

A COMPARATIVE STUDY OF GROWTH AND NUTRITION IN BARLEY AND RYE AS AFFECTED BY LOW-WATER TREATMENT

By R. F. WILLIAMS* and R. E. SHAPTER†

[Manuscript received March 31, 1955]

Summary

A comparative study of growth and nutrition in barley and rye was made with two water treatments. The low-water treatment was of an intermittent character and harvests were made after each of the five periods of water stress. Yield reductions due to low-water treatment were highly significant at all five harvests and for both species. The severity of the effects on various plant parts was conditioned by the stage of development of those parts.

The importance of leafiness, as measured by the leaf weight ratio, is stressed as a factor determining interspecific and treatment effects on transpiration rate and the transpiration ratio. An increase in the ratio of roots to shoots has been regarded as a typical response of plants to low-water treatment, but the *immediate* response in the present experiment was a reduction in the root weight ratio. This effect was later reversed in barley but not in rye. The inflorescence weight ratio was reduced by treatment in barley but not in rye. Stem height was unaffected by low-water treatment in rye but was reduced in barley.

The data were examined by classical growth analysis procedures and it was shown that, for successive harvest intervals, net assimilation rates on a leaf nitrogen basis were depressed by treatment in accordance with its severity. There was a tendency for nitrogen to be excluded from the leaves and to accumulate in the "stems" as a result of wilting. Phosphorus intake by the shoots was considerably reduced by low-water treatment, and there were initial decreases in relative leaf phosphorus for both species. This effect was reversed later. Relative contents of silica also tended to be reduced by treatment. The relative contents of potassium, calcium, and magnesium were increased by treatment in the tissues of barley, but these effects were less pronounced in rye. Rye absorbed very much less sodium than did barley, and there were chemically equivalent but relatively smaller differences in the intake of chlorine. There was also evidence for selective absorption of manganese, relative contents being higher in rye than in barley.

The results and the relevant literature are discussed in terms of the growth patterns of the experimental plants. It was found that those plant parts which are growing most actively during the period of low-water treatment are those which suffer the greatest check to their growth and it is indicated that many of the effects on the ratios of plant parts are no more than indirect consequences of this fact. In other cases, such effects could arise directly from the action of water shortage on morphogenetic processes.

Distribution indices for dry weight change are examined, and for many cases there were remarkably small immediate effects of low-water treatment. The exceptional behaviour of rye in this respect is thought to be relevant to its drought resistance.

* Division of Plant Industry, C.S.I.R.O., Canberra, formerly Waite Agricultural Research Institute, University of Adelaide.

† Officer of C.S.I.R.O., stationed at Waite Agricultural Research Institute, University of Adelaide.

I. INTRODUCTION

It is now well recognized that a number of factors contribute to drought resistance in plants. Some of these, such as depth of root system, can be studied properly only in the field. We know much less, however, about the physiological characters which enable the plant to withstand severe desiccation, and these factors can rarely be studied effectively in the field. The elucidation of these physiological characters calls for detailed comparative studies of plants possessing well-established differences with respect to drought resistance.

Cereal rye undoubtedly possesses drought-resistant qualities in a high degree, and this paper is based on an experiment in which it was compared with barley, which is not usually regarded as resistant. The work arose indirectly from an experiment designed to investigate the ability of various plant species to grow on and stabilize drifting sand at Pallamana, South Australia. Barley and rye were the only plants to establish themselves successfully, and only the rye survived the combined effects of drought and sand drift (Waite Institute Report 1938, p. 28). Since that time rye has been used quite extensively in southern Australia for sand-drift control (Herriot 1947-8; Sims 1949).

It may well be that the characters which enabled rye to survive under these extreme conditions are also such as cannot adequately be studied in pot culture, but it was hoped that a comparative study of the two species would reveal differences of response to low- and high-water treatment. This did, in fact, prove to be the case, and to that extent the experiment can be regarded as a contribution to the complex problem of drought resistance.

Perhaps the main value of the data to be presented lies in the fact that, for a considerable portion of the life of two plant species, we have accurate information concerning both relative and absolute contents of no less than nine chemical elements, most of which are essential nutrients and all of which are normally present in plants. It is true that the low-water treatment effects on these plant constituents are difficult to interpret with any confidence, but they do shed some light on certain anomalies which exist in the literature concerning the effects of such treatment on nutrient accumulation in plants (Wadleigh and Richards 1951).

II. EXPERIMENTAL METHODS

(a) General

One hundred enamelled pots containing approximately 14 kg of a 2:1 mixture of Waite loam and washed river sand were used for the experiment. Half of these were seeded with barley, *Hordeum vulgare* L. and half with rye, *Secale cereale* L. on April 17, 1939, and the pots mulched with fine gravel to reduce water loss from the surface of the soil. At an early stage the plants were thinned to five uniform seedlings per pot. Until June 5 (day 49) all pots were watered frequently and so as to bring them back to 65 per cent. of the water-holding capacity of the soil. This procedure is not entirely satisfactory, but it was standard practice at the time of the experiment. Field capacity for the soil mixture would have been somewhere between 50 and 60 per cent. of the

water-holding capacity, but soil water would not long have remained above the field capacity after each watering.

After June 5, half of the pots were subjected to a low-water treatment, and were watered to the original level only on July 3 and 24, August 14, and September 4 (days 77, 98, 119, and 140). This gave four treatments, and on five occasions, July 3 and 26, August 16, and September 6 and 27 (days 77, 100, 121, 142, and 163), five pots of each treatment were harvested. For harvests 2, 3, and 4 it will be noted that there is a discrepancy of 2 days between date of watering-up and date of harvest. Only pots for later harvests were watered on the first of these pairs of dates. Low-water pots to be harvested 2 days later were not watered. This unfortunate expedient tends to destroy the strict continuity of the data for the low-water treatments, but not for the high-water treatments.

At each harvest the leaves were separated at the ligule and, from harvest 3 onwards, the inflorescences were separated from the stems. The stem fraction was a composite one and included leaf sheaths as well as the true stems. Roots were carefully washed from the soil and their dry weights were corrected for soil contamination. Both fresh and dry weights were obtained for the above-ground parts. For the chemical analyses, methods for which are briefly stated below, the inflorescences were reunited with the stems. For the sake of brevity this reunited material will be referred to as "stems".

Pot weight records were kept throughout the experiment and transpiration losses were calculated after correcting for the fresh weights of the plants and for losses from the soil surface.

(b) Chemical

(i) *Ash*.—While data for total and soluble ash are of relatively little value by comparison with data for individual elements of which they are composed, they do give a measure of the total inorganic material in these categories. The total ash values of Figure 5 are carbonate-free, and the usual precautions were observed in the preparation of the ash. Soluble ash is that portion of the total ash remaining after subtraction of silica plus free carbon and carbon dioxide (if present). Insoluble ash gives a sufficiently accurate estimate of plant silica.

(ii) *Calcium*.—As a preliminary to this estimation, phosphoric acid, iron, and aluminium were removed by precipitation with ammonia after addition of sufficient ferric chloride to ensure complete removal of phosphate. Manganese was removed by the use of bromine and ammonia. The calcium was precipitated as oxalate and subsequently titrated as usual after solution of the oxalate in dilute sulphuric acid.

(iii) *Magnesium*.—Magnesium was precipitated as magnesium ammonium phosphate in the filtrate from the calcium determination by the usual procedure and with the usual precautions. The magnesium ammonium phosphate was ultimately ignited to magnesium pyrophosphate.

(iv) *Potassium*.—Potassium and sodium were separated as mixed chlorides, the potassium being converted to perchlorate and weighed as such, or in some

cases estimations of potassium were made by precipitating as cobaltinitrite and subsequently converting to perchlorate.

(v) *Sodium*.—Sodium was obtained by difference from the mixed chloride result, or directly by precipitation with uranyl magnesium acetate.

(vi) *Chlorine*.—Chlorine was estimated by the electrometric method devised by Best (1929) and the results checked against the more usual Volhard method after ashing with lime. The values are high for plant material other than chenopodiaceous shrubs, but there seems no reason to doubt their validity, especially as the ash contents are also high. It has been suggested that watering the plants with tap water, which was relatively high in salts, may have been partly responsible.

(vii) *Manganese*.—Manganese was estimated by the colorimetric periodate method.

(viii) *Nitrogen*.—Nitrogen was estimated by the Kjeldahl method, using selenium as the catalyst.

(ix) *Phosphorus*.—Phosphorus was estimated by the gravimetric Lorenz method.

III. PRESENTATION OF DATA

(a) *The Severity of Treatment*

As might have been expected, the interpretation of the results of this experiment is complicated by the necessity to make interspecific comparisons within a soil-water treatment which is unavoidably lacking in constancy. This is so because of the impracticability of maintaining soil water at levels below field capacity. The expedient of submitting plants to intermittent periods of water shortage, as in the present experiment, has the virtue that it imitates more or less accurately what does in fact happen in the field, but the growth characteristics of the plant species to be compared will almost certainly modify the severity of one or more of the periods of water shortage. Species is, to that extent, confounded with water treatment, and the comparison of quantitative attributes of growth and nutrition may be quite spurious. While such a criticism is very obvious with soil-water treatments it is nevertheless applicable to most interspecific comparisons, especially when pot-culture techniques are used.

Some idea of the effect of species on soil-water treatment in the present experiment will be gained from Table 1, which shows for each harvest interval the number of days during which soil water had been reduced below certain arbitrary levels. This information was derived from pot weights and by using a correction for the fresh weights of the plants. At 600 ml per pot the soil was at the permanent wilting percentage, and it will be noted that the plants succeeded in reducing this to less than half during the later harvest intervals. The picture for the case of barley only is presented diagrammatically as part of Figures 1, 2, and 3. Table 1 shows that, for the period prior to harvest 1, the barley plants were subjected to a much more severe water shortage than

were the rye plants. The differences for intervals 1-2 and 2-3 were in the same direction although less marked, but the difference was reversed slightly for

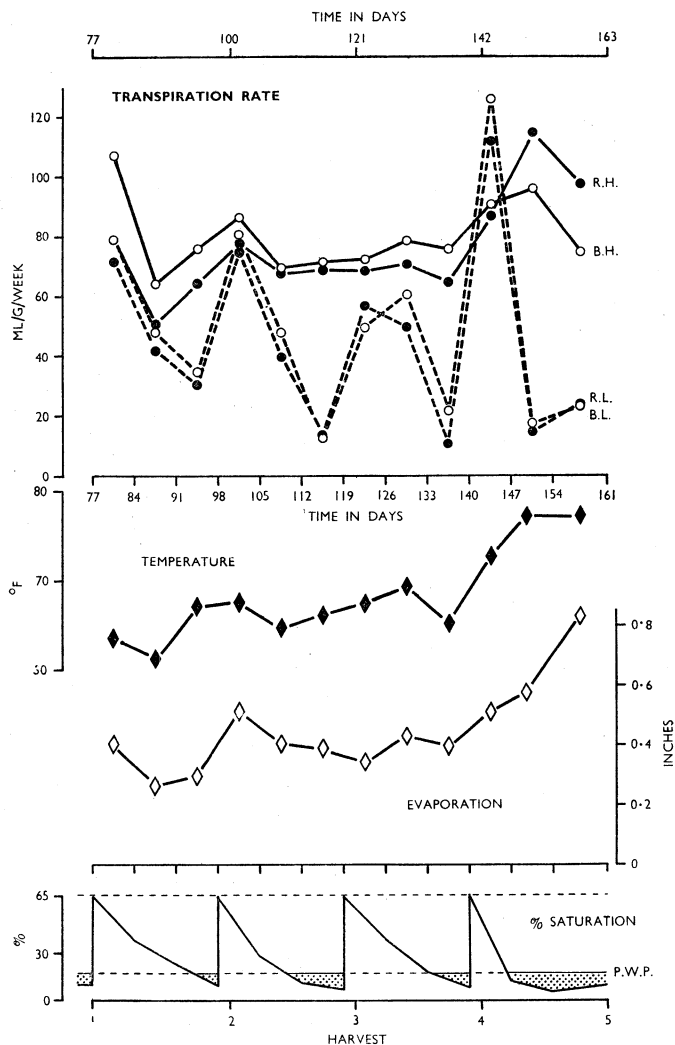


Fig. 1.—Transpiration in ml per g dry weight of leaves per week. The treatment legend is given in Figure 2, but on all figures B.H. = barley, high water, B.L. = barley, low water, R.H. = rye, high water, and R.L. = rye, low water. The temperatures are mean daily maxima within the glasshouse, and the evaporation values are expressed in inches of water per week from an evaporimeter at the open end of the glasshouse. At the bottom of the figure and also in Figures 2 and 3 is a diagram representing the soil-water sequence for the barley low-water treatment. The upper limit of watering, 65 per cent. saturation, was somewhat in excess of the field capacity.

interval 3-4. There was little or no difference in water treatment for interval 4-5. Table 1 also shows that for barley the second and fourth intervals were

considerably less severe than the other three. For rye, only the second interval was markedly less severe than the others.

It must be admitted that, in general, the low-water treatment turned out to be more severe for barley than for rye. This difference might have been reduced if, instead of having five plants per pot in each case, there were more rye than barley plants per pot. Caution is clearly necessary in comparing the responses of the two species to low-water treatment, and for this reason attention will be concentrated on effects which seem to have general validity.

(b) Transpiration Rate

Transpiration rates are presented as water loss per unit dry weight of leaf in Figure 1. To obtain weekly values it was necessary to use interpolations on the leaf weight curves.

TABLE 1
TIME IN DAYS THAT SOIL WATER WAS REDUCED BELOW SPECIFIED LEVELS

Soil Water per Pot	Harvest Interval				
	0-1	1-2	2-3	3-4	4-5
Barley, low water					
At or below 600 ml	15	5	11	7	18
At or below 500 ml	13	3	10	6	17
At or below 400 ml	10	1	8	4	16
At or below 300 ml	—	—	5	2	14
Rye, low water					
At or below 600 ml	11	4	10	9	18
At or below 500 ml	9	2	8	8	17
At or below 400 ml	—	—	5	6	15
At or below 300 ml	—	—	—	2	11

For the control plants, except at late maturity, the transpiration rate is lower for rye than for barley. Williams (1935) found for oats that transpiration rates on this basis were significantly correlated with the nitrogen contents of the leaves. The nitrogen content data of Figure 4 show, however, that such a relation is not present here. Indeed, leaf nitrogen is consistently higher in rye than it is in barley.

As is to be expected, rates within the low-water treatment are governed very largely by soil-water level, though immediate past history seems also to have an effect. The first, fourth, seventh, and tenth weeks of the transpiration record immediately follow the harvesting occasions, and for these weeks the soil-water supply was the same in both treated and control series. Prior to the first week, treatment had been severe, especially in barley, and in barley the rate of transpiration did not recover to the level of the control. For the seventh

week, neither rye nor barley recovered to the level of the controls. On other occasions—the fourth and tenth weeks—the rates equalled or exceeded the

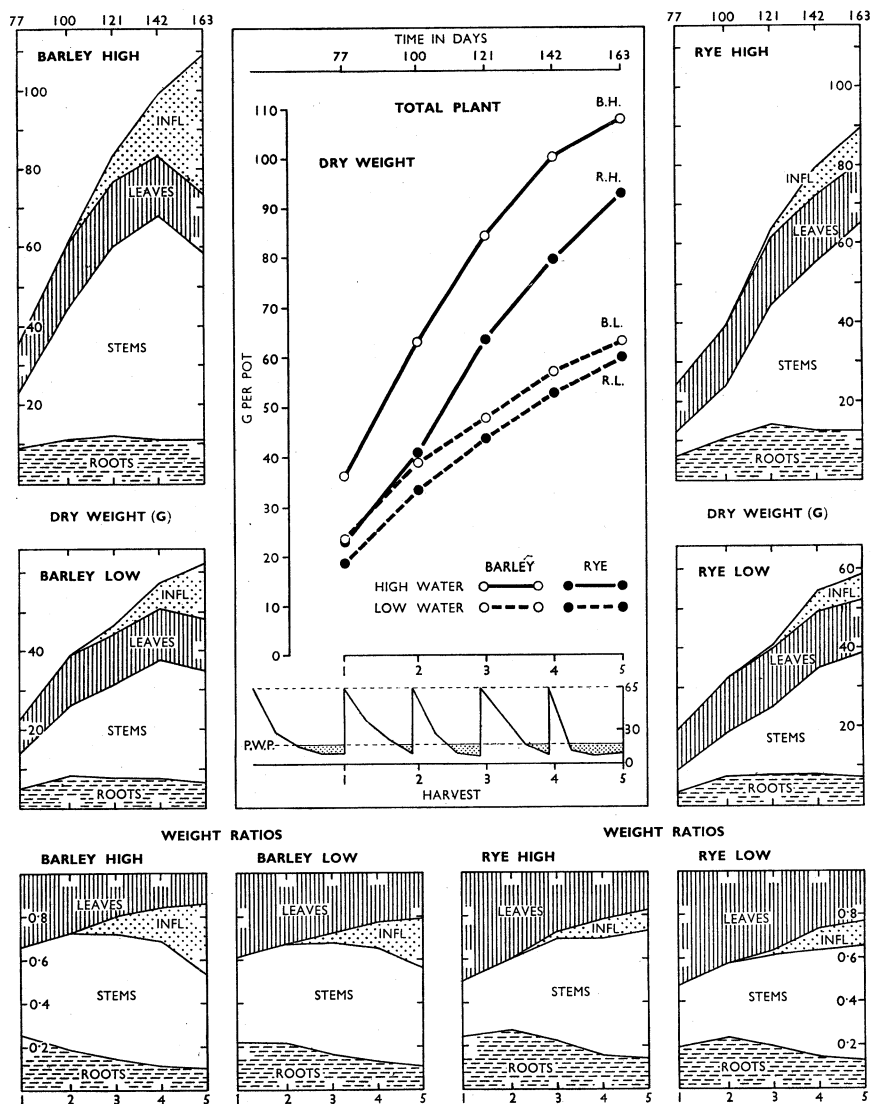


Fig. 2.—Growth (dry weight) of barley and rye as affected by low- and high-water treatments. The marginal figures are summation diagrams of dry matter in roots, stems, leaves, and inflorescences for each treatment separately. At the foot of the page are similar diagrams showing the relative distribution of dry matter between the same plant parts.

rates for the controls, and these occasions were preceded by rather mild low-water treatment.

The fluctuations in the transpiration rates for the controls show a reasonably close agreement with the fluctuations in rate of evaporation from a free water surface.

(c) *Transpiration Ratio*

The transpiration ratio is defined as the ratio of the amount of water transpired to the amount of dry matter formed during the whole or any part of the life-cycle of a plant. Ballard (1933) and Williams (1935) were able to interpret the depressing effects of increased supplies of nitrogen and phosphorus by analysing transpiration ratio into a growth factor and a rate factor, and it is of interest to attempt an interpretation of the specific and treatment differences in the transpiration ratios of the present experiment. The values of Table 2 are based on dry weights for the whole plant including the roots, and are for those portions of the life-cycle ending at the harvests indicated in the table. There are significant interactions between time and treatment class, but these may be neglected for our present purposes.

TABLE 2
TRANSPIRATION RATIOS FOR BARLEY AND RYE SUBJECTED TO HIGH- AND LOW-WATER TREATMENTS

Harvest	Barley		Rye	
	High	Low	High	Low
1	177	171	204	182
2	166	153	188	155
3	164	157	179	160
4	176	158	184	159
5	198	183	211	176

Minimum differences for significance between means ($P = 0.05$) 10.2, ($P = 0.01$) 13.6, ($P = 0.001$) 17.6.

In the control series, the ratio is higher for rye than for barley, and, in the low-water series, rye and barley have virtually the same ratios. Taken together, these effects imply that the transpiration ratio is reduced more by low-water treatment in rye than it is in barley. Looking first at the species difference in the controls, it will be seen that the growth factor would bring about a slight reduction in the ratio for rye as compared with barley. This is so because, if dry matter production is expressed as a percentage of final yield, the curve for barley is always above that for rye. It has also been shown that the transpiration rate per unit weight of leaf tends to be lower in rye than in barley. However, the rate factor of Ballard's original analysis is the somewhat artificial one of rate per unit weight of plant, and he analysed it further as the product of the transpiration rate per unit weight of leaf and the leaf weight ratio (the

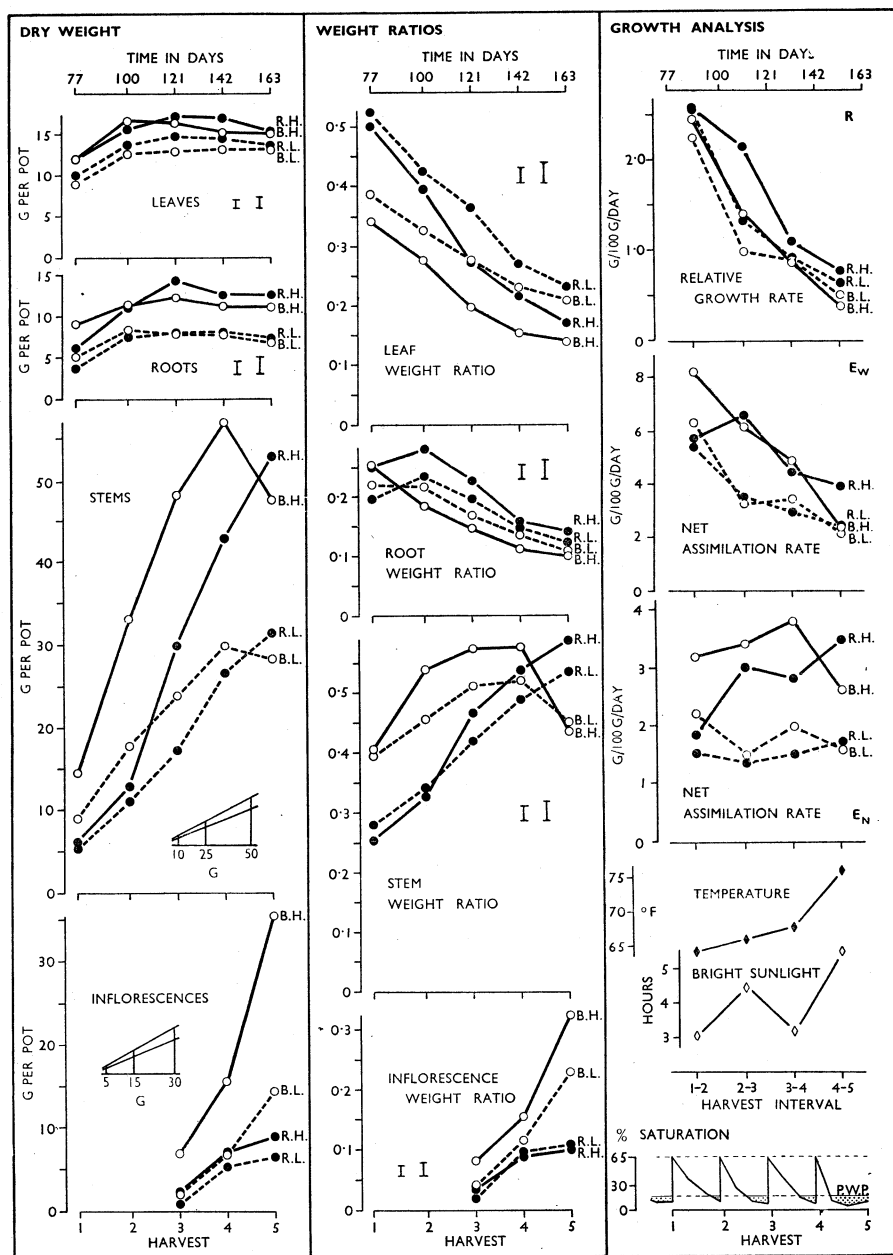


Fig. 3.—Growth (dry weight) curves for the leaves, roots, stems, and inflorescences of barley and rye, weight ratios for these plant parts, and derived data (growth analysis) for the experiment. Where applicable, minimum significant differences are indicated at both 5 per cent. and 1 per cent. levels of significance. For stem and inflorescence dry weights, logarithmic transformations were used, and appropriate minimum significant differences can be read from the inset diagrams. Mean maximum glasshouse temperatures and mean hours of bright sunshine are shown for the four harvest intervals.

ratio of leaf weight to total plant weight). For the present experiment, leaf weight ratios are presented as part of Figure 2. At any one time, the ratio is considerably higher for rye than for barley. That transpiration ratios are higher for rye than for barley may therefore be ascribed to the fact that rye is a more leafy plant than barley.

The reductions in transpiration ratio with low-water treatment are brought about primarily by the reductions in transpiration rate per unit weight of leaf, though the extent of the reductions is modified by the other factors. The growth factor is virtually identical for the low- and high-water treatments of barley, but in rye it would tend to give a higher transpiration ratio with low-

TABLE 3

TOTAL DRY WEIGHT (G PER POT) IN BARLEY AND RYE SUBJECTED TO HIGH- AND LOW-WATER TREATMENTS

Harvest	High Water		Low Water	
	Mean	S.E.	Mean	S.E.
Barley				
1	35.54	1.254	22.94	0.791
2	62.28	1.595	38.34	0.783
3	83.42	1.170	46.99	1.042
4	99.44	2.259	56.32	0.720
5	106.87	1.638	62.25	1.382
Rye				
1	22.24	0.778	18.19	0.482
2	40.15	1.555	32.71	1.134
3	62.70	2.416	43.05	1.570
4	78.62	1.364	51.89	1.258
5	91.75	2.620	58.92	0.868

than with high-water treatment. The effect of treatment on leaf weight ratio in both plants is also such that the transpiration ratio would tend to be increased with low-water treatment. This effect, however, is very much greater for barley than for rye, and it is for this reason that the transpiration ratio is less reduced by low-water treatment in barley.

The importance of leafiness, as measured by the leaf weight ratio, as a factor in water usage is worth stressing. These data show two apparent anomalies. Rye, the more drought-resistant species, is more leafy than barley, and low-water treatment gives a more- and not a less-leafy plant than high-water treatment.

(d) Dry Weight

The dry weight data for the whole plant and for leaves, stems, roots, and inflorescences are presented in a number of ways in Figures 2 and 3. Only total dry weights are presented in tabular form (Table 3), these being basic to the whole experiment. Records of water loss from individual pots had been kept,

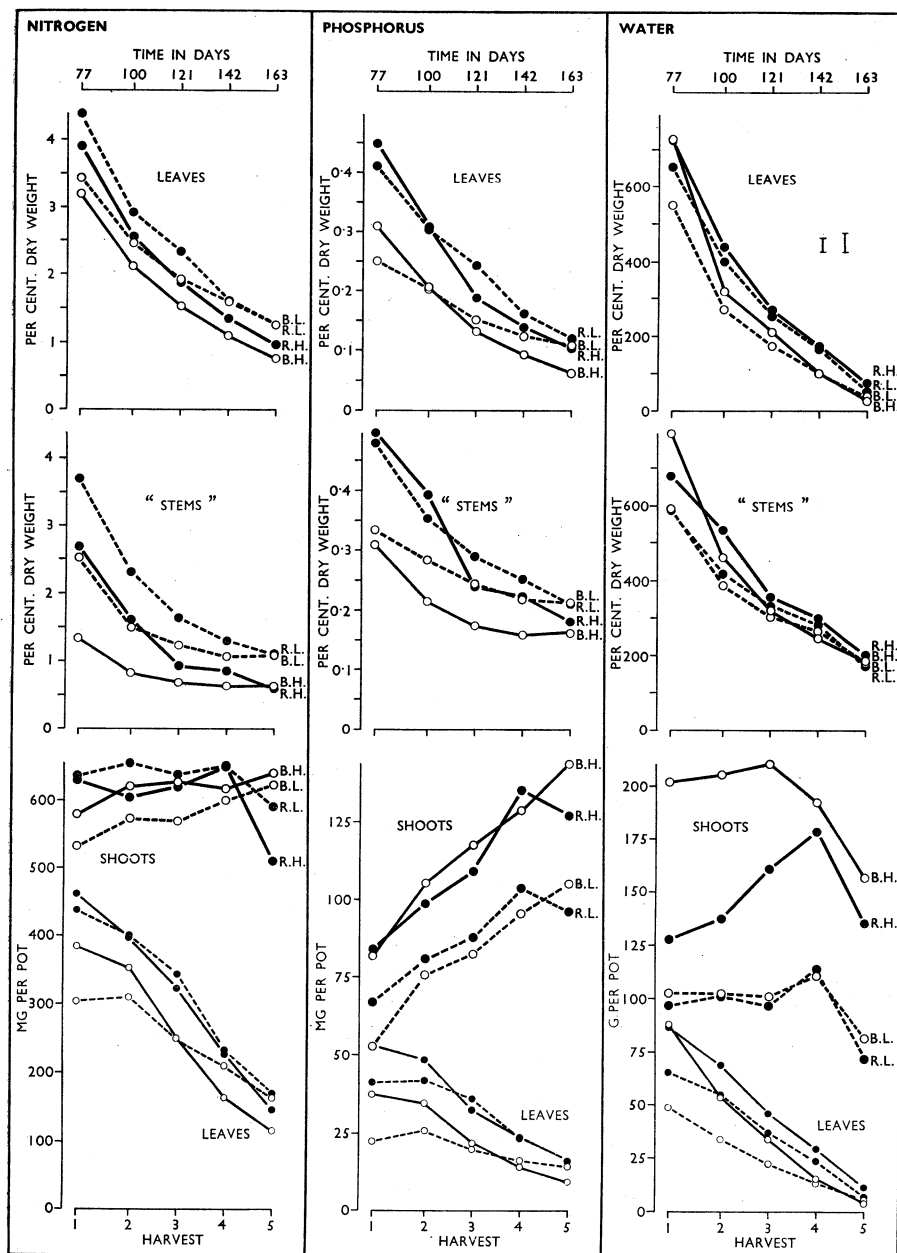


Fig. 4.—Relative and absolute contents of nitrogen, phosphorus, and water in the above-ground parts of barley and rye, as affected by low- and high-water treatments. In this and the succeeding figures, "stems" include the true stems, leaf sheaths, and, when present, inflorescences as well. To aid in distinguishing the absolute data for leaves and shoots, treatment initials have been omitted from the leaf curves.

and it was found possible to use these as ratings for the improvement of the accuracy of mean dry weights (see McIntyre and Williams 1949). The growth curves for the control plants show that vegetative growth was well advanced at harvest 1, the points of inflexion being in the vicinity of harvests 1 and 2 for barley and rye respectively. Leaf and root growth (Fig. 3) were approaching their maxima early in the experiment, and stem growth tends to dominate the picture. Barley has a very much larger inflorescence than rye.

Yield reductions due to low-water treatment were highly significant at all harvests and for both species; even the relatively small effects on rye at harvests 1 and 2 are significant at the 1 per cent. level. Sooner or later the low-water treatment reduced the yields of all plant parts, but the severity of the effect was conditioned by the stage of development of those parts and by the specific differences mentioned above. Stems were more severely affected than leaves, and the inflorescence of barley was more severely affected than that of rye. The effect on root growth was greater than might have been expected from their stage of development at time of treatment, and this effect will be re-examined when considering the weight ratios. The marginal diagrams of Figure 2 present a pictorial version of the distribution of dry matter between leaves, roots, stems, and inflorescences. The upper four diagrams are built up from the absolute weight, and the lower four from the weight ratios.

(e) *Weight Ratios*

The possession of a relatively large root system is a recognized character of many drought-resistant plants, and it has also been claimed (see Miller 1938 for references) that a typical response of plants to low-water treatment is an increased ratio of roots to shoots. By contrast, the *immediate* effect of low-water treatment in this experiment is to give a significantly smaller root weight ratio with both rye and barley. In barley, however, this effect is reversed after the second period of water shortage, and remains so for the rest of the experiment. In rye, the more drought-resistant plant, the root weight ratio is *reduced* at all five harvests, and significantly so for the first three. A difference between rye and barley which may be relevant here is that, for the controls, the root weight ratio rises to a maximum at harvest 2 in rye, but seems to have passed it already by harvest 1 in barley.

Further differences between barley and rye are shown in leaf and stem weight ratios, high initial leaf weight ratios being balanced by low stem weight ratios in rye. These differences and the subsequent trends in these ratios would seem to be expressions of a delayed developmental pattern in rye. This is also reflected, at least in the controls, in a delayed development of the smaller inflorescence of rye.

Specific differences in response to low-water treatment are also found in leaf and stem weight ratios. Initially both ratios are increased in rye, but significantly so only for the stems. For barley, the initial increase in leaf weight ratio is highly significant, but there is no effect on the stem weight ratio. Examination of the subsequent trends in these ratios suggests that there may

be no essential difference in the pattern of response to low-water treatment, however, and the initial differences could well be associated with the more

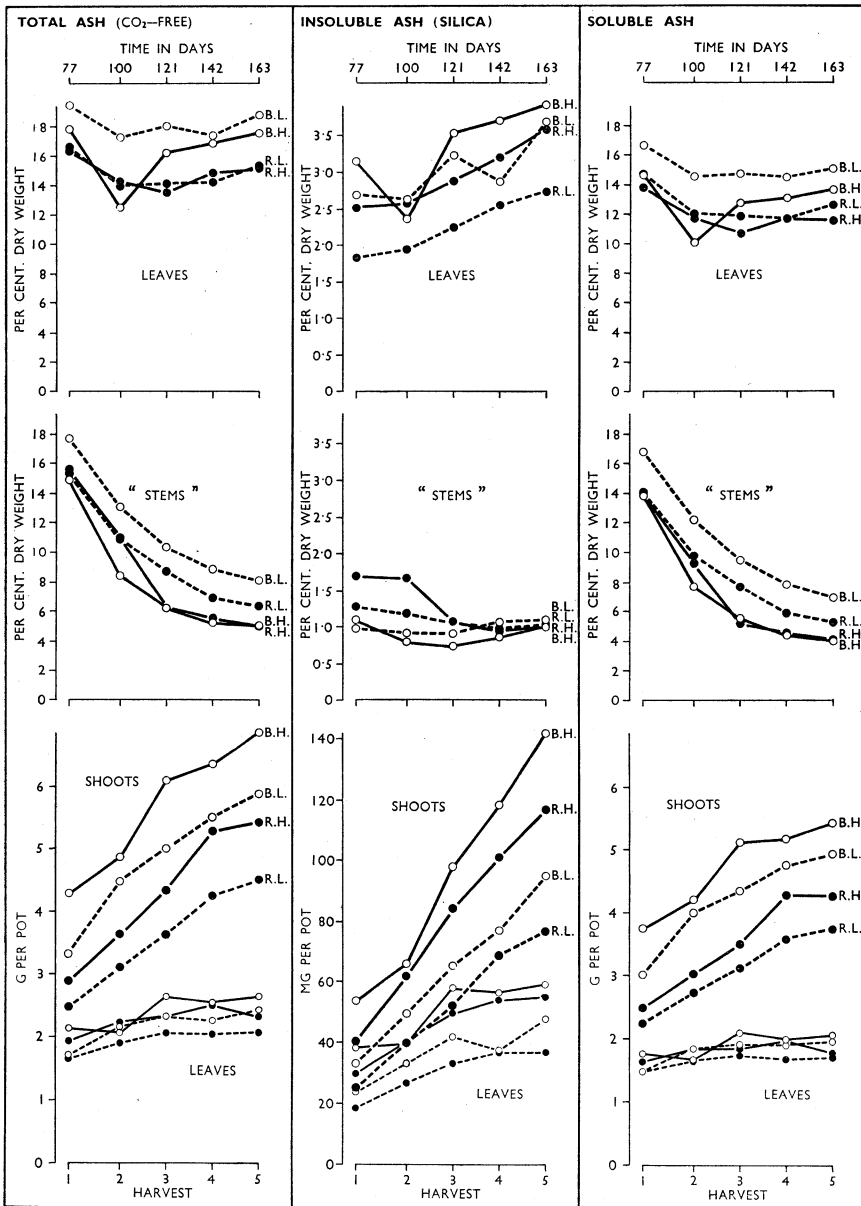


Fig. 5.—Relative and absolute contents of total, insoluble, and soluble ash in the above-ground parts of barley and rye, as affected by low- and high-water treatments.

severe treatment suffered by barley. On the other hand, there remains the curious fact that stem height was quite unaffected by low-water treatment in

rye, but was considerably reduced in barley. Cell elongation was presumably quite unaffected, at least in the primary shoots of rye, by low-water treatment. The number of tillers producing mature heads was considerably reduced by treatment in both barley and rye.

The inflorescence weight ratio was considerably reduced by low-water treatment in barley, but not at all in rye. This fact attests for the drought resistance of rye, and is a result which can scarcely be referred to any difference in severity of treatment. Indeed, rye suffered rather more than did barley during interval 3-4, at which time the inflorescences were growing rapidly. This specific difference in response is well brought out in the four diagrams at the foot of Figure 2.

(f) *Growth Analysis*

Growth rate indices for the experiment are presented in the right-hand panel of Figure 3, and include the relative growth rate R , and net assimilation rates, E_W and E_N , which are based on leaf weight and leaf nitrogen respectively. Mean maximum temperatures for the glasshouse, and mean daily hours of bright sunlight are given for the four harvest intervals, and a soil-water diagram (barley, low water) is repeated at the foot of the page.

No provision was made in this experiment for an initial harvest prior to the first period of treatment. This means that we have no estimate of the effect of this period on the growth indices. However, the much greater reduction in yield in barley at harvest 1 implies a greater reduction in R for this species by low-water treatment. More interest attaches to the values of E_W and E_N , than to those of R , for only in the former can one expect to find any reasonably direct effects of treatment. Moreover, Williams (1946) found that leaf protein was more adequate than leaf weight as an index of the "internal factor" for growth, so that E_N might be expected to be the best available growth index. For the high-water treatment the rising trends in E_N tend to reflect the rising trends in temperature and light; also the depressions in E_N due to low-water treatment follow the severity indices of Table 1 reasonably well. It is a curious fact that E_N tends to be lower for rye than for barley.

The significance of treatment effects can be tested in E_W but not in E_N , and it can be shown that E_W was significantly depressed by low-water treatment for intervals 1-2 and 2-3 in barley, and for interval 2-3 in rye. E_W values tend to converge for later intervals, but there seems no reason to doubt the reality of treatment effects on E_N for intervals 3-4 and 4-5, despite the fact that the significances cannot be assessed.

(g) *Plant Composition and Nutrient Intake*

(i) *General*.—Because of their voluminous character, the data relating to plant composition are presented only in graphical form, but a limited number of sets of numerical data will be available on application to the authors. Statistical treatment is not possible because the material from the five replicates of each harvest class was bulked; however, the sets of data are sufficiently consistent within themselves to justify full discussion of many of the effects.

The data are to be found in Figures 4-7, each figure presenting in columns the values for three distinct plant constituents. At the top of the column in

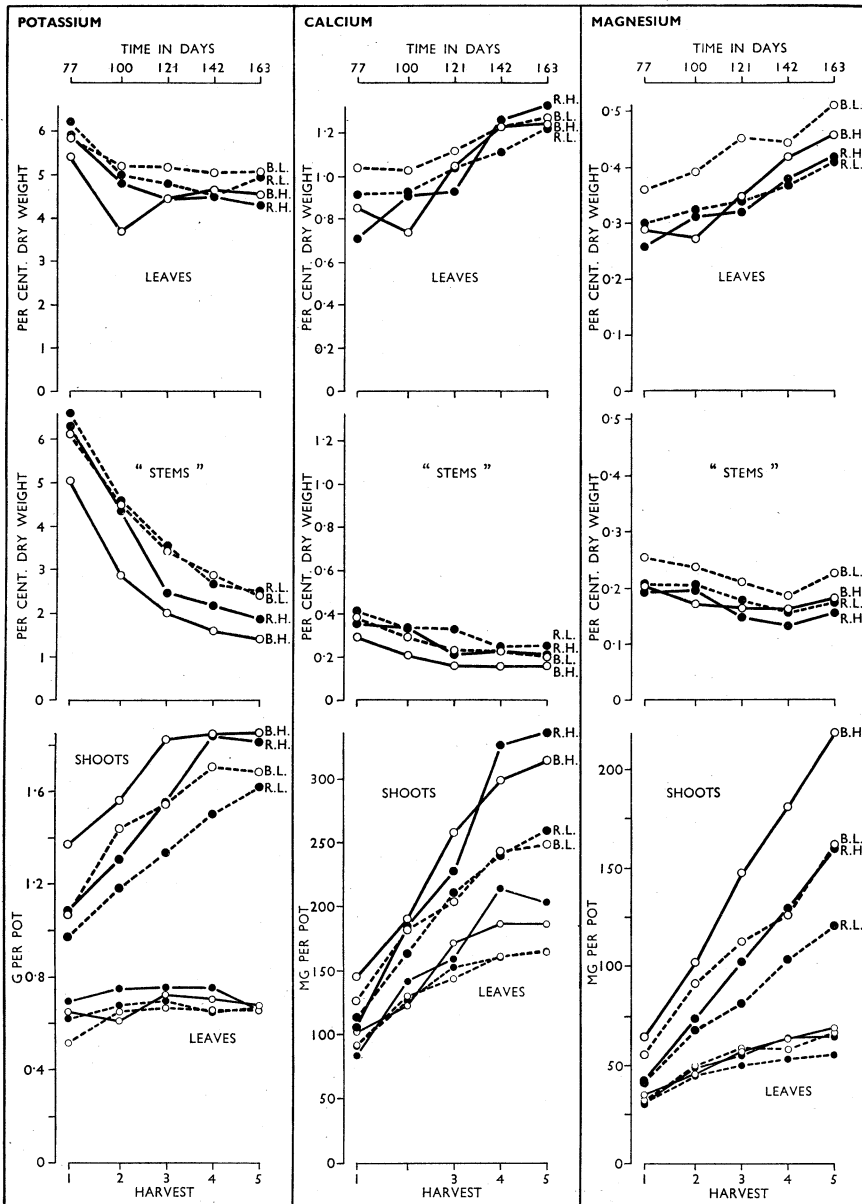


Fig. 6.—Relative and absolute contents of potassium, calcium, and magnesium in the above-ground parts of barley and rye, as affected by low- and high-water treatments.

each case are relative contents for the leaves; then follow relative contents for the "stems". The absolute data are together at the bottom of each column.

It should be remembered that the "stem" fraction of Figures 4-7 includes the inflorescences, the leaf sheaths, and the true stems.

No chemical estimations were made on the roots, so the nearest approach to intake figures is given by the absolute data for the shoots (leaves plus "stems"). Absolute values for the leaves are on the same scale as the shoots, so that "stem" values can be stepped off by difference should these be desired. In most cases there is no confusion between the absolute data for leaves and shoots, but in others the two sets overlap to some extent (especially for sodium, and acid-insoluble ash). Treatment curves are drawn more heavily for the shoots, and treatment initials are included for these but not for the leaf curves.

Nitrogen, phosphorus, and water are presented together in Figure 4 because of several similarities in their trends. Figure 5 presents the trends for total ash, soluble ash, and silica. The first two, which are presented on the same scales, are given for the sake of completeness, though they have little physiological significance. The cations potassium, calcium, and magnesium are together in Figure 6, and possess obvious similarities of trend and treatment effect. Sodium and chlorine also have trends which are linked in a distinctive way (Fig. 7), and manganese is placed with them because sodium and manganese show varying degrees of selective absorption by the plant species under comparison.

In considering the effects of low-water treatment on nutrient intake and relative content, it is necessary to take note of the intake trends for the control series. Nitrogen intake had already ceased in both barley and rye at the time of the first harvest (day 77), but intake was continuous throughout the experiment for silica, magnesium, and possibly also for manganese (data for harvest 5 not available). Shoot intake was also fairly continuous for phosphorus, calcium, sodium, and chlorine. The rate of intake tended to be relatively slower in this group, and there were minor differences between species. Potassium intake ceased rather early in barley but later in rye. Absolute water had attained its maximum at harvest 1 in barley, but rose slowly to harvest 4 in rye.

(ii) *Nitrogen* (Fig. 4).—The relative content of this element for the controls was consistently greater for rye than for barley in the leaves, and in the "stems" it was at first very much greater, but it reduced to equality by harvest 5. These interspecific differences resulted largely from the differences in growth pattern already noted, for the same absolute amount of nitrogen would necessarily be at a higher concentration at any one time in the tissues of the smaller rye plants. Similar considerations apply to the effect of low-water treatment in increasing the nitrogen content of the tissues of both plants, and there is nothing very unexpected in the results.

The absolute data show, however, that the low-water treatment had somewhat delayed the intake of nitrogen by the shoots of barley, and this effect was at first confined to the leaves. That such an effect was slight in the leaves and absent in the shoots of rye, may simply be a reflection of the less severe drought period experienced by rye prior to harvest 1.

There seems, however, to have been a tendency for nitrogen to be excluded from the leaves and to accumulate in the "stems" as a result of wilting,

even though the water content was equally depressed in leaves and "stems" after the soil water had been restored to field capacity prior to harvest 1. It

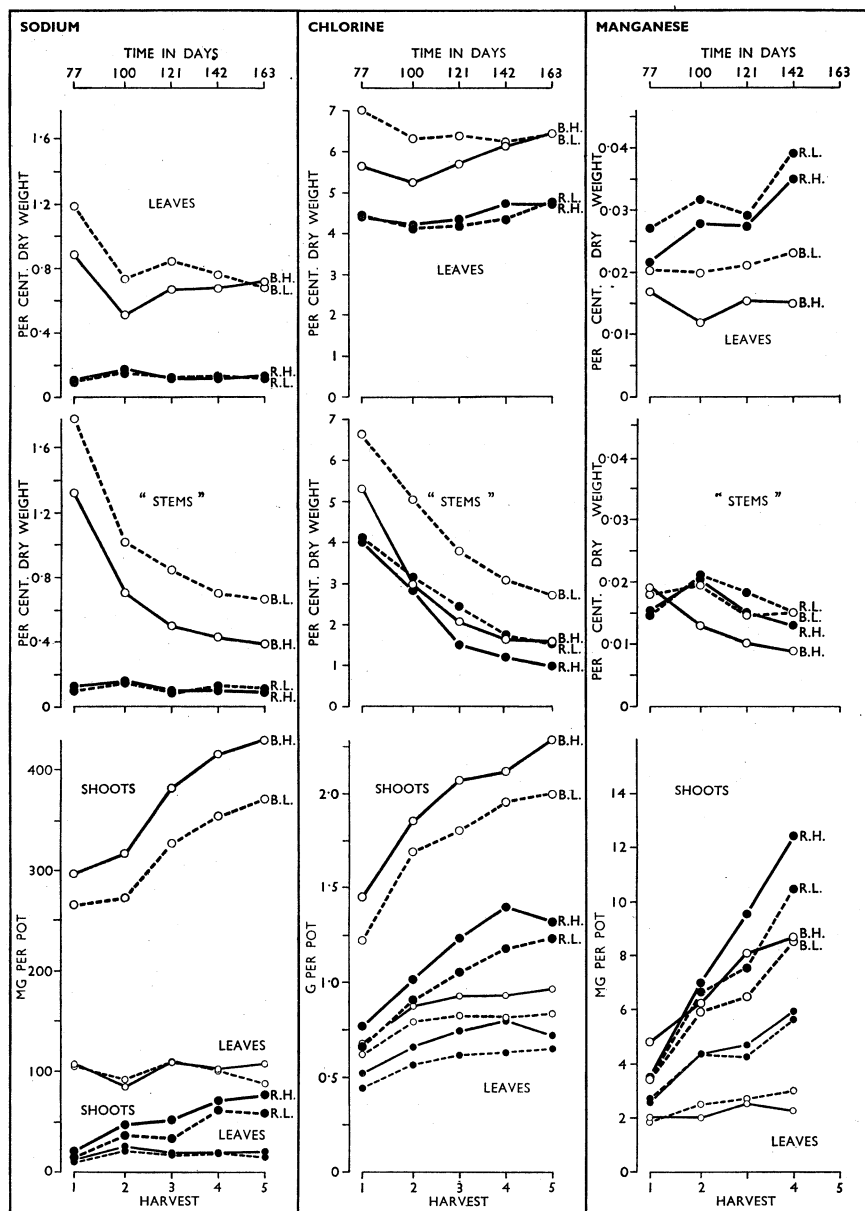


Fig. 7.—Relative and absolute contents of sodium, chlorine, and manganese in the above-ground parts of barley and rye, as affected by low- and high-water treatments.

does not follow that leaf and "stem" water contents were equally depressed during the actual period of wilting, and a fuller understanding of this effect

on nitrogen intake and distribution within the plant calls for a detailed examination of the course of events during the wilting period.

(iii) *Phosphorus* (Fig. 4).—Relative contents of phosphorus for the controls show remarkably similar time trends to those of nitrogen, but early effects of low-water treatment were very different. Instead of an increase there was an initial decrease in the leaf-phosphorus content of both species, and instead of the very big increases in “stem”-nitrogen content there was little initial effect of treatment on “stem” phosphorus. The absolute data show that phosphorus intake by the shoots was considerably reduced by low-water treatment, the greatest effect being in the leaves. The magnitude of this effect is worth stressing. Thus the leaf values, when expressed as a percentage of the control values, are 60 per cent. for barley and 77 per cent. for rye. The corresponding values for nitrogen are 79 per cent. and 95 per cent. respectively.

Nitrogen and phosphorus moved out of the leaves into the “stem” fraction at an increasing rate during the course of the experiment. No such movement of the cations or of chlorine or silica was observed in this experiment.

(iv) *Potassium, Calcium, and Magnesium* (Fig. 6).—Treatment effects on relative content of these three cations are so similar that they may be treated together. However, there are the important differences in intake trends already mentioned for the control series. Thus more than half of the potassium had been accumulated prior to the first harvest by both species, but little more than a quarter of the magnesium had been accumulated in the same period. Calcium is intermediate in this respect. These differences naturally affect the time trends of relative content. Leaf content remained fairly constant for potassium, but rose with time for calcium and magnesium. Potassium content fell rapidly from high initial values in the “stems”. Initial “stem” values for calcium and magnesium, however, were lower than their corresponding leaf values and, though the “stem” values fell at first, they either levelled off or tended to rise during maturation. Similar differences between time trends in potassium and calcium were attributed by Petrie (1934) to the low mobility of calcium and its continued fixation in the tissues. The movement of magnesium within the plant would seem to be governed by similar considerations to those for calcium, though less is known about the forms in which magnesium is chemically fixed in the tissues.

The relative contents of all three cations are consistently increased by low-water treatment in both leaves and stems of barley. Such effects are much less pronounced and somewhat erratic in rye, a difference which may well be due to the difference in severity of treatment. Effects of time and treatment on cation balance (including sodium) will be considered in the discussion.

(v) *Silicon* (Fig. 5).—The element silicon is believed to be absorbed as the silicate ion and to be dehydrated to silica at the cuticular surfaces of the grasses. In the present experiment the time trends of its relative and absolute content are similar to those for magnesium and calcium, but the effects of low-water treatment are quite different. The immediate effect of treatment is a

reduction in the relative content of silica in the tissues, an effect which has a parallel only in the case of phosphorus (Fig. 4). The effect on silica content is erratic in barley but pronounced in rye. It disappears in the "stems" but remains in the leaves of rye as the plants mature.

In view of the very different fates of phosphorus and silicon within the plant, it is difficult to visualize an internal factor which might link these effects. It is perhaps more likely that the low-water treatment reduces the availability of silicate and phosphate ions in the soil, or affects the permeability of the roots with respect to these ions.

(vi) *Sodium and Chlorine* (Fig. 7).—The data for these two elements have many features in common, but the outstanding fact is the strong evidence of selective absorption of sodium as between species. Perhaps the best basis of comparison is that of equivalent percentages (Table 10), from which it will be seen that, at harvest 1, the sodium value is nine times greater for barley than it is for rye. This discrepancy diminishes with time but the difference is still large at harvest 5. Put in another way, the leaves of barley always contained more sodium than the whole of the shoots of rye (Fig. 7). The low equivalent percentages for sodium in rye are balanced mainly by increases in the values for potassium and to a lesser extent by increases in calcium.

Collander (1941) has shown that plants vary greatly in their power to absorb sodium ions when grown in solutions of constant composition. The two cereals, oats and maize, which were included in his study, differed fairly consistently in this respect. Equivalent percentages for sodium were always higher in oats than in maize—in one case nearly seven times higher—but even those for oats were much lower than those reported here for barley.

The relative contents of sodium change rather little with time in rye but fall markedly, especially for the "stems", in barley. The effects of low-water treatment also differ between species, for the relative contents are increased in barley but are little affected in rye.

Time trends and interspecific differences in the relative chlorine contents are very similar to those in sodium for the leaves, but much less so for the "stems". The differences between barley and rye, however, are relatively greater for sodium than for chlorine, and the impression is gained that the chlorine effects follow from and are more or less conditioned by the sodium effects.

(vii) *Manganese* (Fig. 7).—Here again there is evidence of selective absorption, but not to the extent found for sodium. Collander (1941) also found wide variation in his equivalent percentages for this element.

Time trends and treatment effects are similar to those for calcium and magnesium. Rye has taken in relatively more manganese than has barley and this difference tended to widen with time.

(viii) *Water* (Fig. 4).—Water is not usually treated as a plant nutrient, but it is convenient to examine its trends and treatment effects in this place.

The relative water contents show the pronounced downward trends which are to be expected, and the specific and treatment effects are very similar in leaves and "stems".

It is perhaps a little surprising that the very great losses of absolute water from the leaves in all cases did not result in any appreciable loss of potassium from the leaves as predicted by Petrie (1934). The constancy of absolute leaf potassium does not, of course, mean that potassium from old leaves was not re-utilized by younger leaves. This is quite likely, though evidence is lacking in this case.

Watson and Petrie (1940), working with tobacco, found no case in which decrease in absolute leaf-water content preceded net nitrogen export, and this is also true for earlier, less detailed work with gramineous plants by Petrie (1937) and Williams (1938). However, if one may judge from the absolute trends of Figure 4, it does seem possible for the present experiment that net loss of water from the leaves occurred somewhat before net loss of both nitrogen and phosphorus. This may only mean that the nutritional status of the plants was high, so that the demands of developing stems and inflorescences for these nutrients were met to a greater extent from the external medium.

IV. DISCUSSION

(a) *Growth Pattern*

It has often been pointed out that early work on plant response to soil-moisture treatments is of doubtful value because it was based on imperfect knowledge of the physical condition of moisture in soil. This in itself may account for some of the conflicting results which were produced, but confusion has also arisen from a failure to anticipate differences in response traceable to differences in growth pattern of the experimental plants and to the growth stage at which treatment was applied. There has also been a tendency to rely too much on the shoot-root ratio as a single-value index of response to treatment. In what follows, therefore, only those papers which take some account of growth as a factor in response will be considered.

Harris (1914) used nutrient as well as soil-moisture treatments in a study of the ratio of tops to roots in plants. In general, he found this ratio to be decreased by low-water treatment. This result tended to be brought about by a reduction in shoot growth rather than by a direct effect on root growth. In one of his experiments Harris also applied various sequences of low- and high-moisture treatment during three successive stages of growth in wheat. He concluded that his top root ratio was most affected by water treatment during the first of these stages, but his results are difficult to interpret from final yields alone.

Miller and Duley (1925) subjected corn to all possible sequences of "optimum" and "minimum" soil moisture during three successive 30-day periods of growth. Their dry weight data include values for the conclusion of each 30-day period. At the end of the first period, leaf and root weights were greatly reduced, but stem weight was little affected by "minimum" water treatment.

At the end of the second period, "minimum" water during that period also reduced leaf and root weights, but the reduction in stem weight was even greater. At the end of the third period, the main effect of "minimum" water during that period was a reduction in ear weight. There were small but consistent reductions in leaf weight, no effects on stem weight, and a tendency for root weights to be increased. Miller and Duley draw attention to this latter anomaly, but do not attempt an explanation. It is now suggested that where ear development suffers no check, as with "optimum" water, further root growth could have been checked by an intensified competition within the plant for assimilates and mineral nutrients.

It was perhaps to be expected that the application of their "minimum" water treatment at different stages of growth should cause different patterns of response in Miller and Duley's corn plants. A generalization which emerges from the results is that those plant parts which are growing most actively during the period of treatment are those which suffer the greatest check to their growth. The low-water treatments of the present experiments with barley and rye are similar to that of Miller and Duley which received the "minimum" supply during the second and third periods of growth, and the patterns of response are very similar, especially as between barley and corn.

TABLE 4

WEIGHT RATIOS FOR CORN (*ZEA MAYS* L.) AS AFFECTED BY "OPTIMUM" (O) AND "MINIMUM" (M) SOIL-MOISTURE SUPPLY AT THREE SUCCESSIVE 30-DAY PERIODS OF GROWTH*

Weight Ratio	Period 1		Period 2		Period 3	
	O—	M—	—O—	—M—	—O—	—M—
Leaf	0.305	0.341	0.291	0.356	0.306	0.340
Root	0.131	0.137	0.139	0.128	0.114	0.154
Stem	0.263	0.288	0.285	0.266	0.246	0.305
Ear	0.301	0.234	0.285	0.250	0.334	0.201

* Computed from the primary data of Miller and Duley (1925).

Weight ratios for leaf, root, stem, and ear can be calculated from Miller and Duley's data and, since treatment effects are consistent within periods, it is appropriate to present the results (Table 4) as general means at final harvest. Irrespective of when it was applied, "minimum" supply always reduced the ear weight ratio. The effect was greatest for period 3 when the grain was filling, and least for period 2. It is probable that floral initiation took place towards the end of the first period, and the large effect of "minimum" water during this period on ear weight ratio at final harvest may be a reflection of a deleterious effect on floral initiation. The leaf weight ratio was always increased by "minimum" water treatment, but the greatest effect was produced when this was applied during the second period. Root and stem weight ratios were increased

by "minimum" water in the first and third periods but tended to be decreased by this treatment in the second period.

Many of these effects of treatment on the weight ratios of corn (Table 4) are no more than indirect consequences of the fact that those plant parts which are growing most actively at the time suffer the greatest check to their growth. Thus if stem growth is checked severely, leaf and root weight ratios will tend to retain the high values characteristic of the early growth of many plants. It is possible, however, that changes in weight ratios could arise more directly from the action of drought on morphogenetic processes. Indeed, Maximov (1941) has stressed the importance of such effects, particularly those which lead to the formation of the reproductive organs, and quotes at length the findings of Lobov (unpublished data 1939) on the effects of drought on the formation of the spike in wheat. At each successive stage in the development of the spike, drought has its characteristic effect, and this is often not noticeable until long after the drought is over.

TABLE 5

DRY WEIGHT INCREMENTS AND INDICES OF DISTRIBUTION BETWEEN THE LEAVES, ROOTS, STEMS, AND INFLORESCENCES OF FLAX (*LINUM USITATISSIMUM* L.)*

Treatment Interval	Interval (days from sowing)	Water Treat- ment	Total Increment (mg)	Leaves (%)	Roots (%)	Stems (%)	Inflor- escences (%)
Before treatment	64-85	High	212	15	6	79	—
	85-98	High	260	11	5	84	—
First interval of treatment	98-118	High	398	2	1	83	14
	98-118	Low	201	3	-2	82	17
Second interval of treatment	118-136	High	426	-4	4	54	46
	118-136	Low	160	-5	6	56	43

* Computed from the primary data of Tiver (1942).

In the remaining papers to be examined, the level of experimental accuracy permits a more detailed analysis of plant response, and, to this end, distribution indices were computed (Tables 5-9) for relevant harvest intervals of the experiments. Distribution indices are obtained by expressing the increments in dry weight of leaves, roots, stems, etc. for each interval as percentages of the total dry weight increment for that interval. Where such indices are available for a succession of harvests they give quantitative expression to the changing growth pattern, and to the effects of treatment on this pattern. Of special interest is the comparison of indices for the period immediately following the application of low-water treatment.

Tiver (1942) and Tiver and Williams (1943) made parallel studies of growth and development in flax and linseed, and applied a low-water treatment

after flowering. Dry weight increments and indices of distribution are given for flax in Table 5 and for linseed in Table 6. The differences in growth pattern to which Tiver and Williams drew attention are well illustrated by the distribution indices of these tables. Thus, at the time of the first interval of treatment, leaf and root growth had virtually ceased in flax and more than 80 per cent. of the dry matter was going to the stems. With linseed, on the other hand, nearly 30 per cent. was still going to the leaves. The important point for our present purpose, however, is that the low-water treatment had no effect on the distribution indices. It is true that treatment had a rather small effect on the dry weight increment of linseed, but the effect was large for flax. During the second interval of treatment the growth increment was severely reduced in both plants by low-water treatment, yet only in linseed were there any effects on the indices of distribution. Here there were reductions in root and stem indices and rather a large increase in the inflorescence index. The picture gained from the above analysis of weight change and distribution is very dif-

TABLE 6
DRY WEIGHT INCREMENTS AND INDICES OF DISTRIBUTION BETWEEN THE LEAVES, ROOTS, STEMS, AND INFLORESCENCES OF LINSEED (*LINUM USITATISSIMUM* L.)*

Treatment Interval	Interval (days from sowing)	Water Treat- ment	Total Increment (mg)	Leaves (%)	Roots (%)	Stems (%)	Inflor- escences (%)
Before treatment	64-85	High	322	32	13	55	—
	85-98	High	400	23	21	56	—
First interval of treatment	98-115	High	559	27	1	64	8
	98-115	Low	429	28	-1	65	8
Second interval of treat- ment	115-140	High	1267	-3	16	25	62
	115-140	Low	510	-7	10	12	85

* Computed from the primary data of Tiver and Williams (1943).

ferent from that which might be drawn from the weight ratios in these cases (Tiver and Williams 1943, Table 2, p. 202), for it has been shown for both flax and linseed that low-water treatment *reduces* the inflorescence weight ratio and increases the leaf weight ratio. Once again the effects of treatment on these weight ratios must be interpreted as indirect consequences of the growth pattern of the plant and the time of application of treatment. It would be wrong in this case to infer that the inflorescence got less than its share of assimilates as a result of low-water treatment. In the case of linseed, there is even a suggestion that the inflorescence got more than its share with this treatment.

Petrie and Arthur (1943) subjected tobacco plants to a number of water treatments, and the dry weight increment and distribution values of Table 7 were derived from their data. The tobacco seedlings were transplanted on day

51 and differential watering for the low-water series commenced on day 58. In addition, there were early- and late-temporary-drought treatments. In the first of these (E.D.), differential watering began on day 74 and ended on day 81. The late-drought treatment (L.D.) was begun on day 100 and ended on day 112. The pattern of growth for tobacco is well shown by the distribution indices of the high-water treatment. During the course of the experiment the leaf index fell from 83 to 19, the root index rose from 6 to 34, and the stem index rose from 11 to 47. These changes are associated, at least in part, with the incidence of secondary thickening in roots and stems.

TABLE 7
DRY WEIGHT INCREMENTS AND INDICES OF DISTRIBUTION BETWEEN THE LEAVES, ROOTS,
AND STEMS OF TOBACCO (*NICOTIANA TABACUM* L.)*

Treatment Interval	Interval (days from sowing)	Water Treat- ment	Total Increment (g)	Leaves (%)	Roots (%)	Stems (%)
Before treatment	34-41	High	0.047	83	6	11
	41-49	High	0.191	72	4	24
First interval of treatment	49-73	High	7.30	67	13	20
	49-73	Low	3.09	68	12	20
Second interval of treatment	73-85	High	16.41	51	14	35
	73-85	Low	6.04	39	32	29
	73-85	E.D.	14.12	50	17	33
Third interval of treatment	85-99	High	33.6	40	16	44
	85-99	Low	8.2	55	10	35
	85-99	E.D.	32.5	39	15	46
Fourth interval of treatment	99-118†	High	39.8	44	16	40
	99-118†	Low	29.1	48	19	33
	99-118†	L.D.	26.3	32	14	54
Fifth interval of treatment	118†-146†	High	19.9	19	34	47
	118†-146†	Low	16.6	28	25	47
	118†-146†	L.D.	29.8	42	30	28

* Compiled from the original records of an experiment described by Petrie and Arthur (1943).

† Harvesting took more than one day on these occasions.

During the first interval of treatment the dry weight increment was greatly reduced by low-water treatment, but again there was no effect of treatment on the distribution indices. The increments for the second and third intervals of treatment, however, show that the low-water treatment became very severe, so it is not surprising that treatment effects began to appear in the distribution indices as well. The effects are complex and difficult to interpret: the stem index tends always to be depressed by low-water treatment (height growth was

greatly reduced); the leaf index was at first depressed and then increased by treatment; and the root index was much increased and then tended to be depressed by treatment.

The effects of the E.D. treatment (second and third intervals) on dry weight increment are very slight, and it had no effects on the distribution indices. The L.D. treatment (fourth interval), however, had an immediate effect both on the increment and the indices. The leaf index was depressed, the stem index increased, and the root index little affected by treatment. For the final interval, when high-water supply had been restored to the L.D. treatment, these effects were reversed.

TABLE 8

DRY WEIGHT INCREMENTS AND INDICES OF DISTRIBUTION BETWEEN THE LEAVES, ROOTS, AND STEMS OF BARLEY (*HORDEUM VULGARE* L.) AND RYE (*SECALE CEREALE* L.)

Treatment Interval	Interval (days from sowing)	Water Treat- ment	Total Increment (g)	Leaves (%)	Roots (%)	Stems (%)
Barley						
Before harvest 1*	0-77	High	35.5	34	25	41
	0-77	Low	22.9	39	22	39
Second	77-100	High	26.7	18	9	73
	77-100	Low	15.4	24	21	55
Third	100-121	High	21.1	-1	4	97
	100-121	Low	8.7	4	-7	103
Rye						
Before harvest 1*	0-77	High	22.2	50	25	25
	0-77	Low	18.2	52	20	28
Second	77-100	High	17.9	25	31	44
	77-100	Low	14.5	28	29	43
Third	100-121	High	22.6	6	14	80
	100-121	Low	10.3	12	4	84

* Including first interval of treatment.

The data of the present experiment with barley and rye will now be re-examined, and the dry weight increment and distribution indices are to be found in Table 8. Unfortunately, no harvest was taken at the beginning of the low-water treatment, so the values for the period before harvest 1 cannot be taken as a measure of the immediate effect of low-water treatment on dry matter distribution. The distribution indices for this period (0-77 days) are equivalent to weight ratios at harvest 1, and the treatment effects on these ratios are sufficiently small to make it entirely possible that there were no immediate effects of low-water treatment on the distribution indices. With barley for the second interval of treatment, the stem index was greatly depressed, and the indices for roots and leaves were increased by treatment. No such effects were

found with rye for the same interval, and, even admitting that the low-water treatment was less severe for rye, the continued absence of any treatment effect on the stem index during the third interval, does suggest that stem growth in rye was less susceptible to limitation by low-water treatment than it was in barley. Stem height was in fact unaffected by treatment in rye, but was considerably reduced in barley.

TABLE 9

DRY WEIGHT INCREMENTS AND INDICES OF DISTRIBUTION BETWEEN THE LAMINAE, PETIOLES, ROOTS, AND STEMS OF TOMATO (*LYCOPERSICON ESCULENTUM* MILL.)*

Treatment Interval	Interval (days from sowing)	Water Treatment	Total Incre- ment (g)	Laminae (%)	Petioles (%)	Roots (%)	Stems (%)
First experiment							
Before treatment	38-42	Control	1.20	43	18	13	25
During treatment	42-48	Control	2.43	39	20	13	28
	42-48	Moderate	1.86	31	21	11	37
	42-48	Severe	1.17	28	23	12	37
After treatment	48-55	Control	4.18	30	18	13	39
	48-55	Moderate	3.25	36	16	17	31
	48-55	Severe	2.88	39	17	17	28
Second experiment							
Before treatment	36-40	Control	1.23	40	24	14	22
During treatment	40-48	Control	4.84	41	23	10	26
	40-48	Moderate	3.72	36	23	11	30
	40-48	Severe	2.37	33	24	11	32
After treatment	48-56	Control	5.72	27	21	16	36
	48-56	Moderate	4.45	32	19	14	35
	48-56	Severe	3.72	37	19	15	29

* Computed from the primary data of Gates (1955a).

Gates (1955a, 1955b) has made a careful and detailed study of the effects of wilting treatments of short duration on the growth response of young tomato plants. The wilting treatments were at a moderate and a severe level, but, even at the severe level, soil water did not go below the permanent wilting percentage. From an examination of growth rate and weight ratio data for two closely parallel experiments, Gates concluded that his treatment effects could be summarized as a tendency towards senescence during wilting and a return to a more juvenile condition upon re-watering. For purposes of comparison, these data have been presented as dry weight increments and distribution indices in Table 9. The single day recovery period (day 48-49) was too short to give accurate distribution values, and was united with the following period of each experiment.

From the control values it will be seen that, during the rather brief period considered, the lamina index falls, the stem index rises, and the root and petiole indices change very little. Similarly, only the lamina and stem indices are appreciably affected by the wilting treatments. During wilting, lamina indices were depressed and stem indices were increased, and these effects were reversed during recovery after wilting. Gates found that the pattern of translocation between plant parts had been modified by treatment. Translocation to the upper (younger) laminae was impaired but was continued to the stem, and, upon re-watering, the normal course of translocation was quickly resumed. However, it is not possible from the evidence to judge to what extent the translocation of the wilting period was contributed to by the movement to the stems of breakdown products of hydrolysis in the older laminae. In the overall picture these effects of treatment on translocation tend to cancel out, as seems also to be the case with the L.D. treatment of the tobacco experiment (Table 7).

Taking the evidence as a whole, it is remarkable that there are so many cases in which the immediate effects of low-water treatment on the distribution of dry matter between leaves, roots, and stems are quite small. This could mean that the growth of all rapidly-growing regions tends to be equally inhibited by water stress within the plant, and this interpretation would be in keeping with the claim of Maximov (1941) that drought retards the utilization of carbohydrates (in growth) more than it retards the production of them. If it were otherwise, one might expect that the roots, being furthest from the supply, would tend to get less than their proportionate share of the dry matter produced with low-water supply. This does not seem to be the case, except perhaps at a later stage in rye.

In the light of the foregoing analysis of dry weight increments and distribution indices we may now re-examine the significance of the low-water effects on root weight ratios. It was said earlier that an increased ratio of roots to shoots was more or less accepted as a typical response of plants to low-water treatment. This is not always true and must now be modified. It has been shown that such a response can be brought about as an indirect consequence when the root weight ratio is falling at the time of application of treatment. If, as was certainly the case with rye in the present experiment (Fig. 3), this ratio was rising at the time, the result would be a *decrease* in the root weight ratio with low-water treatment. Such an effect, however, would not explain the continued depression of the root weight ratio in rye, for this ratio later falls with time in both treatments (after day 100), and another cause must be sought. In this connection, it may well be questioned whether Maximov's claim that drought retards the utilization of carbohydrates more than it retards the production of them is always correct. In rye, a drought-resistant plant, the distribution indices for the second and third intervals of treatment (Table 8) indicate that leaf growth is favoured, stem growth is little affected, and root growth becomes adversely affected by continued low-water treatment. While this evidence needs confirmation and is too indirect to be used with any confidence, it could mean for this case that the roots, being furthest from the

supply, do in fact get less than their proportionate share of a limited supply of carbohydrates from the leaves. It is suggested, therefore, that the capacity under water stress of juvenile tissues to continue to operate on a restricted supply of carbohydrates may be characteristic of some drought-resistant plants. Such plants would suffer little permanent damage, and would quickly respond to water when it came. Other characteristics of rye which seem to be in keeping with this picture are the absence, in this experiment, of treatment effects on stem height and on inflorescence weight ratio.

(b) Mineral Nutrition

Wadleigh and Richards (1951) have adequately reviewed the literature on the effects of soil-moisture level on the mineral nutrition of plants and they assert that this is dependent on (i) the extent to which growth and, consequently, mineral utilization might be limited by water supply, (ii) the effect of change in thickness of the moisture films on nutrient availability, and (iii) the effect of variation in soil-moisture tension upon microbiological activity. The evidence was such that these authors found some difficulty in making broad generalizations, but they state that decreasing soil-moisture supply is commonly associated with a definite increase in nitrogen content of the plant tissue, a definite decrease in potassium content, and a variable effect upon content of phosphorus, calcium, and magnesium. The first factor of Wadleigh and Richards' analysis seems to have produced fairly pronounced increases of nitrogen, potassium, calcium, magnesium, sodium, chlorine, and manganese content in both leaves and "stems" of barley. This was also the case for nitrogen and possibly manganese in rye, but increases were small or absent for the other elements. These differences in the effects of low-water treatment as between barley and rye are likely to be due in part to the relatively small initial effect of treatment on growth in rye. The depression in yield increased with time, however, and consistent increases in content of potassium, magnesium, and chlorine appeared in the "stem" fraction of rye with low-water treatment. It will be noted that low-water treatment at no time depressed the potassium content of the tissues of either barley or rye, and this in spite of the fact that the soil-water level was reduced well below the permanent wilting percentage in each case.

Treatment responses with respect to phosphorus and silicon contents in barley and rye differ from those in the other elements, and it has already been suggested that the low-water treatment may have reduced the availability of silicate and phosphate ions in the soil. Wadleigh and Richards have attributed the variable effects of water treatment on phosphorus content to differences in fixing power of the soils used by different workers, the implication being that, for soils with a low fixing power, the growth factor will operate to give increases in phosphorus content. The simplest explanation of the reversal in treatment effect on phosphorus content in the present experiment is that the soil factor was dominant as an initial effect but that this was later reversed by the growth factor. Another possibility which should not be overlooked, however, is that water stress in the tissues and particularly in the leaves may ad-

versely affect the synthesis of organic phosphorus compounds or even cause their hydrolysis. Such an effect might increase the inorganic phosphorus content of the roots sufficiently to retard phosphorus intake. Under the conditions of this experiment re-synthesis would be favoured for some time after each watering and, after the initial setback, net utilization of phosphorus could be at a high rate. Inspection of Figure 4 will show that, after harvest 1, the relative rate of intake of phosphorus by the shoots in the low-water treatments was equal to or greater than that in the controls. Williams (1948) has shown that the balance between synthesis and hydrolysis of nucleic acid is rather easily upset by changing internal factors, and it would not be surprising if it were also sensitive to drastic changes in water stress.

Miller and Duley (1925) give relative phosphorus contents of roots, stalks, leaves, and ears for an experiment with corn, concerning which some aspects have already been considered. Treatment effects vary markedly according to the time of application of their "minimum" water treatment and with past history. Before earing, leaf phosphorus was markedly increased by "minimum" water, and, for two of the three possible comparisons, root phosphorus was also greatly increased. Stem phosphorus was slightly decreased by the same treatment. It is difficult to generalize from the results at maturity, and it is suspected that varying degrees of redistribution of phosphorus within the plant during ear development are responsible for the apparent lack of uniformity of response. The case is quite otherwise with nitrogen, potassium, calcium, and magnesium, for the contents of these elements are, with few exceptions, increased by the "minimum" water treatment. In general, the results for corn are very similar to those for barley in the present experiment.

There seems little reason to doubt that the reductions in tissue content of silica with low-water treatment are due to a reduction in availability with treatment.

(c) *Cation Balance*

As values are available for the four major cations present in the tissues it is possible to examine the effects of species, water treatment, and time of harvest on the cation balance of the experimental plants. The data were converted to milliequivalents per pot for the shoots as a whole, and the values of Table 10 are percentages of the totals for sodium, potassium, calcium, and magnesium. The very small values for manganese were not included in the totals, the equivalent percentages for this element being based on the totals for the other four elements.

The differences in relative rates of intake of the five elements (see Figs. 6 and 7) are reflected in the equivalent percentages of Table 10. Thus the values for potassium fall about 10 per cent. on the average, but less in the low- than in the high-water series, and less in barley than in rye. The values for calcium, magnesium, and manganese all rise with time, the greatest increase being for magnesium. The sodium values fall in barley but rise with time in rye.

Attention has already been drawn to the very much smaller equivalent percentages of sodium in rye than in barley. The average values are 3.4 and 19.5 per cent. respectively, the difference being balanced by a reverse effect on potassium, and to a lesser extent on calcium. It seems clear that barley has a much greater capacity than has rye to absorb sodium ions when the two are grown on the same medium. It will also be noted that, at harvest 1, which

TABLE 10
EQUIVALENT PERCENTAGES* OF CATIONS IN THE SHOOTS OF BARLEY AND RYE

Treatment	Harvest	Na (%)	K (%)	Ca (%)	Mg (%)	Mn† (%)
Barley, high water	1	21.3	58.1	11.9	8.7	0.29
	2	19.2	55.8	13.3	11.7	0.32
	3	18.8	52.9	14.6	13.7	0.33
	4	19.0	49.7	15.7	15.6	0.33
	5	18.7	47.5	15.8	18.0	—
Barley, low water	1	23.2	54.9	12.8	9.1	0.25
	2	18.1	56.5	13.9	11.5	0.33
	3	19.4	54.0	14.0	12.6	0.32
	4	18.9	53.5	14.9	12.7	0.38
	5	18.9	50.7	14.7	15.7	—
Rye, high water	1	2.3	74.2	14.1	9.3	0.34
	2	4.0	65.9	18.2	11.9	0.50
	3	3.6	64.3	18.5	13.6	0.56
	4	4.0	61.0	21.2	13.8	0.58
	5	4.2	58.2	21.1	16.5	—
Rye, low water	1	1.8	71.9	16.5	9.8	0.37
	2	3.5	66.4	18.0	12.1	0.53
	3	2.7	64.6	20.0	12.7	0.52
	4	4.3	62.4	19.5	13.8	0.62
	5	3.8	62.0	19.4	14.8	—

* For definition see text.

† Expressed as percentage of totals for other four cations.

immediately follows the first period of the low-water treatment, the equivalent percentage of sodium is slightly increased by treatment in barley, and is appreciably lowered in rye. It is tempting to infer from this rather slender evidence that the selective absorption of sodium is actually increased by low-water treatment, and to wonder whether the low uptake of sodium contributes to the drought resistance of rye. Richards and Shih (1940) using statistical methods were able to predict differences in leaf-water content in terms of the contents of potassium, sodium, calcium, and phosphorus. They found large positive correlations between sodium and water contents and a smaller positive effect of phosphorus. The effects of calcium and potassium were small and rather

complex. This work revealed the hitherto unsuspected importance of sodium as a determinant of tissue succulence in plants but it does not of course supply any information on its effect when the same tissues are subjected to water stress. The concentration of sodium ions in wilted tissues could conceivably produce toxic effects leading to the increase in permeability and the intensification of hydrolytic processes that are postulated by Russian workers (Maximov 1941) as major elements in the physiological effects of drought.

This comparative study stresses the need to take into account both the growth pattern of the experimental plant and the stage at which the drought or low-water treatment is experienced. It is believed that many apparent anomalies in the literature on plant-water relations are due to a failure to recognize the relevance of these points. While the original purpose of this study necessitated an interspecific study, it will be abundantly clear that the comparison of drought-resistant and non-resistant varieties of the same species would have been more helpful for the understanding of drought resistance. Such varieties would not necessarily have the same growth pattern, however, and care would be needed to select examples in which this complication was at a minimum.

V. ACKNOWLEDGMENTS

The authors are indebted to Professor J. A. Prescott, Director, Waite Agricultural Research Institute, for permission to examine and use original records relating to tobacco (see Table 7), and to Mr. C. T. Gates for permission to compile the data of Table 9 from his primary data, and prior to the publication of his work.

VI. REFERENCES

- BALLARD, L. A. T. (1933).—*Aust. J. Exp. Biol. Med. Sci.* 11: 161-76.
BEST, R. J. (1929).—*J. Agric. Sci.* 19: 533-40.
COLLANDER, R. (1941).—*Plant Physiol.* 16: 691-720.
GATES, C. T. (1955a).—*Aust. J. Biol. Sci.* 8: 196-214.
GATES, C. T. (1955b).—*Aust. J. Biol. Sci.* 8: 215-30.
HARRIS, F. S. (1914).—*J. Amer. Soc. Agron.* 6: 65-75.
HERRIOT, R. I. (1947-8).—*J. Dep. Agric. S. Aust.* 51: 319-26.
MCINTYRE, G. A., and WILLIAMS, R. F. (1949).—*Aust. J. Sci. Res. B* 2: 319-45.
MAXIMOV, N. A. (1941).—Collection of papers on plant physiology in memory of K. A. Timiryazev, pp. 299-309. (Acad. Sci. U.S.S.R., Inst. Fiziol. Rast. Timiryazeva.)
MILLER, E. C. (1938).—"Plant Physiology." 2nd Ed. p. 123. (McGraw-Hill Book Co. Inc.: New York.)
MILLER, M. F., and DULEY, F. L. (1925).—*Res. Bull. Mo. Agric. Exp. Sta.* 76: 1-36.
PETRIE, A. H. K. (1934).—*Aust. J. Exp. Biol. Med. Sci.* 12: 99-110.
PETRIE, A. H. K. (1937).—*Aust. J. Exp. Biol. Med. Sci.* 15: 385-404.
PETRIE, A. H. K., and ARTHUR, J. I. (1943).—*Aust. J. Exp. Biol. Med. Sci.* 21: 191-200.
RICHARDS, F. J., and SHIH SHENG-HAN. (1940).—*Ann. Bot. Lond. (N.S.)* 4: 403-26.
SIMS, H. J. (1949).—*J. Dep. Agric. Vict.* 47: 465-72.
TIVER, N. S. (1942).—*Aust. J. Exp. Biol. Med. Sci.* 20: 149-60.
TIVER, N. S., and WILLIAMS, R. F. (1943).—*Aust. J. Exp. Biol. Med. Sci.* 21: 201-9.
WADLEIGH, C. H., and RICHARDS, L. A. (1951).—"Mineral Nutrition of Plants." pp. 411-50. (Ed. Emil Truog.) (University of Wisconsin Press.)

- WAITE AGRICULTURAL RESEARCH INSTITUTE (1938).—Annual Report for 1937-38. pp. 28-9.
(Hassell Press: Adelaide.)
- WATSON, R., and PETRIE, A. H. K. (1940).—*Aust. J. Exp. Biol. Med. Sci.* 18: 313-40.
- WILLIAMS, R. F. (1935).—*Aust. J. Exp. Biol. Med. Sci.* 13: 49-66.
- WILLIAMS, R. F. (1938).—*Aust. J. Exp. Biol. Med. Sci.* 16: 65-83.
- WILLIAMS, R. F. (1946).—*Ann. Bot., Lond. (N.S.)* 10: 41-72.
- WILLIAMS, R. F. (1948).—*Aust. J. Sci. Res. B* 1: 333-61.