Europ. J. Agronomy 72 (2016) 91–98

Contents lists available at ScienceDirect

European Journal of Agronomy

journal homepage: www.elsevier.com/locate/eja

Higher forage yields under temperate drought explained by lower transpiration rates under increasing evaporative demand

Pierre Hainaut[a], Thibaut Remacle[a], Christian Decamps[a], Richard Lambert[a,b], Walid Sadok[c,*]

[a] Earth and Life Institute, Université catholique de Louvain, Croix du Sud 2, L7.05.14, 1348 Louvain-la-Neuve, Belgium
[b] Centre de Michamps ASBL, Horritine 1, 6600, Michamps, Belgium
[c] Department of Agronomy and Plant Genetics, University of Minnesota, 411 Borlaug Hall, 1991 Upper Buford Circle, 55108-6026 St. Paul, MN, USA

ARTICLE INFO

Article history:
Received 13 April 2015
Received in revised form 4 October 2015
Accepted 8 October 2015
Available online 27 October 2015

Keywords:
Drought tolerance
Transpiration
Vapor pressure deficit
FTSW
Forage crops
Yield

ABSTRACT

In temperate regions, perennial forage-based cropping systems are expected to face an increasing frequency of summer droughts over the next decades prompting the need for more resilient cultivars. However, most efforts mainly focus on Mediterranean-type environments where the plant survival is often engaged. Under temperate environments, vapor pressure deficit (VPD) is a key component of drought, because its variation alters the crop transpiration rate (TR) and therefore its ability to fix carbon even in well-watered conditions. Despite this knowledge, there is no available data about the diversity of whole-plant TR responses to VPD and soil moisture among key forage crops such as alfalfa, red clover, cock's foot and perennial ryegrass. Further, field-based evidence is lacking regarding the links between TR responses to VPD and yield under drought. Here, we combined experimental approaches characterizing gas exchange responses to VPD and soil moisture at scales that ranged from the growth chamber to the field, where yields were characterized both quantitatively and qualitatively over the course of 2 years on 8 genotypes from the 4 above species. A significant variability in TR responses to increasing VPD and soil water deficit was found among locally-adapted cultivars. More importantly, TR responses to VPD – but not to decreasing soil moisture – were found to be consistently correlated to relative yield performances under drought, in a way indicating that conservative water use under high evaporative demand promoted higher yield outputs. In contrast, yields under drought were unrelated to canopy temperature and leaf gas exchange measured in the field. Further, no link was found between TR responses to VPD and qualitative yield traits such as digestibility indicating that the hypothesized water saving strategy does not improve yield at the expense of forage quality. This study opens the way for future forage breeding and management strategies taking advantage of the diversity of TR responses to drought to implement climate-change resilient forage-based systems.

1. Introduction

In northern Europe and in several temperate regions across the globe, a large segment of the agricultural productivity is based on grassland and herbage systems, which are expected to be exposed to an increasing frequency of late spring and summer droughts in the coming decades, prompting the need for new germplasm and water-saving cropping systems (IPCC, 2014). Currently, several breeding programs are underway for developing drought-tolerant forage crops. Many of these target Mediterranean-type environments where drought is co-occurring with extreme heat events and where the survival of the plant is often engaged (see the review of Volaire et al., 2014). Given that forage-based systems in temperate regions are not expected to experience such severe patterns of drought in the next decades and that improved crop survival is not an economically viable option for such systems, new resilient, locally-adapted forage cultivars are called for (FAO, 2008). These cultivars should be still well adapted to the colder winter and autumn temperature regimes of such environments while being able to minimize the economic impacts of summer water deficits.

An often-overlooked drought component that operates in well-watered conditions is "atmospheric drought" or vapor pressure deficit (VPD). This environmental variable encapsulates the effects of both temperature (T) and relative humidity (RH) and is the main driver of the crop water loss through is transpiration rate (TR, Monteith, 1995). From an agronomical perspective, the response

* Corresponding author. Fax: +1 6126251268.
E-mail address: msadok@umn.edu (W. Sadok).

http://dx.doi.org/10.1016/j.eja.2015.10.002

of the crop TR to VPD is key because it determines its water needs for achieving economically viable yields. In Mediterranean-type environments, a reduced TR above the VPD threshold of 2 kPa was hypothesized to result in substantial sorghum yield gains in south Australia (Sinclair et al., 2005). Such potential yield benefits were confirmed on soybean in the more temperate climate of continental USA (Sinclair et al., 2010). Crucially, the study showed that such reduced sensitivity of TR to increasing VPD only rarely translated into yield penalties in temperate regions.

Another more known drought component that strongly influences TR is decreasing soil moisture or FTSW (for fractions of transpirable soil water). Similarly to TR response to VPD, simulation analyses clearly indicate that conservative genotypes reducing their TR at higher FTSW are more likely to improve yields in rain-fed environments characterized by late-season water deficit (Sinclair and Muchow, 2001; Sinclair et al., 2010).

The potential benefits resulting from such traits led to several studies investigating the genetic variability in TR response to increasing VPD and to decreasing FTSW for economically important species such as soybean (Sadok and Sinclair, 2009), maize (Gholipoor et al., 2013a,b), pearl millet (Kholová et al., 2010a,b) and wheat (Schoppach and Sadok 2012; Schoppach et al., 2014), leading to breeding programs currently aiming at developing new water-saving cultivars. However, despite their much greater diversity, no studies addressed TR response to drought among non-food crops, with the exception of Wherley and Sinclair (2009) who characterized TR responses to VPD of four C_3 and C_4 turfgrass species in the conditions of central Florida. No such data is available regarding economically strategic perennial forage crops such as alfalfa, red clover, cock's foot and perennial ryegrass grown in temperate conditions. Furthermore, given their perennial characteristics, one key question is whether it is possible to identify a beneficial TR response pattern that will consistently appear during the target summer drought window over consecutive years and after several harvests, which are known to alter key whole-plant functions such a gas exchange, carbon and nitrogen metabolisms (e.g., Aranjuelo et al., 2015).

In addition to the above, direct and straightforward links between whole plant TR responses to VPD and actual yield benefits under non-pot, field-imposed agronomic drought remains poorly documented. For instance on soybean, King et al. (2009) found that a drought tolerant soybean line characterized by a limited TR over a VPD threshold of 2.1 kPa exhibited significantly more water at 15 and 50-cm depths than non-drought tolerant genotypes, but such study did not quantify the associated yield benefits. Furthermore, no data is available regarding the potential consequences of TR-based drought tolerance strategies on key qualitative components of yield. If the quantitative yield benefits resulting from such strategies are offset by dramatic decreases in quality, the economic consequences for the farmer can be potentially grave. Such issue is particularly important for forage crops where quality criteria such as digestibility, protein and carbohydrate contents determine not only the direct economic return but also the health of the livestock.

The main objective of this study was to test the hypotheses that (i) TR responses to increasing VPD and decreasing soil moisture are variable among forage species and cultivars widely used in Belgium and northern Europe and (ii) this variation might explain differential quantitative and qualitative yield performances examined under imposed summer droughts in the field over two consecutive years. We addressed these hypotheses by combining a continuum of experimental approaches characterizing gas exchange response to VPD and soil moisture at scales that ranged from the growth chamber to the field and from the single leaf to the whole plant, and by measuring yields qualitatively and quantitatively in the field. We compared the relevance of field-based canopy temperatures and single-leaf gas exchange measurements with gravimetric, whole plant transpiration measurements as potential predictors of yield performance in the field.

Table 1
Species and cultivars used in the study.

Species (common name)	Cultivars	Origin[a]
Dactylis glomerata L. (Cock's foot)	Foly	RAGT
	Greenly	RAGT
Lolium perenne L. (Perennial ryegrass)	Azur	Caussade
	Cangou	Carneau
Medicago sativa L. (Alfalfa)	Alexis	Barenbrug
	Marshal	LG
Trifolium pratense L. (Red clover)	Amos	DLF-Trifolium
	Pavo	DSP

[a] RAGT: Rouergue Auvergne Gévaudan Tarnais; LG: Limagrain; DSP: Delley Seeds and Plants.

2. Materials and methods

2.1. Genetic material

A total of eight genotypes belonging to 4 forage species (*Dactylis glomerata*, *Lolium perenne*, *Medicago sativa*, *Trifolium pratense*) were selected (Table 1). The cultivars were identified based on previous field experiments that revealed adequate growth in the same environment as the one of the present field study.

2.2. Whole plant transpiration response to increasing evaporative demand

The plants were prepared as in Schoppach and Sadok (2012). For each genotype, four seed per pot were sown on February 28, 2013 at a depth of 2.5 cm in 2.5-l polypropylene plastic pots filled with compost garden soil (DCM Corporation, Grobbendonk, Belgium) mixed with 3 g of slow-release fertilizer (9% N – 11% P – 17% K, Scotts, Sint Niklaas, Belgium). In order to allow for drainage, small holes were drilled in the bottom of the pot. The plants were grown in a greenhouse located at the Université catholique de Louvain in Belgium (50°40'N, 4°36'E), regulated for minimum/maximum temperatures of 16 °C and 25 °C respectively and a 14-h photoperiod. The average temperature during growth was 24 °C (day) and 16.1 °C (night) and the average daily VPD was 2.1 kPa. Thirty days after sowing, the pots were thinned to one plant per pot. Plants were watered every 1–3 days and were grown for 75–85 days before the experiments began. On the evening prior to the measurements, each pot was watered to dripping around 17:00 solar time and covered with an aluminum foil to nullify direct soil evaporation. The following morning, the pots were placed inside a walk-in growth chamber (2.5 m × 1.9 m × 1.3 m, Conviron, Winnipeg, Manitoba, Canada) delivering a photosynthetic photon flux density (PPFD) of 515 μmol $m^{-2} s^{-1}$ at the canopy level.

In order to impose a range of VPD level representative of diurnal field conditions, at least six VPD levels (ranging between 0.7 and 3.2 kPa) were targeted for each genotype, with measurements gathered over 2 consecutive days for a given replicate plant. Similarly to natural conditions, variations in VPD were the result of changes in both temperature (increase from 18 to 31.5 °C) and relative humidity (RH decrease from 70 to 29%) (Sadok and Sinclair, 2009; Schoppach and Sadok, 2012). Low RH was achieved by means of 2–4 industrial humidifiers (0.5 l h^{-1}, Defensor 505, Axair AG, Pfäffikon, Switzerland) and high RH was imposed using an industrial dehumidifier (TTK 350 S, Trotec, Heinsberg, Germany) and/or forcing the incoming air through custom-made desiccant-filled screens (Silica Gel Orange, 2–5 mm with indicator, CarlRoth GmbH, Karlsruhe, Germany). During all VPD treatments, four rotating 30-cm diameter electric fans (Proline DKF30, Kesa Electricals, Hull, United Kingdom)