CHAPTER 6

How Grasses Respond to Drought—A Model

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Drought can be defined as a period when available soil water is much less than that required by the crop for optimal evapotranspiration. The period can be short or protracted. Many of the common forage grasses are well adapted to extended periods of drought. For example, crested wheatgrass and orchardgrass have been reported to survive at least 22 months of drought (Tadmore et al. 1970) in the Negev Desert in Israel due to deep roots and effective quiescence.

Adaptation to drought takes on two forms: 'drought tolerance' refers to the ability to maintain growth through periods of water shortage and 'drought resistance' is the ability to survive, without growth, through dry periods. The two aspects involve different adaptations but are not unrelated since persistence may involve managing water use. While persistence is obviously important for perennial grasses, more important for agricultural production is maintaining vigorous growth for as long as possible since the growing season has a limited number of days. In some respects maintaining good production in dry years is especially important for livestock producers since it is difficult to store feed over years, and poor production will compel farmers to cull their herds which is difficult to reverse.

Optimization of the water resource can be described in terms of 'water use efficiency', or the amount of yield produced with a given amount of water. There are large intrinsic differences between cool season and warm season grasses due to their contrasting photosynthetic pathways. Warm season grasses have potentially higher water use efficiency and even nutrient use efficiency thanks to their C-4 photosynthetic pathway in contrast to C-3 in cool season grasses. However, as this physiology is manifest mainly under warm and sunny conditions, the advantage of C-4 is progressively diminished as the temperature declines. The reason is that cool temperature which favours the growth of cool season grasses is inherently advantageous for water use efficiency. This is because water use efficiency is, in essence, determined by the ratio of CO_2 absorbed: H_2O transpired through the open stomata, and the ratio will tend to be higher (more favourable) when the vapour pressure deficit in the atmosphere is low (i.e. humidity is high) so that less H_2O is transpired while CO_2 is taken up. Low vapour pressure deficit is more common in cool weather. However, when the weather is very cold there is little growth, so water use efficiency is of course very low, and typically grasses will become dormant and often shed their leaves to conserve their resources. Hence greatest water use efficiency often occurs in the early part of the growing season. In temperate

regions, cool season grasses can take advantage of favourable spring conditions producing greater total yields than the potentially more efficient warm season grasses that will grow best later in the season when conditions are less favourable (high vapour pressure deficit, less available soil water) for conserving plant water.
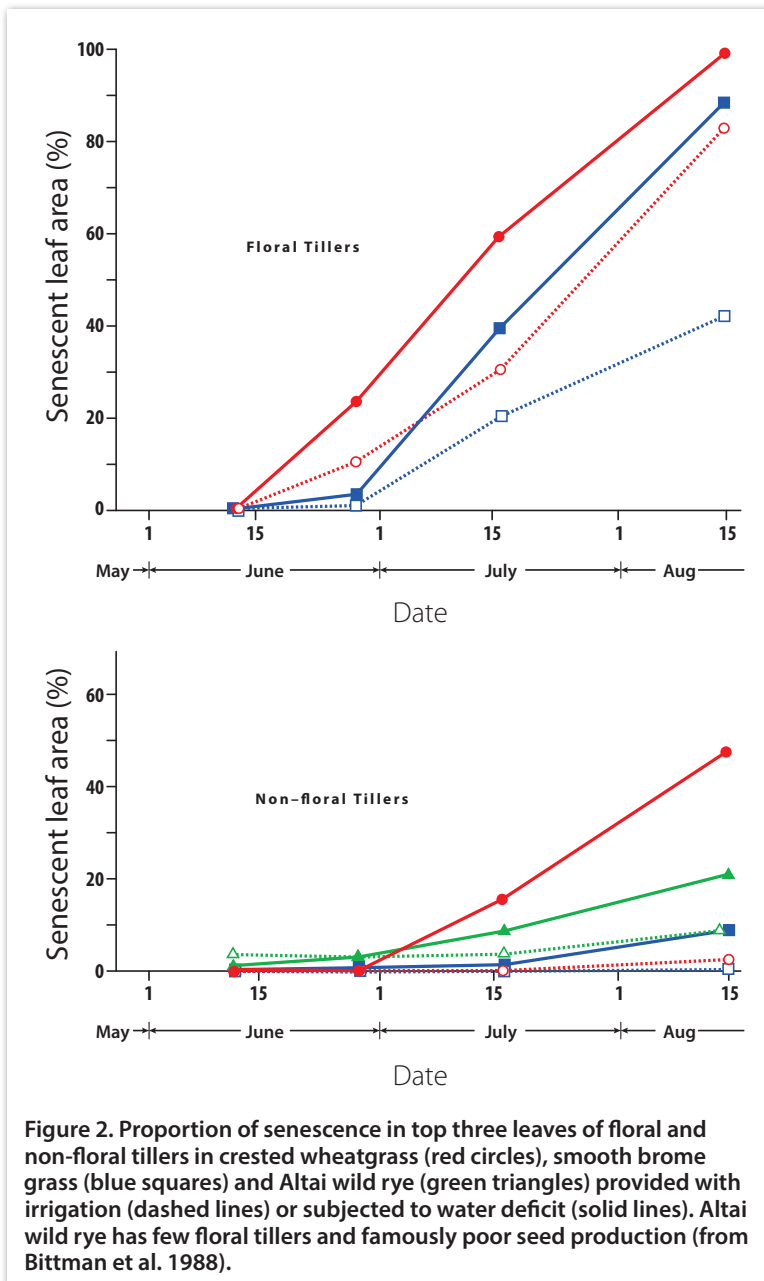
Response to drought in grasses and other plants begins with cessation of cell expansion in the meristematic (growth) regions, followed by a decline of stomatal opening, slowing of cell division and accelerated senescence and loss of older leaves. In extreme drought, desiccation of tissue will cause disruption of cell membranes and tissue death, which is quite different from the orderly cell death of age-related senescence. While this pattern of response to drought is well established in the scientific literature, the implications for crop response strategies are at once subtle and sublime.

Stomatal closure is the first level of defence against desiccation due to drought and many studies have demonstrated a relationship between various indicators of leaf water status and stomatal conductance. However the relationship is not as consistent as might be expected, and is sometimes modulated by other factors. For example, Figure 1 shows a relatively flat response of stomatal conductance in relation to leaf pressure potential (turgor) in the morning in three forage grasses: Altai wild rye (*Leymus angustus*), smooth bromegrass (*Bromus inermis*) and crested wheatgrass (*Agropyron cristatum*) (Frank et al. 1996; Bittman and Simpson 1989). These are three grasses with somewhat different drought resistance strategies; for example crested wheatgrass grows earlier in spring and has a greater tendency for leaf senescence than does smooth bromegrass. Surprisingly, there is no abrupt drop in conductance below the zero pressure potential (calculated as difference between total water potential and osmotic potential and not correcting for apoplastic water) in any of the grasses. In other words, the stomata remain open despite zero turgor in the leaf cells. In the afternoon, there is again no abrupt decline in conductance at zero turgor, but the relationship between pressure potential and conductance is much stronger with greater conductance at high values and lower conductance at low values. The stomata of all three grasses responded abruptly to decreasing light levels or increasing CO_2 concentrations. The rather weak relationship between leaf conductance and leaf pressure potential over a very wide range of values, despite the intrinsic accounting for changes in leaf osmotic potential, was unexpected. These observations suggest that stomatal conductance is actively regulated by the guard cell/subsidiary cell system, probably in response to a signal, and is not a passive response to water loss. But what is the signal and why is a signal needed?
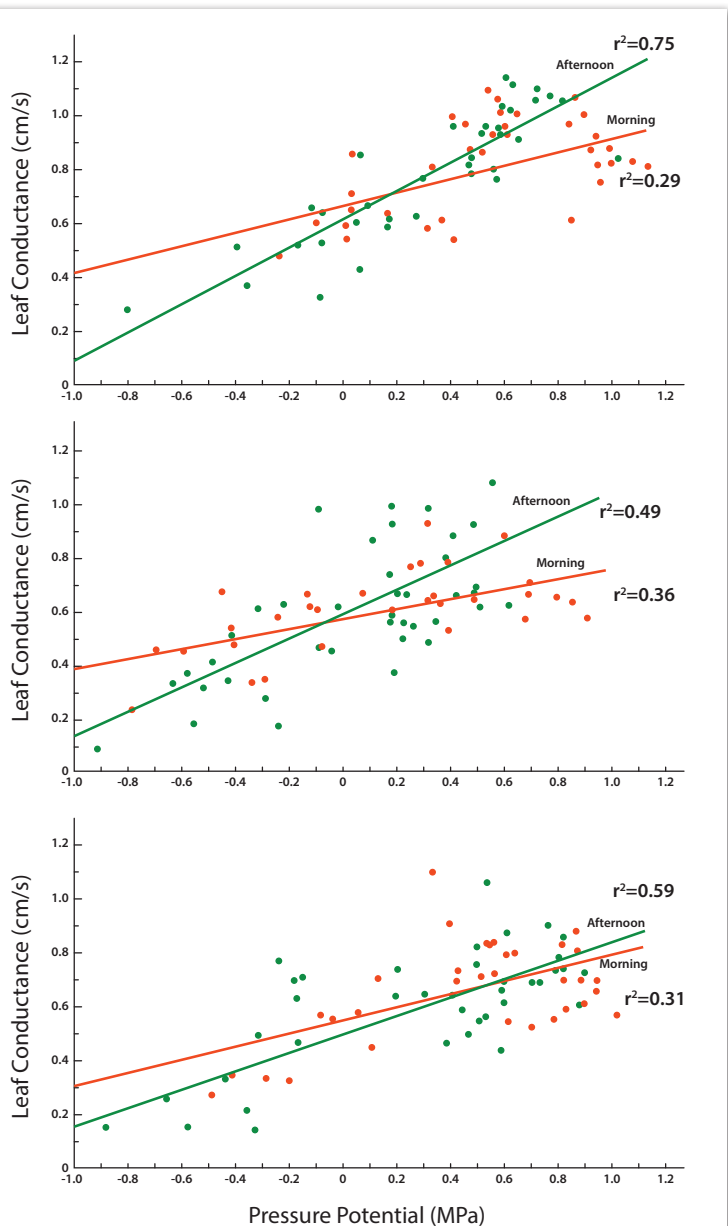
Figure 1. Effect of leaf pressure potential (turgor) on leaf stomatal conductance in Altai wild rye (top), crested wheatgrass (middle) and smooth bromegrass (bottom). Red lines and symbols are morning measurements, and green lines and symbols are afternoon measurements (from Frank et al. 1996; Bittman and Simpson 1989).

Another unexpected response of the three grasses to drought was the weak effect of drought on leaf senescence in non-floral tillers compared to floral tillers (Fig. 2). Since leaf senescence is often considered a drought response by plants to reduce evaporative surface area and therefore conserve water, it is surprising that the non-floral tillers tended to stay green much longer than the floral tillers which had less than half the total leaf area. This suggests that the leaf senescence response to water deficits is related less to conserving water and more to conserving nutrients, with the floral tillers commanding more rapid senescence to mobilize nutrients towards the seed which is a strong sink. Ample seed production is often observed in periods of stress.

Figure 2. Proportion of senescence in top three leaves of floral and non-floral tillers in crested wheatgrass (red circles), smooth brome grass (blue squares) and Altai wild rye (green triangles) provided with irrigation (dashed lines) or subjected to water deficit (solid lines). Altai wild rye has few floral tillers and famously poor seed production (from Bittman et al. 1988).

so they are prone to be rapidly depleted of water. Fine textured soils contain more bound water with lower hydraulic conductivity and the residual water is bound with increasing tenacity as the soil dries out. Since the hydraulic conductivity is low in these soils, extracting tightly held residual water requires a very dense root system.

In scenario one, the soil water is depleted rapidly by the plants leaving little reserve moisture in the soil so plants are at risk of desiccation. For this scenario, tissue growth stops quickly and plant stomata respond soon after, protecting against further plant water loss. By rapidly shutting down, the stomata also limit carbon assimilation, so carbohydrate reserves are likely to decline during the stress period. In scenario two, that of slow drying, there is less long-term risk for the plant that soil water will be depleted. If the soils are also deeply penetrated by fine roots there is additional water security for the plants. It is this scenario that applies to the data presented above.

In the slow drying scenario, tissue growth is reduced more gradually and the stomata remain open longer, causing low leaf water potentials during the day since there will be some ability to recover at night when stomata are closed. There is also sure to be some soil water left for an extended period, albeit in declining amounts, so stopping transpiration is less urgent. Since the stomata remain open after leaf expansion has ceased, there is a tendency for carbon assimilation to continue and for the new carbohydrates (and soil minerals) to accumulate in cells and to some extent also in stem bases and roots. There is also evidence in the literature that cell division continues after cell enlargement has ceased. The slowly stressed plants with a bank of small new cells and a store of carbohydrates and minerals are in a better position to resume growth when water is replenished, compared to the plants whose stomata have closed rapidly. Many producers observe that crop growth may be accelerated following short periods of water shortage and there are many such reports in the literature.

Leaf senescence provides plants with the alternative drought response strategy- that of providing for the next generation by accelerating development and enhancing seed production. The carbon sink for non-floral tillers in roots and buds may be smaller and less compelling than the carbon sink of the seed being produced in floral tillers. Leaf death due to drought-induced senescence is programmed to conserve nutrients and is distinct from tissue injury.

When carbohydrates and other solutes accumulate in cells there is the impression that the cells are osmoregulating, but if plant response to drought is regulated by signals then there may be little benefit to regulating pressure

Combining our findings with many published observations, we have proposed a model for grass reaction to water deficits or drought which is shown in Figure 3 (Frank et al. 1996; Bittman 1985). The model reconciles the dual goals of maintaining growth and ensuring survival, which are at least partly in conflict, as poor growth (to compete for resources) will mean demise in a community of plants as surely as that caused directly by desiccation. We proposed two contrasting scenarios: rapid water-depleting soils and slow water-depleting soils. Rapid depletion is typical of coarse soil texture soils with low organic matter, or limited soil volume for roots due to a soil barrier such as a hardpan or in small greenhouse pots. Slow water depletion reflects deep, fine-textured, organic matter-rich soils which are not overly explored by roots. Coarse textured soils have mostly unbound water with relatively high hydraulic conductivity,
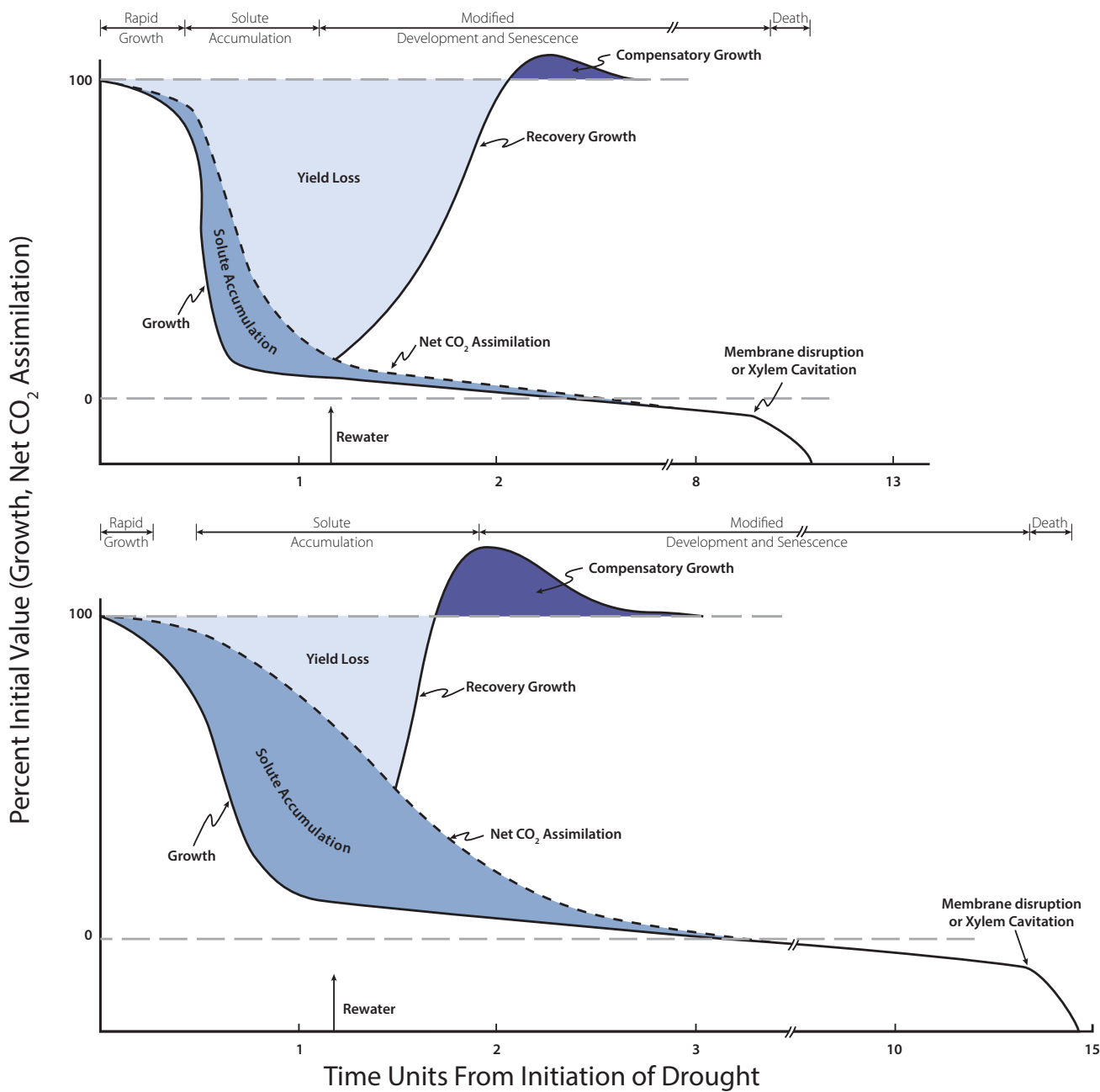
Figure 3. Proposed general model for responses of grasses to drought on rapidly drying (e.g. coarse textured) soils (top) and slow drying (e.g. fine textured) soils (bottom). Four periods of plant response are identified above each graph: rapid growth, solute accumulation, modified development and senescence, and plant death due to rupture of cell membranes or failure of the xylem vessels. The effect of re-watering on growth in the two scenarios is shown by the rising curve.

potential of entire plants to modify a small number of cells. If this is true, then accumulation of solutes is more likely an adaptation to enable compensatory growth than a mechanism for regulating water loss. The signal, whatever it is and however it might be produced and transmitted, informs the plants about the rate of plant water loss, since rapid water loss will invariably mean water depletion and slow water loss will mean that there is little risk of water depletion. Plant response to water is designed more to maximize opportunism in exploiting uneven rainfall than for maintaining growth with limited water. The latter is often the

goal of drought breeding programs. Plant breeders should be selecting germplasm that exhibits rapid growth under favourable conditions, be they more or less frequent, and this is likely what conventional plant breeders have always been doing.

References available online at www.farmwest.com

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