 kPa. Fiscus *et al.* (20) found that the extrapolated regression line intersected the coordinate axes close to the origin as should be expected for plants that transpire actively. Hirasawa and Ishihara (21) analyzed the relationships between leaf water potential and transpiration rate under various evaporative conditions and found that the relationships with a decreasing transpiration rate at low transpiration, with leaf water potential remaining constant, are plotted below the regression line expected for plants that transpire actively. They also indicated that water uptake could not catch up with intensive transpiration in such a case. Our analysis of transpiration rate and leaf water potential corroborated their findings (Fig. 6). Hence, it is thought that water uptake could not catch up with intensive transpiration in the VPD_{la} range of 2.53 to 3.44 kPa in all species except peanut. Hirasawa *et al.* (22) indicated that passive water uptake capacity affected the degree of midday depression in stomatal conductance and the photosynthetic rate in rice plants with lower leaf water potential under the condition of high evaporative demand in which water uptake could not catch up with intensive transpiration, and they proposed that an increased capacity for passive water uptake is essential in maintaining high photosynthetic rates.

Among the four legume species examined, peanut was the one most tolerant to high VPD_{la} with respect to its photosynthetic rate. Pandey *et al.* (23) compared drought responses of legumes in irrigation experiments and found that peanut exhibited greater drought tolerance by maintaining higher leaf water potential and lower canopy temperature than did soybean, mungbean and cowpea. We also observed that peanut maintained higher leaf water potential and transpired actively over a wide range of VPD_{la} (Fig. 3). The superior performance of peanut is probably due to greater water extraction from the soil and less severe wind effects due to a smaller plant height (24).

Notably, peanut exhibited variable gas exchange parameters at constant leaf water potential and did not show significant correlations between leaf water potential and transpiration rate (Figs. 4, 6). These findings suggest that unknown factors in the peanut plant might cause changes in gas exchange parameters, without being mediated by leaf water potential under conditions of varying VPD_{la}. The phytohormone ABA is considered to play a critical role in regulating these phenomena (25-27). In summary, we conclude that, among the four species tested, peanut is the most tolerant to high VPD_{la} in terms of apparent photosynthetic rate and water relation. Further studies are required to clarify the specific mechanisms by which high water potential and water uptake ability are maintained in this species.

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