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Regulation of K^+ Influx in Barley[1]

EFFECTS OF LOW TEMPERATURE

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ABSTRACT

Influx and accumulation of K^+ in barley (*Hordeum vulgare* L. cv Fergus) roots were measured at two temperatures (10°C and 20°C) in plants which had been grown with roots and shoots at 20°C (HT plants), with roots and shoots at 10°C (LT plants), and with roots at 10°C and shoots at 20°C (DT plants). Under conditions where K^+ was in limited supply during the prior growth period, K^+ influx and accumulation were consistently higher in roots of DT and LT plants than in those of HT plants. Thus, it would appear that this low temperature response is not limited specifically to conditions in which temperature differentials are maintained between roots and shoots. Nevertheless, it was generally the case that increases of influx were larger in DT and LT plants so that the temperature differentials may intensify the low temperature response. When K^+ influx was examined over a wide range of root [K^+], it was seen that the characteristic reduction of influx associated with increased internal [K^+] was substantially greater in HT than DT or LT plants. Transfer of plants grown under HT conditions to DT or LT regimes led to both short-term and long-term adjustments of influx. The former became apparent within 6 hours of exposure to the new conditions and decayed within minutes of transfer back to 20°C. The long-term adjustments were only apparent after prolonged exposure (days) to the lower root temperature and these did not decay as rapidly. Regardless of shoot temperature, the transfer of roots from 20°C to 10°C caused a gradual increase of root [K^+] so that 4 days later LT and DT roots contained, respectively, 53.3 and 49.83 micromoles per gram compared to 17.82 micromoles per gram for roots maintained at 20°C.

Most experimental work on ion absorption by higher plant roots has been conducted on plants in which roots and shoots were grown at similar ambient temperatures. However, Clarkson and his co-workers (4, 5, 7) have clearly emphasized that under natural conditions, particularly in spring and fall, temperatures experienced by roots during daylight hours may be several degrees lower than aerial temperatures experienced by shoots. The anticipated reduction of root activity (Q_{10} values for ion uptake, *e.g.* may be between 2 and 3) in relation to that of the shoot might lead to the imposition of a strongly root-limited pattern of growth. Although shoot growth is somewhat limited under these conditions, there is also clear evidence of the acclimation of root activity which apparently reduces the severity of this temperature stress. Clarkson *et al.* (4, 5, 7) have shown that following several days of growth at low temperatures there is increased capacity of transport processes which becomes apparent when these plants are returned to high temperatures. For example, compared to control plants grown at 20°C continuously, plants whose roots had been maintained at 8°C demonstrated increased rates of nutrient absorption, accumulation, translocation, and xylem exudation when these processes were measured at 20°C.

Clarkson and his co-workers (4, 5, 7) have emphasized that the observed responses represent a strategy which compensates for the lower root activity and higher shoot activity associated with the temperature differential. However, similar increases in ion fluxes in response to pretreatment at low temperatures have been demonstrated in a giant alga where differential temperatures were not involved (12, 13). It is therefore important to resolve, in higher plants, whether the stimulation of ion fluxes is due to differential (root/shoot) temperature or due to exposure of roots to low temperature *per se* irrespective of shoot temperature. This may have important implications as to the source(s) of the signal(s) responsible for the observed adjustments of ion fluxes.

Moreover, the extent of the accommodation of ion fluxes may have been considerably underestimated in previous studies. At face value it would appear that roots, maintained at 10°C below shoot temperatures, achieve higher levels of ion accumulation and ion fluxes which are equal to or even slightly higher (on a per unit weight basis) than those of roots where roots and shoots are maintained at the higher temperature. However, it is well documented that ion uptake is negatively correlated with tissue ion concentration (8, 10, 14). Hence, not only have these low-temperature plants achieved parity with respect to the temperature constraints but they maintain equivalent fluxes despite increased tissue concentration. This raises important questions regarding the proposed regulation of ion flux by internal ion concentration. For example, is the apparent negative feedback between internal [ion] and influx (*e.g.* 8, 10, 14) suspended under these conditions? Or, is the relationship between these variables altered as a result of acclimation?

In this paper, we have measured K^+ influx into intact roots of barley plants under conditions which enable us to distinguish the effects of temperature differentials from effects of low temperature *per se*. By measuring influx over a range of external concentrations we have estimated K_m and V_{max} values for influx. Finally, by obtaining influx measurements (at 10°C and 20°C) over a wide range of internal [K^+], in plants grown under various temperature conditions, it has been possible to estimate the extent of temperature acclimation free from the complications associated with simultaneous increases of internal [K^+].

MATERIALS AND METHODS

Germination and Growth of Plants. Seeds of barley (*Hordeum vulgare* L. cv Fergus) were placed on Plexiglas discs (fitted with plastic mesh) and left to germinate in sand in the dark for 2 d at 25 ± 2°C. After washing off adhering sand, the discs were transferred to Plexiglas hydroponic tanks (of 24 l capacity) containing 0.5 mM $CaSO_4$ and modified 0.01 Johnson's solution

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(15) with K^+ at 0.1 mM (as sulfate). The tanks were placed in controlled growth chambers (Conviron, model 811) maintained on 16-h day/8-h night cycles at either 20 ± 1 or 10 ± 1°C and 70% RH. Light was provided (6 mw cm^{-2} at plant level) by Vitalite fluorescent tubes with spectral composition similar to sunlight. Differential root and shoot temperatures (10 ± 1 and 20 ± 1°C, respectively) were achieved by immersing a stainless steel heat exchange coil in the culture solution within the reservoir of the growth tank. Water, at 10°C, was continuously circulated through this coil by a Forma Scientific Refrigerated Unit (model 2325). A continuous mixing and circulation of the culture solution between the reservoir and the main compartment containing the plants, was maintained by means of Lauda, model T-1 circulation pumps. The temperature in the vicinity of roots was monitored frequently and was always found to be within 1°C of the desired (10°C or 20°C) temperatures.

K^+ Influx Measurements. K^+ influx was measured at 20°C and 10°C in intact roots that were prewashed for 5 min in nonradioactive solution (identical to uptake solution in all other respects, including temperature) and aerated continuously. The plants were then transferred, for 10 min, to aerated uptake solutions which contained 0.5 mM $CaSO_4$ plus the desired concentration of K_2SO_4, labeled with $^{86}Rb^+$. These solutions were maintained in a water bath at the desired temperature. The influx was terminated by transferring plants, for 5 min, to an identical but unlabeled solution maintained at 1°C. After determining fresh weights, the roots were ashed in a furnace at 500°C for 24 h. The ash was dissolved in 10 ml of distilled H_2O and the radioactivity obtained by Cerenkov Counting in a Searle Isocap 300 Scintillation Spectrometer.

Determination of K^+ Contents. K^+ concentrations of roots were determined by flame photometry (Instrumentation Laboratory, model IL 443) using aliquots from the aqueous solutions which had been Cerenkov-counted for influx determinations.

Experiment 1: K^+ Influx Isotherms. After germination in sand for 2 d at 25 ± 2°C, seedlings were transferred to their respective tanks under three temperature regimes: (a) both root and shoot at 20°C, henceforth referred to as HT[2] plants; (b) both root and shoot at 10°C, henceforth referred to as LT plants; and (c) roots at 10°C and shoot at 20°C, henceforth referred to as DT plants.

K^+ influx isotherms of HT plants were determined on day 7 from sowing both at 10°C and at 20°C (temperatures of the uptake media). Growth rates of DT and, more so, LT plants were visibly slower than those of HT plants. Consequently, influx isotherms for these plants were determined 10 d after sowing when they appeared to be at the same growth stage as HT plants (fresh weights of roots were similar) (see Ref. 9).

Experiment 2: Regulation of K^+ Influx. Plants were grown under three temperature regimes as described above, K^+ influxes from 0.5 mM $CaSO_4$ plus 0.05 mM K_2SO_4 solution were measured in the morning of day 7 (from sowing) in HT plants and in the morning of day 10 in DT and LT plants at both 10° and 20°C (T_0 samples). After the removal of Time 0 samples, sufficient K_2SO_4 was added to each tank to bring the K^+ concentration to 6 mM. Thereafter, K^+ influxes (at 10°C and 20°C) were determined at hourly intervals until T_5; K^+ influxes of the last samples (T_{24}) were determined the following morning (24 h after the addition of K_2SO_4). K^+ content of roots of all these samples were also determined. Curves describing the relationships between K^+ influx and root [K^+] were based upon values for slopes and intercepts obtained by exponential regression.

Experiment 3: Effect of Duration of Exposure to Low Temperatures upon K^+ Influx. Seeds were germinated as described above, after which seedlings were transferred to HT conditions and left to grow for 4 d. Then, at appropriate times (96, 72, 48, 24, 12, and 6 h prior to influx measurements), samples were transferred to DT and LT treatment tanks. Control (0 h) samples remained at 20°C (HT) throughout. K^+ influxes of all treatments were determined at the same time, from 0.5 mM $CaSO_4$ plus 0.05 mM K_2SO_4 at both 10°C and 20°C. Because plants had been maintained for 4 d under HT conditions, differences in size due to subsequent exposures to DT and LT were relatively small. In this experiment, K^+ concentrations of culture solutions were measured daily and restored, by appropriate additions of K_2SO_4, to 0.1 mM K^+.

Each experiment was repeated, and in each experiment all measurements were replicated three to four times.

RESULTS

Experiment 1: K^+ Influx Isotherms. Temperature regimes during growth had significant effects on V_{max} values for K^+ influx (Table I). At both uptake temperatures, V_{max} values were in the order: DT plants > LT plants > HT plants. Root [K^+] under the different temperature regimes also showed significant differences and were in the order: LT > DT ≫ HT. K_m also showed differences but, as in previous studies (9), considering the errors associated with these estimates, the differences are relatively small.

Experiment 2: Regulation of K^+ Influx. Regardless of the prevailing temperatures during pretreatments to increase internal K^+ status, subsequent K^+ influxes (at 10°C or 20°C) were negatively correlated with root [K^+] (Figs. 1 and 2). Exponential regression gave the following equations:

1. HT plants, influx at 10°C: $Y = 3 \cdot 67.e^{-0 \cdot 042.x}$ ($r^2 = 0 \cdot 95$)
2. HT plants, influx at 20°C: $Y = 9 \cdot 78.e^{-0 \cdot 041.x}$ ($r^2 = 0 \cdot 95$)
3. LT plants, influx at 10°C; $Y = 7 \cdot 85.e^{-0 \cdot 034.x}$ ($r^2 = 0 \cdot 93$)
4. LT plants, influx at 20°C: $Y = 14 \cdot 46.e^{-0 \cdot 029.x}$ ($r^2 = 0 \cdot 97$)
5. DT plants, influx at 10°C: $Y = 8 \cdot 44.e^{-0 \cdot 030.x}$ ($r^2 = 0 \cdot 99$)
6. DT plants, influx at 20°C: $Y = 14 \cdot 75.e^{-0 \cdot 025.x}$ ($r^2 = 0 \cdot 94$)

where Y = influx and x = root [K^+].

However, at both 10°C and 20°C, K^+ influxes into LT and DT plants were consistently higher than influxes into HT plants. This was true at all levels of internal [K^+] encountered. Moreover, K^+ influxes of DT plants were always slightly higher than those of LT plants. Rates of decrease of influx per unit increase in root [K^+] (slopes of the curves) were greater in HT plants than in DT and LT plants, although slopes of the curves did not change as the influx temperature was changed.

Experiment 3: Effect of Duration of Exposure to Low Temperature. Transfer of HT plants to either DT (Table II) or LT (Table III) conditions produced similar effects upon K^+ influx. However, the most apparent and consistent change observed was the gradual increase of root [K^+]. As a consequence, it becomes difficult to separate the effects of acclimation to reduced temperature from those due to increased root [K^+]. For example, despite the increased root [K^+] after 6 h pretreatment (Tables II and III), influx (measured at 10°C) was increased from 1.91 to 2.86 μmol g^{-1} h^{-1} following DT pretreatment and 1.91 to 2.54 μmol g^{-1} h^{-1} following LT pretreatment. In order to isolate these confounding effects, K^+ influx at each interval was predicted from the equations relating K^+ influx and root [K^+] obtained from the regulation experiment (Figs. 1 and 2, experiment 2). In the latter experiment, K^+ influx was measured at 10°C or 20°C in HT, LT, and DT plants. Fluxes obtained were characteristic of the growth conditions, particularly HT as distinct from LT and DT plants. If these equations are used to predict influx at a given root [K^+],

[2] Abbreviations: HT, high temperature; LT, low temperature; DT, differential temperature.

Table I. *V_{max} and K_m Values (Mean ± SE) (Obtained from Hofstee Plots) at 10°C and 20°C Uptake Temperatures for Plants Grown under Three Temperature Regimes (Experiment 1)*

r^2 values for Hofstee plots, respectively, at 10°C and 20°C uptake temperatures were as follows: 20/20°C (HT) plants: 0.95, 0.88; 10/20°C (DT) plants: 0.93, 0.94; 10/10°C (LT) plants: 0.83, 0.87.

Growth Temp. Root/Shoot	Root [K⁺]	V_{max}		K_m	
		10°C	20°C	10°C	20°C
°C	μmol g^{-1}	μmol g^{-1} h^{-1}		mM	
20/20	21.6 ± 0.7	5.10 ± 0.33	8.43 ± 0.72	0.033 ± 0.004	0.033 ± 0.006
10/20	28.8 ± 1.3	7.29 ± 0.54	11.34 ± 0.08	0.045 ± 0.006	0.054 ± 0.007
10/10	32.8 ± 2.8	5.91 ± 0.62	10.18 ± 1.09	0.032 ± 0.007	0.054 ± 0.010

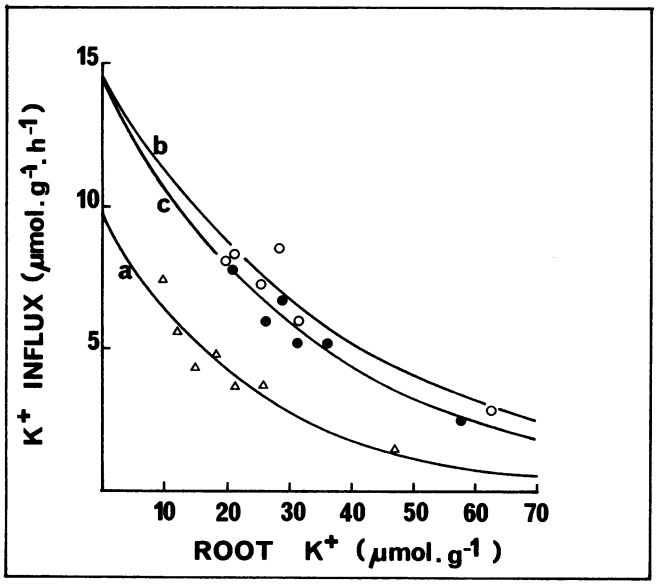

FIG. 1. Regulation of K^+ influx by root K^+ concentration in plants grown at 20°C root/20°C shoot temperature (HT, Δ), 10/20°C (DT, O), and 10/10°C (LT, ●). Uptake temperature was 20°C, see text. The lines were drawn after exponential curve fitting. Intercept and slope values, respectively, were: For HT (a), 9.78, −0.041 (r^2 = 0.95); for DT (b), 14.75, −0.025 (r^2 = 0.94); and for LT (c), 14.46, −0.029 (r^2 = 0.97).

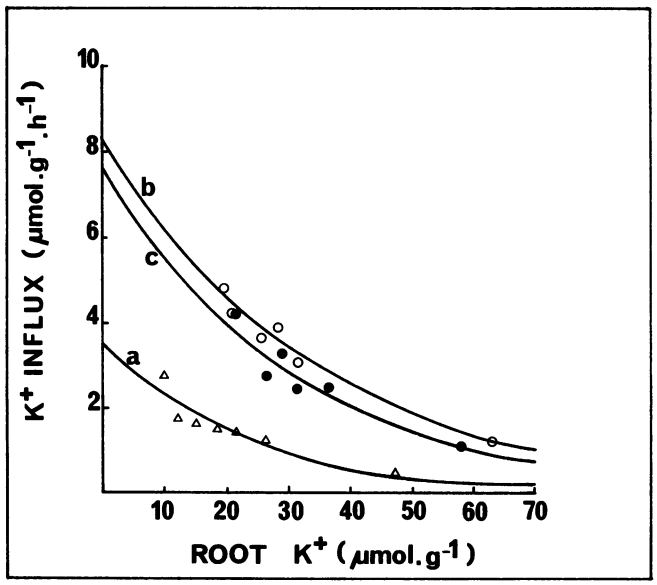

FIG. 2. Regulation of K^+ influx by root K^+ concentration. Uptake temperature was 10°C. Details and symbols as in Figure 1. Intercept and slope values, respectively, were: For HT (a), 3.46, −0.042 (r^2 = 0.95); for DT (b), 8.44, −0.030 (r^2 = 0.99); and for LT (c), 7.85, −0.034 (r^2 = 0.93).

the extent of acclimation (HT to DT or LT conditions) can be assessed from the ratio observed/estimated). For example, using equation 1 (HT plants, influx at 10°C) gives an expected influx of 1.63 μmol g^{-1} h^{-1} for root [K^+] of 17.82 μmol g^{-1} (Table II, line 1). This is close to the observed flux (1.91 μmol g^{-1} h^{-1}, observed/estimated = 1.17) because these HT plants have not yet undergone any acclimation to low temperature. By contrast, according to equation 3, DT plants would have given an influx of 4.93 μmol g^{-1} h^{-1} under the same conditions. The large discrepancy between 1.91 and 4.93 μmol g^{-1} h^{-1} (observed/estimated = 0.39) confirms the lack of acclimation of these HT plants to DT conditions.

In both instances (DT and LT plants), there are clear indications of significant adjustments to the new conditions within 6 h. Thus, 6 h of DT treatment raises the ratio from 1.17 to 2.60 and 0.95 to 1.28 (influx at 20°C (Table II). Thus, the observed influx at 10°C had increased substantially over the expected value for HT plants at the particular root [K^+]. Ratios in column b showed that, while K^+ influx at 10°C was 76% of the 'completely' acclimitized plants, at 20°C influx was only 55% of expected. In fact, as indicated by the ratios in column b, complete acclimation was achieved only after 4 d had elapsed (ratios approaching unity at both influx temperatures). Both DT and LT plants appeared to show a greater degree of acclimation of influx at 10°C than at 20°C, particularly during the first 72 h of low temperature treatment.

DISCUSSION

The results of the experiments detailed above reveal that K^+ influx at a given root [K^+] in the range from 10°C to 20°C is essentially independent of temperature when measured at the growth temperature in plants which have become fully acclimated to that temperature. This is perhaps contrary to expectation, given the high Q_{10} for K^+ influx in barley (9). Indeed, experiments in which plants are grown at elevated temperatures (20–28°C) and uptake experiments subsequently performed at several lower temperatures (2, 3) may generate quite erroneous conclusions regarding the capacity of plants to function effectively at lower temperatures. Such adjustments of ion fluxes have previously been observed by other workers when plants were grown at different root (low)/shoot (high) temperatures (4, 5, 7, 9). These authors have argued that the observed changes represent processes which tend to compensate for the relatively slower growth of roots (due to low temperature) compared to shoot. In our expeiments where roots were grown at low temperatures, an almost equivalent increase in K^+ influx occurred independently of shoot ambient temperature (Figs. 1 and 2; Tables I–III). In a giant alga (*Chara corallina*) also, enhancement in K^+ and Cl^- influxes have been observed when the plants were maintained at low temperatures (12, 13). In the present experiments, plants

Table II. *K+ Influx (ϕ_{obs}, Mean ± SE) Measured at 10°C and 20°C, as a Function of Duration of Exposure to DT Conditions in Plants Previously Grown under HT Conditions*

Estimated K^+ influxes (ϕ_{est}) at that particular root [K^+] according to the equations describing influx as a function of root [K^+] (see "Materials and Methods" and Figs. 1 and 2) for HT conditions and DT conditions and observed/estimated ratios (in parentheses).

Exposure Period	[K^+] Root	Uptake Temp.	ϕ_{obs}	ϕ_{est} (ϕ_{obs}/ϕ_{est})	
				HT	DT
h	$\mu mol\ g^{-1}$	°C	$\mu mol\ g^{-1}\ h^{-1}$	$\mu mol\ g^{-1}\ h^{-1}$	
0	17.82	10	1.91 ± 0.05	1.63 (1.17)[a]	4.93 (0.39)
		20	4.42 ± 0.06	4.67 (0.95)	9.34 (0.47)
6	27.00	10	2.86 ± 0.14	1.10 (2.60)	3.74 (0.76)
		20	4.08 ± 0.16	3.18 (1.28)	7.38 (0.55)
12	30.68	10	2.50 ± 0.09	0.94 (2.66)	3.35 (0.75)
		20	3.36 ± 0.11	2.73 (1.23)	6.71 (0.50)
24	35.91	10	2.22 ± 0.08	0.75 (2.96)	2.86 (0.78)
		20	3.66 ± 0.14	2.20 (1.66)	5.87 (0.62)
48	36.37	10	2.11 ± 0.06	0.74 (2.85)	2.82 (0.75)
		20	3.64 ± 0.35	2.16 (1.69)	5.80 (0.63)
72	43.40	10	1.89 ± 0.08	0.55 (3.44)	2.28 (0.83)
		20	2.63 ± 0.11	1.61 (1.63)	4.84 (0.54)
96	49.83	10	1.50 ± 0.10	0.42 (3.57)	1.88 (0.80)
		20	3.69 ± 0.35	1.23 (3.00)	4.11 (0.90)

[a] Numbers in parentheses, ratios.

Table III. *K+ Influx (ϕ_{obs}, Mean ± SE) Measured at 10°C and 20°C, as a Function of Duration of Exposure to LT Conditions Previously Grown under HT Conditions*

Estimated influxes (ϕ_{est}) at that particular root [K^+] according to the equations describing influx as a function of root [K^+] (see "Materials and Methods" and Figs. 1 and 2) for HT conditions and LT conditions and observed/estimated ratios (in parentheses).

Exposure Period	[K^+] Root	Uptake Temp.	ϕ_{obs}	ϕ_{est} (ϕ_{obs}/ϕ_{est})	
				HT	DT
h	$\mu mol\ g^{-1}$	°C	$\mu mol\ g^{-1}\ h^{-1}$	$\mu mol\ g^{-1}\ h^{-1}$	
0	17.82	10	1.91 ± 0.05	1.63 (1.17)[a]	4.28 (0.45)
		20	4.42 ± 0.06	4.67 (0.95)	8.48 (0.52)
6	24.14	10	2.54 ± 0.09	1.24 (2.04)	3.45 (0.74)
		20	3.31 ± 0.17	3.59 (0.92)	7.01 (0.47)
12	26.08	10	2.35 ± 0.18	1.14 (2.06)	3.23 (0.73)
		20	3.65 ± 0.20	3.31 (1.10)	6.62 (0.55)
24	29.47	10	2.10 ± 0.17	0.99 (2.12)	2.88 (0.73)
		20	3.72 ± 0.19	2.87 (1.29)	5.98 (0.62)
48	34.23	10	2.24 ± 0.18	0.81 (2.76)	2.45 (0.91)
		20	3.64 ± 0.18	2.36 (1.54)	5.18 (0.70)
72	39.11	10	1.55 ± 0.06	0.66 (2.35)	2.07 (0.75)
		20	2.61 ± 0.38	1.93 (1.36)	4.48 (0.58)
96	53.30	10	1.62 ± 0.10	0.36 (4.50)	1.28 (1.27)
		20	2.42 ± 0.07	1.07 (2.26)	2.93 (0.83)

[a] Numbers in parentheses, ratios.

grown at differential root/shoot temperatures demonstrated a slightly, but consistently higher K^+ influx than LT plants. Nevertheless, the major factor in this acclimation process would appear to be the root temperature. Our results clearly show that root [K^+] is significantly greater where roots are maintained at lower temperature, irrespective of shoot ambient temperature (Figs. 1 and 2, Tables I–III; *cf.* Ref. 9). Moreover, root [K^+] increased as the duration of exposure of roots to low temperature increased (Table II and III). It appears, therefore, that one outcome of the altered growth rates and acclimation of ion fluxes is to increase internal [K^+]. The extent to which this result is universally borne out may vary according to variety and level of K^+ supply. Using a continuous supply system where external [K^+] was maintained at 100 μM, we have observed only slight differences in tissue [K^+]. However, preliminary experiments in this laboratory (M. De Silva, unpublished) with winter varieties of cereals indicate that the latter tend to maintain higher tissue [K^+] at low temperature even during continuous K^+ provision.

It is beyond the scope of this paper to evaluate the exact adaptive significance of the increased K^+ accumulation at low temperature, but the parallel with the increased ion accumulation (osmotic adjustment) as a result of saline, drought, and low temperature stress is inescapable. It is well documented that freezing temperatures of some plant tissues are directly correlated with osmotic potentials and that adequate K^+ fertilization is essential for the development of cold hardiness (1).

Our data (Tables II and III) showed two distinct mechanisms for increased K^+ influx into roots exposed to low temperatures (both DT and LT plants). One, which appeared to operate within 6 h of exposure to low temperature, decayed within minutes of returning the roots to higher temperature (henceforth referred to as short exposure effect). The other developed over a much longer period (4 d) and did not decay in such a short time as the first one (henceforth referred to as long exposure effect). It may be that the latter mechanism represents an increased number of transporters as has been proposed by Clarkson (4). This interpretation is consistent with our observation that, while V_{max} of roots grown at low temperature was substantially increased (at both influx temperatures), K_m was either little affected or showed some increase (Table I; *cf.* Refs. 9, 13). In addition, increased membrane fluidity has also been implicated in the stimulation of ion fluxes and water flow in roots pretreated at low temperatures (4, 6, 13, 17). However, there is little definitive information available regarding the biochemical basis of this adjustment. In the short exposure effect, by contrast, any increase in the number of transporters can be immediately discounted because of the short time involved both in the development and the decay of this effect. It has been reported, on the other hand, that when a nonphotosynthetic tissue was exposed to low temperature, the rates of synthesis of unsaturated fatty acids responded immediately and noticeable changes in gross lipid unsaturation occurred within 5 h (11). Thus, the short exposure effects we have observed may well be due to changes in the fluidity of plasma membrane. The difficulty remains, however, in explaining the extremely short time (few minutes) of decay of this effect.

Our results (particularly Figs. 1 and 2) make it abundantly evident that it is essential to consider the flux in conjunction with root [K^+] in order to obtain a clear appreciation of the adjustments of ion influx brought about by low temperature pretreatment. In this regard it is interesting to observe that the relationships between internal [K^+] and influx (slopes of curves in Fig. 1 and 2) were reduced by continuous growth at low temperature but not by the brief exposure (15 min) to low temperatures during prewash and influx measurements. This appears to indicate not only an "expansion of the ion transporting capacity" as proposed by Clarkson and Deane-Drummond (5)

but also an altered sensitivity to negative feedback from tissue [K^+].

Although it is perhaps premature to make a strong argument concerning the low temperature adjustments reported here, we presently prefer the notion that these responses may represent the first indications of a continuous process of osmotic adjustment which renders the plant better able to resist the deleterious effects of freezing temperatures.

LITERATURE CITED

1. BERINGER H, G TROLLDENIER 1978 Influence of K nutrition on the response to environmental stress. *In* Potassium Research—Review and Trends. International Potash Institute, Bern, pp 189–222
2. BLOOM AJ, FS CHAPIN III 1981 Differences in steady-state net ammonium and nitrate influx by cold- and warm-adapted barley varieties. Plant Physiol 68: 1064–1067
3. CAREY RW, JA BERRY 1978 Effects of low temperature on respiration and uptake of rubidium ions by excised barley and corn roots. Plant Physiol 61: 858–860
4. CLARKSON DT 1976 The influence of temperature on the exudation of xylem sap from detached root systems of rye (*Secale cereale*) and barley (*Hordeum vulgare*). Planta 132: 297–304
5. CLARKSON DT CE DEANE-DRUMMOND 1981 Thermal adaptation of nitrate transport and assimilation in roots? *In* I Rorison, JA Lee, eds, Nitrogen as an Ecological Factor. British Ecological Society Symposium, Oxford, pp 1–20
6. CLARKSON DT, KC HALL, JKM ROBERTS 1980 Phospholipid composition and fatty acid desaturation in the roots of rye during acclimatization of low temperature. Planta 149: 464–471
7. CLARKSON DT, MGT SHONE, AV WOOD 1974 The effect of pretreatment temperatures on the exudation of xylem sap by detached barley root systems. Planta 121: 81–92
8. CRAM WJ 1976 Negative feedback regulation of transport in cells. The maintenance of turgor, volume-, and nutrient supply. *In* U. Lüttge, MG Pitman, eds, Transport in Plants II, Part A, Cells. Encyclopedia of Plant Physiology, New Series, Vol 2. Springer-Verlag, Berlin, pp 284–316
9. DEANE-DRUMMOND CE, ADM GLASS 1983 Compensatory changes in ion fluxes into barley (*Hordeum vulgare* L. cv. Betzes) seedings in response to differential root/shoot growth temperature. J Exp Bot 34: 1711–1719
10. GLASS ADM 1976 Regulation of potassium absorption in barley roots. An allosteric model. Plant Physiol. 58: 33–37
11. HARRIS P, AT JAMES 1969 The effect of low temperatures on fatty acid biosynthesis in plants. Biochem J 112: 325–330
12. RAVEN JA, FA SMITH 1978 Effect of temperature on ion content, ion fluxes and energy metabolism in *Chara corallina.* Plant Cell Environ 1: 231–238
13. SANDERS D 1981 Physiological control of chloride transport in *Chara corallina.* I. Effects of low temperature, cell turgor pressure, and anions. Plant Physiol 67: 1113–1118.
14. SIDDIQI, MY, ADM GLASS 1982 Simultaneous consideration of tissue and substrate potassium concentration in K^+ uptake kinetics: a model. Plant Physiol 69: 283–285
15. SIDDIQI MY, ADM GLASS 1983 Studies of the growth and mineral nutriton of barley varieties. I. Effect of potassium supply on the uptake of potassium and growth. Can J Bot 61: 671–678
16. SIDDIQI MY, ADM GLASS 1983 Studies of the growth and mineral nutrition of barley varieties II. Potassium uptake and its regulation. Can J Bot 61: 1551–1558
17. VIGH L, I HORVATH, LI HORVATH, D DUDITS, T. FARKAS 1979 Protoplast plasmalemma fluidity of hardened wheats correlates with frost resistance. FEBS Lett 107: 291–294