

Diurnal Change in Water Droplets Adhering to Rice Panicles at the Booting Stage*

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Abstract : Many water droplets adhere to the surface of a rice panicle located inside the protective sheath of flag-leaf at the booting stage. Since the adhering water is formed by the exudation of liquid water from the plant, we can expect that the amount of adhering water varies diurnally with the change of root pressure. To test this hypothesis, we examined the amount of the adhering water and the bleeding sap from the cut surface of the stub for 24 hours. Wetland rice cultivars, Akenohoshi and Ukonnishiki, were grown under submerged and water-stressed soil conditions. The amount of adhering water changed diurnally in response to the potential evapotranspiration : the amount increased during the night and decreased during the day. A similar trend was also found in bleeding rate, except under drought conditions where both bleeding and adhering water were negligible. Furthermore, the adhering water increased proportionally with the increase of bleeding sap during the night. Bleeding occurs when root pressure develops. These results suggest that the adhering water is formed through the efflux of water under root pressure during the night, and is lost by transpiration during the day.

Key words : Adhering water, Bleeding, Booting stage, *Oryza sativa*, Rice, Water content, Water stress, Young panicle.

穂ばらみ期のイネ幼穂に付着する水滴の日変化 : 津田 誠・藤川哲哉・池田勝彦 (三重大学生物資源学部)

要 旨 : イネの穂ばらみ期に止葉葉鞘に包まれた幼穂の表面には水滴が付着する。この幼穂の付着水は、蒸散と根圧がかかわる水移動に対応して変化するのではないかと推定した。そこで、水稻 (品種アケノホシ, うこん錦) を水田に栽培し、幼穂の付着水と稈切断面からの出液を測定した。土壤乾燥条件下でも同様の測定を行なった。幼穂の付着水は、蒸発散能の変化に追従して夜間に増加し、日中低下した。また、稈切断面からの出液速度も夜間に増加し、日中低下した。付着水の増加量は、日没後の出液量に比例的であった。土壤乾燥条件下では幼穂の付着水および出液は殆ど認められなかった。これらの結果より幼穂の付着水は、夜間には根圧による水移動にともない増大し、日中には蒸散の影響を受けて失われ、変動すると結論した。

キーワード : イネ, 出液, 穂ばらみ期, 水含量, ホストレス, 幼穂。

Water droplets adhere to the surface of a rice panicle located inside the protective sheath of the flag-leaf^{9,10,11}). The water of rice pseud stem, in which the adhering water was included, disappeared rapidly when plants were exposed to a strong wind⁹). Since water is lost by transpiration under such conditions, we can assume that the water adhering on the panicle surface decreases through transpiration. If so, it must be derived from any water movement other than transpiration.

The adhering water has been considered to be derived from liquid water in the plant. In rice the exudation of liquid water through hydrathodes is called guttation²). Since guttation usually occurs when root pressure develops, the formation of adhering water can also be attributed to the development of root

pressure.

We therefore expect that the amount of adhering water on rice panicles at the booting stage decreases with transpiration during the day and increases through the efflux of water under root pressure during the night. To test this hypothesis, we examined the diurnal changes in the amount of water adhering to the panicle and the bleeding sap from the cut surface of stubs in two wetland rice cultivars.

Materials and Methods

The study was conducted at the experimental paddy field at the Faculty of Bioresources, Mie University in 1990. The soil was a sandy loam. Land preparation consisted of soil flooding followed by wet plowing and harrowing to puddle the soil. N, P₂O₅, K₂O 3 gm⁻² were each applied as commercial compound chemical fertilizer, being broadcasted and incorporated before transplanting. Wetland rice cultivars, Akenohoshi and Ukonnishiki, were used. On June 3 27-day old seedlings were

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transplanted with a space of 30 cm between the center of the rows and 30 cm between hills. One row consisted of the same cultivar and the row direction was east to west.

Main treatments were two water regimes: submerged soil and drought conditions. The drought plot was located under a rain shelter and neither flooded nor irrigated from July 10 (37 days after transplanting). Due to the limited space at the rain shelter site, there was only one main plot. Plot sizes were 15.5 m by 1.8 m for the submerged soil plot and 15.5 m by 4.5 m for the drought plot. The depth of flooded water was maintained at approximately 5 cm except for a drought period.

Leaf water potentials, and the amounts of adhering water and bleeding sap were measured when plants were at the booting stage of development. Three sets of measurements were made on the same stems at intervals of three hours from 1500 h on August 14. Within each plot, each of the measurements were obtained on triplicate randomly-selected plants using the most developed stem whose panicle was located inside the flag-leaf sheath.

Leaf water potential measurements were made on flag-leaves with a pressure chamber by standard procedures. Sample leaves were covered with plastic bags just before cutting at the leaf base to prevent water loss during preparing and reading.

The amount of water droplets adhering to the young panicle was determined by following procedures. The stems, which were subjected to pressure chamber measurements, were used. The stems cut at the internode just below the flag-leaf node were placed in plastic bags. The stems being a spindle like shape were brought into the laboratory and weighed. The weight of a sample (S mg) in a plastic bag consisted of the fresh weight of a young panicle (YP mg) and a flag-leaf sheath (LS mg), including a flag-leaf node and a tiny internode of the panicle, and the weight of adhering water (AD mg) as shown in the following:

$$S = YP + LS + AD \quad (1)$$

The stems were taken out of the bags and divided into sheaths and panicles. After water droplets were wiped away with sheets of filter paper, the fresh weight of each organ was determined. The difference between S and the sum of YP and LS was assumed to estimate the weight of adhering water. It took one

minute and a half to determine the fresh weight. Samples were then oven-dried and weighed.

To collect bleeding sap from the stem, they were severed just below the third node counting from the flag-leaf node. A disk of filter paper of 70 mm in diameter was attached to the cut surface of the stub, then covered with a plastic bag. About three hours later sets of a disk and a plastic bag were detached from the stubs and brought into the laboratory. The rate of bleeding per stem (BL mg hr^{-1}) was defined as:

$$BL = \Delta B / \Delta t \quad (2)$$

where ΔB represents the increase in weight of a disk and a plastic bag (mg) during the time for sap collection (Δt hr)^{3,6}.

The general formula⁷) using large-scale parameters was used to estimate the potential evapotranspiration rate from meteorological measurements. The measurements were made at the Experimental Farm of the Faculty of Bioresources, Mie University located 10 km west of the experimental site.

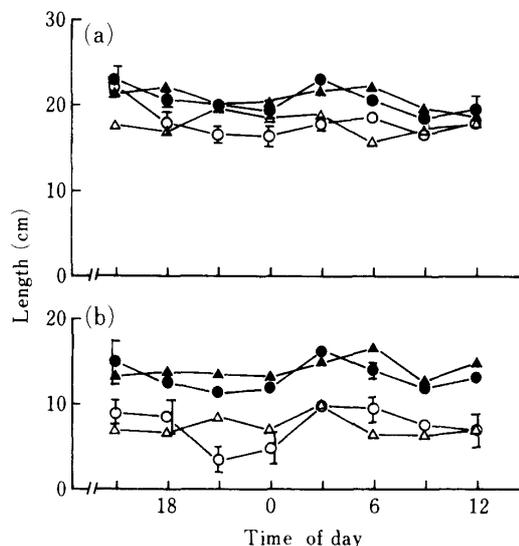


Fig. 1. (a) panicle length and (b) the distance between the auricles of flag and penultimate leaves during the experimental period.

Circles and triangles indicate cultivars Akenohoshi and Ukonishiki. Open symbols indicate water deficit plants and closed ones plants under submerged soil conditions.

Vertical bars indicate upper and lower limits of one standard error of the mean.

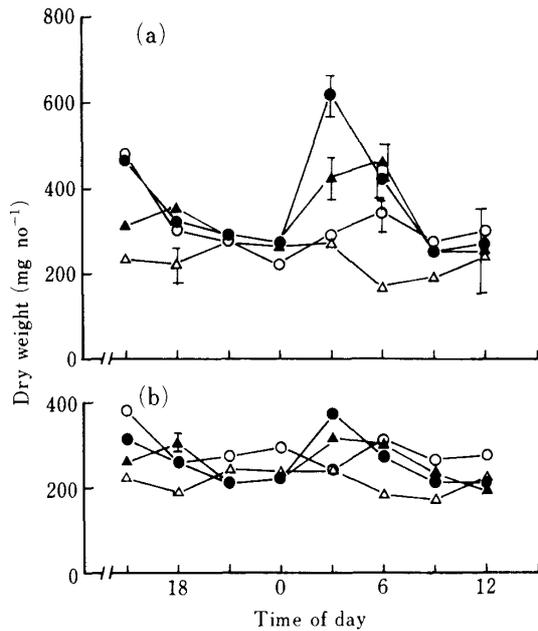


Fig. 2. (a) panicle dry weight and (b) the dry weight of the flag-leaf sheath during the experimental period. Symbols are the same as in Fig 1.

Results

No apparent growth of plant was observed. In the course of the experiment the panicle length as well as the distance between the auricles of flag and penultimate leaves did not increase (Fig. 1). Both of these lengths in plants exposed to soil water stress were shorter than those grown under submerged soil conditions.

Similarly no measurable increase in the weight of panicle and flag-leaf sheath was obtained for the two cultivars under both conditions (Fig. 2). Average weight per panicle of plants under submerged soil conditions was 363 mg for Akenohoshi and 323 mg for Ukonnishiki. Although panicle weight was significantly reduced by water deficit as panicle length, sheath weight was not reduced in both cultivars.

Leaf water potential fluctuated diurnally in concert with change in the potential evapotranspiration under submerged soil conditions (Fig. 3). Leaf water potential recovered progressively toward the afternoon and declined in the morning. Similar diurnal pattern of leaf water potential was also observed in plants subjected to soil water stress conditions, although leaf water potential of stressed

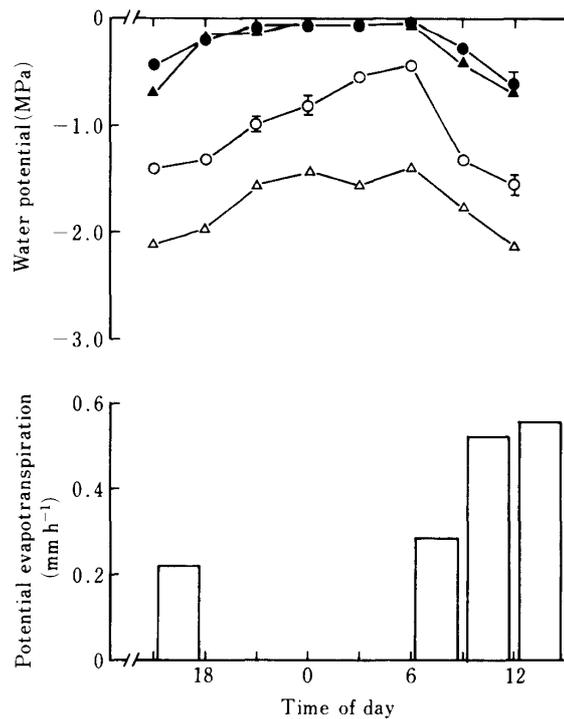


Fig. 3. Diurnal changes in leaf water potential and potential evapotranspiration. Symbols are the same as in Fig 1.

plants was always lower than that of well-watered plants. Leaf water potential of water deficit plants was kept at a higher level in Akenohoshi than in Ukonnishiki.

The rate of bleeding from the cut surface of a stub showed a marked diurnal fluctuation under submerged soil conditions (Fig. 4). Bleeding rate per unit of panicle dry weight increased rapidly after sunset and decreased in the morning. Maximum bleeding rate occurred from 2100 h to 0300 h the following day in plants under submerged soil conditions. For water deficit plants, the bleeding rate was almost zero throughout the day.

The amount of water adhering to young panicle showed a marked diurnal fluctuation, similar to the bleeding rate, except for water deficit plants, in which a very small amount of the adhering water was detected (Fig. 5). Water per unit of panicle dry weight of submerged plant was 0.07 mg mg⁻¹ in the afternoon, but it increased steadily after the sunset with a rate of 0.1 mg mg⁻¹ hr⁻¹, reaching a peak of about 2.6 mg mg⁻¹ at 0900 h. The maximum quantity of adhering water per panicle reached 890 mg. The water declined rapidly late in the morning.

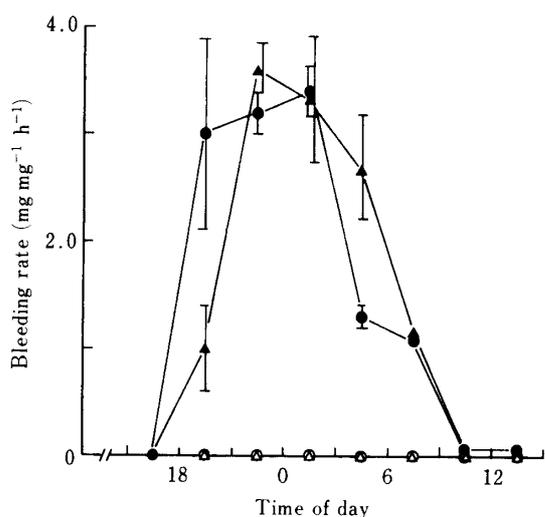


Fig. 4. Diurnal change in the bleeding rate. Values are bleeding rate per unit of panicle dry weight. Symbols are the same as in Fig 1.

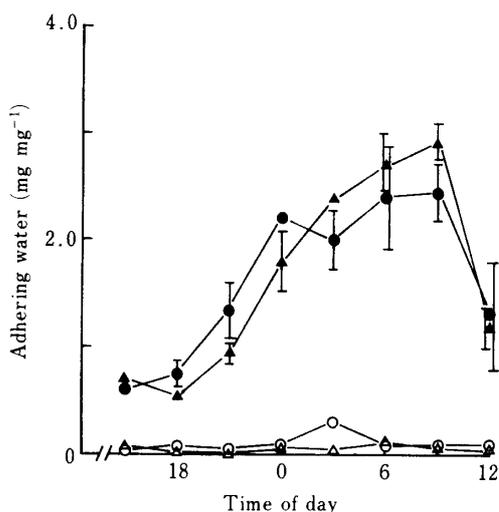


Fig. 5. Diurnal change in the amount of adhering water on panicle surface. Values are water per unit of panicle dry weight. Symbols are the same as in Fig 1.

No diurnal trend was observed in the water content of flag-leaf sheath for the two cultivars under submerged soil conditions (Fig. 6). A slight increase in sheath water content around midnight was detectable in water deficit plants of which water content was smaller as a whole. In the water content of the panicle no diurnal trend was seen with the exception of the water-deficit plants of Akenohoshi whose water content increased, albeit slightly, at night.

Comparison of adhering water with bleeding sap (Fig. 4 vs Fig. 5) reveals that a time window for the increase of adhering water was consistent with that for bleeding: i.e. from 1800 h to 0900 h. Fig. 7 depicts the relationship between the amount of adhering water and bleeding sap during the time window. A linear relationship between them was found under submerged soil conditions. From the slopes of regressions, an increase of bleeding sap of 100 mg should have corresponded to an increase in adhering water of 4.5 mg for Akenohoshi and 6.4 mg for Ukonnishiki.

Discussion

Diurnal measurements of water adhering to rice panicles at the booting stage revealed the drastic fluctuation of adhering water: decrease during the day and increase during the night (Fig. 5). Boyer¹⁾ proposed that water transport through whole plants consisted of water movement for rehydration and dehydration of the mature tissue balanced by three types of water flow. The conservation of mass for water movement through whole plants can be written as follows:

$$\Delta C/\Delta t = A - T - G \quad (3)$$

where C is tissue water content, t time, A and T are the fluxes for absorption and transpiration, and G is the storage flux for growth. Additionally, water flux for guttation (I) occurs in some plants such as rice, so the equation (3) can be written:

$$\Delta C/\Delta t = A - T - G - I \quad (4)$$

Equation (4) states that the rate of change in tissue water content is equal to the sum of four fluxes.

Although rice panicles generally grow at the booting stage, no detectable growth occurred during the experiment (Fig. 1 and 2). We can therefore neglect the water flux for growth. Furthermore, no diurnal fluctuation of tissue water content was observed as seen in panicle as well as in flag-leaf sheath (Fig. 3). Since the change of leaf water content is small for rice (due to decrease to -0.6 or -0.7 MPa of leaf water potential)⁵⁾, we assumed the change of leaf water content in our experiment would also be negligible. Thus, the equation (4) can be simplified as

$$A = T + I \quad (5)$$

The driving force for transpirational flux is the water potential decrease due to dehydra-

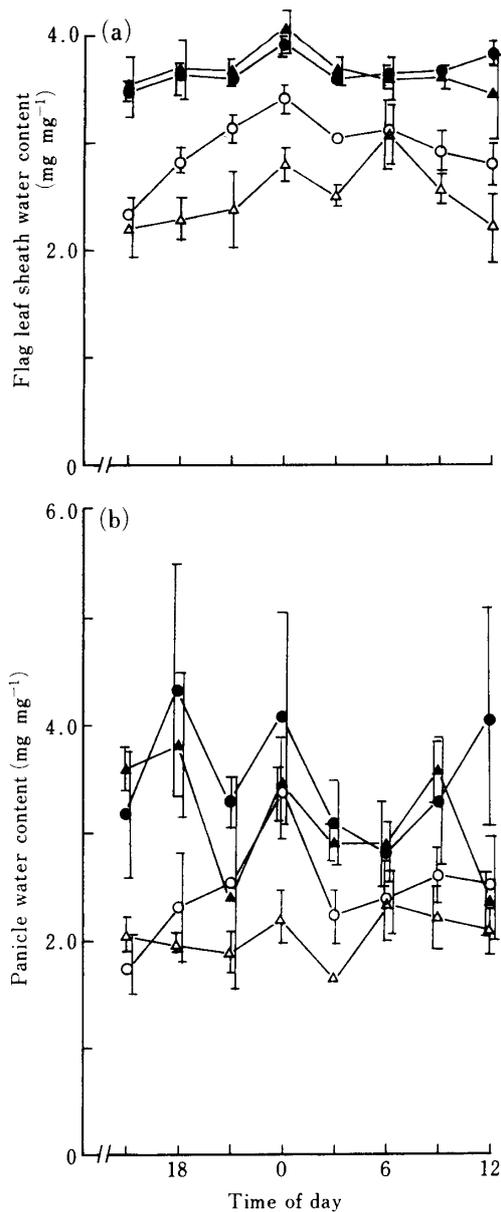


Fig. 6. Diurnal change in the water content of (a) flag-leaf sheaths and (b) panicles. Symbols are the same as in Fig 1.

tion of organs through evaporation. The driving force inducing the flux for guttation is root pressure. Therefore, the flux for transpiration is dominant during the day and that for guttation during the night :

$$\text{day} : A = T \quad (6-a)$$

$$\text{night} : A = I \quad (6-b)$$

The determination of the flux for guttation is difficult. However, our recent data (unpublished) has shown the bleeding flux to be more or less similar to the flux for guttation. Thus bleeding seems to directly reflect guttation. Since the increase in adhering water was in

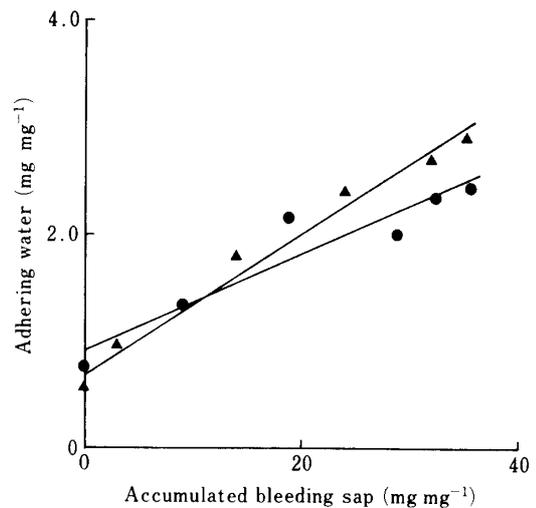


Fig. 7. Relationships between the amount of adhering water and bleeding sap under submerged soil conditions in two rice cultivars Akenohoshi (●) and Ukonnishiki (▲). Values are water and sap per unit of panicle dry weight. Regression lines were calculated using data from 1800 h to 0900 h the following day.

Regression lines are :

$$y = 0.93 + 0.045x, r^2 = 0.89^{**} \quad (\bullet)$$

$$y = 0.74 + 0.064x, r^2 = 0.98^{**} \quad (\blacktriangle)$$

**Statistically significant at 1% level.

proportion to bleeding sap (Fig. 7), the adhering water appeared to be coupled with water flux for guttation. In other words, the adhering water can be attributed to the fraction of water flow for guttation. Thus the adhering water should have increased during the night (Fig. 5) when the flux for guttation is predominant (6-a). It should have decreased due to evaporation during the day when the water flux for adhering water ceases (6-b).

The adhering water increased by only a small fraction of the guttation flux : 4% to 7% of bleeding sap (Fig. 7). This is probably because water driven by root pressure exuded from various sites of the plant other than young panicles, such as hydathodes of leaf tips and edges. Also some fractions of the adhering water might be lost by evaporation, down flow and incorporation by plant tissues.

From the above discussion, we conclude that the diurnal change in the adhering water on the young panicle surface is associated with the transition from one flux for transpiration to another for guttation.

Guttated water is generally considered of

negligible importance but rather harmful to plants: occasionally damage is caused to leaf margins and tips by deposits of salts left by evaporation of guttated water⁴⁾. On the other hand when plants are covered with dew, transpiration decreases in the mornings of dry days. Certainly it appears that under some conditions the transpiration retardant effect of dew could be very important⁸⁾. Since rice plants at the booting stage are susceptible to environmental stresses, there is a possibility that the adhering water protects young panicles from water and/or temperature stress. We need further information about the physiological and ecological roles of the adhering water in rice panicles.

References

1. Boyer, J.S. 1985. Water transport. *Ann. Rev. Plant Physiol.* 38: 473—516.
2. Doi, Y. and K. Yamatani 1953. The guttation from rice seedlings leaves as influenced by root activity. *Bull. Fac. Agric. Yamaguti Univ.* 4: 133—162*.
3. Kuroda, E. and A. Kumura 1990. Difference in single leaf photosynthesis between old and new rice varieties. II. A physiological basis for the difference in stomatal conductance between varieties. *Jpn. J. Crop Sci.* 59: 293—297*.
4. Kramer, P.J. 1969. *Plant and Soil Water Relationships: A Modern Synthesis*. McGraw-Hill, Inc.
5. Hirasawa, T. and K. Ishihara 1978. The relationship between environmental factors and water status in the rice plant. I. On leaf water potential, leaf water content on an areal basis and water saturation deficit in leaf blades. *Jpn. J. Crop Sci.* 47: 655—663*.
6. ———, T. Araki, E. Matsuda and K. Ishihara 1983. On exudation rate from the base of the leaf blade in rice plants. *Jpn. J. Crop Sci.* 52: 574—581*.
7. Priestley, C.H.B. and R.J. Taylor 1972. On the assessment of surface heat flux and evaporation using large scale parameters. *Mon. Weather Rev.* 100: 81—92.
8. Stone, E.C. 1957. Dew as an ecological factor. I. A review of literature. *Ecology* 38: 407—413.
9. Tsuboi, Y. 1961. Ecological studies on rice plant with regard to damages caused by wind. *Bull. Natl. Inst. Agric. Sci. A* 8: 1—156*.
10. Tsuda, M., S. Takami and D. Yokoe 1992. Developmental change in panicle water potential in rice. *Jpn. J. Crop Sci.* 61: 213—217*.
11. ———, ——— 1993. Changes of water potential in rice panicle under increasing drought stress at various stages. *Jpn. J. Crop Sci.* 62: 41—46*.

* In Japanese with English summary or abstract.