

Effects of Temperature and Partial Root Removal on The Relationship Between Root and Shoot Activities in Wheat

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Abstract: Wheat (*Triticum aestivum* L. C. V. Highbury) seedlings were grown in solution culture in a controlled environment with a 14 hour day and 10 hour night regime. The effects of root temperature ranging from 6 to 32°C were investigated, and the optimum root temperature for plant growth was found to be 24°C. The development of shoots and roots followed a thermal time relation. Root appearance started at a lower thermal time than leaves because roots developed earlier. Root-shoot ratio was largest at low and high temperatures with a minimum at the optimum of 24°C. The relationship between relative accumulation rate of nitrogen and relative growth rate of the whole plant was linear.

Both characters were higher in roots than shoots for plants grown at the two lowest temperature (6 and 12°C). The converse was true for plants grown at the two highest temperatures (18 and 24°C). Thus nitrogen appeared to accumulate in the roots of plants grown at low temperatures.

Removing one third of the adventitious, prop roots had no effect on the growth of both shoots and roots, but removing two thirds of these adventitious roots reduced shoot growth significantly especially at root temperatures of 18 and 24°C.

Nitrate nitrogen concentration in shoots and roots and amino nitrogen in shoots were significantly increased as temperature increased. Conversely, concentrations of ammonium and amino nitrogen in roots were significantly decreased as root temperature increased. Total soluble carbohydrates in shoots increased as root temperature increased, but the converse was true in roots. Relative accumulation rate of nitrogen for the whole plant was proportional to the plant relative growth rate.

On the other hand, relative accumulation rates of nitrogen and soluble carbohydrate were greater in the roots of plants grown at low root temperatures. Consequently, low root temperatures of 6 and 12°C markedly reduced the contents of nitrogen fractions (ammonium and amino acid) and soluble carbohydrates in the shoot. This might explain the reason for the reduction in growth of plant shoots at low temperatures.

Additional key words: Wheat, solution culture, temperature, roots, nitrogen.

INTRODUCTION

Temperature exercises profound effects on all physiological activities by differentially influencing the rates of metabolic processes (Steward, 1963). The effect of temperature on the growth of wheat plants illustrates the complexity of the relationships between root and shoot growth. Total growth was found to increase to a maximum as root temperature increased to the optimum. Root growth relative to shoot growth increased as root temperature decreased. Thornley (1972) found that the growth of either root or shoot is totally dependent upon the activities of both root and shoot. Growth depends upon the presence of two substrates, one of which supplies carbon (shoot) and the other nitrogen (roots). The shoot grows as the root supplies nitrogen. When the shoot receives an ample supply it will use most of the products of photosynthesis and little is translocated to the roots. Stele (1969) stated that the proportion of translated carbohydrates and nitrogen is one measure of the relative activities of the two systems, shoots and roots.

The objective of this study was to find out the relationships between the products of root activity (nitrate absorption and reduction and shoot activity (production of carbohydrates) at various root temperatures. This may help to explain why shoot growth is reduced at low root temperature. Previous experiments have shown that low root temperatures affect shoot growth more than root growth, and it is difficult to state which particular factor is responsible for the observed differences in root-shoot ratio. Therefore, in this experiment the root-shoot ratio has been manipulated artificially by partial removal of the adventitious roots.

MATERIALS AND METHODS

Wheat seeds of cv. Highbury were sown in sand which had been previously acid-washed (3% HCl + 1% oxalic acid mixture) for one week, then leached with distilled water until the pH of the leachate was the same as the distilled water and air dried before its use.

Seeding trays were 60 cm long, 30 cm wide and 9 cm deep. The temperature of the sand during germination was in the range 20-21°C. Germination took place on the second day after seeding and by the third day, germination was about 89%. Seedlings were irrigated with distilled water. Four days after seeding, plants of equal size with five seminal roots and one leaf were selected for transplanting. Three plants were transplanted into each plastic jar. Jars used were wide-mouthed, thick-walled, 20 cm, 9 cm in internal diameter, with a capacity of 1200 ml, provided with plastic screw caps.

They were wrapped with aluminium foil, and the caps were painted black to reduce light transmission. Four holes were drilled in each cap, three for the seedlings and one for the aeration tube. Non-absorbent cotton wool was used around the base of the plant stem to support the plants in the holes. Jars were filled with 1200 ml of nutrient solution and placed in water baths on the growth room bench.

The nutrient solution used (Table 1) was almost similar to that of Hoagland and Arnon (1950). Its pH was 5.6. It was checked during the experiment and adjusted with 0.5M HCl or NaOH when necessary.

An air compressor was used to create a flow of air into the nutrient solution in the plastic jars. Air was drawn from the compressor through a polyethylene tube (1.2 cm outer diameter and 0.9 cm bore diameter) and passed into each jar with a piece of polyethylene tubing about 32 cm long (0.8 cm outer diameter and 0.6 cm bore diameter) via a hypodermic needle.

Aeration was almost continuous. The aeration technique served not only as a means of maintaining a high oxygen concentration around the roots, but also as an effective stirring device for mixing the nutrient solution.

The experiments were conducted in the growth room. The average air temperature was about 22°C during the day and 20°C at night; it was measured continuously with a thermograph. The duration of the light period was 14 hours/day with an average light intensity of 0.4 millienstein/m²/sec. The light intensity was measured at the level of the water baths and at the top of the plants with a lambda instruments P.A.R. sensor and a D.C. microvoltmeter. The daily relative humidity recorded by a hydrometer ranged from 50-68% but was mostly around 60%.

Four water baths were used to create the required root temperatures in the experimental work. They were rectangular metal tanks (64 cm long, 30 wide and 21 cm deep) with water maintained at a depth of 16 cm (i.e. the level of the nutrient solution in the jars.). The water was stirred continuously to maintain uniformity of temperature throughout the baths. Two refrigerator units were used to create temperatures lower than 20°C (i.e. growth chamber air temperature). The water baths were randomly arranged on the bench. Temperature in water baths and in plastic jars was checked daily by thermometers.

The nutrient solution was changed once a week, but halfway through the week, the solution lost was made back to its original volume by the addition of distilled water. In both cases, the loss was recorded. The loss of water through evaporation alone, as measured using one jar without plants, was found to be very small.

The first root cutting was made 14 days after transplanting (DAT). One third of the adventitious, prop roots developed were removed from each plant in 4 replicates, and two-thirds were removed another 4 replicates. The remaining 4 replicates were kept as a control. Roots were cut off as close to the point of attachment to the stem as possible by using sharp scissors. Plants were allowed to grow for a further growth period of 10 days before harvesting two replicates at 24 DAT. at 25 DAT, the same process of root cutting was repeated on the remaining replicates and plants were allowed to grow for 10 days further before they were finally harvested (35 DAT).

Soluble carbohydrates were determined in the dry samples according to anthrone method of Fairbairn (1953).

Nitrogen fractions (total-N, $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ and amino-N) were determined in the dry samples according to the method described by Isaac and Johnson (1976).

Statistical analysis was done using the least significant difference (LSD) and Student Newman Keul's multiple range test.

RESULTS AND DISCUSSION

Growth of plant organs:

Control plants showed a normal root system consisting of healthy, thick, branched roots; while the root cutting treatments resulted in plants with very fine, branched roots. Figure 1 shows that removing one-third of the adventitious roots had no effect on the growth of the shoot and roots. However, when two-thirds of the adventitious roots were removed, root growth decreased but not as much as that of the shoots. Shoot growth was significantly reduced by removing two-thirds of the adventitious root system, particularly at the two highest temperatures (18 and 24°C).

Table 1. Composition of the stock nutrient solution used in the study.

a) Macro nutrients

	$\text{NO}_3\text{-N}$	H_2PO_4	K	Ca	Mg	Na	S	Cl
mg/l	10.5	15.5	117	20	24	92	32	35
mM	7.5	0.50	3.0	0.50	1.0	4.0	1.0	1.0

b) Micro nutrients

	Fe	Mn	B	Zn	Cu	Mo
mg/l	3	0.25	0.25	0.025	0.01	0.005
um	54	4.6	23	0.38	0.16	0.15

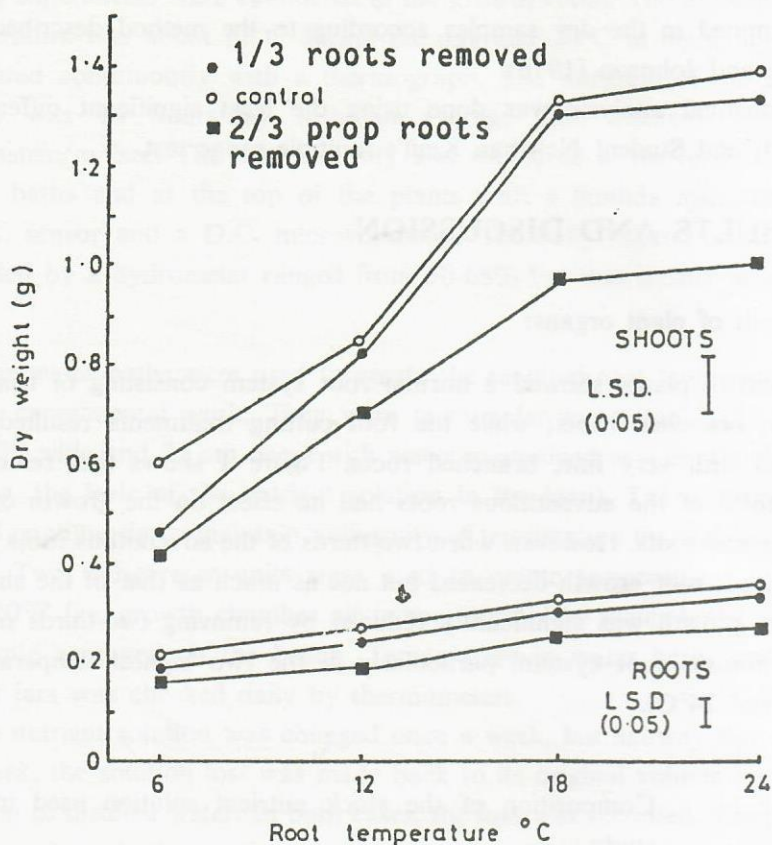


Fig. 1 Effect of root temperature and partial derooting on the dry weight of the shoots and roots for wheat plants grown in solution culture.

Root-shoot ratio was significantly decreased by increasing root temperature to 24°C, but it was not significantly affected by root removal (Fig. 2).

Total and nitrate nitrogen:

Total nitrogen concentration in the roots of plants grown at low root temperatures (6 and 12°C) was higher than that of plants grown at 18 and 24°C. (fig. 3). Total nitrogen and nitrate nitrogen concentrations in the shoot were significantly increased as root temperature increased to

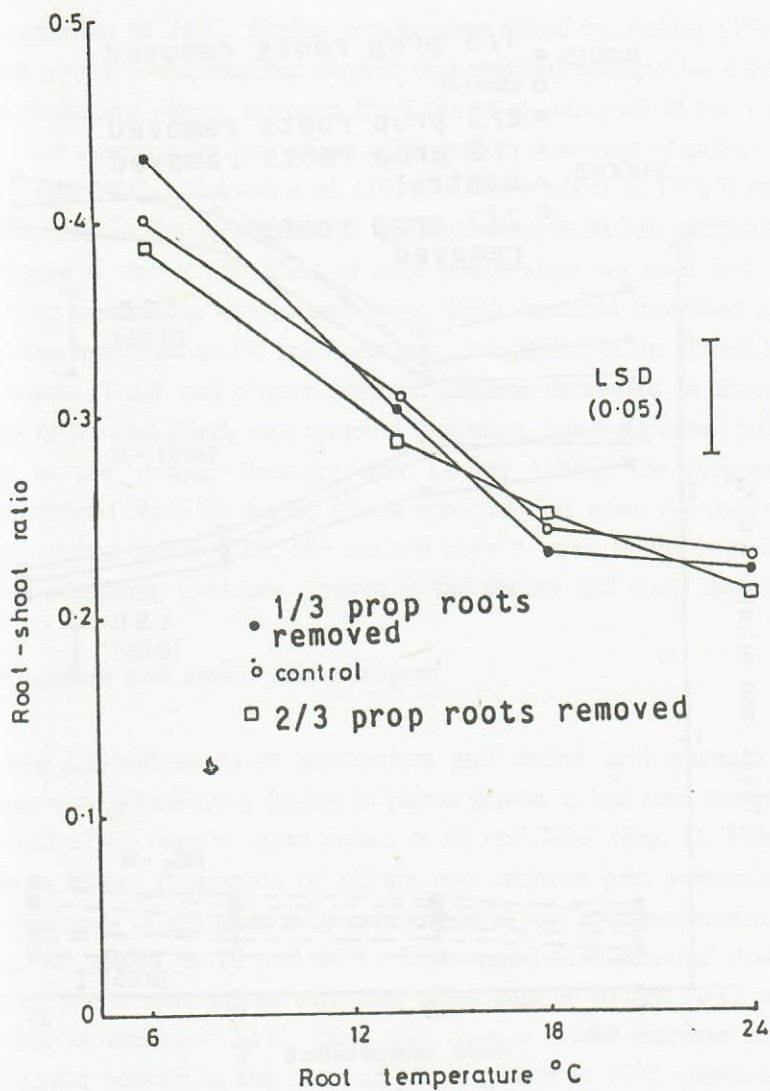


Fig. 2 Effect of root temperature and partial derooting on the root-shoot ratio of wheat plants grown in solution culture.

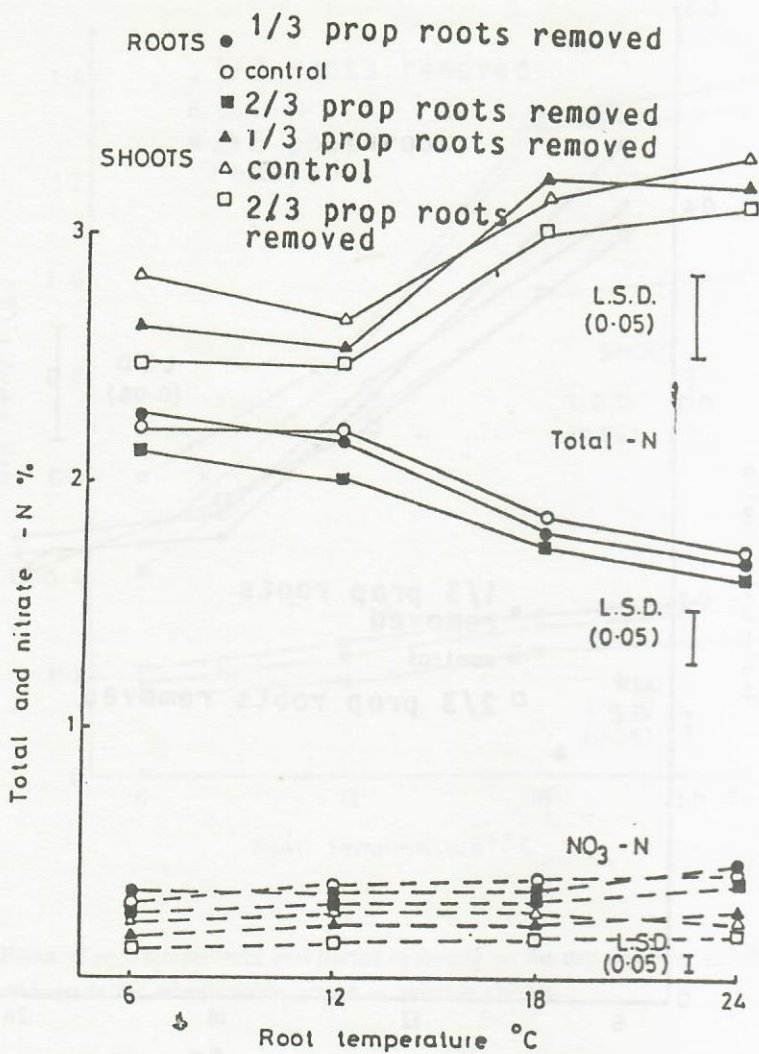


Fig. 3 Effect of root temperature and partial derooting on total and nitrate nitrogen concentration in shoots and roots of wheat plants grown in solution culture at 35 DAT.

the optimum of 24°C. Similar results were found by Ashley (1965) for wheat plants. Data obtained showed that reduced nitrogen (as calculated by subtracting nitrate nitrogen from the total nitrogen) in the roots at low root temperature was about 45% greater than that of plants grown at 18 and 24°C. Clarkson et al. (1982) and Younis et al. (1965) reported an increase in the proportion of reduced nitrogen at low temperature.

Figure 4 shows the effect of root temperature on total and nitrate nitrogen content in shoots and roots. Both contents increased as temperature increased to the optimum and were higher in the shoots than in the roots. Total and nitrate nitrogen content decreased in shoots and roots of the two-thirds root removal treatment, but the greatest reduction was in the shoots. Brouwer and Locher (1965) for ryegrass and Humphries (1951) for barley plants reported that when the root system was reduced below 50%, the mineral supply, even to the root system, became limiting, therefore, growth of the shoots and roots declined.

Ammonium and amino acid nitrogen:

The concentrations of ammonium and amino acid nitrogen in the roots were significantly higher in plants grown at low root temperatures (6 and 12°C) than in those grown at 18 and 24°C (Fig. 5). This shows that a higher proportion of nitrate was reduced into ammonium and amino acids in the roots of plants grown at low root temperatures than in those grown at 18 and 24°C. Drummond (1980) found that, when barley plants were grown with their roots kept at 10 and 20°C and their shoots at constant 20°C, there was over a 3-fold increase in nitrate reductase activity in the roots of plants grown at 10°C compared with those grown at 20°C.

Martin (1970) stated that nitrate is first reduced to nitrite then to ammonium which, once absorbed, may be immediately used in the synthesis of amino acids. Hence energy is conserved when ammonium rather than nitrate is supplied to the plant. Figure 5 clearly shows that the concentrations of ammonium and amino acid nitrogen in the shoots of plants grown at the two lowest temperatures (6 and 12°C) were lower than in the roots. The converse was true for plants grown at 18

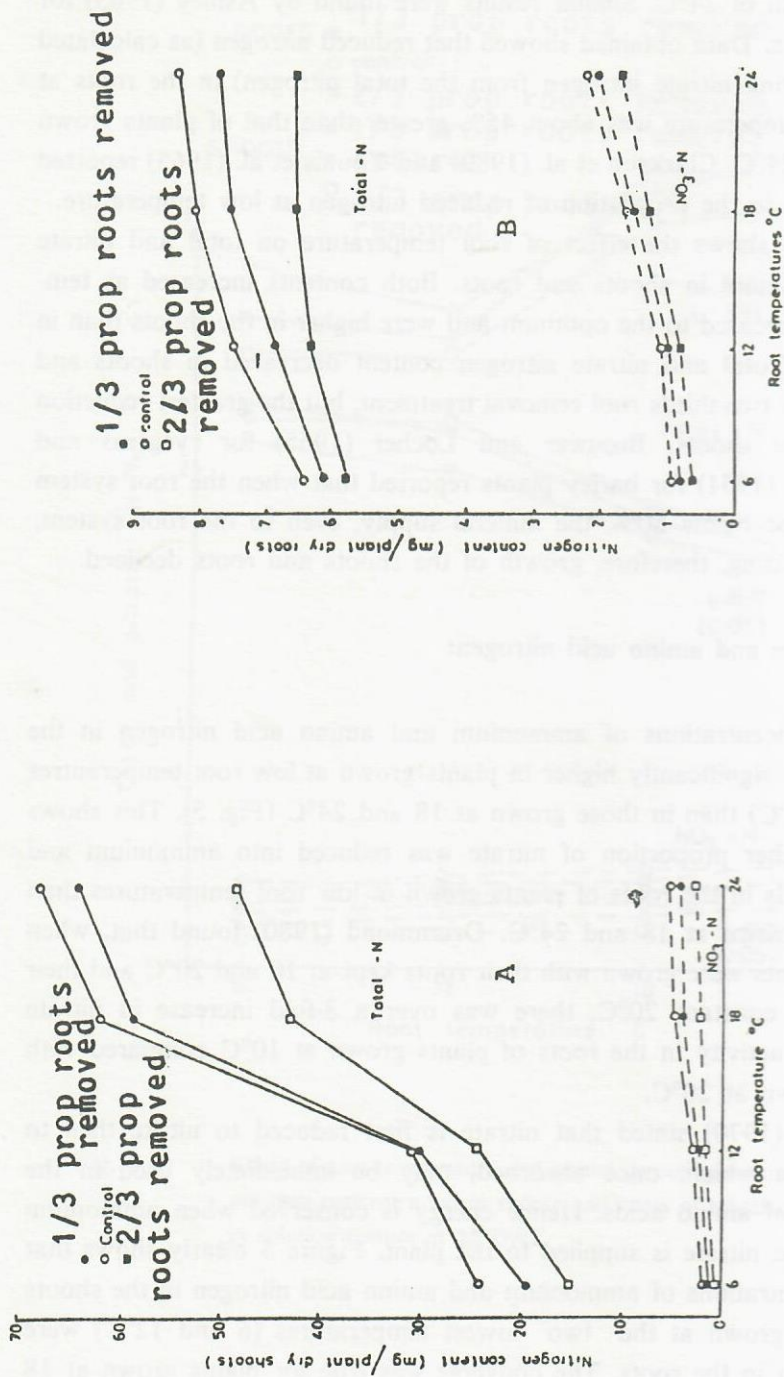


Fig. 4 Effect of root temperature and partial root removal on total and nitrate nitrogen content of the shoots (A) and roots (B) of wheat plants at 35 DAT.

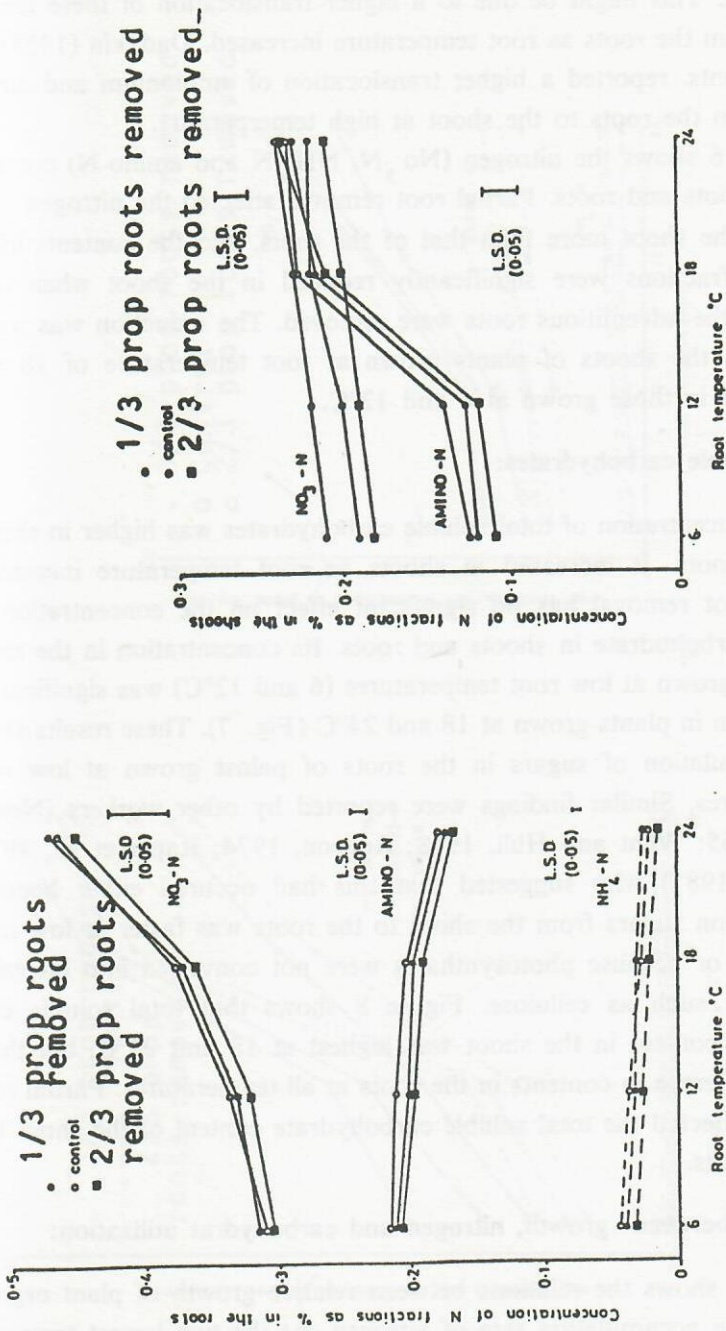


Fig. 5. Effect of root temperature and partial root removal on nitrogen fractions concentration of wheat plants at 35 DAT.

and 24°C. This might be due to a higher translocation of these constituents from the roots as root temperature increased. Dadykin (1955) for maize plants, reported a higher translocation of ammonium and amino acids from the roots to the shoot at high temperature.

Figure 6 shows the nitrogen ($\text{No}_3\text{-N}$, $\text{NH}_4\text{-N}$ and amino-N) contents of the shoots and roots. Partial root removal affected the nitrogen fractions of the shoot more than that of the roots, and the contents of all nitrogen fractions were significantly reduced in the shoot when two-thirds of the adventitious roots were removed. The reduction was much greater in the shoots of plants grown at root temperature of 18 and 24°C than in those grown at 6 and 12°C.

Total soluble carbohydrates:

The concentration of total soluble carbohydrates was higher in shoots than in roots. It increased in shoots as root temperature increased. Partial root removal has no significant effect on the concentration of soluble carbohydrate in shoots and roots. Its concentration in the roots of plants grown at low root temperatures (6 and 12°C) was significantly higher than in plants grown at 18 and 24°C (Fig. 7). These results show an accumulation of sugars in the roots of plants grown at low root temperatures. Similar findings were reported by other workers (Nowakowski, 1965; Went and Hull, 1968; Robson, 1974; Raper et al., 1976; Stephen, 1981) who suggested that this had occurred either because translocation of sugars from the shoot to the roots was faster at low temperatures, or because photosynthates were not converted into insoluble substances such as cellulose. Figure 8 shows that total soluble carbohydrate content in the shoot was highest at 18 and 24°C, but there was no difference in contents in the roots at all temperatures. Partial root removal affected the total soluble carbohydrate content of the shoot but not the roots.

Relations between growth, nitrogen and carbohydrate utilization:

Table 2 shows the relations between relative growth of plant organs and relative accumulation rate of nitrogen. At the two lowest temperatures (6 and 12°C) relative growth rate of the roots (RGR_R) was greater

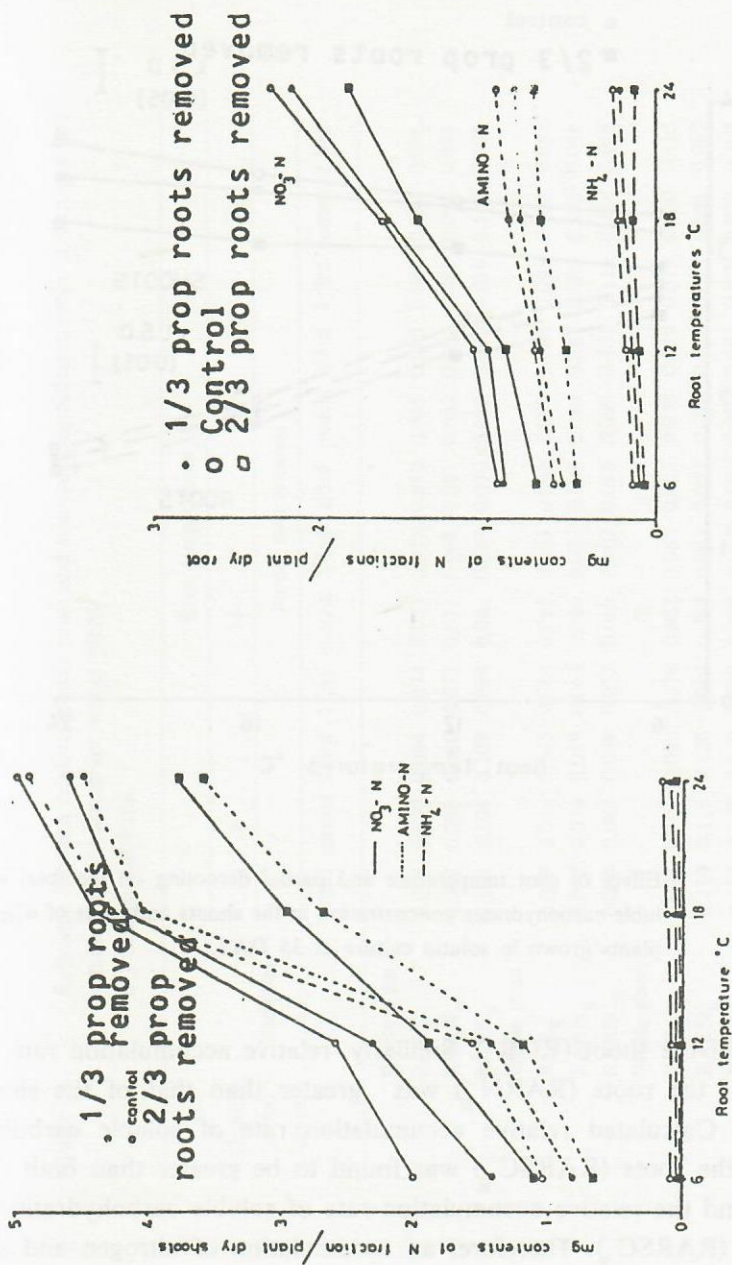


FIG. 6. Effect of root temperature and partial root removal on the contents of nitrogen fractions of wheat plants at 35 DAT.

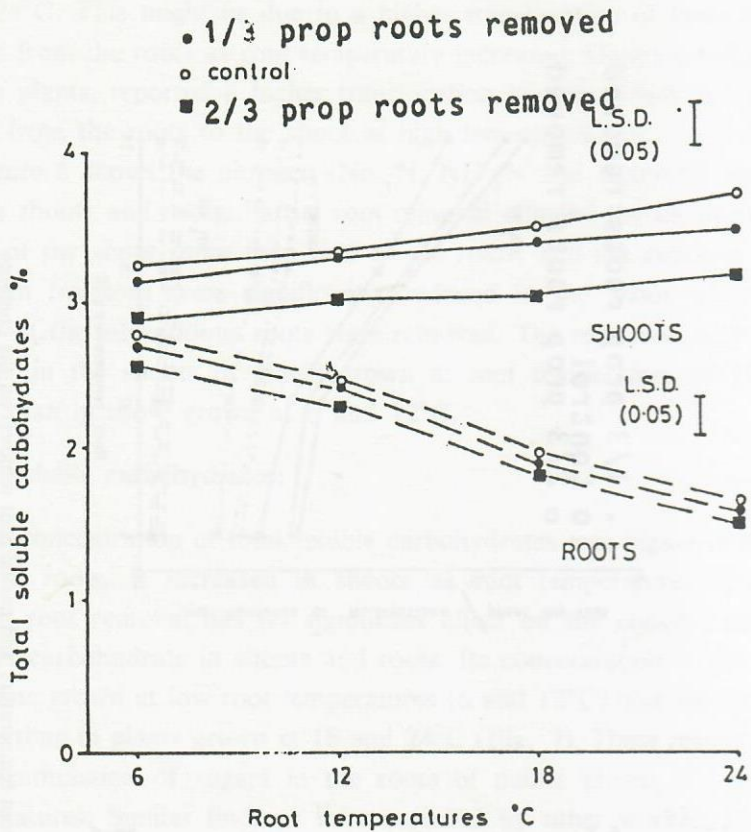


Fig. 7. Effect of root temperature and partial derooting on the total soluble carbohydrates concentration in the shoots and roots of wheat plants grown in solutin culture at 35 DAT.

than that of the shoot (RGR_S). Similarly, relative accumulation rate of nitrogen of the roots ($RARN_R$) was greater than that of the shoot ($RARN_S$). Calculated relative accumulation rate of soluble carbohydrates of the roots ($RARSC_R$) was found to be greater than both the (RGR_R) and the relative accumulation rate of soluble carbohydrates of the shoot ($RARSC_S$). Therefore, an accumulation of nitrogen and soluble carbohydrates occurred in the roots of plants grown at low root temperatures. The converse was true for plants grown at the two highest

Table 2. Relations between relative growth rates and relative accumulation rates of nitrogen and soluble carbohydrates for wheat plants.
a) Macro nutrients.

Growth period (days)	Variables	Root temperatures °C											
		6		12		18		24					
		1/3rd control	2/3rd control	1/3rd control	2/3rd control	1/3rd control	2/3rd control	1/3rd control	2/3rd control				
	Whole plant												
	RGR _P	0.094	0.090	0.094	0.074	0.073	0.072	0.087	0.085	0.083	0.086	0.091	0.096
	RARN _P	0.082	0.088	0.080	0.071	0.072	0.068	0.081	0.082	0.082	0.083	0.090	0.094
	RARS _P	0.101	0.104	0.109	0.086	0.081	0.093	0.090	0.089	0.090	0.096	0.100	0.098
	Whole plant												
	RGR _S	0.079	0.076	0.065	0.064	0.062	0.053	0.092	0.090	0.086	0.093	0.102	0.083
	RARN _S	0.072	0.074	0.069	0.063	0.064	0.051	0.088	0.089	0.087	0.089	0.103	0.098
	RARSC _S	0.086	0.081	0.099	0.072	0.069	0.087	0.098	0.099	0.101	0.115	0.111	0.096
	Whole plant												
	RGR _R	0.091	0.101	0.090	0.078	0.082	0.081	0.083	0.079	0.079	0.079	0.080	0.110
	RARN _R	0.110	0.115	0.120	0.083	0.084	0.091	0.073	0.078	0.078	0.077	0.081	0.097
	RARSC _R	0.117	0.127	0.120	0.099	0.093	0.097	0.083	0.080	0.081	0.079	0.079	0.100

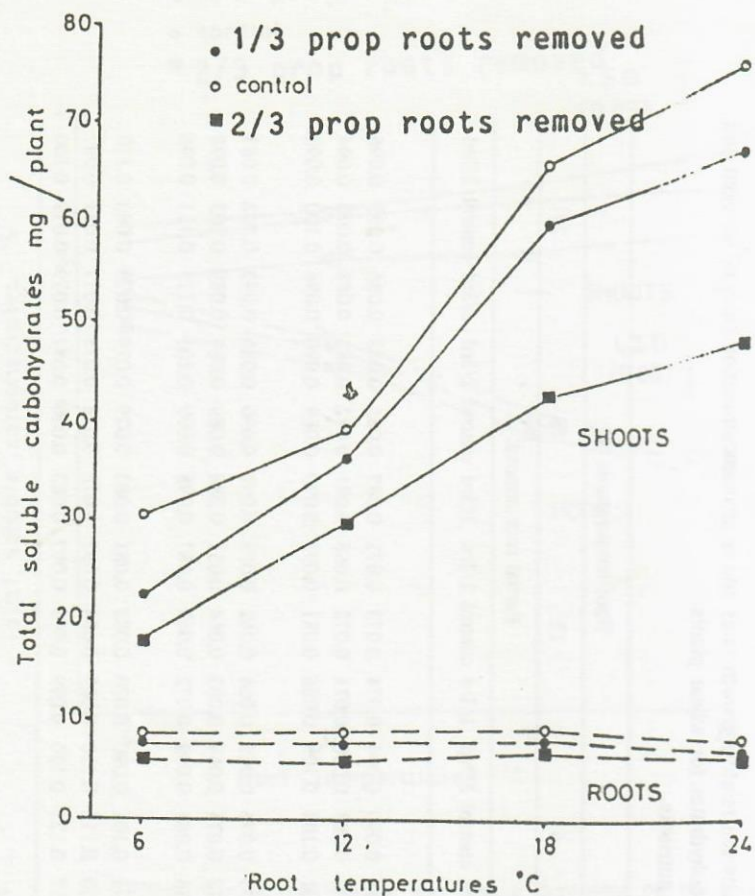


Fig. 8. Effect of root temperature and partial derooting on the total soluble carbohydrates content in the shoots and roots of wheat plants grown in solution culture at 35 DAT.

temperatures (18 and 24°C). Similar results were also found by Minotti and Jackson (1970), Jackson et al. (1976); Raper et al. (1977); who stated that both absorption of nitrate by roots and growth of roots are concurrently and competitively influenced by the rate of flow photosynthates. The nitrates in the roots must be utilized concurrently with the utilization of carbohydrates for root growth grown at 18 and 24°C)

support the concept (Rapper and McCant, 1966 and Raper et al., 1977) that nitrogen uptake by the plants is regulated by the current flux of soluble carbohydrate into the roots. However the accumulation of ammonium and amino acid nitrogen and soluble carbohydrates within the roots grown at the two lowest temperatures (6 and 12°C) might be a reason for the reduction of shoot growth of these plants.

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