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Compendio

Existe escasa información acerca de la manera como el déficit hídrico afecta diferencialmente las hojas de los tallos axilares (macollas) y del tallo principal de la planta de trigo (Triticum aestivum).

Por ello, se sembró trigo de primavera en macetas que se colocaron en una cámara de crecimiento. Después de 7 semanas se midió el efecto del déficit hídrico sobre el contenido relativo de agua (CRA) de las hojas del tallo principal y macollas primarias y secundarias. Las plantas que no fueron sometidas a déficit hídrico mostraron contenidos relativos de agua que aumentaron basipetálicamente en las hojas, pero las diferencias en CRA de las varias hojas fueron relativamente pequeñas. Este efecto, sin embargo, resultó opuesto al de las plantas sometidas a déficit hídrico, donde el CRA de las hojas disminuyó basipetálicamente y la magnitud de las gradientes aumentó, a medida que el déficit hídrico se hizo mayor. Cuando las plantas fueron sometidas a un régimen de déficit hídrico, el CRA de las hojas viejas de las macollas primarias y secundarias disminuyó más que el de las hojas del tallo principal. Se observó que la senescencia prematura de las hojas más viejas en plantas sometidas a déficit hídrico era invariablemente precedido por CRA relativamente bajos. Los estados de desarrollo de los diferentes tipos de raíces se observaron al momento de iniciarse el período de déficit hídrico. El sistema de raíces de las macollas resultó menos desarrollado que el sistema seminal y que el formado a partir de los nudos del tallo principal de la planta.

Introduction

It is a common observation that when plants are subjected to drouth the oldest leaves are the first to die, and if the drouth continues, an accelerated acropetal progression of leaf senescence occurs. In addition to this premature leaf death under

water stress it has been observed that young primary and secondary tillers of cereals often die while the older tillers and main culm survive. A few measurements of relative water contents (RWC) or water potentials in leaves at different insertion levels on the main stems of plants have been made, but we know of no studies showing the water status of leaves of the main culm and tillers of gramineous plants during water stress.

Catsky (5, 6) using the water saturation deficit (WSD) method of determining leaf water content in pot experiments found that leaves of different ages of fodder cabbage (*Brassica oleracea*) wilted unevenly during a drying cycle. The oldest leaves were the first to wilt and die, then the mature leaves, and finally the youngest. On the first day of the drying cycle, when soil moisture levels were

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high, the oldest leaves had the lowest WSD and the youngest the highest. During the second day of the drying cycle the WSD gradient began reversing, and by the third day the youngest leaves had the lowest WSD and the oldest leaves the highest. The same results were also obtained in fodder cabbage by Solarova (15).

Begg *et al.* (3) followed the diurnal trends of RWC of leaves in the upper, middle and lower portions in a canopy of bulrush millet (*Pennisetum typhoides*). Their data showed that during most of the afternoon the RWC was lowest in the bottom layer of leaves, but during nighttime hours the gradient was reversed, and this leaf zone had the highest RWC. In a growth chamber experiment Hoffman and Splinter (8) found the leaf water potentials (LWP) of the bottom leaves of tobacco to be lower than that of center leaves. However, under field conditions Begg and Turner (2) found the opposite result.

Barnes and Wooley (1) observed in field corn (*Zea mays* L.) that between 1500 and 1600 hours with or without moisture stress, the lowest RWC were found in the bottom leaves, but under moisture stress conditions the leaf RWC gradient was much steeper, and was displaced toward lower RWC. Interestingly, the second leaf from the top had the highest RWC in both treatments; however, its RWC was about 5% lower under moisture stress conditions.

Millar *et al.* (11) studied the variation of the leaf water potential (LWP) with leaf position in barley in a greenhouse pot experiment and showed that LWP increased basipetally at soil moisture contents near the field capacity and near the permanent wilting point; however, the LWP were much lower at soil moisture levels near the permanent wilting point. A difference of about -16.5 bars in LWP was observed between the top and bottom leaves when the plants were growing in soil near the field capacity; this contrasted with a value of -5.6 bars when the soil moisture content was near the permanent wilting point.

The objective of this research was to measure gradients of RWC in the leaves of the main culm and tillers of spring wheat, and to study the survivability of tillers and leaves with increasing water deficits during a drying cycle.

Materials and methods

Spring wheat (*Triticum aestivum* cv. Waldron) was planted on September 20, 1969 in pots containing 14 kg of air-dried Tiffany loam soil

and placed in a growth chamber. Soil in each pot was mixed with 6.6 g of ureaformaldehyde, 1.9 g of NH_4NO_3 , 11.1 g concentrated superphosphate and 2.0 g of K_2SO_4 .

After germination at 32 to 38C the chamber was programmed to provide 15 hours of daylight with temperatures of 27.8 ± 0.5 C during the day and 22 ± 0.5 C at night. Light intensities measured with an Isco Spectroradiometer in the center of the growth chamber and at the top of the pots in the 400, 500, 600, 700 nm bands were 4.1, 8.1, 28.9 and 2.1 microwatts/cm⁻²/nm⁻¹, respectively.

The plants were thinned after 10 days to six uniformly spaced plants per pot, and silica sand to a 3-cm depth was added to each pot to reduce soil evaporation. All pots were watered to the approximate field capacity at regular intervals during the first 7 weeks.

After 7 weeks, the water stress period was initiated by withholding water from five randomly selected pots (hereafter referred to as stress pots). Twenty-four hours prior to this all pots were watered to the field capacity. Throughout the investigational period the non-stress pots were watered daily to the field capacity after the RWC measurements had been completed. The stress period was for 7 days. RWC measurements were made on all leaves of the main culm and tillers of a single plant in both the water stress and non-stress pots. The plants chosen for RWC determinations were matched as closely as possible for similar tillering characteristics. On the first day of the drying period RWC measurements were made only on leaves of a single plant from one pot because there was no disparity in treatments, but on the second, fourth, fifth, sixth and seventh days RWC measurements were made on all leaves in both water stress and non-stress pots. The pots containing the plants sampled were discarded after the RWC determinations were made.

The RWC measurements were made just prior to the completion of the "day" period as previously described by Millar *et al.* (11). In addition, the sampling procedure consisted of identifying in the growth chamber the tiller and leaf position of the selected plant. All tillers were tagged on the date of their appearance. After this was done, one tiller at a time was brought from the growth chamber into an adjacent laboratory where its leaves were prepared for RWC measurements as rapidly as possible.

Tillers were identified according to the nomenclature advocated by Percival (12). The main culm or axis was denoted by 1 and the branches on

tillers arising from this axis were designated T11, T12, T13, etc. where T11, T12 and T13 were the tillers arising from the coleoptile node, the node from which the first true leaf arose and the node from which the second true leaf arose respectively. Similarly, a number was added to the primary axes to denote branches (secondary tillers) arising from them (eg. T132 denoted the second branch arising from the third branch of the main culm).

Root data were obtained by examining a total of seven plants selected from four pots. The soil and root matrix were carefully removed from the pots and inverted. A pinboard was placed on top of the inverted mass, and thin 7-inch iron spikes were rammed through the soil and root matrix. The board and soil were then immersed in a tub of water prior to washing away adhering soil from the roots.

Spike development stages in three plants were determined by exposing the apex of the main culm and the primary and secondary tillers. The apices were examined under a binocular microscope and classified according to photographs and descriptions given by Bonnett (4).

Results

RWC for leaves of plants growing under non-stress conditions for 1, 4 and 7 days are given in Figures 1, 2(a), and 3(a), respectively. The detailed RWC data for days 2, 5 and 6 are not presented because of space limitations. The trends displayed in these data are essentially similar to those found on days 4 and 7. RWC of leaves on the main culm and tillers increased basipetally. However, on each day the differences in RWC between corresponding leaves on the main culm and the various tillers were relatively small.

The development of water deficits within the aerial portion of the water stress plant after 4 days of stress is clearly shown by the RWC data contained in Figure 2(b). Gradients of leaf RWC in all tillers and the main culm were now reversed when compared with those of the non-stressed plant: The RWC of the leaves decreased basipetally and the lowest RWC were now found in the lowest leaves of individual branches. Thus, the least difference in RWC between the stressed and non-stressed plants was found in the top leaves of the various branches. However, large changes in RWC in the second leaves from the top on the secondary tillers had occurred when compared to the second leaves of primary tillers and the main culm. The RWC of the lowest leaves on the primary tillers were also much lower than the lowest living leaf of the main culm,

although the RWC of the top two leaves on the primary tillers compare favorably with those on the main culm. Overall, it appeared that as water stress developed, leaves of secondary tillers had a poorer water balance than leaves of primary tillers, and that leaves of primary tillers had larger water deficits than leaves of main culms.

By the seventh day of the drying cycle, when soil moisture was near the permanent wilting point as expressed by water content at 15 bars pressure, RWC had decreased substantially in all leaves which were still alive [Figure 3(b)]. The inverted gradient now extended to the top leaf in all culms except for the second leaf on the main culm which had a RWC about 2% higher than the top leaf. This apparently is not an artifact since one of the authors (R. Jensen, unpublished data) has observed in field-barley plants under severe water stress conditions that the flag leaves on main culms usually die before the second leaf. In addition, Barnes and Wooley (1) showed that the second leaf of a water-stressed corn plant also had a higher RWC than the uppermost leaf.

The age of the tiller, or possibly the position of the tiller, may have an important effect on how well the tiller competes for water. The age of the primary tillers of the stressed plant in Figure 3(b) was: T12 > T13 > T14 > T15 > T16. Examination of the RWC data revealed that all leaves on T16 were dead, and the maximum RWC of the first and second leaves on T12, T13, T14 and T15 were 61.8 and 50.0, 69.9 and 58.2, 62.6 and 32.6, and 54.9 and 46.6 percent respectively. T13 had overall the highest RWC for tillers, but this may be due in part to T12 having more secondary tillers competing for the available water. The oldest portion of the plant, the main culm, had the highest RWC of all culms with both top leaves slightly over 70%.

All live leaves on the secondary tillers after 7 days of stress were at lower RWC than the primary tillers with which they were associated. Comparing RWC to age of secondary tillers on a particular primary tiller, it can be seen [Figure 3(b)] that the younger tiller (T142) on T14 was dead and on T141, the older secondary tiller, both leaves were still alive, but the highest RWC was only 46.7%. This was about 16% lower than the highest RWC on T14. On T13, all the leaves on the younger tiller (T132) were dead, but the older secondary tiller (T131) still had one live leaf with a RWC of 40%. Three secondary tillers are on T12. The youngest tiller (T123) had one live leaf, but its RWC was only 30.3%; all leaves were dead on T122 and on the oldest secondary tiller (T121) both leaves were alive with RWC greater than

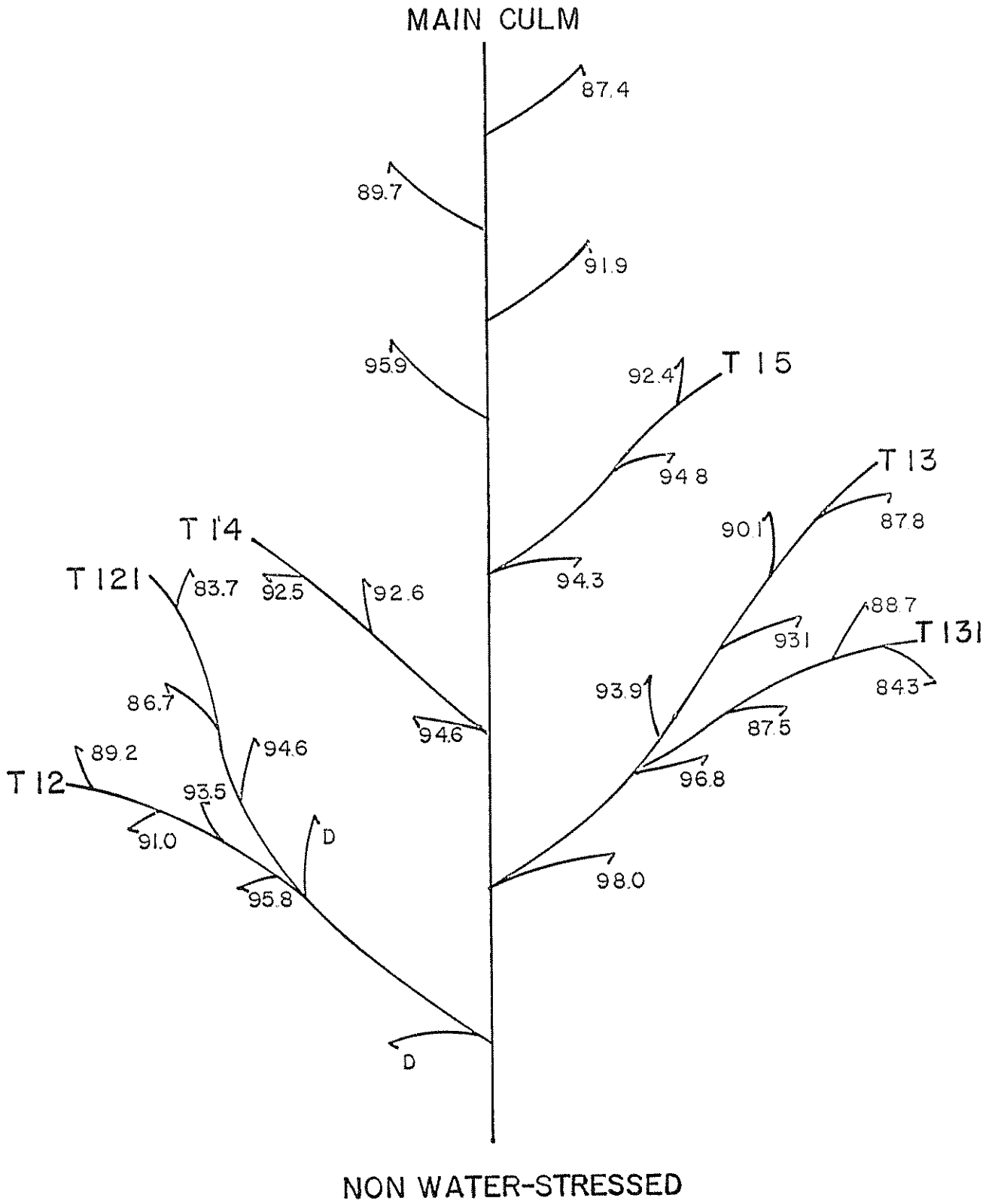


Fig. 1 Relative water contents of the leaves of a wheat plant 1 day after watering (D represents a dead leaf)

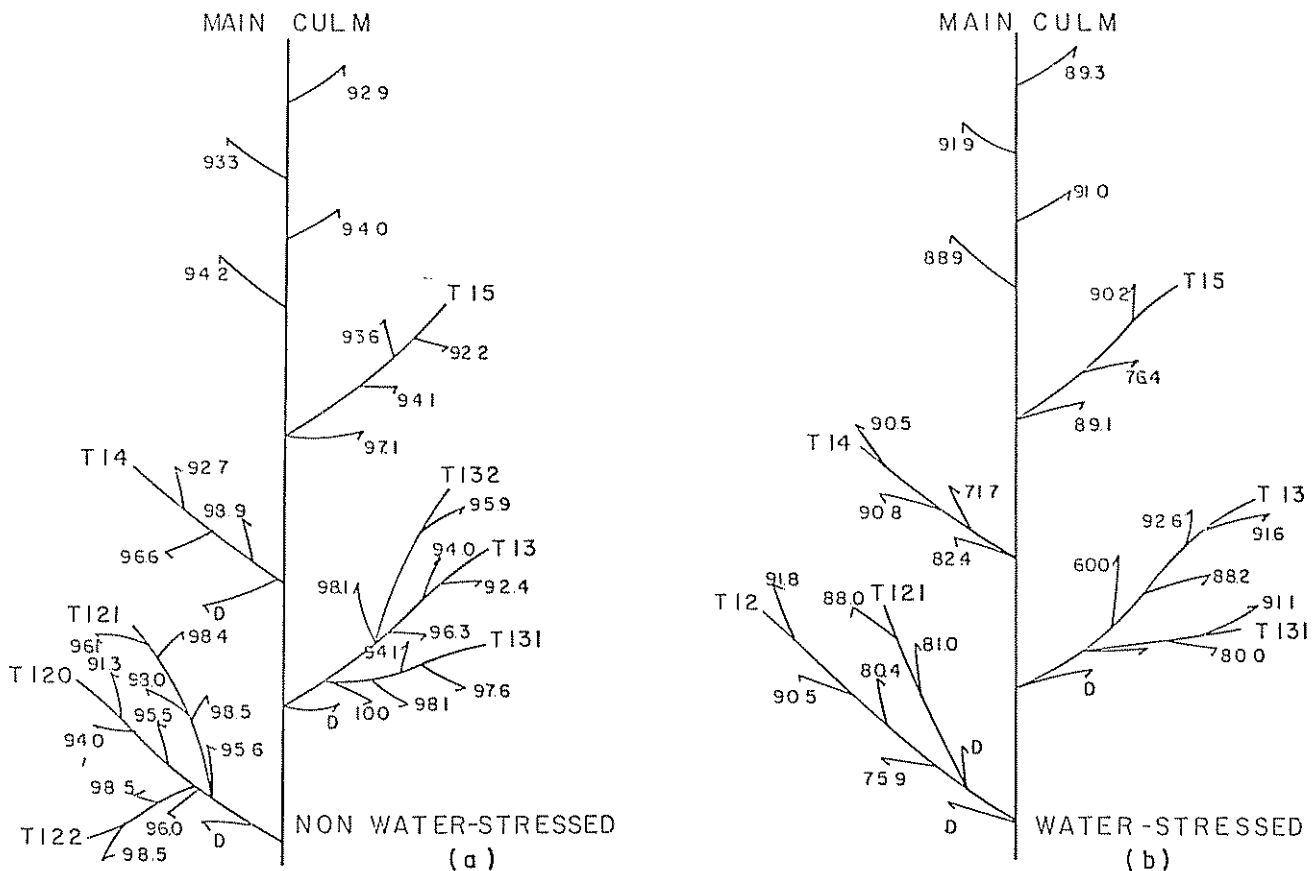


Fig. 2 Relative water contents of the leaves of a non-stressed and a stressed wheat plant after 4 days of stress (D represents a dead leaf).

40%. From this analysis, it would appear that leaf RWC is related to tiller age, but it must be remembered that tiller position and tiller age are closely correlated.

The progress of the decline of RWC with leaf position on the main culm during the 7-day stress period is shown in Figure 4. The first day's data are averages of leaf RWC with respect to leaf position of non-stressed plants for all seven days during the stress period, while the data for the following days are measurements from a single plant which has been stressed for the period indicated. The data clearly show that the lower leaves are the first to show declines in RWC and that the rate of decline in RWC is much more rapid in the lower than the upper leaves. The same general sequence also occurs for leaves on tillers.

An attempt was made to relate RWC to death of leaves on water-stressed plants. The procedure followed was to compare leaves on the tillers and main culms for two consecutive days, noting the RWC on the first day and whether the leaf at the same position was alive or dead the following day.

Less than 5% of the leaves of stressed plants which had RWC in excess of 80% died during the subsequent 24 hours. In contrast, approximately 50% of the leaves which had RWC less than 80% died within 24 hours under the given experimental conditions. It was assumed that premature senescence of these leaves of water stressed plants was caused by water stress because of the difficulty of determining any other cause.

Each of the seven plants studied had well developed, healthy seminal root systems. The 4 to 6 seminal roots on each plant had many lateral roots and appeared better branched than the nodal roots. The internode between the coleoptile node and the first node was healthy in all cases. Most of the adventitious roots were developed from nodes on the main stem, and the adventitious roots from the lower nodes of the main stem were longer and more extensively branched than those arising from higher nodes.

A summary of adventitious root and spike development at the time of the application of the stress treatment is presented in Table 1. The root

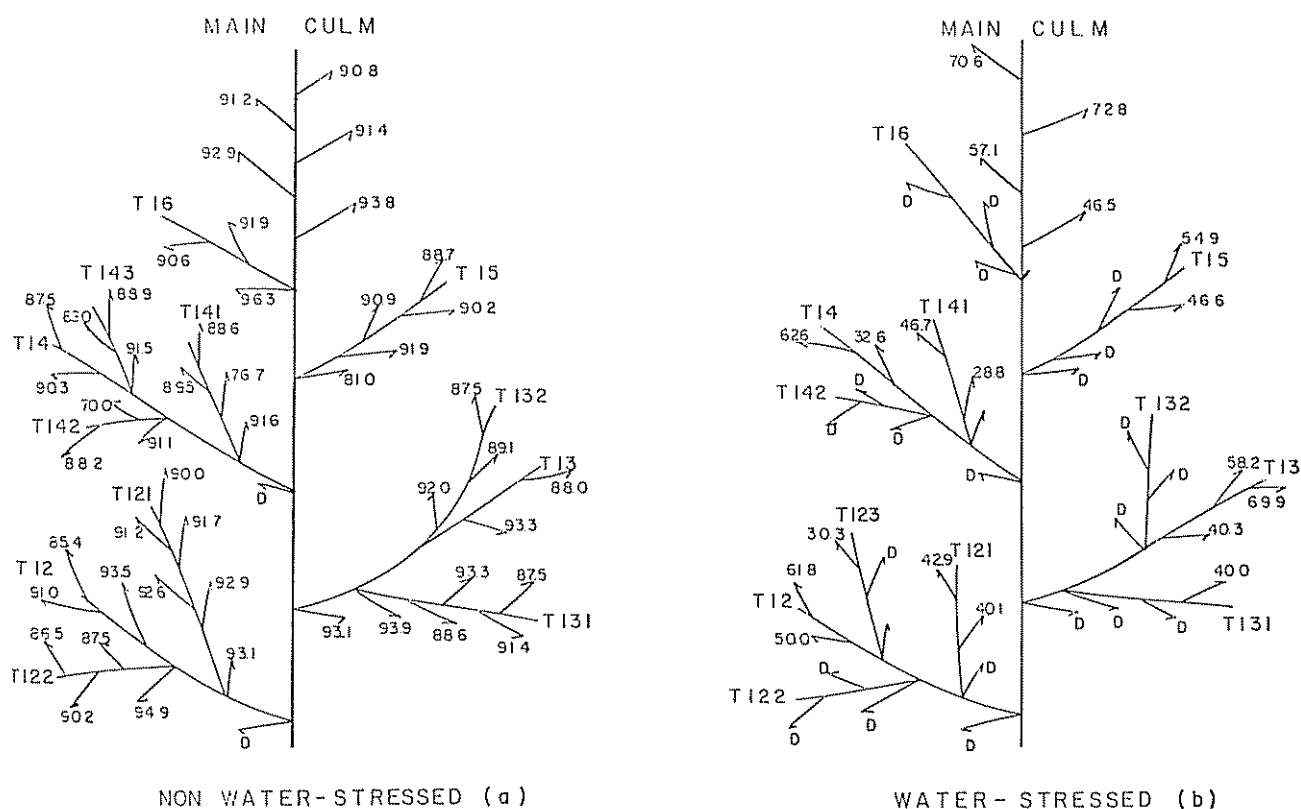


Fig 3 Relative water contents of the leaves of a non-stressed and a stressed wheat plant after 7 days of stress (D represents a dead leaf)

Table 1. Adventitious root growth and stage of development of spikes on the main culm and the primary and secondary tillers of Waldron plants after approximately 7 weeks of growth.

Plant characteristic	Plant part										
	Main culm (T1)	Primary tillers					Secondary tillers				
		T12	T13	T14	T15	T16	T121	T122	T123	T131	T132
Average number roots/plant (>18 cm)	6.1	2	1.7	0.2	0	0	0.2	0	0	0	0
Average number roots/plant (6-18 cm)	1.3	1.5	1.1	0.7	0.1	0	0.1	0	0	0.1	0
Average number roots/plant (1-6 cm)	2.1	1.7	1.6	0.6	0.3	0	0.1	0	0	0.1	0
Roots initials*	a	a	a	a	a	a	a	a	a	a	a
Spike development†	b	b	b	b, c	c	c, d	d, e	-	-	b, f	e, f

* "a" - indicates that root initials present

† "b" - florets of all of the spikelets differentiated; "c" - basal florets only of spikes initiated; "d" - empty glumes only of the spikelets identified; "e" - spikelet branches identified but spikelet parts not differentiated; "f" - spikelets not initiated

system associated with the main culm was much better developed than that of any of the tillers. The root systems of tillers T12 and T13 were also better developed than those of the other primary and secondary tillers. In the T16 and the secondary tillers T122, T123 and T132 there was little if any evidence of development of a root system other than root initials. The root study indicated that the primary tillers T14, T15 and T16 and all of the secondary tillers were completely or largely dependent upon either the seminal root system or the adventitious roots developed on other plant parts for supply of water and nutrients.

Microscopic observations of the stem apices during the stress period revealed a range of spike development from spikelets not initiated on some secondary tillers to florets of all the spikelets being differentiated. Florets of all spikelets on the spikes of the main culm and of the primary tillers T12, T13 and T14 were initiated. The stage of development of the spikes in the main culm and primary tillers was in the order of: main culm >T12 >T13 >T14 >T15. The secondary tillers were not beyond double ridge formation.

Discussion

It is well recognized that the influence of water stress differs according to the portion of the plant examined. For instance, the growth of the leaf of tomato is more susceptible to water-stress damage than that of the stem (7). In the present study the leaves of secondary and young primary tillers as indicated by measurements of RWC and visual observation were particularly adversely affected by water stress.

The adventitious root system associated with the young primary and secondary tillers in our study was poorly developed. As a result the leaves of these tillers would have been dependent for nutrients and water on the seminal roots and the adventitious roots of the main culm and older primary tillers. Viable vascular connections apparently occur between tillers and the main culm for much of the life of the wheat plant (14). Conceivably, the vascular connections between the root system and the main culm and older tillers would be more developed than that leading to the younger tillers. Thus, when water stress occurs the older main culm and older tillers may be in a more favored position.

However, such a simple explanation for the premature death of the leaves of the youngest tillers may not be entirely correct. Tiller senescence is a complex process which is not fully understood (10),

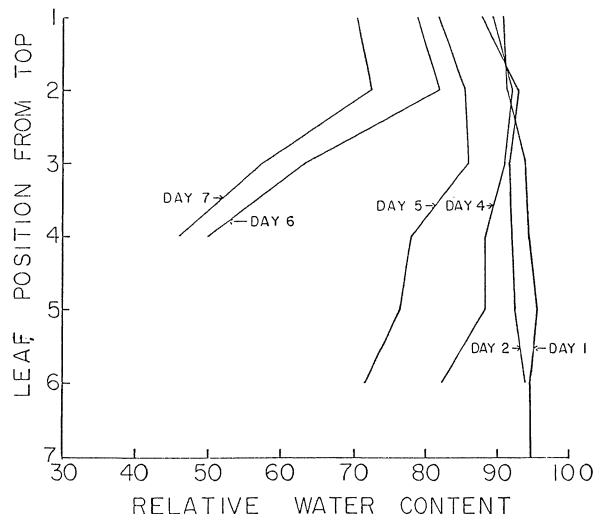


Fig. 4 Effect of leaf insertion level on the main culm on the relative water contents of wheat plants without added water for selected periods.

and the effect of water stress on the controlling mechanisms is not completely clear. The complex, competitive relationship for plant nitrogen among different shoots of a wheat plant was recently illustrated by Rawson and Donald (13). These authors found that when nitrogen in the rooting medium was restricted, movement within the plant of previously accumulated nitrogen was largely limited to the main culm and primary tillers or was transported to the roots. The secondary and tertiary tillers were starved of this nitrogen. However, when the rooting medium was adequately supplied with nitrogen the previously accumulated nitrogen was more evenly distributed.

In the water-stressed plants the lower leaves of the tillers and the main culm normally had a lower RWC than the upper leaves of the corresponding stems. The lower leaves also appeared visually to be more affected by water stress. Hoffman and Splinter (8) using LWP measurements also found such an effect with tobacco. Begg and Turner (2) suggested that such an effect is possibly due to the lower leaves being in a senescent state. The data presented in this paper, however, allows no conclusions to be drawn concerning the LWP, since age of leaves affects the RWC-LWP relationship (9). The tendency for the lower main culm leaves of water stressed plants to have lower RWC was in agreement with the data reported by others for corn (1) and millet (3).

Summary

Little information is available concerning the manner in which drought stress differentially affects the leaves of tillers and of the main culm of wheat

(*Triticum aestivum*). Spring wheat was grown in pots in a growth chamber, and after 7 weeks the effect of water stress on the relative water content (RWC) of the leaves of the main culm and primary and secondary tillers was determined. In non-stressed plants the RWC of the leaves increased basipetally, but the differences in RWC among the various leaves were small. This effect was reversed in water-stressed plants. The RWC of the leaves of these plants decreased basipetally, and the magnitude of the gradients increased with increasing water stress. The RWC of the older leaves of young primary and secondary tillers were reduced to a greater extent by water stress than those of the older leaves of the main culm. Premature senescence of older leaves of stressed plants was preceded by relatively lower RWC. The tiller root systems were less developed than the seminal and the adventitious roots arising from nodes of the main culm. The stage of development of the various branches was recorded at the time of application of the water stress treatment.

Literature cited

1. BARNES, D. L. and D. G. WOOLLEY. Effect of moisture stress at different stages of growth. I. Comparison of a single-eared and a two-eared corn hybrid. *Agronomy Journal*. 61:788-790. 1969.
2. BEGG, J. E. and N. C. TURNER. Water potential gradients in field tobacco. *Plant Physiology* 46:343-346. 1970.
3. BEGG, J. E., J. F. BIERHUIZEN, E. R. LEMMON, D. K. MISRA, R. O. SLATYER, and W. R. STERN. Diurnal energy and water exchanges in bulrush millet in an area of high solar radiation. *Agricultural Meteorology* 1:294-312. 1964.
4. BONNETT, O. I. Inflorescences of maize, wheat, rye, barley and oats: their initiation and development. *Illinois Agricultural Experiment Station Bulletin* 721. 1966.
5. CATSKY, J. Water saturation deficit and the wilting plant. The preference of young leaves and translocation of water from old into young leaves. *Biology Plant* 4:306-314. 1962.
6. CATSKY, J. Water saturation deficit and photosynthetic rates as related to leaf age in the wilting plant. pp. 203-209. In B. Slavik (ed.) *Water stress in plants. Proceedings of Symposium Prague, 1963.* Czechoslovakian Academy of Science. 1965.
7. GATES, C. T. The response of the young tomato plant to a brief period of water shortage. I. The whole plant and its parts. *Australian Journal of Biological Sciences* 8:196-214. 1955.
8. HOFFMAN, G. J. and W. E. SPLINTER. Water potential measurements of an intact plant-soil system. *Agronomy Journal* 60:408-413. 1968.
9. KNIPLING, E. B. Effect of leaf aging on water deficit-water potential relationship of dogwood leaves growing in two environments. *Physiologia Plantarum* 20:65-72. 1967.
10. LAUDE, H. M., J. R. RIDLEY and C. A. SUNESON. Tiller senescence and grain development in barley. *Crop Science* 7:231-233. 1967.
11. MILLAR, A. A., E. DUYSSEN, and GUY E. WILKINSON. Internal water balance of barley under soil moisture stress. *Plant Physiology* 43:968-972. 1968.
12. PERCIVAL, J. *The wheat plant.* E. P. Dutton Co., New York. 1921. 463 p.
13. RAWSON, H. M. and C. M. DONALD. The absorption and distribution of nitrogen after floret initiation in wheat. *Australian Journal of Agricultural Research* 20:799-808. 1969.
14. RAWSON, H. M. and G. HOFSTRA. Translocation and remobilization of C assimilated at different stages by each leaf of the wheat plant. *Australian Journal of Biological Science* 22:321-331. 1969.
15. SOLAROVA, J. Stomata reactivity in leaves at different insertion levels during wilting, pp. 147-154. In B. Slavik (ed.) *Water stress in plants. Proceedings Symposium Prague, 1964.* Czechoslovakian Academy of Science Prague. 1965.