

FORAGE PERSISTENCE UNDER EXTREMES OF COLD AND DROUGHT

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ABSTRACT

In many parts of the world forage production is limited by cold temperatures in winter, and/or drought during the growing season. While these stresses alone are capable of causing plant death it is most commonly their interaction with defoliation stress that leads to a decline in grassland productivity and the introgression of less favourable plant species. In intensive livestock systems, the desire to maximize forage production and utilization, coupled with economic pressures, may result in management strategies that enhance rather than minimize the effect of these stresses. While the physiological basis of plant injury caused by cold temperatures and water stress has received much attention in recent years, less emphasis has been placed on understanding these phenomena as they develop under field conditions. In many environments, the identification of plant characteristics and management strategies that enhance stand persistence may be of greater economic value than increased production *per se*. There is a need not only to understand the nature and economic significance of catastrophic damage, resulting from extreme cold or water stress, but also for an increased understanding of the incremental and cumulative nature of such damage over average years. While grassland management has long been acknowledged as both an art and a science, producers need well defined management strategies that have predictable outcomes.

KEYWORDS

Winter kill, winter hardiness, water stress, persistence, defoliation, grass, legume.

INTRODUCTION

Outside the world's most favourable climatic regions for forage production, two of the major constraints to plant productivity are cold temperatures and lack of moisture. While annual crops are able to avoid such constraints by completing their life cycle prior to the onset of cold or drought, perennial forages must persist through such unfavourable times.

This paper will look at plant adaptations to stresses - stress due to low temperatures during winter and stress due to lack of water, or drought. In each case we will emphasize the interaction between cold or drought stress and stress due to defoliation. The majority of our comments on winter survival will refer to the extreme cold experienced in northern continental climates such as the Canadian prairies, although we will also refer to problems of over-wintering in more temperate climates. In relation to drought, we will be emphasizing intermittent severe drought. The authors will draw on their own experiences of winter stress and drought conditions in Canada and Australia respectively.

Both drought and cold tolerance are complex traits (Wilkins, 1991). The onset of winter is a more predictable phenomenon than drought, but the length and severity of both winters and droughts vary considerably at any one location.

Where seasonal water deficits are a predictable recurring event, native grassland plants have evolved drought strategies that enhance persistence. More damaging to grassland persistence are the intermittent severe droughts that threaten plant survival, especially when grazing pressure is not alleviated during the drought.

While our understanding of some of the short term physiological changes that occur in response to low temperatures and water deficits has increased significantly in recent years, there have been relatively few field studies under natural stress conditions. Only when we are able to integrate our understanding of resistance phenomena at the sub-cellular and tissue level with an increased level of understanding at the plant and community level will we be able to provide useful management guidelines to producers.

PERSISTENCE

Persistence is a crucial attribute of perennial pastures which enables them to supply feed for grazing animals cost effectively. Under moderate temperate climates such as those experienced in the UK, seeded pastures may persist for many decades, or possibly centuries. Recent assessments of pastures in the 'high rainfall' parts of south eastern Australia, however, have shown that few pastures are still dominated by the species widely sown in recent decades (Kemp and Dowling, 1991). Under the extreme continental conditions of the Canadian prairies many producers expect to re-seed their permanent pastures every five to ten years (Entz et al., 1995).

As permanent forage stands thin due to death of seeded species, they are typically invaded by less productive weedy species. These degraded pastures often produce only small quantities of feed of low quality. Since the legume component of a mixed sward is frequently the most palatable to livestock it is often the first to disappear.

Persistence through periods of cold or drought requires either the ability to maintain a low level of growth throughout the stress period or the ability to become dormant. Dormancy requires the conservation of both meristematic tissue and energy reserves so that growth can recommence when the environmental constraints are released.

THE STRESS CHALLENGE

Winter. Winter throughout the world is a season of short day lengths and lower temperatures. In an extreme continental climate, typical of much of the Canadian prairies, air temperatures are commonly below 0°C for five or more months of the year and may remain below -20°C for several weeks at a time with occasional lows of -40°C. During these winter months plants are often covered by an insulating blanket of snow that moderates the temperature at the soil surface. Nevertheless, the perennial plant is faced with the challenge of maintaining viable tissues at extremely low temperatures, in the absence of current photosynthesis, for a period of several months. Where the effects of latitude are mitigated by adjacent oceans, winter temperatures may not be as severe, but extreme fluctuations in temperature can challenge a plant's ability to maintain a hardened condition. In temperate climates, plants may grow slowly throughout much of the winter period, their growth rate being limited by low temperatures and low levels of irradiance. Defoliation during this time may reduce plant vigour.

Drought. Droughts are an inevitable and recurring feature of World agriculture, however, relatively few drought studies have been conducted, even in Australia. Despite attempts to predict droughts, and reduce their impact, they are still the single most important factor affecting world food security (McWilliam, 1986).

Carr (1966) defined an agricultural drought to occur 'when soil moisture and rainfall are inadequate during the growing season to support healthy top growth to maturity and to prevent extreme crop stress and wilt'.

The effects of drought tend to accumulate gradually (Gillette, 1950) and may persist for long periods of time, making it difficult to determine when a drought actually starts and finishes. The severity of drought is also difficult to define, and will be influenced by human intervention and the type of vegetation. Droughts differ from one another in intensity, duration, and spatial coverage (Wilhite, 1982, cited in Meyer et al, 1993).

Forage crops frequently face the additional stress of defoliation during periods of water shortage, and while many forage species can survive either of these stresses alone, the combined effects frequently lead to plant death. Where plants are physiologically well adapted to survive the conditions of water shortage, it is often decisions related to stocking density and defoliation frequency that determine the persistence and subsequent vigour of the sward.

For both winter and drought, the inherent variability, and inability to predict the severity or longevity of the stress period, presents the major challenge to both plant and manager.

Defoliation. Forage species exhibit different levels of tolerance to defoliation stress. These differences relate to the plant's ability to maintain a positive carbon balance under different frequencies and intensities of defoliation (Richards, 1993). Plants that are well adapted to withstand defoliation often have a plant structure that maintains a significant leaf area below the defoliation height and protected meristems that escape defoliation. Caldwell et al. (1981) identified two possible strategies associated with recovery from defoliation, a conservative response where root:shoot ratio is maintained, and a more opportunistic response where shoot growth is favoured over root maintenance in order to rapidly re-establish leaf area. The effects of defoliation interact strongly with environmental conditions that limit growth.

As grazing production systems throughout the world become more intensive, the management of defoliation intensity, frequency, and timing becomes more crucial to plant persistence as the defoliated plant has fewer reserves with which to survive stress periods. Nevertheless, in contrast to the communal grazing systems in many countries, more intensive management does provide the opportunity to control defoliation and hence manage plant reserves.

WINTER INJURY AND ACCLIMATION

Winter injury to plants may result from physical, physiological and biotic stresses (Larsen, 1994). Cold temperature injury includes that resulting from inter- or intra-cellular freezing of unhardened tissues, damage due to anoxic conditions resulting from ice encasement, physical damage to roots due to soil heaving and damage caused by low temperature fungi. The prevalence of these various kinds of damage depends on the geographic location and plant genotype and is further influenced by a range of management practices.

In Scandinavia for example, where the effects of latitude are moderated by adjacent oceans, physical stresses such as frost and ice encasement may predominate in coastal regions, where the temperature is less stable, while biotic stresses such as low temperature fungi are the major threat to forage persistence further inland (Larsen, 1994). Under continental conditions, extremely low temperatures often prevent fungal development, and death due to

freezing is the main stress, coupled with the extreme length of time for which the hardened condition must be maintained.

Freezing stress. Freezing injury is of two main types - primary direct injury due to intra-cellular freezing, and secondary freeze dehydration injury due to extra-cellular freezing (Levitt, 1979). Intra-cellular ice formation is generally lethal to plant tissue (Guy, 1990).

Extracellular freezing causes dehydration stress as water moves out of the cells, osmotic stress due to removal of water from the vacuole and mechanical stress caused by ice growth and cell contraction (Li, 1994). Levitt (1979) describes freezing tolerance as the ability to avoid extracellular ice formation and to tolerate intercellular freezing. Many species of temperate plants exhibit some ability to undergo cold acclimation or hardening such that ice forms between, rather than within, cells. Limin and Fowler (1987) rated the cold hardiness of 18 grass species grown on the Canadian prairies and found maximum hardiness ratings (measured as lethal temperature at which 50% of plants were killed) ranged from -18°C for seedling reed canary grass (*Phalaris arundinacea* L.) to -37°C for kentucky bluegrass (*Poa pratensis* L.). Management effects can limit a genotype's ability to fully express its genetic potential to harden if carbohydrate accumulation is restricted in the fall through an inappropriate harvesting schedule, or high levels of irrigation or nitrogen fertilization (McKenzie et al., 1988).

Ice Encasement. Death due to ice encasement can occur when standing water freezes, or when warming temperatures cause partial thawing of the snow pack such that the water percolates down through the snow and re-freezes at the soil surface.

Solid ice is nearly impermeable to respiratory gases and death due to ice encasement results from the development of anoxic conditions (Andrews, 1996). Any factors that relieve the anoxic condition by allowing some gaseous diffusion, such as part of the canopy protruding above the ice, markedly reduce the toxic effects (Freyman, 1969). Where icing is frequent, the use of a strong bunch grass and greater stubble height could be beneficial, however, too much carryover may promote growth of snow molds.

Timothy (*Phleum pratense*), and Bering's hairgrass (*Deschampsia berengensis*) exhibit enhanced tolerance to anoxic conditions associated with a lower rate of accumulation of fermentation end products (Gudleifsson et al., 1986; Gudleifsson, 1994; Crawford and Braendle, 1996) and may offer the possibility to breed for enhanced tolerance to anoxic conditions.

Heaving. Frost heaving occurs when ice layers form in wet soil during freeze thaw cycles (Beuselinck et al., 1994). The expanding ice layer thrusts the roots and crowns of tap rooted species, such as alfalfa (*Medicago sativa*), above the soil surface where they are fully exposed to cold air temperatures and the desiccating action of winds. The use of species or genotypes with a fibrous root system can reduce the problem, as may growing tap rooted alfalfa in mixtures with a rhizomatous grass such as smooth brome grass (*Bromus inermis*).

Disease. Where winter temperatures are moderate and snow cover persists for several months, low temperature fungi can be the major cause of winter injury in perennial grasses and legumes (Hannukkala, 1994). Damage occurs most frequently under persistent snow cover and at surface soil temperatures of -5 to +1°C (Orr et al., 1996). The most effective means of preventing such damage comes from the development of resistant genotypes. Reducing the amount of carryover, by late fall cutting, may reduce disease incidence, however,

in the absence of disease such a practice can reduce spring yields (Halling, 1994a, 1994b). The presence of disease during the growing season can also affect plant vigor and the degree of winter hardening (Takeda, 1994).

Acclimation. Solberg et al. (1994) describe winter-hardiness as a complex character determined by tolerance to low temperatures, long lasting snow cover, ice, and low-temperature fungi. If we accept the premise that under continental conditions the most significant cause of plant death over winter is freezing injury, then management will most significantly impact survival through its effects on winter hardening in the fall.

Carbohydrate accumulation has long been implicated in the attainment of a hardened condition. Levitt (1956) considered the accumulation of soluble sugars in perennating organs during winter hardening essential for survival of plants in temperate regions. Among perennial forages, winter hardy ecotypes that have evolved in latitudes far from the equator, or at high altitudes, tend to accumulate higher concentrations of soluble sugars in the autumn than do non-hardy, low latitude or low altitude genotypes (Klebesadel, 1971; Duke and Doehlert, 1981; Collins and Rhodes, 1995).

Initiation of the hardening process occurs in response to shortening daylengths and declining temperatures (Shih et al. 1967; Paulsen, 1968; Habeshaw and Swift, 1978; Fuller and Eagles 1980). The specific environmental conditions will vary from species to species. In perennial ryegrass (*Lolium perenne* L.), the minimum temperature experienced during diurnal fluctuations is more critical than the mean daily temperature (Eagles and Williams, 1992). In some species the period of acclimation is strongly associated with a decline in above ground growth rate (fall dormancy response). Other species, that may achieve a similar level of acclimation, are able to maintain their top growth throughout the autumn (Van Esbroeck et al., 1995).

Breeders of alfalfa have used the "fall dormancy" response as a selection criteria for winter hardiness (Heinrichs et al., 1960; Smith 1961; Larson and Smith, 1963; Barnes et al., 1979). Heichel and Henjum (1990) used a reciprocal grafting technique to determine that herbage production per plant in alfalfa was controlled by the fall-dormant member of the graft. They suggested that one or more graft transmissible factors may be involved in the expression of fall dormancy traits.

Carbohydrate and Nitrogen pools. While an increase in carbohydrate content seems to be observed in nearly all plants during cold hardening, the amount of carbohydrate accumulated is not necessarily correlated to the maximum level of frost tolerance achieved, nor does the rate of accumulation necessarily parallel the rate of increase in cold tolerance. McKenzie and McLean (1980a) showed that alfalfa plants with low energy reserves were unable to attain the same level of cold hardiness as those with higher energy reserves. However, work with orchard grass (*Dactylis glomerata*) (King, unpublished data) suggests that genotypes which accumulate similar levels of soluble sugars in the autumn do not necessarily achieve equal levels of freezing tolerance. Thus, the presence of large pools of carbohydrate will not guarantee survival of a hardened plant if the critical temperature limit is exceeded.

Carbohydrate storage has also been correlated with the ability to maintain a hardened condition during periods of fluctuating temperatures. Cold resistance may be reduced during warm periods in winter (Suzuki, 1981; Sunde, 1994) and ability to reharden with the onset of colder temperatures is favoured by high energy reserves

(McKenzie et al., 1988). Initial regrowth in the spring is also dependent on stored reserves of energy. The level of non-structural carbohydrate in overwintering tissues may also affect spring seed production in grasses (Aamlid, 1996).

Early work on alfalfa by Graber et al. (1927) concluded that both taproot carbohydrate and nitrogen reserves were important for regrowth and persistence of alfalfa. Since that time the role of nitrogen pools has been largely ignored. A recent review by Volenec et al. (1996) suggests a role for nitrogen pools in supporting regrowth following defoliation and in early spring. Further work is needed to elucidate the relative importance of carbon and nitrogen pools in relation to winter survival.

DROUGHT INJURY AND ADAPTATION

Water stress initially reduces plant growth rates through closure of stomates, leaf rolling, lower rates of photosynthesis and reduced leaf expansion. This may be followed by leaf senescence, especially of flowering tillers, and ultimately death of meristematic tissue. In extreme cases, cavitation in xylem vessels may occur. A detailed review of the effects of drought on grasses has been published by Frank et al. (1996).

Adaptation to water stress. The three strategies by which plants survive drought are: drought escape, drought avoidance and drought tolerance (Whalley, 1973; Ludlow, 1989). Drought escape is the ability of a plant to complete its life cycle in a short period of time while adequate moisture is available (Whalley, 1973). Persistence of the species occurs via a persistent seed bank. Drought avoidance (Whalley, 1973) is the ability of the plant to maintain a high level of water in its tissues during periods of low soil water potential, and has also been described as dehydration postponement (Kramer, 1980). Drought tolerance occurs when a plant's tissue water status is reduced by drought but not detrimentally (Whalley, 1973; Kramer, 1980). Drought tolerance is achieved through osmotic adjustment, decreased cell size, increased cell elasticity, and protoplasmic tolerance to low water potential (Turner, 1979). Mechanisms of drought avoidance include increases in stomatal and cuticular resistance, reduced leaf area, reduced radiation absorption, and increased root density and rooting depth (Turner, 1979). Drought tolerant perennial grassland species often combine these strategies.

Carbohydrates. The role of storage carbohydrates in forage persistence under drought conditions relates both to their role in osmotic adjustment and in supporting regrowth tissue following defoliation.

In the short term, carbohydrates accumulate in water-stressed plants because growth is impaired before photosynthesis declines (Dina and Klikoff, 1973; Hsiao, 1973; Deregibus et al., 1982). Non-structural carbohydrates stored in the bases of elongating leaves may serve as a substrate for biosynthesis or aid in osmotic adjustment (Darbyshire and Henry, 1978; Volenec and Nelson, 1984a, 1984b). Under extended periods of water stress, conditions which encourage or prevent the accumulation of non-structural carbohydrates, appear to be influenced by genotype, water deficit and defoliation events (Julander, 1945; Busso et al., 1990; Mott et al., 1992; Volaire, 1994; McKenzie, 1996).

Following defoliation, energy for regrowth is provided by current photosynthesis and/or non-structural carbohydrates stored in stem bases, rhizomes or stolons (Davies, 1965; Davidson and Milthorpe, 1966a, 1966b; Smith, 1974; Booyesen and Nelson, 1975). The relative contribution from current or previously stored carbohydrates will be

largely influenced by the quantity of leaf lamina remaining. Thus, the ability to re-grow following a period of drought and defoliation will depend in part on the presence of residual photosynthetic area, active meristems, and carbohydrate storage.

DEFOLIATION STRESS AND WINTER INJURY

In continental climates where growth ceases for several months over winter, fall management can be critical to subsequent winter survival. Smith (1972) suggested that alfalfa plants required six weeks of uninterrupted regrowth prior to the first killing frost to ensure that the crop entered winter in a sufficiently hardened condition and with a high level of non-structural carbohydrate. McKenzie and McLean (1980b) working in northern Alberta confirmed this requirement. The length of the required fall rest period has been tested in several other growing environments (Yager and Tesar, 1968; Reynolds, 1971; Mays and Evans, 1973; Marten, 1980; Sholar et al., 1983) with varying results. In general the requirement for a fall rest period is less critical in more moderate climates. Since it is difficult to predict the time of the first fall frost, Tesar and Yager (1985) concluded that the guideline for the northern latitudes of the USA should be based on a requirement for alfalfa to reach 10% bloom prior to the final fall harvest. However in northern Canada under a two cut system, regrowth following the first harvest may not reach 10% bloom.

There has been little work published on the effects of fall harvest date on winter hardiness in grasses. In Alberta, work on orchard grass showed that the final fall harvest date significantly affected winter survival, spring regrowth, and the total non-structural carbohydrate content with which plants entered and came out of winter (King and Van Esbroeck, 1991). However, it was also found that differences in winter-hardiness between cultivars of orchard grass were not strongly correlated to the amount of carbohydrate they accumulated in the fall. Further tests, looking at the interaction between fall harvest date and stubble height, suggested that the effect of fall cutting date might be mitigated as much through its effect on the snow trapping potential of the remaining stubble as on the accumulated carbohydrate storage (King and Van Esbroeck, 1993). Clearly these relationships need to be more accurately defined for different climatic regions.

Ultimately it is the producer who balances the need to harvest forage material at a particular maturity level and quality, against possible consequences relating to winter hardiness and stand longevity.

In more temperate climates, where forage growth is maintained over much of the winter, sward persistence and species composition can be affected by the timing and severity of defoliation during the winter months. White clover persistence and production under temperate maritime conditions in the UK is dependent on the amount of stolon that over-winters and the number of branch buds present in the spring (Collins et al., 1991; Rhodes et al., 1994). In mixed perennial ryegrass-white clover swards, hard grazing in early winter favours the initiation of growing points and carbohydrate accumulation in white clover stolons relative to perennial ryegrass (Laidlaw and Stewart, 1987). Maintaining a short sward height in perennial ryegrass-white clover swards during winter and early spring, enhanced clover branching during mild periods of winter growth, and encouraged rapid clover canopy development in the spring (Laidlaw et al., 1992). In white clover-orchardgrass pastures in West Virginia, USA, a brief fall grazing period favoured a grass dominated sward, whereas an extended grazing period favoured white clover growth (Belesky and Fedders, 1995). Withholding spring nitrogen applications and avoiding stolon burial due to grazing during wet soil conditions in the spring also enhanced clover persistence (Laidlaw et al., 1992).

DEFOLIATION STRESS AND DROUGHT INJURY

Neither drought nor grazing stress alone are primary causes of mortality of well adapted plants. However, when plants concurrently experience both drought and defoliation stress, mortality increases. Whilst vegetative legumes may virtually disappear from pastures during stressful climatic periods (Sheath and Hodgson, 1989), grasses are relied on as the more drought resistant component for stable, productive pastures. Hence, it is important that perennial grasses be well managed if they are to be maintained in a pasture.

The adverse effects of drought on pastures have been recorded in several environments. In the traprock region of Queensland, Australia, the loss of valuable native species during the severe drought of 1965 resulted in a decline in soil cover from 15% to 8% (Clarkson and Lee, 1988). Twelve months following the end of the drought, botanical composition was still depleted, and yield recovery was only apparent where stocking rates were low. In the 1968-69 drought in Queensland, the loss of Rhodes grass (*Chloris gayana*), glycine (*Neonotonia wightii*) and Siratro (*Macroptilium atropurpureum*) resulted from the combination of drought and high stocking rates. Nevertheless, green panic (*Panicum maximum* var. *trichoglume*) survived well under these conditions (Silvey and Jones, 1990). The loss of Siratro in Australia between 1968 and 1982 was mainly attributed to high set-stocking rates and below-average summer rain (Jones and Bunch, 1988).

Mott et al. (1992) found that for grazing-sensitive species such as *Themeda triandra*, grazing during a post-drought recovery period killed regrowing tillers. Such a plant tended to have a poor carbon balance compared with more resilient grasses such as spear grass (*Heteropogon contortus*) and Guinea grass (*Panicum maximum*).

Even in the relatively moderate climate of New Zealand, populations of perennial grasses (Weeda and Goold, 1990) and legumes (Sheath et al., 1990) can be reduced dramatically by combinations of grazing and drought stress. Legumes suffer from the double punishment of being susceptible to drought and highly palatable to livestock (Scott, 1996).

The effects of defoliation during drought may be mediated through their effect on carbohydrate storage and the plant's energy balance. Early studies by Julander (1945) indicated that *Agropyron* and *Andropogon* species accumulated carbohydrate reserves during drought, but severe defoliation prevented such accumulation. Volaire (1994) found that, under Mediterranean conditions, water soluble carbohydrate concentrations were reduced in orchard grass (*Dactylis glomerata*) populations by intense defoliation in spring and severe water stress in summer. In a further study Volaire (1995) identified summer semi-dormant genotypes that accumulated high levels of carbohydrate during summer drought and had good fall regrowth. Less persistent summer active genotypes, which drew down their carbohydrate reserves over the summer, were also identified. In South Africa, the response of perennial ryegrass under a range of defoliation frequencies and intensities was correlated to non-structural carbohydrate levels in the first season, and again to non-structural carbohydrate levels and the number of surviving tillers in a second season (McKenzie, 1996).

Pasture losses do not occur immediately a drought takes hold. Gammon (1983) found in southern Africa, where veld condition was poor, that extensive plant losses were usually the result of years of mis-management over a number of drought years. Similarly, Busso and Richards (1995) found that a mild water stress and an annual defoliation did not limit herbage accumulation by either crested

wheatgrass or bluebunch wheatgrass after a single season, but that regrowth was restricted following a second season.

In a trial on the Northern Tablelands of NSW, Australia, examining the mortality thresholds of six perennial grasses under controlled conditions of drought and defoliation, more plants died under a moderate drought treatment than under a more severe drought (Boschma et al., 1996). This suggests that plants were most susceptible when attempting to grow from depleted reserves when moisture levels were limited.

In the same trial, at the end of a drought period, plants which had been moderately defoliated had higher energy reserves than plants which had been severely defoliated (King et al., 1996). Thus a moderate drought stress, combined with continued defoliation, may be more detrimental to the persistence of pasture species which are not dormant than a more severe drought.

DISCUSSION: PERSISTENCE VS. PRODUCTIVITY

The ability to survive either cold or drought is dependent on the maintenance of viable meristematic tissue and the conservation of resources throughout the period of stress until such time as more favourable growing conditions prevail.

In relation to winter survival, it is important that plants harden in anticipation of cold temperatures and do not deharden in response to “false springs”. For winter hardy species where hardening is correlated with the slowing of leaf initiation and leaf expansion rates in the fall, early closure of pastures may be essential to stand longevity. Although defoliation of plants during fall can provide low cost feed at a time when forage production is limited, it may reduce stand persistence. In environments where winters are long and the growing seasons are short, maximizing the length of the grazing season may provide short term economic gains. However, when re-establishment costs are amortized over a longer time period, preservation of a vigorous perennial stand may be more profitable. On the Canadian prairies, extending the length of the grazing season has been identified as a research priority. However, the expectation that this can be achieved using current perennial species may be unrealistic. It may be more appropriate to look for alternative feed sources during the fall, such as sowing annual forage species or fodder crops to provide late season grazing. If perennial plants are defoliated around the time of the first killing frost, regrowth is restricted and total non-structural carbohydrate stores are not compromised. Therefore, stockpiling late season growth from perennial pastures, to be swathed and grazed once plant growth has ceased is an approach that is currently gaining attention.

Where winters are more temperate, defoliation during periods of slow winter growth must be managed to maintain plant vigour and a desirable species mixture. Where soils are not frozen over winter, indirect damage through soil compaction can also affect long term yield. Effects of fall, winter and early spring defoliation on tiller or branch number may affect stand longevity and has only been quantified for a few species.

Persistence during drought can be achieved through a strategy of conservative growth, or the cessation of growth, and the conservation of dormant meristems and energy reserves. Kemp and Culvenor (1994) suggested that, for Australian conditions, adjustment to water stress that aids plant survival may be a better strategy than adjustment for growth. Within *Phalaris aquatica* it has been possible to select for different strategies associated with various levels of bud dormancy. Thus “Sirocco” phalaris is highly summer dormant (Oram

1990) while “Sirolan” phalaris, which does not have highly dormant buds, has very vigorous growth which better exploits the available soil water (Oram and Freebairn, 1984).

Where soils are deep, selection for deeper rooting genotypes and a shift in the shoot:root ratio under increasing water deficits may prolong the growth period. Where conservative growth rates are maintained, regulating stocking density will be crucial to the maintenance of a positive carbon balance. Plants that become dormant in response to increasing water deficits and conserve energy for regrowth when the water balance improves, offer the opportunity for long term sward stability. Maximizing the number of growing points that survive a dry season will enhance recovery, and selecting for high tiller and bud survival coupled with summer inactivity has been suggested by Biddiscombe et al. (1977). However, this may only be achieved by sacrificing current production and short term profitability.

The discounted cost of additional feed supplied by sown pastures depends to a large extent on the longevity of the pasture. A pasture lasting for ten years can produce extra feed at a cost which is one third that of a pasture lasting only three years (Scott, 1996). Pasture establishment costs are high and in many environments unprofitable. The costs of grazed pasture in the field are much lower than the cost of purchased grains, hay or silage. This emphasises the importance of managing pastures for longevity and hence the need to understand plant mortality under the stresses of cold or drought.

Work done in Ontario by Stonehouse (1992), indicates that there is a trade-off between the short-term profits that can arise from greater crop specialization coupled with higher economic and environmental risks, and longer-term sustainability achieved through greater diversification and lower risks economically and environmentally. There are significant economic benefits to the long term maintenance of a vigorous forage sward and long-term economic consequences to the loss of valuable species. Thus, there is a need to convince the livestock producer of the long-term value to be derived from looking after the pasture resource within a related series of sensible short-term actions.

CONCLUSIONS AND FUTURE DIRECTIONS

As researchers we often approach complex phenomena by studying the component parts, leaving the grassland manager to integrate the information and apply it to the practical management of grasslands. This is particularly true in the areas of stress survival and persistence. Phenomena that are easily measured in the laboratory or greenhouse setting have received more attention and research support than the integrative studies which operate in a more realistic biological time frame. As a result, we have a fairly sophisticated understanding of many of the physiological changes that take place within tissues and cells, in response to low temperatures and low levels of water availability. However, appropriate management strategies are yet to be defined.

While long term integrative studies are expensive and results accrue only slowly, they ultimately provide information that is easily transferred to the end user. Long term field studies also offer the opportunity for collaboration between scientists from different disciplines.

In order to increase our understanding of plant persistence, there is first a need for better documentation of the economic value of plant loss due to cold and drought stress. This relates both to severe conditions and the small cumulative losses which accrue annually in

response to more moderate levels of cold and drought stress.

Further international co-operation in identification and testing of germplasm for cold and drought resistance should be encouraged. Similarly, the freezing and drought tolerance of a wide number of species should be assessed under field conditions. By increasing the hardiness of important forage species by 1 to 4°C their geographic range could be significantly extended.

In relation to water stress, genotypes within species that exhibit contrasting survival strategies, either through conservative growth or a dormancy response to water stress, should be identified.

There is a need to further increase our understanding of the effects of defoliation frequency, intensity, and timing on plant survival under conditions of water stress, and during plant hardening. The susceptibility of plants to defoliation damage during the recovery period following cold or drought stress, and any interactions with levels of soil nutrients also needs to be quantified.

Species responses to cold and drought stress need to be incorporated into crop models, thereby allowing models to be used in a predictive fashion to determine suitable defoliation frequencies. A better understanding of species response would also enable GIS techniques to be used to better identify areas of adaptation in relation to cold and drought. There remain many challenges ahead.

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