Optimal stomatal behaviour under stochastic rainfall

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HIGHLIGHTS

- We predict response of stomatal opening to soil water level under random rainfall.
- We optimise stomatal behaviour for the highest long-term average carbon gain.
- This model captures general features of stomatal response to environment.
- However, notable discrepancies suggest additional factors also shape this response.

ABSTRACT

Vegetation CO_2 uptake is always accompanied by water loss. The balance in this gas exchange is controlled by the stomata, through which CO_2 and water vapour diffuse between the leaf and the atmosphere. The optimal stomatal behaviour theory proposes that vegetation should optimise its stomatal behaviour such that, for given water availability, photosynthesis is maximised. In this paper, we optimise stomatal conductance as a function of soil water content for the maximum expected value of photosynthesis rate. This optimisation process is considered under stochastic rainfall. The optimal solution is largely shaped by two constraints: the risks of soil water exhaustion and surface runoff, which results in an inverse S-shaped curve of stomatal conductance along the soil water gradient. We derive the optimal functional relationship between stomatal conductance and soil water content under varying rainfall frequency, mean annual precipitation and atmospheric CO_2 concentration. Comparisons with large-scale observational data show that the model is able to broadly capture responses of photosynthesis, transpiration, and water use efficiency along rainfall gradients, although notable discrepancies suggest additional factors are important in shaping these responses. Our work provides a theoretical framework for analysing the vegetation gas exchange under environmental change.

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1. Introduction

As both CO_2 and water vapour pass through the stomatal aperture, plant CO_2 uptake is always accompanied by water loss. The diffusion rates of both gases increase with stomatal conductance (g_s). Consequently, the dynamics of photosynthesis and transpiration are closely coupled by the behaviour of stomata. The physiology of photosynthesis and transpiration are each well studied, but their interdependence and how it responds to the changing environment are not fully understood (Ainsworth and Rogers, 2007). Thus, understanding stomatal behaviour is a prerequisite for reliable predictions of photosynthesis and transpiration.

There have been many efforts to model stomatal behaviour (Damour et al., 2010). These models can be divided generally into mechanistic, empirical, and optimisation approaches. Each of these approaches has advantages and disadvantages. Mechanistic models attempt to predict stomatal behaviour from an understanding of the mechanisms governing their opening (Buckley, 2005; Buckley et al., 2003; Dewar, 2002, 1995). These models can provide insights into how stomata function (Buckley, 2005). However, our knowledge of stomatal mechanisms is imperfect (Mott, 2009; Mott and Buckley, 1998; Mott and Peak, 2007), meaning that such models can currently only capture some aspects of stomatal behaviour. In addition, mechanistic models of plant function usually require many parameters to describe the processes, few of which can be estimated from available data (Dewar et al., 2009).

Many empirical models of stomatal conductance have been proposed (Ball et al., 1987; Jarvis, 1976; Leuning, 1995). These models have been developed from experimental observations in a range of environmental conditions and C_3 plant species. Many of these models follow a so-called 'Ball-Berry' formulation in which

g_s is linked to net photosynthesis rate (A) under given atmospheric CO_2 concentration (c_a) and vapour pressure deficit (D). These models are widely used as they are straightforward to parameterise and easy to incorporate into other models of plant function. The downside to such empirical models is that, without any mechanistic understanding or theoretical explanation of stomatal behaviour, the model parameters and their relationship with plant physiological traits and environmental conditions cannot be generalised. Such models provide predictive power but little biological insight.

Optimisation models provide a third means to model stomatal behaviour. Plants appear to actively regulate stomatal opening (Hari et al., 1999; Katul et al., 2010), highlighting the 'regulatory' role of stomata in balancing the need for photosynthetic CO_2 uptake against the need to control water loss (Sperry, 2000; Sperry et al., 2002a). This observation opens the possibility for models to identify the stomatal behaviour that most benefits the plant. In this spirit, Cowan and Farquhar (1977) proposed that natural selection should favour stomatal behaviour that maximises net carbon gain (photosynthesis, A) for a fixed amount of water (transpiration, E). Mathematically, this top-down approach aims to minimise.

$$E - \lambda A,$$

with respect to g_s, where λ is a Lagrange multiplier. This leads to the following optimisation constraint:

$$\frac{\partial E}{\partial A} = \lambda,$$

where λ is equivalent to the constant marginal water cost of plant carbon gain (mol H_2O mol^{-1} CO_2). The optimal theory of stomatal behaviour represents an alternative approach that may allow us to understand why stomata are controlled as they are, as it requires far fewer parameters while still providing solution with a top-down explanation. This theory has been successfully implemented in global vegetation models (Bonan et al., 2014; De Kauwe et al., 2015).

In this paper, we extend this optimisation theory to consider optimal stomatal behaviour when water availability is not fixed, but rather is determined by the rainfall regime. We assume that vegetation should maximise its long-term average photosynthesis rate. The balance in gas exchange is especially essential when the supply of water is limited. Thus, to understand the 'regulatory' role of stomata, we optimise g_s as a function of soil water content. The quantitative dependence of g_s on soil water content will be a result of the optimisation. Similar work has been done by Mäkelä et al. (1996). They applied this optimisation theory to a highly simplified situation – a single dry down. In this well-defined environment, they predicted the optimal functional relationship between g_s and soil water content quantitatively. Their results explicitly show how vegetation will adjust its water consumption rate during soil drying for maximum total carbon gain. However, due to the unrealistic single dry-down assumption, it is not clear if their conclusions can be widely applied.

Our approach, unlike that of Mäkelä et al. (1996) considers an infinite number of dry downs. Stomatal behaviour is optimised under stochastic rainfall (i.e., rainfall is treated as a stochastic process). Both the occurrence and depth of rainfall events are random. By following Rodriguez-Iturbe et al. (1999), we first derive the probability density function (PDF) of soil water content. Then, the optimal stomatal behaviour can be identified by maximising the expected value of photosynthesis rate. We demonstrate the derivation of this optimal stomatal behaviour and

compare the predicted optimal behaviour against a range of global datasets.

2. Methods

In brief, the optimal stomatal regulation under stochastic rainfall is found in two steps: deriving the probability distribution of soil water content and then maximising the expected value of photosynthesis rate ($\bar{A}$). Following Rodriguez-Iturbe et al. (1999), the probability density function (PDF) of soil water content is derived from the stochastic process of rainfall based on the soil moisture balance equation (Eq. (2)). Then, for any given stomatal behaviour, the corresponding $\bar{A}$ can be calculated. The optimal stomatal behaviour can be found by maximising $\bar{A}$.

2.1. Deriving the probability density function of soil water content

Following Rodriguez-Iturbe et al. (1999), we derive the probability density function of soil water content (Eqs. (3) and (4)), which describes the probabilistic behaviour of soil water content, based on the soil moisture balance equation (Eq. (2)).

We treat the soil as a simple one-layer reservoir. Soil water is intermittently filled by rainfall events while its loss occurs via only vegetation transpiration and surface runoff. All the other common loss terms, such as deep infiltration, soil evaporation, and canopy interception, are ignored for simplicity. We consider the relative soil moisture, w (dimensionless), vertically averaged over the rooting zone of depth Z (m), as the state variable describing the soil moisture dynamics. We define w as 1 when soil is saturated and as 0 at the permanent wilting point. We further assume that vegetation transpiration stops at the permanent wilting point. This is just a preliminary attempt to prevent vegetation from xylem cavitation, which happens when water potential in the soil-leaf continuum drops too low (Sperry, 2000; Sperry et al., 2002a). As a result, w can never drop below 0.

We assume that the canopy is well coupled to the atmosphere so that the vegetation transpiration rate, E, can be described by Fick's laws of diffusion

$$E(g_s(w)) = E(w) = \frac{lLp}{nZ}Dag_s(w) = hDg_s(w); \quad h = \frac{lLp}{nZ}a \qquad (1)$$

where l (m^2 mol^{-1}) converts unit typically used for stomatal conductance, g_s (mol m^{-2} s^{-1}), to unit consistent with the time derivative of w (i.e., s^{-1}); L is the constant leaf area index (m^2 m^{-2}); a is the ratio of the diffusivities of water vapour and CO_2; D is the vapour pressure deficit (mol mol^{-1}); $g_s(w)$ represents stomatal behaviour, which defines stomatal conductance, g_s, as a function of w; p (second per day) is the effective day length. Importantly, the functional form of $g_s(w)$ is not given as a prior here, but the outcome of the optimisation approach described below. However, as we have assumed that transpiration stops at $w = 0$, it follow$_s$ that $g_s = 0$ at $w = 0$ as well, which can be considered as a boundary condition.

Following Rodriguez-Iturbe et al. (1999), we idealise rainfall as a Poisson process with frequency k (day^{-1}). Each rainfall event is assumed to carry a random depth with exponential distribution of mean $1/\alpha$ (m). The soil water capacity (i.e., $w = 1$) is the product of soil porosity, n (dimensionless), and the depth of soil, Z (m). Both n and Z are assumed to be constant over time and space. To be consistent with w, the average rainfall depth $1/\alpha$ is normalised as a relative measurement, $1/\gamma$, where γ (dimensionless) equals α/nZ. Infiltration from rainfall leads to an increment in w. However, the amount of infiltration from each rainfall event is not always the same as the rainfall depth. This is because when rainfall depth exceeds the available soil water storage (i.e., $1 - w$), the extra