水文・水資源学会誌
J. Japan Soc. Hydrol. & Water Resour.
Vol. 10, No. 1 (1997) pp. 32-43

Determining Factors of Ranges of Water-use Efficiency, Net Assimilation Rate and Transpiration Rate

— An Analysis Using α - β Method —

水利用効率・純光合成速度・蒸散速度の決定要因

— α - β 法を用いた解析 —

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The factors determining water-use efficiency, net assimilation rate and transpiration rate were investigated using two parameters α (ratio of total conductance to CO_2 to total conductance to H_2O) and β (ratio of total conductance to latent heat to total conductance to sensible heat, or surface moisture availability). The characteristics of water-use efficiency were detected from several data sets of field observations with porometric method as follows, (1) Water-use efficiency was higher in the morning than in the afternoon. (2) Water-use efficiency was higher in winter than in summer. (3) Water-use efficiency values were scattered mainly from 10^{-1} to 10^2 (mg/g), and the fluctuation of water-use efficiency with species was smaller than that with environmental conditions. These characteristics of water-use efficiency reflect the difference of the diurnal and seasonal variation patterns of transpiration rate and net assimilation rate. The phenomena (1) and (2) were mainly caused by the differences in vapor pressure deficit, and partly by the differences in α , and the phenomenon (3) was caused by the little differences in α with species. Furthermore, the ranges of values of water-use efficiency, net assimilation rate and transpiration rate were discussed using two parameters, α and β .

Key words: Water use efficiency, Net assimilation rate, Transpiration rate, α - β method

本研究は野外観測から得られた水利用効率、純光合成速度、蒸散速度の決定要因を二つのパラメータ α (CO_2 フラックスに対する全コンダクタンス/ H_2O フラックスに対する全コンダクタンス)、 β (潜熱フラックスに対する全コンダクタンス/顕熱フラックスに対する全コンダクタンス)を用いて説明したものである。観測から明らかになった水利用効率の特性は、以下の3点であった。(1)午前中の水利用効率は午後より高い。(2)冬の水利用効率は夏より高い。(3)水利用効率の値は 10^{-1} から 10^2 (mg/g)の範囲に分布しており、樹種間差より環境条件の違いによる変動のほうが大きい。これらの特徴は純光合成速度と蒸散速度の日変化および季節変化の違いを反映したものである。解析から、(1)、(2)はおもに飽差の違い、一部には α の違いが原因となって起こり、(3)は α の樹種間差があまりないことによることが分かった。また、水利用効率、純光合成速度、蒸散速度の値の範囲が α 、 β を用いて説明された。

キーワード：水利用効率、純光合成速度、蒸散速度、 α - β 法

1. INTRODUCTION

Water-use efficiency is one of the most significant parameters in discussing net assimilation rate and transpiration rate. It has been

often analyzed in the field of crop production study (e.g., Sinclair *et al.*, 1984) mainly because of the need to investigate crop field management to get maximum production with minimum water loss. Water-use efficiency is also

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useful as an index to clarify the differences of diurnal and seasonal variation patterns of net assimilation rate and transpiration rate (e.g., Kosugi *et al.* 1994; Kosugi and Kobashi 1994). In this study how the water-use efficiency of several tree species is determined in situ is investigated. And the ranges of the values of water-use efficiency, net assimilation rate and transpiration rate are discussed.

II. THEORY

In this study, water-use efficiency (*WUE*) (mg/g) is defined as the ratio of net assimilation rate to transpiration rate ($=A_{\text{mg}}/E_g$). Bowen ratio (B_o), i.e., the ratio of sensible heat flux to latent heat flux ($=H/\epsilon E_{\text{hg}}$), is a similar parameter concerned with the process of H_2O diffusion. Sensible heat flux, latent heat flux ($\propto \text{H}_2\text{O}$ flux), and CO_2 flux between leaf and the atmosphere are represented as follows,

$$H = \rho_a C_p C_H u (T_l - T_a) = \rho_a C_p \frac{1}{r_a} (T_l - T_a) \\ = C_{\text{pmol}} g_{bw} (T_l - T_a) \quad (1)$$

$$\epsilon E_{\text{hg}} = \epsilon \rho_a C_E u (q_s(T_l) - q_a) \\ = \epsilon \rho_a \frac{1}{r_a + r_c} \{q_s(T_l) - q_a\} \quad (2)$$

$$E_g = 18 \frac{g_{bw} g_{sw} (W_i - W_a)}{g_{bw} + g_{sw}} \quad (3)$$

$$A_{\text{mg}} = 0.044 \frac{g_{bc} g_{sc} g_i (C_a - \Gamma_*)}{g_{bc} g_{sc} + g_{sc} g_i + g_i g_{bc}} \quad (4)$$

where H is the sensible heat flux (Wm^{-2}), ρ_a is the density of air (kg m^{-3}), C_p is the specific heat capacity of air ($\text{JK}^{-1} \text{kg}^{-1}$), C_{pmol} is also the specific heat capacity of air ($\text{JK}^{-1} \text{mol}^{-1}$), C_H is the bulk transfer coefficients for sensible heat, u is the wind speed (m s^{-1}), T_l is the leaf temperature, T_a is the air temperature, r_a is the aerodynamic resistance (s m^{-1}), l is the latent heat of vaporization of water (Jkg^{-1}), E_{hg} is the transpiration rate ($\text{kg m}^{-2} \text{s}^{-1}$), ϵE_{hg} is the latent heat flux (Wm^{-2}), C_E is the bulk transfer coefficients for latent heat, $q_s(T_l)$ is the saturation specific humidity at leaf temperature, q_a is the specific humidity of the air, r_c is the canopy resistance (s m^{-1}), E_g is the transpiration

rate ($\text{g m}^{-2} \text{s}^{-1}$), W_i is the mole fraction of water vapor in the stomata (mol mol^{-1}), W_a is the mole fraction of water vapor in the air (mol mol^{-1}), g_{bw} is the boundary layer conductance to H_2O ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), g_{sw} is the stomatal conductance to H_2O ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), A_{mg} is the net assimilation rate ($\text{mg m}^{-2} \text{s}^{-1}$), C_a is the ambient CO_2 concentration ($\mu\text{mol mol}^{-1}$), Γ_* is the CO_2 compensation point without dark respiration ($\mu\text{mol mol}^{-1}$), g_{bc} is the boundary layer conductance to CO_2 ($\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and $g_{bc} = g_{bw}/1.6^{(2/3)}$, g_{sc} is the stomatal conductance to CO_2 ($\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) and $g_{sc} = g_{sw}/1.6$ (Ball, 1987; von Caemmerer and Farquhar, 1981), g_i is the 'internal' conductance ($\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) (Kosugi *et al.*, 1994). In this study, aerodynamic resistance (r_a) (s m^{-1}) is assumed to be equal to boundary layer resistance ($\rho_a \text{mol}/g_{bw}$) (s m^{-1}) and canopy resistance (r_c) (s m^{-1}) is assumed to be equal to stomatal resistance ($\rho_a \text{mol}/g_{sw}$) (s m^{-1}) for simplification, though they have different meanings precisely. Eq. (1) to Eq. (4) can be reformed as follows using the total conductances to sensible heat (g_{bw}) ($\text{mol air m}^{-2} \text{s}^{-1}$), H_2O (g_{tw}) ($\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), and CO_2 (g_{tc}) ($\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), respectively,

$$H = C_{\text{pmol}} g_{bw} (T_l - T_a) \quad (5)$$

$$E_g = 18 g_{tw} (W_i - W_a) \quad (6)$$

$$A_{\text{mg}} = 0.044 g_{tc} (C_a - \Gamma_*) \quad (7)$$

To convert the unit of conductance from $\text{mol m}^{-2} \text{s}^{-1}$ to ms^{-1} , conductance in the unit of $\text{mol m}^{-2} \text{s}^{-1}$ must be derived by the mole density of air ($\rho_a \text{mol}$) (mol m^{-3}). From Eq. (5) and Eq. (6), Bowen ratio (B_o) can be represented as follows,

$$B_o = \frac{H}{\epsilon E_{\text{hg}}} = \frac{g_{bw}}{g_{tw}} \frac{C_{\text{pmol}} (T_l - T_a)}{l \cdot 0.018 (W_i - W_a)} \quad (8)$$

From Eq. (6) and Eq. (7) water-use efficiency (*WUE*) (mg/g) is given by,

$$WUE = \frac{A_{\text{mg}}}{E_g} = \frac{g_{tc}}{g_{tw}} \frac{0.044 (C_a - \Gamma_*)}{18 (W_i - W_a)} \quad (9)$$

To discuss the relationship between H and ϵE_{hg} , β , surface moisture ability and $0 \leq \beta \leq 1$, which is defined as follows, is often used,

$$C_E = \beta C_H \quad (10)$$

This equation can be modified using Eq. (1), Eq. (2) and Eq. (3) as follows using the concept of resistance or conductance,

$$\frac{1}{r_a + r_c} = \beta \frac{1}{r_a} \quad (11)$$

or

$$\beta = \frac{g_{tw}}{g_{bw}} \quad (12)$$

In Eq. (12) β can be renamed as 'the ratio of total conductance to latent heat to total conductance to sensible heat'. In this study, a new coefficient, α , 'the ratio of total conductance to CO₂ to total conductance to H₂O' and $0 \leq \alpha \leq 0.625$, is proposed as follows,

$$\alpha = \frac{g_{tc}}{g_{tw}} \quad (13)$$

Putting Eq. (12) and Eq. (13) into Eq. (7) yields the following equation,

$$A = \alpha \beta g_{bw} (C_a - \Gamma_*) \quad (14)$$

In the same way putting Eq. (12) into Eq. (6) yields,

$$E = \beta g_{bw} (W_i - W_a) \quad (15)$$

Using Eq. (12) and Eq. (13), Bowen ratio and water-use efficiency are given by,

$$B_o = \frac{H}{\epsilon E_{ng}} = \frac{1}{\beta} \frac{C_{pmol}(T_i - T_a)}{\epsilon \cdot 0.018(W_i - W_a)} \quad (16)$$

$$WUE = \frac{A_{mg}}{E_g} = \alpha \frac{0.044(C_a - \Gamma_*)}{18(W_i - W_a)} \quad (17)$$

As the fluctuation of $C_a - \Gamma_*$ is small, water-use efficiency is mainly determined by the change of water mole fraction difference between the atmosphere and the intercellular space ($W_i - W_a$) and the ratio of total conductance to CO₂ to total conductance to H₂O (α).

III. OBSERVATIONS

Several series of field observations were carried out in different sites and conditions to clarify the patterns of diurnal and seasonal change of CO₂ and H₂O exchange between leaves and the atmosphere. The method used to measure the CO₂ and H₂O fluxes was porometry. Net assimilation rate and transpiration rate were measured in situ on intact leaves using the LI-6200 portable photosynthesis system (Li-Cor,

Inc., Lincoln, Nebraska, USA).

Observation No. 1 (OBS No. 1) was carried out at Kyoto University in 1989 to clarify the diurnal and seasonal pattern of CO₂ and H₂O fluxes of leaves of three temperate evergreen broad-leaved trees in situ (Shibata *et al.* 1991; Kosugi *et al.* 1994). Observation No. 2 (OBS No. 2) was carried out at Kyoto University from 1994 to 1995 additionally to compare the diurnal and seasonal pattern of CO₂ and H₂O fluxes of leaves of three evergreen broad-leaved trees and four deciduous broad-leaved trees (Kosugi *et al.* 1997). Observation No. 3 (OBS No. 3) was carried out in a buffer green zone in Akou, Hyogo Prefecture, Japan, from 1991 to 1994 to clarify the diurnal change of CO₂ and H₂O fluxes of leaves of four temperate evergreen and one deciduous broad-leaved trees in different seasonal and soil moisture conditions (Kosugi and Kobashi, 1994; Kosugi *et al.* 1997). Observation No. 4 (OBS No. 4) was carried out in Tokuyama Experimental Field of Kyoto University Forest, Yamaguchi Prefecture, Japan, in 1994. Two kinds of conifers, 12 evergreen and 13 deciduous trees and 4 grasses were observed to obtain some information on the deviation of CO₂ and H₂O fluxes of leaves of different types of trees, as well as grasses. (Table 1).

Fig. 1, Fig. 2 and Fig. 3 show the diurnal change of water-use efficiency on each observation day of OBS No. 1, No. 2, and No. 3, respectively. Fig. 4 shows the diurnal change of water-use efficiency of various kinds of tree species and grasses on each observation day of OBS No. 4. Several characteristics of water-use efficiency can be detected from these observational results. The values of water-use efficiency were scattered mainly from 10⁻¹ to 10² (mg/g). Diurnal and seasonal change of water use efficiency can be detected from Fig. 1 and Fig. 2, which show that water-use efficiency was higher in the morning than in the afternoon and higher in winter than in summer. Fig. 3 and Fig. 4 show that the fluctuation of water-

Table 1 A summary of observation site, location, period and materials

No.	Name of site	Location	Period	Materials
OBS No.1	Naehata	35.02N 135.47E	1989	3 evergreen broad-leaved trees
	(Kyoto Univ.)	60m a.m.s.l.		
OBS No.2	Nakaniwa	35.02N 135.47E	1994-1995	3 evergreen broad-leaved trees
	(Kyoto Univ.)	60m a.m.s.l.		4 deciduous broad-leaved trees
OBS No.3	Akou	34.44N 134.22E	1991-1994	4 evergreen broad-leaved trees
	(Hyogo Pref.)	<20m a.m.s.l		1 deciduous broad-leaved trees
OBS No.4	Tokuyama	34.03N 131.50E	1994	12 evergreen broad-leaved trees
				13 deciduous broad-leaved trees
				2 conifers and 4 grasses.

Fig. 1 Diurnal change of water-use efficiency on each observation day of OBS No. 1

use efficiency with species was smaller than that with environmental conditions. These characteristics of water-use efficiency reflect the differences of diurnal and seasonal variation patterns of transpiration rate and net assimilation rate.

IV. DISCUSSION

Fig. 5 shows the relationship between g_{bw} and β with contour-lines of g_{sw} . The value of g_{bw} is fixed in one value with porometric method using a chamber with a fixed shape and a constant wind speed, and in this study g_{bw} used in the LI-6200 was $2.0\text{mol m}^{-2}\text{s}^{-1}$. As the value of

Fig. 2 Diurnal change of water-use efficiency on each observation day of OBS No. 2

Fig. 3 Diurnal change of water-use efficiency for each observation period of OBS No. 3

Fig. 4 Diurnal change of water-use efficiency of various kinds of tree species and grasses on each observation day of OBS No. 4

Fig. 5 Relationship between g_{bw} and β with contour-lines of g_{sw}
Note: Contour lines of g_{sw} are drawn using Eq. (12) and Eq. (3).

g_{sw} was mostly under $0.6 \text{ mol m}^{-2} \text{ s}^{-1}$ in the case of tree species of OBS No. 1 to OBS No. 4, β was mostly under about 0.3 and usually under 0.2, which corresponds to $g_{sw}=0.5 \text{ mol m}^{-2} \text{ s}^{-1}$. Kondo and Watanabe (1992) summarized the value of β of various vegetation covers, reporting values ranging from 0.1 to 0.4 in several vegetations except rice paddy, which showed the values ranging from 0.5 to 0.8. These β values at the scale of canopy correspond to the upper line of β obtained from leaf-scale observations in this study, probably as a result of the difference in the scale of measurement used.

Fig. 6 shows the relationship between g_{sw} and α with contour-lines of g_i with the observed data from OBS No. 1 to OBS No. 4 plotted on each chart. From this figure, α should be under 0.625, and observed α often showed the values under 0.2 and sometimes large values over 0.4 in the zone of $g_{sw}<0.1$.

From Eq. (17), water-use efficiency is determined by vapor pressure deficit and α . Fig. 7 shows the relationship between vapor pressure deficit and water-use efficiency with contour lines of α , and with the observed data from OBS No. 1 to OBS No. 4 plotted on each chart. Since the deviation of α was often from 0.01 to 0.2 in the observations of this study, the observed water-use efficiency was plotted in the zone between the two contour lines in each chart. As α also fluctuated less compared with $W_i - W_a$, the change of vapor pressure deficit mainly regulated the diurnal and seasonal change of water-use efficiency. Thus water-use efficiency was mainly regulated by vapor pressure deficit, and the similar values for water-use efficiency were observed with different species in conditions of similar vapor pressure deficit. It can be also said that large water-use efficiency was observed in winter and in the morning mainly because of the small water vapor deficit.

From Eq. (14), net assimilation rate is determined by α and β since $C_a - \Gamma_*$ fluctuates very little with the condition of ambient CO_2 concen-

tration and g_{bw} is assumed to be constant. Fig. 8 shows the relationship between α and β with contour lines of net assimilation rate and with the observed data from OBS No. 1 to OBS No. 4 plotted on each chart. This figure represents the probable value of net assimilation rate with various pairs of α and β . As α must be under 0.625 and was often from 0.01 to 0.2, and β was also often from 0.01 to 0.2 in the observations in this study, net assimilation rate was often plotted in the shadow region in the figure.

From Eq. (15), transpiration rate is determined by vapor pressure deficit and β as g_{bw} is assumed to be constant. Fig. 9 shows the relationship between vapor pressure deficit and β with contour lines of transpiration rate and with the observed data from OBS No. 1 to OBS No. 4 plotted on each chart. This figure represents the probable value of transpiration rate with various pairs of vapor pressure deficit and β . As β is often from 0.01 to 0.2 in the observations in this study, transpiration rate was often plotted in the shadow region in the figure.

V. CONCLUSIONS

In this study, the factors determining water-use efficiency, net assimilation rate and transpiration rate at the leaf-scale were investigated using two parameters α (ratio of total conductance to CO_2 to total conductance to H_2O) and β (ratio of total conductance to latent heat to total conductance to sensible heat). The characteristics of water-use efficiency were detected from several data sets of field observations with porometric method as follows,

- (1) Water-use efficiency was higher in the morning than in the afternoon.
- (2) Water-use efficiency was higher in winter than in summer.
- (3) Water-use efficiency values were scattered mainly from 10^{-1} to 10^2 (mg/g), and the fluctuation of water-use efficiency with species was smaller than that with environmental conditions. These characteristics of water-use efficiency reflect the difference of the diurnal and

Fig. 6 Relationship between g_{sw} and α with contour-lines of g_i with the observed data from OBS No. 1 to OBS No. 4

Note: Contour lines of g_i are drawn using Eq. (13), Eq. (4) and the value of $g_{bw}=2.0$.

Fig. 7 Relationship between vapor pressure deficit and water-use efficiency with contour lines of α with the observed data from OBS No. 1 to OBS No. 4

Note: Contour lines of α are drawn using Eq. (17) and the value of $C_a - \Gamma_* = 320$.

Fig. 8 Relationship between α and β with contour lines of net assimilation rate with the observed data from OBS No. 1 to OBS No. 4

Note: Contour lines of net assimilation rate, A , are drawn using Eq. (14) and the value of $C_a - \Gamma_s = 320$, $g_{sw} = 2.0$.

Fig. 9 Relationship between VPD and β with contour lines of transpiration rate with the observed data from OBS No. 1 to OBS No. 4

Note: Contour lines of transpiration rate, E , are drawn using Eq. (15) and the value of $g_{bw} = 2.0$.

seasonal variation patterns of transpiration rate and net assimilation rate.

It was clarified that phenomena (1) and (2) were mainly caused by the differences in vapor pressure deficit, and partly by the differences in ratio of total conductance to CO_2 to total conductance to H_2O (α). This analysis also showed that phenomenon (3) was caused by the little differences in the ratio of total conductance to CO_2 to total conductance to H_2O (α) with species. The ranges of values of water-use efficiency, net assimilation rate and transpiration rate could be also explained using the two parameters, α and β .

The parameter α , in addition to surface moisture ability β , is considered to be a useful number for any studies which express heat and H_2O fluxes using Eq. (1) and Eq. (2), to expand into CO_2 flux. This α - β method is considered to be suitable for rough estimation of fluxes at large scale, for example, using remote-sensing data.

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(Received: July. 12, 1996, Accepted: Sept. 5, 1996)