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ADAPTATION OF FORAGE SPECIES TO DROUGHT

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Abstract

Variability in rainfall is the single greatest cause of variation in forage production for a given site. Current climate scenarios predict future annual rainfall to decrease at some geographic regions. The intensity of future rainfall is also predicted to increase at other regions, with the expectation of greater variability in soil moisture. The adaptation of forage species to drought is an issue that is likely to remain with us into the future.

Precise definitions are critical to water relations work, and imprecise use of terms has complicated comparisons of some studies on plant response to drought. Drought is a purely relative term, being abnormally low rainfall. Its duration and intensity will vary between locations. The intensity of drought is measured as water potential (-MPa) (relatively difficult), or water deficit (mm) (well suited to modeling) or soil water content (g/g, cm³/cm³, %). None of these measurements has a linear effect on plants. Drought resistance is a virtually meaningless term. Plant water reserves are trivial compared to the demand from the environment, and plants are virtually incapable of resisting drought. Forage plants do vary in tolerance to the intensity and duration of water deficit. Definition is further complicated by the scale of reference; at the plant-scale the plant might tolerate a level of water deficit, however tissues such as primordial are protected and do not encounter stress. At the tissue-scale certain cell components might be protected by osmotic adjustment, which allows some water loss by the plant but maintains turgor and some plant function.

Since growth is largely the physical response of cells to turgor, opportunity for plants to continue growth in the face of water deficit is limited. Plants that could continue growth at low water deficit might be useful during mild and short-term drought, but would likely be at a disadvantage as drought intensified. Recovery from drought is related to preservation of growing points during water deficit, compensatory growth in surviving tissue, and the rate of mobilization

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of root reserves. Plants with rapid recovery are likely to be vulnerable to false-breaks, and appropriate definition of environmental conditions is necessary for plant breeding.

Drought effects on plant quality characteristics are variable. Although increased quality might result from OA, drought invariably decreases plant quality through reduced leaf:stem ratio, accelerated flowering and lignin accumulation

Among the exciting developments in plant water relations are the reports that tolerance to water deficit of some grass species is improved through association with endophytic fungi.

Whole pasture responses to water deficit are poorly understood. Biodiversity theory suggests that sward stability (production and persistence) is greatest for species rich pastures, however research in this area is sparse.

Optimum defoliation during water deficit involves managing the trade-off between benefits of maintaining leaf area for a) carbon fixation for osmotic adjustment and root growth, b) providing an insulation layer preventing soil heating & evaporation, c) ensuring low water potential in the plant to access meager water reserves in the soil. Invariably, at high water deficit (low water status) it is preferable to the plant to have low green leaf area to minimize leaf water loss and heating from radiation. If this does not occur through grazing, it will result from leaf senescence.

There are few options for meeting animal requirements during water deficit. Importing stock feed, reducing animal intake and reducing stocking rate are significant costs to graziers. Excessive defoliation can, however, slow eventual recovery from water deficit, loss of growing points, and depletion of plant energy reserves.

Many forage cultivars have been bred to improve forage production during drought. Molecular technologies offer the potential for greater understanding of the role of specific genes in controlling plant responses to water deficit.

Introduction

In the millennia since famine forced Abraham from Canaan into Egypt (Genesis 12:10) mankind has encountered drought (Woodhouse and Overpeck, 1999). Today, the literature is virtually unanimous that variation in soil moisture resulting from variable rainfall is the single greatest cause of variation in forage yield. Numerous authors have found strong relationships

between forage yield and either soil moisture or rainfall (Rickard and Fitzgerald, 1970; Baars and Coulter, 1974; Radcliffe, 1979; Alcock and Al-Juboury, 1981; Lambert *et al.*, 1983). Although other factors such as temperature, radiation, day length, soil fertility and soil depth have large effects on plants, they are inherently less variable at any point in time or space.

Most drought research has been with non-forage species. Ludlow and Muchow (1990) have summarized the suitability of 16 traits for row-crop production in water-limited environments. Characteristics such as rooting depth & density, early vigor, developmental plasticity, low root hydraulic conductance, low root hydraulic conductance, osmotic adjustment, low lethal water status, reduced stomatal conductance, leaf movements, leaf reflectance, heat tolerance, low epidermal conductance, and transpiration efficiency are clearly of mutual value in both crop and forage plants. Other characteristics such as leaf area maintenance and matching phenology to water supply are of uncertain value in forage plants. Of little value to forage plants are characteristics ensuring grain harvest, such as mobilization of pre-anthesis dry matter and photoperiod sensitivity. Emphasis in this review will be on the areas where demands on forage plants are unique from other plants:

- 1) most forage plants are perennial and are required to provide feed for use during a drought as well as survive after a drought,
- 2) all forage plants are subjected to defoliation (grazing or cutting); the severity often increases during drought,
- 3) many forage plants are grown in drier environments than are cropped,
- 4) forages have a requirement for quality in addition to yield; quality characteristics of forages are uniquely affected by drought.

The literature is prolific on the topic of drought. A search of the AGRICOLA database for (drought or water) found 158,860 references. Further refinement to (drought, water or moisture) and (pasture or forage) found 1,916 references. Among this literature are several excellent reviews and readers are referred to Levitt (1980), Jones *et al.* (1981), Morgan (1984), Ludlow and Muchow (1990), Belhassen (1996) and Thomas (1997) for further reading on adaptation of plants to drought, and to Turner and Begg (1978), Kemp and Culvenor (1994) and Frank *et al.* (1996) for specific discussion of forage species.

Current climate change scenarios predict future annual rainfall to decrease in some geographic localities (Campbell, 2001). The intensity of future rainfall is also predicted to

increase at other localities sites, with the expectation of greater variability in soil moisture (Campbell, 2001). The adaptation of forage species to drought is an issue that is likely to remain with us into the future.

Definitions

Precise definitions are critical to water relations work, and imprecise use of terms has complicated comparisons of some studies on plant response to drought. There are numerous definitions of drought (Table 1), with none being universally accepted (Passioura 1996). Du Pisani *et al.* (1998) note that no absolute objective biophysical criteria have been identified for quantifying the onset and end of drought. The most consistent element in definitions of drought is a negative impact of dry weather on mankind. This can include reduced yield, food quality or water supply, or increased production costs or fire risk. In this respect drought is largely a human construct, with definitions varying in how dry weather and its impact are determined. Dry weather not affecting production (or conceivably improving production) would not be drought.

Meteorologically-based definitions typically define drought by a minimum threshold for rainfall over some period of time (Passioura, 1996). Such definitions have the advantage of being simple but the limitation of not considering any impact on plants. In some cases drought is defined as some critical (low) proportion of seasonal norms. In this case definition of drought can have regional specificity, where what is accepted as drought in one region might not be regarded as drought in another (Jones *et al.*, 1981). It also follows in this case that water deficit could reduce yield and not necessarily be the consequence of drought, and furthermore that irrigation responses could occur in the absence of drought. Du Pisani *et al.* (1998) also suggest caution in reporting return times for drought, since the statistical error in predicting infrequent low-rainfall events can be high.

Biologically-based definitions typically define drought in terms of a growth-limiting water deficit. For example, Rickard and Fitzgerald (1970) define agricultural drought as when soil moisture in the root zone is at or below wilting point (50-60 mm water deficit). They went on to show a strong relationship between pasture production and days of agricultural drought (range 2-96 days).

Sociologically-based definitions often include some climatic thresholds, but also involve consideration of impacts on production, farm costs and rural communities, often on a regional basis (du Pisani *et al.*, 1998). Such definitions often have the objective of determining the requirement for government intervention and aid.

Drought has components of duration and intensity. The duration of drought has been reported to vary from as short as 2 days (Rickard and Fitzgerald, 1970) to as long as 20 years (Woodhouse and Overpeck, 1999). The intensity of drought is measured as soil water status, with units of water potential (-MPa), soil water deficit (mm) or soil water content (g/g, cm³/cm³, %). None of these measurements has a linear effect on plant or animal production, at critical points a small change in a water status can result in a large effect on the plant.

Drought resistance is described by Passioura (1996) as a nebulous term encompassing the various strategies for plants to tolerate or escape drought (Levitt, 1980). Although it is used widely, drought resistance is in reality a misnomer since the potential for plants to truly resist the dominating effect of their environment is trivial. Boswell and Espie (1998) describe the ability of a rangeland forb (*Hieracium pilosella*) to preferentially remove water from a “halo” at the limit of its rooting circle and maintain a more favourable water status immediately under the plant, however such a mechanism is not reported in forage species. Drought tolerance can be subdivided into tolerance at high potential (dehydration avoidance (Levitt, 1980)) or tolerance at low potential (dehydration tolerance (Levitt, 1980)) (Jones *et al.* 1981). In the former case cells are protected from dehydration and do not encounter stress (Tardieu, 1996).

Drought adaptation is the process of change in a plant that increases its ability to tolerate drought. A vast number of responses to drought have been reported in plants and most cases (but not all (Bray, 1993)) confer some adaptive advantage to a plant to survive but not necessarily produce during drought. Clearly, time is required for adaptation to occur and in ryegrass (*Lolium perenne*), a slowly applied stress resulted in a smaller effect (40% reduction) on photosynthesis than a rapidly imposed stress (80% reduction) (Jones *et al.*, 1980a). Usually plants have a suite of interacting responses that in combination confer drought adaptation. Since the occurrence of any particular response does not necessarily confer adaptation, breeding for a single trait might not necessarily result in improved field performance. Furthermore, the absence of any particular response does not necessarily imply drought sensitivity since Barker *et al.* (1993b) found varying

levels of osmotic adjustment and cell wall elasticity in a range of grass species that were all well adapted to drought.

Summary of Plant Responses to Drought

Community responses to drought

The literature is clear that species vary in their tolerance to water deficit. Species such as cocksfoot (*Dactylis glomerata*) and tall fescue (*Festuca arundinacea*) are more abundant in moderately dry environments (Jackson, 1974) and species such as big bluestem (*Andropogon gerardii*) and wheatgrass (*Agropyron cristatum*) are more abundant in dry environments (Barnes, 1985; Frank *et al.*, 1996). These species have traits conferring tolerance to both water deficit and variation in the severity of water deficit, and contribute to adaptation of the pasture community to survive and produce during future drought.

Natural reseeding by annuals is frequently cited as a drought avoidance strategy (Levitt, 1980). This is successful in subterranean clover (*Trifolium subterraneum*) since this species has wide occurrence in dry environments and can replace white clover (*T. repens*) in non-irrigated pastures (Rickard and Fitzgerald, 1970). The rapid growth of annuals upon relief from water stress can allow them to exploit spaces in a sward better than their slower growing perennial competitors. In contrast however, some studies have found that during their growth phase, annual species have greater sensitivity to drought than perennials (e.g. annual compared to perennial ryegrass (Norris and Thomas, 1982)) and out-of-season drought can result in decreased abundance of annuals in pasture (Espigares and Peco, 1995).

The study of Tillman and Downing (1994) that reports a strong positive relationship between biodiversity (species richness) and recovery from drought in grassland is in contrast with Sankaran and McNaughton (1999) who found greatest yield from simpler species mixtures in a dry environment. Conceptually, one might imagine that a mixture of species (and genotypes within a species) might be better able to exploit a range of conditions in a variably dry environment, however insufficient evidence has been collected to fully quantify all the circumstances where this might apply.

Morphological responses to drought

Morphological responses to drought are dramatic and obvious. For example, water stressed ryegrass has smaller, thicker and shorter leaves, deeper ridging on adaxial leaf surfaces, a slower rate of leaf expansion and slower leaf appearance (Leafe *et al.*, 1977; Jones *et al.*, 1980b). Collectively, these responses have adaptive value since they reduce the radiation load on leaves and reduce water use. Ritchie and Burnett (1971) found in sorghum and cotton that as leaf area index decreases below 3, actual evapotranspiration becomes less than potential evapotranspiration.

Among the most important plant responses to drought is continued root growth. Whether greater absolute growth than watered controls, greater root:shoot ratio compared to watered controls (Jones *et al.*, 1980b) or deeper root growth (Caradus and Woodfield, 1998) the ability of plants to maintain access to soil water reserves is critical to surviving drought.

In addition to impaired leaf expansion, the rate of tiller appearance is slower in drought stressed ryegrass (Korte and Chu, 1982; Barker *et al.*, 1985). Death processes are generally not affected by drought and the death rate of tillers present at the start of drought were similar to watered controls (Korte and Chu, 1982; Barker *et al.*, 1985). Grazing managements or cultivars with a high population density before drought can have faster recovery upon relief from stress (Barker *et al.*, 1985; Kemp and Culvenor, 1994; Brock and Caradus, 1996).

Anatomical and physiological responses to drought

As water deficit develops, the plant relative water content and leaf water potential decrease. Since growth is related to cell turgor, the first plant process to be affected is the rate of cell expansion. Over time this results in reduced plant size, a higher stomatal density, smaller epidermal cells and increased chlorophyll concentration compared to watered controls (Leafe *et al.*, 1977). As a direct consequence of dehydration, cellular contents become concentrated and osmotic potential decreases. Continued photosynthesis and reduced utilization of water soluble carbohydrates contribute to a further decrease in osmotic potential (Brown and Blaser, 1970). This osmotic adjustment has considerable adaptive value since it helps maintain cell turgor and contributes to compensatory growth upon re-watering (Horst and Nelson, 1979).

Reduced leaf turgor ultimately impairs stomatal function and causes leaf rolling. These process increase stomatal resistance, reduce CO₂ exchange and elevate leaf temperature. Plants with C4 metabolism are relatively less affected since their unique CO₂ pathway allows carbon accumulation to continue despite greater stomatal conductance.

At moderate stress levels, expression of abscisic acid (ABA) will trigger innumerable biochemical and molecular responses as precursors to total loss of leaf (or in extreme cases plant) function. Production of osmoprotectants such as proline is proposed to offer protection to nucleic acids. As water stress develops, senescence processes are initiated, beginning with the export of leaf metabolites towards meristematic areas and ultimately resulting in leaf excision.

Biochemical and molecular responses to drought

As cellular contents become concentrated through dehydration, plant metabolism responds through altered enzyme kinetics and concentration of reaction substrates and products. An increase in the activity and concentration of α -amylase (hydrolyzing starch to fructose and glucose) due to water stress has been found in maize (Maranville and Paulsen, 1970) and barley (Jacobsen *et al.*, 1986). Jacobsen *et al.* (1986) went on to show the increase in α -amylase resulted from de novo synthesis regulated ultimately by genetic transcription. In maize and forage sorghum, drought can decrease the activity of nitrate reductase, resulting in accumulation of nitrate to levels toxic to stock (Foyer *et al.*, 1998).

The basis of virtually all plant responses whether fast or slow, direct or indirect lies encoded within the genome. Given the complexity of these responses it is likely suites of genes are involved in the expression of these responses. Considerable progress has been made in identifying molecular responses since 1990, and reviews on this subject include Bray (1993) and Belhassen (1996). The production and expression of heat shock proteins during water stress has been characterized and the genetic control identified (Key *et al.*, 1981; Heikkila *et al.*, 1984; Guerrero and Mullet, 1988). Although these responses might be derived from the genome, the short and severe duration of the stress imposed during experimental conditions may be unrelated to responses occurring with field conditions. Further work is required to establish adaptive benefit (Bray, 1993).

The gene Rab21 in rice has been found to be activated by ABA, water stress (Mundy and Chua, 1988) and cold (Hahn and Walbot, 1989). This gene may be involved in synthesis or control of the enzyme sucrose synthetase (Hahn and Walbot, 1989), and therefore has the potential to exert a direct effect on one of the important contributors to osmotic adjustment. The gene pMAH9 from maize, which encodes a glycine rich protein, is activated by water stress and ABA accumulation (Gomez *et al.*, 1988). Glycine rich proteins such as osmatin and thaumatin can comprise up to 12% of total cellular protein of stressed cells, and likely have a role in protein storage or osmotic adjustment (Singh *et al.*, 1987). New molecular technologies offer the potential for greater understanding of the control of plant responses to drought (Bray 1993).

Pasture Perenniality

Pasture-based animal production requires a year-round supply of forage to meet animal requirements and any drought-induced interruption in this supply will either reduce production or increase costs. The effect of drought on systems can be differentiated between i) those effects on a system adapted to an anticipated water deficit (usually summer) and ii) those effects of an unexpected (often severe) water deficit. In this later case, there are few management options, other than purchase of additional feed (usually at a demand-inflated price) or decrease in stock numbers. Options for production during anticipated water deficit include:

- a) stock management to minimize animal requirements during dry seasons e.g. as non-lactating/non-pregnant breeding stock,
- b) maximize production during wet seasons e.g. finish lambs early or on-farm conserved feed,
- c) use of specialty forage crops which can accumulate biomass to feed during drought (e.g. brassica crops, feed-sorghum),
- d) use of specialty pasture species e.g. C4 grasses, lucerne, tall fescue, chicory.

It remains unavoidable in pastoral agriculture that maintaining a conservative stocking rate and “emergency” feed supplies are production costs of a variably dry environment (Illius *et al.*, 1998).

Opinion varies in the acceptability of human intervention in ensuring pasture perenniality following drought. Ecologically-speaking, perenniality is a functional requirement of grassland, however in pastoral systems this function is complemented to varying extents by human

intervention through reseedling. Annual species (most notably subterranean clover) are dependant on natural reseedling. Perennial species are largely dependant on vegetative propagation, and the role of reseedling in perennial species is subject to debate (Hume and Barker, 1991). With the negative relationship between drought production and drought survival (Knight, 1973) managers are faced with the dilemma of deciding what are acceptable levels of pasture production and relative costs of natural vs. interventionist re-establishment following drought.

Since growth is largely the physical response of cells to turgor, opportunity for plants to continue growth in the face of water deficit is limited. Plants that could continue growth at low water deficit might be useful during mild and short-term drought, but would likely be at a disadvantage as drought intensified. Ecologically-speaking, there are few advantages for a plant to continue growth in dry conditions. Some species might gain advantage over others for resources (lights & nutrients) by having some growth during short-lived dry periods, however in general plants gain greatest advantage from avoiding prolonged dry periods. The ability of plants to continue production during drought is of less value than the benefit of plants to survive drought (Volaire *et al.* 1998a).

As a consequence of being perennial, forage species will encounter a range in climatic conditions. Over their typical 5-50 year lifetime, pastures will need to be adapted to both drought and wet years. In contrast, row-crops are established annually and a manager has the option of varying the cultivar sown in response to current or projected climate. Kemp and Culvenor (1994) consider the dilemma of selecting a ryegrass cultivar that might survive a long Australian drought but be less productive during wet seasons.

Defoliation (Grazing and Cutting)

Forage plants differ from most other plant species in that they are subjected to grazing, the severity of which often increases during drought as feed becomes scarce. Apart from the benefit of water conservation under short pasture, the effects of defoliation are largely detrimental to plant survival during drought. These effects include reduced photosynthesis and impaired osmotic adjustment, impaired root growth, reduced water potential gradient – preventing water uptake from the soil, sudden loss of the transpiring surface with consequential heating (Barker and Chu, 1985).

In general, close and infrequent grazing will give high pasture growth under wet conditions (Appadurai and Holmes, 1964; Brougham 1970) but will result in poor pasture growth during drought (Appadurai and Holmes, 1964). Baker and Jung (1968) observed high plant losses following defoliation during drought, and suggested it might be more important to have precipitation at the time plants are defoliated rather than later in the growth period. Jackson (1974) found that undefoliated cocksfoot had a leaf water potential up to 0.4 MPa lower than defoliated plants during water deficit. In the case where a plant was maintaining its water status slightly above the permanent wilting point, defoliation could put the plant into immediate and severe water deficit stress (Jantti and Kramer, 1956; Jantti and Heinonen, 1957).

The only benefit of defoliating pasture during drought appears to be water conservation. Goode (1955) found that short mowing of grass conserved water at 45-90 cm soil depth. It was not clear if this was caused by a reduced transpiring surface or from impaired root mass/depth. Mitchell and Kerr (1966) also found greater soil water depletion by tall ryegrass (less so for tall white clover), attributable to greater radiation and elevated temperature in the tall stand. Neither of these studies demonstrated if these swards were able to benefit from this conserved water for continued growth during drought or improved survival following drought.

Defoliation management to increase tiller density prior to drought can result in a greater population of tillers surviving drought and a faster recovery following relief of drought (Brougham 1970; Barker *et al.*, 1985; Kemp and Culvenor, 1994). These studies used close defoliation prior to drought and avoided close defoliation during drought, consistent with the recommendation of Appadurai and Holmes (1964). This recommendation is not readily compatible with grazing practice where feed deficits during drought make it difficult to avoid close grazing.

Dry environments

In geographic regions where soils are too steep, sandy, infertile or dry to be suitable for row cropping, the predominant land use is often extensive pastoral farming. Pasture establishment in these environments is often impossible, or dependent on low cost methods with variable success (Awan *et al.*, 1993; Awan *et al.*, 1996). The forage species in these regions frequently encounter extreme water deficits and require adaptations giving tolerance to

prolonged and severe drought. In such environments most forage production is likely to come from brief periods of rainfall, and drought escape would be the best plant strategy. Perennials would be dependant on extreme dehydration avoidance strategies, with little benefit likely to result from dehydration avoidance strategies.

Among the exciting recent discoveries is the role of fungal endophytes in conferring environmental tolerance in a number of grass species (Saikkonen *et al.*, 1998). While there is clear evidence that endophytes confer resistance to some insects, the benefits in conferring drought tolerance are less clear. Some reports show greater tolerance to drought in endophyte-infected tall fescue (Buck *et al.*, 1997; Assuero *et al.*, 2000) and ryegrass (Ravel *et al.*, 1995), however, other reports show no benefit from the plant-endophyte association (Barker *et al.*, 1997). Clearly further work is required clarifying conditions where the benefit occurs. Evidence of an interaction between the plant host and the endophyte strain on physiological responses is of considerable interest (Assuero *et al.*, 2000) and also requires closer investigation.

Quality

Nutritive value is an important component of forage quality, and knowledge of situations where quality might be affected by drought is of importance. Factors affecting forage quality during drought include the frequent accumulation of dead material in the sward, the loss of legumes from the sward, direct effects on fibre and protein in the remaining green forage, and in some instances the accumulation of anti-quality constituents (alkaloids and nitrate)

The amount of dead material in pasture has a huge effect on forage quality. In most cases drought will not increase the rate of leaf death, however, non-decay of dead material during dry conditions usually results in an increase in the dead content of pasture and a resulting decrease in quality. During grazing, animals will attempt to avoid dead material and the influence of accumulating dead matter during drought does not always have a proportional decrease in the forage consumed by stock.

Species vary in both their forage quality and response to water deficit. As a consequence, changes in botanical composition during drought can be accompanied by a change in forage quality. Although legumes have a higher temperature optimum for growth than most grasses and are typically more active during summer, they also tend to be more sensitive to water deficit.

Since legumes are the highest quality components of pastures, their loss from the sward during drought will result in decreased forage quality.

As plants respond to drought they typically show accelerated maturity, increased fibre, altered leaf:stem ratio, breakdown of protein and elevated water soluble carbohydrate status. These factors can result in an unpredictable effect on forage quality. In lucerne (Mir Hosseini Dehabadi *et al.*, 1994) and other legumes species (Pederson *et al.*, 1992), drought increased the leaf:stem weight ratio with the result of improved quality but drastically reduced yield.

Anti-quality components that accumulate in forages during water stress include alkaloids and nitrate. One consequence of the endophyte-grass association is production of alkaloids including lolitrem in ryegrass and ergovaline in ryegrass and tall fescue. These alkaloids are typically (but not exclusively) localized in plant crowns and are largely not consumed by stock. With the occurrence of drought, ergovaline concentrations can increase above 1-2 ppm in leaves and stems and become toxic to stock (Barker *et al.*, 1993a). Furthermore, as feed supplies become limited, animals will progressively graze near the plant crowns and can encounter toxic levels of these alkaloids. In C4 grasses (e.g. maize, forage sorghum, sudangrass and pearl millet) decreased activity of nitrate reductase during drought (Foyer *et al.*, 1998) can result in toxic nitrate levels, and testing is recommended prior to grazing these species (Pickrell *et al.*, 1991)

Breeding for adaptation to drought

Considerable variation exists within species for the array of traits related to their production and survival during drought, and this allows scope for selection of plant-types adapted to drought (Table 2). Reviews in this area include Johnson and Asay (1993), Kemp and Culvenor (1994) and Ceccarelli and Grando (1996).

Researchers vary in their views on which traits are of importance in drought-prone environments. Tardieu (1996) argues there is sufficient scope for selection of dehydration avoidance traits to continue growth during water deficit and that transferring genes for desiccation tolerance may have no impact on agronomic yield. In an alternative view, Volaire *et al.* (1998a) argue that in environments with extreme (80 day) drought the best strategy is to avoid growth during drought

and select for traits of desiccation tolerance, thus increasing plant survival during drought. Clearly plants are required to be bred for specific environments.

Traditional genetics has made some progress in identifying genes associated with drought tolerance. Morgan (1984) found with crossing high and low osmoregulating near-isogenic wheat lines, a tendency for F4 and F6 progeny to segregate into groups that were predominantly high or low in osmoregulation. He concluded this trait might be controlled by a single gene, however, considering the complexity of osmotic adjustment it is difficult to propose a mechanism with only one controlling enzyme (or mRNA or gene). In a similar case, with crosses within the big bluestem – sand bluestem (*Andropogon gerardii*) complex, Barnes (1985) found that osmotic potential at full turgor and stomatal conductance of hybrids were most similar to big bluestem. This might suggest relatively simple genetic inheritance, however, in some cases hybrids were intermediate in character and more complex genetic inheritance may be involved.

The development of new molecular tools such as restriction fragment length polymorphisms (RFLP), chromosome markers, and quantitative trait locus analysis (Quarrie, 1996) will allow further progress in identifying the genetic control of plant adaptation to water deficit and in breeding forages with improved drought tolerance.

Conclusions

In addition to the drought adaptations in common with other crop plants, there are demands on forage plants are unique from other species. Most forages are perennial and are required to provide feed for use during a drought as well as recover after a drought; annual species are expected to survive in successive years through natural reseeding. Survival and production in non-drought periods are frequently better strategies than continued production into drought. All forage plants are subjected to defoliation (grazing or cutting) and the severity often increases during drought. In low-input, extensive pastoral agriculture forage plants are grown in drier environments than are cropped and frequently encounter extreme drought stress. In addition to yield, forages are required to have sufficient quality for stock; quality characteristics of forages are uniquely affected by drought. With an increasing world population, fixed water resources, and predictions for climate change, it is likely that adaptation of forage species to drought will remain of interest into the future.

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Table 1 - Definitions of drought

Term	Definition	Reference
crop water stress index (CWSI)	calculated from radiation, wind speed, air temperature, humidity, and canopy temperature (USA)	Feldhake <i>et al.</i> (1997)
drought exceptional conditions (DEC)	A 1 in 25 year event – based on meteorological conditions, impact on farms and rural communities (A)	White <i>et al.</i> (1998)
disaster drought	<70% of average rainfall over 2 years (SA)	Schulze cited by du Pisani <i>et al.</i> (1998)
disaster drought	<50% of average rainfall over 6 months (SA)	Venter cited by du Pisani <i>et al.</i> (1998)
drought	when the 12-month rainfall deficit exceeds monthly average rainfall (SA)	Herbst <i>et al.</i> cited by du Pisani <i>et al.</i> (1998)
severe rainfall deficiency	3-month rainfall is in the lowest 10% of occurrences (SA)	Erasmus cited by du Pisani <i>et al.</i> (1998)
disaster drought	3-month rain is in the lower 5% of historical events (SA)	Erasmus cited by du Pisani <i>et al.</i> (1998)
disaster drought	<30% of average rainfall over 3 months (SA)	Erasmus cited by du Pisani <i>et al.</i> (1998)
disaster drought	Return time 1-in-5 years (SA)	Fouche cited by du Pisani <i>et al.</i> (1998)
disaster drought	Return time of 1-in-14 years (SA)	de Jagger cited by du Pisani <i>et al.</i> (1998)
prolonged Mediterranean drought	80 days without rainfall (F)	Volaire <i>et al.</i> (1998a)
agricultural drought	15 days without rain (NZ)	Rickard (1960), cited by Coulter (1966)
agricultural drought	soil moisture at or below wilting point (nominally 50 mm of water deficit) (NZ)	Rickard & Fitzgerald (1970)
drought days	the number of days soil moisture at or below wilting point (NZ)	Rickard & Fitzgerald (1970)
partial drought	29 days with <7 mm rainfall (NZ)	cited by Coulter (1966)

Abbreviations: SA = South Africa, A = Australia, NZ = New Zealand, F = France, USA = United States of America

Table 2 - Summary of forage adaptations to drought

Response	Continued vegetative growth	Plant survival/enhanced recovery
Community responses		
tolerant perennials	in some cases	important for cocksfoot and ryegrass, no difference between species (Volaire <i>et al.</i> , 1998a)
annuals	no	natural reseeding (Hume and Barker, 1991; Espigares and Peco, 1995)
biodiversity		positive relationship (Tilman and Downing, 1994)
Morphological responses		
deep root system	e.g. alfalfa and tall fescue	superior survival in cocksfoot and ryegrass (Volaire <i>et al.</i> , 1998a), Ludlow and Muchow (1990)
reduced leaf area index	LAI<3 impairs water use in crops, conserves water use (Ritchie and Burnett, 1971)	
survival of leaves	negligible and resulted in little production during drought (Volaire <i>et al.</i> , 1998a)	negative association with survival (Knight, 1973)
survival of tillers, high population density		was critical in post-drought production (Korte and Chu, 1982; Barker <i>et al.</i> , 1985; Volaire <i>et al.</i> , 1998a; Brock and Caradus, 1996)
Maintenance of water status	cocksfoot had slower water depletion than ryegrass and produced into drought (Jackson, 1974)	Volaire <i>et al.</i> , (1998a)
Early flowering		was associated with drought survival (Volaire & Lelievre)
Early flowering		Was useful in cocksfoot but not ryegrass (Volaire <i>et al.</i> , 1998a)
early vigor	Ludlow & Muchow (1990)	

