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Water use efficiency in perennial forage species: Interactions between nitrogen nutrition and water deficit

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ABSTRACT

Interactions between nitrogen and water may vary between N_2 fixing species and species that rely only mineral soil nitrogen. Here we compared above ground biomass accumulation (W), nitrogen uptake (N), evapotranspiration (ET) of alfalfa (*Medicago sativa* L.) and tall fescue (*Festuca arundinacea* Schreb.) during regrowth periods under contrasting supply of water (irrigated vs non-irrigated) and N (for non-fixing species). Using previously published data, we estimated the dynamics of the two components of ET, evaporation from soil (E) and transpiration (T), in order to analyse the impact of E/T, of the transpiration efficiency (TE = W/T) and the role of crop N nutrition on water use efficiency (WUE = W/ET). In tall fescue, limiting N supply reduced WUE by both increasing E/T ratio and decreasing TE. Water limitation in both alfalfa and tall fescue led to crop nitrogen deficit. This drought-induced N deficiency resulted in a proportional reduction in TE irrespective of the source of N for the plant. We propose that the ratio N/T, representing the apparent N concentration of water transpired by the crop, is relevant for analysing N-water interactions. Comparisons of dynamics of N/T ratio must be done at similar biomass or similar transpiration because N and T are related allometrically.

1. Introduction

Water and N supply are two major limitations in crop production (Sinclair and Rufty, 2012). Recent reviews on the interactions between water and nitrogen (N) highlight the reduction in water use efficiency caused by N deficit and the reciprocal impact of water deficit on the N economy of crops and pastures (Sadras et al., 2016; Sinclair and Rufty, 2012; Gonzales-Dugo et al., 2010). Crop responses to the combination of water and N supply is thus important for evaluating the interactions among crop management, species, cultivar and environment.

Many studies analysed water use efficiency (WUE) as the relationship between biomass or grain yield and evapotranspiration (ET) (Dagdelen et al., 2006; Fischer, 1979; Garafolo and Rinaldi, 2013; Kresovic et al., 2016; Suyker and Verna, 2009; Tolk et al., 1998; Yimam et al., 2015). Separating the components of ET, soil evaporation (E) and crop transpiration (T) (Cooper et al., 1987; de Wit, 1958):

$$WUE = \frac{W/T}{1 + {}^{E}\!/_{T}} \quad (1)$$

highlights that biomass per unit ET (WUE) increases with transpiration efficiency (W/T) and smaller E/T fraction. Further, TE is related to CO_2 assimilation, transpiration, stomatal control of gas exchange, and plant nutritional status (Jones, 2004; Monneveux et al., 2006; Schulze and Hall, 1982), thus providing a solid physiological basis to investigate effects of N on WUE. Methods to separate E and T include statistics (Hanks et al., 1969), modelling (Fandino et al., 2015; Sanchez et al., 2015; Sutanto et al., 2012), microlysimeters (Villalobos and Fereres, 1990), and isotope discrimination (Wang et al., 2015; Yidana et al., 2016).

Nitrogen deficit reduces both (i) the crop leaf area index (LAI, Bélanger et al., 1992a), hence increasing E/T (Ritchie, 1972); and (ii) leaf photosynthesis and radiation use efficiency (RUE, biomass per unit of intercepted radiation) (Bélanger et al., 1992a; Gastal and Bélanger, 1993; Sadras et al., 2016; Sinclair and Muchow, 1999). On the other hand, water deficit can decrease N availability in legumes by impairing N_2 fixation (Durand et al., 1987), and in both legumes and grasses by decreasing availability of mineral N in soil, as mineralisation and N transport from bulk soil to rhizosphere are constrained in dry soil (Hungria and Vargas, 2000; Marino et al., 2007; Serraj et al., 1999). The ratio between N uptake and ET or T has been used to capture N-water interactions, and their effect on water use efficiency (French and Schultz, 1984a; Sadras, 2004; Sadras and Rodriguez, 2010; Sadras

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Nomenclature

Symbols

E (mm) Soil evaporation from the beginning (cutting) to the end of regrowth period
ET (mm) Evapotranspiration from the beginning to the end of regrowth period
E_t (mm) Soil evaporation from the beginning of the regrowth ($t = 0$) until time t
ET_{max} (mm) Maximum ET in the absence of water and N limitations
ET_t (mm) Evapotranspiration from the beginning of regrowth ($t = 0$) until time t
N_{crit} (kg ha^{-1}) Critical n uptake defined as the minimum N uptake for achieving maximum above ground biomass at time t
N_t (kg ha^{-1}) Quantity of nitrogen accumulated in shoot at time t
NNI (unitless) Nitrogen nutrition index calculated as the ratio between N_t and nc corresponding to W_t
PAR_i (MJ) Quantity of PAR intercepted by the canopy
RG_i (MJ) Quantity of global radiation intercepted by the canopy
RUE (g MJ^{-1}) Radiation use efficiency calculated as the ratio between biomass W_t and the cumulative photosynthetically active radiation (PAR_i) intercepted by the crop
T (mm) Crop transpiration from beginning to the end of regrowth period
TE (kg mm^{-1}) Transpiration efficiency estimated as the ratio between shoot biomass W_t and crop transpiration T_t
TE_{max} (kg mm^{-1}) Maximum transpiration efficiency estimated as the ratio between maximum shoot biomass W_m and crop transpiration T_t
T_t (mm) Crop transpiration from the start of regrowth period ($t = 0$) until time t
T_m (mm) Maximum transpiration in the absence of water and N limitations
W (t ha^{-1}) Shoot biomass per unit soil area at the end of the regrowth period
W_m (t ha^{-1}) Maximum shoot biomass per unit soil area in the absence of water and N limitations
W_t (t ha^{-1}) Shoot biomass per unit soil area at time t during regrowth
WUE (kg mm^{-1}) Water use efficiency estimated as the ratio between shoot biomass and evapotranspiration
WUE_t (kg mm^{-1}) Water use efficiency at time t

et al., 2016).

This paper focuses on perennial forage species, and the objectives are to examine the following hypothesis:

1. Does TE vary between seasonal growth cycles, in relation to seasonal variation in growth potential (water and N non-limiting) and climatic conditions?
2. How do crop N status and water availability affect TE? As a consequence, how to use crop N status as a benchmark for comparisons of TE among different crops or growing conditions?
3. Is the ratio between crop N uptake and transpiration useful for analysing interactions between water and N affecting crop growth and transpiration efficiency?
4. Are the water-N relations different according to the main source of N, namely N_2-fixation in legumes or soil mineral N in grasses?
5. To test these hypotheses, we compared tall fescue (*Festuca arundinacea* Schreb.) and alfalfa (*Medicago sativa* L.) for which production is directly linked to shoot biomass.

2. Conceptual framework

We used dynamic accumulation variables recorded during the regrowth of alfalfa and tall fescue: (i) shoot biomass W_t (t ha^{-1}), (ii) N uptake N_t (kg ha^{-1}) and (iii) evapotranspiration ET_t (mm), where the subscript "t" is time (day) since beginning of regrowth (date of cutting). Data were sourced from previous publications (Section 3).

2.1. Separation of soil evaporation (E) and crop transpiration (T)

For annual crops, it has often been assumed that the X-intercept of the regression line between biomass or yield and crop ET accumulated during the growing period is an approximate measure of soil evaporation, and the slope a measure of transpiration efficiency (French and Schultz, 1984a,b; Grassini et al., 2009; Hanks et al., 1969; Sadras, 2005; Sadras and Rodriguez, 2010). In contrast to this seasonal approach, here we focused on the dynamic accumulation of both crop biomass W_t and ET_t during each regrowth period between successive cuttings. Regrowth after cutting features a lag-phase in the W_t-ET_t plot that needs consideration (Fig. 1). Here we used a dynamic analysis based on W_t and ET_t for discriminating E_t and T_t during regrowth.

Just after cutting, i.e. at $t = 0$, as most leaf area has been removed, the proportion of solar radiation transmitted to the soil is high, and, depending on soil surface moisture, soil evaporation can be high while transpiration is low, depending on residual leaf area. As crop LAI increases with time during regrowth, E_t/T_t progressively declines and WUE_t progressively increases.

Plotting W_t versus ET_t for each regrowth period, we can fit a linear regression by assuming that $T_t >> E_t$ and $dW_t/dET_t \approx dW_t/dT_t$ when W_t is sufficiently large. Assuming little variation in both weather and plant N status during the regrowth period, then dW_t/dT_t could be considered as constant, and extrapolation of the W_t vs ET_t regression allows the determination of the X-intercept that estimates soil evaporation. With:

$$W_t = K \times (ET_t - d) \quad (2)$$

where d is the Y-intercept and assuming that

$$ET_t = E_t + T_t \text{ and that } dE_t/dt \ll dT_t/dt \quad (3)$$

then K can be considered as an estimate of transpiration efficiency (TE):

$$W_t = K \times T_t \quad (4)$$

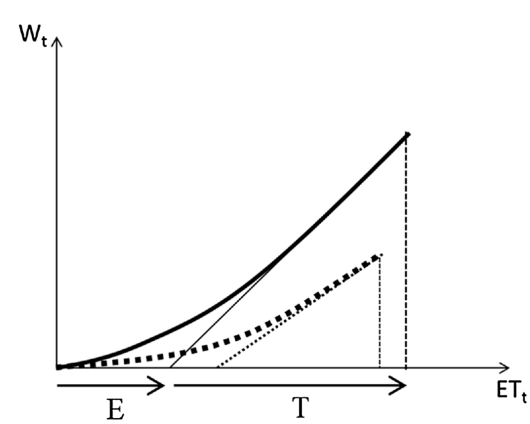

Fig. 1. Diagram of the method for discriminating soil evaporation (E) and crop transpiration (T), and calculating transpiration efficiency (TE) by linear extrapolation of the regression line between biomass accumulation (W_t) and evapotranspiration (ET_t) in perennial pastures. TE is estimated by the slope of regression line (K) and E is estimated by X-intercept. Solid curve represents non-limiting N and water and dashed curve represents limiting N and water.