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ON THE CONSERVATIVE BEHAVIOR OF BIOMASS WATER PRODUCTIVITY[1]

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INTRODUCTION

Food production and water use are two closely linked processes. As the competition for water intensifies worldwide, water in food production must be used more efficiently. Of the different steps in water use in the crop production process, the most fundamental is the exchange of water lost by transpiration for the assimilation of carbon dioxide. The net gain of carbon and energy by the plant in this process then leads to the production of biomass. It turned out that for biomass production, the efficiency of water use is relatively constant after the variation in two key environmental factors, evaporative demand of the atmosphere and air carbon dioxide concentration, are accounted for by normalization.

This conservative behaviour has been analyzed and discussed in detail several times in the past half century (e.g., de Wit, 1958; Tanner and Sinclair, 1983). In light of the urgent need to answer the question of how much the efficiency of water use in agriculture can be improved, and to further analyse the implications for agricultural systems sustainability (e.g., Fereres et al., 1993), we are revisiting the issue here to see how conservative biomass water productivity is and the extend of possible improvements.

The conceptual basis for the conservative behaviour is reviewed and the ways to normalize for evaporative demand and carbon dioxide concentration illustrated. It is hoped that this discourse will help to focus better the potential means to improve the efficiency of water use, and also lead to a simple means of modelling crop productivity based on water use.

THEORETICAL FRAMEWORK AND EXPERIMENTAL EVIDENCE

The focus of this note is biomass water productivity (WP_b), also referred to as biomass water use efficiency (WUE_b) in the literature. From an agronomic standpoint, it is the amount of crop biomass output per unit of water consumed in transpiration by the crop and evaporation from the soil (together, evapotranspiration). From a physiological standpoint, only the water transpired is considered because evaporation from the soil is not in exchange for carbon assimilated. Here, WP_b is defined as the aboveground dry matter (kg m^{-2}) produced per unit of water transpired (m^3 m^{-2}, or mm). Therefore, the units of WPb are g m^{-2} mm^{-1} or g biomass per m^3 of water transpired (g m^{-3}). Only above-ground biomass is considered in our discussion as for most crop species, except root crops, only a small portion of the total biomass is in roots and because there is a general homeostatic growth response towards a near constant root:shoot ratio.

In developing the theoretical background and the appropriate framework for analyzing the constancy of WP_b, we follow a stepwise scaling-up approach, from leaf to whole crop field, in the analysis of the two basic processes involved, water transpiration (T) and net carbon assimilation (A), and its conversion to biomass.

At the leaf level, we define photosynthetic water productivity (WP_p) as the ratio of leaf net carbon dioxide assimilation (A_l) to leaf transpiration (T_l), both expressed as flux rates on a leaf area basis

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(μmol m^{-2} s^{-1} for A_l, and mol m^{-2} s^{-1} for T_l) and directly proportional to the gas gradient (CO_2 for A_l and vapour for T_l) and inversely proportional to the resistance encountered along the path (e.g., boundary layer, stomatal, metabolic). Plants have apparently evolved physiological mechanisms to keep the importation (from ambient air to leaf interior via stomata) and depletion (from leaf interior to the cellular carboxilating sites) of CO_2 in balance most of the time so that the leaf-internal CO_2 concentration (c_i) is conservative. This implies that photosynthetic capacity and stomatal opening are coordinated and operate in concert in the leaf. This suggests that when one of the two opposing processes, either the importation or depletion, is perturbed, the other adjusts with some lag to keep the system in balance and c_i nearly constant. There has been substantial experimental evidence showing that for many species, c_i tends to remain constant under a range of conditions including temperature, radiation, water and salinity stresses, especially when the stress develops gradually, as it generally occurs in the field. The ample evidence of the tendency of c_i to remain constant at a constant ambient CO_2 concentration (c_a), i.e. a constant c_i/c_a ratio, is an indication that stomata perform at the leaf scale in a manner that leads to a constant WPp.

At the canopy level, we define, canopy photosynthetic water productivity (WP_p^c) as the ratio of canopy net carbon dioxide assimilation (A_c) to canopy transpiration (T_c). As we scale up from leaf to canopy, there are additional features that must be taken into account because the consideration is now on a land area basis instead of leaf area basis. The extent of radiation capture by a crop depends on the amount of leaf area, on the geometric arrangement of the leaves within the canopy, as well as on the angle and intensity of incident radiation. As is the case at leaf level, the process of T_c shares the same source of captured energy as A_c. Of the total captured solar radiation, though, only the fraction that is photosynthetically active (PAR) is effective in CO_2 assimilation, while the whole spectrum is used for transpiration. PAR, however, is a fairly constant fraction of the incident solar radiation as is the ratio of absorptance of PAR to non-PAR radiation for the leaves of many species. Consequently, any change in the amount of radiation captured by the canopy would affect in a similar way A_c and T_c so that also WP_p^c tends to remain constant.

At crop field level, the variable we want to focus on is the biomass water productivity (WP_b). Changing from A_c to biomass requires an analysis of the respiratory costs in relation to A_c and of the chemical composition and carbon cost of the biomass. A constant WP_b, then, would be expected only if the relationship between assimilation and respiration is also linear. This seems the case, provided that the composition of biomass does not change significantly. More and more evidence is appearing indicating an approximate fixed ratio of assimilation to respiration for crops (e.g., Albrizio and Steduto, 2003) where the reproductive organ has no high protein and/or oil content, such as soybean and sunflower. Constant WP_b seems to be the case even under varying environmental conditions. Although WP_b addresses situations where only aboveground biomass is considered, constant WP_b has also been described for root and tuber crops.

NORMALIZATION OF BIOMASS WATER PRODUCTIVITY FOR CLIMATE

To extrapolate water productivity values between climatic zones and between atmospheric CO_2 statuses, there is a need to normalize them for the climate, specifically, for the evaporative demand of the atmosphere and for the atmospheric CO_2 concentration, respectively. Ways of normalizing WP_b for the evaporative demand of the atmosphere (Steduto and Albrizio, 2005) and for the atmospheric CO_2 concentrations (Hsiao, 1993) are expressed by Eq. (1) and Eq. (2), respectively, where WP_p^* is the normalized value of WP_b. In Eq. (1), the summation is over a total number of time intervals (n), with i being the running number designating each interval and ti the length of the interval (in days); Biomass denotes the gain in biomass from the beginning to the end of the summation period. In Eq. (2), the subscript "o" indicates the reference situation; the summation is over a number of days (n); Δw is the water vapour concentration difference between the leaf intercellular air space and the atmosphere.

$$WP_b^* = \frac{\text{Biomass}}{\sum_{i=1}^{n} t_i \left(\frac{T_c}{E_0}\right)_i} \qquad (1)$$

$$WP_b^* = WP_{b,o} \frac{\sum_{i=1}^{n} (c_a)_i}{\sum_{i=1}^{n} (c_{a,o})_i} \frac{\sum_{i=1}^{n} (\Delta w_o)_i}{\sum_{i=1}^{n} (\Delta w)_i} \qquad (2)$$

CONCLUSION

The implications that the near constancy of WP_b has in the improvement of water productivity in agriculture cannot be overemphasized. The presented stepwise approach from leaf to the whole crop has provided a conceptual and theoretical framework to explain the basis for the constancy of biomass water productivity. An important implication of normalizing biomass water productivity is that it allows the comparison of water productivity data across the globe on equal footing, after accounting for differences due to variations in evaporative demand of the climate, and in atmospheric carbon dioxide concentration when applicable. Such comparisons will reveal more definitively the intrinsic properties of the crop or the management practices that alter such productivity. Most importantly, normalized WP_b will provide a head start in knowing the WP_b values at a new location or new time period when CO_2 concentration is different, whether in the future or in the past. This offers an invaluable tool for modelling purposes, providing an effective way of extrapolating WP_b values between different locations and seasons. Crop modelling based on radiation use efficiency (RUE), in fact, has a limited normalizing capability (Steduto and Albrizio, 2005).

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