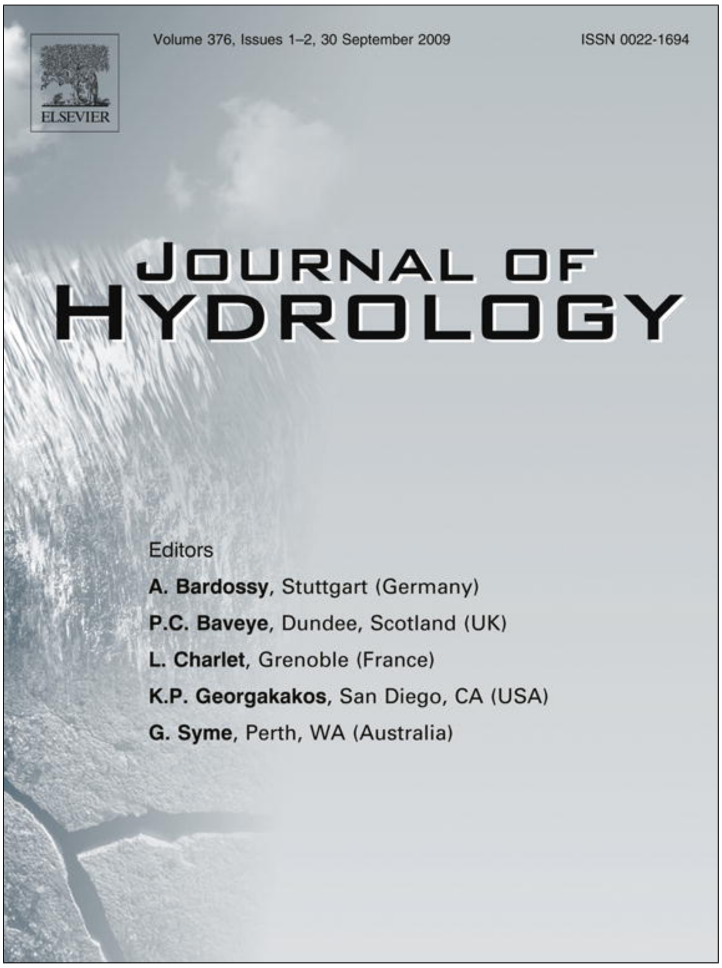
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Leaf water absorption and desorption functions for three turfgrasses

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Summary

Plant leaf can absorb water when the leaf is in contact with water. This happens when the rainfall is intercepted by plant leaves, where the intercepted part of rain remains on the leaf surface. When the intercepted water is either absorbed or subsequently evaporated into the atmosphere, the plant leaves can dissipate water through the desorption process until the plant is dry or rewatered. In this paper, two symptomatic models in the form of exponential functions for leaf water absorption and leaf water desorption were derived and validated by experimental data using leaves of three turfgrasses (Tall fescue, Perennial ryegrass and Kentucky bluegrass). Both the models and measured data showed that the rate of leaf water absorption was high at the low initial leaf water content and then gradually leveled off toward the saturated leaf water content. The rate of leaf water desorption was high at the high initial leaf water content then decreased drastically over time toward zero. The different plant leaves showed different exponents and other parameters of the functions which indicate the difference of plant species. Both the absorption and desorption rates were relatively higher for the Kentucky bluegrass and lower for the Tall fescue and Perennial ryegrass. The concept of specific leaf area (*SLA*) was used to understand the saturated leaf water content (C_s) of the three turfgrasses. Linear relationships were found between C_s and *SLA*. The leaf water absorption and desorption functions are useful for deriving physiological parameters of the plant such as permanent wilting leaf water content, naturally irreducible leaf water content, exponential leaf water absorption coefficient, and exponential leaf desorption coefficient, as well as for evaluating the effects of rainfall interception on plant growth and water use efficiency.

Introduction

Water attached on the surface of plant leaves plays an important role in the recovery of the plant especially in the arid environment, and may be beneficial to the plant by decreasing the vapor-pressure deficit on the leaf surface and thus allowing stomatal opening and photosynthesis. In the process of interception of rainfall or irrigation, plant leaves or canopies can intercept a large amount of water, which is dissipated not only through evaporation, but also absorbed by plant itself. Therefore, the need arises to develop methods for evaluating the amount of leaf water absorption during rainfall and leaf water desorption during subsequent evapotranspiration.

Researches have shown that plant leaf can absorb water when the leaf is immerged in water. In natural conditions, this process takes place during rainfall interception and evaporation processes. Rainfall interception by vegetation is an important micro-hydrologic process which affects water availability for other processes such as infiltration, runoff and evapotranspiration (Gómez, et al., 2001). The gross rainfall on the canopy is eventually separated into four parts: interception, evaporation, throughfall and stemflow (Liu, et al., 2007). The intercepted part of rain can be used by plant through absorption which increases with the amount and time of rainfall until the canopy is saturated (Klaassen, et al., 1998), whereas the remaining is attached to the plant and subsequently evaporates into the atmosphere. Factors affecting the amount of rainfall interception include leaf size, shape and orientation (Armstrong et al., 1987), leaf area index, plant height and density (Kang, et al., 2005; Wang, et al., 2006), rainfall intensity, drop size, wind speed, air temperature, relative humidity, etc. However, the characteristics of water absorption and desorption by plant leaf itself are not clear when the leaf is in ~~at~~ the water environment and when the leaf is out of water environment. Previous studies have largely focused on the total amount of interception and its subsequent evaporation, neglecting the absorption part by plant leaves. In fact, it is generally understood that plant leaves can absorb water from air, fog, and dew. For example, leaves of epiphytes and non-epiphytes in Xishuang Banna of China can absorb fog water (Zheng, et al., 2006). The air humidity was observed to have direct effects on leaf water potential, relative water content and leaf growth (Leuschner, 2002; Luo et al., 1992). Dew droplets that condense on plant canopies can provide moisture that helps them survive the dry season (Willis, 1985). In agriculture, dew may be beneficial to crops by decreasing the vapor-pressure deficit in the vicinity of the dew drops and thus allowing stomatal opening and photosynthesis (Slatyer, 1967). Moreover, despite the small amount of free liquid water involved in the process of dew formation, it can play an important role in the recovery of water content in plants after extreme water loss (Went, 1955). These features are similar to the rain intercepted by plant leaves which absorb water.

The motivation of this study came from the observations of turf. Turfgrass is a plant community with high density and low mowing. When small amount of rainfall or sprinkle irrigation takes place, the major part of rain is intercepted by the canopy of turfgrasses and less amount of water falls down beneath the grass and infiltrates into the root zones. But the visual effect of the turf was different from the situation of no rainfall. Therefore, the experiments were conducted using turfgrasses in particular.

The objectives of the study were to: (1) derive the leaf water absorption and desorption functions to characterize the ability of a plant leaf to use intercepted water; and (2) experimentally determine the parameters of the absorption and desorption functions for the three turfgrasses, namely Tall fescue (*Festuca arundinacea* Schreb.), Perennial ryegrass (*Lolium perenne* L.) and Kentucky bluegrass (*Poa pratensis* L.). . The results can be used to evaluate the effects of rainfall interception on turfgrasses growth and water use efficiency.

Theoretical considerations

Leaf water absorption function

Rainfall or sprinkler irrigation can be intercepted by plant leaves which can absorb water. Absorption is an interfacial phenomenon resulting from the differential actions of physical and physiological attractions occurring in different phases. Despite complex mechanism of absorption, the rate of water absorption is higher in the initial period when the leaves are relatively dry. With the increase of water uptake, foliar cells swell and the rate of water absorption tends to slow down and the leaf water content will gradually reach its maximum value. Further increase in absorption should not be possible during the saturated condition, given that the moisture capacity is constricted by the plant itself and its environment. Physically, the dynamic leaf water content should vary between the initial leaf water content and the saturated leaf water content. Thus, a symptomatic function can be assumed here to indicate that at any time the rate of leaf water absorption is proportional to the difference between the saturated leaf water content and the current leaf water content,(or leaf moisture deficit):

$$\frac{dC}{dt} = k\left(C_s - C\right) \tag{1}$$

where C is the dynamic leaf water content at any time, C_s is the saturated leaf water content, k is the absorption exponential coefficient of the leaf (or the curve number of the absorption function), t is the absorption time.

Noting that when t = 0, the dynamic leaf water content is defined as the initial leaf water content, namely, $C = C_i$, solution of Eq. (1) results in:

$$\alpha = \frac{C - C_i}{C_s - C_i} = 1 - e^{-kt} \quad ,0 < \alpha < 1, \;\; C_i < C < C_s \tag{2a}$$

or

$$C = C_i + (C_s - C_i)(1 - e^{-kt}), \;\; C_i < C < C_s \tag{2b}$$

where α is the absorbing water saturation of the leaf, C_i is the initial leaf water content.

Eq. (2a) or Eq. (2b) is the leaf water absorption function, in which the parameters, C_s, k, and C_i, can be determined through experiments.

Leaf water desorption function

During the desorption process, the dynamic leaf water content should vary between the saturated leaf water content and the naturally irreducible leaf water content. Thus, it can be assumed again that at any time during desorption, the rate of leaf water desorption is proportional to the difference between the present leaf water content and the naturally irreducible residual leaf water content:

$$\frac{dC}{dt} = -f\left(C - C_{ir}\right) \tag{3}$$

where f is the desorption exponential coefficient of the plant ($f > 0$), C_{ir} is the naturally irreducible residual leaf water content. The negative sign indicates the falling trend of C with time t. Noting that when $t = 0$, $C = C_s$, solution of Eq. (3) results in:

$$\beta = \frac{C - C_{ir}}{C_s - C_{ir}} = e^{-ft}, \quad 0 < \beta < 1, \quad C_{ir} < C < C_s \tag{4a}$$

or

$$C = C_{ir} + (C_s - C_{ir})e^{-ft}, \quad C_{ir} < C < C_s \tag{4b}$$

where, β is the relative desorption saturation of the leaf, C_{ir} is the naturally irreducible residual leaf water content, f is the desorption exponential coefficient of the plant or the desorption curve number.

Eq. (4a) or (4b) is the leaf water desorption function. The exponential coefficient f and the irreducible leaf water content C_{ir} can be determined through experiment. In extremely dry conditions, $C_{ir} = 0$.

Fig. 1 shows the absorption and desorption function curves (corresponding to Eqs. 2a and 4a). It can be seen that the rate of absorption (or the slope of the absorption curves) is extremely high at the initial low leaf water saturations, and then gradually decreases toward the saturated leaf water content. For the reversed process, the rate of desorption is high at the high initial water saturations but decreases drastically over a short periods of time. Both the absorption and desorption rates increase with the increasing exponential coefficients k or f.

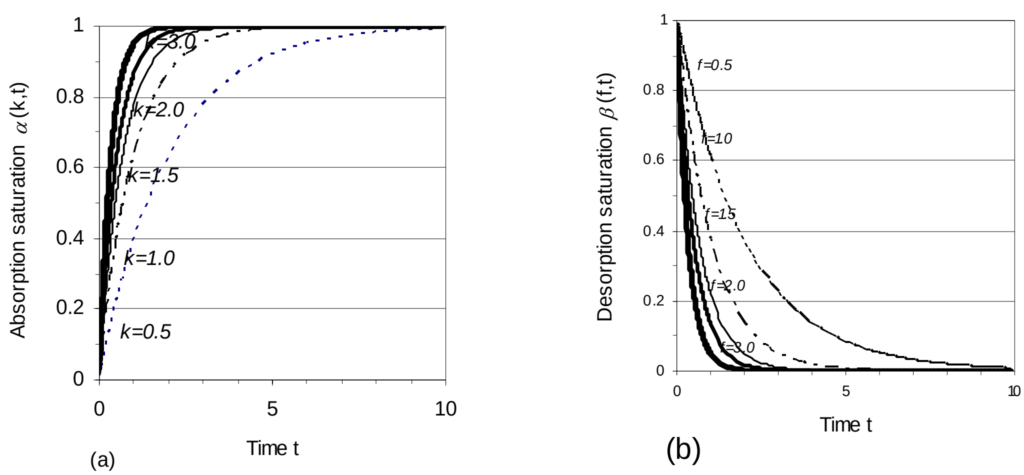


Fig. 1. Leaf water adsorption function in (a) and the leaf water desorption function in (b).

Materials and methods

Three popular turf grasses, namely Tall fescue (*Festuca arundinacea* Schreb.), Perennial ryegrass (*Lolium perenne* L.), and Kentucky bluegrass (*Poa pratensis* L.), were used to study the dynamics of leaf water absorption and desorption functions. The plants were grown in laboratory pots under room temperatures with sufficient irrigation. The leaf water absorption and desorption experiments were carried out when the plants were fully grown, with the full heights reached at 10 cm for Tall fescue, 7 cm for Perennial ryegrass, and 7 cm for Kentucky bluegrass.

Measurement of leaf water absorption

The randomly selected whole blades of leaves were excised from the plants, weighed immediately and recorded as the initial weight. They were then soaked in distilled water with the leaves covered with a filter paper to prevent the leaves from floating above the water surface. During absorption, the leaf blades were weighed every15 minutes in the first 2 hours, then every 30 minutes in the next two hours, and finally every one hour until eventually there were no more changes in the leaf weight (a total of 15 measurements). Each of the successive weight was recorded as the current weight, and the final weight as the saturated weight. For each measurement, the leaves were first wiped using cheese cloth to remove excess water and then weighed with an electronic balance under the indoor temperatures around 26 °C and about 60 ± 5% relative humidity. The leaf blade's dry weight was determined after drying the blades in the oven for 48 h at 80 °C.

The dynamic leaf water content (C) and the saturated leaf water content (C_s) were calculated using:

$$C = \frac{CW - DW}{DW} \quad (5)$$

$$C_s = \frac{SW - DW}{DW} \quad (6)$$

where, CW is the current leaf weight, DW is the dry leaf weight, and SW is the saturated leaf weight. The unit of water content can be expressed as the ratio of water lost and dry leaf weight, namely, g/g.

The relative leaf water content R_c is defined as:

$$R_c = \frac{CW - DW}{SW - DW} \quad (7)$$

The total amount of leaf water absorption TA is defined as:

$$TA = \frac{SW - IW}{DW} \quad (8)$$

where IW is the initial leaf weight.

Measurement of leaf water desorption

The excised leaf blades were brought to 100% relative leaf water content by placing leaves in distilled water for 3 hours. These leaves, after being gently wiped to remove excess water, were weighed with an electronic balance and recorded as the saturated leaf weight. During the water desorption process, leaf blades were weighed every 0.5 to 1 hour in the first 6 hours, then every 12 and 24 hours until there were no changes in the leaf weight. The 24-h total amount of leaf water desorption TD is defined as:

$$TD = \frac{SW - CW_{24h}}{DW} \quad (9)$$

where $CW_{24\,h}$ is the leaf weight when the leaf has been out of water for 24 hours.

Measurement of specific leaf area (SLA)

The leaf area measurements were made on the green leaves using digital scanning. The pixel number of a leaf in every picture was calculated using commercial software PhotoShop (Adobe Photoshop 7, 2002). Grid lines were inserted in the picture and then the number of pixels over a unit area (1 cm^2) was counted. The leaves were then oven-dried to a final constant weight at 80°C for a minimum of 24 hours. The leaf area was calculated using:

$$LA = \frac{I}{i} \quad (10)$$

where LA is the leaf area, I is the pixel number of the entire leaf, i is the pixel number over the unit area (1 cm^2). The specific leaf area was calculated as:

$$SLA = \frac{LA}{DW} \quad (11)$$

where SLA is the specific leaf area (Anyia, et al., 2004).

Results and discussion

Leaf water absorption

From Eq. 2a or 2b, it can be alternatively shown that the incremental amount of leaf water absorption is:

$$\Delta C = \Delta C_{\max}(1 - e^{-kt}) \quad (12)$$

where $\Delta C = (C - C_i)$ is the difference between the current leaf water content and the initial leaf water content or the increment of leaf water absorption, $\Delta C_{\max} = (C_s - C_i)$ is the maximum difference between the saturated leaf water content and the initial leaf water content, which represents the leaf water absorbing capacity. The regression equations based on the experimental data for the three turfgrasses are:

Perennial Ryegrass:

$$\Delta C = 0.6186(1-e^{-1.0645t}),\ R^2 = 0.7057 \quad (13)$$

Kentucky bluegrass:

$$\Delta C = 0.6375(1-e^{-2.2093t}),\ R^2 = 0.7917 \quad (14)$$

Tall fescue:

$$\Delta C = 0.4253(1-e^{-1.7226t}),\ R^2 = 0.6834 \quad (15)$$

These equations indicated that the leaf water absorption functions are different for the three turfgrasses. The exponential factor k is about 2.2093 for Kentucky bluegrass, 1.7226 for Tall fescue and 1.0645 for Perennial ryegrass, which means the leaf of Kentucky bluegrass absorbs water more quickly than that of Tall fescue and Perennial ryegrass. The rate of leaf water absorption increases rapidly in the early period of time then levels off later (Fig. 2a).

Using another form of Eq. 2b, the relationships between the leaf water content and the absorption time can be obtained as:

Perennial Ryegrass (PR):

$$C = 3.2207 + 0.6186(1-e^{-1.0645t}) \quad (16)$$

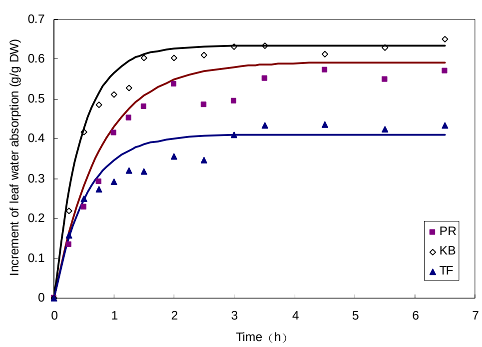
Kentucky Bluegrass (KB):

$$C = 2.1732 + 0.6375(1-e^{-2.2093t}) \quad (17)$$

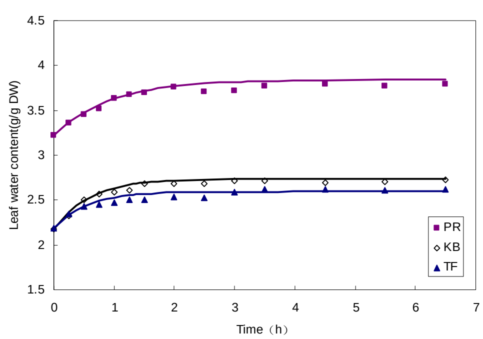
Tall Fescue (TF):

$$C = 2.1830 + 0.4253(1-e^{-1.7226t}) \quad (18)$$

The above equations, as also shown in Fig. 2b, indicate that the Perennial ryegrass has the highest initial leaf water content at 3.221 g.g^{-1}, followed by the Tall fescue at 2.183 g.g^{-1} and Kentucky bluegrass at 2.173 g.g^{-1}. Comparing parameters in Eq. 2b with that in Eqs. 16-18, one can also find out that the saturated leaf water content C_s is 3.84 g.g^{-1} for the Perennial ryegrass, 2.81 g.g^{-1} for the Kentucky bluegrass, and 2.61 g.g^{-1} for the Tall fescue.



(a)

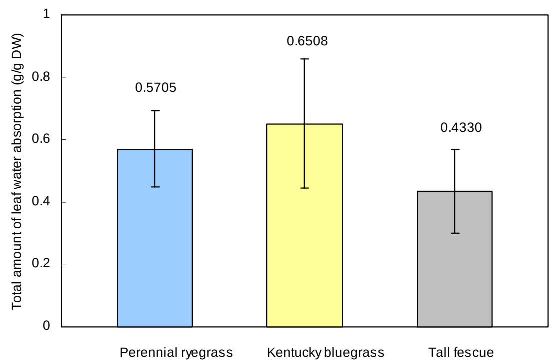


(b)

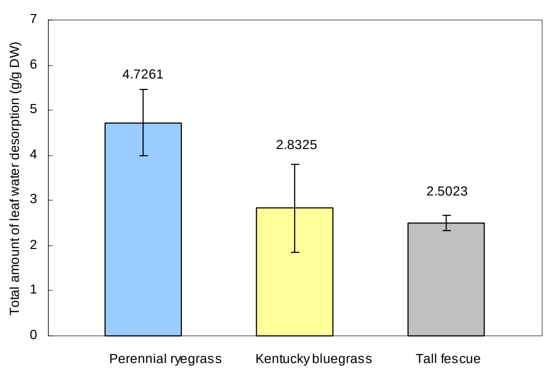
Fig. 2. Leaf water absorption processes of three turfgrasses (Perennial ryegrass (PR), Kentucky bluegrass (KB) and Tall fescue (TF)). (a) Incremental leaf water content and (b) dynamic leaf water content (DW means leaf dried weight).

Physiologically, water enters the plant through cell walls then access protoplast and vacuole. The main mode of water absorption in the cell wall is absorption and expansion; in the vacuole it is infiltration and sop, and in the protoplast it involves all the processes. Absorption and expansion (or swelling) in hydrophilic colloid is rapid and intense at the start of the process. It slows down when the plant becomes swollen. A large amount of water can be absorbed and stored through absorption and expansion. It is gradually stored in the plant water for subsequent desorption or respiration.

Fig. 3 shows the total amount of leaf water absorption and desorption for the three turfgrasses. It is apparent that the total amount of absorption (*TA*) is an order of magnitude smaller than that of the desorption (*TD*). This indicates that at the start of the absorption experiment the leaf water content was already higher, thus the total amount of the absorbed water is small. The desorption rate is very high during the initial periods (see Fig. 1 and Fig. 4). In 24 hours of desorption, the leaf weight is close to the dried weight. The experimented maximum water absorption of the leaves was 0.4 - 0.65 time of their dry weight, whereas the maximum amount of desorption was 2.5 - 5 times of the dry weight.



(a)



(b)

Fig. 3. Total amount of leaf water absorption and desorption of three turfgrasses. (a) Water absorption and (b) water desorption.

Leaf water desorption

Fig. 4 shows the relationships between the leaf water content and the desorption time for the selected three turfgrasses. The highly correlated regression equations are:

Perennial ryegrass (PR):

$$C = 0.3384 + 4.4692e^{-0.4110t}, \ R^2 = 0.8971 \tag{19}$$

Kentucky bluegrass (KB):

$$C = 0.1102 + 2.7800e^{-1.0486t}, \ R^2 = 0.8567 \tag{20}$$

Tall fescue (TF):

$$C = 0.1624 + 2.3965e^{-0.6385t}, \ R^2 = 0.7536 \tag{21}$$

In the desorption process, the leaf water content rapidly decreased in the first few hours and then gradually decreased toward zero (Fig. 4). The exponential factor *f* is 1.0486 for Kentucky bluegrass, 0.6385 for Tall fescue and 0.411 for Perennial ryegrass. This means that the rate of leaf water desorption is highest in Kentucky bluegrass, at medium levels in Tall fescue and slower in Perennial ryegrass

The naturally irreducible residual leaf water content (C_{ir}) is a key parameter in Eqs. 4, manifesting the terminal leaf water content of the plant in the environment. Comparing Eq. 4 with Eqs. 19, 20, and 21, it can be determined that the naturally irreducible residual leaf water content (C_{ir}) of the Perennial ryegrass is 0.338 g/g, 0.162 g/g for Tall fescue and 0.11 g/g for Kentucky bluegrass.

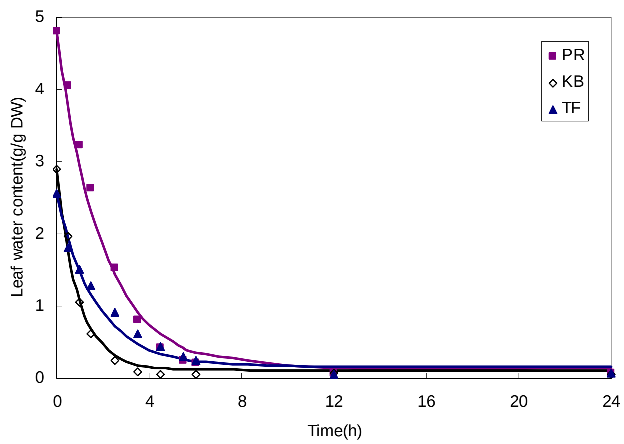


Fig. 4. Leaf water desorption processes for three turfgrasses (PR is Perennial ryegrass, KB is Kentucky bluegrass, and TF is Tall fescue. DW means leaf dried weight).

Comparison the leaf water absorption exponential factor *k* and the desorption exponential factor *f* for the three turfgrasses, it shows that the k value varied between 1.1 and 2.2 whereas the *f* value varied between 0.4 to 1.0. These different curve numbers (see Fig. 1) mean that, in general, the absorption process occurs much faster than the desorption process in these turf grasses.

Relative water content

The relative water content has been recognized as a more important indicator of water status than other parameters under drought stress conditions. It is closely related to the cell volume, and therefore it more closely reflects the balance between water supply to the leaf and the transpiration rate (Dhanda, et al., 1998). Studies have proved that desorption has positive correlations with relative water content, transpiration rate, stomata conductance and water potential (e.g., Zhang, et al., 2005).

In order to reduce water loss, stomata openings are smaller under drought stress conditions. Once stomata are closed, cuticular transpiration determines the rate of water loss (Larcher, 1985), in which diffusion of water molecules occurs across the cuticular membrane (Kerstiens, 1996). Thus, when stomata are closed, water loss mainly reflects epidermis conduction differences, and these differences are probably related to cuticle resistance, the amount of wax, leaf curl, and other characteristics (Ma, et al., 1998).

On the other hand, cuticular waxes play an important role in plant water loss (Ristic, et al., 2002). Waxes are accumulated at the outer surface of the cuticle. Estimates of the thickness of the cuticular wax layer ranges from 0.1 to 5 μm for 23 plant species (Riederer et al., 2001). Grasses also have cuticle on their epidermis. Leaf cuticle thickness of the Kentucky bluegrass is about 0.58 μm on the upper epidermal surface and about 1.23 μm on the lower epidermal surface (Wang, et al., 2002). The epidermis wax content of 14 Tall fescue varieties ranged from 7.12 mg/g to 10.87 mg/g (Zhang, et al., 2007) while the epidermis wax content of 6 wheat varieties ranged from 2.49 mg/g to 3.51 mg/g (Huang, et al., 2003). As cuticle is made from hydrophobic lipids, it seems likely that differences in water permeability of the cuticle membrane play a dominant role (Ristic, et al., 2002).

The desorption function quantifies the above processes. However, the saturated water content C_s in the function may change with the environmental conditions. The relationships between the leaf water desorption rates (*DR*) and the relative leaf water content (R_c) can be obtained for the three grasses as:

Perennial ryegrass:

$$DR = 0.0250R_c + 0.0023,\ R^2 = 0.9095 \quad (22)$$

Kentucky bluegrass:

$$DR = 0.0657R_c + 0.0009,\ R^2 = 0.8686 \quad (23)$$

Tall fescue:

$$DR = 0.0645R_c - 0.0035,\ R^2 = 0.7565 \quad (24)$$

Thus, it is apparent that the relative leaf water content strongly affects the water desorption rate.

Specific leaf area (SLA)

Larger specific leaf area means that the leaves of the same weight have larger area. As one of the most important traits in determining plant ecological functions, *SLA* is influenced by many structural and anatomical traits, including leaf dry matter concentration, leaf thickness, leaf water content, the proportion of vascular and sclerenchyma tissues, and the proportion of cell wall components (Sugiyama，2005). As an indictor of leaf thickness, *SLA* has often been observed to decrease under drought conditions (Liu et al., 2004; Vile et al., 2005） which is assumed to be a way to improve water use efficiency (WUE), because thicker leaves usually have a higher density of chlorophyll and proteins per unit leaf area and hence have a greater photosynthetic capacity than thinner leaves (Liu et al., 2004).

Fig. 5 shows the relationships between saturated leaf water content (C_s) and specific leaf area (SLA) for three turfgrasses. The apparent linear relationships between C_s and *SLA* for the three turfgrasses are:

Perennial ryegrass:

$$C_s = 0.0108SLA + 1.7431,\ R^2 = 0.7466 \quad (25)$$

Kentucky bluegrass:

$$C_s = 0.0107SLA - 0.1807,\ R^2 = 0.8115 \quad (26)$$

Tall fescue:

$$C_s = 0.0154SLA - 0.1938,\ R^2 = 0.6688 \quad (27)$$

The coefficients of above equations indicate that the co-varying slopes (incremental needs for SLA) are similar. However, the intercept values show that the leaves of the Perennial ryegrass need an order of magnitude higher value of SLA to be saturated at the initial growing state.

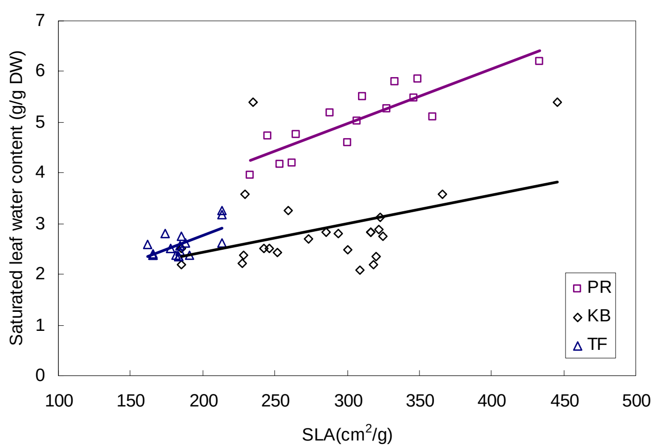


Fig. 5. The relationships between saturated leaf water content and specific leaf area (SLA) for three turfgrasses (PR is Perennial ryegrass, KB is Kentucky bluegrass, and TF is Tall fescue. DW means leaf dried weight).

Conclusions

Leaf water absorption and desorption are interfacial phenomena. Although the mechanisms of the interfacial physics or physiology of water absorption and desorption are not yet absolutely clear, the dynamics processes of leaf water absorption and desorption with time have been examined by many researchers.

In the present work, two symptomatic mathematical models were developed to characterize the leaf water adsorption and desorption processes of a plant. They can be used to quantitatively determine the dynamic changes of leaf water content and to obtain the characteristic plant parameters such as the saturated leaf water content, the permanent wilting leaf water content and the naturally irreducible leaf water content.

The developed leaf water absorption and desorption models were tested against the experimental data. Three turfgrasses (namely, Perennial ryegrass, Kentucky bluegrass and Tall fescue) were studied in the laboratory experiments using excised leaves of the three turfgrasses. Both the models and the measured data showed that the rate of leaf water absorption was high at the initial leaf water content and then gradually decreased toward the saturated leaf water content. The rate of leaf water desorption was high at the high initial leaf water contents but decreased drastically over time.

Among the three turfgrasses studied, the maximum absorbed water weight of the excised leaves were 0.4 - 0.65 times their dry leaf weight as the leaves were initially high in water content. However, the amounts of total water desorption were 2.5 - 5 times their dry leaf weight as the leaves were allowed to dry for a long time. The Kentucky bluegrass absorbs water more quickly than Tall fescue and Perennial ryegrass. In the reversed process of leaf water desorption, the Kentucky bluegrass also loses water more quickly than Tall fescue and Perennial ryegrass.

The concept of specific leaf area (*SLA*) was used to understand the saturated leaf water content (C_s) of the three turfgrasses. Linear relationships were found between C_s and *SLA*, which can be used to differentiate plant species and their water use efficiencies. Further researches are oriented to study the mechanisms of the leaf water absorption and desorption as well as to improve the models through field experiments on ~~or~~ the live plant leaves under real or simulating rainfall conditions.

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