

ROLE OF STOMATAL OSCILLATIONS ON TRANSPIRATION, ASSIMILATION AND WATER-USE EFFICIENCY OF PLANTS

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ABSTRACT

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The objective of this study was to evaluate the average transpiration rate and CO₂ assimilation rate and water-use efficiency during steady-state limit cycle oscillations (time varying cyclic changes) in stomatal pore width both for a hydropassive feedback loop model and for a comprehensive model with both hydropassive and CO₂ feedback effects. The results were compared with the corresponding values for the non-time varying pore width (pore width corresponding to a theoretically predicted unstable focus). The hydropassive model predicts that the oscillations of stomata under dry ambient conditions conserve moisture. The comprehensive model which incorporates CO₂ feedback loop suggests that such oscillations not only reduce transpiration rate, but also improve water-use efficiency.

INTRODUCTION

Stomatal pores are microscopic openings on the surface of a leaf which permit CO₂ and water vapor exchange between the leaf interior and the environment (Fig. 1). Carbon dioxide enters the leaf through open stomata and is utilized in photosynthesis. Water vapor diffuses out of the leaf when stomatal pores are open. Thus, stomata play the crucial role of permitting sufficient entry of CO₂ while avoiding excessive water loss.

Stomata change their width continuously in response to changes in the surrounding environment. Delwiche and Cooke (1977) modelled hydropas-

NOMENCLATURE

a_0	semi-major axis of elliptical stoma, mm
d	pore depth, mm
l	maximum leaf dimension in downward wind direction, mm
n	number of stomata per unit area, mm
r	mean pore radius, mm
v	mean ambient wind velocity, mm/s
w	width of elliptical pore, mm
A	rate of CO ₂ assimilation, mol/s
C_m	water vapor concentration at the wet mesophyll wall, mol/mm ³
C_{ta}	water vapor concentration in the turbulent atmosphere, mol/mm ³
$C_{cav}^{CO_2}$	CO ₂ concentration in the cavity, mol/mm ³
$C_{ta}^{CO_2}$	atmospheric CO ₂ concentration, mol/mm ³
D_{CO_2}	diffusion coefficient for CO ₂ , mm ² /s
D_{wv}	diffusion constant for water, mm ² /s
E	transpiration rate, g/(mm ² h)
R_{st}	stomatal resistance, MPa
WUE	water use efficiency
α	antagonism ratio
δ_{ias}	mean intercellular air space path length, mm
ϵ_g	guard cell elastic modulus, MPa
ϵ_s	subsidiary cell elastic modulus, MPa
ξ	proportionality constant
π_g	guard cell osmotic pressure, MPa
π_s	subsidiary cell osmotic pressure, MPa
π_g^o	guard cell osmotic pressure at incipient plasmolysis, MPa
π_s^o	subsidiary cell osmotic pressure at incipient plasmolysis, MPa
a	$\frac{\delta_{ias} + \xi\sqrt{l/v}}{D_{wv}}$
b	$\frac{2(d+r)}{n\pi a_0 D_{wv}}$
p	$\frac{\delta_{ias} + \xi\sqrt{l/v}}{D_{CO_2}}$
q	$\frac{2(d+r)}{n\pi a_0 D_{CO_2}}$
A_{max}	$\frac{C_{ta}^{CO_2}}{C_m - C_{ta}}$
E_{max}	$\frac{a}{C_{cav}^{CO_2}}$
F_{max}	$\frac{p}{q/p}$
K_A	q/p
K_E	b/a

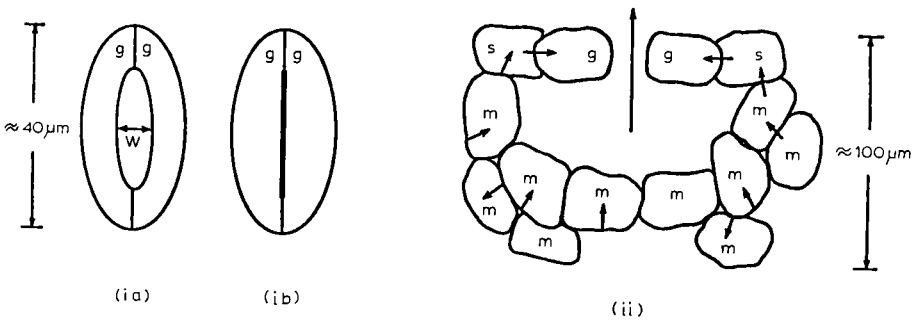


Fig. 1. Stomatal apparatus: (i) view looking onto the leaf surface, (a) pore open, (b) pore closed; (ii) cross-sectional view with arrows representing various water fluxes; g, guard cell; s, subsidiary cell; m, mesophyll cell.

sive aspects of stomatal dynamics. Their hydropassive loop model consisted of two coupled nonlinear differential equations of the following form:

$$\dot{P}_g = f_1(P_g, P_s, \tilde{\pi}_g) \quad (1)$$

$$\dot{P}_s = f_2(P_g, P_s, \tilde{\pi}_g) \quad (2)$$

where P_g is guard cell turgor pressure, P_s subsidiary cell turgor pressure, and $\tilde{\pi}_g$ metabolically controlled part of the guard cell osmotic pressure. Note that the dot above P_g and P_s denote time differentiation. Delwiche and Cooke (1977) assumed $\tilde{\pi}_g$ to be constant. The exact functional forms of f_1 and f_2 are given in Delwiche and Cooke (1977) and Upadhyaya et al. (1983). This hydropassive loop model exhibited a steady state limit cycle (time varying) oscillation of pore size of 20 min under *constant* environmental conditions (Fig. 2).

Rand et al. (1981) analyzed this model and showed that it exhibits a steady state oscillation for a certain range of parameter values. In particular, they showed that a Hopf bifurcation occurs (a stable focus corresponding to non-time varying pore width changes to an unstable focus resulting in a limit cycle [time varying] oscillation of pore width) as the osmotic pressure in the guard cell is changed. When the osmotic pressure in the guard cell is high, the stoma opens to an equilibrium width (stable focus) under steady environmental conditions. As the osmotic pressure in the guard cell is decreased, a critical value of osmotic pressure is reached at which the stable focus corresponding to non-time varying pore width becomes unstable (unstable focus). Because of differences in equations (1) and (2) when the stoma is open versus when it is closed, a stable limit cycle surrounds this unstable equilibrium point resulting in steady state oscillations (Fig. 2). Note that the Hopf bifurcation itself leads to an unstable focus. The guard cell osmotic

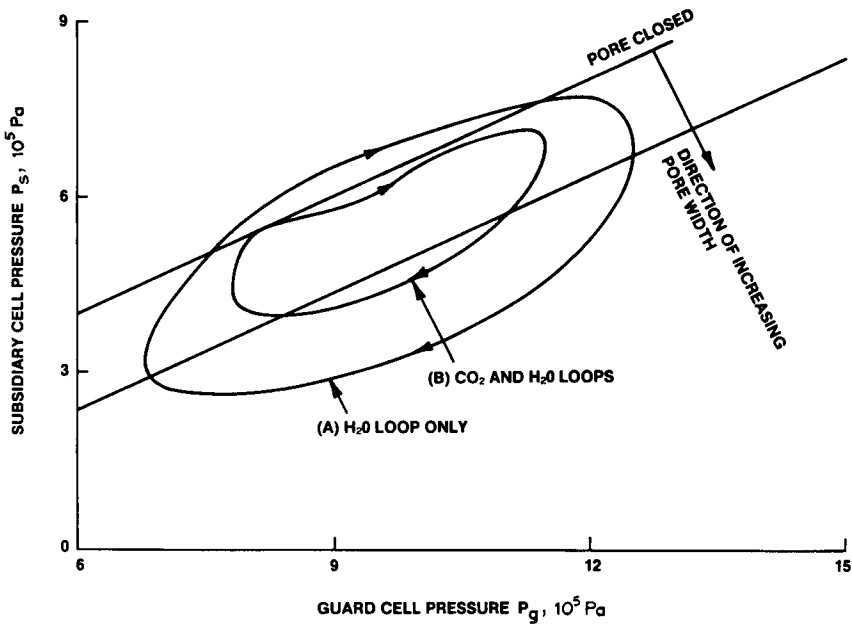


Fig. 2. Limit cycles in phase plane.

pressure at which Hopf bifurcation occurs depends on ambient conditions and material properties of the guard cell complex (cf. Fig. 1). If the stomatal pore is open when this critical osmotic pressure is reached, then steady state limit cycle oscillation will result. Steady state stomatal oscillations may result when the guard cell osmotica is decreased from a high to a low value (and vice versa). Such a reduction in osmotica may occur due to release of the plant hormone ABA at low soil water potential.

A bifurcation also occurs when the humidity in the turbulent atmosphere is decreased or when the plant's resistance to water uptake is increased. The plant's resistance to water uptake and the difference in water vapor concentration between wet mesophyll cell walls and the turbulent atmosphere appear as a product in our model. Therefore, the response of the plant to an increase in the atmospheric humidity is similar to the response of the plant to a decrease in the plant resistance.

Upadhyaya et al. (1980, 1983) developed a comprehensive model of stomal dynamics which incorporates a CO_2 -based feedback control in the model developed by Delwiche and Cooke. They assumed that CO_2 is metabolized in the guard cell into malic acid as a result of PEP carboxylation. They also assumed the existence of a proton pump (chemiosmotic hypothesis) across the guard cell-subsidiary cell membrane which actively expulses H^+ ions to subsidiary cells and OH^- ions to guard cells when

sufficient energy is available (either due to sunlight or oxidative phosphorylation in mitochondria). This active ion transport across the guard cell-sub-sidiary cell membrane generates a pH difference and an electrical potential difference across the membranes separating the guard cell and subsidiary cells. This electrical potential difference results in a shuttle of potassium (from subsidiary cells to guard cell) and malate ions (from guard cells to subsidiary cells). The increased potassium ions in the guard cell lead to an increased osmotic potential ($\tilde{\pi}_g$) and hence an increased stomatal pore width. Upadhyaya et al. (1983) showed that the electrical potential difference across the guard cell-sub-sidiary cell membrane can be expressed as:

$$E = f_3(q, C_{cav}^{CO_2}) \quad (3)$$

where E is electromotive force (emf) across the guard cell-sub-sidiary cell membrane, q hydrogen pump capacity, and $C_{cav}^{CO_2}$ CO_2 concentration in sub-stomatal cavity.

Moreover, potassium flux, metabolically controlled guard cell osmotic pressure and $C_{cav}^{CO_2}$ are governed by the following equations:

$$\dot{N}_g = f_4(E, N_g) \quad (4)$$

$$\tilde{\pi}_g(t) = f_5(N_g(t)) \quad (5)$$

$$C_{cav}^{CO_2} = f_6(P_g, P_s) \quad (6)$$

where N_g is amount of potassium ion in the guard cell, and t time.

Upadhyaya et al. (1983) have derived explicit expressions for functions f_3 , f_4 , f_5 , and f_6 . In essence, equations (3) through (6) are equivalent to:

$$\tilde{\pi}_g = f_7(P_g, P_s, \tilde{\pi}_g) \quad (7)$$

although, the complexity of equations (3) through (6) makes it difficult to solve them explicitly in the form of equation (7). They solved the coupled nonlinear system of equations (1) through (6) numerically and showed that this model exhibits a limit cycle behavior which may be thought of as a 'superposition' of a long (about 20 min) period hydropassive loop-controlled oscillation and a short (about 2 min) period CO_2 loop-controlled oscillation (Fig. 2). These characteristics agree with the experimental work of Apel (1966, 1967).

These steady-state oscillations are predicted to occur for a certain range of parameter values. What purpose, if any, such oscillations play in conserving moisture or improving plant water use efficiency (i.e., mass of CO_2 assimilated per unit mass of water vapor lost) is not known. The objective of the present study is to compare the effect of limit cycle oscillations (time varying, cyclic) of pore width on: (a) transpiration rate; (b) CO_2 assimilation rate; and (c) water use efficiency of the plant, with the non-time varying

(constant) pore width corresponding to an unstable focus that would have resulted if that focus were stable (i.e. if stoma did not exhibit limit cycle oscillation).

REVIEW OF LITERATURE

Stomatal pore widths have been observed to oscillate in even under steady environmental conditions (Karmanov and Savin, 1964; Ehrlert et al., 1965; Apel, 1966, 1967; Lang et al., 1969; Bars, 1971) Barrs (1971) has reviewed the oscillations in leaf conductance. Cowan (1977) has reviewed stomatal behavior with respect to changes in the environment. Two reviews by Raschke (1975, 1979) cover the literature on various aspects of stomatal mechanics. Upadhyaya et al. (1983) have given a comprehensive review of the literature on stomatal movements.

MODEL STUDIES

Model behavior

The qualitative response of the hydropassive loop model to changes in soil water potential, atmospheric humidity, and plant resistance to water uptake depends on the antagonism ratio (mechanical advantage of subsidiary cells over guard cells – see Cooke et al., 1976), the guard and subsidiary cell elastic moduli, and the guard and subsidiary cell osmotic pressures at incipient plasmolysis. For this study, we selected parameter values which resulted in a realistic behavior of the model – i.e., the equilibrium width of the stoma increases with an increase in either atmospheric humidity, soil water potential, or overall plant conductivity. Under these circumstances it can be shown that:

$$(1 + \pi_s^o/\epsilon_s) > \alpha(1 + \pi_g^o/\epsilon_g) \quad (8)$$

where π_g^o , π_s^o are osmotic pressure in the guard and subsidiary cells at incipient plasmolysis, ϵ_g , ϵ_s elastic moduli of guard and subsidiary cell, and α is antagonism ratio.

Because of the presence of radial micellation, the guard cell elastic modulus is quite high (about 7 MPa) according to Raschke (1979). This study uses a value of 6 MPa. Equation (8) can be satisfied for various combinations of α , ϵ_g , π_g^o , and π_s^o . In this study we used the following values:

$$\pi_g^o = 1.5 \text{ MPa} \quad \epsilon_g = 6 \text{ MPa}$$

$$\pi_s^o = 2 \text{ MPa} \quad \epsilon_s = 2 \text{ MPa}$$

$$\alpha = 1.5$$

TABLE 1

Parameters used in this study

Plant resistance to water uptake	$R_p = 8 \times 10^6 \text{ Pa s/mm}$
Water vapor concentration in the wet mesophyll walls, cm	$= 30 \times 10^{-3} \text{ mm}^3/\text{mm}^3$
Hydrogen pump capacity	$q = 18 \times 10^{-10} \text{ moles}/(\text{mm}^2 \text{ s})$
Maximum enzymatic velocity for PEP carboxylation	$V^* = 8.5 \times 10^{-13} \text{ mol/s}$
Guard cell elastic modulus	$\epsilon_g = 6 \text{ MPa}$
Subsidiary cell elastic modulus	$\epsilon_s = 1.5 \text{ MPa}$
Guard cell osmotic pressure at incipient plasmolysis	$\pi_g^o = 1.5 \text{ MPa}$
Subsidiary cell osmotic pressure at incipient plasmolysis	$\pi_s^o = 2 \text{ MPa}$

Almost all other parameter values used in this study are the same as those used by Upadhyaya et al. (1983). The parameters which differ from those used in this previous paper are given in Table 1.

Upadhyaya et al. (1981) conducted several simulation studies to evaluate the performance of this model. They found that the stomatal pore width increased linearly with an increase in the osmotic pressure in the guard cell. This behavior was in agreement with the experimental results reported by Raschke (1979) and Hsiao (1976). Moreover, in the simulation studies the stomatal pore width increased slightly when the ambient humidity increased, and the pore width decreased when the soil water potential was decreased. They also found that the transpiration rate increased linearly with increased pore width for pore widths less than 10 μm . The CO_2 assimilation rate increased very rapidly with the increased pore width up to a pore width of 2 μm and then remained more or less constant for higher pore widths. The water use efficiency decreased very quickly as pore width increased to about 2 μm and remained fairly constant with further increases in pore width. The above model predictions are consistent with real life behavior of leaf stomata (Nobel, 1974).

Stomatal oscillations

This model predicts the occurrence of a limit cycle oscillation when either guard cell osmotic pressure, soil water potential, or atmospheric humidity is reduced from a high value to low value, or when the plant resistance to water uptake is increased from a low value to high value, provided equation 8 is satisfied. It should be noted that a given species of plant may or may not exhibit stomatal oscillations, depending on the parameter values of the guard cell complex (i.e., if the atmospheric humidity decreases from a high

value to a low value, some plant species may exhibit stomatal oscillations whereas other species may not). Moreover, the value of relative humidity at which the bifurcation occurs, i.e. a time nonvarying pore width suddenly becomes a time varying pore width (limit cycle oscillation) also depends on parameter values used in the model. The parameter values used in this study were selected to demonstrate the model behavior. These values may not correspond to parameter values for a specific species.

A quasi-static decrease in atmospheric humidity is probably responsible for the steady state oscillations of stomatal pore size observed in many plant species during late afternoon. Therefore, in this study, guard cell osmotic pressure and soil water potential are maintained constant while the atmospheric humidity is changed.

For these conditions, the transpiration rate, E , is calculated using the following expression:

$$E = D_{\text{wv}} \frac{C_{\text{m}} - C_{\text{ta}}}{R_{\text{st}}} \quad (9)$$

where D_{wv} is diffusion constant for water vapor, R_{st} = stomatal resistance, C_{m} = water vapor concentration at the wet mesophyll wall, and C_{ta} = water vapor concentration in the turbulent atmosphere. Stomatal resistance to water vapor diffusion was calculated using the following equation (Cooke and Rand, 1980):

$$\frac{R_{\text{st}}}{D_{\text{wv}}} = a + \frac{b}{w} \quad (10)$$

where

$$a = \frac{\delta_{\text{ias}} + \xi \sqrt{l/v}}{D_{\text{wv}}}$$

$$b = \frac{2(d+r)}{n\pi a_0 D_{\text{wv}}}$$

and δ_{ias} is mean intercellular airspace path length, ξ proportionality coefficient, l maximum leaf dimension in the downward wind direction, v mean ambient wind speed, d stomatal pore depth, r mean stomatal pore radius, n number of stomata per unit area, a_0 semi-major axis of elliptical stoma, and w stomatal pore width. Equation (9) can be rewritten as:

$$\begin{aligned} E &= \frac{\left(\frac{C_{\text{m}} - C_{\text{ta}}}{a} \right) w}{b/a + w} \\ &= \frac{E_{\text{max}} w}{K_E + w} \end{aligned} \quad (11)$$

where

$$E_{\max} = \frac{C_m - C_{ta}}{a}$$

$$K_E = b/a$$

The amount of CO_2 fixed by the green leaves minus the CO_2 released due to respiration and dark respiration is net assimilation. Rand and Cooke (1980) have developed the following expression for CO_2 assimilation:

$$A = D_{\text{CO}_2} \frac{C_{ta}^{\text{CO}_2} - C_{cav}^{\text{CO}_2}}{R_{st}} \quad (12)$$

where D_{CO_2} is diffusion coefficient for CO_2 , $C_{ta}^{\text{CO}_2}$ = atmospheric CO_2 concentration, and $C_{cav}^{\text{CO}_2}$ = CO_2 concentration in the cavity. Equation (12) can be rewritten as:

$$A = \frac{C_{ta}^{\text{CO}_2}}{p + q/w} - \frac{C_{cav}^{\text{CO}_2}}{p + q/w} \quad (13)$$

where

$$p = \frac{\delta_{ias} + \xi\sqrt{l/v}}{D_{\text{CO}_2}}$$

$$q = \frac{2(d+r)}{n\pi a_0 D_{\text{CO}_2}}$$

But $C_{cav}^{\text{CO}_2}$ is a function of atmospheric CO_2 concentration and the stomatal pore with (Rand and Cooke, 1980). Therefore:

$$C_{cav}^{\text{CO}_2} = f(w, C_{ta}^{\text{CO}_2}) \quad (14)$$

Equation (13) can be rewritten as:

$$\begin{aligned} A &= \frac{\left(\frac{C_{ta}^{\text{CO}_2}}{p}\right)w}{q/p + w} - \frac{\left(\frac{C_{cav}^{\text{CO}_2}}{p}\right)w}{q/p + w} \\ &= \frac{A_{\max}w}{K_A + w} - \frac{F_{\max}w}{K_A + w} \end{aligned} \quad (15)$$

where

$$A_{\max} = \frac{C_{ta}^{\text{CO}_2}}{p}$$

$$K_A = q/p$$

$$F_{\max} = \frac{C_{cav}^{\text{CO}_2}}{p}$$

Water use efficiency is obtained by dividing equation (15) by (11):

$$WUE = A/E \quad (16)$$

When the stomatal pore width undergoes limit cycle oscillation, transpiration rate E (equation 11), assimilation rate A (equation 15), and hence water use efficiency WUE (equation 16) change with time in a cyclic manner. Therefore, these quantities may be integrated over one time period and the results may then be normalized to a base time of 1 h, i.e.

$$\bar{E} = \frac{3600}{\tau} \int_0^{\tau} E \, dt \quad (17)$$

$$\bar{A} = \frac{3600}{\tau} \int_0^{\tau} A \, dt \quad (18)$$

$$\overline{WUE} = \frac{\bar{A}}{\bar{E}} \quad (19)$$

where \bar{E} = normalized transpiration rate, \bar{A} = normalized assimilation rate, \overline{WUE} = normalized water use efficiency, and τ = time period for cyclic oscillation.

The transpiration rate, CO_2 assimilation rate, and water use efficiency are evaluated for the above case for the following situations:

(1) The stoma opens to its equilibrium width corresponding to stable or unstable focus predicted by the hyropassive loop model and does not oscillate. If the equilibrium point is stable, this pore width is realized. If the equilibrium point is unstable, this pore width is not attainable in reality; it is used in this analysis for comparison purposes only. This pore width is predicted by equating the right hand side of equations (1) and (2) to zero (i.e. $\dot{P}_g = \dot{P}_s = 0$) and solving for P_g and P_s . Once P_g and P_s are known, pore width is obtained as follows (Cooke et al., 1976):

$$w = \begin{cases} b_0 + b_g P_g + b_s P_s & \text{if } b_0 + b_g P_g + b_s P_s \geq 0 \\ 0 & \text{if } b_0 + b_g P_g + b_s P_s < 0 \end{cases} \quad (20)$$

(2) The stoma exhibits steady-state oscillations governed by the hydro-passive feedback loop (Delwiche and Cooke, 1977).

(3) The stoma exhibits steady state oscillations governed by both hydro-passive and CO_2 -based feedback loops (Upadhyaya et al., (1983).

RESULTS AND DISCUSSION

Figures 3 through 5 represent, respectively, the variations in the rate of transpiration, the rate of CO_2 assimilation, and water use efficiency as the

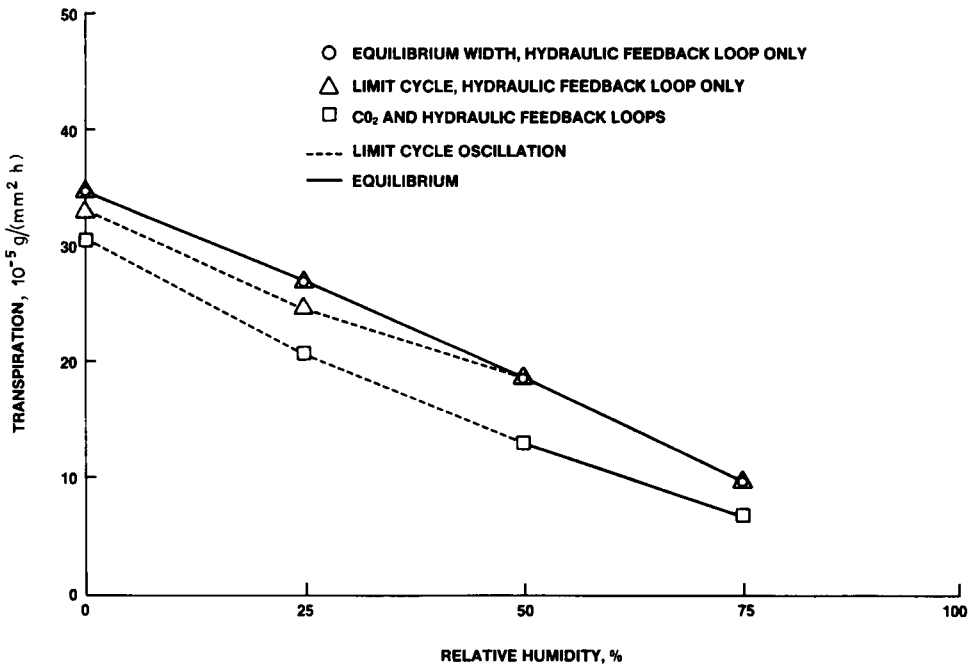


Fig. 3. Transpiration vs. atmospheric humidity at constant soil water potential and guard cell osmotic pressure.

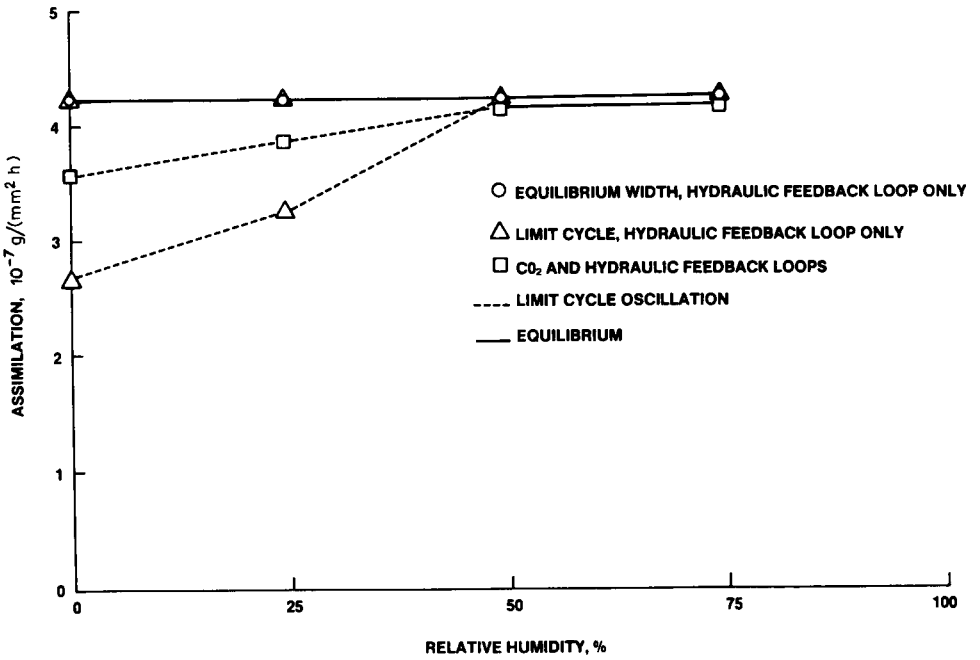


Fig. 4. CO₂ assimilation vs. atmospheric humidity at constant soil water potential and guard cell osmotic pressure.

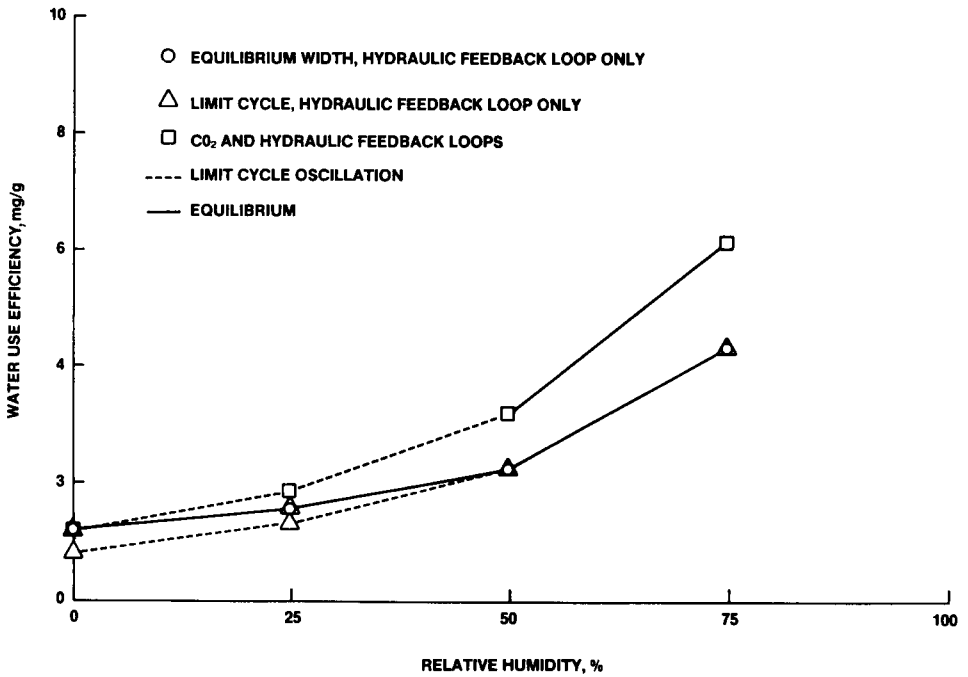


Fig. 5. Water use efficiency vs. atmospheric humidity at constant soil water potential and guard cell osmotic pressure.

atmospheric humidity changes. Note that above 50% relative humidity hydropassive oscillations cease. Below 50% humidity hydropassive oscillations increase in amplitude as the humidity decreases. Transpiration decreases as the humidity decreases. This decrease happens at the cost of a decrease in the CO₂ assimilation and water use efficiency. Inclusion of the CO₂ loop further reduces the transpiration rate and results in a CO₂ assimilation rate intermediate between that occurring during hydropassive limit cycle oscillations and that occurring in the absence of oscillations. However, with the inclusion of CO₂ loop water use efficiency is higher than in these other two cases. Although our model exhibited limit cycle oscillation below 50 percent relative humidity because of parameter values we chose, the limit cycle oscillations occur only under very dry conditions in nature. Changes in the atmospheric humidity occur naturally during the course of a day in the field. During late afternoon when the atmospheric humidity is low, some plant species may exhibit stomatal oscillations. If this oscillation occurs, it appears to reduce transpiration and improve water use efficiency of the plant.

CONCLUSIONS

Stomatal oscillations occur as the humidity in the ambient atmosphere is reduced. These oscillations are induced by a hydropassive feedback mechanism. As the atmospheric humidity decreases, the amplitude of these oscillations increases, and the amount of water vapor lost to the surrounding atmosphere decreases. *Thus, hydropassive oscillations tend to conserve water under dry atmospheric conditions.* This moisture conservation occurs at the cost of a reduced rate of CO₂ assimilation and reduced water use efficiency.

Incorporation of the CO₂ feedback mechanism in the hydropassive model further reduces the amount of water vapor lost at low ambient humidity and improves the water use efficiency. This mechanism is important under dry ambient conditions. However, this reduction in water loss occurs at the cost of a reduced rate of CO₂ assimilation.

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