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Analytical approach to relate evapotranspiration, canopy-atmosphere coupling level, and water deficit sensitivity

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ABSTRACT: The decoupling factor (Ω) reflects the leading mechanisms responsible for canopy transpiration and allows to know the relevance of the control of stomatal or canopy conductance on transpiration (T). The Ω is strongly dependent on water availability and can be a good approach to describe how plants minimize excessive water loss by increasing the dominance of biotic factors that controls evapotranspiration under water deficit conditions. We provided an overview of how the Ω concept can be broadly used and applied for studying the sensitivity of evapotranspiration and water conservation potential of canopies under water deficit conditions. A decoupling condition indicates that, under water deficit, the increase of canopy resistance will not have control over the transpiration. Therefore, a structural context of the canopy in which predominantly uncoupled regions will have a lower capacity to reduce evapotranspiration and avoid water losses. Furthermore, because of the water deficit, stomatal closure restricts photosynthesis more than transpiration, and water use efficiency can be lower in decoupled canopies compared to more coupled ones. Yet, we summarized the characteristics that depict structural context predisposing coupled or decoupled conditions that can indicate the capacity of canopy/crop to reduce excessive water losses and maintain a high assimilation/transpiration relation under water deficit.

Key words: transpiration, water deficit, vapor pressure deficit, decoupling factor.

INTRODUCTION

Radiation, air temperature, air humidity and wind are meteorological elements involved in determining evaporation and transpiration. Both processes occur simultaneously such as evapotranspiration and are controlled by biophysical conditions (aerodynamic resistance, stomatal conductance, surface conductance) and crop management (Allen et al. 2006). The amount of water evaporated during evapotranspiration is related to the energy received per unit area in the form of latent heat of vaporization (λE). Therefore, the λE flux (LE) is a direct expression of evapotranspiration, in which 2.45 MJ per m2 is required to vaporize 1 kg or 1 mm of water (Rosenberg et al. 1983).

The main driving force of the biophysical interaction between the biosphere and the atmosphere is the radiative energy from solar radiation. Although evapotranspiration is directly linked to this available energy (which is the primary driver of vapor transport), there is a considerable influence of the biotic factors (Nassif et al. 2014, Paulino Junior et al. 2017, Spinelli et al. 2018). The decoupling factor was proposed by Jarvis and McNaughton (1986). It allows to understand the ability of plant canopy and the atmosphere to exchange momentum, energy, and mass (Steduto and Hsiao 1998), reflects the dominant mechanisms responsible for the canopy evapotranspiration, and contributes to explain how evapotranspiration is controlled in vegetated surfaces (Paulino Junior et al. 2017, Sutherlin et al. 2019). Conceptually, the extreme values of Ω mean are:

- $\Omega \rightarrow 1$, implying that the net radiation is the only contributor to the evapotranspiration process and that vegetation is completely decoupled from the atmospheric conditions;

- $\Omega \to 0$, indicating complete coupling of vegetation with atmospheric vapor pressure deficit (VPD) and wind speed (Marin et al. 2016).

According to Jarvis and McNaughton (1986) and McNaughton and Jarvis (1991), Ω describes the sensitivity of evapotranspiration to biological and environmental controlling factors like radiation, wind speed, vapor pressure deficit, or surface conductance (Zhang et al. 2016). In other words, Ω is an index to assess:

- whether the evapotranspiration process is mainly controlled by the vegetation in terms of surface conductance or mainly limited by the energy available (radiation);
- how different vegetation types control the evapotranspiration fluxes in land–atmosphere interactions (Paulino Junior et al. 2017, Sutherlin et al. 2019).

Ω represents the magnitude of the coupling effect of the canopy and the aerodynamic conductance in controlling rates of canopy evapotranspiration (Kumagai et al. 2004) and characterizes the extent to which stomatal and canopy conductance may control transpiration (water vapor and CO_2 exchange) (Steduto and Hsiao 1998). Still, Ω is useful to quantify the relative importance of VPD in controlling the evapotranspiration (Ferreira 2017, Spinelli et al. 2018, Sutherlin et al. 2019).

Under water deficit conditions, the primary survival strategy in plants is to avoid excessive water loss and prevent dehydration. Although the stomatal closure or the increase in canopy resistance is an immediate response, the impact on the reduction of transpiration (for controlling water loss) and its consequence on carbon assimilation depends on the natural degree of coupling of canopies to the atmosphere. Likewise, the natural coupling or uncoupling condition of the different species is conditioned by their biophysical environment and their phenotypic characteristics.

This review aims to provide an overview around the decoupling factor (Ω) concept and its potential use to analyze the capacity of the canopy to reduce excessive water losses and the possible impacts on assimilation under water deficit. The following question is addressed in this review: how is omega modulated under water deficit?; and how does it impact water vapor and CO_2 exchange?

METHODOLOGY

Data sources and search strategies

This review was conducted according to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) methodology (Moher et al. 2009) by asking a question, choosing the eligibility criteria and keywords, searching the literature, excluding, and selecting the papers, assessing the quality of the articles, extracting the required information, and presenting data. The eligible articles published until 2022 were searched in three databases, including Scopus, ScienceDirect, and Web of Science. The search process was accomplished using the keywords "omega", "decoupling factor", "water deficit", and "evapotranspiration". Additional articles were taken into consideration by hand searching, mainly those that are theoretical bases for the subject. Metadata was not used in this review.

Study selection

The papers related to the subject of interest were selected by studying the abstracts and titles. Afterwards, the full texts of the selected papers were obtained. The main criteria for including papers were the link between water deficit and Ω, as well as retrospective articles than depict the theoretical approach for evapotranspiration and its relation to the Ω decoupling factor. We excluded studies that did not link the relation between Ω and evapotranspiration, or papers that work each one individually. After the exclusion of the irrelevant articles, the remaining papers were reviewed meticulously, and a careful review of titles and abstracts was done. We continued with a full-text checking of the articles related to the main criteria for inclusion. Figure 1 presents the flow diagram for the selection process of papers.

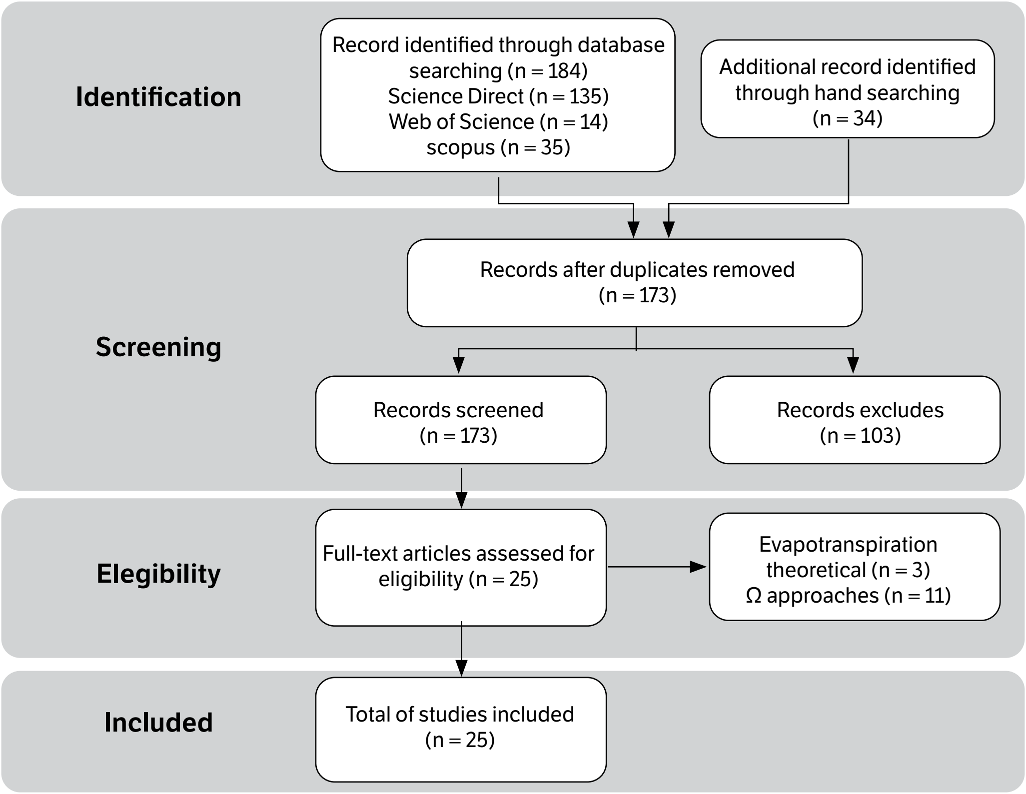

Figure 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses flow diagram showing the selection process of papers.

RESULTS

The searches produced 173 records after duplicates were removed. We identified 135 potentially relevant studies in Science Direct, 14 in Web of Science, 34 in Scopus, and 34 by hand searching. After reading the full reports, we considered 25 studies. The studies were reported between 1985 and 2022, involving different species. The first reports related to water availability were cited by Jarvis (1985) for soybean and alfalfa. After that, some reports were found for grasslands, forests (evergreen broadleaf forests, evergreen oak, lowland dipterocarp forest, rain forest) (Köstner et al. 1992, Khatun et al. 2011, Nassif et al. 2014, Ferreira 2017, De Kauwe et al. 2017, Spinelli et al. 2018, Sutherlin et al. 2019), woody crops, Kernza crop (Sutherlin et al. 2019), sugarcane (Nassif et al. 2014), almond (Spinelli et al. 2018), and maize (Steduto and Hsiao 1998). Grass species have a greater number of studies on the subject.

Three studies (Penman 1948, Monteith 1965, Marin 2021) were chosen to develop the theoretical basis of evapotranspiration and as a previous context of Ω concept. Sixteen studies (Jarvis and McNaughton 1986, Jones 1990, McNaughton and Jarvis 1991, Köstner et al. 1992, Steduto and Hsiao 1998, Marin et al. 2001, Khatun et al. 2011, Marin and Angelocci 2011, Nassif et al. 2014, Marin et al. 2016, Ferreira 2017, De Kauwe et al. 2017, Spinelli et al. 2018, Marin et al. 2019, Sutherlin et al. 2019, Marin 2021) substantiated the conceptual and theoretical meaning of the Ω, its sense regarding the link between plant canopy and the atmosphere.

In general, studies describe Ω as an indicator of the dominant mechanisms responsible for the evapotranspiration of the canopy and a good approach to describe the sensitivity of evapotranspiration to stomatal closure. Eleven studies (Jarvis 1985, Kumagai et al. 2004, Aires et al. 2008, De Kauwe et al. 2017, Ferreira 2017, Paulino Junior et al. 2017, Silva et al. 2017, Spinelli et al. 2016, 2018, Sutherlin et al. 2019, Alves et al. 2022) developed the Ω concept under water deficit conditions. Studies demonstrated how Ω is strongly dependent on water availability, and how its variable value depicted the importance of atmospheric and surface factors in controlling evapotranspiration.

DISCUSSION

Evapotranspiration

The process of water evaporation is an exchange, in which a humid surface delivers water vapor in exchange for the heat of the air above the said surface (Monteith 1965). This exchange only works if there are two fundamental components:

- an energy source providing latent heat of evaporation from the degradation of net radiation (energy component);
- a mechanism to remove water vapor. This mechanism is driven both by a sinking force and by the turbulent transport of water vapor (aerodynamic component) (Penman 1948, Marin 2021).

In the *aerodynamic component*, evaporation is a mass diffusion process in which there is a sink force governed by the gradient flow theory described by Eq. 1:

$$E = (e_{sur} - e_{air})f(u) \tag{1}$$

in which: Evaporation rate = related to the difference in the water vapor content; E = the evaporation per unit of time; e_{sur} = the vapor pressure of the evaporating surface; e_{air} = the actual vapor pressure of the surrounding air; $f(u)$ = a function of the horizontal wind speed.

difference e_{sur}–e_{air} = the gradient force directed by the pressure difference between the air and the evaporating surface (Penman 1948).

The main resistance to evaporation from the surfaces is a thin layer of air (1–3-mm thick) near the surface in which the movement of air is not turbulent and the transport of vapor through this layer occurs by molecular diffusion (sublaminar boundary layer). Penman (1948) parameterized $f(u)$, and the result is Eq. 2:

$$E = 0.33(e_{sur} - e_{air})U_2^{0.76} \tag{2}$$

in which: e_{air} = the actual vapor pressure of the air at a sufficient height not to be affected by evaporation; U_2 = the air velocity at 2 m.

The *energy component* is based on the concept that the energy for generating water vapor is defined by the energy balance. The shortwave and longwave components of the radiation balance determine the amount of energy available or used for the system. With this amount defined, the way of use or destination of that energy becomes relevant since it can be used mainly for water evaporation or for air heating (Penman 1948, Marin 2021) (Eq. 3):

$$Rn = LE + H \tag{3}$$

An air mass can be described by its temperature and vapor pressure. That is, the total heat content is the sum of the sensible heat content (which depends on the temperature) and the latent heat content (which depends on the vapor pressure). A change in latent heat content has an equal and opposite change in sensible heat content. To illustrate the concept, when liquid water carried by an air mass evaporates, there is an increase in the latent heat content in that air mass. Because the evaporation process involves a loss of internal energy, the air will cool down, thus reducing the sensible heat content (Monteith 1965).

Transport of latent heat (LE) is governed by the vapor pressure gradient (e_{sur}–e_{air}), and the transport of sensible heat (H) is driven by the temperature gradient (T_{sur} – T_{air}). Since these two are the main sinks of the incoming energy, it is useful to define the link between LE and H, in terms of the Bowen relationship: $\beta = \frac{H}{LE}$. which can also be written as pressure and temperature gradients, and ϒ is the psychrometric constant (Eq. 4):

$$\beta = \frac{\Upsilon\,(T_{sur} - T_{air})}{(e_{sur} - e_{air})} \tag{4}$$

in which: T_{sur} = the surface temperature; T_{air} = the temperature of the air above the surface.

From Bowen ratio, we obtain $H = \beta LE$; replacing Rn in the equation, we obtain $Rn = LE + \beta LE$ and, therefore, Eq. 5:

$$LE = \frac{Rn}{(1+\beta)} \tag{5}$$

Replacing the expression for Bowen ratio in terms of pressure and temperature gradients, we obtain Eq. 6:

$$LE = \frac{Rn}{1 + \frac{\Upsilon\,(T_{sur} - T_{air})}{(e_{sur} - e_{air})}} \tag{6}$$

By combining the aerodynamic component with the energy component, we obtain Eq. 7 (Penman 1948):

$$ET = \frac{\mathrm{Rn}\Delta + \mathrm{VPD}\ \Upsilon}{\Delta + \Upsilon} \tag{7}$$

in which: Δ = the slope of the vapor pressure curve at equilibrium temperature ($\mathrm{hPa{\cdot}K^{-1}}$); γ = the psychrometric coefficient ($0.67\ \mathrm{hPa{\cdot}K^{-1}}$); VPD ($e_{sur} - e_{air}$) = the air vapor pressure deficit (hPa), which is a function of air temperature and relative humidity.

Monteith (1965) extends Penman's method (1948) to plant surfaces considering aerodynamic and surface resistance factors. Like Penman (1948), he defines an energy component in which latent heat is consumed at a rate of Eq. 8:

$$LE_1 = \frac{\Delta Rn}{\Delta + \gamma} \tag{8}$$

and an aerodynamic component where the evaporation rate from a surface follows the gradient (surface T – T of the surrounding air). This approximation includes the specific heat of the air (*pc*) and the time in which 1 cm^3 of air exchanges heat with 1 cm^2 of surface (*ra*) (Eq. 9):

$$LE_2 = \frac{pc(T_{sur} - T_{air}{}')}{ra} = \frac{pcD}{ra} \tag{9}$$

Therefore, evapotranspiration is given by Eq. 10:

$$ET = LE_1 + LE_2 = \frac{\Delta Rn}{\Delta + \gamma} + \frac{pc\ DPV}{ra} \tag{10}$$

Considering that, $e_{sur} - e_{air} = \Upsilon(T_{sur} - T_{air})$, the equation can be written as (Eq. 11):

$$ET = \frac{\Delta Rn + cp\ [(e_{sur} - e_{air})/ra]}{\Delta + \gamma} \tag{11}$$

This equation is analogous to Penman's (1948) one. However, Monteith (1965) included the canopy (*rc*) and aerodynamic resistances (*ra*) (Marin 2021). In this approach, the transpiration rate is proportional to the difference between the vapor pressure at the leaf surface (e_{sur}) and the actual vapor pressure of the surrounding air (e_{air}). The term ($e_{sur} - e_{air}$)/ra (external diffusion rate) indicates a potential difference that maintains a current or flow of water vapor that passes through an *external resistance to diffusion "ra"* present in the air surrounding the leaf. Similarly, the rate of diffusion within the leaf is stated in terms of the gradient between the saturation vapor pressure of the air in contact with the cell walls surrounding the substomatal cavity $e_{s(sub)}$, and the vapor pressure at the surface of the leaf e_{sur}. The term ($e_{s(sub)} - e_{sur}$)/*rl* (internal diffusion rate), then, indicates a potential difference that maintains a flow of water vapor that crosses the internal resistance of the r_l leaf (stoma + cuticle + cell walls, under conditions of water deficit). When the leaves are turgid, with enough water for transpiration, the resistance of the cell walls is zero, and the resistance of the stoma is low and much lower than the cuticle. The resistance in this case is due to the stomata, their size and population on the leaf (Monteith 1965).

When both external and internal diffusion rates are equal (Eq. 12):

$$\frac{e_{s\,(sub)} - e_{sur}}{rl} = \frac{e_{sur} - e_{air}}{ra} \tag{12}$$

Solving for $e_{s(sub)} - e_{sur}$, we obtain Eq. 13:

$$e_{s(sub)} - e_{sur} = (1 + \frac{rl}{ra})\,(e_{sur} - e_{air}) \tag{13}$$

in which: $e_{sur} - e_{air}$ can be replaced by $\frac{e_{s(sub)} - e_{sur}}{(1 + \frac{rl}{ra})}$ to alternatively be written as Eq. 14:

$$\Upsilon^{*} = \Upsilon\,(1 + \frac{rl}{ra}) \tag{14}$$

The psychrometric constant Υ is replaced by Υ^{*} in the evapotranspiration equation to obtain the equation of latent heat of transpiration of a leaf or cultivation surface (Monteith 1965). Finally, the development of the Penman-Monteith equation is obtained (Eq. 15):

$$ET = \frac{\Delta Rn + pc\,\rho_{ar}\,[(e_{sur} - e_{air})/ra]}{\Delta + \Upsilon\,(1 + \frac{rl}{ra})} \tag{15}$$

Monteith (1965) extended the concept of resistance from the vegetated surface to a total surface resistance, *rs*, which describes the resistance to the flow of vapor through the stomata, of the total area of the leaf and the soil surface (Allen et al. 2006, Marin 2021), where (Eq. 16 and Eq. 17):

$$\Upsilon^{*} = \Upsilon\,(1 + \frac{rs}{ra}) \tag{16}$$

$$ET = \frac{\Delta Rn + pc\,[(e_{sur} - e_{air})/ra]}{\Delta + \Upsilon\,(1 + \frac{rs}{ra})} \tag{17}$$

Transpiration and decoupling factor

The total flux of water vapor from a crop is the sum of the transpiration of all radiation-intercepting leaves, and the evaporation from the soil surface under the crop. Transpiration plays an important role both because of its contribution to the total flow of water vapor and because of the variety of factors that control it (Monteith 1965). Transpiration depends on net radiation (*Rn*), VPD, temperature (*T*), wind speed (*u*), and stomatal conductance (*gs*). These variables vary within the canopy and through the atmosphere above the crop surface. Stomatal conductance (*gs*) determines and controls the VPD of the leaf surface directly, but its relationship with transpiration is not strictly direct (Jarvis and McNaughton 1986). The effect of gs on transpiration could be direct only if it were considered like a single stoma.

In this scenario, a change in the conductance of a single stoma would generate an equal change in the transpiration of that single stoma. Consequently, transpiration would be controlled by the movement of the guard cells and the stomatal geometry. Despite this, the contribution of water vapor from that single stoma would not be enough to modify the VPD gradient of the leaf surface.

At the leaf level, in which there is a population of stomata, the relationships between stomatal conductance, foliar VPD, and transpiration are not direct. In the leaf blade, the conductance of the stomata changes in unison, significantly altering the VPD of the leaf surface and generating a change in the water vapor gradient along the leaf boundary layer. In this case, the influence of conductance on transpiration will be determined by the relationship between the VPD of the leaf surface and the external VPD of the air environment beyond the leaf boundary layer. These effects are described by Jarvis and McNaughton's (1986) equation, in which the sensitivity of transpiration to conductance is given by Eq. 18:

$$\frac{dE_l}{E_l} = (1 - \Omega_l) dg_s/g_s \quad \text{and} \quad \frac{dE_c}{E_c} = (1 - \Omega_c) dg_c/g_c \tag{18}$$

In these equations, the change in leaf (E_l) and canopy (Ec) transpiration due to a change in stomatal conductance g_s and canopy conductance g_c is estimated. Ω_l and Ω_c are the *leaf and canopy decoupling factors*, respectively. This variable describes the degree of coupling of canopies to the atmosphere by depicting how closely the VPD of the leaf surface is related to the air outside the leaf boundary layer. It is a dimensionless value between 0 and 1 that depends on the temperature and the size of the conductance (as they are sites of water evaporation) and the conductance of the leaf boundary layer (which defines the VPD gradient near the leaf surface) (Jarvis and McNaughton 1986).

If Ωl/c → 1, the conditions at the leaf surface are completely decoupled from the air conditions outside the leaf boundary layer, that is, $\text{VPD}_{\text{leaf/canopy}}$ and VPD_{amb} are decoupled. Under these conditions, there is no effect of stomatal or canopy conductance on transpiration. Stomatal conductance regulates the VPD of the leaf surface, but not transpiration. Transpiration is regulated by the joint effect of net radiation, temperature, the conductance ratio of the foliar boundary layer of the two leaf surfaces (adaxial and abaxial), wind speed, the VPD_{env} (external to the leaf boundary layer).

In contrast, when $\Omega_{l/c} \rightarrow 0$, $\text{VPD}_{\text{leaf/canopy}}$ equals VPD_{env}, the conditions at the leaf surface are fully coupled to the air conditions outside the leaf boundary layer. In this case, the stomatal closure regulates transpiration. At intermediate values of $\Omega_{l/c}$, there is an intermediate control of stomatal conductance in transpiration. If the value of $\Omega_{l/c}$ decreases from 1 to zero, the stomatal conductance control gradually increases. Therefore, transpiration will be regulated by the joint effect of stomatal conductance, net radiation, temperature, conductance ratio of the foliar boundary layer of the two leaf surfaces (adaxial and abaxial), wind speed, and VPD_{env} (Jarvis and McNaughton 1986, Marin and Angelocci 2011, Nassif et al. 2014, Marin 2021).

In the same way, if there is an increase in the sensitivity of transpiration to the control of g_s or g_c, the rate of evapotranspiration will be called *imposed evapotranspiration* ET_{imp}. In contrast, if $\Omega_{l/c}$ goes from zero to 1, the sensitivity of transpiration to changes in *gs* or total *gc* is very low. In this case, the evapotranspiration is called *equilibrium evapotranspiration* ET_{eq} (Jarvis and McNaughton 1986, Marin and Angelocci 2011, Nassif et al. 2014, Marin 2021). Therefore, the equation for the dominant mechanisms driving evapotranspiration in terms of surface-atmosphere coupling is Eq. 19:

$$ET = ET_{eq} + (1 - \Omega_c) ET_{imp} \tag{19}$$

This indicates that, at the leaf and crop scale, the evapotranspiration response to changes in conductance depends on the Ω factor (Jones 1990). It is important to notice that Ω_c (canopy) will always be larger than Ω_l (leaf) (Jarvis and McNaughton 1986).

Authors such as Jarvis and McNaughton (1986) and Jones (1990) have reported some typical and unique values for different canopies of unstressed covers such as conifers, tomato, oats, cotton, potatoes, beans, strawberries, citrus, among others. However, these values were calculated for the entire canopy, from measurements of *gs*, or estimated in the mixed layer. More recently, Marin et al. (2001), Marin and Angelocci (2011), Nassif et al. (2014) and Marin et al. (2016) obtained Ω determinations from *gs* measurements through the canopy in exposed and shaded leaves in the upper, middle, and lower part of the canopy throughout the day between 9 and 4 p.m. in *Citrus latifolia Tanaka* trees, sugarcane, and several other crops. In these studies, the *gs* values were expressed as the canopy resistance to vapor diffusion (*rc*) and the decoupling factor (Ω) was calculated using the expression of Jarvis and McNaughton (1986) (Eq. 20):

$$\Omega = \frac{1}{1 + \left[\left(\frac{2rc}{(\frac{s}{\Upsilon} + 2)}\right)\right] * ra} \tag{20}$$

in which: *ra* = the aerodynamic resistance of the canopy; ϒ = the psychrometric constant.

An alternative equation of the equation is Eq. 21:

$$\Omega = \frac{ra}{1 + \left[\left(\frac{\Upsilon}{s + \Upsilon}\right)\right] * rc} \tag{21}$$

Equations 20 and 21 show that the decoupling factor (Ω) is a function of *rc* (1/*gc*) and *ra* (1/*ga*); if *rc/ra* is low, Ω will be close to 1, and if *rc/ra* is high, Ω will tend to zero. This indicates that Ω is an indicative of the control of these resistances on the evapotranspiration of vegetation. Therefore, the dynamics of vapor transport can be understood by studying Ω.

Structural context of Ω

The decoupling factor (Ω) is not considered a fixed canopy characteristic (Spinelli et al. 2016, 2018), as it depends on environmental conditions, canopy characteristics, planting arrangements and density, and even plot size (Jones 1990). Within the same canopy, there may be Ω variations, since, along the different strata, there is diversity in leaf distribution, leaf area, leaf density, stomatal density, as well as temperature gradients, VPD and wind speed generated by microenvironments within the canopy (Jarvis and McNaughton 1986). Ω is also highly dependent on leaf area index (LAI).

Spinelli et al. (2018) reported that in *Prunus dulcis* high LAI was determinant of higher Ω values, and that only when senescence caused a fall in LAI a decrease in Ω was observed. The Ω also varies with the time of the day. Köstner et al. (1992) reported large variations in the daily pattern in forests, and Nassif et al. (2014) reported a daily variation between a range between 0.2 and 0.7 in sugarcane during the wet season. Ω has also been shown to depend on wind speed and its effect on *ra*, as well as on temperature and its relationship with the vapor pressure (Monteith and Unsworth 2013). These microenvironmental conditions, canopy characteristics, time of day, and environmental conditions make up what is called the *structural context* in which a canopy, plant, or leaf is found (Jarvis and McNaughton 1986).

Other factors such as the presence of windbreaks cause decoupling conditions even in rough crops (Jones 1990). Because of windbreaks, this can decrease crop boundary layer conductance (Jarvis 1985). Consequently, it could be said that the variations in Ω are due to the diversity of *structural contexts* within a canopy of a vegetation cover. This indicates that there are places in the canopy or crop where stomatal control of evapotranspiration predominates and others where evapotranspiration is controlled by the radiative environment and net radiation (Jarvis 1985, Jarvis and McNaughton 1986, Spinelli et al. 2016, 2018, Sutherlin et al. 2019).

Decoupling factor Ω dynamics under water deficit

The relationship between water availability and degree of coupling is currently well-known (Jarvis and McNaughton 1986, Sutherlin et al. 2019). Jarvis and McNaughton (1986) observed an increase in coupling ($\Omega \rightarrow 0$) because of water deficit, since the most coupled canopies are more controlled by stomatal conductance and, therefore, by fluctuations of water in soil. Other researchers have reported the increase in the canopy resistance and a decrease in aerodynamic resistance that cause a greater coupling during water deficit events (Aires et al. 2008, De Kauwe et al. 2017, Ferreira 2017, Paulino Junior et al. 2017, Silva et al. 2017, Spinelli et al. 2018, Sutherlin et al. 2019, Alves et al. 2022). Khatun et al. (2011) also found this increased coupling because of water stress in Asian forests. Rana and Katerji (1998) reported that in sorghum canopies under water limited conditions the greater coupling caused evapotranspiration to depend only on canopy resistance (*rc*). In contrast, when there is an increase in soil water content (SWC) and LE, there is an increase in the values of Ω, which indicates a positive correlation between SWC and LE with Ω. In other words, increases in LE occur with a more uncoupled condition ($\Omega \rightarrow 1$) because of lower water deficit thanks to higher SWC (Sutherlin et al. 2019).

During the periods with limiting soil moisture or water deficit, plants reduce the stomatal conductance (g_s) (higher *rc*) due to the canopy experiencing a larger saturation deficit (high VPD) and high temperature (Aires et al. 2008; Alves et al. 2022). In this condition, Ω approaches 0, being those low values an indicative that evapotranspiration is strongly controlled by VPD and g_s (Jarvis 1985, Aires et al. 2008, Ferreira 2017, Alves et al. 2022). The high coupling to the atmosphere in response to high VPD causes higher canopy resistance (*rc*), a condition that drastically reduces transpiration and canopy evapotranspiration. This high control of stomatal conductance prevents the excessive losses of water, maintain essential metabolic activities, and minimize dehydration caused by high demand of the atmosphere (Jarvis 1985, Jarvis and McNaughton 1986, Spinelli et al. 2016, 2018, Alves et al. 2022).

Without great limitations or fluctuations of water in the soil, a canopy can have a greater advantage if it increases the decoupling ($\Omega \rightarrow 1$), since the transpiration is not affected by the stomatal conductance and the water content in the soil (Sutherlin et al. 2019). When soil moisture decreases, the lower water available and higher VPD could cause mortality in vegetation. Therefore, a canopy could have greater advantage in situations of water deficit if it starts to increase coupling ($\Omega \rightarrow 0$), since it would have greater control over water losses by increase surface resistance and the stomata close to retain water (Aires et al. 2008, Sutherlin et al. 2019, Alves et al. 2022). However, under severe water deficit, there is a dramatic decline in transpiration rate as a result of absolute stomatal closure, whatever the value of Ω (Jarvis 1985).

But *how much should the conductance change to restrict transpiration under water deficit?* Jarvis and McNaughton (1986) states that, in a crop or canopy regions with $\Omega \rightarrow 0$ value (in well-watered conditions), more sensitive reductions in evapotranspiration occur in response to stomatal closure induced by water deficit (Jarvis 1985) and a *smaller change in conductance is required to restrict evapotranspiration* (due to the dependence of E on *gs*). Therefore, in canopies naturally coupled (due to its *structural context*), water deficit has more impact on evapotranspiration reduction (Ferreira 2017).

In $\Omega \rightarrow 1$ situation, a large decrease would be required in stomatal conductance or a large increase in canopy resistance to restrict evapotranspiration because transpiration is not very sensitive to changes in conductance and it is mainly controlled by net radiation. Therefore, as the Ω decrease when water deficit increases, having a decoupled ($\Omega \rightarrow 1$) canopy as high as possible makes that the impact in evapotranspiration is as low as possible when stomata close (lower *gs*) or canopy resistance (*rc*) increase (Jarvis 1985, Ferreira 2017, Spinelli et al. 2018). This low sensitivity of transpiration to changes in *gs* and *rc* indicates that trying to control leaf water potential by manipulating conductance is ineffective. This is one of the reasons why anti-transpiring products have not good results when $\Omega \rightarrow 1$ (Jones 1990) It could be indicated that, in those circumstances that predispose a predominance of stomatal control of transpiration (low Ω values), evapotranspiration is more sensitive to large changes in soil water content.

The degree of coupling could help to identify the capacity of canopy/crop to reduce excessive water losses under water deficit

The plant's primary necessity is to maintain its water content. In this sense, plants evolved adaptations to survive in a much more coupled environment through developing control mechanisms like stomatal regulation on transpiration. However, such mechanisms are not as effective in a decoupled crop canopy (Jarvis 1985). Indeed, the potential for water conservation is greater in the more coupled canopies to the atmosphere than in decoupled ones (Fereres and Soriano 2007, Spinelli et al. 2018).

The Ω could be functional to determine the sensitivity of evapotranspiration to canopy resistance during water deficit, as demonstrated by Spinelli et al. (2016, 2018) in *Prunus dulcis*. On the other hand, there are certain conditions or structural context of the vegetation that are typically better able to reduce water losses under drought. A decoupled condition means that the canopy/crop can minimally control its transpiration rate via stomatal regulation (Jarvis 1985, Aires et al. 2008, McNaughton and Jarvis 1991, Alves et al. 2022, Spinelli et al. 2018). Even under water deficit, stomatal closure response has a low impact on the reduction of evapotranspiration, and a large increase in canopy resistance may result in a marginal reduction in transpiration (Spinelli et al. 2016, 2018). Therefore, a *structural context* of canopy or crop in which uncoupled regions predominate will be less able to reduce evapotranspiration and avoid water losses under water deficit conditions (Spinelli et al. 2018). On the other hand, in a highly coupled conditions, canopy resistance control is higher and able to reduce the evapotranspiration because stomatal closure immediately limits the excessive losses of water. Therefore, a *structural context* in which more coupled regions predominate will have a high capacity to reduce evapotranspiration and maintain a water-saving strategy under water deficit conditions.

Linking the decoupling factor (Ω) with CO_2 exchange

In conditions of water deficit, the closure of the stomata is the first and main mechanism that limits the loss of water. The cost of stomatal closure is a lower permeability of the leaves to CO_2, which limits the assimilation of carbon (Brodribb and Holbrook 2003, Nadal-Sala et al. 2021). At the beginning of water stress, the decrease in photosynthesis is caused by stomatal limitations (Mafakheri et al. 2010, Kamanga et al. 2018), due to the diffusive resistance of the stomata to the entry of CO_2. Stomata close rapidly, resulting in decreased transpiration and net photosynthesis caused by decreased supply and diffusion of CO_2 to carboxylating enzymes (Flexas and Medrano 2002, Galmés et al. 2007, Li et al. 2007, Mafakheri et al. 2010). With the progress of water deficit and water stress, the absorption of CO_2 is mainly limited by non-stomatal limitations caused by the reduction of mesophyll conductance and photochemical and enzymatic limitations (Galmés et al. 2007, Varone et al. 2012).

As previously indicated, the degree of coupling increases under conditions of water deficit, and such coupling indicates greater control of evapotranspiration by stomatal conductance as a strategy to limit water losses. However, this also indicates lower carbon assimilation. In a decoupled canopy, the impact of increasing *rc* over evapotranspiration is low, but it causes stomatal limitations to photosynthesis. However, the high VPD and the low SWC on which the increase in coupling occurs for reducing evapotranspiration and minimizing excessive water loss cause metabolic damage and effects on the plant's primary metabolism related to non-stomatal limitations to photosynthesis. Therefore, the increased coupling under water deficit is directly associated with stomatal limitations and non-stomatal limitations from plant water stress.

From another point of view, in a decoupled canopy under well-watered conditions, evapotranspiration works as an equilibrium evapotranspiration ET_{eq}, which depends only on available radiation. However, under water deficit, when *rc* increases as a result of an increase of coupling, evapotranspiration starts to work at an imposed evaporation rate ET_{imp}, which depends on the saturation deficit and *rc* only. This means that, when in a decoupled canopy evapotranspiration works at an imposed rate, at the same time, the carbon assimilation is limited by both stomatal and non-stomatal limitations to photosynthesis. Therefore, Ω allows not only to know if evapotranspiration works at ET_{eq} or ET_{imp}, or if canopy increases its control over water vapor flux but recognized possible stomatal and non-stomatal limitations at the ecosystem level that affects CO_2 assimilation.

Beyond this, the impact on carbon exchange associated with the degree of coupling could be studied in terms of carbon assimilation/transpiration relation or water use efficiency (Spinelli et al. 2016, 2018). It is generally accepted that, under water deficit, the induced stomatal closure must increase water use efficiency (Rouhi et al. 2007, Spinelli et al. 2016, 2018). However, in a decoupled canopy stomatal closure may restrict photosynthesis more than it restricts transpiration (Jarvis 1985, Jarvis and McNaughton 1986, Spinelli et al. 2016, 2018). In consequence, water use efficiency could be lower compared to more coupled canopies. A proposed explanation is that, in an unstressed decoupled canopy, *rc/ra* is low, which means that the stomatal-canopy resistance is relatively unimportant compared to the larger aerodynamic resistance (Nassif et al. 2014, Ferreira 2017, Spinelli et al. 2016, 2018). However, under water deficit conditions, a canopy gets more coupled by *rc* increases, which causes inherent limitations to CO_2 assimilation. Furthermore, *ra* decreases, but the aerodynamic resistance for CO_2 is higher than for water vapor due to the excess resistance for CO_2 (Steduto and Hsiao 1998), which could cause additional limitations for CO_2 fluxes from the turbulent activity of the surface boundary layer.

Considering the points discussed, we agree with Steduto and Hsiao (1998): "The degree of coupling between the plant canopy and the atmosphere characterizes the extent to which stomatal and canopy conductance may control water vapor and CO2 exchange". Although forests, tree canopies, and tall, rough vegetation are generally considered more closely coupled than pastures or low-growth crops (Jarvis and McNaughton 1986, Köstner et al. 1992, Rana and Katerji 1998, Spinelli et al. 2018), we try to summarize characteristics that depict *structural context* predisposing coupling or decoupling conditions that could indicate the capacity of canopy/crop to reduce excessive water losses and maintain a high assimilation/transpiration relation under water deficit. Table 1 indicates some characteristics that could predispose crops to higher/lower coupling conditions.

Table 1. Structural context of Ω which determines the capacity of canopy/crop to reduce excessive water losses and maintain a high assimilation/transpiration relation under water deficit.

Low Ω High capacity of canopy/crop to reduce excessive water losses, higher water use efficiency	High Ω Low capacity of canopy/crop to reduce excessive water losses, lower water use efficiency
• Low leaf area index; • Canopy with small leaves; • Hypostomatic leaves; • Tree-like canopy; • Senescence; • Leaves more exposed to the wind, from the periphery; • Spaced crops; • Crop edges; • Sunrise and sunset.	• Leaf area index large, or increasing; • Leaves are large, the larger the blade, the more decoupled it is; • Amphiestomatic leaves; • Low, smoother canopies; • Areas exposed to low wind speed; • Continuous canopies; • Hours close to noon; • Windbreaks around fields.

Source: adapted from Jarvis and McNaughton (1986).

Decoupling indicates low sensitivity of transpiration to canopy resistance. This means that, under mild or moderate water deficit events, the stomatal closure, and the increase in the resistance of the canopy (as the first biological response) will not have control over the transpiration, and indirectly over the leaf water potential. This condition causes a low water use efficiency due to the increase in canopy resistance and has a greater restriction in the carbon fluxes than for water vapor. For these reasons, a decoupling condition could be disadvantageous when facing water deficit conditions.

CONCLUSION

Nowadays, we know that the coupling level increases under conditions of water deficit, causing the evapotranspiration to depend only on the resistance of the canopy (*rc*), and this increased coupling could be associated with stomatal limitations of photosynthesis, mainly in presence of mild and moderate water deficit. However, the impact of this greater coupling on CO_2 exchange between canopies with different Ω values is still not well understood.

From the central work of Jarvis and McNaughton (1986), the decoupling coefficient Ω is a basic measure of the degree of the aerodynamic coupling between plants and the boundary layer. However, its interpretation could go beyond the description of the characteristics of the land surface and the partition between equilibrium or imposed evapotranspiration.

This paper shows that it is possible to delineate a *structural context* that predisposes high Ω values and a low capacity to get into a water-saving strategy under water deficit conditions. A decoupled canopy has an imbalance in the restrictions of carbon and water fluxes by increases in canopy resistance, being greater for carbon fluxes and having a potentially large impact on gross primary productivity. This decoupling condition could be disadvantageous under water deficit conditions. Therefore, in low and smooth canopies, it is important to accurately determine the switch between imposed and equilibrium evapotranspiration and the impact on water use efficiency. This gains relevance for future research in irrigation management related to deficit irrigation in high LAI crops which seeks to impose limited but not severe stress.

Through the analysis of Ω, the environmental controls of evapotranspiration and gross primary production fluxes under the contrasting soil water availability could be studied. Ω and its underlying theory could give new information about carbon–water interactions. Future studies could be developed to study temporal scales of water and carbon fluxes interactions, and the intrinsic link between carbon and water fluxes through stomatal conductance/canopy resistance at the ecosystem level, as well as at the leaf level.

AUTHORS' CONTRIBUTION

Conceptualization: F. E. Martínez. M. and Marin, F. R.; **Methodology:** F. E. Martínez. M.; **Formal Analysis:** M. E. Martínez. M.; **Writing – Original Draft:** F. E. Martínez. M.; **Writing – Review and Editing:** Marin, F. R.

DATA AVAILABILITY STATEMENT

All dataset were generated and analyzed in the current study.

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