

Plant drought survival under climate change and strategies to improve perennial grasses. A review

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Abstract The three cool-season perennial forage grasses cocksfoot/orchardgrass, *Dactylis glomerata* L., tall fescue, *Festuca arundinacea* Schreb. syn. *Lolium arundinaceum* (Schreb.) Darbysh., and phalaris/harding grass, *Phalaris aquatica* L., are of major economic and ecological importance in regions with summer-dry environments. This review considers the constraints that these species are likely to experience under current and predicted increase of droughts due to climate change scenarios in south-eastern Australia, the southern Great Plains of USA and the Western Mediterranean Basin. The review identifies research required to maximise the development and use of C3 cool-season grasses with enhanced resilience to drought while considering the concern of some regulators that these grasses may be potential weeds. The state of knowledge of factors influencing plant drought survival and therefore recovery after stress and long-term persistence is discussed in the light of adaptive strategies. The major research needs identified to enhance traits conferring drought survival include (1) increasing the depth and density of grass root systems to strengthen dehydration avoidance; (2) exploring the

biochemical, molecular and hydraulic bases of dehydration tolerance and improving techniques to measure this trait; (3) breaking the trade-off between summer dormancy and forage yield potential and improving understanding of environmental, biochemical and genetic controls over summer dormancy; (4) identifying non-toxic endophyte strains compatible with summer-dormant cultivars of tall fescue to enhance drought survival; and (5) enhancing seed production capability of new cultivars as well as the development of agronomic management packages for promoting stable mixtures combining perennial grasses and legumes. The weed potential of newly introduced summer-dormant cultivars is concluded to be minor. The research directions proposed here should improve pasture grass resilience and forage crop sustainability in Mediterranean and temperate summer-dry environments under the future drier and warmer conditions associated with climate change.

Keywords Summer dormancy · Dehydration tolerance · Dehydration avoidance · Drought survival

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1 Introduction

1.1 Projected climates and impact on pastures and grasslands

Grasslands cover 70 % of the world's agricultural surface and support crop-livestock farming systems that contribute to the livelihoods of more than 800 million people worldwide (2013). Furthermore, they produce forage for many of the world's grazing animals both in developed and developing nations and provide crucial ecosystem services including carbon sequestration, protection and enrichment of the soil and preservation of biodiversity (Gaujour et al. 2012). However, the stability of both native and sown grasslands and the sustainability of the pastoral agriculture which is dependent on them will be challenged by global climate change (Tubiello et al. 2007). Depending upon the greenhouse gas emission scenario chosen, the projected increases in mean global annual temperature vary by between 2.5 and 4.3 °C in most crop-growing regions in the world by 2080 to 2099 (IPCC 2014). Despite the fertilisation effects of increased atmospheric CO₂, extreme events including severe heat waves and droughts may become more frequent in a changing climate compounding the level of stress on grassland plants (Schar and Jendritzky 2004; Brookshire and Weaver 2015).

To give these predictions a regional perspective, the projected changes in climate for southern Australia, the Southern Great Plains of the USA and southern Europe will be proposed as examples of the types of challenges that grasslands are predicted to experience in the near future.

1.1.1 The case of southern Australia

In southern Australia, severe droughts of great intensity, duration and extent have, since British settlement, been a major constraint to agriculture (Verdon-Kidd and Kiem 2009). As an example, the so-called Millennium Drought, which lasted with varying intensity from approximately 2002 to 2009, has had a strong detrimental effect on southern Australian agriculture (Kirkegaard and Hunt 2010) particularly by increasing the level of farmer debt. However, it has also awakened some farmers to the increased flexibility that grazing animal enterprises when mixed with cropping provide to farm viability, in comparison

to enterprises based solely on the cropping of annual species (Nordblom et al. 2015). Associated with these events, there has been renewed interest in ways to improve the persistence of pasture plants under drought, an example in the cool-season pasture scene being the renewed introduction into the market of tall fescues with the summer dormancy trait (Miller 2000). In southern Australia, located between latitudes 30° and 43° S, depending on the greenhouse gas emission scenario chosen, the climate is expected to experience between 2 and 8 % more evapotranspiration, temperatures will increase by between 1.5 and 3 °C, and annual rainfall will decline by between 2 and 5 %. Moreover, the more northerly part of this region is likely to receive between 2 and 5 % more rainfall in summer than currently (www.climatechangeinaustralia.gov.au). It is likely there will be specific challenges that drier, warming climates will pose to much of the current C3 grass germplasm we use in these latitudes. For example, in southern Australia, the length of the cool season appears to be shortening including a later start to autumn rains that begin the growth of cool-season species together with an earlier finish to their growing season at the end of spring (Wang et al. 2009).

1.1.2 The case of the Mediterranean Basin

In Europe, a decline in summer precipitation, with associated increases in solar radiation and temperature, both enhancing evapotranspiration, will lead to more frequent and more intense droughts (Lehner et al. 2006). Thus, the widespread devastating drought and heat wave observed over Europe in the summer of 2003 (Ciais et al. 2005) might become more usual. Indeed, in the Mediterranean Basin, the rate of warming may lead to an additional month of summer (Giannakopoulos et al. 2009). This increasing water deficit will also worsen in winter since ten of the 12 driest winters since 1902 have occurred in just the last 20 years (Hoerling et al. 2012). Therefore, pasture establishment failures and long-term degradation from drought are expected to become more common (Briske et al. 2003). Around the Mediterranean Basin, mixed crop-livestock farming systems contribute significantly to the rural economy. In southern Europe, livestock farming provides high-added value animal products (typically cheese and meat), but the recent decrease in grazing pressure, brought about by the widespread population shift from rural to urban areas, negatively impacts the landscape since the lack of farmers allows shrub encroachment, thus increasing wildfire frequency. In Northern Africa, animal production is widespread and mostly extensive, often with a strong negative impact because of overgrazing on rangelands. However, greater production of animal products is required to satisfy the need of growing populations (Delgado et al. 1999; FAO 2009). In Morocco for example, public actions ('Plan Vert') have been implemented to foster livestock farming. In all cases, a key determinant for the sustainability of animal production is self-

sufficiency in on-farm forage supply, to counterbalance the increasing cost of feed stuff sourced off-farm (Abdelguerfi and El Hassani 2011; Taher Sraïri 2011). All around the Mediterranean Basin, rangelands and grasslands cover over 50 % of the land surface and about 270 million ha in the arid and semi-arid belt receiving 100–400 mm annual rainfall (CIHEAM 2009). They provide forage resources as well as many ecosystem services including carbon sequestration, protection against soil erosion, increased water infiltration and biodiversity preservation (Turner et al. 2011). However, in the southern Mediterranean countries, areas available for grazing are diminishing due to the expansion of production of rain-fed annual cereals, to meet increasing demand for human food (Lelievre and Volaire 2009). Millions of hectares of fallow and rangeland have disappeared while stocking rates increased due to imported grains and by-products subsidised by governments. Thus, grazing at higher stocking rates is allocated to drier and poorer rangelands: the remaining rangeland is drastically degraded due to overgrazing, leading to a dramatic loss of biodiversity, vegetation cover, greater soil erosion and a diminishing ability to provide ecosystem services.

Perennial grasses dominate in most natural grasslands and provide the principal nutrition for ruminant livestock. However, the genetic diversity of these palatable species is declining due to habitat destruction and overgrazing (CIHEAM 2009). In the Northern Mediterranean countries, stocking rates tend to decrease along with an increase of extensive permanent pastures that cannot provide sufficient forage resources in all seasons. As a consequence, and around the whole Mediterranean Basin, complementary forage crops are crucial to secure farming systems and increase productivity and stability of animal production.

1.1.3 The case of the Southern Great Plains of the USA

According to the recent report of the U.S. Global Change Research Program (Karl et al. 2009), climate change is projected to progress in the USA during this century. USA average temperature has risen more than 1 °C over the past 50 years, and further temperature increase will depend on the amount of greenhouse gases emitted globally and climate sensitivity to those emissions. By the end of the century, the average USA temperature is projected to increase by approximately 4 to 6 °C under the higher emissions scenario or by approximately 2.2 to 3.6 °C under the lower emissions scenario. Future changes in total precipitation are more difficult to project than changes in temperature. For example, climate models suggest that northern areas are likely to become wetter, and southern areas drier, especially in winter and spring. The models also agree that much of the Southeast and West will experience reductions in precipitation and increases in drought severity and duration. These changes will have dramatic effects on agricultural production (Motha and Baier 2005).

In the Southern Great Plains of the USA, located between latitudes 32° and 38° N, a bimodal pattern of precipitation with peaks in May and September, severe water deficits accompanied by extreme heat in summer and relatively mild winters have shaped the primary and secondary productions from agroecosystems. One of the most important crops with the ability to compensate for these weather extremes is winter wheat (*Triticum aestivum* L.), cultivated on approximately 6.5 million hectares (Pinchak et al. 1996). In this region, wheat is a dual-purpose crop (31 % for grain-only, 20 % for forage-only and 49 % for dual-purpose use) providing winter forage for cattle and a grain crop at maturity in early summer (Hossain et al. 2004). In the past decade, the disturbed pattern of autumn precipitation has threatened timely planting of dual-purpose wheat, often resulting in a lack of forage for cattle to graze into the winter and early spring. In the 1970s and 1980s, introduced cool-season but summer-active perennial grasses became an important source of high-quality forage to complement dual-purpose wheat and perennial warm-season C4 grass pastures, saving producers about US\$100 ha⁻¹ annually (Reuter and Horn 2002). Changing climatic conditions (Nielsen-Gammon 2011) is considered one reason for the increasing failure of these summer-active, introduced, cool-season perennial grasses which are at the margin of their zone of adaptation in these naturally C4 grass-dominated ecosystems (Malinowski et al. 2003; Gillen and Berg 2005). As a result, improved cool-season perennial grasslands based on summer-active cultivars are short-lived and require frequent reestablishment, increasing the cost of winter forage for cattle and driving the search for alternative forage options.

1.2 The role of C3 versus C4 perennial forage grasses

For the development of sustainable pastures in the light of these warming projections, the question arises regarding the relative importance of C3 and C4 grasses in future Mediterranean and temperate summer-dry environments. The current role of C3 grasses in grazing animal breeding and production in these regions is critical, and while the forage contribution of C4 species may increase (Johnston 1996), the role of C3 species is likely to remain important even as the climate warms, for the following reasons. C3 species generally have a lower optimum temperature for peak growth than C4 grasses (Pau et al. 2013; Still et al. 2003). These grasses are better adapted to the lower radiation intensity of the cooler seasons with maximum growth at lower temperatures and vapour pressure deficits when water use efficiency is higher (Lelièvre et al. 2011). In addition, the forage of C3 grasses is of markedly higher nutritive quality than that of most C4 species with resulting benefits for animal production (Minson 1990; Minson and McLeod 1970). C4 grass species have the disadvantage that they produce little forage during the cooler seasons because of sub-optimal temperatures and radiation

intensity. This was recently demonstrated in a comparison between a suite of C3 and C4 grasses at multiple sites across temperate southern Australia (Reed et al. 2008b). In addition, C4 species tend to be much more sensitive to frost, in some cases to such a degree that frost can destroy their entire swards. The cold, often wet soils to which all the grasses were exposed in this multi-site experiment also had a deleterious effect on C4 grass persistence. Thus, the C3 grasses in the same study as that of Reed et al. (2008b) had superior persistence compared to all C4 grasses except *Pennisetum clandestinum* (Nie et al. 2008). Nevertheless, there is little doubt that drier and warming climates will pose serious challenges to persistence of many of the current C3 grass cultivars used in these regions. The question, ‘In a warming climate is there still an important role for cool-season perennial pasture grasses in the future, or should the focus be redirected to C4 warm season species’, is pertinent and has a different answer in different regions. Thus, in those regions with mild winters, including south-west Western Australia and the northern inland New South Wales region of south-eastern Australia, significant development of pasture technology based on C4 warm-season grasses is occurring. While some of this development is based on the perception that such species will be better adapted to future climates (Timbal et al. 2006; Charles and Fu 2012), some is based on observations that there are few well-adapted, persistent C3 cool-season grasses available to commercial agriculture particularly in northern NSW where summer rainfall predominates (Culvenor and Boschma 2005). Indeed, early indications in northern inland NSW suggest that C4 grass species have better adaptation (Harris et al. 2009) although in the cooler, frost-prone Tableland districts of this region C3 grasses are likely to remain dominant. However, even with a warming and drying climate for much of the Mediterranean Basin, southern Australia and the Southern Great Plains of USA, cool-season, C3, perennial grasses are likely to remain important for farmers with grazing livestock both in terms of environmental adaptation and livestock production. Nevertheless, it will be necessary to strengthen the environmental resilience of these grasses especially by enhancing their tolerance to drought and heat.

This review will identify research required to maximise the development and use of cool-season grasses with enhanced adaptation to drought and high temperature and highlight technical and regulatory constraints to the release and adoption of these grasses.

2 Strengthening drought survival strategies of perennial grasses

An increased frequency and severity of drought, defined here as ‘a period of sub-optimal moisture availability reducing potential plant productivity and in severe cases threatening plant

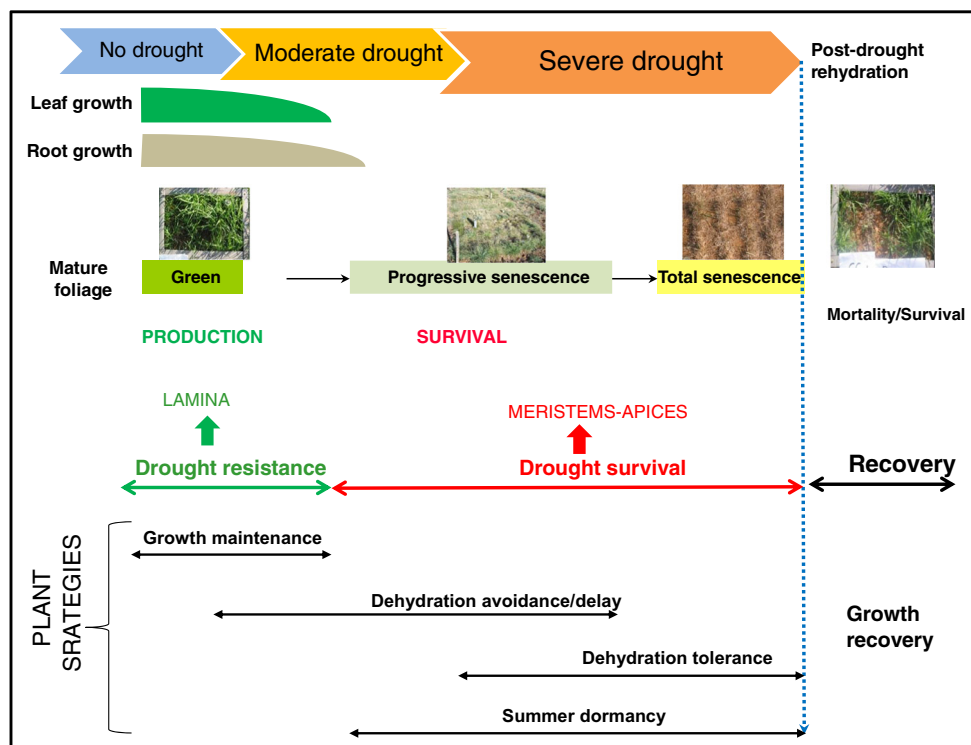
survival’ (Passioura 2006) along with raised temperatures, are likely to be two key factors threatening the productivity and stability of cool-season grasslands and sown pastures in the future. These two factors also interact with one another so that as temperature rises (other things being equal), so also does vapour pressure deficit which in turn increases the rate of transpiration from plants per unit of CO₂ uptake, leading to a reduction in water use efficiency (Ritchie 1983) and increasing the rate at which water deficit stress is experienced.

The majority of research on the effects of water deficit has dealt with annual rather than perennial crops so that the conceptual framework necessary to understand drought resistance and survival in perennial grasses has been slower in developing than that for annual crops. The ‘drought resistance framework’ of Turner (1986; 1997, 2003), although developed primarily with annual crops, seeks to identify the specific physiological and biochemical characteristics that lead to improved plant yields in drought-prone environments. The strategies these characteristics comprise are termed drought escape, dehydration avoidance (syn. postponement, delay) and dehydration tolerance (Turner 1986; 1997). In the case of perennial grasses, plants able to resist moderate drought and maintain aerial growth have to avoid and/or tolerate leaf dehydration. Conversely, plant responses facilitating survival of severe drought are mainly associated with both dehydration avoidance and tolerance primarily occurring in meristematic tissues, as these may be the sole plant organs surviving severe drought. In some species and genotypes, summer dormancy is another combination of strategies which confers efficient survival of meristematic tissues through the dehydration avoidance and tolerance of these organs (Volaire and Norton 2006). Making this distinction between the responses of mature and meristematic tissues seems crucial to properly analyse and understand the strategies of perennial grasses to contrasting drought intensities (Volaire et al. 2014). These various drought resistance and survival strategies as used by perennial cool-season grasses are graphically depicted in Fig. 1.

2.1 Drought escape—the importance of reliable seed production

At the whole plant level, ‘drought escape’ is a strategy primarily used by annual plants to ensure that growth, reproduction and seedset are completed before the onset of dry conditions, with the plant existing as a seed during the season when abiotic conditions are most threatening to survival (Kooyers 2015) An example of how ‘drought escape’ has been a key breeding objective is seen in the Australian wheat industry where plant breeders have sought to better match plant phasic development to the environment. For the relatively dry Australian environments, in contrast to Europe, this has

Fig. 1 Plant adaptive strategies and responses at the whole plant level (aerial and root growth, leaf senescence) involved in drought resistance and drought survival successively, under increasing drought intensity. Drought resistance is defined as the plant ability to maintain biomass production (at leaf level) under moderate drought while drought survival is the ability of meristems and apices to survive and regrow upon conclusion of drought after rehydration (source Volaire et al. 2014 EJA, with permission from publisher)



required the development of earlier maturing cultivars. While perennial plants cannot escape from stressful seasons, the correct phasing of flowering and seedset to ensure that these processes occur at a time of year when they can be successfully completed is essential to long-term survival. Thus, a positive correlation between earliness of heading and ability of plants to survive subsequent drought has been shown in cocksfoot (Voltaire and Lelievre 1997).

2.2 Dehydration avoidance/delay and rooting system improvement

While drought-escaping species only grow with sufficient water supply, the extent to which a plant regulates its water potential as soil water deficit increases indicates whether a species copes with water deficit by responses primarily characteristic of either dehydration avoidance or dehydration tolerance (Kramer 1980; Levitt 1980). Thus, a species is considered to use dehydration avoidance (syn. dehydration delay/postponement) if it must maintain high tissue water potential during periods of moisture deficit. Traits characteristic of the dehydration avoidance strategy include high sensitivity of stomatal conductance to water deficit, osmotic adjustment, conservation of water through leaf modifications such as rolling, paraheliotropism and waxiness to reduce heat load and transpiration as shown in a range of grass species from both the North American semi-arid prairies (Hardy et al. 1995) and Australian rangelands (Bolger et al. 2005).

In phalaris, the early onset and high level of senescence of herbage were observed to reduce transpiration (McWilliam 1968) while the development of an extensive root system and/or superior hydraulic conductance to maximise soil water uptake was noted as being important for ongoing production under drying conditions in tall fescue (Garwood and Sinclair 1979). Dehydration-avoiding plants are able to survive extended dry spells but can only do so if able to maintain high tissue water status. Indeed, McWilliam and Kramer (1968) demonstrated in phalaris that dehydration avoidance through the development of an extensive, deep root system (Cashmore 1934) and the ability to readily senesce foliage during summer is of great importance for the maintenance of the high plant water content that is typically observed in this grass. They showed that if this water harvesting ability is compromised by severing the root system, the plants rapidly die.

Although research to develop roots of annual cereals better able to optimise yield in water-limited environments continues apace with examples already in wheat (Palta et al. 2011; Wasson et al. 2012), this work remains to be commenced in perennial forage grasses. Techniques to facilitate screening of roots across genotypes have been developed utilising both destructive and non-destructive methods (Flavel et al. 2012), with the common objective of improving the adaptation of crops to both the biotic (Watt et al. 2003; Sprague et al. 2007) and abiotic soil factors (Rahnama et al. 2011) which induce stress. These techniques need to be applied in the development of perennial forages to strengthen root systems and

thereby enhance plant persistence, although so far few of the more advanced phenomic techniques have been applied with these species (Walter et al. 2012). Enhanced dehydration avoidance, for example through denser or deeper rooting, may be useful in many situations of water deficits (Fig. 2). Thus, in south-eastern Australia, summer rainfall is predicted to increase leading to the possibility that subsoil moisture may accumulate over summer so that cool-season grasses which can access this moisture from depth could have improved productivity and persistence.

2.3 Dehydration tolerance to improve survival of drought

A species is considered to use dehydration tolerance as a strategy if it allows its water potential to fall in response to increasing moisture deficit (Levitt 1980). The primary indicator of dehydration tolerance is the level of the plant water content at death, i.e. lethal plant water content. Specifically, dehydration tolerance increases as lethal water content declines (Flower and Ludlow 1986, 1987). This trait seems to be mediated by mechanisms which maintain the integrity of cell membranes as tissue moisture content declines. LEA proteins including

dehydrins, sugars such as fructans (Demel et al. 1998) and the level of reactive oxygen species have been implicated in this trait (Turner 2003) although research to better understand its biochemical and molecular basis is required (Verslues et al. 2006; Oliver et al. 2010). Plants with high leaf dehydration tolerance typically maintain growth for longer into a dry period than a dehydration avoider, and although often associated with development of an extensive root system, they tend not to shed their foliage to the same degree as dehydration avoiders and so are better able to utilise incident rainfall for growth if and when it occurs.

Among the perennial grasses, cocksfoot (irrespective of whether a summer-dormant or summer-active cultivar) is more dehydration tolerant at the meristem level than either tall fescue or phalaris. Thus, the meristems of cocksfoot were reported to dry to approx. 0.54 g H₂O/g dry weight during a drying cycle, whereas those of tall fescue dried down to 0.72 while phalaris dried to 0.70 g H₂O/g dry weight immediately before death (Norton et al. 2014). Related to this greater dehydration tolerance is the ability of cocksfoot to survive at soil moisture contents lower than either tall fescue (Volaire and Lelievre 2001) or phalaris (Norton et al. 2014). However, the processes involved in the ability of the perennial herbaceous plant to survive and recover after tissue dehydration require better characterisation (Craine 2013; Hoover et al. 2014). In particular, the hydraulic thresholds of mortality in perennial grasses should be investigated with recent methodological developments that allow the measurement of vulnerability to cavitation associated with drought survival in trees (McDowell et al. 2008; Reich 2014) (Lens et al. 2013). Over the last decade, methods to measure dehydration tolerance in forage crop species have evolved (Volaire and Lelievre 2001) and these have been extended to, *Poa bulbosa* L. (Volaire et al. 2001), and modified to compare the dehydration tolerance of perennial grasses with barley (Volaire 2003) and wheats of both annual and perennial habit (Larkin et al. 2014). More recently, a glasshouse-based method to measure and scale dehydration tolerance incorporating the components, (1) final soil water content, (2) duration of survival after stomatal closure and (3) percentage of surviving plants, has been developed and has been used to compare for the first time the three cool-season perennial grasses most important in regions with Mediterranean climates, tall fescue, cocksfoot and phalaris (Norton et al. 2014). This method not only highlighted the differences that occur between species but also identified intra-specific variation, e.g. within phalaris, and so can be of use to plant breeders. This method needs further refinement particularly to be able to account for differences in plant vigour after termination of the drying cycle and should possibly be further extended to include final tissue moisture content in the determination. It also needs to be modified to accommodate larger numbers of genotypes and perhaps, most importantly, needs field validation. Nevertheless, the method offers



Fig. 2 Assessment of intra-specific variability in the root system and root traits of cocksfoot

the potential to screen for this trait which is important for both forages and annual crops. One of the areas of greatest applicability might be in screening seedlings of genotypes for differences in survival under drying soil conditions. Given the need to sow many cool-season crops in early autumn, e.g. dual-purpose grain/grazing cereals and canola (*Brassica napus* L.), with the consequent high risk of dry soil conditions post-sowing, any difference in the ability of the seedling of one genotype to survive over another confers the potential to maintain a satisfactory crop density and thus yield potential.

Desiccation tolerance, which could be considered as an extreme form of dehydration tolerance, is the ability of plant tissues to maintain viability and recommence growth upon rehydration after tissues have become air dry. It has not been observed within the important cultivated C₃ perennial pasture grasses, including cocksfoot, perennial ryegrass (Volaire 2002; Volaire et al. 1998), tall fescue (Volaire and Lelievre 2001) or phalaris (McWilliam and Kramer 1968; Norton et al. 2014).

2.4 Summer dormancy to improve survival of extended, extreme drought

Summer dormancy is defined as an endogenously controlled and coupled series of processes comprising the cessation or reduction of leaf growth, the complete or partial senescence of herbage and, in some cases, the endogenous dehydration of meristems (Volaire and Norton 2006). These responses are expressed consistently under the environmentally inductive conditions typical of Mediterranean summers and also under non-limiting water conditions (Volaire and Norton 2006; Norton et al. 2008). The trait is induced under the short photoperiods and low temperatures of Mediterranean climate winters with studies showing that cocksfoot and tall fescue must be exposed to these conditions for the trait to be fully expressed under the subsequent long photoperiods and high temperatures of summer (Norton et al. 2006a; Norton et al. 2006b). Summer dormancy is a trait which has evolved primarily for enhancing plant survival and is expressed by some of the cool-season perennial grasses mainly originating in semi-arid and arid Mediterranean climates where the summer-dry period typically lasts 4 months or more (Cooper 1963). Recent research has demonstrated this trait to be very powerful in improving survival over long and intense dry spells in the field with a suite of papers demonstrating the utility of the trait in cocksfoot and tall fescue in the Mediterranean Basin (Volaire 2002; Volaire et al. 2005; Norton et al. 2006a; Norton et al. 2006b; Shaimi et al. 2009; Pecetti et al. 2009; Annicchiarico et al. 2011), southern USA (Malinowski et al. 2005; Malinowski et al. 2009) and south-eastern Australia (Culvenor and Boschma 2005; Norton et al. 2001; Hackney et al. 2006; Hayes et al. 2010a).

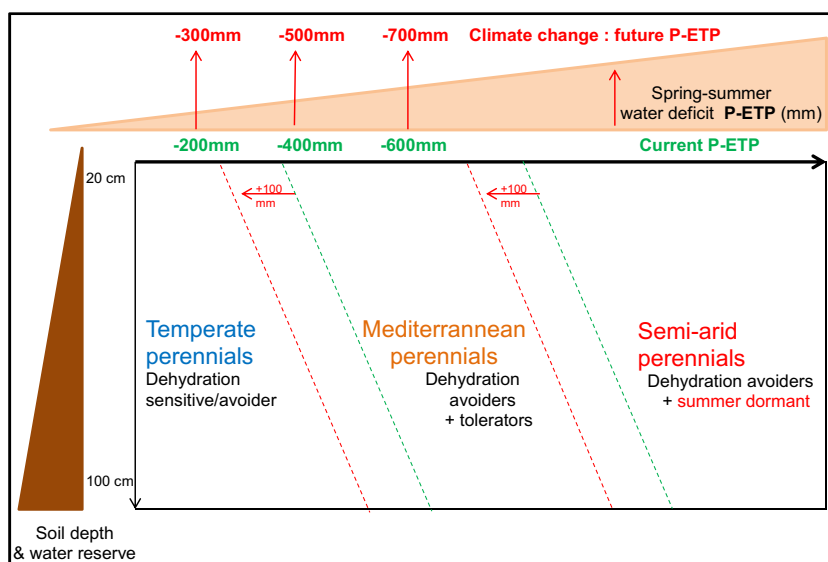
The potency of the summer dormancy trait in ensuring survival and thus maintaining the density of the pasture sward was

well demonstrated in cocksfoot and tall fescue cultivars contrasting in expression of this trait over a number of dry periods of over 3 months which subjected swards to cumulative evapotranspiration (CE) levels of from 650 to 870 mm, the last dry period coinciding with the severe dry spell and heat wave that afflicted much of western Europe in the summer of 2003 (Norton 2007). Over the dry spells of 650 and 790 mm CE, the summer-dormant cocksfoot Kasbah and the non-dormant but drought tolerant Mediterranean cv Medly maintained their sward densities. However, when the drought intensity was increased to 870 mm CE, while the Kasbah sward remained unchanged, Medly was unable to maintain its pre-summer sward cover experiencing a decline to 78 % of its original density (Norton et al. 2006a). Under the dry spell of 790 mm CE, the temperate cocksfoot cultivar Lutetia could only maintain 39 % of its pre-drought cover in contrast to both Kasbah and Medly which remained unchanged. The robust drought tolerance of cv Medly under moderately severe droughts and the poor drought survival of Lutetia have been subsequently confirmed by Poirier et al. (2012). More recent observations in Australia have again highlighted the ability of the summer dormancy trait to enhance survival. Thus, after an extended dry period over the spring/summer period of 2012/2013 during which cumulative evapotranspiration totalled 880 mm, cv Kasbah had been able to maintain 51 % basal cover while other less dormant hispanica populations had declined to 24 % cover with the intermediate cv Currie able to maintain only 12 % cover (Culvenor et al. 2016).

In an earlier study with tall fescue, the summer-dormant cv Flecha maintained 100 % of its pre-summer sward density under the dry spells of 650 and 790 mm CE with a slight decline to 98 % cover when drought intensity increased to 870 mm CE. In contrast, the non-dormant cultivar Demeter could only keep 75 % of its pre-summer sward alive under both the 650 and 870 mm CE droughts (Norton et al. 2006b). Such observations as these, particularly in the light of impending changes in the climate toward a drier and hotter future, have convinced many pasture scientists that the summer dormancy trait merits greater exploitation both for forage production and to help maintain agricultural system sustainability. Figure 3 illustrates the relationships between drought intensity and grass survival as influenced by the drought strategy used by the particular genotype. These relationships are depicted under current and a potential future climate change scenario and are influenced by the level of soil water available.

Before the full potential of the summer dormancy trait can be realised, some pressing problems must be addressed. These have been well summarised by West et al. (2009) who observed that the trade-off between high summer dormancy expression and low forage yield, often also associated with early flowering, must be broken (Knight 1965). As dormancy, by definition means absence of growth, this goal may be considered unrealistic. This is because the three attributes, high dormancy, long

Fig. 3 Present and future adaptation of the perennial forage species, cocksfoot and tall fescue, depending on their drought adaptation strategies and according to (x) current (green) and future (red) average cumulative water deficit across spring and summer (P precipitation, ETP potential evapotranspiration) as influenced by (y) the soil water reserve



duration of dormancy and early flowering, almost always seem strongly correlated. Given the potency of the dormancy trait, it would potentially be attractive if a cultivar with comparable dormancy to cocksfoot cv Kasbah could be developed which would only be inactive for 3 months rather than the 5-month period exhibited by Kasbah. The low forage productivity of many summer-dormant populations is a disincentive to adoption of cultivars with this trait, even though the superior persistence of these plants provides some compensation to this drawback. In this context, the recent publication of research exploring the possibility of breaking this trade-off is timely (Kallida et al. 2016). Even though these researchers observed that high summer dormancy was negatively correlated with annual biomass production (-0.34 , $P < 0.005$), they did note that some progeny had both high dormancy and high productivity indicating the potential to break this trade-off. It is interesting to note that comparable research to this with similar results had occurred with phalaris more than 30 years previously (Oram 1984). Phalaris is not commercially important in the Mediterranean Basin, but as it originates from that region, it is reasonable to assume that its ecophysiological responses and associated genome have many similarities. Scientists specialising in cocksfoot or tall fescue would therefore be wise to note knowledge advances in phalaris.

The second knowledge gap, related to the first, concerns the generally poor understanding of the environmental controls causing induction, expression and release of summer dormancy. Related to this is the lack of information about the relationship between flowering and dormancy induction, and this has important implications because it influences key management decisions such as sowing time. Questions including whether dormancy can be induced independent of flowering need to be addressed. Filling these gaps becomes critical particularly if there is a desire to use the trait in environments where to date it has not been used (West et al. 2009).

P. bulbosa (Ofir 1986; Ofir and Dorenfield 1992; Ofir and Kerem 1982; Ofir and Kigel 1998, 1999, 2003; Ofir and Kigel 2006) and *Hordeum bulbosum* (Ofir 1975, 1976, 1981; Ofir and Koller 1972, 1974; Ofir et al. 1967) are the summer-dormant grasses about which most is known regarding controls over dormancy. This research has mainly been performed in a phytotron. To more efficiently use this trait in the commercially important forage grasses including cocksfoot, tall fescue and phalaris, research in these species directed at a greater understanding of the trait is necessary. The research to tackle both of these problems should be directed not only at understanding environmental controls but also focus on the biochemical and genetic aspects of trait induction, expression and release with effects on productivity explained. Indeed, in phalaris, while the positive contribution of deep roots to dehydration avoidance and the associated drought survival is clear, it still remains to be definitively demonstrated whether and how much summer dormancy enhances drought survival (Norton et al. 2012).

Another problem relates to the difficulty of reliably phenotyping summer dormancy in tall fescue. To date, only lower levels of summer dormancy, termed ‘incomplete summer dormancy’, have been observed in populations of tall fescue in contrast to cocksfoot which contains populations expressing higher levels of dormancy, termed ‘complete summer dormancy’ (Norton et al. 2008; Volaire and Norton 2006) (Fig. 4). Preliminary research has begun to address the difficulty of accurately phenotyping summer dormancy in tall fescue (Bhamidimarri et al. 2012). However, extra research is needed to improve the reliability of trait measurement in this species addressing such questions as definition of the appropriate environmental conditions for phenotyping. There is a strong case for collaborative research between scientists from different regions of the world to work together to address this problem. A measurement system comparable to that developed to assess fall dormancy in lucerne (alfalfa, *Medicago*

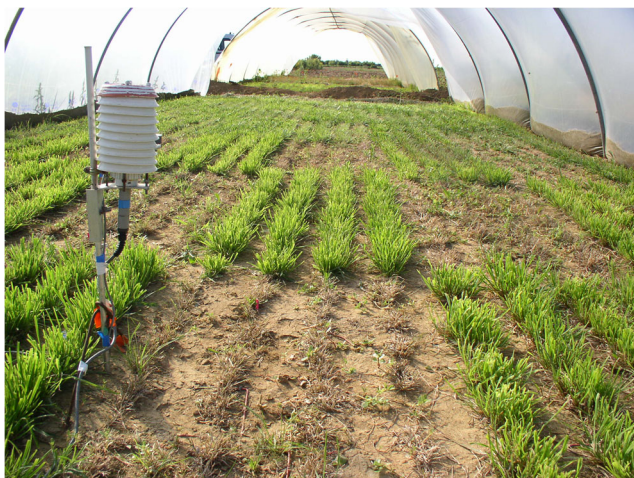


Fig. 4 Measurement of summer dormancy expression in the field under full irrigation over summer. The green, actively growing swards are the Mediterranean cocksfoot cv Medly, whereas the adjoining, senescent swards belong to the highly summer-dormant cocksfoot cv Kasbah

sativa L.) would be an appropriate goal because this system has been uniformly accepted and used among researchers and it has contributed to the progress evident in that very important forage species (Teuber et al. 1998).

Another hurdle in the development of summer-dormant grass technology is the requirement for farmer management packages to allow the establishment and maintenance of compatible, stable grass/legume mixtures (Butler et al. 2008; Butler et al. 2011). This can be particularly problematic at establishment because in grass/legume mixtures, farmers have very few herbicide options for weed control and the young seedlings can easily be out-competed by aggressive weeds (Dear et al. 2007). An understanding of the growth rhythms of all pasture components whether of annual or perennial habit will also be important in selecting the most suitable companion for the summer-dormant grass. The appropriate genotypic components of these mixtures will vary across climatic gradients. The development of principles to guide the degree of expression that must be exhibited by a trait to ensure plant survival in any particular environment will be necessary. For example, to know how much summer dormancy expression is required for a grass to survive in a 400-mm rainfall Mediterranean semi-arid climate may well be necessary.

Finally, as research has not addressed the effects of summer dormancy on reproductive growth, this must occur to ensure commercial availability of seed of cultivars with this trait. Given the central importance of successful seed production to the commercial survival of any cultivar, and the failure to produce adequate seed supplies of key forage species, e.g. cultivars of *Dactylis glomerata* ssp. *hispanica*, there is a clear need for plant breeders and agronomists to place greater emphasis on the development of cultivars with a seed yield high enough for them to be commercially attractive. The unreliability of seed yields is also cited by seed growers of summer-

dormant tall fescue cultivars as a constraint to seed supply chain certainty. The concurrent development of agronomic management guidelines to assist seed producers is clearly essential.

2.5 Drought tolerance—the role of endophytes

Plants of native tall fescue populations are often hosts to symptomless fungal endophytes of the genus *Epichloë coenophiala* (Leuchtman et al. 2014), formerly *Neotyphodium coenophialum* (Hill et al. 1990; Ball et al. 1993). Indeed, there is growing evidence that *Epichloë* spp. endophytes have played a substantial role in the evolutionary adaptation of cool-season perennial grasses to drier and hotter regions of southern Europe (Lewis et al. 1997; Lewis 2000). There is an increasing body of literature describing complex morphological, physiological and metabolic adaptations of cool-season grasses to a broad range of abiotic and biotic stresses as a result of associations with these endophytes (Malinowski and Belesky 2000; Saikkonen et al. 2004). These studies focused almost exclusively on the interactions between grasses originating from the more northern zones of origin, for which symbiosis with the endophytes became vital to their survival in drier and hotter environments. It has been proposed that tall fescue evolved separately north and south of the Mediterranean Sea, as suggested by a lack of cross-compatibility between ecotypes collected in the two regions (Hunt and Slepser 1981; Slepser 1985). Indeed, DNA sequence analysis grouped tall fescue into the southern ecotypes (originating from North Africa, Western Mediterranean, Iberia and southern Italy, bounded in the north by the Pyrenees and the Alps) and northern ecotypes originating from northern Europe into Iberia, Morocco and northern Italy (Craven et al. 2005). Both tall fescue groups harbour the endophytes; however, the endophytes (designated FaTG-2 and FaTG-3) in some of the southern ecotypes of tall fescue (from southern Spain, Algeria and Sardinia) are genetically, biochemically and morphologically different from *E. coenophiala* (Christensen et al. 1993; Clement et al. 2000; Piano et al. 2005). *E. coenophiala* is commonly found in northern tall fescue and in those tall fescue lineages introduced from northern Europe into North America, Australia and New Zealand (Craven et al. 2009).

The role of endophytes in summer-dormant tall fescue is far less understood. The infection frequency of native accessions of summer-dormant tall fescue is usually high (Clement et al. 2001; Piano et al. 2005; Pecetti et al. 2007), suggesting an important ecological role similar to that in continental tall fescue ecotypes. In fact, some of the benefits of endophyte infection are similar for both fescue types, i.e. in terms of tolerance to soil mineral imbalance (Malinowski et al. 2004). Because summer-dormant tall fescue already possesses a highly efficient mechanism of drought avoidance, one may speculate that infection with endophytes would not add

significant improvement in drought tolerance as it is observed for continental tall fescue (Malinowski et al. 2005). Assuero et al. (2000) observed a beneficial role of endophytes for both continental and Mediterranean tall fescue genotypes under controlled growth conditions. In contrast, Flecha summer-dormant tall fescue grown in north Texas for several years did not express any significant increase in persistence whether infected with the endophyte or not (Malinowski et al. 2005; Malinowski et al. 2009). However, after devastating long-term droughts in Texas during 2010–2014, for the first time, a significant positive effect of an endophyte strain (AR584) on survival of an experimental summer-dormant tall fescue breeding line was observed (Malinowski, unpublished data).

Future research should identify novel endophyte strains compatible with summer-dormant tall fescue cultivars similar to those achieved for summer-active tall fescue (Bouton et al. 2002). Studies evaluating effects of the most common novel endophyte strains AR501, AR542 and AR584 on biochemistry and physiology of summer-dormant tall fescue confirm, with the exception of the horse (Bourke et al. 2009), a lack of tall fescue toxicoses in grazing animals (Simpson and Mace 2012; Young et al. 2015). However, altered patterns of bio-protective alkaloids in tall fescue plants infected with the novel endophytes may result in insufficient protection of host grasses against certain insects (Hunt and Newman 2005) that may have unknown long-term consequences for stability of novel associations in managed agroecosystems.

3 Regulatory constraints to use of drought tolerant cool-season grasses—putative weed potential

In the USA, there is currently concern that the introduction of summer-dormant tall fescue may result in the species becoming invasive to native flora. Continental (summer-active) tall fescue was introduced to the USA in the 1800s (Hoveland 2009), and it has become the most important cultivated pasture grass, occupying over 15 million ha (Buckner et al. 1979). Continental tall fescue is a strong competitor with native vegetation, and it has been reported being invasive in Arkansas, Georgia, Idaho, Missouri, New Jersey, Oklahoma, Tennessee, Washington and Wisconsin (USDA-NISIC 2013; USDA-NRCS 2013).

Summer-dormant tall fescue is genetically (Craven et al. 2005) and physiologically (Norton et al. 2006b) distinct from the summer-active variant; thus, its potential to be invasive should not be considered similar. These grasses evolved in association with annual species in Mediterranean grasslands (Naveh 1960). Annual species dominate these plant communities and complete their growth cycles before the onset of summer drought, thus minimising competition for limiting resources with the summer-dormant grasses (Fernández-Alés et al. 1993). Preliminary research suggests that summer-dormant grasses originating from the Mediterranean Basin

and introduced to Mediterranean environments of California have very limited potential for invasiveness when compared with introduced Mediterranean annuals and native summer-dormant grasses (Vaughn et al. 2011). Thus, initial attempts to establish and grow lucerne and summer-dormant tall fescue mixtures in north Texas and southern Oklahoma have proven unsuccessful (Stein et al. 2009). Malinowski et al. (2011) also observed that summer-dormant tall fescue was less competitive than continental tall fescue when both types were grown in binary mixtures with alfalfa, especially when constrained by low soil moisture availability in summer. Summer-dormant tall fescue may be able to coexist only with species expressing a similar growth pattern (Malinowski et al. 2008) and may not be tolerant of a summer-active competitor (Assuero et al. 2002). In non-native environments such as those of the Southern Great Plains, summer-dormant tall fescue is not expected to be able to take advantage of summer soil moisture, in contrast to native temperate and warm-season flora, because its growth pattern is highly restricted. Therefore, summer-dormant tall fescue is not likely to become invasive in environments dominated by warm-season perennial and annual plant species that actively grow during summer when soil moisture is available.

It is true that the introduction of exotic forage species has in some cases led to them becoming invasive weeds, and caution and responsibility need to be exercised in this activity. However, it is possible to ascertain the potential invasiveness of a plant during initial field evaluation so that this introduction can be halted if danger signs, e.g. aggressive spreading into neighbouring plots, occur. The experience in other environments where summer-dormant grasses have been introduced should inform consideration of this issue. The first summer-dormant cultivars in Australia were commercialised in the late 1960s/early 1970s when the cocksfoot cultivars Kasbah and Berber, tall fescue cv Melik and phalaris cv Sirocco were released (Oram 1990). It is important to note that the introduction and release of these exotic plants into diverse southern Australian environments have not led to the development of any of these cultivars into environmental weeds. This contrasts with the situation of summer-active phalaris cultivars which are regarded as showing weed potential in some situations in higher rainfall areas (Carr et al. 1992). Considering the important advantages that grasses with the summer dormancy trait confer particularly in terms of drought survival, and the low likelihood of negative impacts, it should be questioned whether current controls over release of grasses with this trait are warranted.

4 Conclusion and future directions

This paper has highlighted research issues which can mainly be classified as questions of clarification of the phenomics of these species. The addressing of these questions will assist in

the more rapid deployment of genomic selection, which offers much, but so far has delivered little in the improvement of forage species (Barth 2012). A major reason for the slow uptake of these technologies is that they have been relatively expensive until recently so that the relatively small size of the market for new pasture cultivars has made the expense difficult for companies to justify together with the fact that the highly heterozygous, cross-pollinating genetic composition of most cool-season grasses adds great complexity to the task (Wang and Brummer 2012). Consequently for forage plants, these technologies have so far primarily been employed for research and development purposes at publically funded institutions. However, the declining cost of these technologies means that their employment more widely is now becoming likely (Hayes et al. 2013; Resende et al. 2014).

Irrespective of breeding methodology, the long-term sustainability of perennial forage crops rests on the improvement of pasture persistence, i.e. maintaining and increasing density over the long term of the sown species, will remain an important objective of pasture plant breeders. Persistence is important for farmers because when optimised, it ensures that pastures need to be resown less frequently, helping to reduce production costs while protecting often fragile landscapes. However, persistence is a phenomenon with multiple components and presupposes tolerance to biotic and abiotic factors which place life-threatening stress on the plant.

This review has considered those abiotic factors, moisture deficit and high temperature, which future climate change scenarios indicate are most likely to constrain the survival and thus persistence of pasture plants in the future. In summary the main recommendations for future research include:

- Increasing the depth and density of grass root systems to strengthen dehydration avoidance;
- Improving understanding of the biochemical and molecular bases of dehydration tolerance and improving techniques to measure this trait;
- Breaking the trade-off between summer dormancy and yield and improving understanding of environmental, biochemical and genetic controls over summer dormancy;
- Identifying non-toxic endophyte strains compatible with and add value to summer-dormant tall fescue cultivars by enhancing persistence and production;
- Enhancing seed production capability of new cultivars;
- Designing agronomic management packages for promoting stable mixtures combining summer-dormant, cool-season perennial grasses and legumes.

The research directions proposed here should improve pasture grass survival in Mediterranean and temperate summer-dry environments under the future drier and warmer conditions associated with climate change. However, the need for dispassionate assessment of the potential for these species to

become environmental weeds is also necessary for the release of grasses with these superior adaptive traits.

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