

Water use of selected cover crop species commonly grown in South African fruit orchards and their response to drought stress

Z. Ntshidi ^{a,b,*}, S. Dzikiti ^{a,b,c}, D. Mazvimavi ^b, N.T. Mobe ^{a,b}, Y.P. Mkunyana ^b

^a Council for Scientific and Industrial Research (CSIR), Smart Places Cluster, Stellenbosch, South Africa

^b Department of Earth Science, University of the Western Cape, South Africa

^c Department of Horticultural Science, University of Stellenbosch, South Africa



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ABSTRACT

Cover crops are widely planted in orchards for a variety of reasons. These include suppressing soil erosion, nutrient cycling, phytosanitary purposes, general orchard aesthetics etc. However, there is need to balance these benefits against use of scarce resources such as water and nutrients. Currently no information exists on how different cover crop species use water in orchards and how they cope with drought stress. The aim of this study was therefore to compare the transpiration dynamics of various cover crop types in order to identify species with conservative water use rates. Studied species included: 1) two exotic legumes i.e. Lupine (*Lupinus albus* L.), and Common vetch (*Vicia sativa*), 2) three exotic grasses i.e. Tall fescue (*Festuca arundinacea*), Rye grass (*Lolium perenne*), and Kikuyu grass (*Pennisetum clandestinum*) and; 3) grasses that are indigenous to sub-Saharan Africa i.e. African Lovegrass (*Eragrostis capensis*) and Rhodes grass (*Chloris gayana*). The crops were planted in pots under controlled greenhouse conditions. Transpiration rates were quantified using miniature stem heat balance sap flow gauges and by manual weighing. Drought stress was imposed by withholding irrigation at selected intervals and the responses were quantified through changes in the water relations of the plants. The study showed that exotic legumes had the highest daily water use which peaked at about 2.4 L per square metre of leaf area per day, followed by exotic grasses at 1.5–2.0 L/m²/d. The indigenous grasses used the least water ranging from 0.8 to 1.2 L/m²/d. The indigenous grasses largely displayed an isohydric response to drought stress by maintaining their leaf water status with increasing soil water deficit. The exotic species, on the other hand, showed risk taking behaviour (anisohydry) wherein both the transpiration and leaf water status decreased sharply as drought stress increased. Consequently, some exotic species failed to recover when stress was relieved. From a water use perspective, this study demonstrates that indigenous grass species are more appropriate as cover crops in South African orchards because of their low transpiration rates and the ability to cope with extended periods of water deficit.

1. Introduction

In South Africa as elsewhere in the world, cover crops are commonly planted between tree rows in orchards for various purposes. They are important in maintaining the soil structure (Fageria et al., 2005), encouraging water infiltration (Busscher et al., 1996), reducing soil erosion, reducing mud and dust, and maintaining an acceptable surface for moving farm machinery (Hartwig and Ammon, 2002; Panagos et al., 2015). Cover crops can also enhance soil fertility, e.g. through nitrogen fixation and increasing the organic matter content in the soil (Reicosky and Forcella, 1998; Chen et al., 2003). They also play a role in

suppressing weeds, and hosting beneficial natural organisms that control pests and diseases in orchards (Sarrantonio and Gallandt, 2003; Guerra and Steenwerth, 2012). This in turn results in the reduced use of agrochemicals, mainly pesticides and herbicides that are harmful both to humans and the environment.

Various plant species are often used as cover crops in orchards worldwide. These include both grasses and legumes (Wilson et al., 1982). Fynbos, a sclerophyllous shrub dominated by species of the *Proteaceae*, *Ericaceae* and reed-like *Restionaceae* which is endemic to the Cape Floral Regions (Rebelo et al., 2006), is also being used in some commercial orchards in South Africa (Johan Burger, pers. comm.).

* Corresponding author. Council for Scientific and Industrial Research, Smart Places Cluster, 11 Jan Cilliers Street, Stellenbosch, 7599, South Africa.

E-mail addresses: zntshidi@gmail.com (Z. Ntshidi), sdzikiti@gmail.co.za (S. Dzikiti), dmazvimavi@uwc.ac.za (D. Mazvimavi), tmobe@csir.co.za (N.T. Mobe), ymkunyana@gmail.com (Y.P. Mkunyana).

Table 1

Summary of water use measurements in grasses in different parts of the world.

Species	Measurement method(s)	Water use	Reference	Scale	Country
Tussock grass	Sap flow/gravimetric/gas exchange/modelling	44.4–166.7 mol H ₂ O m ⁻² d ⁻²	Ramírez et al. (2006)	Individual plant	Spain
Prairie grasses	Sap flow	≤4 g/h	Senock and Ham (1995)	Individual plant	USA
Grassland	Bowen ratio energy balance technique	~695 mm/year	Everson et al. (2011)	Stand/catchment	South Africa
Kikuyu grass	Lysimetry	~4.41 mm/d	Van Vuuren (1997)	Stand level	South Africa
Creeping bent grass	Lysimetry	~4.21 mm/d	Van Vuuren (1997)	Stand level	South Africa
Kikuyu grass	Neutron probes (soil water balance)	~775 mm/year	Marais et al. (2006)	Individual plant	South Africa
Buffel grass	Neutron probes (soil water balance)	~782 mm/year	Marais et al. (2006)	Individual plant	South Africa
Bioenergy grass crops	Sap flow	850–1150 mm/season	Erickson et al. (2012)	Individual plant	USA
Perennial Pasture grasses	Neutron probes (soil water balance)	~400 mm/season	Parry et al. (1992)	Individual plant	New Zealand
Turf grass	Crop coefficient	1407 acre feet/year	Shapiro et al. (2015)	Stand	California
Buffalo grass	Crop coefficient	871 acre feet/year	Shapiro et al. (2015)	Stand	California
Legumes	Neutron probes (soil water balance)	266 mm/year	Siddique et al. (2001)	Single plant	Australia
Warm season legumes	Neutron probes (soil water balance)	19.6 kg/ha/mm	Rao and Northup (2009)	Single plant	USA
Cover crops	Neutron probes (soil water balance)	~252 mm/year	Nielsen et al. (2015)	Single plant	USA

Grasses, rather than legumes, are by far the most commonly found cover crops species in orchards (Roper, 1992). A major question surrounding the use of cover crops in orchards revolves around whether the benefits derived from them exceed the losses, particularly of scarce resources such as water and nutrients (Jannoyer et al., 2011). For example, during recent devastating droughts in South Africa (2016–2018), many farmers instinctively removed cover crops supposedly to lower the orchard water use (Wiehann Steyn, pers. comm.). Given that currently no accurate quantitative information exists on the water use of cover crops, these actions beg the following questions: Firstly how much water do cover crop species use in orchards under semi-arid sub-tropical conditions? Secondly, how does this water use differ between species? Thirdly, how do orchard management practices e.g. of the cover crops, influence overall orchard water use? An ideal cover crop maximizes the benefits while at the same time reducing costs e.g. through excessive water use and competition for resources with the orchard trees (Jannoyer et al., 2011).

Water use in orchards is driven by factors such as the evaporative demand of the air (includes available energy, as well as the influence of other climatic factors such as wind speed and relative humidity), available soil moisture (irrigation and rainfall), and by management (e.g. canopy cover, cultivar, mowing practices, irrigation system, irrigation frequency etc.) (Dragoni et al., 2005; Dzikiti et al., 2018; Gush et al., 2019). Given the large number of cover crop species used in commercial fruit orchards and the complex interactions between the factors influencing their water use, this study focused on a representative selection of cover crop types. These were selected from the major crop groupings i.e. exotic legumes, exotic grasses, and grasses that are indigenous to sub-Saharan Africa. Secondly, to gain detailed insights on how the different species respond to specific water use drivers, the study was conducted under controlled conditions in a greenhouse. This allowed the selected species to be exposed to similar environmental conditions and for the influence of specific stressors to be studied independently (Dzikiti et al., 2007). Thirdly, the greenhouse experiments also eliminated the confounding influence of trees in orchards, mostly competition for resources e.g. light, nutrients, water, and variations induced by uneven irrigation on the orchard floor. In this way effects of specific environmental factors were studied.

The water use of grasses has been studied before using different techniques as summarized in Table 1. Besides the work by Everson et al. (2011) on grassland in the KwaZulu-Natal Drakensberg in South Africa, no comparative studies exist on the water use and drought stress responses of grass and legume cover crops. Detailed quantitative information on the water use of cover crops is required to improve water resources management in orchards. The specific objectives of this study were therefore to compare the water use rates of selected cover crop species subjected to similar growing conditions. As most cover crops are often irrigated in orchards, the second objective was to study how the different species responded to drought stress. We use this information to

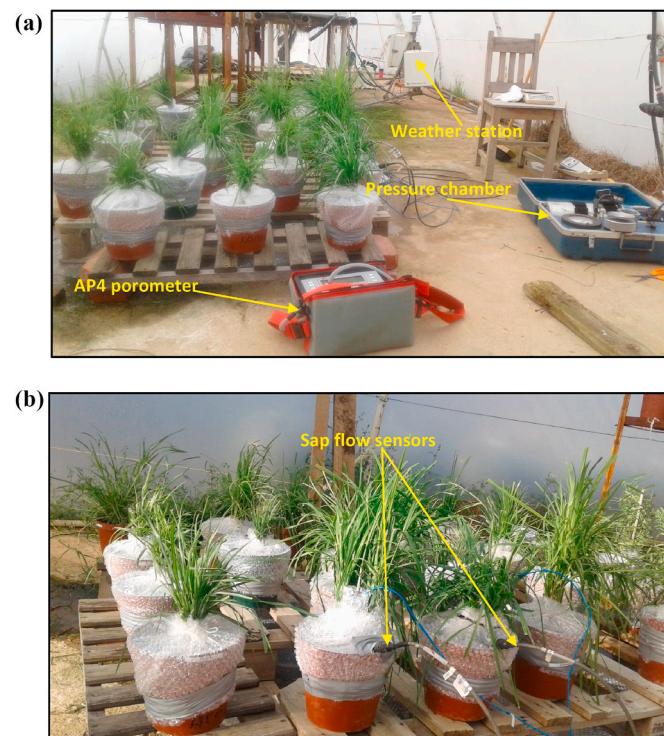


Fig. 1. Setup in the greenhouse showing: (a) position of the weather station in relation to the potted plants; (b) sap flow sensors installed in pots wrapped with plastic.

provide recommendations on the most appropriate cover crop species for orchards under semi-arid conditions based on their water requirements and resilience to drought stress.

2. Materials and methods

2.1. Plant material

Given the wide range of cover crop species planted in commercial orchards, we selected only seven species for practical reasons. These were categorized into three groups namely exotic legumes, exotic grasses, and grasses that are indigenous to sub-Saharan Africa. Two legumes were studied i.e. Lupine (*Lupinus albus* L.), and Common vetch (*Vicia sativa*). Although these are planted in some orchards, they are not widely used in South African orchards. Instead exotic grasses are more common, and for this study, we selected three types namely Tall fescue (*Festuca arundinacea*), Rye grass (*Lolium perenne*), and Kikuyu grass

Table 2

Summary of sap flow gauges used to measure water use during the stress trial. CTRL represents the control treatment.

Gauges	Species	Gauge type	Heater resistance (Ohms)	Input volts	Stem diameter (cm)	Leaf area (cm ²)	Treatment
Gauge 1	Eragrostis	SGA2	95.1	2.3	2.4	26.85	CTRL
Gauge 2	Eragrostis	SGA2	93.6	2.3	2.2	21.72	Stress
Gauge 3	Lupine	SGA5	180.8	4	4	89.48	CTR
Gauge 4	Lupine	SGA5	177.9	4	3.8	77.64	Stress
Gauge 5	Rye	SGA5	179.6	4	2.6	33.24	CTRL
Gauge 6	Rye	SGA5	186	4	2.5	29.78	Stress

(*Pennisetum clandestinum*). Of these, Tall fescue is more popular among fruit farmers in South Africa for unclear reasons. Indigenous grasses are not planted in most instances. Rather farmers simply manage the natural grasses in the same way as they do the exotic species although the seeds of indigenous species are also sold commercially. Two indigenous grasses were selected namely the African Lovegrass (*Eragrostis capensis*) and Rhodes grass (*Chloris gayana*). The cover crops were planted in pots as seeds sourced from a local hardware outlet.

2.2. Experimental layout

The cover crops were planted in 2½ litre pots in a greenhouse at the Department of Agronomy, Stellenbosch University (33°56'30.49"S; 18°51'58.89"E; 330 m asl) in January 2017. The greenhouse measured about 15 m × 5 m × 3 m (Fig. 1) and it was covered with a UV stabilised transparent plastic sheeting with a transmittance of about 88%. About 40 seeds were planted per pot for each grass species. These were thinned to 35 plants per pot after emergence. For the legumes, 20 plants were planted per pot as these tended to be bulky. There were five plant pots per species, so data were collected in five replicates. A standard commercially available potting mixture was used as the growing medium. This comprised of garden soil, compost, sand, sphagnum peat moss, coir fibre, composted pine bark, perlite, vermiculite, limestone, and fertilizers in varying proportions. Irrigation was applied to each pot using a drip irrigation system that delivered about 2 L of water per hour. Each pot received two to three pulses of irrigation per day each lasting about 25 min depending on the weather conditions. The plant pots were randomly arranged in the greenhouse (Fig. 1).

2.3. Microclimate and soil measurements

Weather conditions inside the greenhouse were measured using an automatic weather station installed in the middle of the greenhouse (Fig. 1a). The equipment comprised a pyranometer (Model SP 212 Apogee Instruments, Inc., Logan UT, USA) which measured the solar irradiance. The sensor was installed on a horizontal levelling fixture mounted on a north facing cross bar to avoid self-shading. Air temperature and relative humidity were measured using a temperature and humidity probe (Model: HMP60 Campbell Scientific, Inc., Logan UT, USA) installed at a height of about 2.0 m above the ground. The soil water potential was measured using electronic tensiometers (Model: 200SS Campbell Scientific, Inc., Logan UT, USA). All the sensors were connected to a data logger (Model: CR1000 Campbell Scientific, Inc., Logan UT, USA) programmed with a scan interval of 10 s and the output signals were processed at hourly and daily intervals.

2.4. Transpiration, stomatal conductance and leaf water status

To understand the daily water use dynamics of the different cover crop species transpiration was measured using two independent methods. These included gravimetric monitoring in which plant pots were weighed at hourly intervals on selected days (Xin et al., 2008) using a precision balance (Model SNUG III Jadever; Taiwan, China) that measured mass to the nearest 0.1 g. The second method involved using miniature stem heat balance sap flow gauges (Model SGA 2 & 5;

Dynamax Houston, USA) (Van Bavel and Van Bavel, 1990) and details are shown in Table 2. For the gravimetric method precautions were taken to suppress evaporation from the open soil by wrapping the pots with plastic during measurements (Fig. 1). Sap flow sensors were used to collect transpiration data over long periods when gravimetric measurements were not practical. At the end of each measurement cycle, all the plants were cut and their leaf area measured using the leaf area meter (Model Li-3000, Li-COR Inc., Nebraska, USA). The transpiration data was normalized with the transpiring leaf area to eliminate bias due to plant size variations. These data, collected over several days, formed the baseline data showing the typical responses of each cover crop species to climatic driving factors when the plants were well-watered.

To establish quantitative relationships between leaf water status and the extent of stomatal opening for the various species, the leaf water potential was measured concurrently with the stomatal conductance when the available soil water was not limiting. These data were collected hourly from sunrise to sunset on selected cloudless days. The leaf water potential was measured using a Scholander-type pressure chamber (Model: 615 PMS Instrument Company, Albany, OR, USA) while the stomatal conductance was measured using a diffusion porometer (Model AP4: Delta-T Devices, Cambridge, UK).

2.5. Assessing cover crop response to water deficit

The choice of micro sprinkler irrigation system in orchards (whether narrow or wide range) is informed, not only by the desire to encourage the development of an extensive root system, but also to supply water to cover crops and to maintain biodiversity (Jannoyer et al., 2011). Wide range micro sprinklers inevitably use larger amounts of water than narrow range ones (Knox et al., 2012). Therefore the selection of drought tolerant cover crops is essential in orchards with drip irrigation or narrow range micro sprinklers. To assess the sensitivity of the different species to drought stress, we used plants grown in 20 L containers with higher water storage capacity. One pot of a selected species was well-watered while drought stress was imposed on a second pot by withholding irrigation over a number of days. The transpiration, plant water status, stomatal conductance and soil water potential were measured over drying cycles typically lasting 5–6 days. The stress was relieved at the end of the cycle and data collection continued during the recovery phase. We calculated a transpiration reduction coefficient (T_R , %) to quantify the impact of water stress on transpiration calculated as:

$$T_R = (1 - T_s/T_c) \times 100 \quad (1)$$

where T_c is the daily transpiration per unit leaf area (L/m²/d) for the control treatments, and T_s is the daily transpiration per unit area (L/m²/d) for the drought stress treatments. Because of the need for continuous data during the drying cycle, the transpiration measurements were taken using the stem heat balance sap flow gauges. Also given equipment limitations, the data were collected on only three species namely Lupine, Rye and *Eragrostis* grass representing each of the three crop groupings.

2.6. Statistical analysis of variance (ANOVA)

A one-way analysis of variance (ANOVA) was used to determine

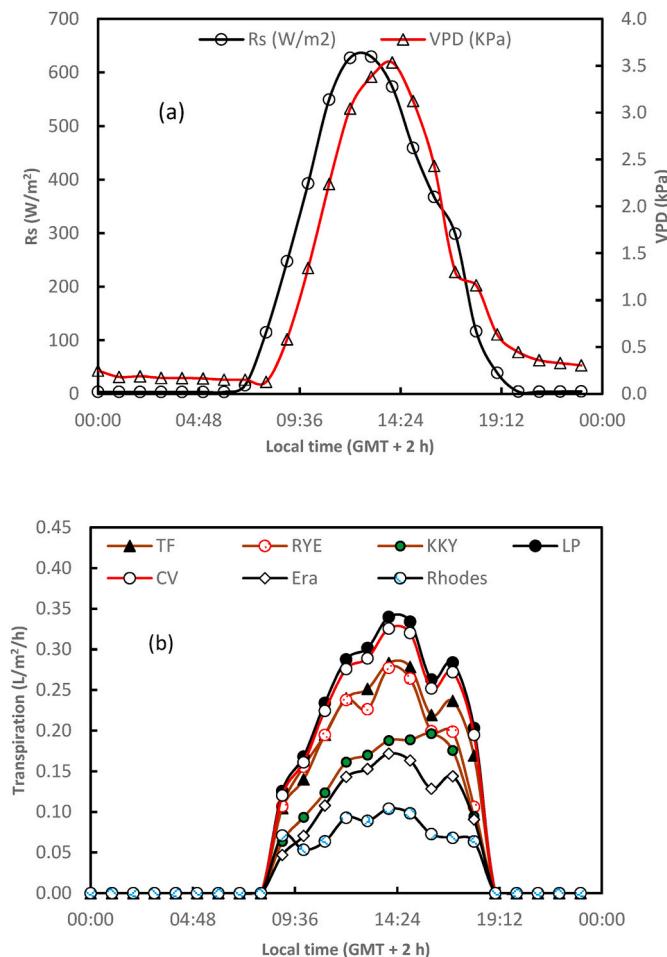


Fig. 2. (a) Typical clear day showing the solar radiation (Rs) and the vapour pressure deficit (VPD) of the air in the greenhouse, (b) Different cover crop species' water use, recorded on 20 September 2017. TF (Tall fescue), KKY (Kikuyu), LP (Lupine), CV (Common vetch) and Era (Eragrostis).

whether there were any statistically significant differences in the water use of the different cover crop species. The water use of each species from 5 different replicates of the same species were used. The differences were compared within the species, also to other species. We tested the hypothesis:

$$Cw_1 = Cw_2 = Cw_3 = \dots Cw_z \quad (2)$$

where: Cw is the average water use for each treatment.

3. Results

3.1. Climatic factors and transpiration dynamics

The diurnal course of the key climate drivers of water use namely the solar radiation (Rs) and the vapour pressure deficit of the air (VPD) on a typical cloudless day on 20 September 2017 is shown in Fig. 2a. Solar radiation peaked at 600 W/m^2 around noon at 12:00 (Local time = GMT + 2 h) while the VPD reached a maximum of about 3.5 kPa about 2 h later at 14:00 (Local time = GMT + 2 h). The maximum air temperature recorded on this day exceeded 40°C , typical of greenhouse conditions. Also on this day, all the plants were well-watered, so the transpiration values represent the baseline water use for each species when water availability is not limiting. The transpiration data were collected using the gravimetric method, so each value in Fig. 2b is an average of measurements from five plant pots.

The exotic legumes (Lupine and Common vetch) had the highest hourly transpiration rates which exceeded $0.30 \text{ L/m}^2/\text{h}$ (Fig. 2b). This was followed by the exotic grasses at around $0.28 \text{ L/m}^2/\text{h}$. Among the exotic grasses, Kikuyu grass that originates from the tropical and subtropical climates in East Africa, had the lowest water use rates close to $0.20 \text{ L/m}^2/\text{h}$. Overall the indigenous grasses (*Eragrostis* and Rhodes grass) had the lowest transpiration rates that peaked between 0.10 and $0.16 \text{ L/m}^2/\text{h}$. The daily total transpiration per unit leaf area summarized in Fig. 3 followed the trend described above. These ranged from 2.3 to $2.5 \text{ L/m}^2/\text{d}$ for the legumes, 1.5 – $2.1 \text{ L/m}^2/\text{d}$ for the exotic grasses and 0.8 – $1.2 \text{ L/m}^2/\text{d}$ for the indigenous grasses.

Water use by plants is driven by the evaporative demand of the air (mainly climatic factors), the available soil water, as well as total leaf area. So, under the well-watered conditions, the solar radiation incident on the crops and the VPD were the main drivers of water use in this experiment. Unlike some irrigated orchard tree species e.g. apple (Dzikiti et al., 2018) and some citrus cultivars (Gush and Taylor, 2014), the relationship between the hourly transpiration and solar radiation was curvilinear showing a strong hysteresis effect between the morning to midday rise and the midday to sunset decline in transpiration illustrated in Fig. 4a,c,e,g,i. Within each hysteresis loop the coefficient of determination was very high ranging from 0.91 to 0.98. The reasons for the hysteresis effect are unclear, but the capacitance (buffering effect) of the internally stored water controlling stomatal functioning due to changes in leaf water status could be a factor (Steppe et al., 2006). In contrast, the relationship between the hourly transpiration and the VPD was

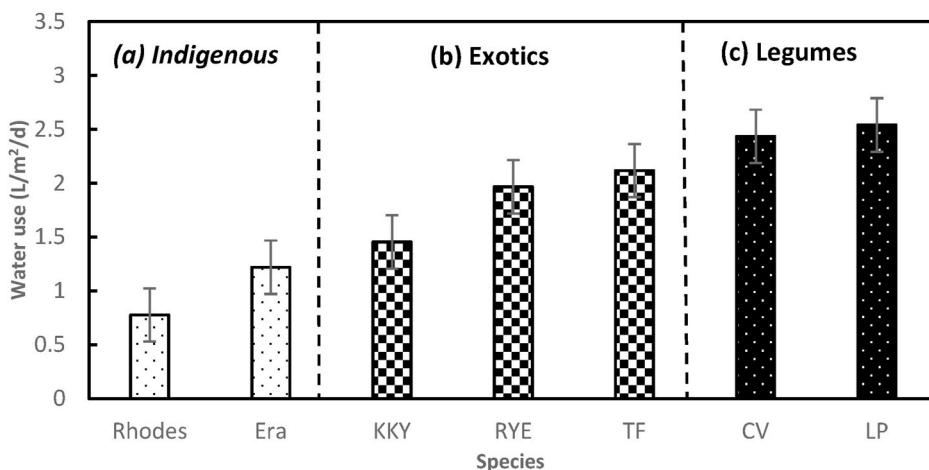


Fig. 3. Transpiration rates of different cover crop species.

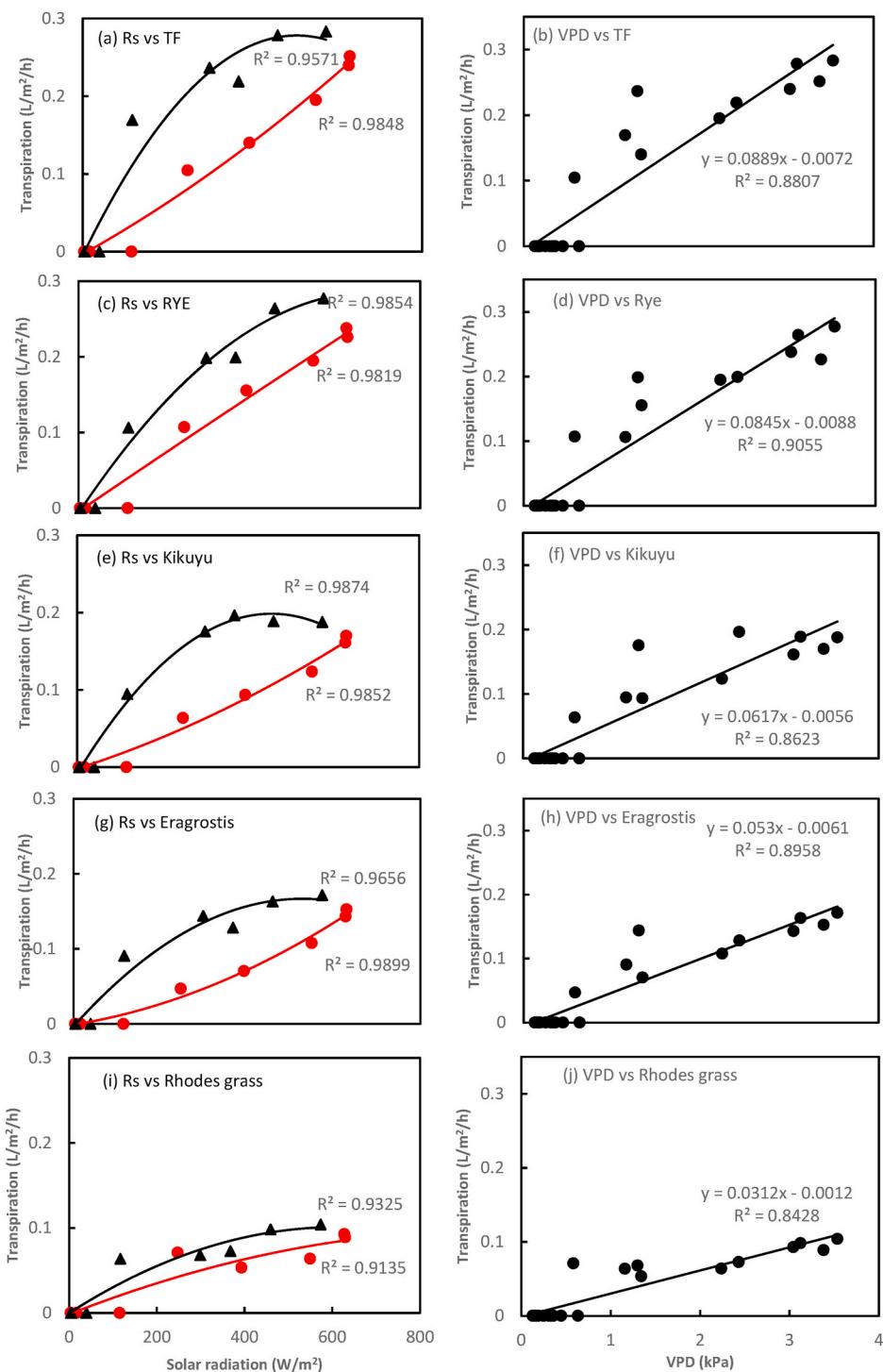


Fig. 4. Correlation of cover crop transpiration with weather variables i.e.; (a) Tall fescue (TF) with solar radiation (Rs), (b) TF with VPD, (c) Rye grass (RYE) with Rs, (d) RYE with VPD, (e) Kikuyu (Kky) with Rs, (f) Kky with VPD, (g) Eragrostis (Era) with Rs, (h) Era with VPD, (i) Rhodes grass (Rhodes) with Rs and (i) Rhodes with VPD. The red line shows the morning curve while the black line shows the afternoon curve, demonstrating the hysteresis effect between solar radiation and transpiration. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

strongly linear suggesting that the VPD had a very limited effect on the stomatal function. This again is in contrast to what has been observed for various tree species in which stomata begin to close when the VPD exceeds values just above 1.0 kPa. The responses to the climate driving variables were similar for all cover crop species.

As expected, the diurnal trend in the stomatal conductance for all the species was strongly related to the transpiration trend, but differences in magnitude between the various species were also quite apparent (Fig. 5). However, there was a significant difference in the timelags between stomatal opening (in response to light stimuli) and the commencement of transpiration (in response to the water potential

gradient) which was as much as 2 h for some species (data not shown). While this observation is not quite expected for such small plants, it supports the hysteresis observed with the solar radiation (in Fig. 3) likely related to the capacitance effects associated with the various species. The ranges of the measured stomatal conductance (G_s) was approximately 0–100 mmol/m²/s for the indigenous cover crops including Kikuyu, 0 to just above 150 mmol/m²/s for Tall fescue and rye and 0 to close to 200 mmol/m²/s for the legumes. The stomatal conductance trends were clearly consistent with the transpiration trends.

The effect of drought stress imposed over a five day period from 28/11/2017 to 02/12/2017 on the water relations of Lupine, Rye grass and

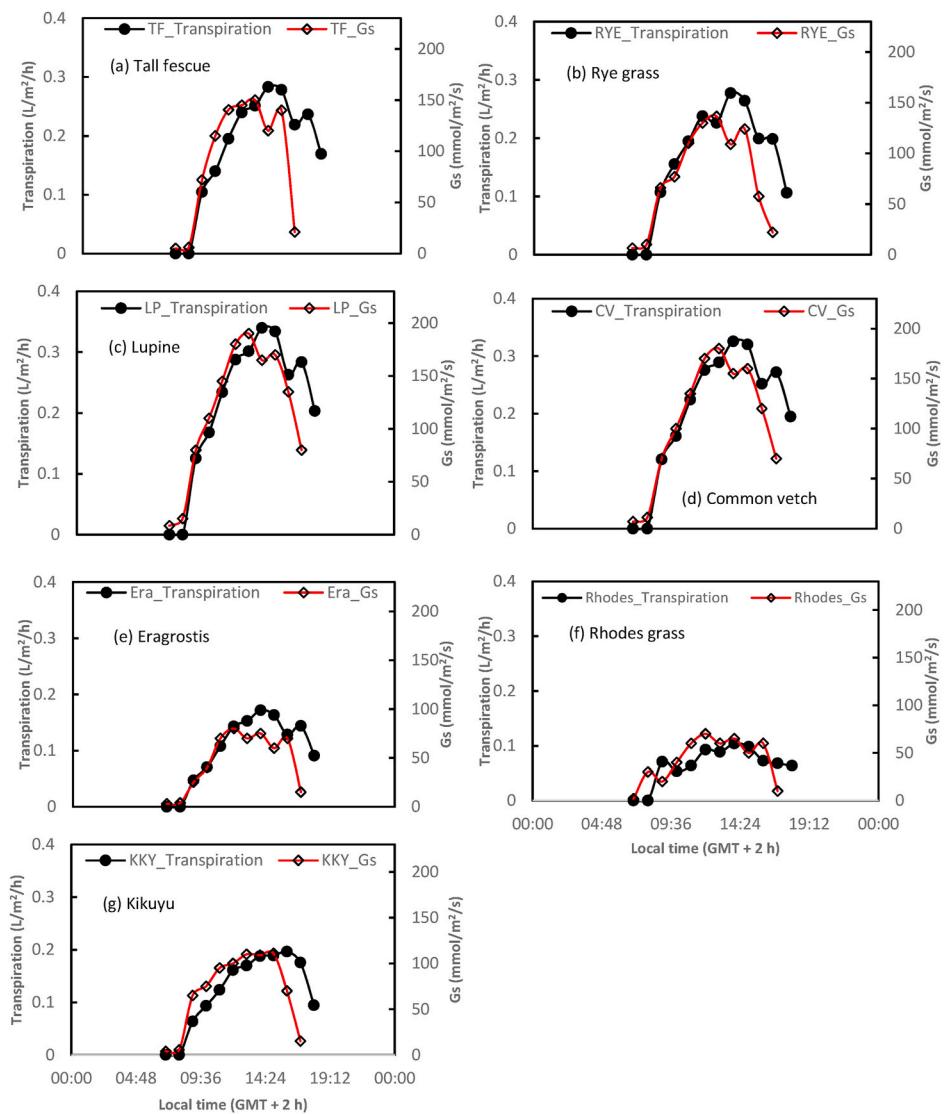


Fig. 5. Transpiration of each cover crop species in relation to the stomatal conductance (Gs) presented in the order (a) TF, (b) RYE, (c) Era, (d) Rhodes, (e) Lupine (LP), (f) Common Vetch (CV) and (g) KKY.

Eragrostis are shown in Fig. 6. All the days were cloudless except for small patchy clouds on the last day of the drying cycle (data not shown). For the control Lupine (Fig. 6a), the stomatal conductance range was fairly consistent over all the days. The same can be said about the leaf water potential which never dropped below -1.5 MPa. However, for the stressed Lupine, some closure of the stomata was apparent although there was a much clear decline in the leaf water status to below -2.0 MPa (Fig. 6b). The associated decline in the transpiration rates with increasing soil water tension are illustrated in Fig. 7a and b. Plants that allow their water status to drop with increasing stress or atmospheric evaporative demand, such as Lupine are called anisohydric plants. Rye grass also showed a similar response to Lupine although the minimum leaf water potential for the well-watered control plants was much higher at -0.98 MPa (Fig. 6c). The leaf water potential declined to about -1.70 MPa under stress (Fig. 6d). The associated transpiration changes for Rye grass for the control and stress treatments are illustrated in Fig. 7 c and d.

Although similar treatments were imposed on the indigenous *Eragrostis*, its response was different from that of the exotic species (Fig. 6 e and f). Firstly, the minimum leaf water potential for *Eragrostis* was much higher dropping to only -0.70 MPa for the control plants (Fig. 6e). Transpiration (Fig. 7a) for this species did not vary substantially

between days. The reason for this consistent response is because the *Eragrostis* actively regulated its stomatal aperture as shown by the cyclic changes in the stomatal conductance whose trajectory is very different from that of the exotic species. Even if similar levels of water stress were imposed on the *Eragrostis*, it is clear from Fig. 6 f and 7 f that both the leaf water status and transpiration hardly dropped. Plants that actively regulate their stomatal aperture to maintain the leaf water status and minimize transpiration losses like *Eragrostis* are isohydric plants. Under severe drought stress, the leaf water potential for *Eragrostis* did not drop below -1.0 MPa (Fig. 6f). Even when the drought stress was relieved, Lupine did not recover from the severe stress as the non-recoverable water deficit threshold had been exceeded.

We calculated the rate of decline of transpiration as a result of drought stress for the three species through a transpiration coefficient and the data is shown in Fig. 8. The rate of decline was faster for Lupine while it was slowest for the indigenous *Eragrostis*.

4. Discussion

In this study we, for the first time, compared the water requirements of a range of cover crop species grown in commercial fruit orchards. We also investigated their responses to drought stress. While the benefits of

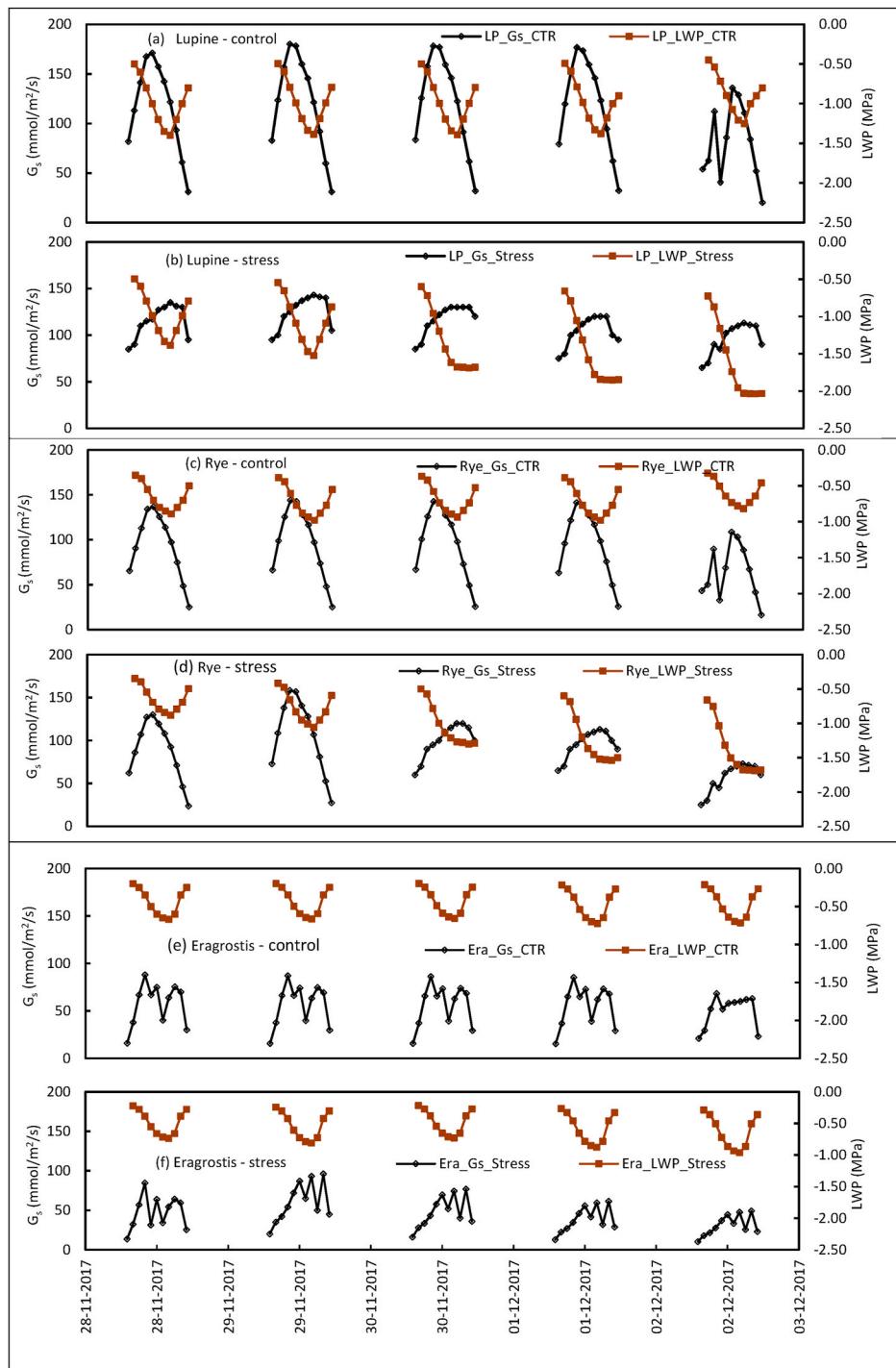


Fig. 6. Comparison of stomatal conductance (G_s) with total leaf water potential (LWP) for Lupine (legume), Rye (exotic) and Eragrostis (indigenous), over a wet-dry period from 28/11/2017 to 02/12/2017.

cover crops in orchards are well documented (Reicosky and Forcella, 1998; Chen et al., 2003; Jannoyer et al., 2011), an important information gap exists regarding their impacts on the water resources. Therefore this study focused on both grasses and legume cover crops, but mostly on grasses which are widely planted in orchards in South Africa and elsewhere. A significant finding from this research is that cover crops that are endemic to sub-Saharan Africa (e.g. *Eragrostis* and Rhodes grass) had substantially lower transpiration rates per unit leaf area than their exotic counterparts. In addition these indigenous grasses also proved to be tolerant to severe drought stress, consistent with observations made on grass species endemic to semi-arid tropics studied by Cardoso et al.

(2015). The legumes had the highest water use rates, but they were also most susceptible to water deficit in the root zone. Therefore this study suggests that legume cover crops are least suited to orchards in water scarce countries such as South Africa, Spain Australia etc. They are more suited to areas where water is not limiting.

The range of water uses by the widely planted exotic grasses lay between that of exotic legumes and the indigenous grasses. Within the exotic grass species, the Tall fescue had the highest water use rates also as reported by Holloway-Phillips and Brodrribb (2011). These authors focused only on the Tall fescue and Rye grass and they attributed the higher water use rates by Tall fescue to its deep and extensive root

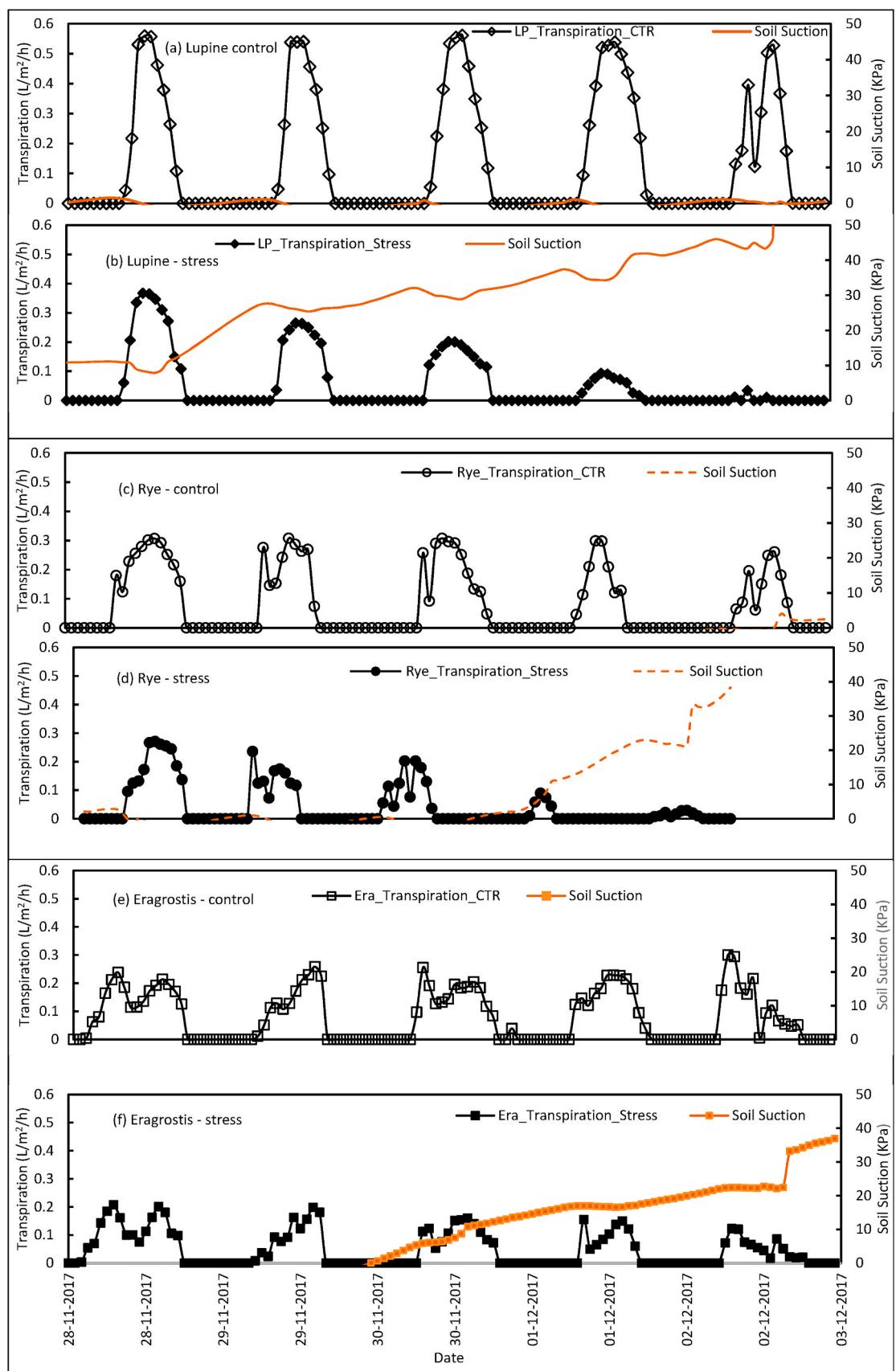


Fig. 7. Comparison of transpiration against soil water availability for Lupine (legume), Rye (exotic) and Eragrostis (indigenous), over a wet-dry cycle from 28/11/2017 to 02/12/2017.

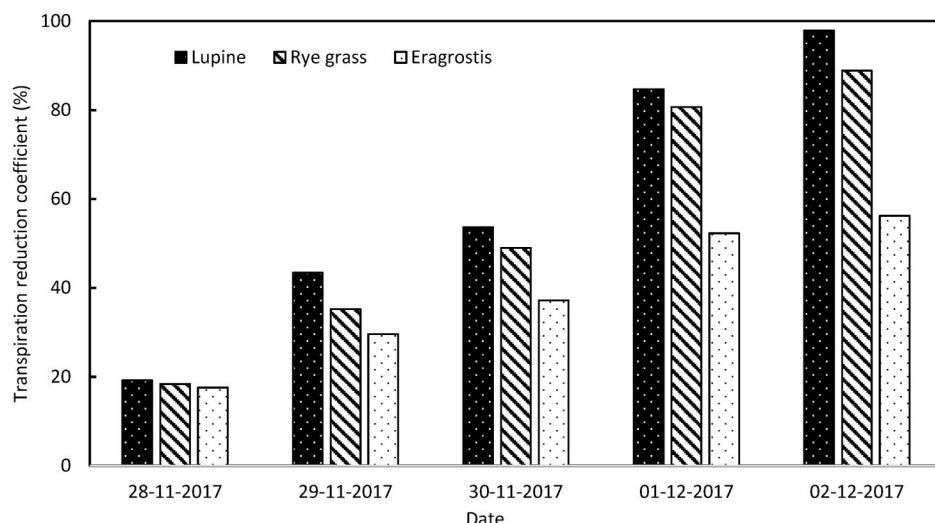


Fig. 8. Transpiration reduction coefficient for the three species during the stress cycle.

system which is able to supply water to the evaporating sites in the leaves when soil availability is limiting. This study also provided insights on the mechanisms by which the different species responded to stress. For example, the indigenous grasses actively reduced water losses thorough cyclic stomatal oscillations which kept the leaf water status fairly high. Such isohydric responses have also been reported on grasses by [Cardoso et al. \(2015\)](#) and [Holloway-Phillips and Brodribb \(2011\)](#). On the other hand, the exotic species displayed the risky anisohydric behaviour wherein the stomata did not actively regulate water losses leading to a precipitous decline in the leaf water potential such that some species, especially the legumes, did not recover from severe drought stress.

A number of studies have quantified the water use of grasses under different levels of drought stress (e.g. [Marais et al., 2006](#); [Koech et al., 2015](#)). But most of the studies were done under field conditions where the evapotranspiration rather than the transpiration component of water use was measured. So this study also provides insights on how climatic factors drive water use in the different species. For example, the relationship between the hourly solar radiation and transpiration showed a significant hysteresis effect for all the species. Unlike orchard tree crops whose stomatal movements are sensitive to the atmospheric VPD (e.g. [Dzikiti et al., 2017](#); [Mobe et al., 2020](#)), this was not the case for the cover crops studied here. The VPD did not cause stomatal closure which was unexpected given the prevalence of this phenomenon in other plant forms. For apple trees for example, the transpiration is linearly related to the solar radiation ([Ntshidi et al., 2018](#)). However, for citrus trees, the relationship is curvilinear as illustrated by [Dzikiti et al. \(2007\)](#) and a hysteresis effect was also observed between the transpiration and the solar radiation. The reasons for the hysteresis phenomenon may be related to the hydraulic properties of the plant especially the hydraulic resistance and capacitance ([O'Brien et al., 2004](#); [Zhang et al., 2014](#)). Evidence of the high hydraulic resistance in the transpiration stream of the grasses was shown by the time lags between the opening of the stomata and the commencement of water up take from the soil which was as high as 2 h for Tall fescue for example. According to [Holloway-Phillips and Brodribb, 2011](#)), more than 60% of the hydraulic resistance of grasses resides in the leaves. Therefore the presence of significant foliage on the cover crops (see Fig. 1) could have contributed to the hysteresis effect.

5. Conclusions

This study provides insights on how different cover crop species impact water resources in fruit orchards. Exotic legumes for example,

had at least three times higher water use than the indigenous grasses under similar growing conditions. Yet the legumes were also most susceptible to water deficit because of their risk taking anisohydric responses to environmental stress. Exotic grasses that are commonly planted in orchards also had high water use rates and a weak response to drought stress, although they were marginally better than the legumes. Therefore, indigenous grasses are more suited as cover crops in the semi-arid tropical and sub-tropical regions because their physiology is more adapted to the harsh growing conditions. They do not need regular irrigation to survive. However, it is important to note that the water saving benefits of the indigenous cover crops demonstrated here should be considered together with other benefits in order to make informed choices when prioritizing species to plant.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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