

Water Relations of Cool-Season Grasses'

ALBERT B. FRANK

*USDA-ARS
Mandan, North Dakota*

SHABTAI BITTMAN

*Agricultural and Agri-Food Canada
Agassiz, British Columbia, Canada*

DOUGLAS A. JOHNSON

*USDA-ARS
Logan, Utah*

Availability of soil water is the single most important factor modifying sustained productivity and persistence of cool-season grasses. Water deficits resulting from intermittent or prolonged periods of drought can lead to significant reductions in leaf area, which is critical in determining dry matter production and forage quality in cool-season grasses.

Water is of special importance in forage production in temperate regions of the world. In the semiarid Northern Great Plains of North America, more than 50% of the yearly variation in forage yield can be attributed to precipitation, usually that received in spring or late fall of the previous year (Table 5-1). Water also has a substantial effect on yield in more mesic environments such as the United Kingdom (Garwood et al., 1979).

Drought has an immediate and direct effect on forage productivity because leaf expansion ceases quickly with onset of water deficit. Also, forages often are relegated to poor soils, which have low water-holding capacity. Management factors such as cutting and grazing, and environmental factors such as low or high temperatures, interact with water status in influencing both yield and persistence. Drought also influences the nutritional quality of forage (e.g., carbohydrates, leaf senescence), and xeromorphic characters such as a thick, waxy cuticle and rigid, lignified cell walls lower the nutritional value of the forage. Severe drought may contribute to stand loss with subsequent economic conse-

¹ Common names for plants have been used throughout the chapter. Refer to the appendix for the scientific name.

Copyright © 1996 American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, 677 S. Segoe Rd., Madison, WI 53711, USA.
Cool-Season Forage Grasses, Agronomy Monograph no. 34.

FRANK ET AL.

Table 5-1. Relationship between water (soil water and/or precipitation) and forage yields on the Northern Great Plains.

Period

Correlation coefficient
(r) Source

Crested wheatgrass

Crested wheatgrass
Smooth brome grass
Russian wildrye
Crested wheatgrass
Crested wheatgrassNative range
Native range unfertilized fertilized
Native range

Growing season precipitation

April-May precipitation April-May precipitation April-May precipitation May precipitation August-May 15 precipitation May-June precipitation

Fall soil water, 0-0.6 m June precipitation Fall soil water, 0-2 m and April-July precipitation0.85 Kilcher & Heinrichs,
19660.89 Stitt, 1958
0.90 Stitt, 1958
0.93 Stitt, 1958
0.89 Power & Alessi, 1970
0.70 Sneva, 1977

0.86 Smoliak, 1956

0.82 Johnston et al., 1969
0.68
0.84

Rogler & Haas, 1947

quences, and soils used for raising forages may be subjected to erosion caused by loss of ground cover during re-establishment of the sward. Livestock producers are particularly vulnerable to the effects of drought because they require a stable supply of forage.

In this chapter we will discuss mechanisms of plant response to drought, whole plant responses to soil water deficits, and the effects of water deficits on physiological processes that control growth, development, and dry matter accumulation in forage grasses.

MECHANISMS OF PLANT RESPONSE TO DROUGHT

Although classification of plant responses to drought varies among authors, we prefer to use the categories suggested by Turner (1986), who classifies plant adaptations into three categories: (i) drought escape, (ii) dehydration postponement, and (iii) dehydration tolerance. These include morphological, physiological, anatomical, and phenological adaptations and have been discussed in relation to pasture plants by Turner and Begg (1978) and in general by Turner and Begg (1981) and Ludlow (1989).

Drought Escape

This mechanism, accomplished through rapid phenological development, involves the capacity of a plant to complete its life cycle before drought becomes limiting. Perennial, cool-season grasses are not true drought escapers because their life cycle is not completed after seeds are produced. In the Northern Great

Plains, crested wheatgrass displays a drought-escape tendency by initiating growth early in spring (Bittman & Simpson, 1987; Frank & Ries, 1990), producing seeds earlier and undergoing more rapid leaf senescence than other grasses such as smooth brome grass and western wheatgrass. Crested wheatgrass then becomes quiescent during hot dry summers and reinitiates growth in fall if water is available.

Two introduced annual, cool-season grasses, which are prominent in the California annual grasslands, soft brome grass and slender oat, are more typical drought escapers. These species survive summer drought as seed produced in spring and are able to produce viable seed even with early drought (Ewing & Menke, 1983). These annual species compete successfully by using available soil water and completing their life cycle up to 60 d earlier in spring than the native perennial grasses (reviewed by Gordon et al., 1989).

Dehydration Postponement

Dehydration postponement mechanisms allow the plant to maintain a favorable internal water content or tissue water potential during drought. These mechanisms include: reduction of water loss, maintenance of water uptake, maintenance of cell volume, and osmotic adjustment (Turner, 1986).

Reduction of Water Loss

Leaf Attributes

Water loss from leaves is affected by stomatal distribution, surface ridging, epicuticular waxes, leaf rolling, leaf orientation, pubescence, and leaf senescence, but the relationships are often unexpected or contradictory. For example, density and size of stomata are positively related to transpiration (Wilson, 1975a; Anderson & Briske, 1990) and in smooth brome grass, stomatal density may be related to yield (Walton, 1974). However, a negative relationship between stomatal frequency and photosynthesis is found in corn (Heichel, 1971).

Stomata of temperate grasses are usually more numerous on adaxial (top) than on abaxial (bottom) leaf surfaces, although in some species stomata are confined to the adaxial surface (e.g., rough rescue) while in others stomata are either evenly divided or more numerous on abaxial surfaces [e.g., western wheatgrass, Indian ricegrass (Redmann, 1985)]. An interesting variation is Texas needlegrass which has 83% of its stomata on the adaxial surface; however, because of a twist at the leaf base, the adaxial surface is oriented abaxially so that the species functionally resembles the cohabiting warm-season grasses (Anderson & Briske, 1990). A greater proportion of leaf conductance from the adaxial surface has been reported for several temperate Gramineae and in some species the proportion increases under water deficit (Morgan, 1977; Bittman & Simpson, 1989a). No simple relationship exists between stomatal distribution and dryness of habitat in grass species; however, as the habitat becomes drier, any selective advantage of proportionately more adaxial or abaxial stomata seemingly becomes smaller (Redmann, 1985; Anderson & Briske, 1990; Foster & Smith, 1986).

Stomata on adaxial leaf surfaces of temperate grasses are frequently located on the bottom of grooves. This arrangement should decrease transpiration by reducing turbulence or increasing thickness of leaf boundary layer at the stomatal opening, but surprisingly studies on perennial ryegrass and tall fescue have shown that this attribute is actually associated with rapid transpiration (Wilson, 1975b; Silcock & Wilson, 1981). High humidity within the grooves and the leaf boundary layer may enable stomata to remain open longer during drought.

Epicuticular wax often forms on grass leaves under hot, dry conditions. Transpiration in tall fescue was increased by removal of epicuticular waxes (Pitcairn et al., 1986). Genetic lines of intermediate wheatgrass with epicuticular waxes had higher radiation reflectance, lower midday canopy temperature, and higher predawn leaf water potential than nonwaxy lines (Jefferson et al., 1989b). Surprisingly, waxy lines of Altai wildrye used water less efficiently on wet soil and had higher leaf temperature on dry soils compared to nonwaxy lines. No relationship was found between waxiness and yield in Altai wildrye lines at two contrasting soil water levels (Jefferson et al., 1989a). Yield and waxiness were negatively correlated in crested wheatgrass at both moderate and low soil water, and wax had no effect on cuticular transpiration from excised leaves (Jefferson et al., 1989b). Lawrence and Ratzlaff (1988) found a positive relationship between yield and waxiness in lines of Altai wildrye only in wet years.

Leaves of many grass species roll during drought due to changes in turgor in rows of bulliform cells. Under drought conditions, leaf rolling reduces heat load and transpiration (Johns, 1978; O'Toole & Cruz, 1980). Transpiration of tall fescue leaves was reduced by up to 65% when leaves were artificially rolled (Renard & Demessemaeker, 1983). Leaf rolling contributed to the relatively high productivity of tall fescue under drought (Johns, 1978). In crested wheatgrass, leaf rolling occurred as a threshold response, which corresponded closely with zero turgor in the leaves as their water potential declined from -1.8 MPa before head emergence to -2.6 MPa after head emergence (Bittman & Simpson, 1989a). In pastures, bison urine decreased folding of Kentucky bluegrass leaves at low leaf water potentials, probably due to the increased N (Day & Detling, 1990). Though leaf rolling seems to reduce transpiration, Redmann (1985) suggested that relatively high humidity within rolled leaves may enable stomata to remain open, thus helping to maintain transpiration during periods of water deficit. Leaves of the warm-season grass, little bluestem, with 99% abaxial stomata, roll adaxially leaving the stomata exposed, suggesting that leaf rolling during drought may serve to reduce heat load more than transpiration (Anderson & Briske, 1990).

Stomatal Control

When water is ample, the rate of transpiration influences the rate of soil water loss, hence the onset of drought. Soil water depletion rates influence species composition in mixed-grass communities (Jackson & Roy, 1986). High leaf conductance was responsible for rapid depletion of soil water and greater plant water deficit in orchardgrass and Italian ryegrass than in perennial ryegrass (Thomas, 1986a). Leaf or stomatal conductance of cool-season grasses in well-watered soil ranged from less than 2 mm s⁻¹ (0.002 m s⁻¹) to more than 12 mm s⁻¹

(0.012 m s^{-1}) depending on species and experimental conditions. Leaf conductances of cool-season Poaceae often exceed those of warm-season grasses (Downes, 1969; Noitsakis & Berger, 1984). High leaf conductance is of little advantage for photosynthesis in temperate grasses (Wilson, 1975a) and may be associated with a greater requirement for N by temperate than tropical grasses (Monson et al., 1986). Among the cool-season grasses, stomatal or leaf conductance of crested wheatgrass was less than western wheatgrass and Russian wildrye, but similar to orchardgrass and smooth bromegrass (Frank & Barker, 1976). Higher conductance in young than in old leaves was observed in only some of the species tested (Frank, 1981). Early season depletion of soil water by crested wheatgrass (Eissenstat & Caldwell, 1988) is evidently due to early leaf development (Bittman & Simpson, 1987) and not to high leaf conductance (Bittman & Simpson, 1989a).

The response of stomata to drought varies among grass species. For example, leaf conductance of orchardgrass was 33% greater than perennial ryegrass under well-watered conditions, but 25% lower during drought (Thomas, 1986a). Crested wheatgrass had lower conductance than Altai wildrye both under favorable soil water and during prolonged drought (Bittman & Simpson, 1989a). Interestingly, leaf conductance in droughted smooth bromegrass was increased by mycorrhiza [*Glomus fasciculatum* (Thaxter sensu Gerd.) Gerd. and Trappe] enabling greater photosynthetic rates and more effective extraction of soil water (Bildusas et al., 1986).

The relationship between stomatal conductance and tissue water status varies among species and is influenced by experimental conditions, particularly rate of onset of drought. Species exhibited a wide range of values for leaf water potentials at which stomatal conductance was reduced to 50% of maximum rate in different experiments (Table 5-2). Responsiveness of stomata to tissue water deficit in temperate grasses was influenced by N status (Ghashghaie & Saugier, 1989) and time of day (Bittman & Simpson, 1989a), and differed between reproductive and vegetative plants of perennial ryegrass (Thomas & Evans, 1990). High vapor pressure deficits decreased leaf conductances in perennial ryegrass (Woledge et al., 1989) and crested wheatgrass (Nowak et al., 1988). High vapor pressure deficits increased the responsiveness of stomata to drought in nongrass species (e.g., Turner et al., 1985). Curiously, in crested wheatgrass, soil water

Table 5-2. Values of leaf water potential at which stomatal or leaf conductance was reduced to 50% of maximum rate in some cool-season grasses growing in controlled (C) or field (F) environments.

Species	Growing condition	Leaf water potential MPa	Source
Perennial ryegrass	C	-1.0	Sheehy et al., 1975
Perennial ryegrass	F	-1.4	Jackson, 1974
Perennial ryegrass	F	-1.0	Jones et al., 1980b
Orchardgrass	F	-1.4	Jackson, 1974
Tall fescue (high N)	C	-1.82	Ghashghaie & Saugier, 1989
(low N)	C	-1.25	Ghashghaie & Saugier, 1989
Tall fescue (wind)	C	-2.5	Grace & Russell, 1977
Thickspike wheatgrass	F	-1.32	Ripley & Saugier, 1978

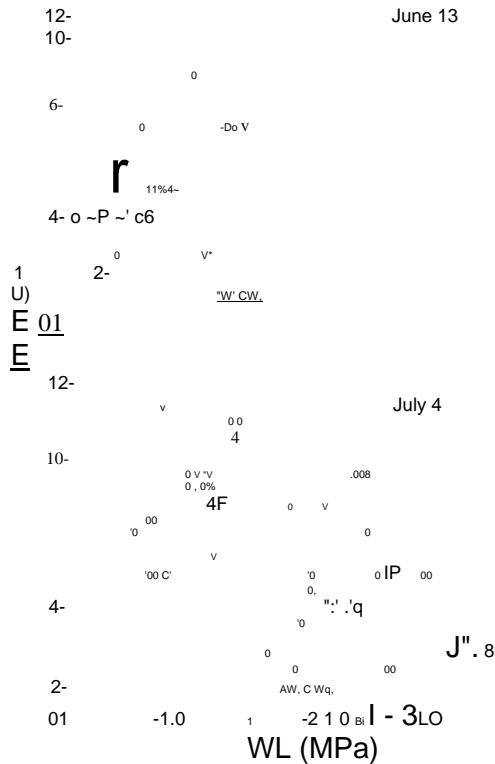


Fig. 5-1. Relationship between leaf conductance (g/L) and leaf water potential (WL) of Altai wildrye (AWr, V) crested wheatgrass (CWg, o), and smooth bromegrass (13r, o) on two dates. Vertical arrows indicate zero turgor for each species (from Bittman & Simpson, 1989a).

content influenced the effect of vapor pressure deficit on CO₂ assimilation rate but not on leaf conductance (Nowak et al., 1988). Greater sensitivity of stomata to leaf water loss during afternoons than mornings (Bittman & Simpson, 1989a) may be due to higher vapor pressure deficit in the afternoons. Response of stomata to vapor pressure deficit is thought to be a safety system for preventing excessive water loss during periods of high evaporative demand (Cowan, 1982). Reducing water loss when vapor pressure deficits are high conserves water and improves water-use efficiency (WUE).

The closing response of stomata to declining leaf water potential ranges from rapid, thresholdlike (reviewed by Jones, 1988) to gradual (e.g., Ripley & Saugier, 1978; Bittman & Simpson, 1989a). Threshold response, often observed in potted plants, is usually associated with rapid water loss; although in perennial ryegrass the rate of water loss had no effect on stomatal sensitivity (Jones et al., 1980b). The decline in leaf conductance with leaf water potential was steep in previously well-watered orchardgrass but gradual in plants acclimated to water deficit (Noitsakis & Berger, 1984). Under slow field drying, stomata of crested wheatgrass, smooth bromegrass, and Altai wildrye responded gradually to declining leaf water potentials (Fig. 5-1) (Bittman & Simpson, 1989a). A wide range of water potentials was associated with 50% reduction from maximum leaf conductance (particularly on July 4) and even at very low leaf water potentials (less than **-3.0 MPa**), leaf conductance was seldom below 2 mm s⁻¹ (0.002 m s⁻¹).

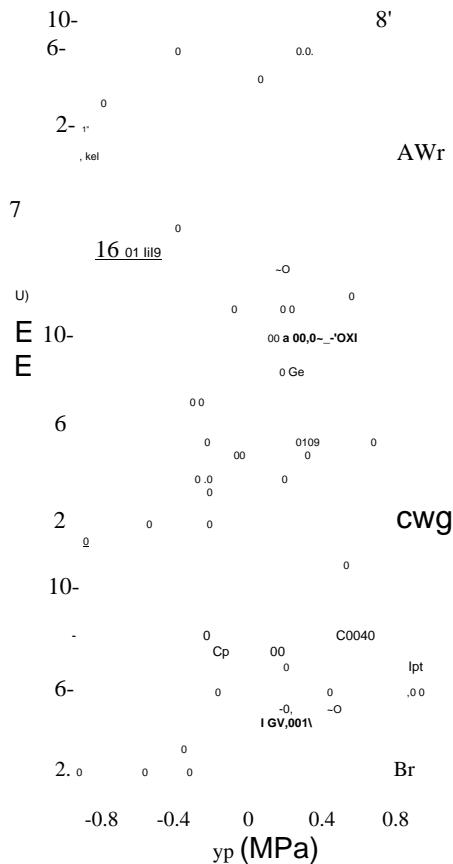


Fig. 5-2. Relationship between leaf conductance (g) and pressure potential (Wp) in Altai wildrye (AWr), crested wheatgrass (CWg), and smooth bromegrass (13r). Each data point represents an average of four measurements of XvLI xVP and 9L within a single plot; (○) morning and (●) afternoon. All regressions were significant at $P < 0.01$.

AWr: morning, $9L = 0.68 + 0.25 Wp$ ($r^2 = 0.29$); afternoon, $0.62 + 0.52 Vp$ ($r^2 = 0.75$). CWg: morning, $9L = 0.58 + 0.19 Nfp$ ($r^2 = 0.36$); afternoon, $0.59 + 0.46 Nfp$ ($r^2 = 0.49$). 13r: morning, $9L = 0.56 + 0.25 Wp$ ($r^2 = 0.31$); afternoon, $0.51 + 0.35 VP$ ($r^2 = 0.59$). (from Bittman & Simpson, 1989a).

A weak relationship between leaf water potential and stomatal conductance in slow-drying plants has been attributed to osmotic adjustment, which allows plants to maintain bulk leaf turgor (e.g., Noitsakis & Berger, 1984). Slow stomatal response to water loss in itself contributes to accumulation of solutes which lowers osmotic potential, providing positive feedback, to help stomata remain open (see "Whole Plant Response to Water Deficits"). However, under slow field drying even the relationship between leaf turgor and leaf conductance was weak in crested wheatgrass and smooth bromegrass with no evidence of stomatal closure near zero turgor (Fig. 5-2) (Bittman & Simpson, 1989a). Similarly, Richter and Wagner (1982) reported that stomata of durum wheat closed only well after pressure potentials reached zero. Because guard cells can adjust osmotically independent of surrounding leaf tissue (Ludlow, 1980) by taking up K^+ and Cl^- and producing organic acids (Raschke, 1976), a direct relationship between

bulk leaf turgor and leaf conductance need not exist. In fact, recent investigations with several species did not support a direct link between stomatal closure and tissue water status (reviewed by Davies & Zhang, 1991).

Growing evidence suggests that stomata of grasses respond directly to soil water content, rather than plant water status (e.g., Nowak et al., 1988; Blaikie et al., 1989), probably mediated by a signal transported from roots in the transpiration stream (Davies & Zhang, 1991). Several signals have been proposed including abscisic acid (ABA), cytokinins, and inorganic ions. Thomas (1972) suggested that water traveling through plants, carrying cytokinins from the roots, regulated stomatal conductance and shoot growth in orchardgrass and timothy; he proposed that the transpiration stream itself mediates plant response to the environment. An alternative explanation is that stomatal response is mediated by rate of tissue water loss (Jones & Rawson, 1979; Renquist et al., 1982; Bittman, 1985). Because rate of water loss is related to rate of soil water depletion, responding to rate of water loss enables plants to adjust their responses to a range of soil conditions (see section on water uptake). Whether stomata respond to a chemical signal from the roots or to rate of water loss, the strategy of stomatal response apparently is to maximize efficient removal of water from the soil (while preventing irreversible tissue damage) and not to maintain a favorable tissue water status.

Maintenance of Water Uptake

Rate of plant dehydration is influenced by rates of water loss and of uptake, the latter is governed by root distribution, root hydraulic properties, and soil properties. During drought, plants that take up water rapidly must endure periods with dry soil. Rapid water uptake by crested wheatgrass early in the growing season, made possible by high root densities and early leaf production (Bittman, 1985), competitively favors this species over the later-growing bluebunch wheatgrass (Eissenstat & Caldwell, 1988). Later seasonal growth using stored soil water is characteristic of many native grasses of the Northern Great Plains and complements early growing species such as crested wheatgrass and Russian wildrye in season-long grazing systems.

Movement of water to roots in unsaturated soils is very slow, so rapid water uptake by plants requires high root densities. Loss of soil water often decreases shoot/root ratios, usually by reducing shoot more than root growth (reviewed by Turner & Begg, 1978). Drought actually increases root growth in some pasture grasses (Molyneux & Davies, 1983), with much of the additional growth coming from lateral root initiation and elongation (Jupp & Newman, 1987). Continued root growth during a drought period is enabled by osmotic adjustment in the roots, which helps maintain turgor (Greacen & Oh, 1972). Even quite small increases in root-length densities (0.2 cm cm^{-3}) at 55-cm soil depth enhanced water uptake and soil water depletion in tall fescue relative to white clover (Burch & Johns, 1978). Roots of western wheatgrass stopped growing when soil water potential ranged from -0.8 MPa at 5 cm to -1.4 MPa at 35-cm soil depth (Majerus, 1975). Whether a large root biomass and continued root growth during drought is agronomically advantageous depends on specific growing conditions such as

soil **depth, depth of water infiltration, and frequency and magnitude of precipitation** events. More deep roots give species such as orchardgrass and tall fescue an advantage over shallow-rooted species such as perennial and Italian ryegrass during drought (Garwood & Sinclair, 1979; Thomas, 1986a). In semiarid areas with permanent grass cover, soil recharge of water below 60- to 90-cm depth occurs infrequently (Read & Winkelman, 1982); hence deep roots found on adapted species (see discussion above) probably contribute more to survival than growth (Redmann, 1976). Grasses such as Altai wildrye, with deep root penetration and a comparatively uniform root profile (Bittman, 1985), are probably adapted to soils with a deep-perched water table.

An interesting variation on function of deep roots, called hydraulic lift, has been reported (Caldwell & Richards, 1989; Caldwell et al., 1991). Deep-rooted big sagebrush extracted water in daytime from deep in the soil and at night released it back to the soil near the surface (reverse potential gradient). This water was reabsorbed during the daytime by the big sagebrush and by the associated crested wheatgrass, thereby increasing daytime gas exchange. This phenomenon also may prolong activity of fine roots during drying cycles and, by flushing localized depletion zones near roots, may facilitate nutrient uptake in drying soils (Caldwell et al., 1991).

Drought caused death of root cortex of perennial ryegrass starting at a soil water potential of -2 MPa, but root tips of this mesic species survived to -10 MPa (Jupp & Newman, 1987). Damage to roots by nematodes (*Meloidogyne graminis*) reduced drought resistance of endophyte-free tall fescue plants (West et al., 1987). Mycorrhizal infection decreased soil-plant flow resistance in smooth brome grass by 35% and increased leaf conductance by as much as 64%, although total shoot production was reduced by 15% probably because photosynthate was consumed to sustain mycorrhiza (Bildusas et al., 1986).

Resistance to water flow in the soil-plant system is well recognized. Major zones of hydraulic resistance include the soil-root interface (Faiz & Weatherly, 1978), within the roots (probably at the endodermis) (Burch, 1979) and in the xylem vessels (Greacen, 1977), although the relative importance of these resistances is not well-known. Water potential gradients of 1.8 to 2.3 MPa between rhizomes and leaves in pine reedgrass suggest a resistance to water flow in the xylem (Svejar, 1986). Flow rate through xylem vessels is thought to vary with the fourth power of their radius (Zimmerman, 1983), although there is no estimate for the additional resistance of cell walls between xylem cells or through the nodes where the xylem vessels of grasses anastomose (Hayward, 1938).

While large vessels have much greater water-conducting capacity than small vessels, their water columns also are more prone to embolism or cavitation (Zimmerman, 1983). Increases in hydraulic resistance with dehydration (Blizzard & Boyer, 1980) may be due to cavitation in large xylem vessels. Cavitation has been reported in corn (Tyree et al., 1986), but not in cool-season grasses. The outer ring of small vascular bundles with narrow xylem vessels in stems of temperate grasses (Hayward, 1938) may serve as a robust, low volume back-up system to the larger inner vessels for water transport. An interesting possibility is that with relief of drought, large vessels are resupplied with water from small vessels at the stem nodes, where the large and small vessels anastomose.

The role of soil water status in regulating drought responses of plants is gaining prominence. Bittman (1985) explained how stomatal response might be affected by soil. The nature of shallow, coarse-textured soils is such that they give up their water easily to the plant, dry out rapidly, and maintain little water reserve. Consequently, stomata must react rapidly to curtail water loss soon after soil water content begins to decline (see "Whole Plant Response to Water Deficits"). Soils that dry slowly (deep, fine-textured) maintain reserves of water that resist uptake by plants so rapid reaction by stomata is not required. This water reserve buffers plants against desiccation and reduces the risk of declines in leaf water content.

Maintenance Of Cell Volume

Elasticity of cells affects the relationship between relative water content and the components of tissue water potential; inelastic tissue loses less water but maintains less pressure potential with declining leaf water potential than elastic tissue (reviewed by Tyree & Jarvis, 1982). Elasticity is influenced by cell wall thickness, cell size, and Young's modulus of elasticity which is affected by lignification of cell walls.

Drought seems to reduce cell expansion more than cell division because typically leaves developed under drought have small cells (Lawlor, 1972; Jones et al., 1980b). Small cells adjust more osmotically than large cells (Cutler et al., 1977), although this effect may be slight (Tyree & Jarvis, 1982). Cells growing during drought usually have thick cell walls (Levitt, 1980; Cutler et al., 1977), but results are inconsistent concerning whether drought increases or decreases lignification of cell walls (see "Forage Quality"). Small, thick-walled cells are rigid and retain more water with declines in leaf water potential than thin-walled cells. Drought increased the capacity to retain tissue water with declining leaf water potential (modulus of elasticity) in thickspike wheatgrass (Maxwell & Redmann, 1978a), perennial ryegrass (Thomas, 1987), and bulbous canarygrass (Sambo & Aston, 1985), although the opposite was observed in wheat (Melkonian et al., 1982). Maxwell and Redmann (1978a) concluded that the ability of grasses to retain tissue water with declining leaf water potential is related to drought resistance. The less drought resistant intermediate wheatgrass lost more water with declining leaf water potential than drought-resistant crested wheatgrass and western wheatgrass (Frank et al., 1984). However, Burch and Johns (1978) reported that drought-resistant tall fescue lost more water as leaf water potential decreased than drought-susceptible white clover.

Assessing the importance of modulus of elasticity is difficult because it is not known whether loss of water content or water potential is more limiting to growth. In practice, large differences in modulus of elasticity may have only a small effect on desiccation tolerance (Turner, 1979). It is possible that elasticity characteristics of a leaf are a coincidental result of growth, cell expansion and lignification and not an adaptation to drought. Tissue elasticity proved to have low genetic heritability in perennial ryegrass so there was little potential for genetic improvement (Thomas, 1987).

Table 5-3. Osmotic adjustment in cool-season grasses grown in field (F) and controlled (C) environments.

Species	Growing conditions	Osmotic adjustment MPa	Source
Orchardgrass	C	0.4-0.6	Gavande & Taylor, 1967
Bulbous canarygrass	C	0.4-0.9	Sambo, 1981
Tall fescue	C	0.7	Sambo, 1981
Orchardgrass	C	0.9-1.2	Sambo, 1981
Bulbous canarygrass	C	0.65-0.85	Sambo & Aston, 1985
Tall fescue	C	0.08-0.49	West et al., 1990
Perennial ryegrass	C	0.43-0.80	Thomas, 1986b
Orchardgrass	C	0.43	Thomas, 1986b
Bluebunch wheatgrass	F	1.7	Dibble & Spomer, 1987
Thickspike wheatgrass	F	0.3	Maxwell & Redmann, 1978b
Crested wheatgrass	F	0.2-0.5	Bittman & Simpson, 1989b
Smooth bromegrass	F	0.2-0.4	Bittman & Simpson, 1989b
Altai wildrye	F	0.2-0.3	Bittman & Simpson, 1989b

Osmotic Adjustment

Declines in osmotic potential of more than 1 MPa during periods of drought occur in many cool-season grasses (e.g., Sambo & Aston, 1985). In part, the decline in osmotic potential results directly from the loss of tissue water, which concentrates the solutes in the cells. The decline in osmotic potential also is the result of osmotic adjustment, which refers to the accumulation of solutes or osmolytes in cells at the same relative water content. In cool-season grasses the solutes are principally carbohydrates (Brown & Blaser, 1970), although inorganic ions (Sambo, 1981) and proline (see Proline) also have been reported. Osmotic adjustment has been demonstrated for many agriculturally and ecologically important cool-season grasses (Table 5-3). Osmotic adjustment values vary with experimental conditions, especially rate of dehydration, but are usually in the range of 0.4 to 0.7 MPa. In long-term field experiments osmotic adjustment values may include the effects of increasing maturity, yielding an exaggerated estimate of adjustment to drought (e.g., Dibble & Spomer, 1987). In fact, separating the effects of drought and maturation on osmotic adjustment is difficult in long-term experiments in the field.

The contribution of osmotic adjustment to drought resistance in plants has been extensively reviewed (Morgan, 1984). Osmotic adjustment enables plants to maintain turgor despite tissue water loss; turgor is required to r - stomata to stay open and for cells to expand. Reported values of water potential and relative water content at zero-turgor in temperate grasses vary widely due in part to differences in osmotic adjustment (Table 5-4). Leaf expansion in Harding grass ceased at leaf water potential of -1.5 MPa with no osmotic adjustment, but continued to -2.8 MPa when turgor was maintained (Sambo, 1981). Sustained growth of both roots and leaves of tall fescue during a drought period was credited to low osmotic potential (Burch & Johns, 1978). However, when genotypes of perennial ryegrass were selected for increased osmotic adjustment, they did not have improved leaf growth during drought (Thomas & Evans, 1989); (see "Leaf Expansion").

Table 5-4. Water potential and relative water content at zero turgor.

Species	Growing conditions	Relative water content Source	
		Water potential	
		MPa	%
Crested wheatgrass	Field	-2.78	Frank, 1983
Western wheatgrass		-2.40	Frank, 1983
Intermediate wheatgrass			-2.30 Frank, 1983
Crested wheatgrass	Field	-1.97 to -2.74	88-96 Frank et al., 1984
Western wheatgrass		-1.95 to -2.15	88-96 Frank et al., 1984
Intermediate wheatgrass			-1.63 to -2.26 88-94 Frank et al., 1984
Crested wheatgrass	Greenhouse	-1.65	Johnson, 1978
Intermediate wheatgrass			-1.45 Johnson, 1978
Russian wildrye		-1.60	Johnson, 1978
Wheatgrass hybrids	Greenhouse	-1.84 to -2.16	Johnson &
Bromegrass		-1.94	Brown, 1977
Thickspike wheatgrass	Field	-2.40	73 Maxwell & Red mann, 1978a
Smooth bromegrass	Greenhouse	-1.77	Brown, 1977
Intermediate wheatgrass			-1.77 Brown, 1977

Accumulation of solutes causing osmotic adjustment results primarily from a change in the source-sink relationship during drought (Brown & Blaser, 1970). Increasing photosynthetic rates (i.e., the source of solutes) by CO₂ enrichment increased osmotic adjustment in wheat (Sionit et al., 1981). Solutes accumulate because stomata remain open and photosynthesis continues after cell expansion has ceased during a period of drought, particularly when dehydration is slow (Bradford & Hsiao, 1982). Orchardgrass showed no osmotic adjustment when dehydration was rapid, but adjusted 0.2 to 0.7 MPa under slow dehydration and restricted watering (Thomas, 1986b). Perennial ryegrass had leaf osmotic potential (corrected to full turgor) of -1.2 MPa when rapidly dried, whereas slowdried plants had values near -1.6 MPa. In some situations, osmotic adjustment resulted not from a decrease in sink size, but rather from the redistribution of assimilates within the plant (Thomas & Evans, 1989).

Despite substantial evidence for the occurrence and benefits of osmotic adjustment, some researchers question the biological significance of this phenomenon for both stomatal control and growth (e.g., Bittman, 1985; Gollan et al., 1985; Munns, 1988). The relative importance of solute accumulation during drought for maintaining growth and gas exchange, for sustaining respiration during periods of quiescence, and for supporting recovery growth needs quantification for cool-season grasses.

Dehydration Tolerance

This mechanism of drought adaptation involves the ability of a plant to endure low tissue water potentials. Desiccation tolerance of tissue seemingly involves both an increase in the synthesis of soluble proteins having intrinsic stability and stabilization of membrane structure by increased sucrose content derived from hydrolyzed starch (Gaff, 1989). Gaff reported on numerous desiccation tolerant grass species, all but one (bulbous bluegrass) belonging to warm-

season grass genera. These grasses withstood water potentials well below -100 MPa and relative water contents below 10%, and survived up to 300 d of drought. Desiccation tolerance may be most beneficial in environments with intermittent drought (Ludlow & Muchow, 1990). In effect, the strategy of desiccation tolerance is the same as "drought escape" described earlier, although the mechanism is different. Gaff (1989) suggested that desiccation tolerant grasses can be useful as colonizers on bare shallow soils in and areas. A few species even show promise for pastures in subtropical and tropical areas periodically subjected to severe drought.

PHYSIOLOGICAL EFFECTS OF WATER LOSS

Range of Tissue Water Loss

Tissue water loss is a daily occurrence when transpiration exceeds water uptake. Grass species differ widely in the amount of dehydration they undergo diurnally or through a drought period. Diurnal reduction of leaf water potential reached 1.5 MPa in thickspike wheatgrass (Redmann, 1976), 1.7 MPa in pine reedgrass (Svejcar, 1986), 1.3 MPa in Harding grass (Sambo, 1981), 1.5 MPa in orchardgrass; and 1.0 to 1.2 MPa in perennial ryegrass (Jackson, 1974; Jones et al., 1980b). As soil water deficit increases, the diurnal decline in leaf water potential decreases (Svejcar, 1986; Distel & Fernandez, 1987).

The minimum leaf water potentials of semiarid grasses during extended periods of drought ranged from -2.5 to -4.0 MPa. For example, Frank (1983) reported minimum values of -2.5 to -3.2 MPa for several wheatgrass species, and Bittman and Simpson (1989b) reported a value of -3.9 MPa for both smooth bromegrass and crested wheatgrass. Minimum values for spider grass reached about -4.0 MPa (Distel & Fernandez, 1987). No reports were found of water potentials much below -4.0 MPa in temperate grasses growing in the field, so this value may represent a typical lower limit. Mesic grasses (orchardgrass, ryegrasses) had higher minimum leaf water potentials (-2.0 to -2.5 MPa), perhaps due to either self-regulation or milder droughts (e.g., Jackson, 1974; Jones et al., 1980a; Norris, 1985). Minimum relative water contents in cool-season grasses are usually greater than 70% and rarely fall below 60% (e.g., Maxwell & Redmann, 1978a; Sambo & Aston, 1985; Thomas, 1986b; Bittman & Simpson, 1989b). Early in a drought cycle, leaf water potentials were severalfold more negative than soil water potentials (Bittman & Simpson, 1989b), but later the upper layers of soil may dry (by evaporation) well below leaf water potentials so that plants must take up water from lower soil horizons.

Meristematic regions in grasses are sheltered from the environment by leaf sheaths and isolated from adjacent tissue because of the undeveloped vascular system. Water potential in the meristematic bases of emerging leaf blades was higher by 0.5 to 0.7 MPa than in expanded leaves in thickspike wheatgrass and western wheatgrass (Maxwell & Redmann, 1978b) and 1.2 MPa higher in tall fescue (West et al., 1990). Low leaf water potential in the autumn may enhance winter survival of some temperate grasses by suppressing growth of snow molds [*Fusarium nivale* (Fr.) Ces. and *Typhula ishikariensis* Imai.] (Tronsmo, 1986).

Leaf Expansion

Decrease in leaf growth has a more direct effect on the productivity of forages than other crops because leaves often comprise 20 to 75% of total yield (Bittman et al., 1988) and an even higher proportion of total nutrients. Leaf expansion is more sensitive to water deficit than are other physiological processes (Bradford & Hsiao, 1982). Leaf expansion of the semiarid adapted western wheatgrass began to slow when soil water potential fell below -0.5 MPa at 5- and 15cm depth and -0.1 MPa at 25- and 35-cm depth (Majerus, 1975). Leaf expansion ceased when soil water potential reached -3.0 MPa at 5 cm and -1.5 MPa at 35cm depth. Leaf elongation of perennial ryegrass declined, at an integrated soil water potential of about -0.15 MPa (Lawlor, 1972). In that study leaf elongation began to decline at leaf water potentials of -0.2 MPa, fell to 50% of maximum at -0.6 MPa, and stopped at -1.6 MPa. Leaf expansion rate in rescue grass decreased by 50% with only 0.2 to 0.3 MPa decline in leaf water potential (Chu & McPherson, 1977). However, after the rapid initial drop, leaf expansion rate became progressively less sensitive to water loss. Drought reduced elongation rate of perennial ryegrass less at night than during the day (Chu et al., 1979; Jones et al., 1980a).

When plants are gradually subjected to water deficit, leaf expansion may persist even after considerable water loss. Leaves of Italian ryegrass in the field continued to grow for 100 d without rain (Norris, 1982). Leaf expansion of fieldgrown perennial ryegrass was maintained at one-third the rate of irrigated controls at leaf water potential of -1.6 MPa (Jones et al., 1980a). In that study, decline in leaf water potential of -1.4 MPa during the day produced little change in leaf expansion rate. Plants of tall fescue, orchardgrass, and Harding grass cv. Australia that were preconditioned to drought maintained leaf expansion to water potentials of -2.4 to -3.4 MPa, although unconditioned plants of Harding grass stopped growth at -1.5 MPa, near zero-turgor potential (Sambo, 1981).

Slowly dehydrating plants undergo osmotic adjustment, which helps maintain positive turgor potentials (see "Osmotic Adjustment")~ The driving force of cell expansion is turgor pressure (Green, 1968), which must be exerted in the meristematic regions. Most measurements of leaf turgor are averages for entire leaves. West et al. (1990) demonstrated that osmotic adjustment in leaf bases of tall fescue is 0.4 MPa greater than in adjacent leaf tissues, although Thomas and Evans (1989) reported only a 0.1 MPa difference in perennial ryegrass, and that only at night. Nevertheless, because the leaf bases are protected from water loss and have higher water potentials than the exposed leaf portions (Maxwell & Redmann, 1978b; West et al., 1990), turgor values are likely to be higher in the leaf bases. Hsiao et al. (1985) demonstrated a linear relationship between leaf elongation rate and turgor potential in the leaf elongation zone of corn. In contrast, Renquist et al. (1982) reported that expansion rate of strawberry leaves was influenced more by water flux through the plants than by turgor force. Similarly, Passioura (1988) showed that rate of elongation was independent of turgor potential in wheat. Perhaps turgor has a direct influence on short-term growth, whereas long-term growth is governed more by changes in the yielding threshold of cell walls and cell wall softening, as proposed by Tyree and Jarvis (1982).

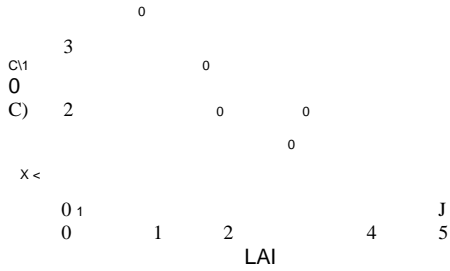
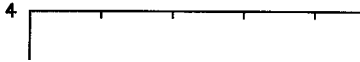


Fig. 5-3. Relationship between unit leaf area rate of "gross" photosynthesis at high irradiance levels (P_{gross}/LAI) and LAI for irrigated (○) and water-stressed (●) field swards of perennial ryegrass (from Jones et al., 1980a).

In areas with intermittent drought, rapid growth during favorable periods is obviously advantageous and may enable even drought-sensitive species to produce well. In regions where most water is available in early season, precocious species such as crested wheatgrass are likely to produce a greater quantity of leaves than slower-growing species such as Altai wildrye, which adjust their leaf expansion to water availability over a longer time period (Bittman & Simpson, 1987). The leaves of crested wheatgrass are predisposed to senescence to reduce the transpiring surface when water is depleted.

The interaction between leaf area and stomata in controlling gas exchange of grass crops has been studied. Johns and Lazenby (1973) reported that stomata regulated water loss from tall fescue and orchardgrass in spring when conditions were cool and moist, whereas leaf area controlled water loss when the air was hot and dry in summer. Water deficit reduced leaf size and total leaf area in barley, permitting stomata to remain open and photosynthesis to continue long into the drought period (Legg et al., 1979). Altai wildrye produced a smaller leaf area than crested wheatgrass or smooth brome grass under drought, but compensated with higher leaf conductance (Bittman & Simpson, 1989a). The relationship between leaf area and photosynthesis was perhaps most elegantly demonstrated in perennial ryegrass (Jones et al., 1980a). Given swards with the same leaf area, leaves of droughted plants photosynthesized 40% less than those of irrigated plants (Fig. 5-3). However, when leaf area index of unirrigated swards was 2.5 units lower than irrigated swards, photosynthetic rates of unirrigated swards equaled those of irrigated swards. Low rates of transpiration helped to prolong leaf growth in orchardgrass further demonstrating the interdependence of leaf area and stomatal conductance (Jackson, 1974). Because of mutual compensation by leaf area



and leaf conductance, improving drought resistance by selecting for stomatal control or leaf resistance (e.g., Wilson, 1975a; Gay, 1989) may prove difficult.

Reduction in leaf expansion contributes to increasing concentration of photosynthates in plants during drought both by helping to maintain photosynthetic activity (above) and by eliminating a sink for photosynthates (Brown & Blaser, 1970). Photosynthates that accumulate during drought help maintain turgor (thus sustaining leaf and root growth and leaf conductance), are necessary for respiration and recovery growth (see "Recovery"), and influence the nutritional quality of the forage.

Leaf Senescence

Drought usually increases leaf senescence in plants; but, grass crops vary widely in sensitivity of leaf senescence to drought (Bittman et al., 1988; Thomas, 1986b). Leaf senescence is generally thought to contribute to drought resistance by reducing transpiration. Despite having much greater leaf area, nonflowering tillers of both crested wheatgrass and smooth brome grass underwent less leaf senescence during drought than flowering tillers (Bittman et al., 1988). This suggests that the benefit of leaf senescence is more the conservation of nutrients than of water and shows that drought advances the maturity of flowering, but not nonflowering tillers. In the same study, drought slowed the rate of lignin accumulation, a process normally associated with increasing maturity. There is evidence that drought may suspend the aging of young leaves in the warm-season grass, guineagrass (Ludlow & Ng, 1974). Mott and McComb (1975) reported that drought delayed development before floral initiation, but accelerated it after. Death beginning with the upper leaves of nonflowering tillers is the result of drought injury which differed from hormonally controlled leaf senescence (Bittman, 1985).

Photosynthesis, Respiration And Translocation

Rate of photosynthesis in vegetation of the semiarid Northern Great Plains, consisting mostly of thickspike and western wheatgrass, was strongly related to soil-water status and air temperature (Redmann, 1978). In the Central Great Plains, maximum photosynthetic rate of western wheatgrass occurred in June when soil moisture, temperature, and plant maturity were most favorable (Monson et al., 1986). Further south in the Great Plains, photosynthetic rates of beardless wheatgrass were twice as high in May as in June (DePuit & Caldwell, 1975). Under favorable spring conditions, photosynthetic rates of crested wheatgrass, which also is well-adapted to the Great Plains, were nearly constant through the day in spring but fell in the afternoons under hot, dry summer conditions (Nowak et al., 1988). Summer drought conditions increased the sensitivity of photosynthetic rates to both high temperature and vapor pressure deficit.

A relationship between photosynthetic rate and tissue water content was shown for perennial ryegrass (Sheehy et al., 1975; Wilson, 1975a). For most species, the decline in photosynthetic rate with water loss is due more to stomatal closure than to decreasing mesophyll photosynthetic capacity. In some species

the photosynthetic capacity does not diminish even when CO₂ assimilation rate approaches zero (reviewed by Chavez, 1991). Nevertheless, high light intensity and heat, which often accompany drought, predispose plants to photoinhibition and may cause a decline in mesophyll photosynthetic activity. Solutes that accumulate during drought (especially sugars, phosphate, and sulphate) inhibit the activity of enzymes involved in CO₂ fixation, usually when relative water content is in the range of 70 to 40%. The carbon dioxide compensation point of perennial ryegrass increased from 50 to 400 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$ as leaf water potential declined from -0.7 to -1.5 MPa (Sheehy et al., 1975), perhaps due to feedback from the accumulation of photosynthates. Although N-deficient tall fescue plants photosynthesized more slowly when water was ample, they were less sensitive to declining water content and recovered more rapidly from drought than high-N plants (Ghashghaie & Saugier, 1989). Accumulation of sugars during drought (osmotic adjustment) apparently does not directly interfere with photosynthesis, although the sugars may be part of a coordinated regulation between synthesis and translocation, a regulation that may lead ultimately to leaf senescence (Chavez, 1991).

Slow dehydration may inhibit photosynthesis at a relatively favorable water status (relative water content of 80% and leaf water potential of -1.8 to -2.5 MPa), and this may be due to a metabolic slowdown associated with reduced availability of CO₂ (Chavez, 1991). This decline is not associated with membrane damage as it is largely reversible with rehydration. Water potentials as low as -9 MPa did not cause permanent membrane damage to guineagrass, a warmseason grass (Ludlow & Ng, 1976). Irreversible damage to chloroplasts generally occurred at relative water contents below 30% (Chavez, 1991); however, no data are available for temperate grasses. Because tissue water levels are usually maintained at higher levels even under prolonged drought (see "Tissue Hydration"), direct injury to the photosynthetic apparatus in grasses is probably uncommon (see Fig. 5-4).

Comparatively little information exists concerning the effects of water deficit on respiration in cool-season grasses. Under favorable water conditions one-third of the carbohydrates synthesized by smooth bromegrass during the day were respired at night (Holt & Hilst, 1969). Water deficit reduced dark respiration in perennial ryegrass, particularly when water loss was rapid, perhaps because overall biochemical activity and growth was reduced (Jones et al., 1980a). In contrast, leaf water potentials of -2 MPa increased dark respiration by 40% in wheat (Kaul, 1966). Respiration during extended or severe drought may deplete stores of carbohydrates (Chu et al., 1979; Lawlor & Khanna-Chopra, 1984). Respiration losses of stored carbohydrates during drought, which are especially rapid when temperatures are high (Trlica & Singh, 1979), deplete stores of carbohydrates (Mela & Youngner, 1976; Lawlor & Khanna-Chopra, 1984) and reduce the potential of grasses for survival and recovery (Julander, 1945) (see Fig. 5-4).

Translocation in cool-season grasses is reduced during drought because of both a decrease in photosynthesis and accumulation of assimilates in sink regions (Wardlaw, 1969). The balance between retention of sugars in chloroplasts and translocation of sugars to other plant parts is determined by the drought resistance strategy of the plants (Trlica & Singh, 1979). In crested wheatgrass, water

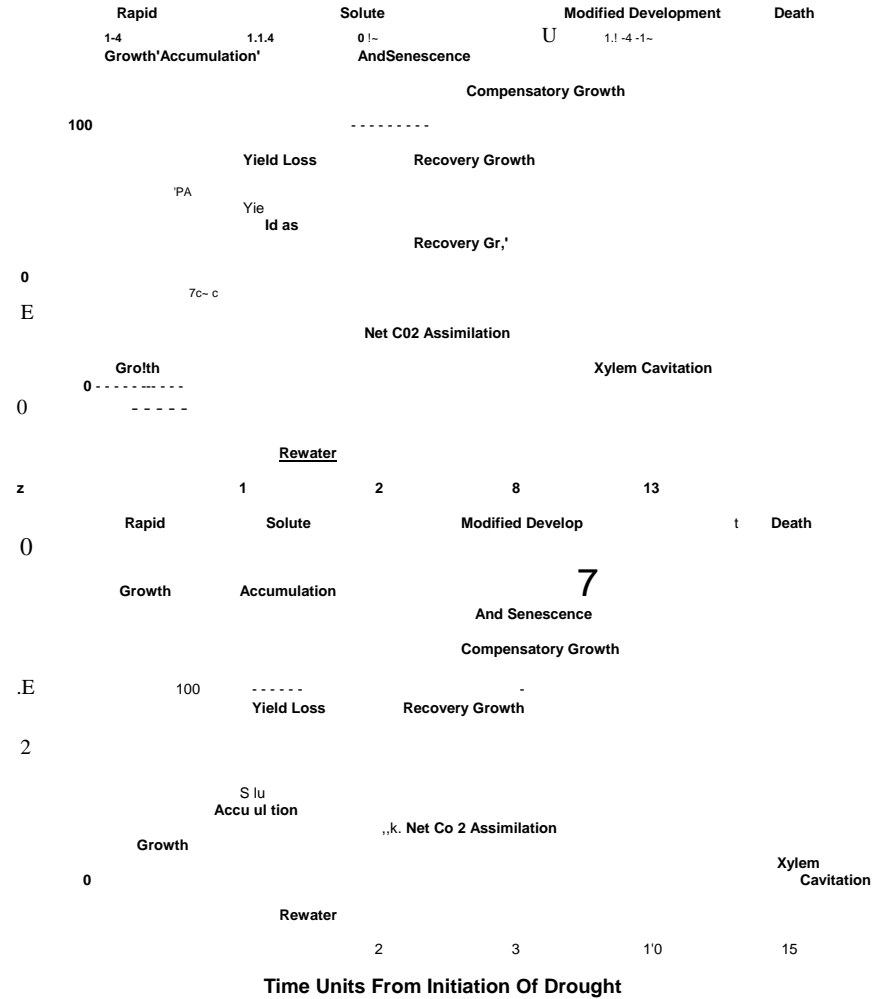


Fig. 5-4. General model for drought resistance in grasses on light textured (top) and heavy textured (bottom) soils. Four periods of plant response are identified above each graph: rapid development, solute accumulation, modified development and senescence, and rapid death due to cavitation of xylem vessels. The effect of rewatering on growth of plants on the two soil types is shown by the rising curve (from Bittman, 1985).

deficit increased movement of carbohydrates downward to roots and crowns, but reduced translocation towards the shoot where meristematic and cell expansion activities were low (Sosebee & Wiebe, 1971). The translocation system itself and the velocity of transport generally is not affected by drought, although few definitive studies exist (Wardlaw, 1969; Milburn & Kallarackal, 1989). A robust translocation system enables plants to continue transporting nutrients from senescing tissue to storage areas during prolonged drought.

Chemical Composition

Proline

Metabolic changes that occur in droughted plants cause changes in cellular chemical constituents. Free proline often accumulates in plants during drought (Aspinall & Paleg, 1981). Proline, inorganic ions, particularly K, and to a lesser extent soluble sugars, also may accumulate and are important for osmotic adjustment in plants (Ford & Wilson, 1981). Bokhari and Trent (1985) reported that droughted plants of tall fescue and western wheatgrass had higher concentrations of proline than nonstressed plants. Droughted western wheatgrass had about 2.5 times more proline than stressed tall fescue. Researchers differ in their interpretation of the accumulation of proline during drought. Stewart and Hanson (1980) suggest that proline accumulation in response to drought in barley is not an adaptive metabolic response. Barnett and Naylor (1966) and Sivaramakrishnan et al. (1988) proposed that proline accumulation allows storage of N and C for use as an energy source when drought is relieved with no direct effect on drought resistance. Much of the research on proline accumulation has been conducted in controlled environments where drought develops more quickly than in the field. Frank (1994) sampled field-grown western and crested wheatgrass from the threeleaf to the seed set stage that was grown at 50, 100, and 150% average rainfall and 10 and 100 kg ha⁻¹ of N fertilizer. He found that proline concentrations were higher at the highest water deficit (50% rainfall) and greater N rate (100 kg ha⁻¹). Proline concentration increased with plant maturity in the more drought-resistant western wheatgrass, but decreased with plant maturity in the more drought-escaping crested wheatgrass.

Carbohydrates

Soil water deficits generally reduce leaf area and affect biochemical processes that result in reduced photosynthesis and concentration of storage carbohydrates (Trlica & Singh, 1979). Cool-season grasses are classified as fructan accumulators; however, Chatterton et al. (1987) reported that the form of carbohydrate present depended on the air temperature at which the plants were grown. At 20°C crested wheatgrass synthesized more sucrose but at 5°C plants produced more starch than sucrose. Cool-season grasses store nonstructural carbohydrates in stems, sheaths, and roots (Caldwell et al., 1981).

The effects of drought on carbohydrates varies depending on species, degree of stress, and plant developmental stage (Brown & Blaser, 1965; Trlica & Cook, 1971; Wardlaw, 1968). Brown and Blaser (1970) concluded that an increase in soluble carbohydrates in droughted orchardgrass was due to a greater reduction in utilization than synthesis of photosynthetic products. Carbohydrate concentrations of grasses are generally at a low level shortly after initiation of spring growth and peak at plant maturity (White, 1973; Daer & Willard, 1981; Sims et al., 1982). Severe defoliation, such as grazing or clipping, generally reduces storage carbohydrates (Buwai & Trlica, 1977). However, in cool-season grasses, regrowth following defoliation may be less correlated with concentra-

tion of nonstructural carbohydrates than with either the efficiency of C allocation and utilization for synthesis of new foliage or with meristematic activity (Davidson & Milthorpe, 1966; Richards & Caldwell, 1985; Busso et al., 1990). Dependence of grasses on carbohydrate reserves for regrowth is limited to only about 2 to 5 d (Davidson & Milthorpe, 1966; Richards & Caldwell, 1985). Richards and Caldwell (1985) estimated that under typical grazing situations at least 89 to 99% of the C in regrown tissues of crested wheatgrass and bluebunch wheatgrass is derived from new photosynthate. Because growth processes are curtailed before photosynthesis when plants are exposed to water stress, carbohydrates typically accumulate in cool-season grass tissues (Trlica & Cook, 1972; Busso et al., 1990). This accumulation of total nonstructural carbohydrates may facilitate rapid regrowth after water stress is relieved.

WHOLE PLANT RESPONSE TO WATER DEFICITS

General Plant Response Model

Bittman (1985) presented a generalized graphical model for plant response to water stress for cool-season forage grasses growing on coarse- and fine-textured soils (Fig. 5-4). The model assumes that plant growth is mediated by available soil water. Growth is portrayed as being rapid when water is ample, but restricted when water is limited. Key elements of the drought-response model include:

1. Differences in rate of dehydration are caused in part by environmental factors such as atmospheric vapor pressure deficit and soil depth and texture. Plants also vary in their rate of dehydration by their control of water loss from leaf surfaces and their ability to extract soil water. Grasses adapted to mesic environments, such as timothy and perennial ryegrass, have shallow roots and exhibit faster dehydration than deep-rooted grasses, such as crested wheatgrass and Russian wildrye growing on deep, fine-textured soils in semiarid environments.
2. The rate of water loss will influence the rate of change in growth rate and the concomitant accumulation of solutes; this, together with the duration of the dehydrated condition, will determine extent of recovery from drought and overall effect of the drought on forage yield.
3. Between cessation of growth and tissue damage is a period of relative quiescence when rate of water loss is slight, physiological activity is low, and leaf senescence is accelerated. Many grasses can endure a long period of quiescence (crested wheatgrass has survived 660 d with essentially no water), but growing days are lost. Tissue damage refers to loss of photosynthetic capability, death of buds, and cavitation of xylem vessels.

Germination And Emergence

Water deficits in the top 10 cm of the soil are critical to seedling establishment. The small mass of seeds of cool-season grasses typically requires that seed-

ing depth be less than 2 cm, which increases the risk of seedling desiccation and establishment failure. Germination of the seed and development of seedling roots are dependent on timely precipitation after sowing or adequate stored soil water. After germination occurs, seedling establishment is dependent on adequate soil water and favorable environmental conditions for root development and penetration into typically moist underlying soil layers.

Because soil water deficits near the seed can change rapidly, researchers have devised controlled techniques that use osmoticum to predict germination under water deficits. Differences in minimum water potentials for seed germination were found among grasses under controlled conditions [-0.35 to -0.55 MPa for crested wheatgrass (Johnson & Asay, 1978); -0.3 to -0.6 MPa for annual ryegrass, 'Kentucky 3 V tall fescue, and Kentucky bluegrass (Wright et al., 1978); -0.9 MPa for Russian wildrye (Berdahl & Barker, 1980)]. Unfortunately, results from controlled environment studies may fail to accurately reflect actual seedling establishment in the field (Asay & Johnson, 1983).

Aboveground Growth And Development

Because water is the most limiting factor to forage grass production in semiarid, and often in humid regions where short-term droughts are frequent, plants must possess water conserving traits to extend the water supply. Leaves are the most nutritious part of the grass plant, but also represent the primary transpiring surface from which water is lost. Under water deficit conditions factors that reduce leaf area to conserve water also reduce forage yield and quality. Short-term water deficits generally cause a decrease in dry matter yield and forage quality through reduction in leaf area and plant size. Long-term water deficits can result in stand losses, especially in marginally drought-tolerant species.

Dominant factors controlling leaf initiation and development in cool-season grasses include temperature (Laude, 1971) and water (Slatyer, 1971). The rate of leaf exertion on the stem is primarily controlled by air temperature or accumulated growing degree-days. Floral tillers develop a set number of leaves under normal growing conditions. Frank and Ries (1990) studied the number of leaves and rate of leaf exertion for crested wheatgrass and western wheatgrass grown under a rain shelter at 50, 100, and 150% average rainfall and 10 and 100 kg N ha⁻¹. In both species the number of leaves on the main stem during the initial spring and a regrowth period was related to the accumulated growing degree-days (Fig. 5-5). Water and N treatments did not affect the relationship between rate of leaf exertion and accumulated growing degree-days in these grasses. Similarly, Norris (1982) found that orchardgrass produced leaves at the same rate under droughted and irrigated conditions, but rate of leaf appearances differed between droughted and irrigated tall fescue, Italian ryegrass, and perennial ryegrass.

Leaf rolling is a common response to drought in cool-season grasses that results in reduced water loss from the leaf through decreases in leaf area, radiation load on the leaf, and boundary layer conductance (Johns, 1978; O'Toole & Cruz, 1980). Johns (1978) suggested that the yield advantage of tall fescue compared to other temperate grasses was due mainly to leaf rolling during drought.

FRANK ET AL.

12

0

z 4

INITIAL GROWTH FORAGE
 $HAUN = -0.0829 + 0.0122(GDD)$
 $r = 0.9804$
 $n = 1242$

REGROWTH FORAGE ~
 $HAUN = -2.7818 + 0.0022(GDD)$
 $r = 0.84^{**}$
 $n = 478$



Fig. 5-5. Regression of Haun growth stage (Haun, 1973) and accumulated growing degree-days for initial spring growth and regrowth forage of crested wheatgrass grown at 10 and 100 kg N ha⁻¹ and 50, 100, and 150% rainfall during 1984, 1985, and 1986. The average date to accumulate 800, 1600, and 2400 growing degree-days was 6 June, 7 July, and 28 August, respectively, (from Frank & Ries, 1990).

Leaf senescence, which reduces transpiring leaf area, also is a common response to water deficits in cool-season grasses. Bittman et al. (1988) showed that leaf senescence was greater for floral tillers than vegetative tillers in both crested wheatgrass and smooth bromegrass under both dryland and irrigated conditions. Drought increased rate of leaf senescence more in floral than vegetative tillers in crested wheatgrass and smooth bromegrass. Among species, floral and vegetative tillers of crested wheatgrass senesced more rapidly than smooth bromegrass (Fig. 5-6). Leaves of vegetative tillers of dryland crested wheatgrass also senesced more rapidly than either smooth bromegrass or Altai wildrye, but no differences were observed under irrigation. The greater senescence in droughted crested wheatgrass may be related to its lower leaf water potential than smooth bromegrass or Altai wildrye. Maximum leaf water potentials to induce leaf senescence occurred from -1.95 to -2.65 MPa in crested wheatgrass and from -1.85 to -2.25 MPa in smooth bromegrass (Bittman et al., 1988).

Growth potential on semiarid grasslands during spring is highly dependent on stored soil water (Table 5-1). In contrast, yield potential on humid grasslands is rarely limited by drought during early spring. Sneva (1977) reported that precipitation received from July, August, or September to March, April, May, or June the following year was significantly correlated ($r = 0.61-0.84$) with regrowth and mature dry matter yield of crested wheatgrass through a 12-yr period in Oregon. In the Northern Great Plains, Rogler and Haas (1947) showed that for 20 yr during the period from 1918 through 1945 native grassland production was correlated with the previous fall soil water for both the 0- to 0.9- and 0- to 1.8-m depth increments ($r = 0.72$ and 0.74 , respectively). Fall soil water also was associated with animal gains the following year in their study.

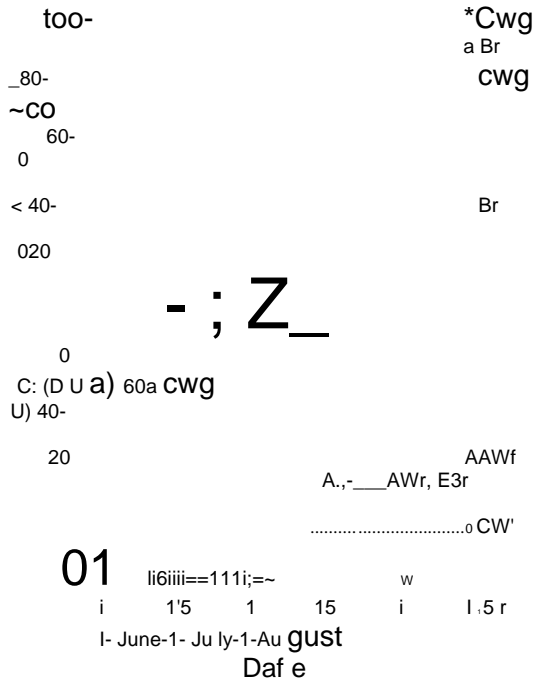


Fig. 5-6. Percentage senescence of the upper three leaves on floral (top) and vegetative (bottom) tillers of crested wheatgrass (CWg) and bromegrasses (Br) and nonfloral Tillers of Altai wildrye (AWr). Solid lines are for dryland plots and broken lines are for irrigated plots. Vertical bars represent least significant difference (P < 0.05) for the sampling date (from Bittman et al., 1988).

Root Growth

The development of an extensive root system is essential for establishment and continued productivity of grasses. In a review of seedling establishment, Hyder (1971) concluded that successful establishment of grasses required a well-developed adventitious root system; the seminal root system alone is not capable of providing adequate water to the grass plant after establishment. Adventitious roots form at the stem nodes, but only if the stem nodes are in moist soil for at least 2 d. Cornish (1982) reported that surface drying of adventitious root primordia for surface-sown seeds of bulbous canarygrass and perennial ryegrass precluded production of adventitious roots even when the seminal roots were in moist soil. After formation of the adventitious root system, the seminal roots are less important to plant persistence or productivity. In a split-root study the adventitious root system in timothy had about 100 times more biomass than the seminal roots 18 wk after seeding (Williams, 1962).

The formation of adventitious roots differs among grass species. Newman and Moser (1988) found that forage grasses adapted to the subhumid regions (creeping foxtail, reed canarygrass, smooth bromegrass, and tall fescue) developed more adventitious roots at the three-leaf stage than grasses adapted to the

Table 5-5. Effective depth of water extraction of some cool-season grasses.

Species	Effective depth of water extraction cm	Source
Humid grasses		
Rough stalk meadow grass	40	Garwood & Sinclair, 1979
Timothy	70	Garwood & Sinclair, 1979
Orchardgrass	70	Garwood & Sinclair, 1979
Perennial ryegrass	80	Garwood & Sinclair, 1979
Tall fescue	> 100	Garwood & Sinclair, 1979
Semi-arid grasses		
Crested wheatgrass	120	Frank & Bauer, 1991
Western wheatgrass	> 120	Frank & Bauer, 1991
Intermediate wheatgrass	120	Frank & Bauer, 1991

semi-arid regions (Russian wildrye, fairway crested wheatgrass, intermediate wheatgrass, and western wheatgrass). In contrast the fewer adventitious roots that formed on the semi-arid grasses at this early developmental stage likely would be a competitive disadvantage in a water-limited environment.

Mature grasslands contain from 56 to 95% of total biomass in roots (Marshall, 1977) with the majority of roots in the upper 30 cm of the soil profile. Grass species differ in their ability to extract soil water mainly because of differences in rooting depth and distribution (Garwood & Sinclair, 1979). Grasses adapted to semi-arid regions have a greater effective depth of water extraction than humid grasses (Table 5-5). Under drought a greater rooting depth and soil volume exploration generally is associated with higher forage yields, greater drought tolerance, and improved plant water status.

Defoliation by grazing or cutting reduces total root biomass and depth of penetration, often causing reduced forage yield and stand persistence. Defoliation of Thurber needlegrass to 2.5-cm stubble at the early boot compared to the anthesis stage reduced spring dry matter yields by 46 to 51% and root mass by 34 to 45% the following spring when soil water was limiting (Ganskopp, 1988). Such severe defoliation often results in reduced stand vigor and predisposes the stand to further reductions should water or temperature stress be severe.

Water-Use Efficiency

Sinclair et al. (1984) indicated that WUE has been used to describe a wide range of various observations covering a variety of diverse time and process scales. The term is sometimes used to refer to instantaneous determinations of WUE, which are based on the amounts of carbon dioxide assimilated divided by either the amount of water transpired or by stomatal conductance. The WUE also refers to the seasonlong accumulation of biomass divided by the ~ amount of water used to produce that biomass and will be used that way here.

Research has shown that numerous climatic factors, plant characteristics, and soil characters influence WUE (Stone, 1975; Taylor et al., 1983; Stanhill, 1986). Although most of this research has been conducted with annual seed crops, some research has been conducted with cool-season grasses. Smika et al. (1965)

reported that WUE of grass stands in North Dakota dominated by western wheatgrass increased with increasing rates of N fertilizer. Similarly, Power (1985) reported a threefold increase in WUE with fertilization in several grasses including western wheatgrass, crested wheatgrass, intermediate wheatgrass, smooth brome grass, Russian wildrye, and creeping foxtail. In that study the quantity of available water required for maximum WUE increased with N supply. Fertilized coolseason grasses apparently take up more water than nonfertilized grasses by extracting water to greater depths (Lorenz & Rogler, 1967). Wight and Black (1978) found similar results on a mixed prairie upland range site in northeastern Montana and reported that the efficiency of overwinter soil water recharge was increased with fertilization. Frank et al. (1985) examined clonal lines of crested wheatgrass, western wheatgrass, and intermediate wheatgrass and found that morphological development earlier in the growing season, when vapor pressure deficits are low, resulted in higher WUE.

Bleak and Keller (1973) found that 62% of the total variance for water requirement in 'Nordan' crested wheatgrass was genetic and suggested that selection for WUE would be effective. Frank et al. (1987) reported that prediction of WUE of field-grown clones of crested wheatgrass, intermediate wheatgrass, and western wheatgrass based on gas exchange data obtained in a controlled environment were not reliable. Barker et al. (1989) found clonal variation for WUE in cultivars or strains of crested wheatgrass, western wheatgrass, intermediate wheatgrass, and reed canarygrass. Because environmental influences on WUE were high, they indicated that effective plant evaluation and selection would be extremely difficult, time consuming, and costly. They concluded that development of more effective screening techniques would be necessary for reliable selection for improved WUE.

Direct evaluation of WUE in species, cultivars, or breeding lines by measurement of growth and water consumption is time consuming both in the field and controlled environments. An indirect method of measuring WUE that has shown promise in evaluating WUE in plants that fix C by the C₃ pathway (such as cool-season grasses) involves analysis of C isotope composition (Rundel et al., 1989). Stable isotopes do not undergo radioactive decay and are atoms whose nuclei contain the same number of protons, but have a different number of neutrons. Carbon has two stable isotopes, ¹²C and ¹³C. The ¹²C form comprises approximately 99% of the C in the earth and its atmosphere, whereas the ¹³C isotope form represents only about 1%. The C isotope composition of plant tissue can be measured by drying, grinding, and combusting the harvested tissue. The composition of the combusted CO₂ is then analyzed with an isotope-ratioing mass spectrometer.

The ratio of ¹³C/¹²C varies in plants due primarily to discrimination by diffusional and enzymatic processes. Farquhar et al. (1982) developed a theory that the level of discrimination against ¹³C compared with ¹²C during CO₂ fixation provides a long-term, integrated estimate of instantaneous WUE. Farquhar et al. (1988) attributed this association to independent linkages through internal CO₂ concentration inside the leaf. Because internal CO₂ concentration is affected by diffusional and biochemical processes that contribute to changes in instantaneous WUE, measurements of C isotope discrimination (Δ) were hypothesized to be

useful in characterizing WUE in C3 plants (Farquhar & Richards, 1984). Since that initial work, numerous studies have reported consistent negative associations between WUE and A (Farquhar et al., 1989).

A negative association between WUE and A has been demonstrated in several cool-season grasses including crested wheatgrass (Johnson et al., 1990; Johnson & Bassett, 1991; Read et al., 1991, 1992), Altai wildrye (Johnson et al., 1990), tall fescue (Johnson & Bassett, 1991; Johnson, 1993), as well as orchardgrass and perennial ryegrass (Johnson & Bassett, 1991). Significant genetic variability for A was found in crested wheatgrass (Johnson et al., 1990). In addition, broad-sense heritabilities for A in crested wheatgrass were about 0.50 (Johnson et al., 1990), and estimates of narrow-sense heritability were more than 0.75 (Read et al., 1993).

The presence of significant genetic variation for A and the magnitudes of the heritabilities for A indicate that genetic improvement for WUE can be effectively achieved in crested wheatgrass through indirect selection for A. Consequently, selection for low A is a promising screening tool for improving WUE in crested wheatgrass and possibly other cool-season grasses. Additional research is needed to document the association between forage yield and A.

Seed Production

Literature dealing with the effects of water deficits on seed production in cool-season grasses is scarce. Factors affecting seed production are presumably similar among cool-season grasses and will be generalized. Both leaf and spikelet primordia originate in the apex of grasses. The sequence of physiological events that result in an apex becoming reproductive or remaining vegetative are mediated by both temperature and photoperiod. Although most cool-season grasses typically form reproductive apices in the spring, Russian wildrye forms reproductive apices in the fall (Lawrence & Ashford, 1964). The inflorescences of cool-season grasses are mainly determinate in growth, suggesting that inflorescence size is determined early in plant development or by about the five- to sixleaf stage. This occurs in early spring when the atmospheric evaporative demand is low, and soil water supplies are often adequate. High atmospheric evaporative demand and drought during anthesis can result in low pollen viability and reduced seed numbers. Seed filling and seed quality require adequate water for photosynthate production and translocation to the developing seed.

Forage Quality

Decline in forage quality with plant development is caused by an increasing proportion of stem tissue, loss of leaves by senescence, and increased lignification of both stems and leaves. Reports on the effect of drought on nutritional quality have been contradictory. Garwood et al. (1979) found that drought had an inconsistent effect on the digestibility of cool-season grasses, and Harris and Lazenby (1974) reported no effect. Dent and Aldrich (1963) reported higher digestibility in perennial ryegrass, timothy, and orchardgrass under low compared

to high rainfall. Water deficit sometimes increases (Wilson, 1983) and other times decreases (Pitman et al., 1981) the digestibility of warm-season grasses. Surprisingly, while drought increased leaf senescence, it decreased the rate of seasonal decline in digestibility and slowed the increase in acid detergent fiber (ADF) and acid detergent lignin in crested wheatgrass, smooth brome grass and Altai wildrye (see "Whole Plant Response to Water Deficits") (Bittman et al., 1988).

Effect of drought on digestibility varies because several processes are involved, and the severity of drought differs. While drought retards stem development (Wilson, 1983) and increases soluble carbohydrates (see discussion above), it causes thickening of cell walls (Cutler et al., 1977) and may either decrease (Bittman et al., 1988; Wilson, 1983) or increase (Pitman et al., 1983) lignification. High leaf temperature, which often is associated with plant water deficit, may decrease herbage digestibility (Hacker & Minson, 1981), while high light levels, also common during drought, contribute to increased digestibility (Van Soest et al., 1978). Xeromorphic structures characteristic of plants in dry habitats, such as thick cell walls, thick cuticle, and highly lignified tissue are associated with low digestibility.

Drought has been shown to decrease N (Gifford & Jensen, 1967; Bittman et al., 1988), increase N (Misra & Singh, 1982), or have inconsistent effects (Garwood et al., 1979) on N concentration in cool-season grasses. Drought had no effect on N concentration of some tropical grasses (Wilson, 1983). The drought effect on N concentration is apparently determined by distribution of N and water in the soil profile. When water deficits developed rapidly, N concentrations were high and some of the N was present in the nitrate form (Garwood et al., 1979). Alternatively, when subsoil moisture was ample and most of the soil N was near the surface, growth continued without N uptake so that levels in the plant declined. In extreme situations, growth may be slowed by drought-induced nutrient deficiency. Plant uptake of P is particularly sensitive to drought (Bittman et al., 1988).

Recovery

Where drought is intermittent, seasonal productivity is influenced by rate and extent of recovery from water deficit (see "Whole Plant Response to Water Deficits"). Both orchardgrass and smooth brome grass maintained green leaf tissue during drought (Thomas, 1986b; Bittman & Simpson, 1987), allowing assimilation and growth to continue rapidly after water was replenished. In contrast, drought readily induces leaf senescence in crested wheatgrass so that it is rarely found in areas with intermittent drought. Leafe et al. (1977) demonstrated that maintaining its green leaf area also helped perennial ryegrass sustain growth during drought.

Droughted plants may grow more rapidly after rewatering than well-watered plants (Lawlor, 1972). For example, rate of leaf extension: after drought in rescue grass equaled the rate of well-watered plants in 4 to 6 d and eventually exceeded it by as much as 20% (Chu et al., 1979). Final yield was proportional to the number of nondrought days so that the loss of final yield from drought was due to loss of growing time (see "Whole Plant Response to Water Deficits"). Regrowth of Italian ryegrass plants after 4 d of drought exceeded that of well-

watered plants in number of shoots and root dry weight so that the brief drought period had little effect on yield (Corleto & Lauda, 1974). Rapid recovery from drought is considered one of the drought resistance attributes of orchardgrass (Thomas, 1986a). The more drought-resistant tall fescue and orchardgrass recovered from drought more rapidly than perennial and Italian ryegrass (Norris, 1982). Tall fescue swards that had been droughted during the summer and then defoliated had better fall regrowth than swards that were irrigated (Horst & Nelson, 1979). Similarly, timothy plants that were droughted and then harvested regrew more rapidly than well-watered plants (Mela & Youngner, 1976). Rapid recovery growth in tall fescue persisted for several days after rewatering (West et al., 1990). Recovery growth of perennial ryegrass was more rapid in vegetative than reproductive plants (Thomas, 1987).

Rapid regrowth is often attributed to accumulation of carbohydrates and other solutes (Thomas, 1987) in leaves (see "Osmotic Adjustment"), stem bases (Horst & Nelson, 1979), roots (Mela & Youngner, 1976), crowns and roots (Busso et al., 1990), and meristematic leaf bases (West et al., 1990). The supply of carbohydrates in meristematic regions of tall fescue persisted for 3 to 6 d after rehydration. The accumulation of solutes is due to both a change in the source-sink relationship (see "Osmotic Adjustment") and to the redistribution of assimilates within the plant (Thomas & Evans, 1989; Lawlor, 1972). Slow dehydration, which favors accumulation of solutes, should promote better recovery (Fig. 5-4). Accelerated regrowth in droughted plants also is due to the accumulation of unexpanded cells in meristematic regions during drought (Thomas, 1987; Lawlor, 1972).

In contrast to leaf expansion, canopy photosynthesis of perennial ryegrass recovered slowly after a drought period, although final rates equaled those of well-watered plants (Sheehy et al., 1975). This "hysteresis," also was evident in tall fescue plants receiving ample N and was attributed largely to slow recovery of stomatal conductance due to slow dissipation of ABA in guard cells (Ghashghaie & Saugier, 1989). In contrast, photosynthetic rates after rewatering in guineagrass warm-season exceeded those of well-watered leaves probably because drought suspended aging of these leaves (Ludlow & Ng, 1974).

Mortality

Few studies have documented death due to drought in adapted cool-season grasses, which suggests that drought may not be a common cause of mortality of mature grasses in the field. Tadmor et al. (1970) reported that crested and intermediate wheatgrass survived 660 d of drought, and orchardgrass survived 3 yr in the Negev Desert in Israel. Crested wheatgrass showed no mortality after a year with 49% of mean precipitation (Ganskopp & Bedell, 1981). Crested wheatgrass swards have survived over 40 yr (Dormaar et al., 1978), and individual plants are thought to survive more than 15 to 20 yr (Looman & Heinrichs, 1973) under fluctuating precipitation in the Northern Great Plains. Survival of cool-season grasses during long periods of quiescence is due to deeply penetrating roots, which maintain a small supply of water enabling meristematic regions to survive (McWilliam & Kramer, 1968; Redmann, 1976), and to carbohydrate reserves,

which provide a substrate for respiration and recovery growth (Julander, 1945). Rogler (1951) reported that much of the needleandthread was killed during the drought years of 1934 and 1936, but it recovered considerably afterwards. Dormancy of axillary buds also is essential for drought survival as demonstrated in cultivars of bulbous canarygrass (Oram, 1984; Oram & Freebairn, 1984).

Population reductions caused by drought are less likely in pure stands than in mixed communities where a drought-resistant species may crowd out a less-resistant species through time. Crested wheatgrass was more competitive than bluebunch wheatgrass with big sagebrush and downy brome grass due to early depletion of water (Eissenstat & Caldwell, 1988). Drought, combined with other factors such as clipping, may reduce carbohydrate reserves (Roundy et al., 1985) and root biomass (Mohammad et al., 1982), thus reducing persistence. However, light defoliation (40%) improved drought persistence compared to no defoliation in crested wheatgrass and Russian wildrye by reducing transpiration (Mohammad et al., 1982). Because drought increases carbohydrate reserves in stem bases (Brown & Blaser, 1970), it may increase grazing (Busso et al., 1989) and cold tolerance, and spring vigor of grasses, contributing to their survival, particularly in mixed communities.

Plant mortality is probably more common in seedlings (Roundy et al., 1985), especially in the one- to three-leaf stage (Lichthardt & Weaver, 1985) and young shoots (Bittman, 1985) than in mature grass plants. Young plants may be more susceptible to drought due to less root development, poorer development of the vascular system, thin cell walls, weak membranes, shortage of carbohydrate reserves, etc. In young shoots the upper emerging leaves are most susceptible to drought injury; in contrast leaf senescence always begins with the older, lower leaves (Bittman, 1985). Drought injury and sudden death may be caused by cavitation of xylem vessels cutting off water supply to leaf tissues; young stems seemingly do not possess the small hypodermal vascular bundles found in mature stems (Hayward, 1938).

SUMMARY

Recent studies have caused some familiar concepts in plant water relations to be re-examined. Attempts to find selection factors for improving yield and survival of plants during drought have often not produced the desired or expected results (e.g., leaf ridging in perennial ryegrass, Wilson, 1975b; osmotic adjustment in wheat, Morgan, 1983; leaf waxes in wheatgrass and wildrye, Jefferson et al., 1989a, b; osmotic adjustment in perennial ryegrass, Thomas & Evans, 1989) despite early promise. Drought responses of plants are very interactive and a change in one characteristic may lead to compensation by other characteristics. Attempts to find generalized responses to tissue water loss (e.g., leaf conductance to plant water potentials) are hampered by the interdependence of plant characteristics, and we are often unable to distinguish cause from effect.

The observation that drought responses may correlate more closely with soil water than plant water status underscores the difficulty: of relating plant responses to tissue water deficit. The question of response must be redefined not how does water potential influence leaf conductance-rather how do the

two responses covary in response to changing soil water? The nature of this covariance represents the drought resistance strategy of the plant, which is both genotype and environment specific. Future studies will be most useful when they are based on clearly defined hypotheses rather than descriptive observations.

Discovery of direct influence of soil water on stomatal response and leaf expansion may change the direction of future drought research because it helps change our perception of water from that of an environmental factor producing stress to that of a resource. Drought may be viewed as a problem of resource limitation and not of environmental stress (or strain). As soil water is depleted it becomes exponentially less available, due to sharp decreases in soil water potential and soil hydraulic conductivity, and there is little biological solution possible. When water supplies decline, drought-resistant plants reduce and modify their physiological activities, remain quiescent, and ultimately exhibit injury, recovery, or mortality. The best chance for improving yield under drought is through understanding how plants efficiently utilize their limited water resource.

REFERENCES

- Anderson, V.J., and D.D. Briske. 1990. Stomatal distribution, density and conductance of three perennial grasses native to the southern true prairie of Texas. *Am. Midl. Nat.* 123:152-159.
- Asay, K.H., and D.A. Johnson. 1983. Genetic variability for characters affecting stand establishment in crested wheatgrass. *J. Range Manage.* 36:703-706.
- Aspinall, D., and L.D. Paleg. 1981. Proline accumulation. Physiological aspects. p. 206-240. *In* L.G. Paley and D. Aspinall (ed.) *Physiology and biochemistry of drought resistance in plants*. Acad. Press, Sydney, Australia.
- Barker, R.E., A.B. Frank, and J.D. Berdahl. 1989. Cultivar and clonal differences for water-use efficiency and yield in four forage grasses. *Crop Sci.* 29:58-61.
- Barnett, N.M., and A.W. Naylor. 1966. Amino acid and protein metabolism in bermuda grass during water stress. *Plant Physiol.* 41:1222-1230.
- Berdahl, J.D., and R.E. Barker. 1980. Germination and emergence of Russian wildrye seeds coated with hydrophilic materials. *Agron. J.* 72:1006-1008.
- Bildusas, I.J., R.K. Dixon, F.L. Pfeleger, and E.L. Stewart. 1986. Growth, nutrition and gas exchange of *Bromus inermis* inoculated with *Gloniufasciculatum*. *New Phytol.* 102:303-311.
- Bittman, S. 1985. Physiological and agronomic responses to drought of three forage grasses: Crested wheatgrass, smooth bromegrass and Altai wildrye. Ph.D. diss. Univ. Saskatchewan, Saskatoon, SK.
- Bittman, S., and G.M. Simpson. 1987. Effect of soil water deficit on yield, leaf area, and net assimilation rate of three forage grasses: Crested wheatgrass, smooth bromegrass, and Altai wildrye. *Agron. J.* 79:768-774.
- Bittman, S., and G.M. Simpson. 1989a. Drought effect on leaf conductance and leaf rolling in forage grasses. *Crop Sci.* 29:338-344.
- Bittman, S., and G.M. Simpson. 1989b. Drought effects on water relations of three cultivated grasses. *Crop Sci.* 29:992-999.
- Bittman, S., G.M. Simpson, and Z. Mir. 1988. Leaf senescence and seasonal decline in forage quality of three temperate grasses as influenced by drought. *Crop Sci.* 28:546-552.
- Blaikie, S.J., K.B. Kelly, and W.K. Mason. 1989. Effects of ameliorating exposed subsoil prior to sowing on the water relations and productivity of pasture during gin irrigation cycle. *Aust. J. Agric. Res.* 40:97-106.
- Bleak, A.T., and W. Keller. 1973. Water requirement, yield, and tolerance to clipping of some cool-season, semiarid range grasses. *Crop Sci.* 13:367-370.
- Blizzard, W.E., and J.S. Boyer. 1980. Comparative resistance of the soil and plant to water transport. *Plant Physiol.* 66:809-814.
- Bokhari, U.G., and J.D. Trent. 1985. Proline concentrations in water stressed grasses. *J. Range Manage.* 38:37-38.

- Bradford, K.J., and T.C. Hsiao. 1982. Physiological responses to moderate water stress. p. 263-324. In O.L. Lange et al. (ed.) Encyclopedia of plant physiology, new series. Vol. 12B. Springer-Verlag, Berlin, Germany.
- Brown, R.W. 1977. Water relations of range plants. p. 96-140. In R.E. Sosebee (ed.) Rangeland plant physiology. Soc. Range Manage. Denver, CO.
- Brown, R.H., and R.E. Blaser. 1965. Relationship between reserve carbohydrate accumulation and growth rate in orchardgrass and tall fescue. *Crop Sci.* 5:577-582.
- Brown, R.H., and R.E. Blaser. 1970. Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (*Dactylis glomerata*). *Crop Sci.* 10:213-216.
- Burch, G.J. 1979. Soil and plant resistances to water absorption by plant root systems. *Aust. J. Agric. Res.* 30:279-292.
- Burch, G.J., and G.C. Johns. 1978. Root absorption of water and physiological responses to water deficits by *Festuca arundinacea* Schreb. and *Trifolium repens* L. *Aust. J. Plant Physiol.* 5:859-871.
- Busso, C.A., R.J. Mueller, and J.H. Richards. 1989. Effects of drought and defoliation on bud viability in two caespitose grasses. *Ann. Bot.* 63:477-485.
- Busso, C.A., J.H. Richards, and N.J. Chatterton. 1990. Nonstructural carbohydrates and spring regrowth of two cool-season grasses: Interaction of drought and clipping. *J. Range Manage.* 43:336-343.
- Buwai, M., and M.J. Trlica. 1977. Defoliation effects on root weights and total nonstructural carbohydrates of blue grama and western wheatgrass. *Crop Sci.* 17:15-17.
- Caldwell, M.M., and J.H. Richards. 1989. Hydraulic lift: Water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia* 79:1-5.
- Caldwell, M.M., J.H. Richards, and W. Beyschlag. 1991. Hydraulic lift: Ecological implications of water efflux from roots. p. 423-436. In D. Atkinson (ed.) *Plant root growth. An ecological perspective.* Br. Ecol. Soc. Spec. Publ. 10. Blackwell Sci. Publ., London.
- Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurec. 1981. Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid Agropyron bunchgrasses. *Oecologia* 50:14-24.
- Chatterton, N.J., P.A. Harrison, J.H. Bennett, and W.R. Thornley. 1987. Fructan, starch and sucrose concentrations in crested wheatgrass and redtop as affected by temperature. *Plant Physiol. Biochem.* 25:617-623.
- Chavez, M.M. 1991. Effects of water deficits on carbon assimilation. *J. Exp. Bot.* 42:1-16.
- Chu, A.C.P., and H.G. McPherson. 1977. Sensitivity to desiccation of leaf extension in prairiegrass. *Aust. J. Plant Physiol.* 4:381-387.
- Chu, A.C.P., H.G. McPherson, and G. Halligan. 1979. Recovery growth following water deficits of different duration in prairie grass, *Bromus catharticus*. *Aust. J. Plant Physiol.* 6:255-264.
- Corleto, A., and H.M. Lauda. 1974. Evaluating growth potential after drought stress. *Crop Sci.* 14:224-227.
- Cornish, P.S. 1982. Root development in seedlings of ryegrass (*Lolium perenne* L.) and phalaris (*Phalaris aquatica* L.) sown onto the soil surface. *Aust. J. Agric. Res.* 33:665-677.
- Cowan, I.R. 1982. Regulation of water use in relation to carbon gain in higher plants. p. 589-613. In O.L. Lang et al. (ed.) *Encyclopedia of plant physiology, new series.* Vol. 12B. Springer-Verlag, Berlin, Germany.
- Cutler, J.M., O.W. Rains, and R.S. Loomis. 1977. The importance of cell size in the water relations of plants. *Physiol. Plant.* 40:255-260.
- Daer, T., and E.E. Willard. 1981. Total nonstructural carbohydrate trends in bluebunch wheatgrass related to growth and phenology. *J. Range Manage.* 34:377-379.
- Davidson, J.L., and F.L. Milthorpe. 1966. The effect of defoliation on the carbon balance in *Dactylis glomerata*. *Ann. Bot.* 30:185-198.
- Davies, W.J., and J. Zhang. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Ann. Rev. Plant Physiol. Mol. Biol.* 42:55-76.
- Day, T.A., and J.K. Detling. 1990. Changes in grass leaf water relations following bison urine deposition. *Am. Midl. Nat.* 123:171-178.
- Dent, J.W., and D.T.A. Aldrich. 1963. Interrelationship between heading date, yield, chemical composition and digestibility in varieties of perennial ryegrass, timothy, cocksfoot and meadow fescue. *Natl. Inst. Agric. Bot. J.* 9:261-281.
- Deput, E.J., and M.M. Caldwell. 1975. Gas exchange of 3 cool semidesert species in relation to temperature and water stress. *J. Ecol.* 63:835-858.

- Dibble, M.S., and G.G. Spomer. 1987. Cell water potential components in the adaptation of *Pseudoroegneria spicata* (Pursh) A. Love to various habitat moisture conditions. *Bot. Gaz.* 148:73-78.
- Distel, R.A., and O.A. Fernandez. 1987. Leaf water potential trends in three grasses native to semiarid Argentina. *J. Range Manage.* 40:203-207.
- Dormaer, J.F., A. Johnston, and S. Smoliak. 1978. Long term soil changes associated with seeded stands of crested wheatgrass in southwestern Alberta, Canada. p. 623-625. *In* D.N. Hagler (ed.) *Proc. 1st Int. Range Cong.*, Denver, CO. 14-18 August. *Soc. Range Manage.*, Denver, Co.
- Downes, R.W. 1969. Differences in transpiration rates between tropical and temperate grasses under controlled conditions. *Planta (Berlin)* 88:261-273.
- Eissenstat, D.M., and M.M. Caldwell. 1988. Competitive ability is linked to rates of water extraction. *Oecologia* 75:1-7.
- Ewing, A.L., and J.W. Menke. 1983. Reproductive potential of *Bromus mollis* and *Avena barbata* under drought conditions. *Madrono* 30:159-167.
- Faiz, S.M.A., and P.E. Weatherly. 1978. Further investigations into the location and magnitude of the hydraulic resistance in the soil:plant system. *New Phytol.* 81:19-28.
- Farquhar, G.D., J.R. Ehleringer, and K.T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* 40:503-537.
- Farquhar, G.D., K.T. Hubick, A.G. Condon, and R.A. Richards. 1988. Carbon isotope fractionation and plant water-use efficiency. p. 21-40. *In* P.W. Rundel et al. (ed.) *Stable isotopes in ecological research*. *Ecol. Stud.* Vol. 68. Springer-Verlag, New York.
- Farquhar, G.D., M.H. O'Leary, and J.A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* 9:121-137.
- Farquhar, G.D., and R.A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* 11:539-552.
- Ford, C.W., and J.R. Wilson. 1981. Changes in levels of solutes during osmotic adjustment to water stress in leaves of four tropical pasture species. *Aust. J. Plant Physiol.* 8:77-91.
- Foster, S.R., and W.K. Smith. 1986. Influence of stomatal distribution on transpiration in lowwind environments. *Plant Cell Environ.* 9:751-759.
- Frank, A.B. 1981. Effect of leaf age and position on photosynthesis and stomatal conductance of forage grasses. *Agron. J.* 73:70-74.
- Frank, A.B. 1983. Plant water relationships of crested, pubescent, slender, and western wheatgrass. p. 399-401. *In* J.A. Smith and V.W. Hays, (ed.) *Proc. 12th Int. Grass. Congr.*, Lexington, KY. 15-24 June 1981. Westview Press, Boulder, CO.
- Frank, A.B. 1994. Physiological comparisons of crested wheatgrass and western wheatgrass to water. *J. Range Manage.* 47:40-466.
- Frank, A.B., and R.E. Barker. 1976. Rates of photosynthesis and transpiration and diffusive resistance of six grasses grown under controlled conditions. *Agron. J.* 68:487-490.
- Frank, A.B., R.E. Barker, and J.D. Berdahl. 1984. Pressure-volume characteristics of genotypes of three wheatgrass species. *Crop Sci.* 24:217-220.
- Frank, A.B., R.E. Barker, and J.D. Berdahl. 1987. Water-use efficiency of grasses grown under controlled and field conditions. *Agron. J.* 79:541-544.
- Frank, A.B., and A. Bauer. 1991. Rooting activity and water use during vegetative development of crested and western wheatgrass. *Agron. J.* 83:906-910.
- Frank, A.B., J.D. Berdahl, and R.E. Barker. 1985. Morphological development and water use in clonal lines of four forage grasses. *Crop Sci.* 25:339-344.
- Frank, A.B., and R.E. Ries. 1990. Effect of soil water, nitrogen, and growing degree-days on morphological development of crested and western wheatgrass. *J. Range Manage.* 43:257-260.
- Gaff, D.F. 1989. Desiccation tolerant resurrection grasses for dryland areas. p. 1537-1538. *In* *Proc. 16th Int. Grass. Congr.*, Nice, France. 4-11 October. *French Grass. Soc.*, Versailles, France.
- Ganskopp, D. 1988. Defoliation of Thurber needlegrass: Herbage and root responses. *J. Range Manage.* 41:472-476.
- Ganskopp, D.C., and T.E. Bedell. 1981. An assessment of vigor and production of range grasses following drought. *J. Range Manage.* 34:137-141.
- Garwood, E.A., and J. Sinclair. 1979. Use of water by six grass species. 2. Root distribution and use of soil water. *J. Agric. Sci. (Cambridge)* 93:25-35.
- Garwood, E.A., K.C. Tyson, and J. Sinclair. 1979. Use of water by six grass species. 1. Dry-matter yields and response to irrigation. *J. Agric. Sci. (Cambridge)* 93:13-24.

- Govande, S.A., and S.A. Taylor. 1967. **Influence of soil water potential and atmospheric evaporative demand on transpiration and energy status of water in plants.** Agron. J. 59:4-7.
- Gay, A.P. 1989. Assessment of the response to selection for leaf water conductance in *Lolium perenne* L. Ann. Bot. 64:593-598.
- Ghashghaie, J., and B. Saugier. 1989. Effects of nitrogen deficiency on leaf photosynthetic response of tall fescue to water deficit. Plant Cell Environ. 12:261-271.
- Gifford, R.O., and E.H. Jensen. 1967. Some effects of soil moisture regime and bulk density on forage quality. Agron. J. 59:75-77.
- Gollan, T., N.C. Turner, and E.D. Schulze. 1985. The responses of stomata and leaf gas exchange to vapor pressure deficits and soil water contents. III. In the schrophyllous weedy species *Nerium oleander*. Oecologia 65:336-362.
- Gordon, D.R., J.M. Welker, J.W. Menke, and K.J. Rice. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasiz*) seedlings. Oecologia 79:533-541.
- Grace, J., and G. Russell. 1977. The effect of wind on grasses. J. Exp. Botany 28:268-278.
- Greacen, E.L. 1977. Mechanisms and models of water transfer. p. 163-196. In J.S. Russell and E.L. Greacen (ed.) Soil factors in crop production in a semi and environment. Univ. Queensland Press, St. Lucia, Australia.
- Greacen, E.L. and J.S. Oh. 1972. Physics of root growth. Nat. New Biol. 235:24-25.
- Green, P.B. 1968. Growth physics in *Nitella*: A method for continuous *in vivo* analysis of extensibility based on a micro-manometer technique for turgor pressure. Plant Physiol. 43:1169-1184.
- Hacker, J.B., and D.J. Minson. 1981. Digestibility of plant parts. Herb. Abstr. 51:459-482.
- Harris, W., and A. Lazenby. 1974. Competitive interaction of grasses with contrasting temperature responses and water stress tolerances. Aust. J. Agric. Res. 25:227-246.
- Haun, J.R. 1973. Visual quantification of wheat development. Agron. J. 65:116-119.
- Hayward, H.E. 1938. The structure of economic plants. MacMillan Co., New York.
- Heichel, G.H. 1971. Stomatal movements, frequency and resistances in two maize varieties differing in photosynthetic capacity. J. Exp. Bot. 22:644-649.
- Holt, D.A., and A.E. Hilst. 1969. Daily variations in carbohydrate content of selected forage crops. Agron. J. 61:239-242.
- Horst, G.L., and C.J. Nelson. 1979. Compensatory growth of tall fescue following drought. Agron. J. 71:559-563.
- Hsiao, T.C., W.K. Silk, and J. Jing. 1985. Leaf growth and water deficits: biophysical effects. p. 239-266. In N.R. Baker et al. S.E.B. Sem. Ser. 27. Cambridge Univ. Press, London.
- Hyder, D.N. 1971. Morphogenesis and management of perennial grasses in the United States. p. 89-98. In K.W. Krestlow and R.H. Hart (ed.) Plant morphogenesis as the basis for scientific management of range resources. Proc. Workshop U.S.-Australia Rangelands Panel. Berkeley, CA. 29 March-5 April. USDA-ARS Misc. Publ. 1271.
- Jackson, D.K. 1974. The course and magnitude of water stress in *Lolium perenne* and *Dactylis glomerata*. J. Agric. Sci. (Cambridge) 82:19-27.
- Jackson, L.E., and J. Roy. 1986. Growth patterns of Mediterranean annual and perennial grasses under simulated rainfall regimes of southern France and California. Oecol. Plant. 7:191-212.
- Jefferson, P.G., D.A. Johnson, and K.H. Asay. 1989a. Epicuticular wax production, water status and leaf temperature in Triticeae range grasses of contrasting visible glaucousness. Can. J. Plant Sci. 69:513-519.
- Jefferson, P.G., D.A. Johnson, M.D. Rumbaugh, and K.H. Asay. 1989b. Water stress and genotypic effects on epicuticular wax production of alfalfa and crested wheatgrass in relation to yield and excised leaf water loss rate. Can. J. Plant Sci. 69:481-490.
- Johns, G.G. 1978. Transpirational, leaf area, stomatal and photosynthetic responses to gradually induced water stress in four temperate herbage species. Aust. J. Plant Physiol. 5:113-125.
- Johns, G.G., and A. Lazenby. 1973. Defoliation, leaf area index, and the water use of four temperate pasture species under irrigated and dryland conditions. Aust. J. Agric. Res. 24:783-795.
- Johnson, D.A. 1978. Environmental effects on turgor pressure in range grasses. Crop Sci. 18:945-948.
- Johnson, D.A., and K.H. Asay. 1978. A technique for assessing seedling emergence under drought stress. Crop Sci. 18:520-522.
- Johnson, D.A., K.H. Asay, L.L. Tieszen, J.R. Ehleringer, and P.G. Jefferson. 1990. Carbon isotope discrimination: potential in screening cool-season grasses for water-limited environments. Crop Sci. 30:338-343.

- Johnson, D.A., and R.W. Brown. 1977. Psychrometric analysis of turgor pressure response: A possible technique for evaluating plant water stress resistance. *Crop Sci.* 17:507-510.
- Johnson, R.C. 1993. Carbon isotope discrimination, water relations, and photosynthesis in tall fescue. *Crop Sci.* 33:169-174.
- Johnson, R.C., and L.M. Bassett. 1991. Carbon isotope discrimination and water use efficiency in four cool-season grasses. *Crop Sci.* 31:157-162.
- Johnston, A., S. Smoliak, A.D. Smith, and L.E. Lutwick. 1969. Seasonal precipitation, evaporation, soil moisture and yield of fertilized range vegetation. *Can. J. Plant Sci.* 49:123-128.
- Jones, M.B. 1988. Water relations. p. 204-242. In M.B. Jones and A. Lazenby (ed.) *The grass crop. The physiological basis of production.* Chapman and Hall, London.
- Jones, M.B., E.L. Leafe, and W. Stiles. 1980a. Water stress in field-grown perennial ryegrass. 1. Its effect on growth, canopy photosynthesis and transpiration. *Ann. Appl. Biol.* 96:87-101.
- Jones, M.B., E.L. Leafe, and W. Stiles. 1980b. Water stress in field-grown perennial ryegrass. 11. Its effect on leaf water status, stomatal resistance and leaf morphology. *Ann. Appl. Biol.* 96:103-110.
- Jones, M.M., and H.H. Rawson. 1979. Influence of rate of development of leaf water deficits from photosynthesis, leaf conductance, water use efficiency and osmotic potential in sorghum. *Physiol. Plant.* 45:103-111.
- Julander, O. 1945. Drought resistance in range and pasture grasses. *Plant Physiol.* 20:573-599.
- Jupp, A.P., and E.I. Newman. 1987. Morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L. *New Phytol.* 105:393-342.
- Kaul, R. 1966. Effect of water stress on respiration in wheat. *Can. J. Bot.* 44:623-632.
- Kilcher, M.R., and D.H. Heinrichs. 1966. Performance of some grass-alfalfa mixtures in southwestern Saskatchewan during drought years. *Can. J. Plant Sci.* 46:177-184.
- Laude, H.M. 1971. Effect of temperature on morphogenesis. p. 25-33. In K.W. Kreitlow and R.H. Hart (ed.) *Plant morphogenesis as the basis for scientific management of range resources.* Proc. Workshop U.S.-Australian Rangelands Panel, Berkeley, CA. 29 March-5 April. USDAARS Misc. Publ. 1271.
- Lawlor, D.W. 1972. Growth and water use of *Lolium perenne*. *It. Plant growth. J. Appl. Ecol.* 9:99-105.
- Lawlor, D.W., and R. Khanna-Chopra. 1984. Regulation of photosynthesis during water stress. p. 379-382. In C. Sybesma (ed.) *Advances in photosynthesis research.* Vol. 4. Martinus Nijhoff/ Dr. W. Junk Publ., the Hague, the Netherlands.
- Lawrence, T., and R. Ashford. 1964. Seed yield and morphological development of Russian wild ryegrass as influenced by grazing. *Can. J. Plant Sci.* 44:311-317.
- Lawrence, T., and C.D. Ratzlaff. 1988. Effects of selection for foliage color on the seed and forage yield of Altai wild ryegrass. *Can. J. Plant Sci.* 68:1003-1007.
- Leafe, E.L., M.B. Jones, and W. Stiles. 1977. The physiological effects of water stress on perennial ryegrass in the field. p. 165-185. In K.W. Kreitlow and R.H. Hart (ed.) *Plant morphogenesis as the basis for scientific management of range resources.* Proc. Workshop of U.S.Australian Rangeland Panel, Berkeley, CA. 29 March-5 April. USDA-ARS Misc. Publ. 1231.
- Legg, B.J., W. Day, D.W. Lawlor, and K.J. Parkinson. 1979. The effects of drought on barley growth: Models and measurements showing the relative importance of leaf area and photosynthetic rate. *J. Agric. Sci. (Cambridge)* 92:703-716.
- Levitt, J. 1980. Response of plants to environmental stresses. p. 93-128. Water, radiation, salt and other stresses. Vol. 2. Acad. Press, New York.
- Lichthardt, J., and T. Weaver. 1985. Tolerance of two and eight week droughts by range grass seedlings. *Proc. Montana Acad. Sci.* 45:46-50.
- Looman, J., and D.H. Heinrichs. 1973. Stability of crested wheatgrass pastures under long term use. *Can. J. Plant Sci.* 53:501-506.
- Lorenz, R.J., and G.A. Rogler. 1967. Grazing and fertilization effect root development of range grasses. *J. Range Manage.* 20:129-132.
- Ludlow, M.M. 1980. Stress physiology of tropical pasture plants. *Trop. Grassl.* 14:136-145.
- Ludlow, M.M. 1989. Strategies of response to water stress. p. 269-281. In K.H. Kreeb et al. (ed.) *Structural and functional responses to environmental stresses.* SPB Acad. Press Publ., the Hague, the Netherlands.
- Ludlow, M.M., and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. *Adv. Agron.* 43:107-153.
- Ludlow, M.M., and T.T. Ng. 1974. Water stress suspends leaf aging. *Plant Sci. Lett.* 3:235-240.
- Ludlow, M.M., and T.T. Ng. 1976. Effect of water deficit on carbon dioxide exchange and leaf elongation rate of *Panicum maximum* var. *Trichoglum*. *Aust. J. Plant Physiol.* 3:401-413.

- Majerus, M.E. 1975. Response of root and shoot growth of three grass species to decreases in soil water potential. *J. Range Manage.* 28:473-476.
- Marshall, J.K. 1977. Biomass and production partitioning in response to environment in some North American grasslands. p. 73-84. In J.K. Marshall (ed.) *The belowground ecosystem: A synthesis of plant associated processes.* Range Sci. Dep. Ser. no. 26. Colorado State Univ., Ft. Collins, CO.
- Maxwell, J.O., and R.E. Redmann. 1978a. Leaf water potential, component potentials and relative water content in a xeric grass, *Agropyron dasystachyum* (Hook.) Scribn. *Oecologia* 35:277-284.
- Maxwell, J.O., and R.E. Redmann. 1978b. Water potential and component potentials in expanded and unexpanded leaves of two xeric grasses. *Physiol. Plant.* 44:383-387.
- McWilliam, J.R., and P.J. Kramer. 1968. The nature of the perennial response in Mediterranean grasses. 1. Water relations and summer survival in *Phalaris*. *Aust. J. Agric. Res.* 19:381-395.
- Mela, T., and V.B. Youngner. 1976. Recovery of three temperate-climate grasses from drought stress. *Ann. Agric. Fenn.* 15:309-315.
- Melkonian, J.J., J. Wolfe, and P.L. Steponkus. 1982. Determination of the volumetric modulus of elasticity of wheat leaves by pressure-volume relations and the effect of drought conditioning. *Crop Sci.* 22:116-123.
- Milburn, S.A., and J. Kallarackal. 1989. Physiological aspects of phloem translocation. p. 264-305. In D.A. Baker and J.A. Milburn (ed.) *Transport of photoassimilates.* Longman Sci. & Technol., London, England.
- Misra, G., and K.P. Singh. 1982. Effect of soil moisture and clipping stresses on the nutrient (N, P and K) concentration, uptake and use efficiency in one temperate and 2 tropical grasses. *Plant Soil* 69:413-421.
- Mohammad, N., D.D. Dwyer, and F.E. Busby. 1982. Responses of crested wheatgrass and Russian wildrye to water stress and defoliation. *J. Range Manage.* 35:227-230.
- Molyneux, D.E., and W.J. Davies. 1983. Rooting pattern and water relations of three pasture grasses growing in drying soil. *Oecologia* 58:220-224.
- Monson, R.K., M.R. Sackschewsky, and G.J. Williams. 1986. Field measurements of photosynthesis, water-use efficiency, and growth in *Agropyron smithii* (C4) and *Bouteloua gracilis* (C4) in the Colorado shortgrass steppe. *Oecologia* 68:400-409.
- Morgan, J.M. 1977. Changes in diffusive conductance and water potential of wheat plants before and after anthesis. *Aust. J. Plant Physiol.* 4:75-86.
- Morgan, J.M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Aust. J. Agric. Res.* 34:607-614.
- Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. *Annu. Rev. Plant Physiol.* 35:299-319.
- Mott, J.J., and A.J. McComb. 1975. Effects of moisture stress on growth and reproduction of three annual species from an arid region of Western Australia. *J. Ecol.* 63:825-834.
- Munns, R. 1988. Why measure osmotic adjustment? *Aust. J. Physiol.* 15:717-726.
- Newman, P.R., and L.E. Moser. 1988. Seedling root development and morphology of cool-season and warm-season forage grasses. *Crop Sci.* 28:148-151.
- Noitsakis, B., and A. Berger. 1984. Relations hydriques chez *Dactylis glomerata* et *Dichanthium ischaemum* cultivés sous deux régimes hydriques contrastés. *Acta Oecol./Oecol. Plant.* 5:75-88.
- Norris, I.B. 1982. Soil moisture and growth of contrasting varieties of *Lolium*, *bacrylis*, and *Festuca* species. *Grass Forage Sci.* 37:273-283.
- Norris, I.B. 1985. Relationships between growth and measured weather factors among contrasting varieties of *Lolium*, *Dactylis* and *Festuca* species. *Grass Forage Sci.* 40:151-159.
- Nowak, R.S., J.E. Anderson, and N.L. Toft. 1988. Gas exchange of *Agropyron desertorum*: Diurnal patterns and responses to water vapor gradient and temperature. *Oecologia* 77:289-295.
- Oram, R.N. 1984. Inheritance of conditional dormancy in over-summering buds of *Phalaris aquatica* L. *Euphytica* 33:313-319.
- Oram, R.N., and R.D. Freebairn. 1984. Genetic improvement of drought survival ability in *Phalaris aquatica* L. *Aust. J. Exp. Agric. Anim. Husb.* 24:403-409.
- O'Toole, J.C., and R.T. Cruz. 1980. Response of leaf water potential, stomatal resistance and leaf rolling to water stress. *Plant Physiol.* 65:428-432.
- Passioura, J.B. 1988. Root signals control leaf expansion in wheat seedlings growing in a drying soil. *Aust. J. Plant Physiol.* 15:687-693.

- Pitcairn, C.E.R., C.E. Jeffree, and J. Grace. 1986. Influence of polishing and abrasion on the diffusive conductance of leaf surface of *Festuca arundinacea* Schreb. *Plant Cell Environ.* 9:191-196.
- Pitman, W.C., E.C. Holt, B.E. Conrad, and E.C. Bashaw. 1983. Histological differences in moisture stressed and non-stressed kleingrass forage. *Crop Sci.* 23:743-755.
- Pitman, W.D., D.M. Vietor, and E.C. Holt. 1981. Digestibility of kleingrass forage growth under moisture stress. *Crop Sci.* 21:951-953.
- Power, J.F. 1985. Nitrogen- and water-use efficiency of several cool-season grasses receiving ammonium nitrate for nine years. *Agron. J.* 77:189-192.
- Power, J.F., and J. Alessi. 1970. Effects of nitrogen source and phosphorus on crested wheatgrass growth and water use. *J. Range Manage.* 23:175-178.
- Raschke, K. 1976. How stomata resolve the dilemma of opposing priorities. *Philos. Trans. R. Soc. London, B* 273:551-560.
- Read, D.W.L., and G.E. Winkelman. 1982. Residual effects of nitrogen and phosphorus fertilizer on crested wheatgrass *Agropyron cristatum* under semiarid conditions. *Can. J. Plant Sci.* 62:415-426.
- Read, J.J., K.H. Asay, and D.A. Johnson. 1993. Divergent selection for carbon isotope discrimination in crested wheatgrass. *Can. J. Plant Sci.* 73:1027-1035.
- Read, J.J., D.A. Johnson, K.H. Asay, and L.L. Tieszen. 1991. Carbon isotope discrimination, gas exchange, and water-use efficiency in crested wheatgrass clones. *Crop Sci.* 31:1203-1208.
- Read, J.J., D.A. Johnson, K.H. Asay, and L.L. Tieszen. 1992. Carbon isotope discrimination: Relationship to yield, gas exchange, and water-use efficiency in field-grown crested wheatgrass. *Crop Sci.* 32:168-175.
- Redmann, R.E. 1976. Plant-water relationships in a mixed grassland. *Oecologia* 23:283-295.
- Redmann, R.E. 1978. Seasonal dynamics of carbon dioxide exchange in a mixed grassland ecosystem. *Can. J. Bot.* 56:1999-2005.
- Redmann, R.E. 1985. Adaptation of grasses to water stress-leaf rolling and stornate distribution. *Ann. Mo. Bot. Gard.* 72:833-842.
- Renard, C., and W. Demessemaeker. 1983. Effects of wind velocity on stomatal conductance and consequences of leaf rolling on water uptake in tall fescue. *Biol. Plant.* 25:408-411.
- Renquist, A.R., J. Breen, and L.W. Martin. 1982. Stomatal behavior and leaf water status of strawberry in different growth environments. *Sci. Hort. (Amsterdam)* 18:101-110.
- Richards, J.H., and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with *Agropyron* species. *J. Appl. Ecol.* 22:907-920.
- Richter, H., and S.B. Wagner. 1982. Water stress resistance of photosynthesis: Some aspects of osmotic relations. p. 45-53. *In* R. Marcelle et al. (ed.) *Effects of stress on photosynthesis*. Junk Publ., the Hague, the Netherlands.
- Ripley, E.A., and B. Saugier. 1978. Biophysics of natural grassland evaporation. *J. Appl. Ecol.* 15:459-480.
- Rogler, G.A. 1951. A twenty-five year comparison of continuous and rotation grazing in the Northern Plains. *J. Range Manage.* 4:35-41.
- Rogler, G.A., and H.J. Haas. 1947. Range production as related to soil moisture and precipitation on the Northern Great Plains. *Agron. J.* 39:378-389.
- Roundy, B.A., G.J. Cluff, J.K. McAdoo, and A.E. Raymond. 1985. Effects of jackrabbit grazing, clipping, and drought on crested wheatgrass seedlings. *J. Range Manage.* 38:551-555.
- Rundel, P.W., J.R. Ehleringer, and K.A. Nagy (ed.). 1989. *Stable isotopes in ecological research*. *Ecol. Stud.* Vol. 68. Springer-Verlag, New York.
- Sambo, E.Y. 1981. Osmotic adjustment as a mechanism of drought resistance in crop and forage species. *J. Sci. Technol. (Malawi)* 2:21-37.
- Sambo, E.Y., and M.J. Aston. 1985. Evidence for osmotic adjustment in *Phalaris tuberosa* L. cv. Australian and Siroso. *Aust. J. Plant Physiol.* 12:481-486.
- Sheehy, J.E., R.M. Green, and M.J. Robson. 1975. The influence of water stress on the photosynthesis of a simulated sward of perennial ryegrass. *Ann. Bot.* 39:387-401.
- Silcock, R.G., and D. Wilson. 1981. Effect of watering regime on yield, water use and leaf conductance of seven *Festuca* species with contrasting leaf ridging. *New Phytol.* 89:569-580.
- Sims, P.L., R.E. Sosebee, and D.M. Engle. 1982. Plant and vegetation responses to grazing management. p. 4-31. *In* D.D. Briske and M.M. Kothmarm (ed.). *Natl. Conf. Grazing Manage. Technol.* College Station, TX 10-12 November. Texas A&M Univ., College Station, TX
- Sinclair, T.R., C.B. Tanner, and J.M. Bennett. 1984. Water-use efficiency in crop production. *BioScience* 34:36-40.

- Sionit, N., B.R. Strain, H. Hellmers, and P.J. Kramer. 1981. Effects of atmospheric CO₂ concentration and water stress on water relations of wheat. *Bot. Gaz.* 142:191-196.
- Sivaramakrishnan, S., V.Z. Patell, D.J. Flower, and J.M. Peacock. 1988. Proline accumulation and nitrate reductase activity in contrasting sorghum lines during mid-season drought stress. *Physiol. Plant.* 74:418-426.
- Slatyer, R.O. 1971. Effects of water stress on plant morphogenesis. p. 3-13. *In* K.W. Kreitlow and R.H. Hart (ed.) *Plant morphogenesis as the basis for scientific management of range resources*. Proc. Workshop U.S.-Australian Rangelands Panel, Berkeley, CA. 29 March-5 April. USDA-ARS Misc. Publ. 1271.
- Smika, D.E., H.J. Haas, and J.F. Power. 1965. Effects of moisture and nitrogen fertilizer on growth and water use by native grass. *Agron. J.* 57:483-486.
- Smoliak, S. 1956. Influence of climatic conditions on forage production of shortgrass rangeland. *J. Range Manage.* 9:89-91.
- Sneva, F.A. 1977. Correlations of precipitation and temperature with spring, regrowth, and mature crested wheatgrass yields. *J. Range Manage.* 30:270-275.
- Sosebee, R.E., and H.H. Wiebe. 1971. Effect of water stress and clipping on photosynthate translocation in two grasses. *Agron. J.* 63:14-17.
- Stanhill, G. 1986. Water use efficiency. *Adv. Agron.* 39:53-85.
- Stewart, C.R., and A.D. Hanson. 1980. Proline accumulation as a metabolic response to water stress. p. 173-189. *In* N.C. Turner and P.J. Kramer (ed.) *Adaptation of plants to water and high temperature stress*. John Wiley & Sons, Inc., New York.
- Stitt, R.E. 1958. Factors affecting yield and quality of dryland grasses. *Agron. J.* 50:136-139.
- Stone, J.F. (ed.). 1975. *Plant modification for more efficient water use*. Elsevier Sci. Publ. Co., Amsterdam.
- Svejar, T. 1986. Comparative water relations of *Carex geyeri* and *Calamagrostis rubescens*. *Bot. Gaz.* 147:71-77.
- Tadmor N.H., M. Evenari, and L. Shahan. 1970. Runoff farming in the desert. IV. Survival and yields of perennial range plots. *Agron. J.* 62:695-699.
- Taylor, H.M., W.R. Jordan, and T.R. Sinclair (ed.). 1983. *Limitations to efficient water use in crop production*. ASA, CSSA, and SSSA, Madison, WI.
- Thomas, H. 1986a. Water use characteristics of *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. plants. *Ann. Bot.* 57:211-223.
- Thomas, H. 1986b. Effect of rate of dehydration on leaf water status and osmotic adjustment in *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. *Ann. Bot.* 57:225-235.
- Thomas, H. 1987. Physiological responses to drought of *Lolium perenne* L.: Measurement of, and genetic variation in, water potential, solute potential, elasticity and cell hydration. *J. Exp. Bot.* 18:115-125.
- Thomas, H., and C. Evans. 1989. Effects of divergent selection for osmotic adjustment on water relations and growth of plants of *Lolium perenne*. *Ann. Bot.* 64:581-587.
- Thomas, H., and C. Evans. 1990. Influence of drought and flowering on growth and water relations of perennial ryegrass populations. *Ann. Appl. Biol.* 116:371-382.
- Thomas, N. 1972. Some morphological and physiological consequences of changing plant density. Ph.D. diss. McGill Univ., Montreal.
- Trlica, M.J., Jr., and C.W. Cook. 1971. Defoliation effects on carbohydrate reserves of desert species. *J. Range Manage.* 24:418-425.
- Trlica, M.J., and C.W. Cook. 1972. Carbohydrate reserves of crested wheatgrass and Russian wildrye as influenced by development and defoliation. *J. Range Manage.* 25:430-435.
- Trlica, M.J., and J.S. Singh. 1979. Translocation of assimilates and creation, distribution and utilization of reserves. p. 537-571. *In* R.A. Perry and D.W. Goodall (ed.) *Arid-land ecosystems: Structure, functioning, and management*. Vol. 1. Int. Biol. Progr. 16. Cambridge Univ. Press., England.
- Tronsmo, A.M. 1986. Host water potentials may restrict development of snow mold fungi in low temperature-hardened grasses. *Physiol. Plant.* 68:175-179.
- Turner, N.C. 1979. Drought resistance and adaptation to water deficits in crop plants. p. 343-370. *In* H. Mussell and R.C. Staples (ed.) *Stress physiology in crop plants*. Wiley-Interscience, New York.
- Turner, N.C. 1986. Crop water deficits: A decade of progress. *Adv. Agron.* 39:1-51.
- Turner, N.C., and J.E. Begg. 1978. Responses of pasture plants to water deficits. p. 50-66. *In* J.R. Wilson (ed.) *Plant relations in pastures*. CSIRO, Melbourne, Australia.
- Turner, N.C., and J.E. Begg. 1981. Plant-water relations and adaptation to stress. *Plant Soil* 58:97131.

- Turner, N.C., E.D. Schulze, and T. Gollan. 1985. The response of stomata and leaf gas exchange to vapour pressure deficits and soil water content. 11. In the mesophytic herbaceous species *Helianthus annuus*. *Oecologia* 65:348-355.
- Tyree, M.T., E.L. Fiscus, S.D. Wullschleger, and M.A. Dixon. 1986. Detection of xylem cavitation in corn under field conditions. *Plant Physiol.* 82:597-599.
- Tyree, M.T., and P.G. Jarvis. 1982. The role of water in plants. p. 35-77. In O.L. Lange (ed.) *Encyclopedia of plant physiology*. New Set. Vol. 12B. Springer-Verlag, Berlin.
- Van Soest, P.J., D.R. Mertens, and B. Deinum. 1978. Pre-harvest factors influencing quality of conserved forage. *J. Anim. Sci.* 47:712-720.
- Walton, P.D. 1974. The genetics of stomatal length and frequency in clones of *Bromus inermis* and the relationships between these traits and yields. *Can. J. Plant Sci.* 54:749-754.
- Wardlaw, I.F. 1968. The control and pattern of movement of carbohydrates in plants. *Bot. Rev.* 34:79-104.
- Wardlaw, I.F. 1969. The effect of water stress on translocation in relation to photosynthesis and growth. 11. Effect during leaf development in *Lolium temulentum* L. *Aust. J. Biol. Sci.* 22:1-16.
- West, C.P., E. Izekor, D.M. Oosterhuis, and R.T. Robbins. 1987. Endophytic fungus effects on tall fescue tolerance of drought and nematodes. *Arkansas Farm Res.* 36:3.
- West, C.P., D.M. Oosterhuis, and S.D. Wullschleger. 1990. Osmotic adjustment in tissues of tall fescue in response to water deficit. *Environ. Exp. Bot.* 30:149-156.
- White, L.M. 1973. Carbohydrate reserves of grasses: A review. *J. Range Manage.* 26:13-18.
- Wight, J.R., and A.L. Black. 1978. Soil water use and recharge in a fertilized mixed prairie plant community. *J. Range Manage.* 31:280-282.
- Williams, R.E. 1962. On the physiological significance of seminal roots in perennial grasses. *Ann. Bot.* 25:129-136.
- Wilson, D. 1975a. Leaf growth, stomatal diffusion resistances and photosynthesis during droughting of *Lolium perenne* populations selected for contrasting stomatal length and frequency. *Ann. Appl. Biol.* 79:67-82.
- Wilson, D. 1975b. Stomatal diffusion resistances and leaf growth during droughting of *Lolium perenne* plants selected for contrasting epidermal ridging. *Ann. Appl. Biol.* 79:83-94.
- Wilson, J.R. 1983. Effects of water stress on in vitro dry matter digestibility and chemical composition of herbage of tropical pasture species. *Aust. J. Agric. Re& 34:377-380.*
- Woledge, J., J.A. Bunce, and V. Tewson. 1989. The effect of air humidity on photosynthesis of ryegrass and white clover at three temperatures. *Ann. Bot.* 63:271-279.
- Wright, D.L., R.E. Blaser, and J.M. Woodruff. 1978. Seedling emergence as related to temperature and moisture stress. *Agron. J.* 70:709-712.
- Zimmermann, M.H. 1983. Xylem structure and ascent of sap. Springer-Verlag, Berlin.

Purchased by RUA

for Official Use