ROOTING DYNAMICS AND WATER STRESS IN WHEAT: POTENTIAL IMPACTS OF GRAZING

Tony Svejcar

U.S. Department of Agriculture, El Reno, OK 73036

Introduction

For many years the use of wheat (Triticum aestivum L.) for winter forage has been popular in the Southern Great Plains. The concept of using annual cereal crops for both forage and grain yield, provides the producer with an extra source of income in the form of animal weight gain. The timing of growth is particularly important because forage is produced during a period when conventional forage species are dormant. However, little information is currently available regarding the physiological response of annual grain crops to defoliation during the vegetative phase. Research concerning plant response to defoliation has centered around perennial range and pasture species. In these species the primary concern is stand survival; with annual cereals, the primary concern is grain available for harvest after grazing. This paper deals with some of the relationships known to exist among water stress, rooting patterns and grain yields in wheat and the ways these relationships may be altered by grazing.

Review of Literature

Water Stress

In many regions, water is the factor most limiting to crop production (Kozlowski, 1968). Few plants growing in natural environments escape water stress for more than a few days at a time (Hsiao et al. 1976). Leaf water potential declines during the day even in well irrigated wheat plants (Jones, 1977). The level of water stress induced by environmental variables influences grain yield in wheat.

During the flowering and grain-filling stages, the wheat plant must produce adequate assimilate to support grain growth. In order to produce the necessary assimilate, plants must maintain a reasonably high stomatal conductance, allowing CO_2 to diffuse into the photosynthetic tissues of the leaf. The level of stomatal conductance is important in controlling photosynthesis (Brix, 1962; Hinckley et al. 1978; Wong et al. 1979). Water stress tends to lower stomatal conductance, (Raschke, 1975). Johnson et al. (1974) found that transpiration was linearly related to flag leaf water potential in both wheat and barley (Hordeum vulgare L.). Thus, much of the reduction in yield caused by water stress can be associated with reduction in assimilate supply. The assimilate use pattern also changes. More current assimilate goes into grain in stressed than in non-stressed wheat plants (Johnson and Moss, 1976). Also, more stored assimilate is transferred to the grain in stressed plants (Gallagher et al. 1976).

The stage of plant development during which water stress occurs is critical in terms of the various yield components and total yield.

Fischer (1980) felt that seed number was the yield component most sensitive to water stress and that this yield component was most affected by stress near flowering. Johnson and Kanemasu (1982) also found reduced kernals/spikelet if preanthesis water levels were low. However, Johnson and Moss (1976) imposed water stress on wheat plants during grain- filling, and measured a 14% reduction in kernal weight and 20% reduction in grain yield. Thus, the component of grain yield most influenced by water stress will depend on the period during which stress is imposed.

A point not considered in the previous discussion is stress during the vegetative and early reproductive phases. During these periods, stress may cause reduction in tiller number. Thus assimilate supply during flowering and grain-filling would not completely explain yield reductions. Johnson and Kanemasu (1982) found that under field conditions head number per square meter was an important component of yield. The recent work of Klepper et al. (1982) indicates how tiller development and number can be influenced by prior stress.

Rooting Dynamics

There are a number of mechanisms the wheat plant might use to cope with stress. From a detailed greenhouse study, Blum et al. (1983) concluded that drought resistance in wheat was related to osmotic adjustment, maintenance of stomatal permeability and turgor under stress, and total root mass production under stress. As one would expect, the water available for plant growth is directly related to the volume of soil occupied by plant roots (Taylor and Klepper, 1978). By maintaining sufficient rooting density a plant is able to partially avoid the sudden drop in water potential associated with drought (Hurd, 1968; Townley-Smith and Hurd, 1979).

Many factors influence root growth; however, wheat roots have a definite pattern of development (Klepper et al. 1984). The number of roots on any culm can be predicted from the number of leaves on the culm ($r^2 = 0.9$), indicating that root and shoot development are linked. In their study the presence or absence of roots and relative order of branching wasn't affected by fertility, row spacing or planting density, whereas branch number and length were affected. Most studies of above- and below-ground dynamics have emphasized relative rates of phytomass production. Anderson-Taylor and Marshall (1983) found that spring barley root systems reached maximum phytomass 6 weeks from sowing when shoot weight was only 50% of its value at maturity. Growth of the barley root system was characterized by rapid increases in weight with time which ceased abruptly just before the ear of the main shoot emerged. Thus, tillers produced after that point were not well rooted and tended to die.

With winter wheat, Gregory et al. (1978) observed exponential increases in total root weight until the beginning of April, then linear increases until mid-June (anthesis), with a slight decrease after that point. Lupton et al. (1974) found that wheat root growth was relatively constant before flowering, compared to sigmoidal curves for the aerial parts. Thus it appears that root growth tends to be fastest during the vegetative phase, with a leveling out during the reproductive period. The magnitude of root growth will be very much influenced by species and environment.

The root/shoot ratio of plants increases with water stress (Turner, 1979). The mechanism for the increase lies in the sensitivity of leaf cell enlargement to small water deficits, causing reduction in crop growth rate and even leaf shedding (Turner and Begg, 1978). Thus the root/shoot ratio is altered because water stress reduces leaf growth more than root growth. However, Passioura (1981) listed a number of studies in which an absolute increase in root growth under water stress was observed. The adaptive significance of root/shoot adjustment lies in the fact that the plant must match water supply to water demand. Kummerow (1980) points out that the ratio of absorbing root surface to photosynthetically active leaf area may be more relevant to plant growth than simple root/shoot ratios. However, Kummerow was dealing with a much more complex system than that of a field crop.

There is some controversy concerning the optimum relationships between root growth and grain yield in cereals. Passioura (1976, 1972) has suggested that early water use in wheat should be limited to maintain sufficient soil water during the later reproductive stages. To limit water use, either rooting volume, or hydraulic conductance of the roots must decrease. This argument is intended for areas where stored soil water is important during reproductive growth. Passioura (1981) also pointed out that the "cost" of producing and maintaining an extensive root system can be considerable. Thus, it would follow that a plant should reduce leaf area to match rooting volume rather than increase rooting volume to match transpiring leaf area. With wheat growing on stored water, Richards (1983) found that removing leaf area during early growth reduced early water use and increased grain yields compared to control plants.

On the other side of the controversy, a number of studies have shown a positive link between early root production and the ability of wheat to produce grain under drought (Blum et al. 1983; Hurd, 1964, 1968, 1974; Sandhu and Laude, 1958). Hurd (1974) suggested that water distribution in the soil profile may help explain the controversy. He postulated that when moisture is available deep in the soil profile extensive root proliferation would allow the plant to use this resevoir of water for later growth. However, if rooting were restricted by a compaction layer or a soil profile were sufficiently shallow, Passioura's logic would apply. Distribution of precipitation is also very important in considering the two arguments. Conserving water early in growth is only important where rainfall is limited during critical growth stages.

Influence of Grazing on Rooting Dynamics

Most work on defoliation has dealt with perennial range and pasture species. In many cases clipping rather than grazing was used to remove leaf area. Much of the work relating defoliation to root growth was conducted 30-50 years ago in the central and southern Great Plains. The results are consistent in that defoliation (grazing or clipping) reduced rooting mass compared to unclipped controls (Crider, 1955; Albertson, et al. 1953; Weaver and Darland, 1947; Biswell and Weaver, 1933). Weaver (1950) found that several native grasses produced more roots on good compared to poor condition range, implying that heavy grazing reduced root production.

The pattern of defoliation has been shown to influence root growth. Carmen and Briske (1982) found that if dependent little bluestem (Schizachyrium scoparium [Michx.] Nash) tillers were defoliated they could still produce nodal roots. However, if the parent tiller was also defoliated, the rooting ability of the dependent tiller was impaired. In perennials, the number of seasons of defoliation also influences level of root reduction (Archer and Tieszen, 1983). The importance of maintaining a balance between root and shoot systems has been emphasized by Caldwell et al. (1981). They have shown that root growth stoppage following defoliation constitutes a mechanism by which the plant can conserve resources and reestablish necessary photosynthetic leaf area following defoliation.

If grazing influences root growth of wheat in a manner similar to perennial plants, we can assume that above a certain level of grazing rooting biomass will be reduced. The subsequent effect of reduced rooting on grain yield will depend on distribution of rainfall and the soil profile on which the wheat is growing. The effects may be positive or negative depending on specific environmental conditions and physiological adaptations of the plant. There are a number of potentially detrimental effects of grazing on yield (eg. growing point removal, trampling, etc.) which have not been considered in this discussion. Certainly water relations is only one of many factors that must be considered in assessing plant response to grazing.

Conclusions

Water relations is an important aspect of both forage and grain yield in wheat. The stage during which water stress occurs will greatly influence it's effect on grain yield components. Some authors have suggested that stress near flowering has the greatest influence on grain yield by reducing seed number. However, stress earlier in growth may reduce tiller numbers while stress after flowering can reduce seed size.

The dynamics of rooting is an important factor influencing water relations. Wheat roots have definite developmental patterns associated with above ground phenology. In terms of phytomass production, most studies have shown that root mass peaks and may even begin to decline before shoot mass reaches peak levels. There are contrasting philosophies concerning the ideal relationships between root growth and grain production under dryland conditions. One line of thought is that root growth and water use during the vegetative phase should be limited, thereby conserving water for the critical reproductive phase. However, if water is available deep in the soil profile, early proliferation of roots may be an advantage. The optimum root growth pattern will depend on seasonal water trends in a particular soil profile.

Grazing typically reduces rooting mass in perennial grasses, and it probably has the same effect in wheat. The influence of reduced rooting mass on grain yield depends on environmental conditions and the specific soil profile supporting the wheat. Factors other than rooting mass should also be considered in interpreting the effects of grazing on grain yield.

Areas of Needed Research

Grazing effects on rooting of annual cereals is a research topic that has received little attention. There are a number of questions research might attempt to answer:

1) What root length density and rooting depth is necessary to produce a crop under a particular climatic and soil regime?

2) What is the rooting response to various levels of leaf area removal?

3) How do different levels of leaf area removal influence water requirements?

4) Does the ratio of leaf area to root absorbing surface tend to remain constant among levels of leaf area removal?

A "whole plant" approach is needed to define critical growth factors and interactions. Factors such as water use, photosynthesis, energy partitioning and storage, growth morphology, and phenology may all be influenced by grazing and in turn interact with one another. Thus, as many plant factors as possible should be considered in research aimed at elucidating wheat response to grazing. Such information will also be useful to breeders, who in the future may attempt to optimize forage, as well as grain production of winter wheat varieties grown in wheat pasture regions.

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