THE EFFECT OF POTASSIUM NUTRITION ON THE UPTAKE AND DISTRIBUTION OF NUTRIENT IONS IN DEVELOPING POTATO PLANTS

A thesis presented by

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ABSTRACT

Giving potassium to potato plants grown in soil increased the concentration of all cations in the soil solution, but the concentrations in the xylem sap from detopped plants suggested that this effect was over-ridden for Ca^{++} by decreased absorption. Effects on Mg^{++} absorption were less simple; phosphate absorption seemed slightly enhanced, that of nitrate unaffected.

The way metabolic 'sinks' influenced K effects on ion distributions in the plants suggested ions are transferred in the vascular bundles from xylem to phloem elements, so that increasing ion fluxes in the phloem decreases those in the xylem. Thus, giving K increased the quantities of Mg and P going to the tubers but at the expense of supply to the stems and leaves. It also increased the Mg concentration in tuber dry matter and that of another 'sink' - unfolding leaves sampled close to apical meristems before the tubers formed; tuber concentrations of Ca and P were little affected, that of N decreased by dilution.

Giving K did not cause Ca or Mg to move out of leaves, but lessened the flux of these ions to mature leaves.

Extra K given for 23 hours to solution-grown plants increased the flux of ^{14}C-labelled assimilate and the concentrations of water-soluble Mg and P, but not K, in the tubers.

Analysing the phloem translocation theories of Munch and Spanner by considering frictional interactions and ion permeation in the sieve-tubes suggested that the experimental data accorded best with Spanner's theory. A slight amendment of this theory is suggested.

Both cutting all the tubers off the plants and giving them K prolonged their life. Removing tubers influenced ion concentrations in leaves in ways

suggesting ion movements to 'sinks' were governed by a predetermined 'development programme' rather than competition between shoot and tuber 'sinks'.

CONTENTS

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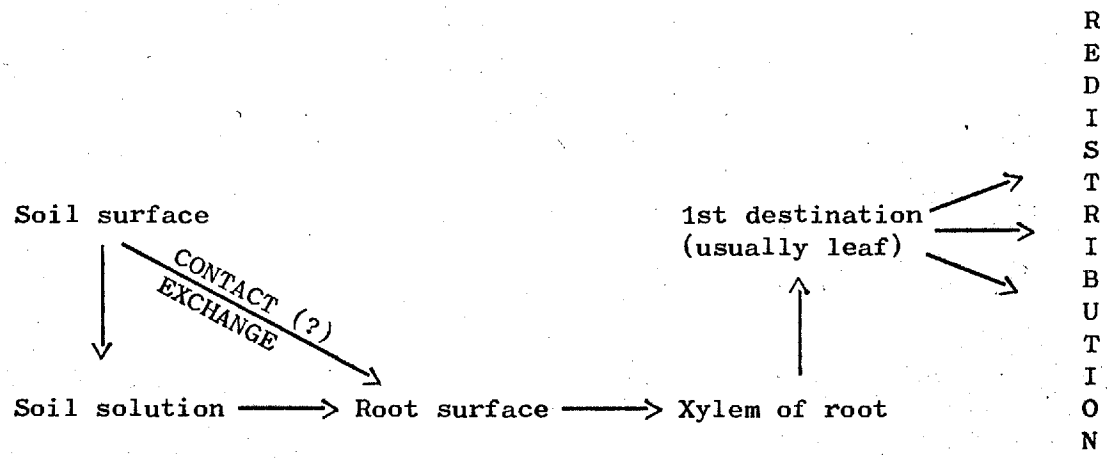
CHAPTER 1

GENERAL INTRODUCTION

Plants probably accumulate potassium more vigorously than any other cation. It is present in the solutions in some plant parts about fifty times more concentrated than in the soil solution, but still surprisingly little is known about its role in the plant. The work to be described was intended to show how added K accumulated and moved in developing potato plants and how its behaviour influenced the absorption and movement of other nutrients.

In this chapter, the different stages of ion absorption and movement, shown below, are described and likely effects of adding K are reviewed.



Soil Surface to Soil Solution

Adding K is likely to influence the desorption of cations more than that of anions. Applying the law of mass action to the exchange equilibrium between K^+ and another cation M^{z+},

$$zK^+ + MX_z \rightleftharpoons zKX + M^{z+}$$

where X^- is an exchange site, shows that adding K to the soil, which increases the K concentration in the soil solution, also increases the concentration of M^{z+}. Different cations will be influenced according to the selectivity of the exchange sites between them and K^+.

Exchange equations proposed by Vanselow (1932), Gapon (1933) and Krishnamoorthy, Davis and Overstreet (1945) did not describe these effects satisfactorily in Rothamsted and Woburn soils (Addiscott, unpublished data) probably because of the heterogeneity of the soil exchange sites. However they can be described in terms of the quantity/intensity relationship (Beckett, 1964) in which gain or loss of K by the soil is related to the activity ratio, the ratio of the activity of K^+ ions to the square root of the sum of the activities of Ca^{++} and Mg^{++} ions, $a_K/\sqrt{a_{Ca+Mg}}$. It can be shown whether the observed effects of K added or removed into the plants on the activities of K^+, Mg^{++} and Ca^{++} accord with an independently-measured quantity/intensity relationship, but quantitative prediction of these activities is not possible.

Although adding K should have no direct effect on the anionic composition of the soil solution, its co-ion will alter it; further, if adding K stimulates the absorption of an anion by the plant, this will affect its concentration.

A note on activities and concentrations. In conventional analysis of an ion in solution its concentration (c_i) is measured. Its chemical potential in an ideal solution would be

$$\mu_i = \mu_i^o + RT \ln c_i$$

where μ_i^o is its chemical potential in a reference state, R the gas constant and T the absolute temperature. The interactions between ionic charges make all solutions non-ideal, and in soil solutions fixed charges on clays

may increase the non-ideality, so in real solutions the chemical potential is redefined as

$$\mu_i = \mu_i^o + RT \ln a_i$$

where a_i is the activity of the ion. The ratio a_i/c_i, the activity coefficient, is a measure of the deviation from ideal behaviour. Polyvalent ions, having multiple charges, are more subject to interactions and have smaller activity coefficients. Activities may be measured directly by ion-specific electrodes or calculated from the ionic strength by one of a series of equations derived by Debye and Huckel (1923).

Because of the charges on clays, much discussion has centred on the adequacy of the ionic composition of the soil solutions for describing the root environment. (See Olsen (1968, 1969) and Franklin & McLean (1963, 1969) for conflicting viewpoints - and data.) Fortunately, in moist, well-structured soils, the argument may be irrelevant because the soil pores may be large enough for most ions not to be close to the clay charges (Khasawneh, 1971).

The concentration, rather than the activity, has been used in much work on ion absorption from solution, but in a typical soil solution the (calculated) activities of mono- and di-valent cations may be only 0.7 and 0.5 times their respective concentrations.

A note on 'contact exchange'. The text diagram on page 9 showed 'contact exchange' directly between the soil surface and the root. Jenny (1951), noting that all ions oscillate within a definite volume round their exchange sites, suggested that roots penetrating these volumes could absorb the ions without their entering the bulk solution. If so, the root environment would not be adequately described by the ionic composition of the soil solution, but 'contact exchange' has never been

unequivocally shown to play an important part in ion absorption, especially in structured soils, and was not taken into account in this study.

Soil Solution to Root Surface

Three mechanisms are recognised by which ions move in the soil to the root surface, diffusion, mass flow in water moving to the root, and root interception, which is not a clearly defined phenomenon; it may imply no more than contact exchange, or it may include the concept of root exploration facilitating the accumulation of ions by diffusion and mass-flow.

The relative importance of the mechanisms varies between ions. Diffusion probably conveys most K^+ (Oliver & Barber, 1966; Drew, Vaidyanathan & Nye, 1966) except possibly when K fertilising makes mass-flow more important (Addiscott & Talibudeen, 1971). Ca^{++} and Mg^{++} ions seem to be moved mainly by mass-flow (Oliver & Barber, 1966; Blanchet, Bosc & Maertens, 1970). Both Olsen, Kemper & Jackson (1962) and Lewis and Quirk (1967) rated diffusion most important for conveying P.

Interactions between ions in diffusion processes have been little studied, but giving K should not much affect the diffusion of other species. Where giving K increases the concentration of other cations in the soil solution it will increase mass-flow transport.

Root interception is difficult to evaluate, and some workers (e.g. Nye, 1968) dismiss it as of no importance. Adding K should not decrease any root interception that occurs provided it causes no osmotic damage.

Interactions in ion transport were expected to be trivial compared with those in other processes and were not investigated.

Root Surface to Root Xylem

Two problems are discussed, (a) the means by which ions are absorbed, and (b) the path they follow.

(a) The means of absorption

Different ions are probably absorbed by different mechanisms, most of which are not yet fully understood.

Passive absorption is the simplest possibility. It implies that an ion moves into the root down a gradient in its electrochemical potential

$$\bar{\mu}_i = \bar{\mu}_i^o + RT \ln a_i + z\mathcal{F}\psi$$

where z is the ion's valency, $\mathcal{F}$ the faraday, and ψ the potential difference between the inside and the outside of the root. ψ is usually negative, and so cations may move down an electrochemical gradient while moving up an activity gradient, whilst anions may not be able to move passively down an activity gradient.

The origin of the potential difference is not yet known. Shone (1969) listed five possibilities; (a) a diffusion potential caused by differential back-diffusion of anions and cations from the xylem (where their concentration is large relative to the surroundings); (b) a 'Donnan' potential resulting from indiffusible charges in the cell walls; (c) an electro-osmotic potential due to salts and water moving past fixed charges in the cells; (d) a 'carrier' potential caused by the movement of a charged carrier (to be discussed); (e) a transport potential due to metabolic

processes transporting anions and cations into the root at different rates. The potential, whatever its nature, seems to be metabolically maintained because metabolic inhibitors much decrease it (Shone, 1968, 1969).

Passive absorption must be inferred with caution because the potential is probably so intimately related to ion movements, and also because passive absorption may appear to occur where an ion is absorbed over an electrochemical potential 'hump' involving no net increase but still needing metabolic intervention. Dunlop and Bowling (1971c) found K^+ and Cl^- ions entered maize roots against an electrochemical potential gradient in each case but later moved down a smaller gradient into the xylem, so that the height of the 'hump' was greater than the net increase.

Cations, except perhaps K^+, often seem to be passively accumulated but anions to be actively accumulated (Bowling & Spanswick, 1964; Bowling, Macklon & Spanswick, 1966; Shone, 1968; Sobey, MacLeod & Fensom, 1970; Dunlop & Bowling, 1971c).

Active absorption of ions is powered ultimately by respiration. Using respiration energy to drive ion absorption may involve separating the hydrogen and hydroxyl ions formed in respiration by a membrane that conducts electrons readily but ions less so. Normal respiration may be written overall:

$$C_6H_{12}O_6 + 6H_2O + 6O_2 \longrightarrow 6CO_2 + 12H_2O + 686 \text{ kcal}$$

but when the ions are separated

$$C_6H_{12}O_6 + 6H_2O \longrightarrow 6CO_2 + 24H^+ + 24e^-$$

$$\downarrow \quad 6O_2 + 12H_2O$$

$$24OH^- + 458 \text{ kcal.}$$

Lundegardh (1939), who first proposed this type of absorption, suggested that membrane-bound cytochrome systems transferred electrons in one direction and anions in the other. In a review, Robertson (1960) noted that it might be possible for the generation of adenosine triphosphate (ATP) to set up a system in which the charges became separated and Mitchell (1961, 1966) suggested such a system. In it, an oxidation-reduction system (powered by reduced nicotinamide adenine dinucleotide produced by the Krebs cycle) drives a proton current which links with a reversible ATPase system generating ATP and also with a cation/proton antiport and an anion/proton symport (systems in which the flow of protons drives cations the other way and anions the same way). The overall effect is that ATP is generated, cations propelled out of the membrane, anions propelled inwards, and the inside of the membrane kept electrically negative. Mitchell's system has been described as operating in the mitochondria of plant (and animal) cells, but the mitochondria may be involved in the ion transport process (Robertson, 1960).

Lundegardh's hypothesis is now mostly rejected, partly because Robertson and Wilkins (1948) showed that some concentrations of the metabolic inhibitor 2,4-dinitrophenol inhibited ion uptake whilst enhancing the cyanide-sensitive respiration which Lundegardh thought was responsible for ion uptake. This objection need not apply to the Mitchell hypothesis.

Examining the second respiration equation shows that no more than 4 g-equiv. of ions can be transported per g-mol of O_2 consumed; if this quotient is exceeded, both these hypotheses fall. There has been much controversy (e.g. Handley & Overstreet, 1955; Sutcliffe & Hackett, 1967; Sutcliffe, 1959; Robertson, 1960) as to whether it is exceeded, but without an unequivocal resolution of the problem. Further, the absence of

competition in absorption between anions, except the halide anions, is an anomaly in these hypotheses, as is the apparent ability of some cells to 'store' the capacity to absorb anions.

The possibility of 'over-efficient' absorption and 'storing' of absorptive capacity suggests that there may be an energy-storing intermediate, presumably ATP, between respiration and absorption, i.e. ATP may be used rather than regenerated when ions are absorbed. No specific linkage between ATP and anion absorption has been shown, although Steward and Millar (1954) hypothesised that it might occur during protein synthesis. For monovalent cations the picture is a little clearer; absorption appears often to obey enzyme kinetics (e.g. Epstein & Hagen, 1952), and Sexton and Sutcliffe (1969) found that the distribution of ATPase along the axis of pea root much resembled the pattern of ion transport found along the root axis of maize by Brown and Cartwright (1953) and Hanson and Khan (1957). Fisher, Hansen and Hodges (1971) found a good correlation between Rb^+ influx into the excised roots of several species and the Rb^+-stimulated part of the ATP-ase activity of the roots. Several results (e.g. Epstein, 1961; Luttge & Laties, 1967) have suggested that there are two absorption systems; system 1 has a large affinity for K and operates mainly at small external K concentrations and system 2 have a small K-affinity and works at larger K concentrations.

No such enzyme systems have been found for divalent cations, and Pitman (1965) and Lazaroff and Pitman (1966) found that mono- and di-valent cations seemed to be absorbed by different mechanisms. Even so, Ca seems necessary for roots to discriminate between K^+ and Na^+ (Epstein, 1961).

It should also be noted that if an ion is passively absorbed but immediately metabolised in a process drive by energy from respiration, it

may appear to be actively absorbed. Nitrate ions may be rapidly metabolised in roots (Dijkshoorn, 1962; Kirkby, 1969) and Loughman and Russell (1957) found phosphate could be rapidly incorporated, via an intermediate, into ATP.

It was implicit in most of the preceding discussion that cations and anions are independently absorbed (except in respect of electrical effects); simultaneous active absorption would imply an amphoteric carrier, which seems unlikely, although Bennett-Clark (1956) suggested lecithin might act in this way. However, Ordin and Jacobson (1955) showed that inhibitors that interfered with glycolysis and the Krebs cycle (and so with ATP replenishment) affected uptake of K^+ and Br^- to different extents, suggesting different mechanisms.

(b) Ion pathways

The pathways followed by ions moved from the surface of the root to its xylem are still speculative. Most probable is the 'Symplasm Theory' of Crafts and Broyer (1938) (also Lundegardh, 1940; Arisz, 1956), whereby the ions move in the cytoplasm of cortical cells to the stele, where they 'leak' into the xylem vessels. The 'symplasm' is a continuum in which the cytoplasm of each cortical cell is connected to that of the next through the plasmodesmata. Another theory suggests that the ions move passively through the 'apparent free space' in the root (Briggs & Robertson, 1957) to the endodermis where they are absorbed and secreted into the xylem vessels (van Andel, 1953; Russell & Shorrocks, 1959; Bowling & Weatherley, 1964). (The 'apparent free space' is the volume of root tissue that is apparently passively penetrated by solute ions in conditions that inhibit active absorption.) A theory of Hylmo (1953) suggests that the barrier to absorption lies in xylem vessels that are not fully differentiated.

These pathways could operate simultaneously. Minchin and Baker (1970) resolved the flux of K^+ through Ricinus roots into water-independent and water-dependent components and suggested that the former moved in the symplasm and the latter through the cellwalls, which probably constitute an appreciable proportion of the apparent free space.

Dunlop and Bowling (1971a, b, c) measured the profiles across maize roots of the activities of K^+ and Cl^- and the potential difference relative to the external solution and concluded that their results accorded best with the symplasm theory. Jarvis and House (1970) have also recently found evidence for the symplasmic pathway.

There has been much discussion about the location of absorption mechanisms in the pathways, especially of the so-called 'system 1' and 'system 2' monovalent cation carriers. Welch and Epstein (1969) claimed the systems worked in parellel across the plasmalemma, but Luttge and Laties (1967) thought 'system 1' could be located in the plasmalemma and control the absorption of ions into the cytoplasm, whereas 'system 2' was placed in the tonoplast to feed ions into the vacuole and only operated (passively) at large external K concentrations, possibly when the cytoplasm was 'full up'. In the latter scheme, only 'system 1' moved ions to the xylem. Minchin and Baker (1970) concluded that the water-independent flux of K^+ they found could cause the 'system 1' effects, but their results did not show that 'system 2' moved K^+.

A feature of the root that may affect absorption is the Casparian Strips in the cells of the endodermis, which are strips of suberised material that appear to be a barrier to permeability; they are unique, which suggests they have a definite function. In the theory of van Andel (1953) and other workers, the endodermis is the barrier to passive

absorption and the site of any active absorption, but the symplasm theory offers no definite function for it, which is sometimes held against the theory. It might, however, act as a barrier to back-diffusion of solutes from the stele. Dunlop and Bowling (1971a) found no change of potential or K^+ activity across the endodermis of a maize root.

(c) Possible effects of K^+ on the absorption of other ions

Added K^+ seems more likely to affect the mechanism than the pathway of ion absorption, except where the two are inter-related.

The simplest interactions would be expected when other monovalent ions competed with K at enzyme carrier sites (e.g. K-Na, Epstein, 1961) and these have been found. However, although mono- and divalent cations seem to be absorbed by different mechanisms, interactions in their absorption are well known (e.g. Overstreet, Jacobson & Handley, 1952; Leggett & Gilbert, 1969; Maas, 1969 (excised roots) and Johansen, Edwards & Loneragan, 1968 (intact barley plants).

Various workers (e.g. Bear, 1950; Dijkshoorn, 1958; Cunningham, 1963a, b, c) have shown that the sum of cations was related to the sum of the anions in plant dry matter. This could occur where an anion carrier actively absorbed anions and caused the passive absorption of cations. If the rate of anion absorption was fixed, increasing the supply of one cation would probably increase its absorption and decrease that of another cation.

Alternatively, K^+ could affect the absorption of divalent cations through its effect on the potential difference between the xylem and the external solution. Shone's (1969) results for maize roots suggest that the relative mobilities of anions and K^+ ions (K^+ slower) may be a major factor causing this potential difference, and so giving K and thereby increasing

the inward flux of K^+ ions should decrease the potential difference. Such an effect was found by Davis and Higinbotham (1969) and Dunlop and Bowling (1971b). Decreasing this (negative) potential difference should decrease the passive absorption of other cations.

Anion absorption may not be much affected by adding K; decreasing the negative potential difference between the xylem and the solution should facilitate anion absorption, but the effect might not be very large compared with the active absorption of anions that often seems to occur. K^+ ions stimulate some ATPase systems and so might enhance anion absorption for which ATP supplied energy.

Redistribution in the Plant

The redistribution of ions in the plant involves two problems, how the ions move and why they move, i.e. the mechanics of translocation and the factors governing ion distribution. These problems are only partially separated.

The Mechanics of Translocation

Upwards. Ions moving from the roots to their first destination in the plant travel in the xylem; the phloem does not seem to be involved (see Biddulph, 1959, for a review). Water is believed to be drawn up through the xylem by transpiration, as a result of the cohesion of the water in the capillary-like xylem vessels (Kramer, 1959). Water seems able to move in either direction in the xylem, but presumably only upwards during transpiration; Baker and Moorby (1969) showed water seemed to move down into potato tubers through the xylem at night. Ions seem mostly to be drawn up dissolved in the water in the xylem stream, although Bell and

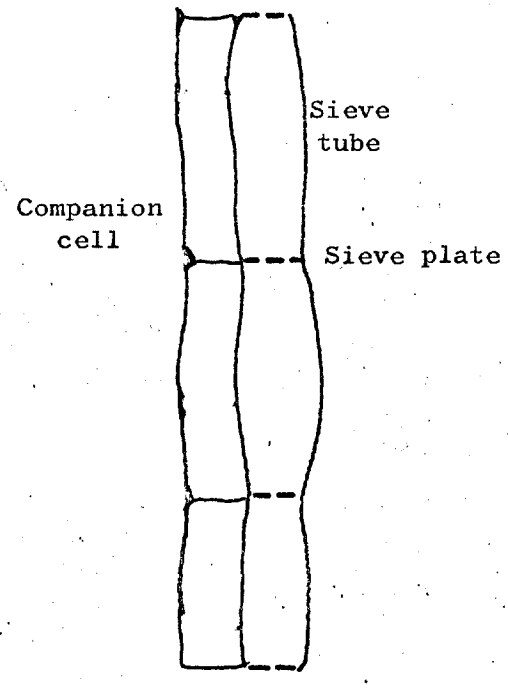
Biddulph (1963) found ^{45}Ca moved up the stem in a way suggesting it moved by a series of exchange reactions. No interactions between K^+ and other dissolved ions seem possible, and Bell and Biddulph (1963) found K did not influence ^{45}Ca movement.

Redistributed ions. The xylem stream tends by its nature to conduct ions to mature leaves, although a proportion of the ions may remain in the stems and petioles. Ions that are redistributed from their first destination probably move mainly in the phloem (Biddulph, 1959). The mechanism of phloem translocation, long a subject of contention, is still not known for certain. Translocation is generally accepted to take place in the sieve tubes of the phloem, which are fairly lengthy tubular elements separated by sieve plates with pores in them (Fig. 1/1a, b); they are accompanied by parallel 'companion cells'. Hypothetical mechanisms depend very much on their exact structure and, in particular, on the location of the considerable amount of fibrillar protein the tubes contain, which may or may not be accumulated in and around the sieve plate pores. (Fig. 1/1b shows some feasible distributions of the protein.) Cytologists disagree on the location of this protein; some find that it is in the pores, but others claim that cutting the material for slide preparation causes a release of pressure that 'blasts' the protein from the tubes into the pores.

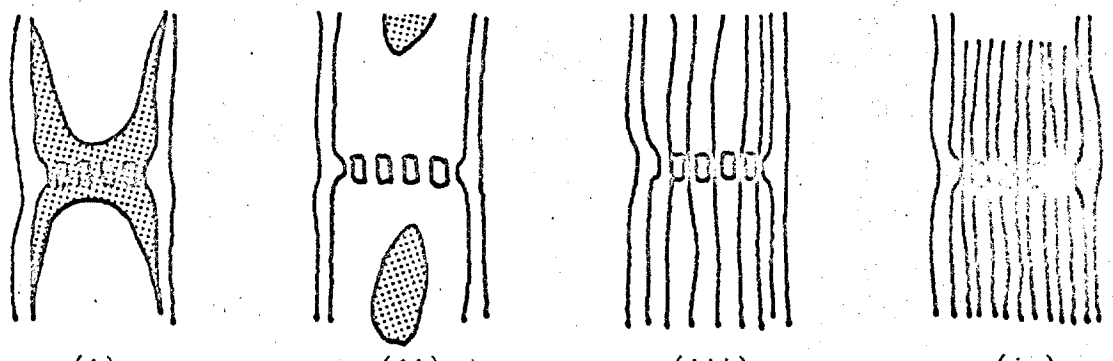
The longest-standing hypothesis is that of Munch (1926), who suggested that water, sugars and ions moved in a bulk flow in the sieve tubes under the influence of an osmotic pressure gradient caused by unequal sugar concentrations, which may be large because soluble sugars are 'loaded' (i.e. have their concentration increased) from the mesophyll tissue to the phloem and 'unloaded' at their destination, giving the concentration profile shown in Fig. 1/2a. Although the Munch hypothesis probably can account for

Fig. 1/1

(a) Sieve tube



(b) Possible distributions of the fibrillar protein



(i) Accumulated in and around the sieve pores
(ii) In discrete globules not in the pores
(iii) In strands passing through the pores
(iv) In transcellular tubules (Thaine)

the quantity of material moved, there are objections to it. First, it depends on the fibrillar protein not being in the pores of the sieve plates; this would make the pressure gradient impossibly large. It is also doubtful whether a large enough osmotic gradient exists in tall trees, and Scholander, Hammel, Hemmingsen and Bradstreet (1964) showed that in mangrove trees the xylem has a large negative pressure which seems unlikely to co-exist easily with the required large positive pressure in the phloem.

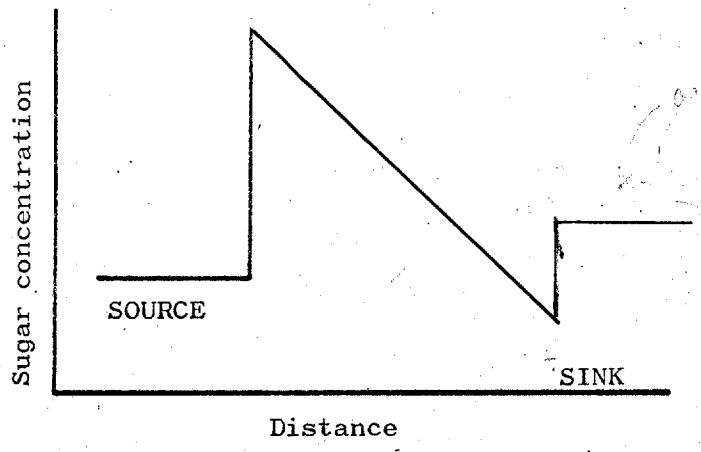
Thaine (1969) suggested that phloem translocation is impelled by peristaltic movements in transcellular tubules (Fig. 1/1b). Aikman and Anderson (1971) showed that taking likely values for the amplitude and velocity of the peristaltic waves led to acceptable velocities of solution flow and a reasonable energy requirement, but again the idea depends on the nature of the fibrillar protein.

Other, not dissimilar, suggestions have included force-generating filaments and protoplasmic streaming in the sieve tubes, although Spanner (1962) questioned whether the sieve tubes have a large enough metabolic rate to operate the latter mechanism.

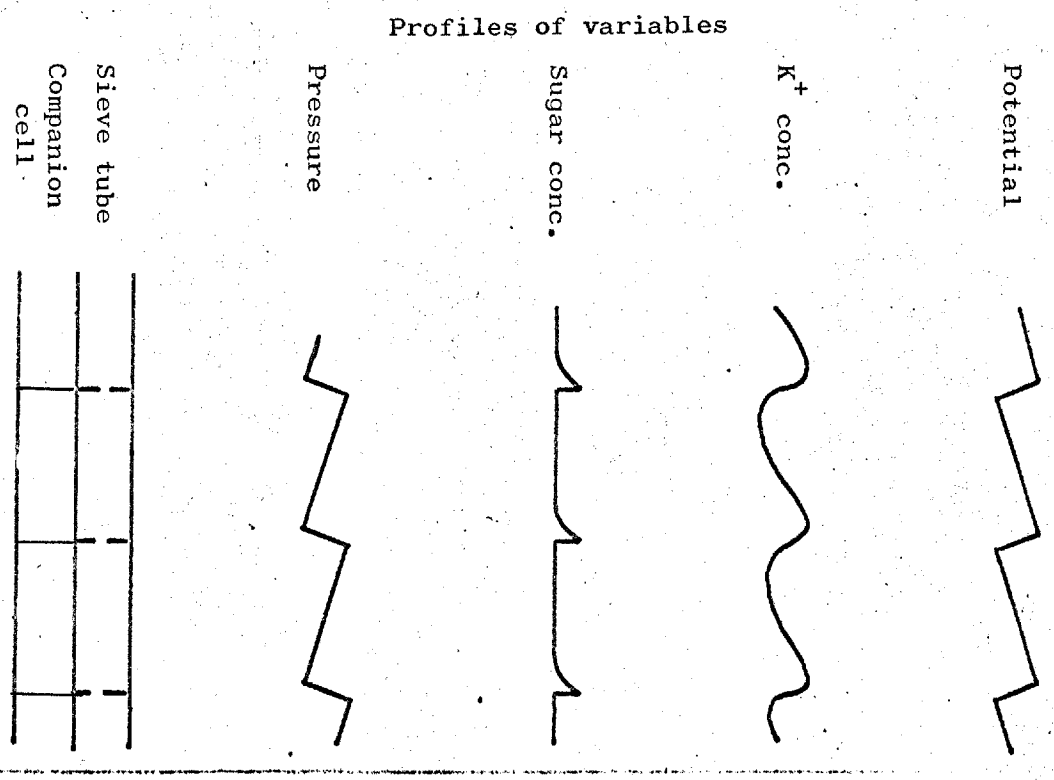
In none of the above mechanisms should varying the concentration of K^+ ions much affect the translocation of other solutes, particularly ions, in the phloem, but in Spanner's electro-osmotic theory (1958), K^+ ions play a vital role. Spanner suggested that phloem transport is assisted by localised circulation of K^+ ions through the sieve plates and back via the companion cells or (Spanner, 1970) weaker parallel sieve tubes; this is hypothetically driven by 'pumping' K from the 'downstream' side of the sieve plate (Fig. 1/2b) into the companion cell or weaker tube, and results in polarisation of the sieve plate, which has been observed by Bowling (1968, 1969), with the 'downstream' side negative. He argued that water

Fig. 1/2

(a) Diagrammatic representation of 'loading' and 'unloading' of the phloem



(b) Diagrammatic representation of Spanner's electro-osmotic theory of phloem transport as originally proposed.



and other substances would partly be carried in the field of the K^+ ions and partly be frictionally impelled by their passage.

Spanner suggested that translocation could be initiated by a discharge of sugar into the upper sieve tube withdrawing water from the companion cell (or weaker tube) and thereby starting the K^+ ions circulating (Fig. 1/2b); the effect would travel down a series of tubes in the same way, and it would be halted when the sugar concentrations at the ends of the tubes were equalised. The system provides for transport in either, but not both, directions.

The hypothesis provides a role for the energy produced in phloem respiration and for the large concentrations of K^+ ions found there (Table 1/1). The most important objection to it lies in the very large K^+ fluxes needed to move the observed sugar fluxes; this is difficult to evaluate because of the small scale (size) of the supposed phenomenon. It has also been argued that anion movements in the phloem would be hindered by the negative sieve-plate potential difference, but Bowling (1968, 1969) found the potential difference was about - 20 mV, which means that monovalent anions would need to be 2.2 times more concentrated above than below the plate to cross it, not an impossibility. Furthermore, Peel and Weatherley (1959) found no inorganic anions in the phloem of Salix and Tammes and Van Die (1964) found only phosphate in that of Yucca, and the organic anions found, such as citrate, might be partly generated and removed in the course of the coupling of the respiration to K 'pumping'; they could then maintain electroneutrality without necessarily moving down the phloem.

Probable profiles of electric potential, turgor pressure and K^+ concentration suggested by the theory are shown in Fig. 1/2b. Bowling (1969)

TABLE 1/1

Concentrations of ions found in the phloem by various workers

	Authors+			
	1	2	3	4
Species	Salix	Yucca	Vitis vinifera	Ricinus
Conc (mM) of				
K^+	51	43	89-100**	60-80
Ca^{++}	Nil	0.35	n.d.*	0.5-1.0
Mg^{++}	n.d.*	2.1	"	n.d.*
Na^+	Trace	0.18	"	9-12
Phosphate	Nil	3.4	"	n.d.
NO_3^-	Nil	Nil	"	n.d.
Cl^-	Nil	n.d.	"	n.d.
pH	n.d.	8.0-8.2	"	8.2

* not determined

** activity measurement

+ 1 Peel, A. J., & Weatherley, P. E. (1959)

2 Tammes, P. M. L. & van Die, J. (1964)

3 Bowling, D. J. F. (1969)

4 Hall, S. M., Baker, D. A. & Milburn, J. A. (1971)

found evidence of the 'saw-tooth' potential profile.

Giving K to the plant should increase the phloem's K^+ concentration and the localised K^+ fluxes, thereby increasing the movements of sugars (see Hartt, 1969), water and all uncharged molecules. The effects on ion movements will depend on how the increased K^+ concentration affects the sieve-plate potential difference.

The factors governing ion distribution

Mobility in the xylem and the phloem. All ions seem to be mobile in the xylem, even if Ca^{++} ions may move differently from others, but ions vary greatly in their apparent ability to move in the phloem and this much influences their redistribution in the plant.

Bukovac and Wittwer (1957) assessed the mobilities of ions in bean plants by the extent to which their isotopes moved away from the leaf to which they were applied. The monovalent cations were the most mobile and Ca^{++}, Sr^{++} and Ba^{++} the least; P and Cl were slightly less mobile than the monovalent cations and Mg^{++} was provisionally placed with Ca^{++}, Sr^{++} and Ba^{++}. However, this experiment was really a test of whether the ions could move out of the leaf and Biddulph, Cory and Biddulph (1959) and Ringeot, Sauer and Gielink (1968) found Ca^{++} seemed to be immobile, not because it cannot move in the phloem, but because it is strongly retained by leaf tissue. The same may be true of Mg^{++}, and Steucek and Koontz (1970) showed Mg^{++} could move in the phloems of bean and barley plants.

Obviously, an important criterion of an ion's mobility in the phloem is its concentration in the solution there; this is difficult to measure, but Table 1/1 summaries the results of some recent work. K^+ was always the dominant ion and, as expected, very little Ca^{++} seems present. Tammes

and van Die (1964) found Mg^{++} six times more concentrated than Ca^{++}, a reversal of the order usually found in the soil solution and the xylem.

'Sink' effects. The twin concepts of 'sources' and 'sinks' of and for photosynthate have proved a useful way of understanding the movements of photosynthetic assimilates in the plant. Mature leaves act as the 'source'; a 'sink' can be defined simply as 'wherever in the plant the products of photosynthesis are utilised' (Beevers, 1969). The most studied 'sinks' have been storage organs such as cereal ears (e.g. Thorne, 1963), beet roots (Thorne & Evans, 1964) and potato tubers (e.g. Nosberger & Humphries, 1965; Moorby, 1968, 1970). 'Sinks' also attract other metabolites such as amino-acids, and they influence ion movements; Kissell and Ragland (1967) found that N, P, K and Mg were substantially redistributed from the vegetative parts to the ears in Zea Mays and Moorby (1968) found N, P and K moved from the haulm to the daughter tubers of potato plants.

It seems accepted that the attractive effect operates through hormones. Various combinations of indolyl-3-acetic acid, gibberellic acids and cytokinins produce it; there seems to be no consistent order of effectiveness and the one present in the smallest amount (relative to its norm) probably has most effect (e.g. Mothes & Engelbrecht, 1961; Davies & Wareing, 1965; Seth & Wareing, 1967; Morris & Thomas, 1968). Precisely how these hormones act is not known; they have the capacity to cause cell proliferation, they are involved in the growth of storage organs and they have specific effects on translocation, but the key facts linking these effects are still to be discovered; they seem likely to be associated with the nucleic acid metabolism of the plant.

'Sink' interactions and plant development. Before a plant forms a storage organ, the 'sink' effects seem quite simple, with the lower leaves

exporting assimilate mainly to the roots and the upper leaves to the developing shoots. This pattern was found for soybean by Thrower (1962), for grape by Hale and Weaver (1962) and for bean plants by Biddulph and Cory (1965). Little is known of the corresponding pattern for mobile nutrient ions, but work by Greenway and Pitman (1965) and Steward and Koontz (1968) suggests K movements may be similar.

When a flower or storage organ forms, this pattern is disrupted and assimilate seems to be directed mainly to the new organ at the expense of shoot and root growth. Murneek (1926) found shoot growth recessed in tomato plants when the fruit formed and Milthorpe (1963) reported similar effects in potatoes. Mobile nutrients seem to behave in the same way (Kissell & Ragland, 1967; Moorby, 1968).

The concept of the 'sink' is essentially a model, albeit a most useful one, for describing and rationalising the movements of metabolites and ions in the plant. The concept may be intrinsically true or it may merely be a representation of the effects of an innate programme of development and senescence, perhaps mediated by the nucleic acid metabolism of the plant and activated by environmental stimuli. The difference between the two points of view can be illustrated by reference to the phenomenon of shoot recession when the tubers form in potato plants.

According to the first viewpoint, the recession in shoot growth reflects competition between the tubers and the shoot with the former gaining the ascendancy. The second viewpoint suggests that the recession arises from a regulated shift of growth activity related to the 'innate development programme'. Heslop-Harrison (1969) discussed these viewpoints and noted that several recent authors have favoured the latter.

Changes in the concentrations of nutrients in leaves were associated with senescence by Kirkby and de Kock (1965) who found that the %Ca increased and the whole cation:anion balance changed going from young to older leaves on brussel sprout plants. Concentrations of P and K in leaves often decrease with age and that of Mg sometimes increases. These effects can be viewed in terms either of competition between 'sinks' or of the 'innate development programme'.

In potato plants, adding K often increases the weight of tubers formed, i.e. enlarges the 'sink'. Giving K can also extend the life of the plant (Dyson & Watson, 1971) and so may affect the 'innate development programme'. Either way, it seems likely to influence the distribution of other nutrients.

The Aim of the Work

The experiments to be described were intended to show how added K behaved in the plant and how it influenced the uptake and distribution of other nutrients. These interactions are interesting partly in their own right and partly because they may throw some light on the overall working of the plant. They are also of practical importance because potato crops usually get heavy K dressings, for example an average of 200 units K_2O/acre* (208 kg K/ha) for maincrop potatoes (Potato Marketing Board, 1970). The interactions of such dressings may prove important in attempts to increase yields while maintaining quality.

The following specific aims were pursued:

1) It seemed likely that adding K to the soil would increase the concentrations of other cations in the soil solution while lessening their uptake by the roots. The relative importance of these effects was therefore tested (Chapter 3).

* 1 unit = 1.12 lb

2) The interactions in root uptake were followed to see if they changed as the plants developed and senesced (Chapter 3).

3) The effects of giving K on other nutrients in potato tubers were measured. The tubers are the best defined 'sink' in the plant and they do not themselves photosynthesise; they thus make the best starting point for determining interactions caused by 'sink' effects (Chapter 4).

4) The apparent consequences of the interactions in the tubers for the nutrient content of the rest of the plant were examined (Chapters 4 and 5).

5) An interaction found in the tubers was sought in another 'sink' (Chapter 6).

6) An experiment was made to investigate whether interactions arising from the formation of tubers accorded better with the concept of competition between tuber and shoot or with that of the 'innate development programme' (Chapter 6).

7) A mechanism for the observed effects was sought (Chapter 7 et seq).

CHAPTER 2

GENERAL METHODS

This chapter comprises a discussion of the methods used and details of methods common to all the experiments made.

Growing Potato Plants

In these experiments, the plants were all grown in the glasshouse in pots or polythene buckets, except in the last experiment where they grew in solution. In both pots and solution the plants grew to maturity and formed tubers. Plants grown in pots were slenderer than those from the field regardless of the size of the pot, possibly because the roots were restricted or because growth started earlier in the warmer glasshouse than in the field. This should not have affected nutrient uptake or distribution. Plants grew to a more normal shape in the solution than in the pots.

The size of the plants much increased with the weight of soil used, 400 g, 2 kg or 3 kg. Plants grew in solution to about the same size as in the largest weight of soil.

Soil preparation

The soil was air-dried before each experiment and sieved to $\frac{1}{8}$ inch. Before planting, it was moistened with deionised water and/or the appropriate nutrient solution and well mixed. One part of quartz (< 2 mm) to two parts of soil was added in the first experiment.

Variety

King Edward potatoes were grown in all the experiments.

Seed pieces

In the first experiment, viable eyes were cut from chitted seed potatoes with a $^{3}/_{8}$ inch cork borer to give a $\frac{1}{2}$ inch long segment. These were incubated in moist sand until roots about 1 inch long had developed, and transplanted into the prepared soil. The method was reliable but gave rather small plants, though in retrospect this can probably be attributed to the weight of soil used.

In the second experiment, small seed potatoes as even in size as possible (about 50 g) were used. These produced sturdier plants, albeit in more soil, but the amounts of nutrients they contained would be a complication in some experiments.

In the third and fourth experiments, excised eyes were used again, but larger ones, taken with an $^{11}/_{16}$ inch cork borer and with a 1 inch long segment of tuber. These gave good plants.

The size and sturdiness of the plants seemed much more influenced by the soil (amount and nutrient content) than the seed pieces.

Watering

Water was given in saucers under the pots unless otherwise stated.

Harvesting

Unless the nature of the experiment dictated otherwise, the plants were separated at harvest into leaves, stems + petioles (afterwards referred to as 'stems'), roots + stolons ('roots'), and tubers. Roots and tubers were washed and blotted free of water. The samples were weighed fresh if % dry matter was needed, dried at 80°C for 24 hours, weighed and ground in a small hammer mill.

Analyses

Dry matter samples were ashed at 450°C for 2 hours and the ash taken up in 5 ml of 5 N hydrochloric acid and evaporated down again; it was finally moistened with 0.5 N HCl and taken up in water.

All solutions were analysed as follows:

Potassium was determined by flame emission on an Evans Electroselenium flame photometer; Calcium* and Sodium*, also by flame emission on a Unicam SP900 spectrophotometer; Magnesium* by atomic absorption also on the SP900; Phosphate[+] by the method of Fogg and Wilkinson (1958) on a Technicon Auto-analyser; Nitrate[+] by the method of Litchfield (1967) also on the auto-analyser.

Nitrogen in dry matter[++] was determined directly by a standard Kjeldahl procedure using K_2SO_4 and $CuSO_4$ catalysts.

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* by V. Cosimini; [+] by Miss B. Messer; [++] by R. J. Avery

CHAPTER 3

THE EFFECTS OF ADDING POTASSIUM ON ION CONCENTRATIONS IN THE SOIL SOLUTION AND IN THE SAP EXUDED FROM DETOPPED PLANTS

Introduction

In Chapter 1, it was suggested that adding K to the soil should increase the concentration of other cations in the soil solution as well as that of K, but that the increased concentration of K may lessen the absorption of other cations by the plant (e.g. Overstreet et al, 1952; Johansen et al, 1968; Andrew & Robins, 1969; Maas, 1969). This chapter describes an experiment intended to show the relative importance of these effects. It also discusses the changes in absorption that occurred as the plants developed.

Effects on the soil solution composition were shown by measuring ion concentrations in water equilibrated with the moist soil and effects on ion absorption by analysing the sap exuded from the xylems of plants cut just above the soil surface.

Methods

The pot experiment

The plants were grown from excised eyes in 400 g of soil from a long-term experiment in Barnfield at Rothamsted, from a plot that has had no fertiliser since 1856. Three plants per pot were grown, to improve the chances of obtaining sap. N, P and Mg at 100, 100 and 20 mg/pot were added as $Ca(NO_3)_2$, $Ca(H_2PO_4)_2$ and $Mg(NO_3)_2$ to the soil which had a pH of

8.0 and an initial exchangeable K content of 16 mg/100 g. There were six K treatments, 0, 20, 80, 160, 300 and 500 mg per pot as K_2SO_4. Two replicates of each treatment were harvested after 28, 44, 63 and 80 days and the last two replicates of each were harvested when the haulms died. Extra N (25 mg/pot) was added between the second and third harvests.

At harvest, the tops were removed just above the soil surface and bent capillary tubes were attached to the stumps with rubber tubing which was sealed with 'Vaseline'. The exuded sap was conducted to a small glass vial and collected for 24 hours, weighed, and analysed for K^+, Ca^{++}, Mg^{++}, Na^+, phosphate and nitrate. (No sap was, of course, collected from the dead plants.)

The treatment of the plant parts is described in the next chapter.

The soil solution

One aliquot of distilled water was shaken successively with three aliquots of the moist soil in a 1:2.5 soil:solution ratio, centrifuged at 6000 rpm and analysed for K^+, Ca^{++}, Mg^{++}, Na^+, phosphate and nitrate. This was done as soon as possible after harvest.

Concentrations and activities

For most purposes in this chapter, the concentrations of the ions in the soil extract are discussed, but the calculated activities are also recorded. These were obtained by an equation of Debye and Huckel (1923):

$$\log_{10} f = - \frac{0.509\, z^2 \sqrt{I}}{1 + 1.5 \sqrt{I}}$$

where f is the activity coefficient of an ion, z its valency, I the ionic

strength of the solution and a the activity = c x f , where c is the ion's concentration.

Because the equation includes the ionic strength, calculating activities in the soil solution necessitated estimating concentrations in the original soil solution rather than the extract. This was done by comparing the volume of water present as moisture in the soil aliquots with the total volume of water (moisture + added water). Assuming that the anions, mostly nitrate, in the soil solution were not absorbed and so were directly diluted, and that the cations obeyed Schofield's ratio law (Schofield, 1947) enabled the concentrations in the original solution to be estimated and I calculated. Possible effects of fixed charges were ignored (see Khasawneh, 1971).

Results

Appendix I contains the data for all ions in tabular form.

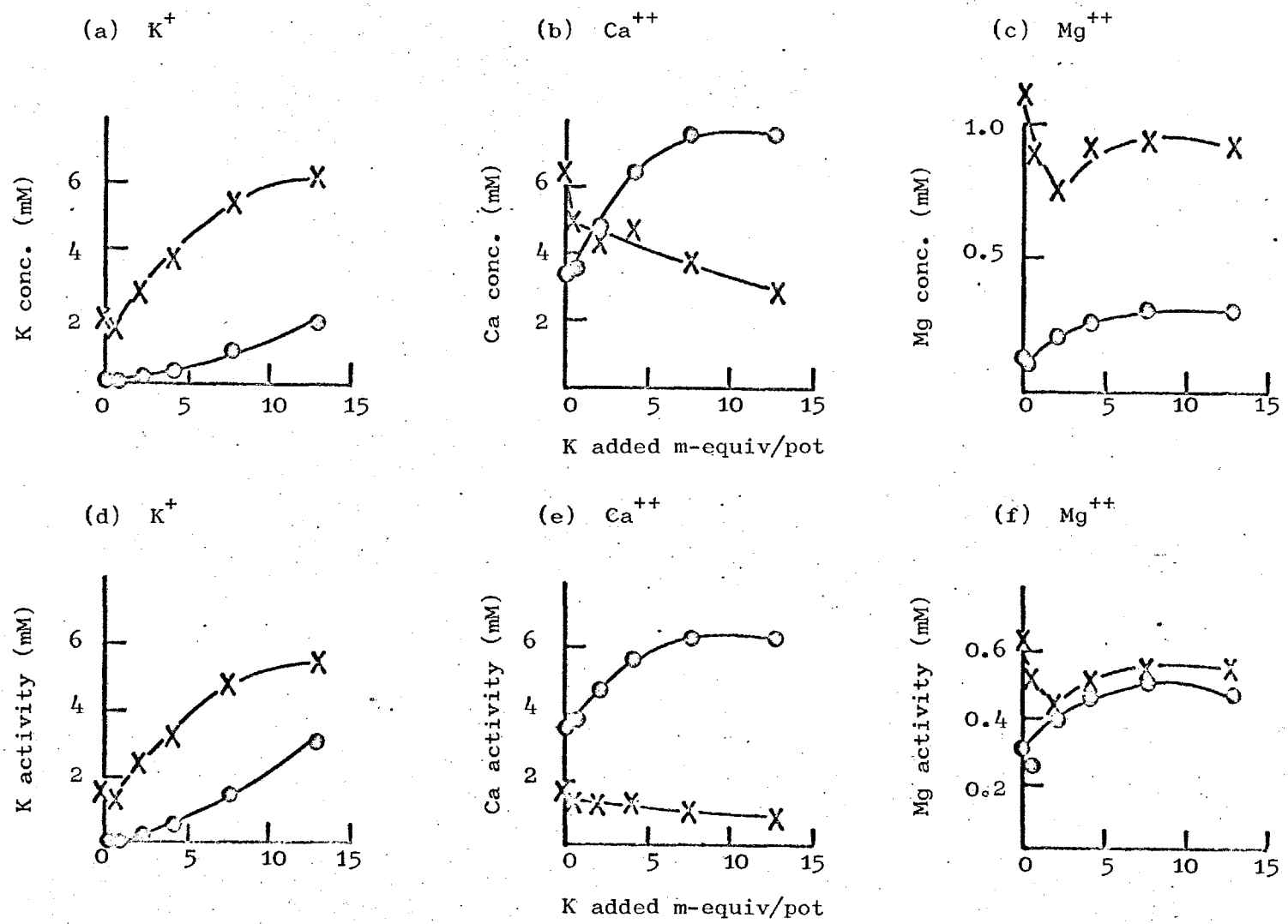
Cations

Fig. 3/1 (a-c) shows the concentrations of K^+, Ca^{++} and Mg^{++} in the soil extract and in the exuded sap at the first (28 day) harvest. Subsequent harvests showed a similar pattern, except that in the second and third harvests the K^+ concentration in the sap was decreased slightly by the largest K addition compared with the previous addition, and in the fourth harvest the concentrations of Ca^{++} and Mg^{++} in the sap were almost constant (although their concentrations in the soil extract increased with added K).

Fig. 3/1 (d-f) shows the calculated activities of K^+, Ca^{++} and Mg^{++} in the soil solution and the exuded sap at the first harvest. The concentration and activity data differed mainly in the relative displacements

Fig. 3/1

(a-c) Concentrations of K^+, Ca^{++} and Mg^{++} in the soil extract (●) and exuded sap (x) plotted against added K.
(d-f) Calculated activities (see text)



of the soil extract (or solution) and sap curves rather than in the shapes of the curves.

Effects in the soil. Fig. 3/1 shows that adding K increased the concentrations of Ca^{++} and Mg^{++} in the soil extract as well as that of K^{+}; this happened at all harvests.

The data was used to derive the potassium quantity/intensity relationship, between gain or loss of K by the soil (K added less K removed by the plant) and the K activity ratio ($a_K/\sqrt{a_{Ca+Mg}}$). This was compared with the relationship independently measured for the soil by equilibrating it with 0.01 M $CaCl_2$ solutions with and without added KCl (Addiscott, 1970). The points for harvests 1 and 2 fell on a smooth curve which was slightly displaced from the previous curve but had a similar shape (Fig. 3/2a); points for harvests 3 and 4 were further displaced in the same direction (Fig. 3/2b), that expected if K were 'fixed' by the soil or otherwise lost from the exchange system. Thus the effects of adding K concurred quite well with the known exchange characteristics of the soil.

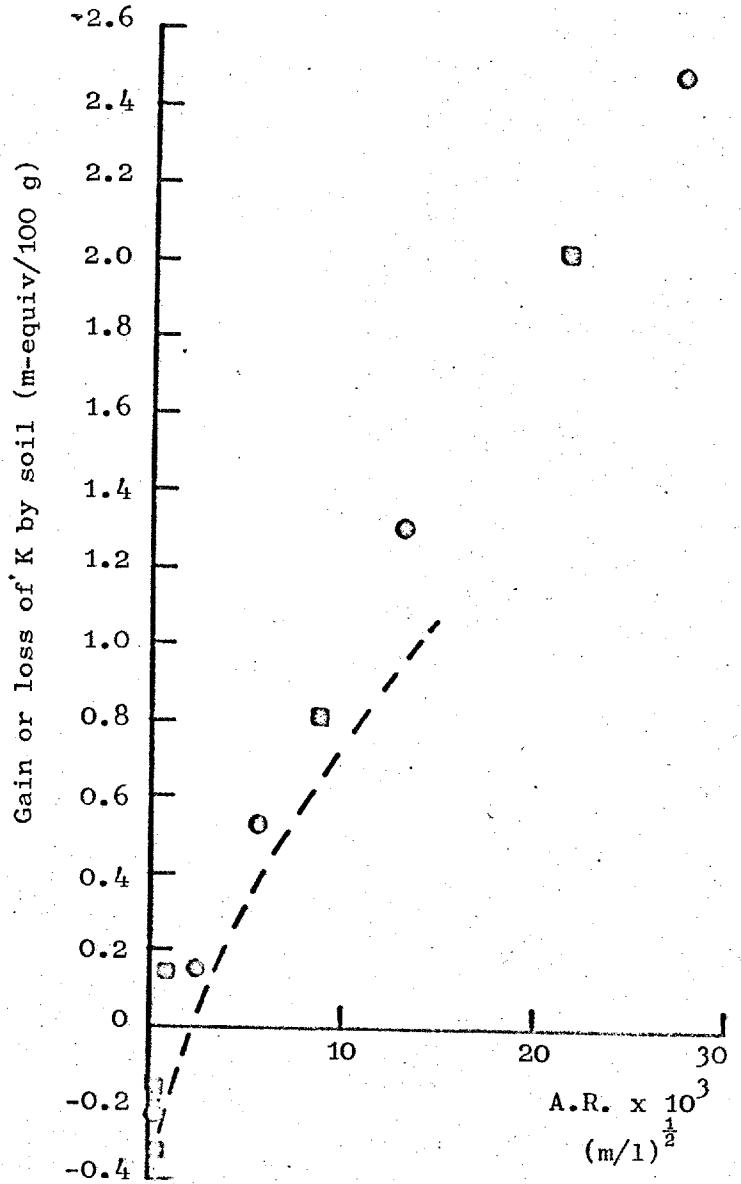
Effects in the plant roots. Because the concentrations of ions in the soil solution were not specifically controlled but allowed to vary naturally, the best measure of their uptake through the roots was probably the ratio

$$\frac{\text{concentration in exuded sap}}{\text{concentration in soil extract}},$$

which was called the 'accumulation ratio'. Fig. 3/3 (a-c) shows that the 'accumulation ratios' for K^{+} and Ca^{++} decreased in a smooth curve as the K^{+} concentration in the soil extract increased, but that for Mg^{++} the curve was not continuous. Fig. 3/3 (d-f) shows $\log_{10}$ (accumulation ratio) plotted

Fig. 3/2

Potassium quantity/intensity relationships for (a) Harvests 1 (●) and 2 (■), (b) 3 (o) and 4 (Δ), compared with the independently-determined curve



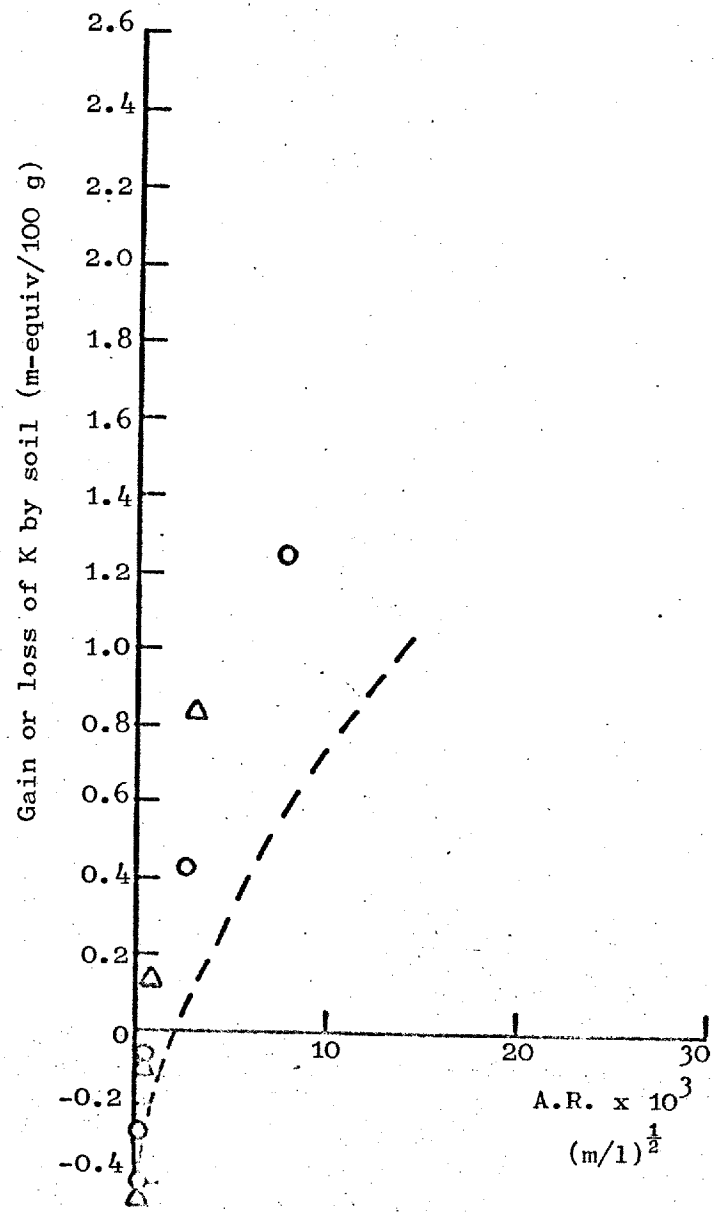
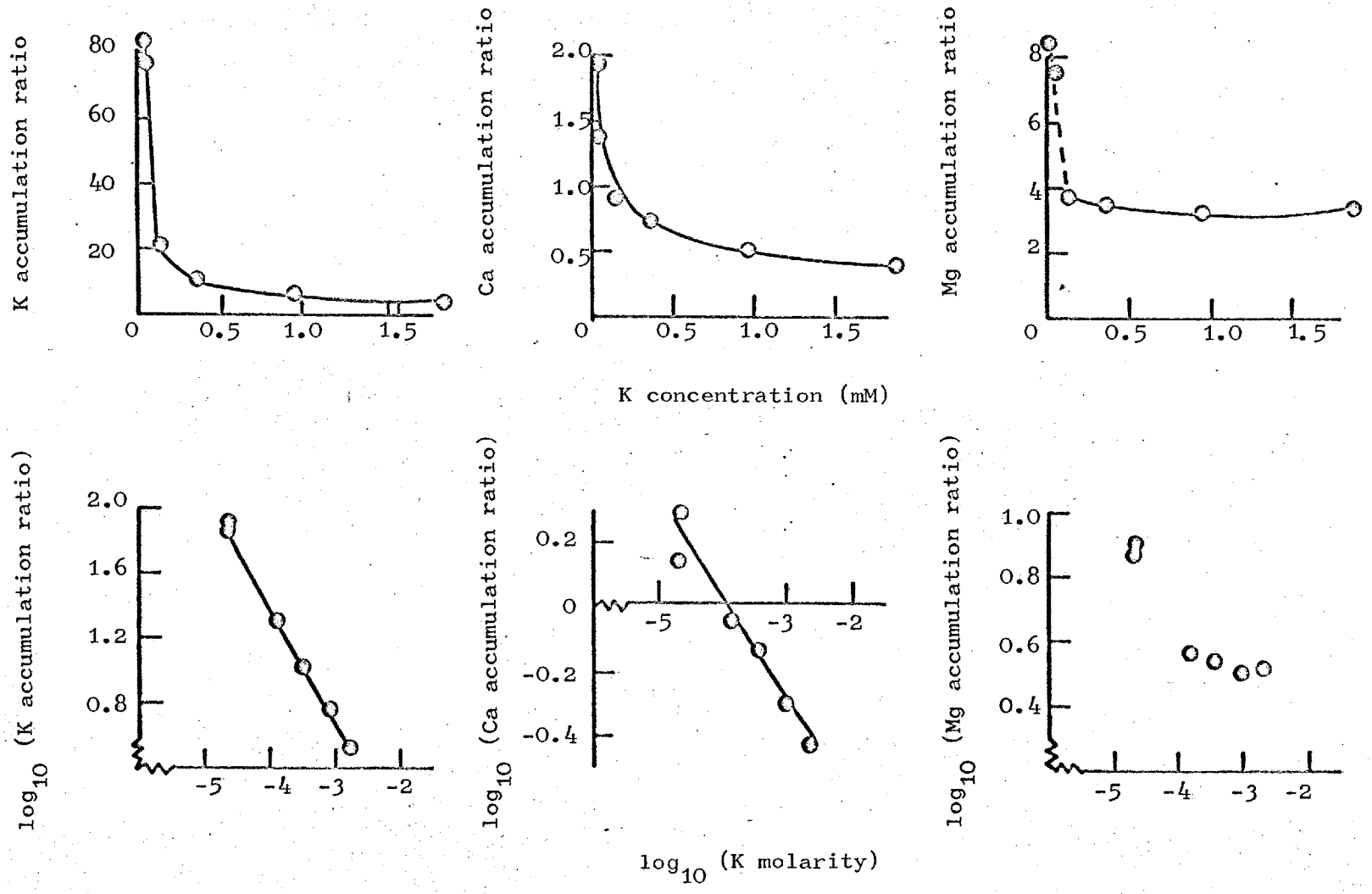


Fig. 3/3

Accumulation ratios for K^+, Ca^{++} and Mg^{++} plotted against K^+ molarity in the soil extract. (a-c) Direct plots. (d-f) Log:log plots.



against $\log_{10}$ (K molarity), giving a straight line for K^+ and Ca^{++} but not for Mg^{++}. Similar plots were obtained from the calculated activity data.

When the linear regressions of $\log_{10}$ (accumulation ratio) on $\log_{10}$ (K molarity) were calculated, using both replicates of each treatment, those for all three cations K^+, Ca^{++} and Mg^{++} were significant and negative (Table 3/1) at all harvests, although, as for Mg^{++} above, the relationships were sometimes better expressed by discontinuous lines (Fig. 3/4).

The relative importance of soil and plant root effects. Fig. 3/1 shows clearly that although adding K increased the Ca^{++} concentration in the soil extract, this effect was over-ridden by decreased absorption of Ca^{++} by the roots, so that the concentration of Ca^{++} was lessened in the exuded sap. The Mg^{++} concentration was also increased in the soil extract; its concentration in the exuded sap decreased with the smaller K additions but increased again with the larger ones. The relationship for Mg^{++} activities (Fig. 3/1f), in particular, suggests that the absorption of Mg^{++} was decreased like that of Ca^{++} but was more influenced by the increased activity in the soil solution, although an alternative explanation is given in Chapter 9. This type of relationship appeared in the second and third harvests but not in the fourth.

Differences in accumulation between cations and between harvests. 'Accumulation ratios' were compared by super-imposing, in Fig. 3/4, the plots of $\log_{10}$ (accumulation ratio) against $\log_{10}$ (K^+ molarity); these were used because of the sharp curvature of some of the unlogged plots. Where straight lines are shown in Fig. 3/4 they are calculated regression lines; discontinuous lines, where judged more appropriate, were fitted by eye.

TABLE 3/1

Values of r^2 for the regressions of $\log_{10}$ (accumulation ratio) on $\log_{10}$ (K molarity)

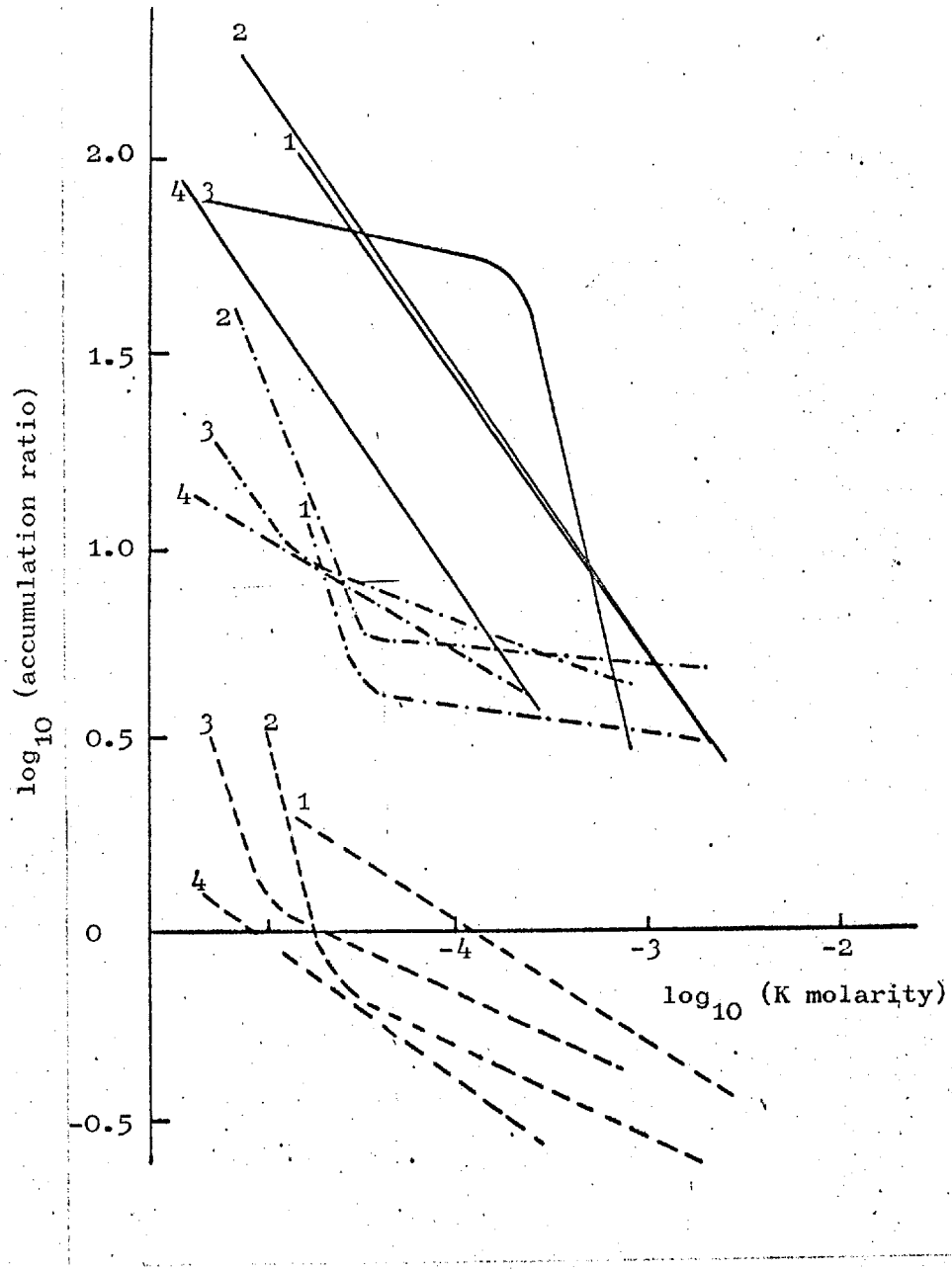
Harvest	r^2 for		
	K^+	Ca^{++}	Mg^{++}
28 days	0.98^{xxx}	0.91^{xxx}	0.53^{xx}
44 days	0.97^{xxx}	0.76^{xxx}	0.52^{x}
63 days	0.71^{xx}	0.75^{xxx}	0.62^{xx}
80 days	0.88^{xxx}	0.75^{xx}	0.79^{xxx}

Significance: x $p < 0.05$; xx $p < 0.01$; xxx $p < 0.001$

Note: The 'accumulation ratio' always decreased as the K molarity increased.

Fig. 3/4

Super-imposed plots of $\log_{10}$ (accumulation ratio) against $\log_{10}$ (K molarity) for K (——), Mg (-.-.) and Ca (---). The numbers denote the harvests.



The accumulation ratios decreased in the order $K^+ > Mg^{++} > Ca^{++}$, except that K^+ and Mg^{++} were reversed at the largest K addition in harvests 2 and 3 (Fig. 3/4). All the accumulation ratios decreased with increasing K concentration, that for K^+ itself most of all.

Variations between harvests were not large. For K^+, the lines for harvests 1 and 2 were almost identical, but by harvest 4 the 'accumulation ratio' had decreased uniformly; the data for harvest 3 may have been influenced by the very variable degree of tuber formation at this stage (see next chapter and Appendix II). The accumulation ratio for Ca^{++} also seemed to decrease between harvests 1 and 4, but for Mg^{++} there was no clear change.

Sodium. No results have been shown for Na^+ because Na^+ concentrations in the exuded sap were not related to those in the soil extract and neither was clearly affected by adding K, although that in the extract increased slightly.

Anions

Effects in the soil. There was no evidence of a direct K effect on the concentrations of nitrate and phosphate in the soil solution, and the amount of each removed by the plant seemed to have most effect.

The total amount of N in the plants was not measured because some plant parts did not yield large enough samples for N analyses as well as for ashing for cation and P analyses (see next chapter). However the concentration of nitrate in the soil extract was negatively related ($r^2 = 0.79^{xxx}$) to the fresh weight of the plant tops at the first harvest, but not in later harvests, suggesting that, initially at least, the nitrate concentration was influenced mainly by the amount of N removed.

The phosphate concentrations in the soil extract were inversely related to the amount of P removed from the soil by the plant (Fig. 3/5). The concentrations were measured in harvests 2, 3 and 4 only, because of technical difficulties at harvest 1.

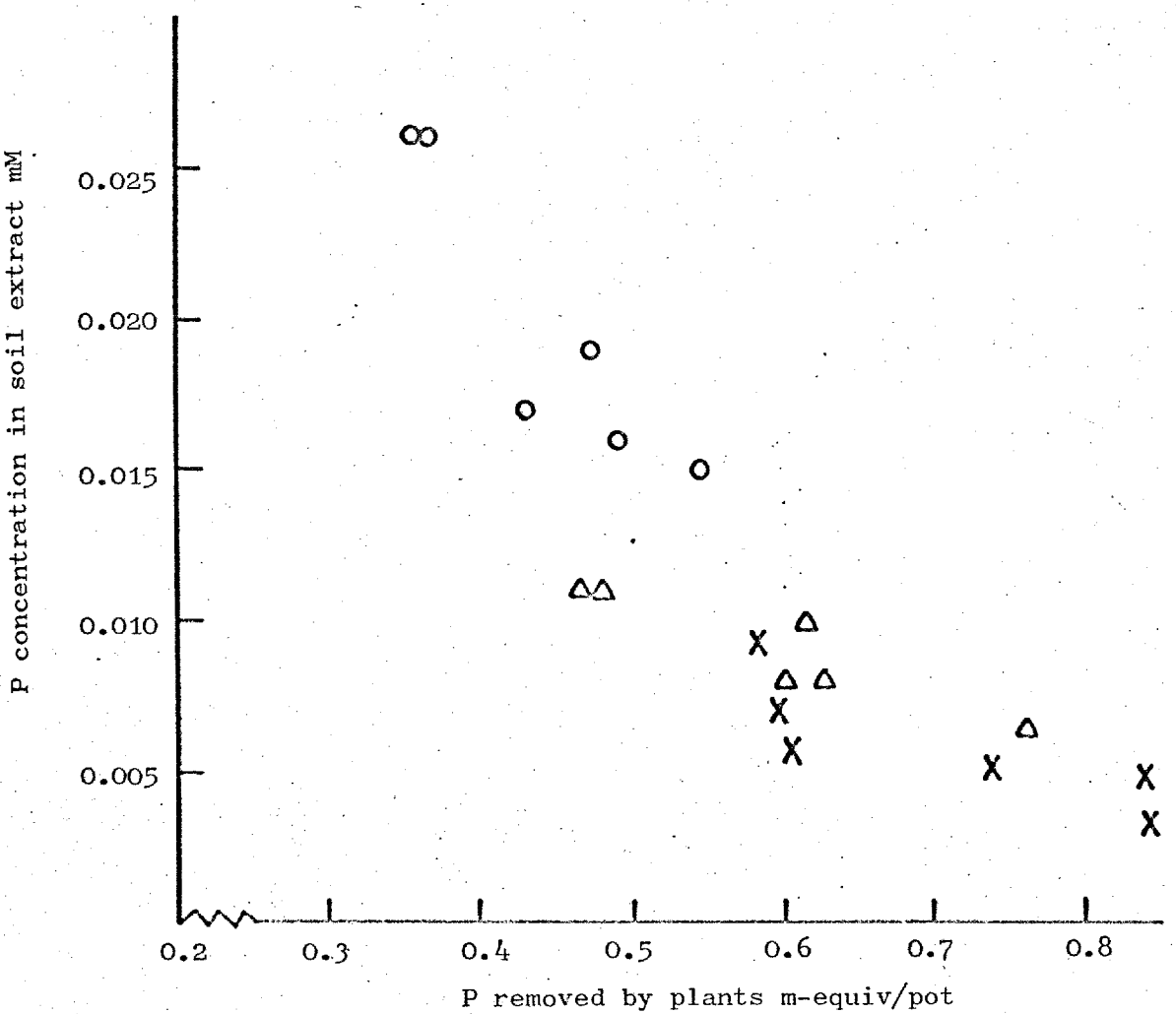
Effects in the plant. Concentrations of nitrate and phosphate in the sap need to be viewed cautiously, because these anions may possibly have been metabolised on absorption and subsequently re-liberated (see Chapter 1).

The concentration of nitrate in the sap was related to its concentration in the soil extract at harvests 1, 2 and 4 (r^2 = 0.65^{xx}, 0.77^{x}, 0.42^{x}) but not in harvest 3, shortly after extra nitrate was added. The mean accumulation ratios (calculated as before) at the four harvests were 3.8, 16.5, 2.6 and 3.1; the large value at the second harvest reflects the shortage of nitrate before more was added. There seemed to be no direct effect of K^+ on nitrate absorption.

The concentration of phosphate in the exuded sap was not related to its concentration in the soil extract or to that of K. However, at harvests 2 and 4 only, the accumulation ratio, which ranged from 42 to 83, increased with the concentration of K in the soil solution, such that $\log_{10}$ (accumulation ratio) was related to $\log_{10}$ (K molarity), just significantly (r^2 = 0.43; sig. at $p < 0.05$) at harvest 2 and almost so (r^2 = 0.37; NS) at harvest 4. Furthermore, at harvest 1, the concentration of phosphate in the exuded sap was positively related to that of K^+ (r^2 = 0.60; sig. at $p < 0.01$). There was thus some evidence that increasing the K concentration in the soil solution enhanced phosphate absorption.

Fig. 3/5

The phosphate concentration in the soil extract plotted against the P removed by the plants. Harvests 2 (o), 3 (Δ) and 4 (x).



Cation-anion relationships

The relationships between the sum of the cation concentrations and that of anion concentrations in the sap were not comprehensively investigated; sulphate and chloride were not determined. However, the concentration sum ($K^+ + Ca^{++} + Mg^{++} + Na^+$) was well related to (nitrate + phosphate) in all four harvests (r^2 = 0.90, 0.57, 0.75, 0.66, all sig. at $p < 0.01$ or 0.001). In the first harvest the relationship was almost 1:1; subsequently the sum of the concentrations of cations was greater than that of anions.

Discussion

It was suggested in Chapter 1 that adding K might influence the absorption of other ions in two ways: (a) a limited capacity for absorbing cations, regulated perhaps by anion absorption, would mean that increasing the amount of K^+ absorbed would decrease the absorption of other cations; (b) if increasing the K^+ supply decreased the negative potential difference across the root, this would decrease the absorption of cations, and possibly enhance that of anions.

The relationship found between the sum of the concentrations of cations and that of anions lends some weight to the first suggestion, but this does not explain why adding K seemed to enhance phosphate absorption.

The phosphate effect could be described by a system in which active absorption of nitrate (the predominant anion) caused a negative sap:solution potential difference which was decreased by increasing the supply of K. However, the phosphate effect could be of metabolic origin and unrelated to potential changes.

The effects of adding K on the absorption of divalent cations, especially Ca^{++}, could arise from either of the suggested causes.

Growing the plants in soil was essential for part of the information obtained, but it precluded measuring the sap:solution potential difference; this would have made it easier to interpret the effects found and needs to be done in a future experiment with plants in solutions.

However, the experiment showed clearly that the lessening of Ca^{++} absorption caused by adding K over-rode the increase it caused in the Ca^{++} concentration of the soil extract. Mg^{++} absorption seemed to be more influenced by the increase in its concentrations in the soil solution. The absorption relationships did not change greatly as the plants grew older.

CHAPTER 4

THE RELATIONSHIPS BETWEEN POTASSIUM AND OTHER IONS IN THE TUBERS AND THEIR EFFECTS IN OTHER PARTS OF THE PLANTS

Introduction

In this chapter, analyses of the various parts of the plants harvested in the experiment described in the previous chapter are used to show the effects of adding K on nutrient distributions in the plants.

The tubers form the best defined 'sink' in the potato plant and were expected to influence ion distributions and interactions between nutrient ions. The effects of adding K on the amounts and concentrations of nutrients in the tubers were first examined and the effects these relationships seemed to have on the nutrients in the rest of the plants are described.

Methods

The pot experiment was described in the previous chapter. The plant parts were prepared and analysed as in Chapter 2, except for the stems and petioles (referred to as 'stems'); these were weighed fresh, macerated under distilled water in a MSE Homogeniser and filtered. The resulting solution was made to volume and analysed, and the solid matter was dried, weighed and analysed. The quantities of nutrients in the soluble and insoluble stem fractions were calculated.

Tubers were just starting to form at the second (44 day) harvest and were collected and analysed from the third harvest onwards.

Results

The relationships between the concentrations of nutrients in the tuber dry matter

Potassium - calcium. Adding K to the soil had little effect on the Ca concentration in the tuber dry matter, which was small (ca. 0.1%) compared with those in the rest of the plant (e.g. up to 6% in the leaf dry matter).

Potassium - magnesium. In all the harvests that yielded tubers, there was a positive linear relationship between %Mg and %K in the tuber dry matter (Fig. 4/1). Thus adding K, as well as increasing the %K in the tuber dry matter, increased its %Mg. The %Mg in the dry matter was also quite small (ca. 0.1%) but Mg concentrations in the rest of the plant were considerably smaller than those of Ca (up to 0.7% Mg in the leaf dry matter).

Potassium - sodium. There were no clear relationships between Na and K in the tubers or any other plant part, and Na is not discussed further.

Potassium - phosphorus. Adding K did not alter the %P in tuber dry matter, although this changed slightly between harvests (Table 4/1).

Potassium - nitrogen. There seemed to be no direct effect of adding K on N in the tuber dry matter, but plotting the %N against the reciprocal of the dry weight of the tubers (Fig. 4/2) suggested that extra growth, mainly caused by adding K, diluted the N content.

The effects of adding K on the amounts and distributions of nutrients in the plants after tuber formation

Fig. 4/3 (a-d) shows the effects of adding K on the amounts of each nutrient in each plant part at 80 days, plotted cumulatively, so that the vertical distance between successive lines represents the quantity of

Fig. 4/1

The concentration of Mg related to that of K in tuber dry matter

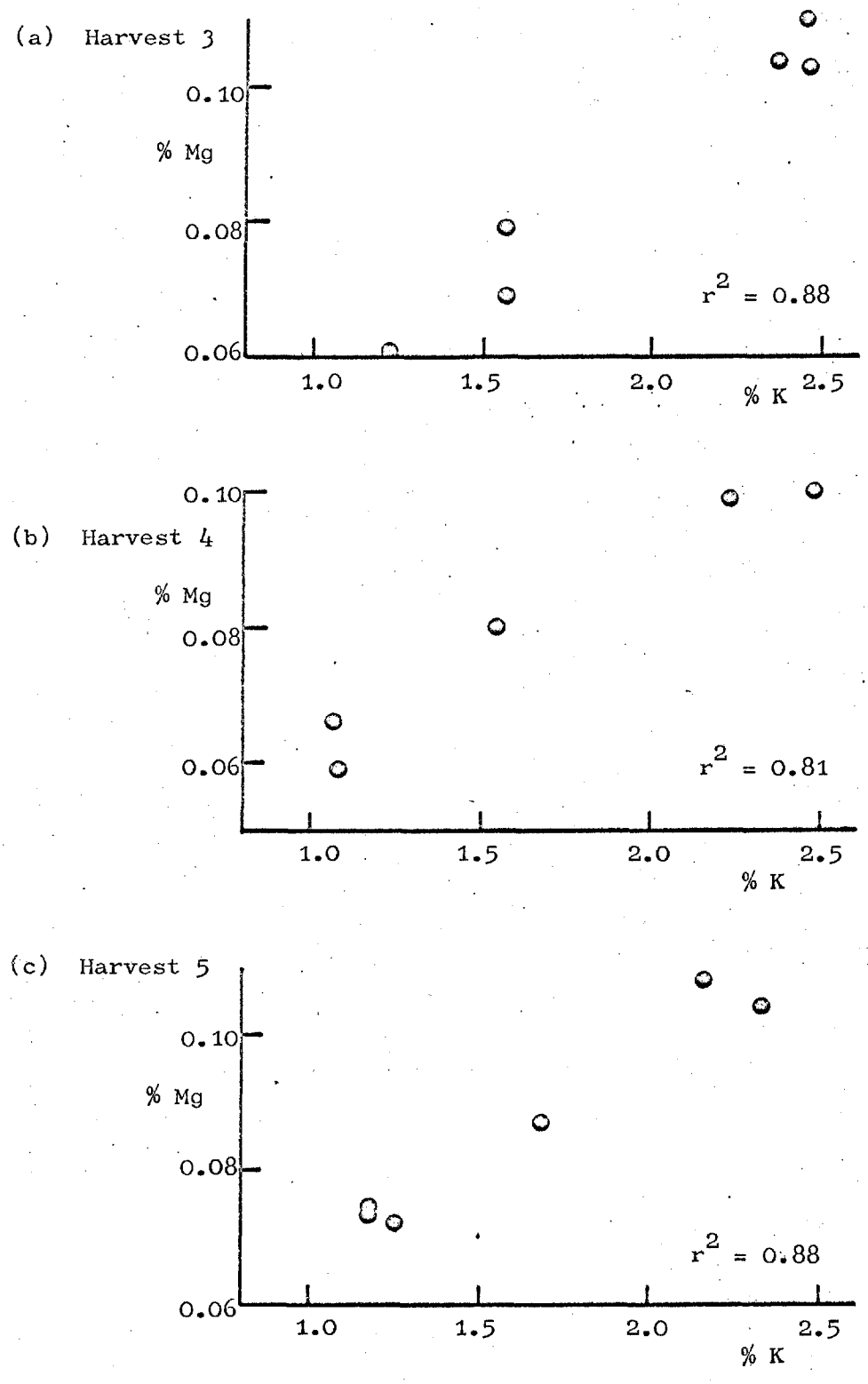


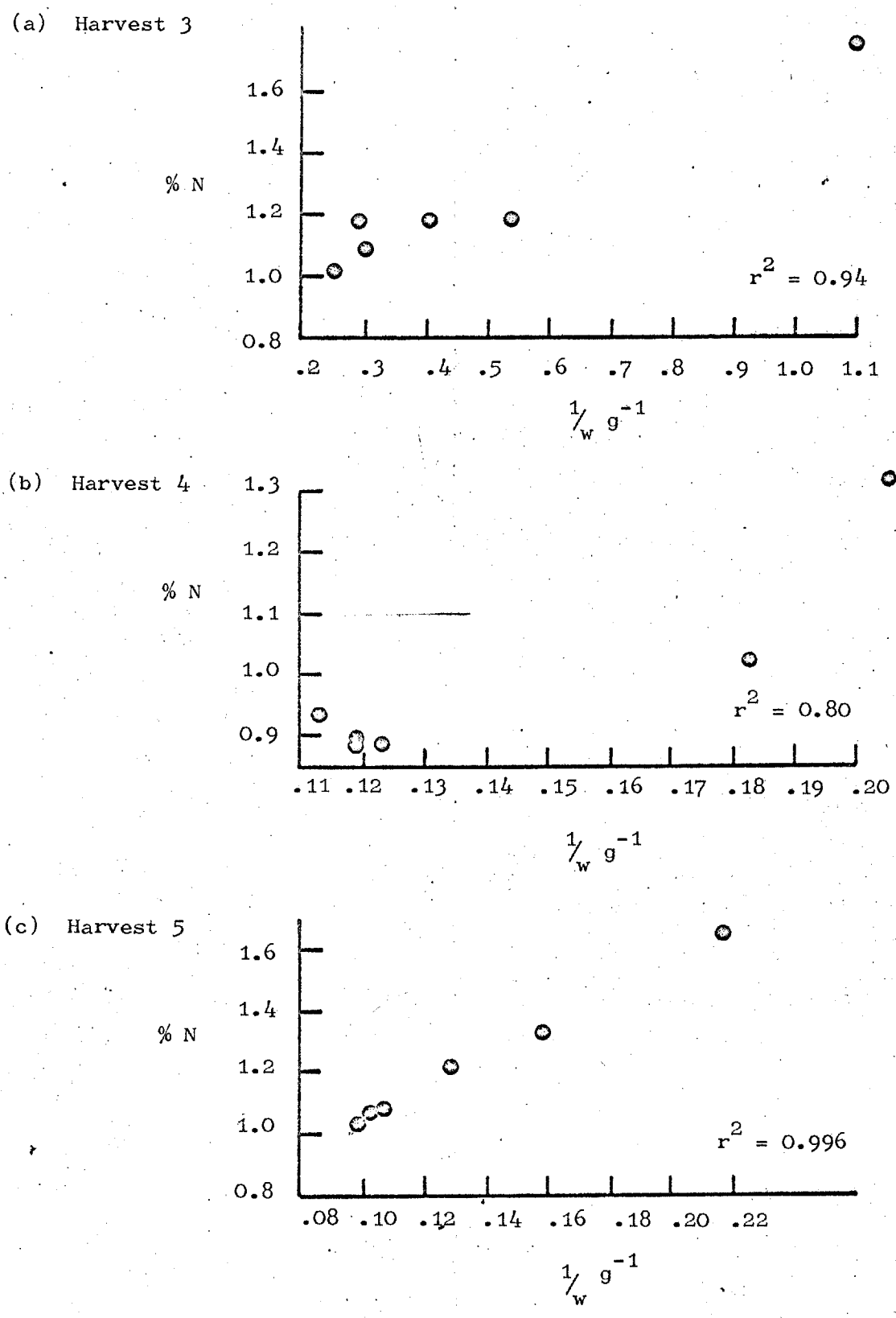
TABLE 4/1

Mean values of %P in the tubers' dry matter

Harvest	Time (days)	%P in tubers
3	63	0.269 ± 0.023
4	80	0.210 ± 0.014
5	at death	0.225 ± 0.012

Fig. 4/2

The N concentration in tuber dry matter related to the reciprocal of its weight of dry matter (w).



nutrient in each plant part. The plants had then been making tubers for about 35 days and any tuber effects should have appeared.

Potassium. Amounts of K in all plant parts were significantly* increased by added K. Most K was in the tubers (Fig. 4/3a).

Calcium. Adding K decreased the quantity of Ca in the plants, mainly because it significantly* lessened the amount in the leaves where most of the Ca was. Little Ca was in the tubers (Fig. 4/3b).

Magnesium. Both the dry weight of the tubers (Appendix II) and their Mg concentration were greater when K was added, so that the quantity of Mg was significantly* increased (Fig. 4/3c). Adding K also slightly increased the Mg content of the roots. There was no increase in overall Mg uptake when K was added and other plant parts therefore contained less Mg, so that adding K increased the proportion of the Mg that was in the tubers.

Phosphorus. The P concentration of the tuber dry matter was unchanged by adding K, but its weight was increased (Appendix II). The resulting (significant) increase in the quantity of P in the tubers (Fig. 4/3d) seemed mainly compensated by extra uptake. Most of the plants' P was in the tubers.

Nitrogen. Adding K slightly increased the quantity of N in the tuber dry matter (though the extra growth tended to dilute it). This did not seem to affect the amount in the leaves, the only other part analysed for N.

Effects at other harvests. At the first (28 day) harvest, adding K did not seem to alter the quantity of any other nutrient in any plant part,

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* Significantly, in this chapter, implies that a regression of the variate discussed on the amount of added K was significant ($p < 0.05$). The regressions are listed in Appendix II.

Fig. 4/3

The quantities of nutrients in different plant parts related to added K (at 80 days). L = Leaves; S(s) and S(I) = Stem soluble and insoluble fractions; R = Roots; T = Tubers.

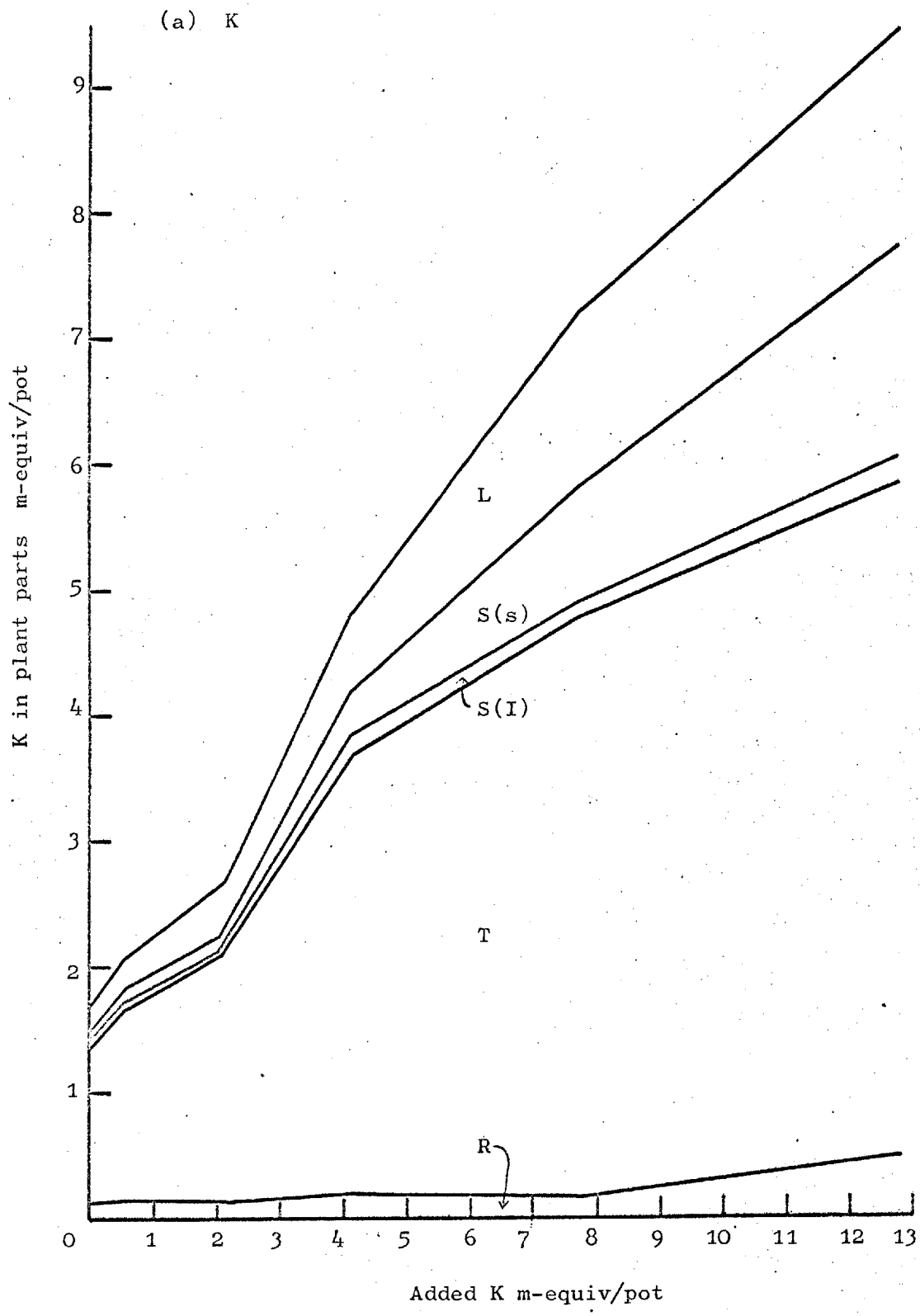


Fig. 4/3 continued

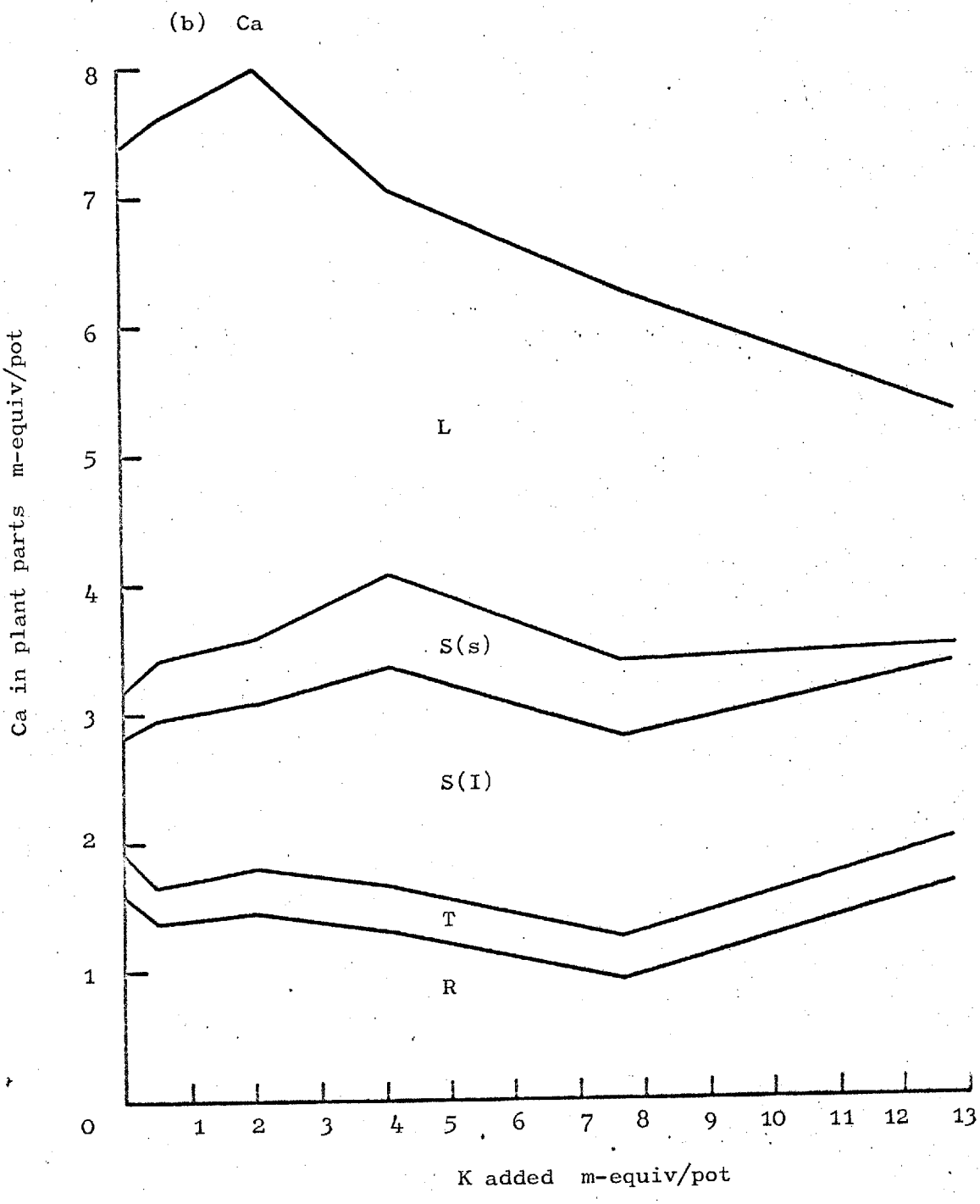


Fig. 4/3 continued

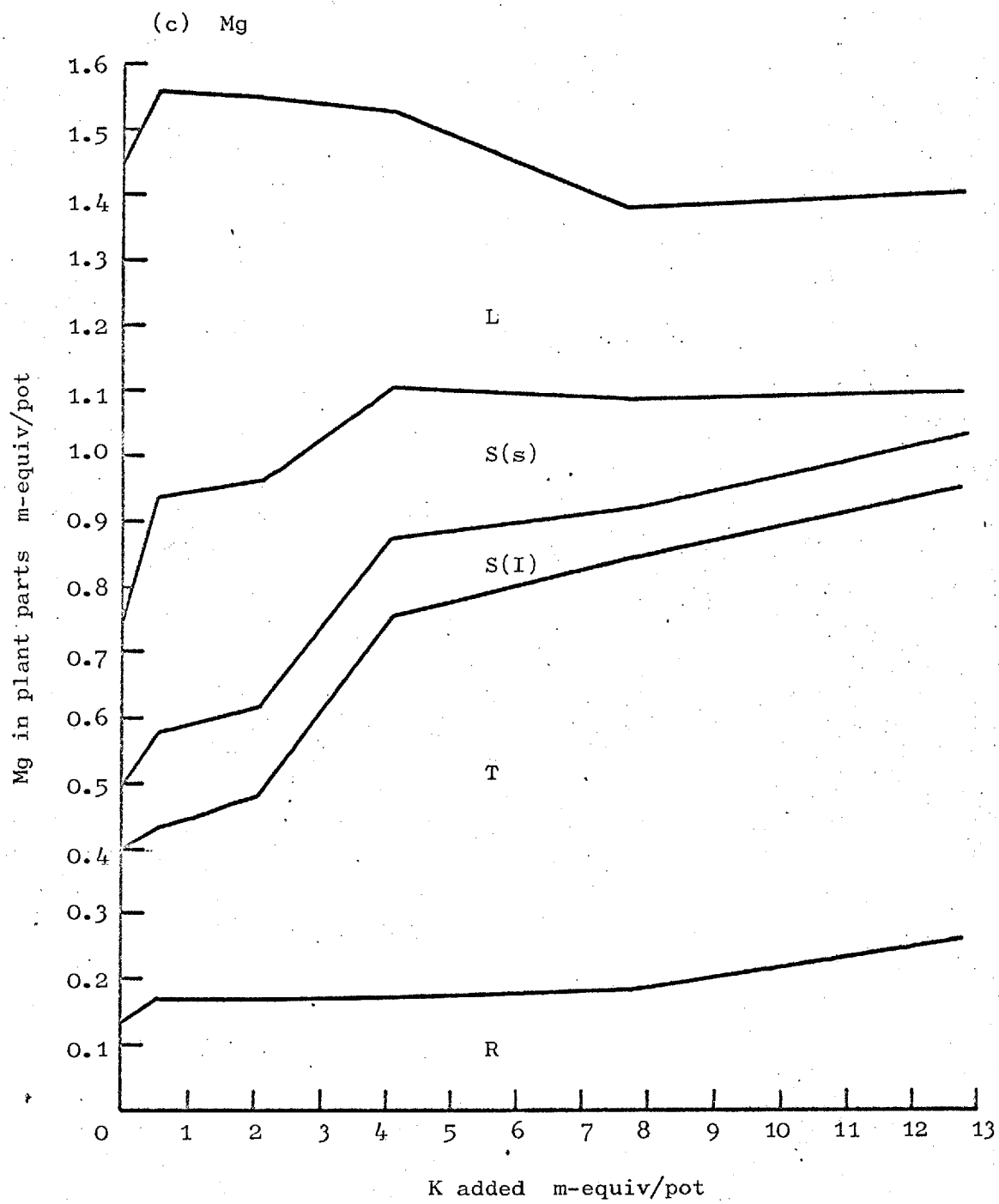
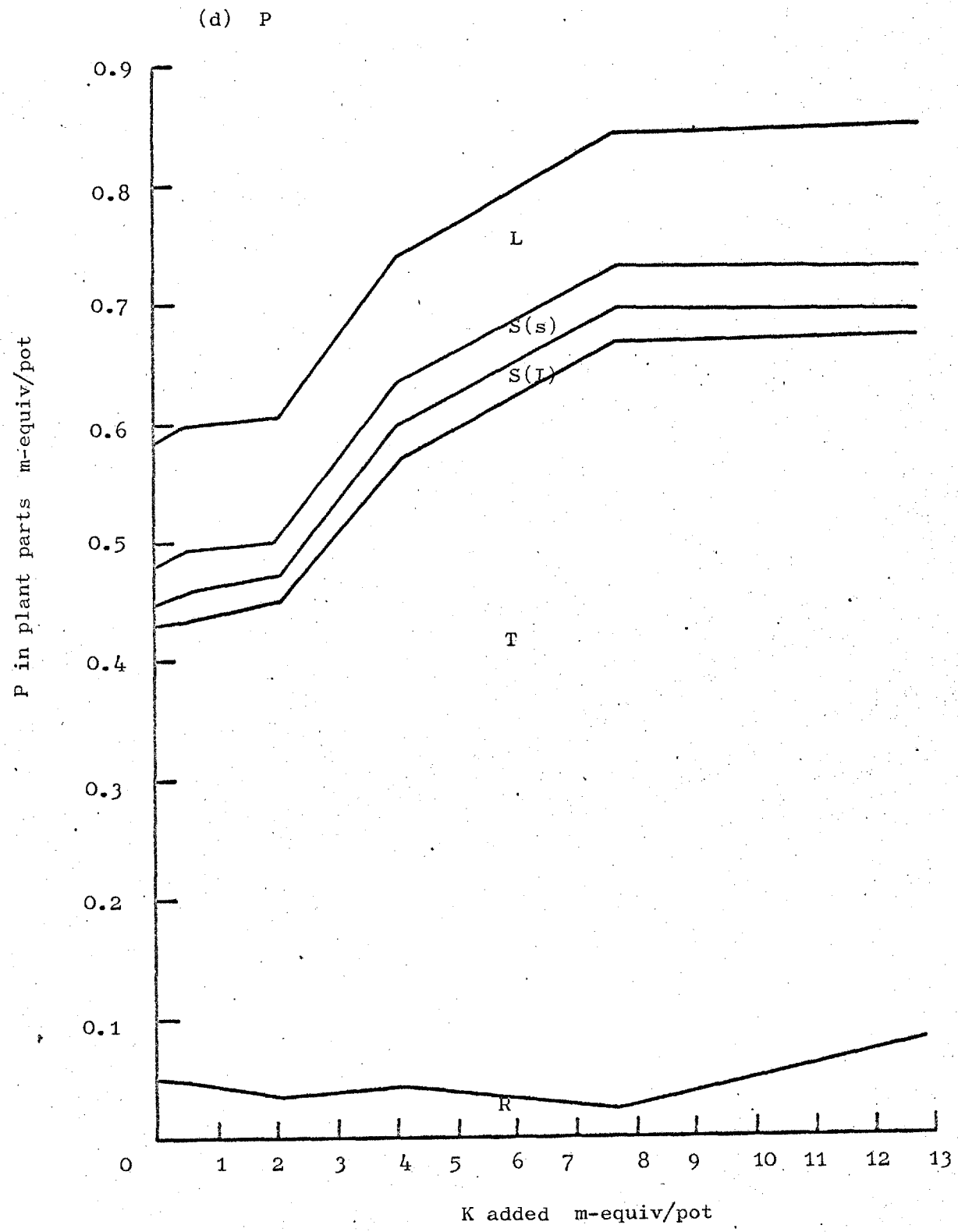


Fig. 4/3 continued



although it decreased Ca and Mg concentrations in the leaves. By 44 days, the quantities of Ca and Mg in the leaves and the total Ca content of the plants were significantly decreased by added K. At 63 days, the degree of tuber formation varied considerably and the nutrient distributions reflected this. The harvest of the dead plants suggested that the trends in the 80-day harvest continued with K and P moving to the tubers, Mg moving to the tubers when K was given, and Ca remaining in the tops.

Appendix II gives the quantities and concentrations of all the nutrients in all the plant parts at all the harvests, and the dry weights, together with the regressions quoted in the text.

Movements of nutrients during tuber formation

Plants harvested at 44 days were just starting to form tubers and those taken at 80 days had been doing so for about 35 days. Thus comparing the quantities of nutrients in the parts of the plants at 80 days with those at 44 days shows how the nutrients moved in the plant during tuber formation, and what effect adding K had on these movements. Fig. 4/4 (a-d) shows the change in nutrient content (quantity at 80 days less that at 44 days) related to the amount of K added for K, Ca, Mg and P.

Potassium. The tubers contained a major share of the plants' K content at 80 days (Fig. 4/3a) and Fig. 4/4a shows that all other parts of the plant lost K during tuber formation, with the soluble stem fraction losing most. The two largest K additions caused less K to be lost from the rest of the plant because more was absorbed from the soil; with the nil or small K additions, much less K could be taken up from the soil during tuber formation.

Fig. 4/4

Changes in the quantities of nutrients in plant parts during tuber formation (44 to 80 days). Legend as for Fig. 4/3.

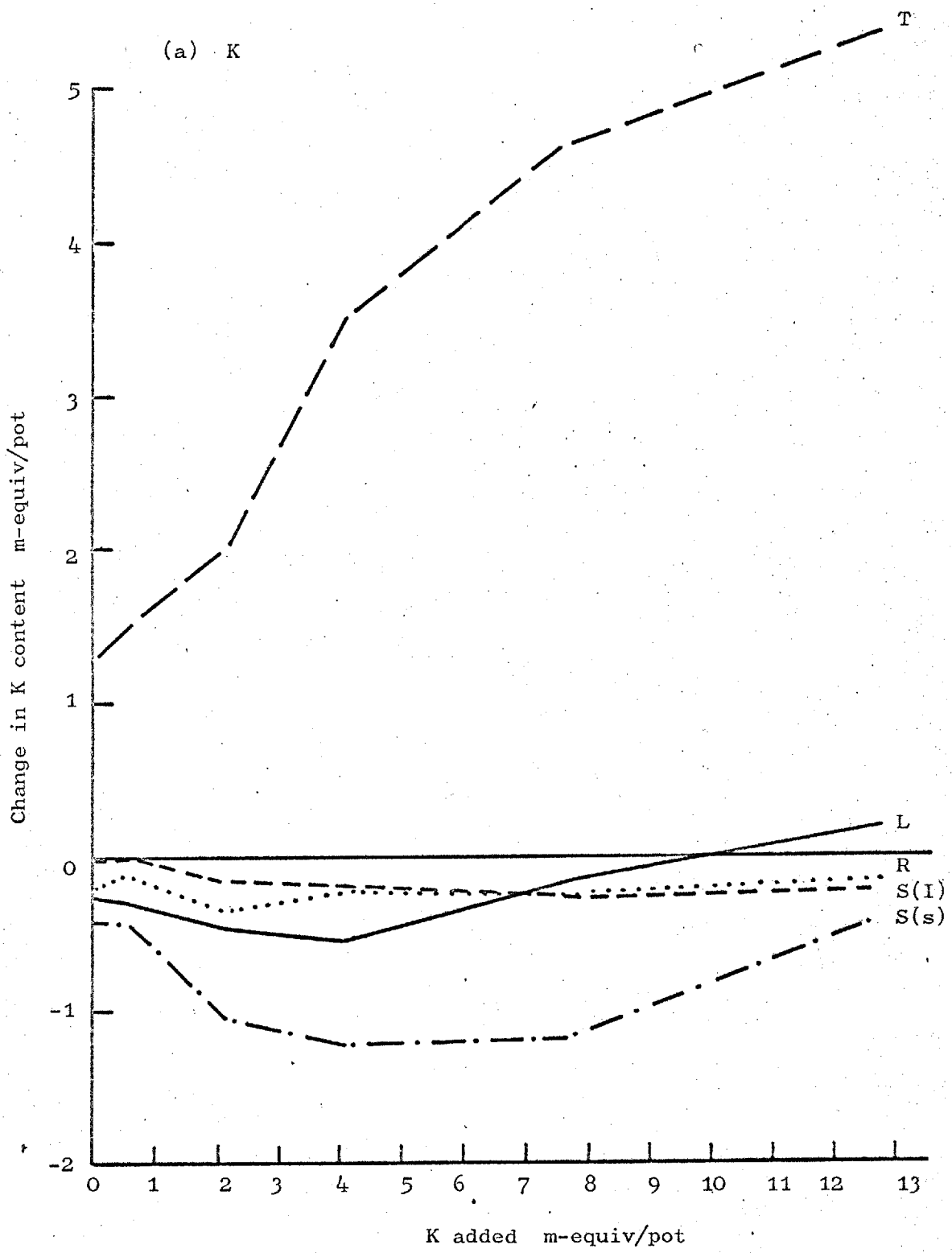


Fig. 4/4 continued

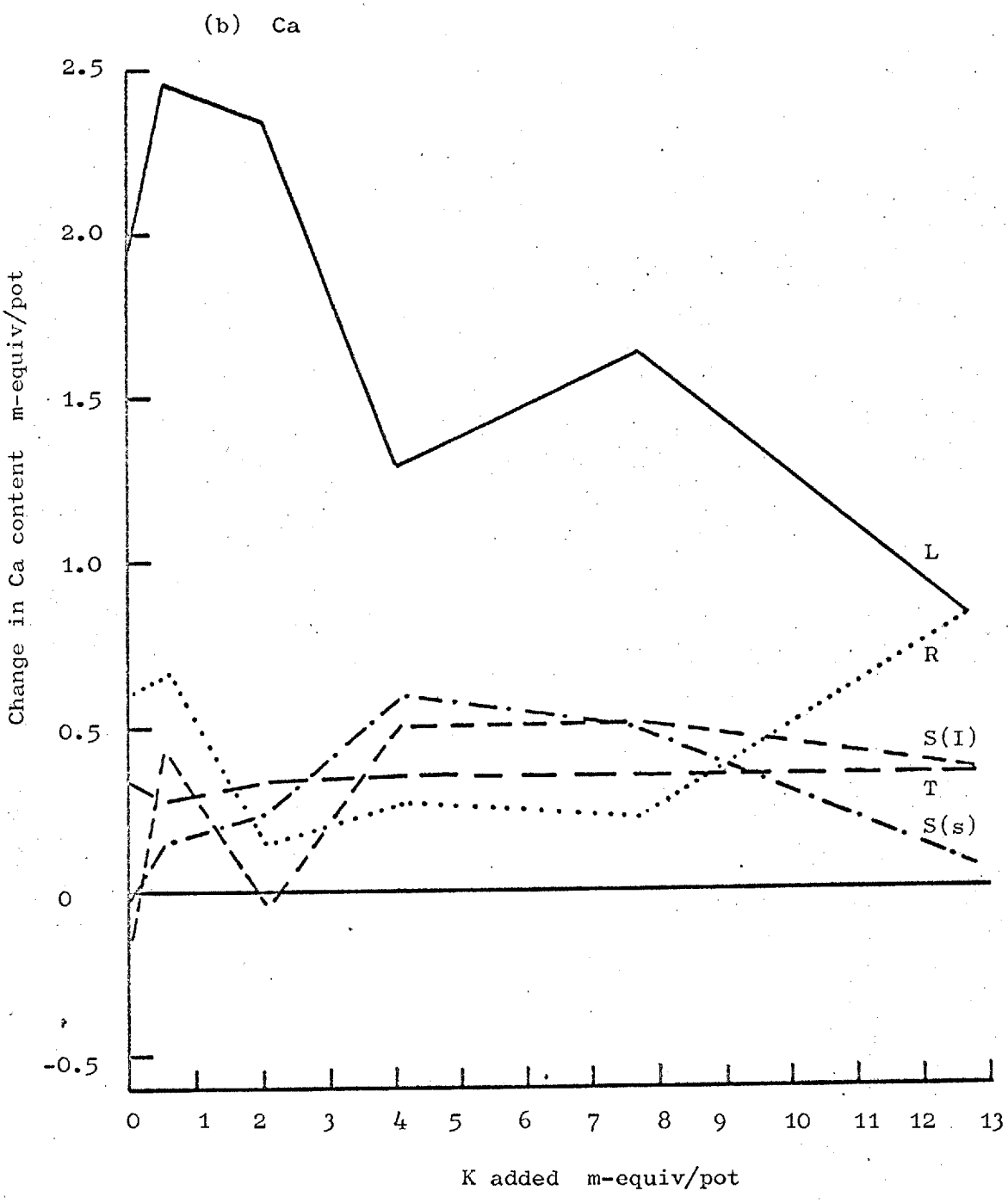


Fig. 4/4 continued

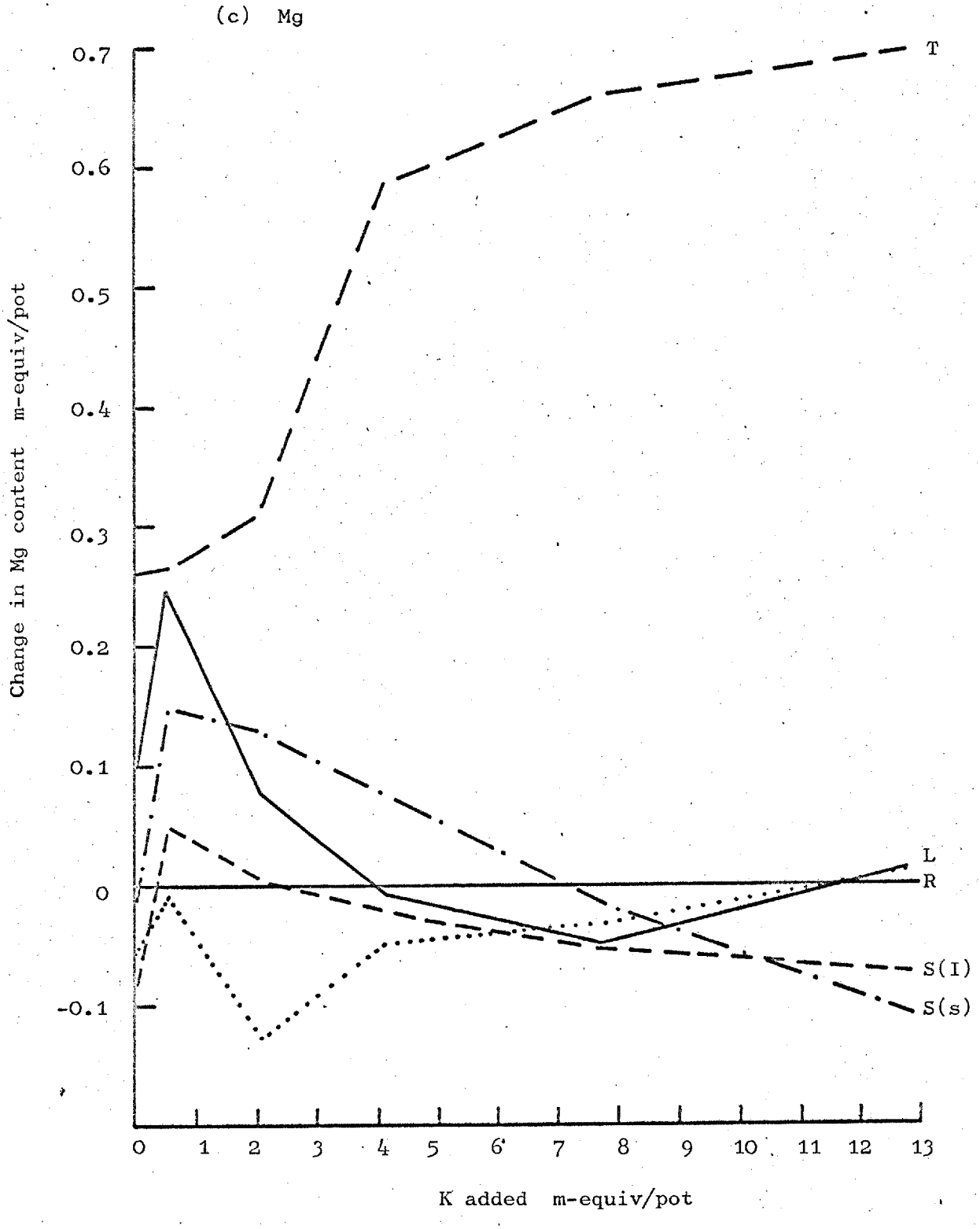
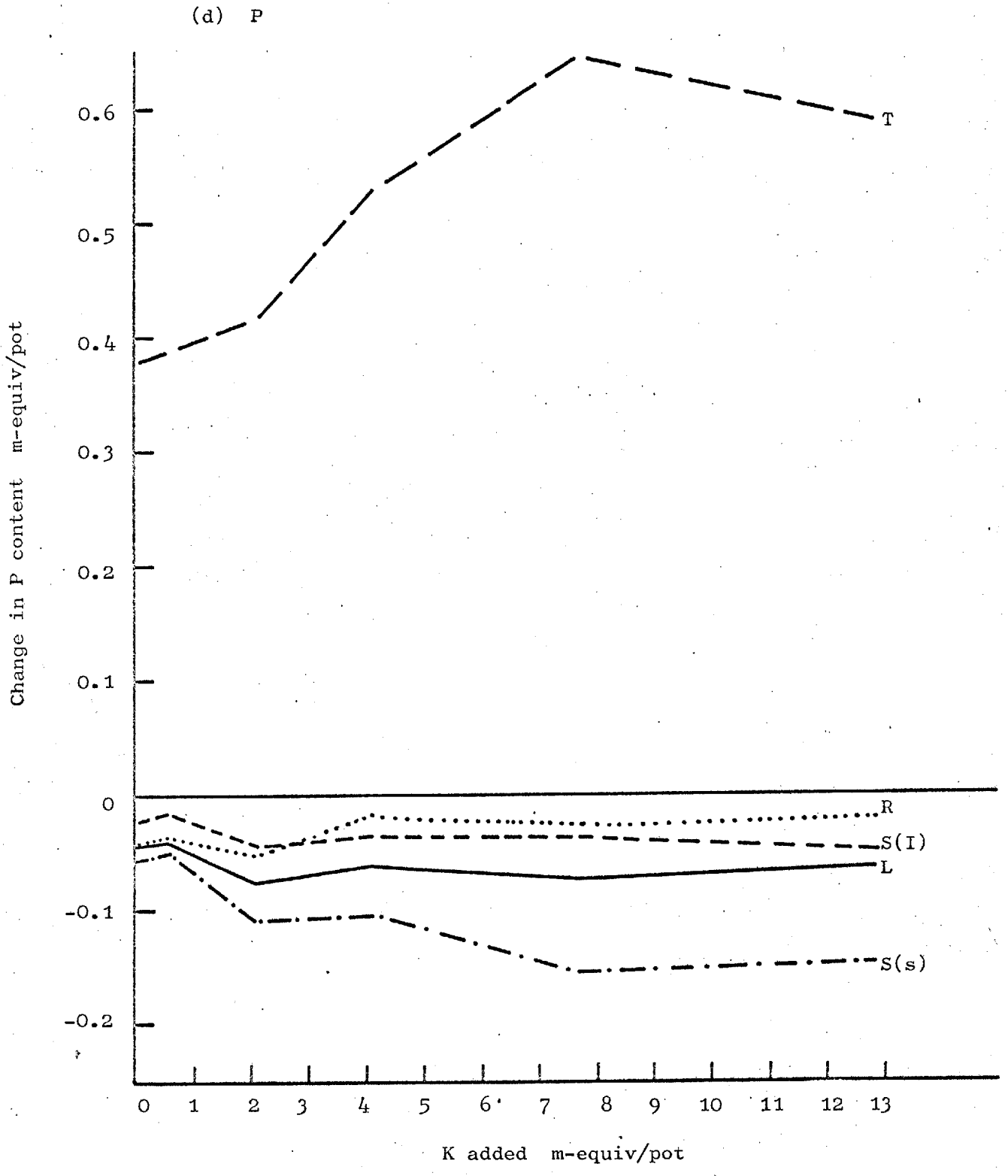


Fig. 4/4 continued



Calcium. All parts of the plant continued to gain Ca while the tubers were forming, with the leaves getting most (Fig. 4/4b), although adding K significantly decreased the Ca gained by the leaves. The amount of Ca entering the tubers seemed too small to affect the rest of the plant.

Magnesium. The plants had a nett gain of Mg from the soil while the tubers were forming; adding K did not affect the quantity of Mg gained but did alter its distribution. Adding K significantly increased the quantity of Mg in the tubers and Fig. 4/4c shows that whilst the leaves were not clearly affected, both stem fractions lost Mg when much K was added; however both leaves and stems seemed to gain some of the intake from the soil when the smaller amounts of K were added, more so than when no K was added at all.

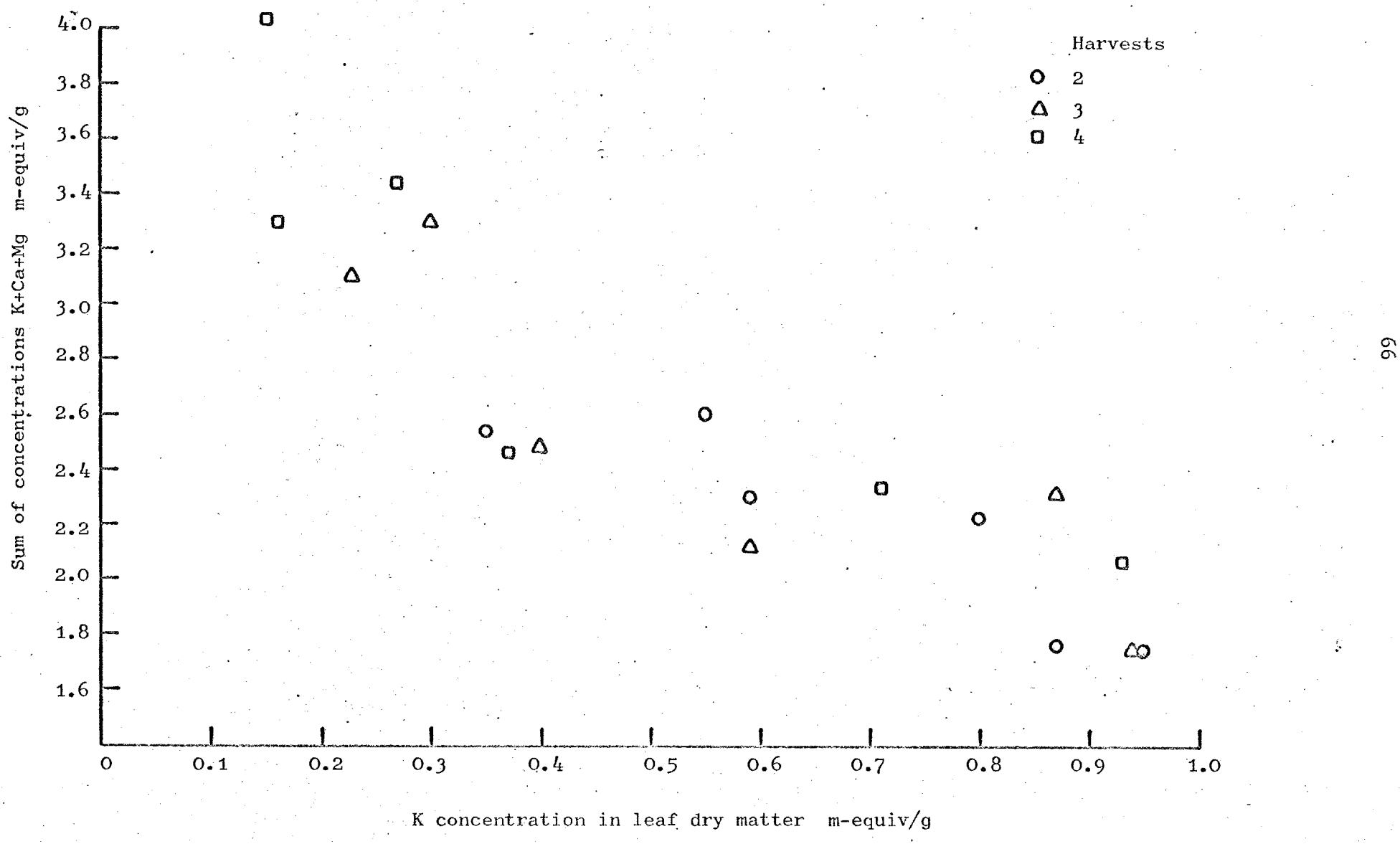
Phosphorus. The tubers held a large proportion of the plants' P content at 80 days (Fig. 4/3d) and all other parts gave up P during tuber formation, the water-soluble stem fraction most (Fig. 4/4d). Adding K significantly increased both the quantity of P in the tubers and the loss of P from the water-soluble stem fraction but not other parts.

Ionic relationships in the leaves and tubers

Leaves. Expressing the nutrient concentrations in the leaves as m-equiv/g of dry matter showed that the sum of the concentrations of K, Ca and Mg was constant in the first harvest at 3.16 ± 0.06 m-equiv/g regardless of the K treatment. (Na concentrations were very small and varied little.) In subsequent harvests, the sum decreased as the concentration of K increased (Fig. 4/5). Thus in the first harvest added K seemed to decrease the leaf concentrations of Ca and Mg simply by replacing them, but later it both replaced them and decreased the total.

Fig. 4/5

The sum of the concentrations of K, Ca and Mg (in m-equiv/g) related to that of K.



An increase in the sum of the cations is one of the symptoms of leaf ageing (Kirkby & De Kock, 1965) and added K might have delayed the increase in the cation sum by delaying the senescence of the plants. This point is taken up again in Chapter 6 and in the final discussion (Chapter 11).

Tubers. The sum of the cations in the tuber dry matter, expressed as m-equiv/g, was not constant. Although the concentration of Mg was linearly related to that of K, the ratio m-equiv K : m-equiv Mg was not constant in respect either of time or added K (i.e. there was a variable intercept in the linear relationship). The ratio varied in the ranges

6.3 - 7.2 : 1 at 63 days

5.4 - 7.1 : 1 at 80 days

and 5.2 - 6.7 : 1 at the final harvest,

where the first figure shown is that corresponding to the smallest K concentration. Adding K thus slightly increased the proportion of K, while that of Mg tended to increase with time.

The rates of accumulation of nutrients in the tubers

Comparing the quantities of dry matter, K, Mg, P and N in the tubers after 63 and 80 days with quantities therein at the final harvest provided an approximate means of comparing the rates of accumulation of these nutrients. Table 4/2 shows these quantities as percentages of the quantities at the final harvest; each percentage is the weighted mean calculated over all six K treatments. K and P seemed to be moved to the tubers slightly in advance of Mg and N; this was suggested by both sets of results. The observation for Mg concurs with the slight increase with time in the proportion of Mg relative to K in the tuber dry matter.

TABLE 4/2

Percentages of the final* quantities of dry matter and nutrients present in the tubers by 63 and 80 days

Time	Percentage of				
	D.M.	K	Mg	P	N
63 days	33.5	35.1	30.8	36.2	32.6
80 days	91.8	86.2	80.2	86.8	74.9

* in the tubers of plants harvested when their haulm died.

Discussion

Potassium and phosphate seem generally accepted as being very mobile in plants (e.g. Bukovac & Wittwer, 1957); that both seemed to be appreciably moved to the 'sink' formed by the tubers concurs with this view. The effect of the added K on P distribution seems simply to have been to enlarge the sink.

Ca is almost immobile in plants probably because it is strongly held in the leaves (Biddulph et al, 1959; Ringeot et al, 1968); thus it seems to have accumulated in the leaves regardless of tuber formation. Krauss and Marshner (1971) suggested tubers could absorb Ca direct from the soil; if so, none need have been moved from the rest of the plant at all. The effect of adding K on Ca accumulation in the leaves may be related to the decrease caused by the added K in the concentration of Ca in the sap exuded from the xylem stream. However, the effect of K on the sum of the cation concentrations implies that the effect might not be quite as simple as it appears, and this point is taken up later.

Mg seemed intermediate in mobility between K and Ca. Fig. 4/4c suggests that the effect of the larger K additions on Mg in the leaves may not have been to mobilise it from the leaves as much as to prevent it reaching them. The effects on the soluble and insoluble Mg in the stems may have been part mobilisation and part prevention. Chapter 5 describes experiments aimed at clarifying these points.

The relationship between the concentrations of Mg and K in the tuber dry matter might be expected in other metabolic sinks and was sought (Chapter 6) in the meristems of the growing shoots before tuber formation. Only Wilkinson (1958) seems to have found such an effect; in apples, he

found a similar relationship with about 10 m-equiv K to 1 m-equiv of Mg. Reasons for the relationship were investigated (Chapters 7 & 9).

The observations described in this chapter have been discussed, in effect, in terms of 'competition' between the tuber 'sink' and the rest of the plant. However it should be noted that the data are equally compatible with the operation of the 'innate development programme' discussed in Chapter 1, and the two descriptions are not completely exclusive.

CHAPTER 5

FURTHER EFFECTS OF ADDED POTASSIUM ON MAGNESIUM DISTRIBUTION AND RECIPROCAL OBSERVATIONS

Introduction

The previous experiment did not show for certain whether adding K decreased the Mg content of the leaves because it caused leaf Mg to be remobilised when the tubers formed or because it decreased the amount of Mg reaching the leaves, probably by increasing that going to the tubers. The question is interesting because it relates to the degree and nature of Mg mobility in the plant. Bukovac and Wittwer (1957) thought Mg was non-mobile when applied to leaves, but Steucek and Koontz (1970) showed by autoradiography that Mg could move from leaves in the phloems of bean and barley plants. If Mg is appreciably remobilised from the leaves to the tubers, it cannot be as strongly held by the leaves as Ca (Biddulph et al, 1959; Ringeot et al, 1968).

In this experiment, potato plants received Mg either initially in the soil or sprayed on the leaves during tuber formation. If Mg is remobilised from the leaves, adding K to the soil should decrease the Mg content of the leaves whichever way the Mg is applied. If added K decreases the Mg reaching the leaves, it should only decrease the quantity of K in the leaves of the plants getting Mg in the soil.

The previous experiment also showed a linear relationship between the concentrations of K and Mg in the tuber dry matter, such that giving K increased the concentration of Mg as well as that of K. The tubers from

the present experiment were therefore analysed to see if the relationship held when both K and Mg additions were varied and if giving Mg increased the K concentration.

Other effects are discussed briefly.

Methods

Potato plants were grown from small seed potatoes, one per pot, in 2 kg of soil from Fosters field at Rothamsted. The soil, like that used in the previous experiment, was a flinty clay loam with a high pH (7.8 in water) and contained 11.7 and 3.05 mg/100 g of exchangeable K and Mg. The soil from the previous experiment was not used because it contained more exchangeable Mg, 8.6 mg/100 g.

Seed potatoes were used here to see if they produced better plants than excised eyes; their nutrient contents (about 9% and 4% respectively of the larger K and Mg additions) were not a problem because effects of additions, rather than absolute amounts, of K and Mg, were tested.

The plants received basal nutrients 0.75 g N and 0.75 g P as $Ca(NO_3)_2$ and $Ca(H_2PO_4)_2$, and an extra 0.3 g N after 64 days. They had nil, 1 or 2.5 g added K as K_2SO_4 in the soil and nil, 120 or 300 mg of Mg as $MgSO_4$ either given initially in the soil or sprayed in three aliquots on the leaves (at 42, 56 and 77 days) from a calibrated sprayer; the amounts of Mg given in the soil and on the leaves were equal. There were thus three K treatments combined with 5 Mg treatments in three replicates.

The plants were harvested at 104 days and separated and analysed for K, Mg, Ca and P as described in Chapter 2. Stems + petioles (unmacerated) and roots + stolons were again taken together.

Analyses of variance were made* on the quantities and concentrations of each nutrient in each plant part, and the results are in Appendix III. Two missing pots were allowed for.

Results

To find whether added K remobilised Mg from the leaves or prevented it reaching them

Fig. 5/1a compares the increases over the control in the quantities of Mg in the leaves caused by adding either amount of Mg without K. Adding the larger amount of Mg caused the larger increase, but whether the Mg was applied in the soil or to the leaves made no significant+ difference.

Fig. 5/1b shows the effect of adding K on the quantity of Mg in the leaves; the change in Mg content is shown as (quantity of Mg when K added) - (quantity when no K added).

When the Mg was given in the soil, adding K significantly decreased the quantity of Mg in the leaves, and the more K was given the more the Mg content was lessened at both Mg levels. However, if the Mg was sprayed on the leaves, adding K did not significantly decrease the quantity of Mg in the leaves; indeed with the larger Mg addition it increased it. Trends in the concentrations of Mg in leaf dry matter followed those in the quantity of Mg (see Appendix III).

These results imply that adding K does not increase mobilisation of Mg from the leaves but rather that it increases the extent to which Mg is prevented from reaching them; how this might happen is considered later. Mg, once in the leaves, may therefore be as strongly retained as Ca, though it is not possible to be certain that sprayed Mg behaves the same as translocated Mg.

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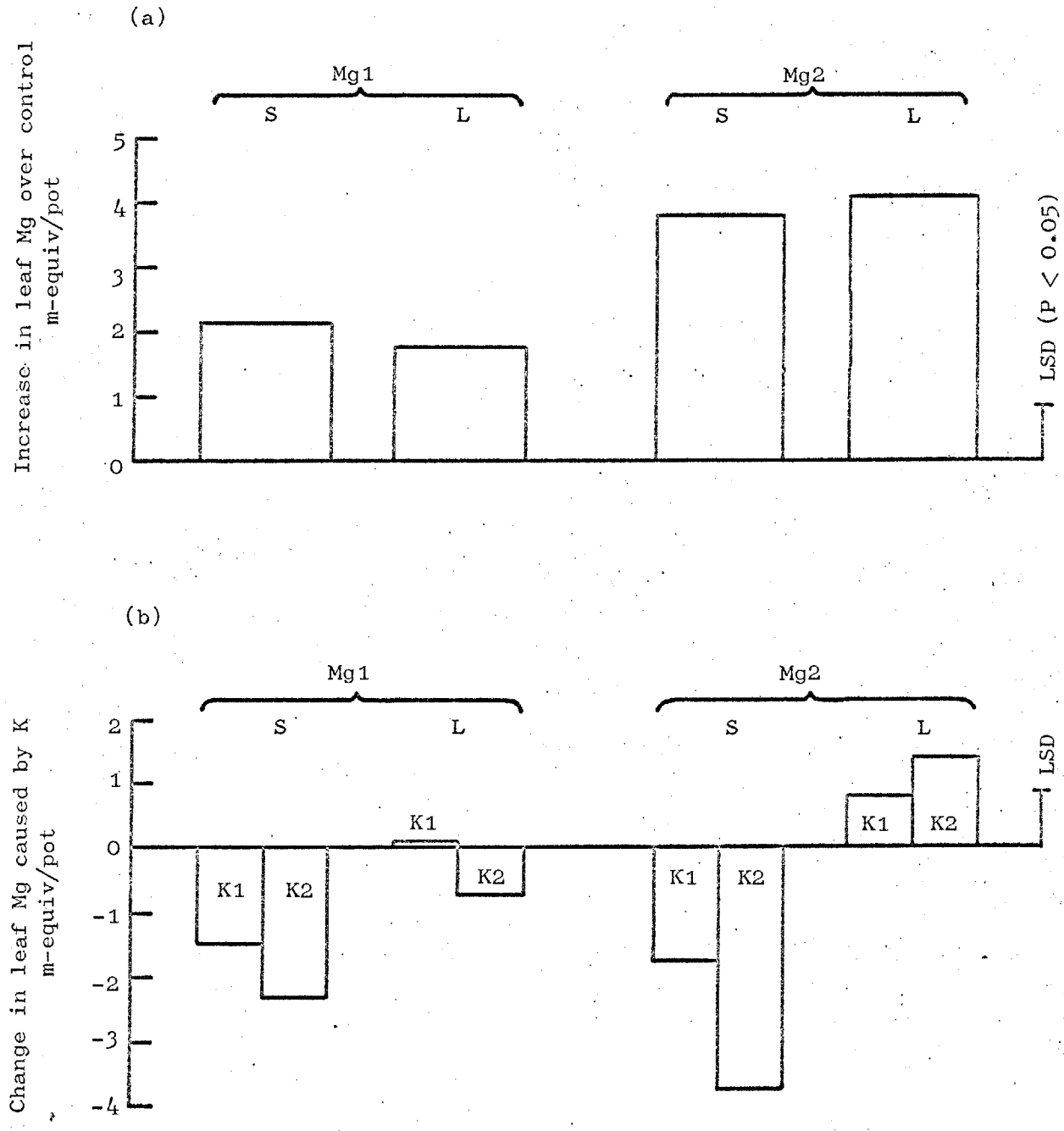
* by J. H. A. Dunwoody

\+ denotes significance at $p < 0.05$ throughout the chapter

Fig. 5/1

(a) Increases in the quantities of Mg in the leaves caused by adding Mg (to soil or leaves) without K.
(b) Effects of K at different Mg treatments.



Legend K1, K2 : 1, 2.5 g K added per pot
Mg1, Mg2 : 120, 300 mg Mg added per pot
S, L : Mg added to the soil, sprayed on the leaves

Effects in the stems and roots

Stems. Fig. 5/2a shows that adding Mg without K only slightly increased the quantity of Mg in the stems except when the larger amount of Mg was given in the soil. The K effects (Fig. 5/2b) were less simple. When either amount of Mg was given in the soil, adding the lesser amount of K increased the quantity of Mg in the stems by increasing their weight without much decreasing their Mg concentration, but giving the larger amount of K significantly decreased both the quantity and concentration of Mg in the stems. When the Mg was sprayed on the leaves, either amount of K decreased the quantity and concentration of Mg in the stems. The difference may mean that stem Mg was partly replenished by Mg given in the soil but not by that sprayed (as expected from the previous section).

Roots. There were few significant effects of K or Mg on the quantity of Mg in the roots, except that when the larger amount of Mg was added to the soil, both K additions significantly increased the quantity of Mg in the roots.

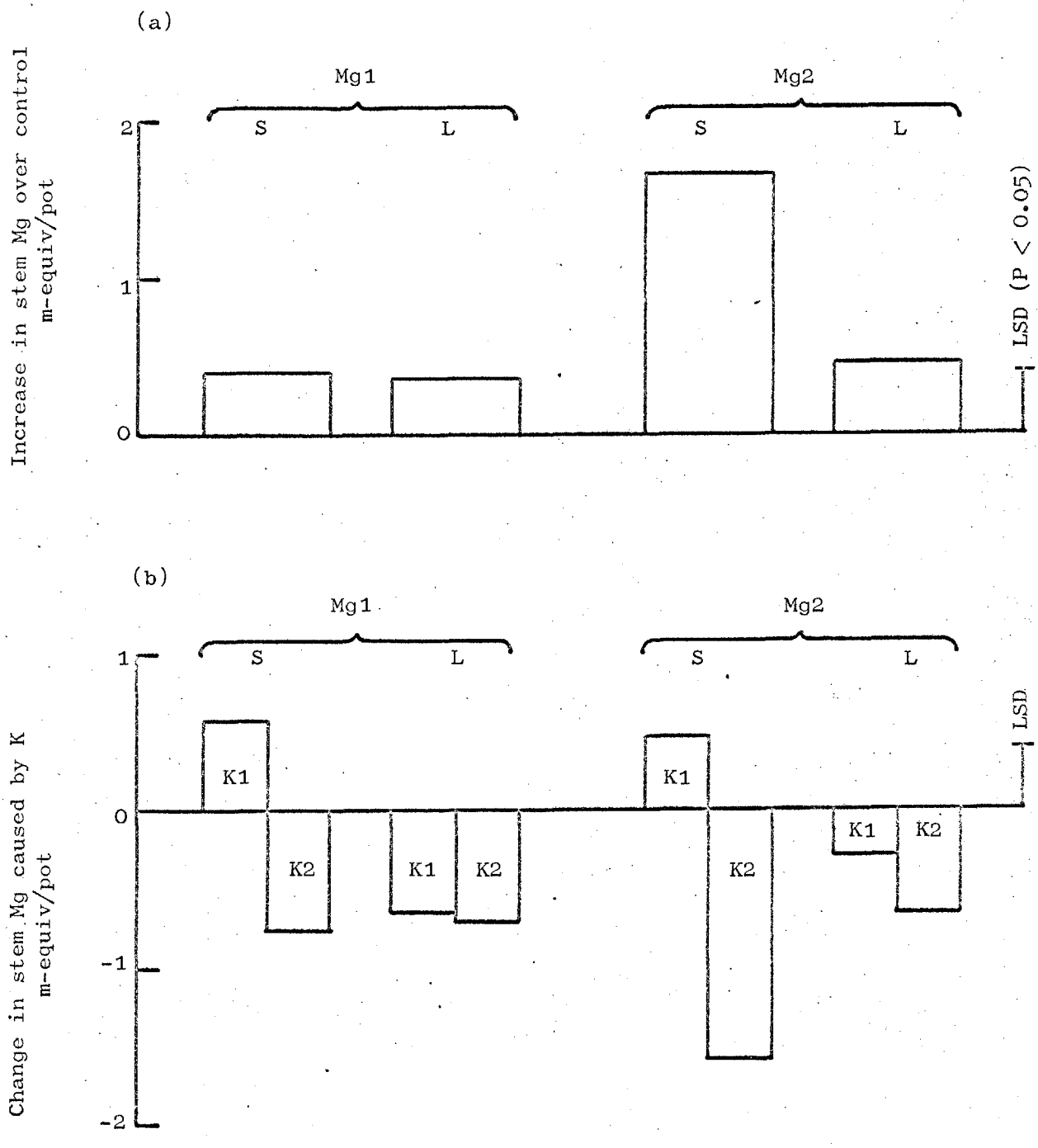
Effects in the tubers

Fig. 5/3 (a,b) shows the effects of added K and Mg on the concentration of Mg in the tuber dry matter, with the effect of each averaged over all treatments of the other. Both amounts of K significantly increased the % Mg in the tuber dry matter but only the larger soil-added Mg treatment did so.

The % Mg in the tuber dry matter was plotted against the % K to see if the relationship found in the previous experiment held in this one, in which the amount of Mg added, as well as that of K, was varied. Fig. 5/3c shows that the value of r^2 (0.68) was significant but smaller than before, and this seemed to be mainly because tubers from plants getting Mg in the soil contained more Mg relative to K than the others.

Fig. 5/2

(a) Increases in the quantities of Mg in the stems caused by adding Mg (to soil or leaves) without K.
(b) Effects of K at different Mg treatments.

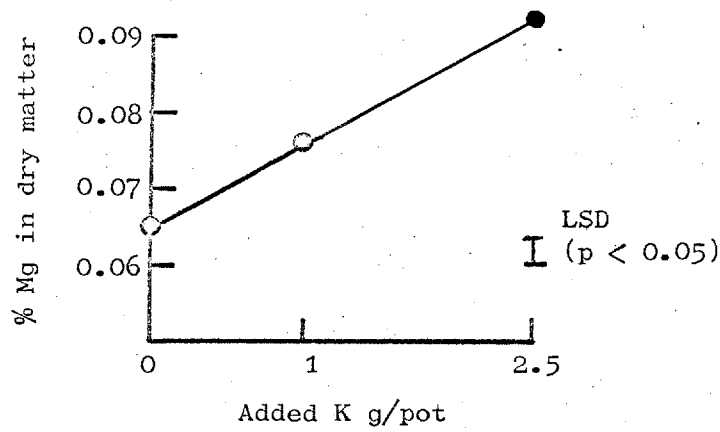


Legend. As Fig. 5/1

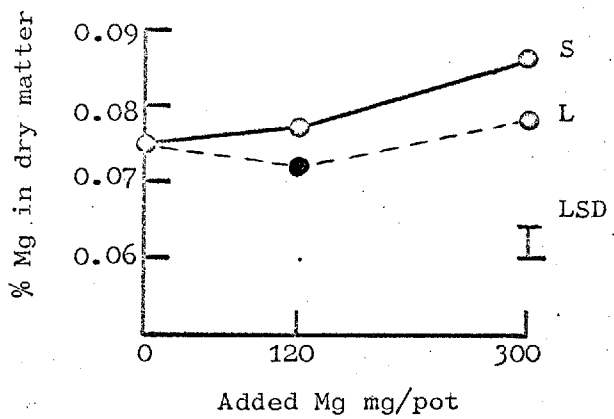
Fig. 5/3

(a, b) The effects of added K and Mg on the % Mg in tuber dry matter. (c) The relationship between % Mg and % K in tuber dry matter. (Open circles denote treatments with soil-added Mg.)

(a)



(b)



(c)

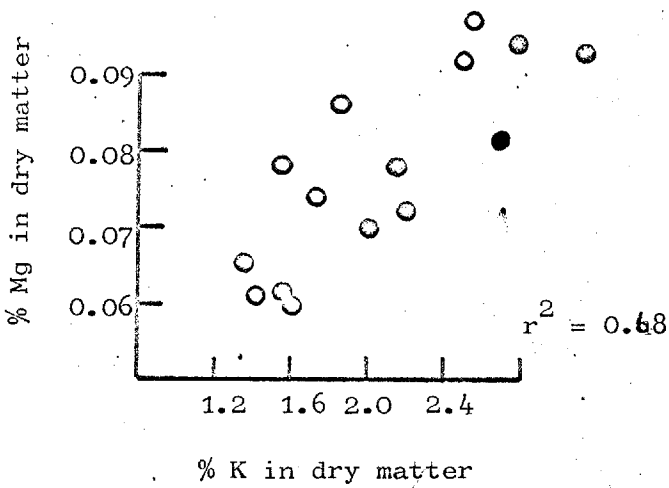


Fig. 5/4 (a,b) shows that adding Mg without K had relatively little effect on the quantity of Mg in the tubers whereas adding K increased it, particularly when Mg was added. Giving K caused the increase by increasing both the weight of tubers formed (Table 5/1) and their Mg concentration.

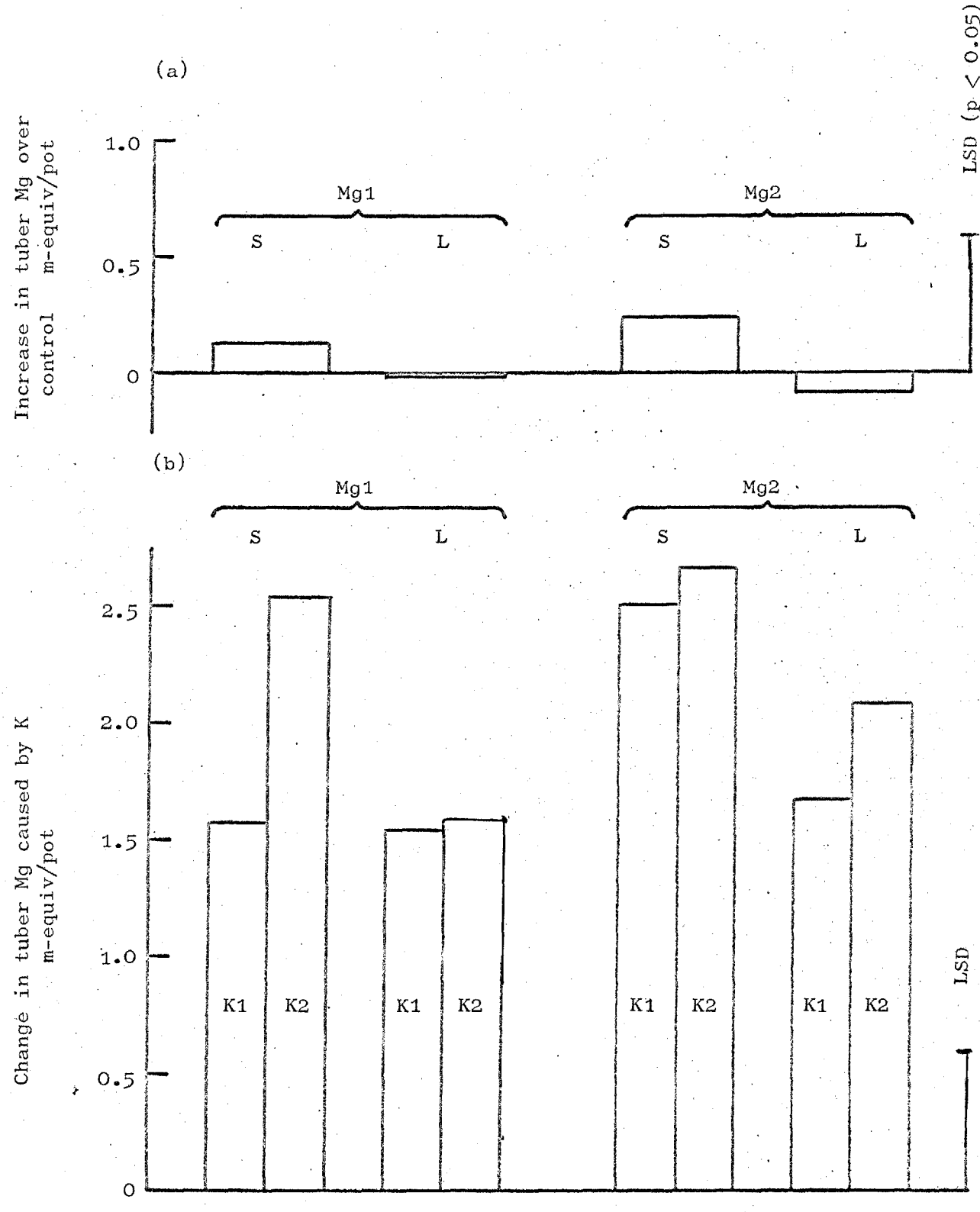
Adding K did not much alter the total Mg uptake of the plants and so it is necessary to find where the extra Mg, moved to the tuber by adding K, came from. When the smaller amount of Mg was given in the soil, the extra Mg in the tubers seemed mainly that prevented from reaching the leaves (the quantities are about right - Figs 5/1 and 5/4), but with the larger amount of Mg given the balance was less satisfactory. No extra Mg came from that sprayed on the leaves and more was found in the tubers than came from the stems. The discrepancy probably arose because the sprayed Mg was not prevented from going on to the petioles and stems from where it might have been absorbed through the epidermis or cork into the phloem and moved to the tubers; this is, perhaps, a flaw in the experiment, though it does not affect the main conclusions.

Reciprocal effects, of Mg on K distribution

Fig. 5/5 (a, b) shows the effects of added K and Mg on the % K in the tuber dry matter, with the effects of each meaned over all treatments of the other. Giving Mg somewhat decreased the concentration of K, probably by diluting it because the quantity of K in the tubers was not decreased. There is thus no reciprocal of the enhancing effect of K on the Mg concentration in the tuber dry matter, and the linear relationship between the concentrations arises purely because of the effect of adding K on the Mg concentration. When K was added as well, giving Mg increased the weight of tuber dry matter formed (Table 5/1) and thus sometimes significantly

Fig. 5/4

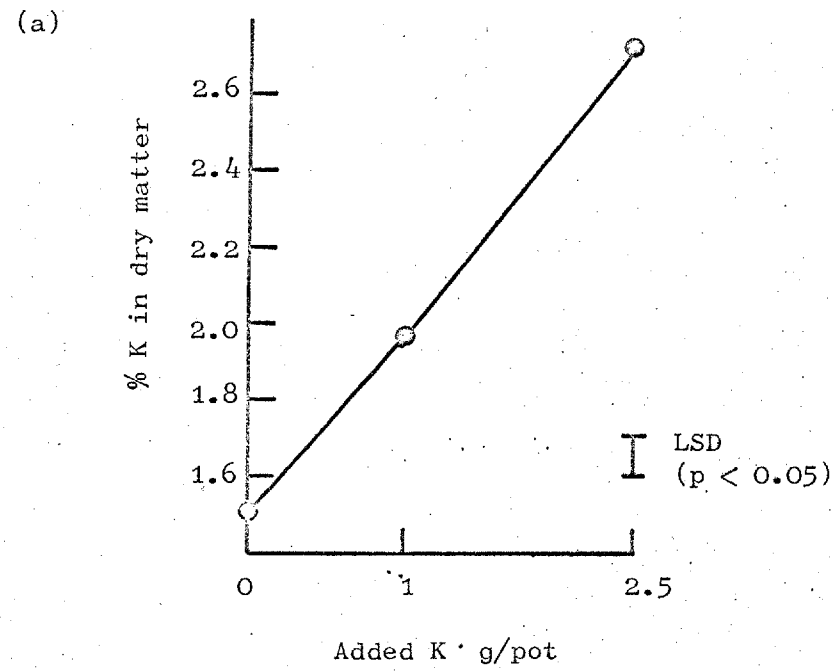
(a) Increases in the quantities of Mg in the tubers caused by adding Mg (to soil or leaves) without K.
(b) Effects of K at different Mg treatments.

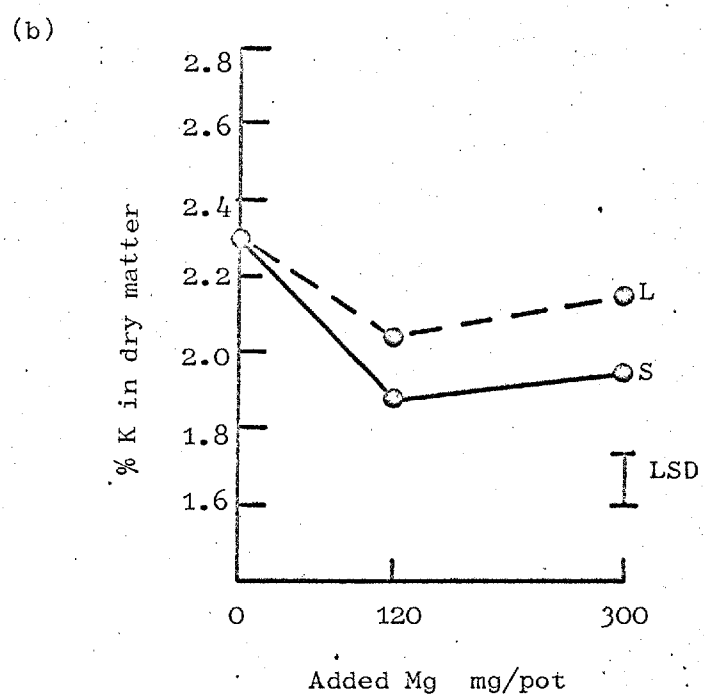


Legend. As Fig. 5/1

Fig. 5/5

(a, b) Effects of added K and Mg on the % K in tuber dry matter





increased the quantity of K in the tubers. This, in turn, meant that the quantities of K in other plant parts were decreased, because overall K uptakes were not much affected. The effects are not described in detail (but see Appendix III), because, although they were sometimes statistically significant, they probably had no great physiological significance and arose because in this soil the amount of Mg available was less than that usually needed for full yield; had more been available these effects would probably have been less apparent.

Effects on other nutrients

Calcium. Giving either amount of K significantly decreased the quantity and concentration of Ca in the leaves; adding Mg did not. Neither K nor Mg much altered the quantities of Ca in other parts, but where they increased growth, they tended to lessen concentration of Ca, probably by dilution.

Phosphorus. Concentrations of P in the tubers were not much changed by adding K or Mg, except that treatments giving the most tuber growth tended to dilute the P. The quantity of P in the tubers therefore varied mainly with the weight of dry matter (Table 5/1). Total P uptake was not much affected by the treatments so that where more P went to the tubers less was in the rest of the plant.

The effects on Ca and P observed accord, where relevant, with those in Chapter 4. Full details are in Appendix III.

Effects on tuber dry matter

Table 5/1 shows the effects of the treatments on the amount and percentage of dry matter in the tubers. In this soil, the larger amount of K given without extra Mg had a clearly adverse effect on the amount and

TABLE 5/1

Effects of added K and Mg on (a) the amount and (b) the percentage of dry matter in the tubers

K added (g/pot)	Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
(a) Dry matter (g/pot)						
0	27.4	29.3	24.9	24.6	25.5	26.3
1	37.8	49.9	49.6	57.6	45.3	48.0
2.5	26.2	50.4	43.7	55.8	43.3	43.9
Mean	30.5	43.2	39.4	46.0	38.1	39.4

S.E.'s* Column mean 1.37; Row mean 1.77
Within table 3.06

(b) Percentage of dry matter						
0	20.7	22.6	19.5	20.7	20.9	20.9
1	20.7	23.0	23.1	24.7	22.8	22.9
2.5	16.8	21.6	19.6	22.8	19.8	20.1
Mean	19.4	22.4	20.7	22.7	21.2	21.3

S.E.'s* Column mean 0.33; Row mean 0.42
Within table 0.73

S denotes Mg added to soil
L denotes Mg sprayed on leaves

* there were 26 degrees of freedom

the percentage of dry matter. When K was given, adding Mg at either level improved both.

Discussion

Biddulph et al (1959) and Ringeot et al (1968) concluded that Ca was almost immobile in plants not because it could not move in the phloem but because the amount that did was very small, the rest being strongly retained by the leaves. Mg could behave similarly, and the results described strongly suggest that where K decreased the quantity of Mg in the leaves, it did so by preventing it from reaching them rather than by increasing its remobilisation, implying that Mg too was strongly held once it was in the leaves.

Mg is found in the phloem in rather larger concentrations than Ca (see Chapter 1). Some may be released from the leaves, but the present results suggest that this is a negligible proportion of what reaches the tubers. However, the results in the previous chapter suggest that nutrients held in soluble form in the stem cells, including Mg were appreciably moved to the tubers. The phloem is probably not isolated from the other cells in the stem, and removal of Mg from the phloem to the tubers would cause a concentration gradient between the other cells, including the xylem, and the phloem, which would induce passive movement of Mg to the phloem. The more Mg was removed from the phloem, the more passive movement would occur. A mechanism whereby increasing the K^+ concentration in the phloem would enhance Mg movement is discussed in Chapters 7, 8 and 9.

The relationship between the concentrations of Mg and K in the tuber dry matter occurred in spite of the variation in the amounts added of both

K and Mg. This was apparently caused by the effects of K on the Mg concentration and not vice versa. This relationship too will be discussed later in terms of the effect of increasing the K^+ concentration in the phloem on the movement therein of Mg.

CHAPTER 6

THE EFFECTS OF GIVING POTASSIUM AND MAGNESIUM AND REMOVING TUBERS ON LEAF NUTRIENT CONCENTRATIONS AND INTERACTIONS DURING SENESCENCE

Introduction

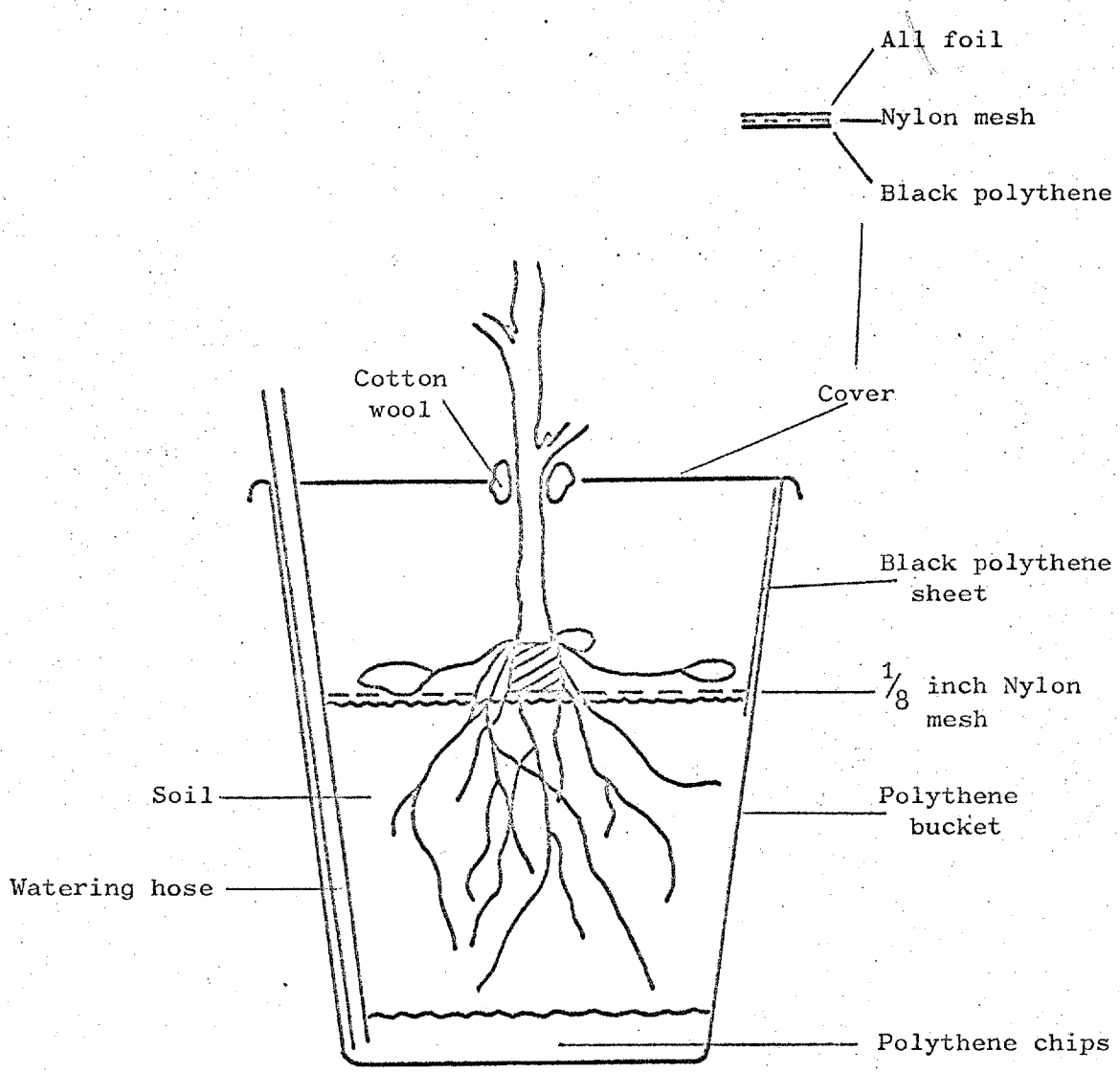
In Chapter 1 (pp 28-29), the concept of the 'sink' was discussed in relation to the phenomena of shoot recession and tuber formation. The effects described so far are equally compatible either with the idea that the 'sink' concept is intrinsically true and that shoot recession reflects competition, with the tubers gaining the ascendancy, or with the idea that an 'innate development programme' regulates the shift of activity from making shoot growth to making tubers and the 'sink' concept merely describes this process.

Leopold, Niedergang-Kamien and Janick (1959), Murneek (1926) and Molisch (1929) all showed that removing the reproductive organs from plants delayed their senescence. Removing tubers from potato plants should therefore delay, but not prevent, the working of the 'innate development programme'; however, it should also largely prevent the tubers competing effectively with the shoot.

The tuber 'sink' was characterised by its ability seemingly to withdraw the mobile nutrients P and K from other plant parts and by the enhancing effect of added K on its Mg concentration. If such effects are common to all sinks, they should appear in the apical meristem of the shoot. Loss of 'sink' character from the shoot as the tubers formed could be expected to involve a decrease in the K and P concentrations and the disappearance of

Fig. 6/1

The equipment used for growing the plants



the 'enhancing effect'. Removing the tubers should only delay such changes if the 'development programme' hypothesis is valid, but largely prevent them if straightforward competition is involved.

These effects were investigated by following the concentrations of nutrients in young unfolding leaves sampled close to the apical meristem. Similar sampling was continued after shoot growth ceased because the leaves from the top of the shoot remain the youngest on the plant and their senescence should reflect that of the whole plant. The plants received added K or Mg or both and all tubers were removed from half the plants of each treatment.

Effects on growth and water use by the plants are also discussed.

Methods

The plants grew in 3 kg of soil from Geescroft field at Rothamsted; this soil was more acid (pH 5.7 in water) and contained more exchangeable Mg (5.8 mg/100 g) than that used in the previous experiment but held a similar amount of exchangeable K (11.3 mg/100 g). They received basal nutrients 1 g N and 1 g P as $Ca(NO_3)_2$ and $NH_4H_2PO_4$, and, where appropriate, 2 g K as K_2SO_4 and/or 0.3 g Mg as $MgSO_4$. The treatments were: control, added K, added Mg, added K + Mg; there were six replicates of each, of which three later had their tubers removed and three did not.

Fig. 6/1 shows the equipment used to grow the plants. Sprouted eyes, cut with an $^{11}/_{16}$ inch cork borer to give a 1 inch long segment, were planted one per pot with the tuber segment on top of an $^{1}/_{8}$ inch nylon gauze, with the roots protruding through the gauze into the soil. The segments were originally covered with moist peat which was removed when the insulating

covers were put on as the plants grew above the rims of the buckets. Water was given through the hoses, enough (by weight) to keep the soil at 0.75 water-holding capacity (measured as in Addiscott and Talibudeen, 1971), and the water use was recorded.

Tubers started to form about 44 days after planting and were removed with scissors or a scalpel on half the plants of each nutrient treatment. A 'tuber' was removed when it was twice the diameter of the stolon.

Leaf sampling. Starting from the tip of the shoot meristem, young leaves (furled or unfurled) were counted and the fourth one, which was usually unfurling or just unfurled, was taken. For consistency, the procedure was retained after shoot growth recessed. Samples were taken 32, 42, 57 and 74 days after planting and were analysed as described in Chapter 2.

Analysis of variance, allowing for one missing pot, was performed* on all the variates to be described.

Results

The effects of added K on Mg concentrations in the 'sinks'

Table 6/1 (a-c) shows the effects of adding K and Mg on the concentrations of Mg in (a) the fully grown tubers on intact plants, (b) the very small tubers cut from the others, and (c) the young leaves cut from the shoot meristem at the first (32-day) sampling. In each case, giving K significantly+ increased the % Mg in the dry matter while Mg had considerably less or no effect, and the K treatment always accounted for at least ten times as much variance as the Mg treatment. The enhancing effect of K on Mg concentration thus appeared in all three 'sinks' and seemed fairly definitely linked with 'sink' function.

---

* by J. H. A. Dunwoody
+ $p < 0.05$, unless otherwise stated

TABLE 6/1

Effects of K and Mg on Mg concentrations in (a) fully grown tubers, (b) cut tubers, and (c) leaflets taken at 32 days

All % Mg in dry matter

(a)		0	K	Mean
	0	0.080	0.095	0.087
	Mg	0.060	0.110	0.085
	Mean	0.070	0.102	0.086
		S.E.'s*	Means	0.0059
			Within table	0.0083
(b)	0	0.111	0.138	0.125
	Mg	0.112	0.156	0.134
	Mean	0.112	0.147	0.129
		S.E.'s+	Means	0.0025
			Within table	0.0035
(c)	0	0.159	0.260	0.209
	Mg	0.184	0.296	0.240
	Mean	0.171	0.278	0.224
		S.E.'s++	Means	0.0041
			Within table	0.0057

* there were 6 degrees of freedom
\+ " " 5 " " "
++ " " 13 " " "

The effect of removing the tubers on K and P concentrations and the K-Mg interaction in the young leaves

Fig. 6/2a shows changes during growth in the % K in the leaf dry matter of plants with and without their tubers and with and without added K. (Mg had little effect on % K and the points show the means for treatments with and without Mg.) When no K was given, removing the tubers had no significant effect on the decrease in the leaf K concentration that occurred when the tubers formed, although it seemed to delay it slightly. With K added, no decrease occurred and there was a larger K concentration in leaves from intact plants.

The P concentration (Fig. 6/2b) was averaged across the K and Mg treatments for plants with and without tubers. Removing the tubers initially (57 days) lessened the decrease in the P concentration that occurred when the tubers formed but later (74 days) increased it. Adding K or Mg had no effect except in the first sampling, when giving K increased the % P in leaf dry matter from 0.72% to 0.81% (sig at $p < 0.01$).

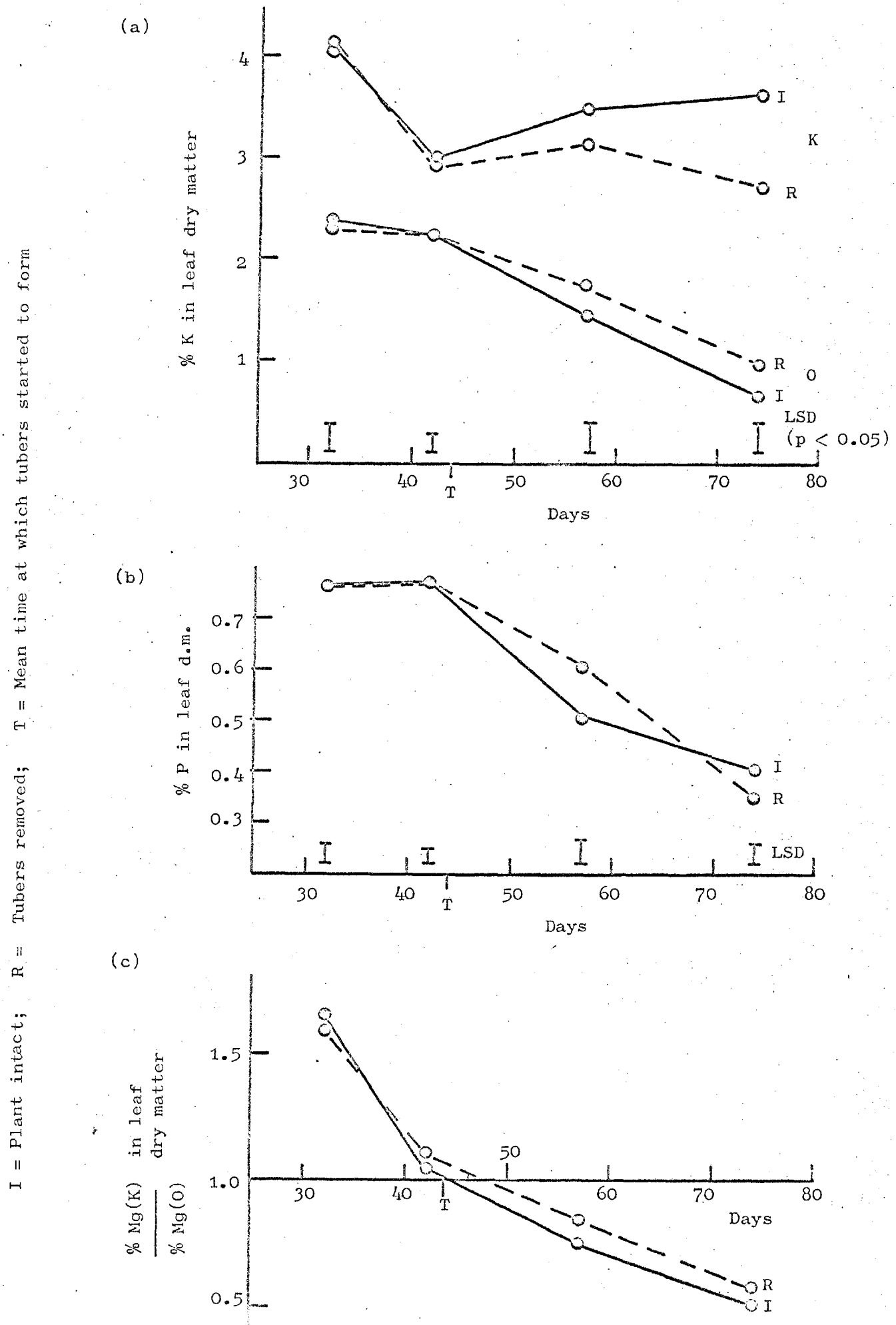
Changes during growth in the effect of added K on the Mg concentration in the leaf dry matter were shown (Fig. 6/2c) by the ratio

$$\frac{\text{\% Mg when K added}}{\text{\% Mg when no K added}}.$$

The points show the means of treatments with and without added Mg, which had little effect. Before tubers formed the ratio exceeded 1.0 (see previous section), but when the tubers formed the ratio became less than 1.0, i.e. giving K decreased % Mg. Removing the tubers slightly delayed the change but did not much affect it. The change seemed to go in a smooth progression and to have started before the tubers formed.

Fig. 6/2

Changes with time in and the effects of tuber removal on (a) % K and (b) % P in leaf dry matter and (c) the ratio of Mg concentrations with and without added K.



I = Plant intact; R = Tubers removed; T = Mean time at which tubers started to form

The effects of removing the tubers and giving K and Mg on cation concentrations in the leaves and on plant senescence

Neither nutrient treatment affected the time the plants took to form tubers (mean 43.6 days). Removing the tubers when they formed increased the total life of the plants by an average of 50 days and giving K by 27 days, but giving Mg had no effect. The K and tuber removal effects were additive (Table 6/2).

Fig. 6/3 (a-c) shows the effects on the sum of the leaf cation concentrations K+Ca+Mg (in m-equiv/g) of (a) removing the tubers, (b) giving K, and (c) giving Mg. The figures show the effects separated with each averaged across the other two. Removing the tubers much decreased the cation concentration sum; giving K initially increased it but significantly decreased it at 74 days; Mg had little effect.

Removing tubers and giving K thus both increased the longevity of the plants and both decreased the cation concentration sum in the leaves, providing further evidence for a link between cation sum and senescence.

The effects of the treatments (again separated) on the individual concentrations of Ca and Mg are shown in Fig. 6/4 (a-f). The Ca concentration in the leaf dry matter was small and constant until the tubers formed and then increased greatly. Removing the tubers halved the rate of increase and giving K decreased it even more; Mg had no effect. As was shown before, the Mg concentration was initially increased by giving K and less so by giving Mg; after tubers formed, removing them or giving K decreased it but giving Mg increased it. These effects are discussed later.

TABLE 6/2

Effects of giving K and removing the tubers on the total life of the plants

	Days		
	0	K	Mean
Plants intact	90	114	102
Tubers removed	136	167	152
Mean	113	140	127

S.E.'s* Means 2.8
Within table 3.9

Above are means of treatments with and without added Mg, which had no effect

TABLE 6/3

Effects of giving K and removing the tubers on the water used between tuber formation (44 days) and the death of the first plants (81 days)

	Litres		
	0	K	Mean
Plants intact	5.17	8.44	6.81
Tubers removed	3.41	6.65	5.03
Mean	4.29	7.54	5.92

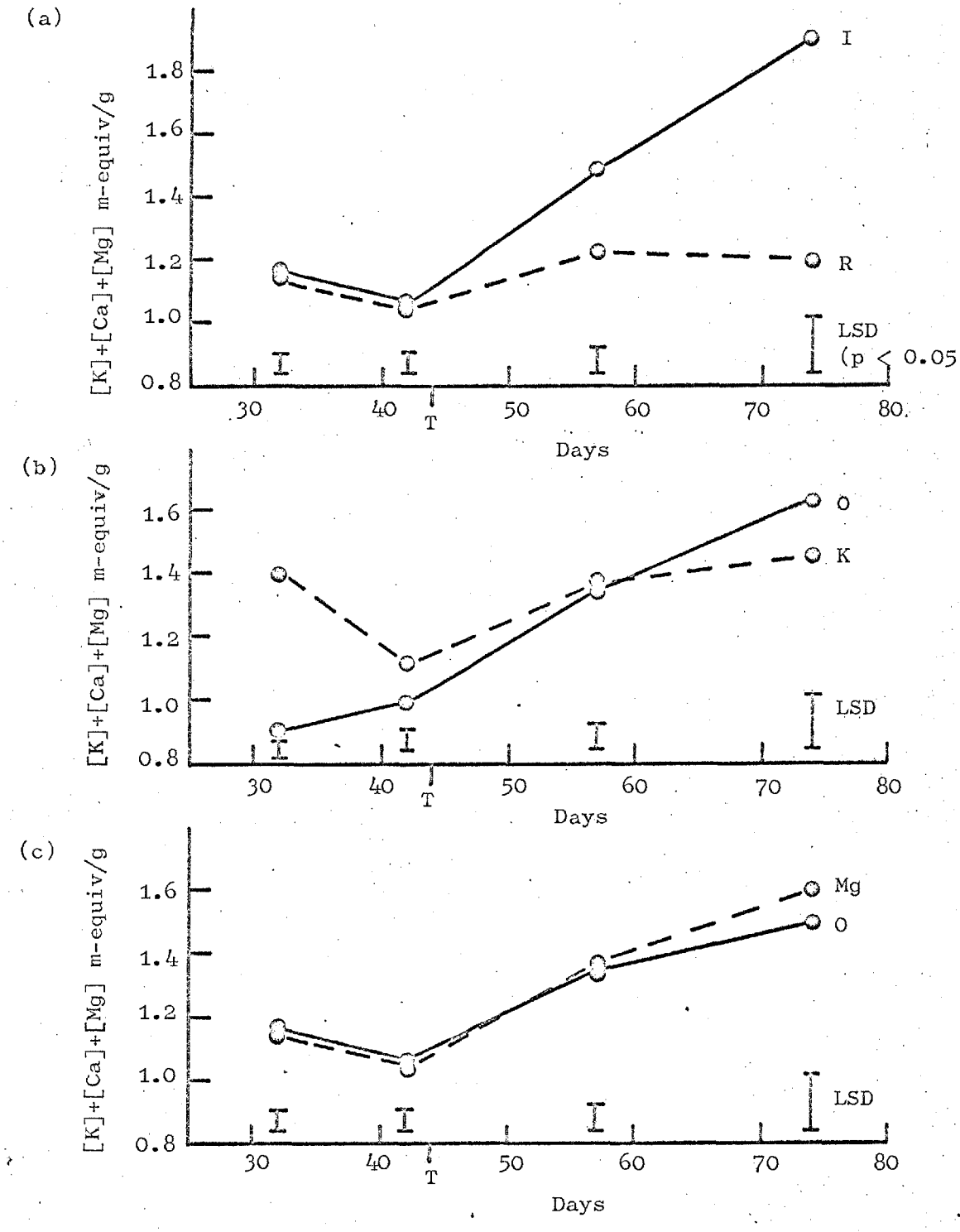
S.E.'s* Means 0.173
Within table 0.244

Means of treatments with and without added Mg

* there were 13 degrees of freedom

Fig. 6/3

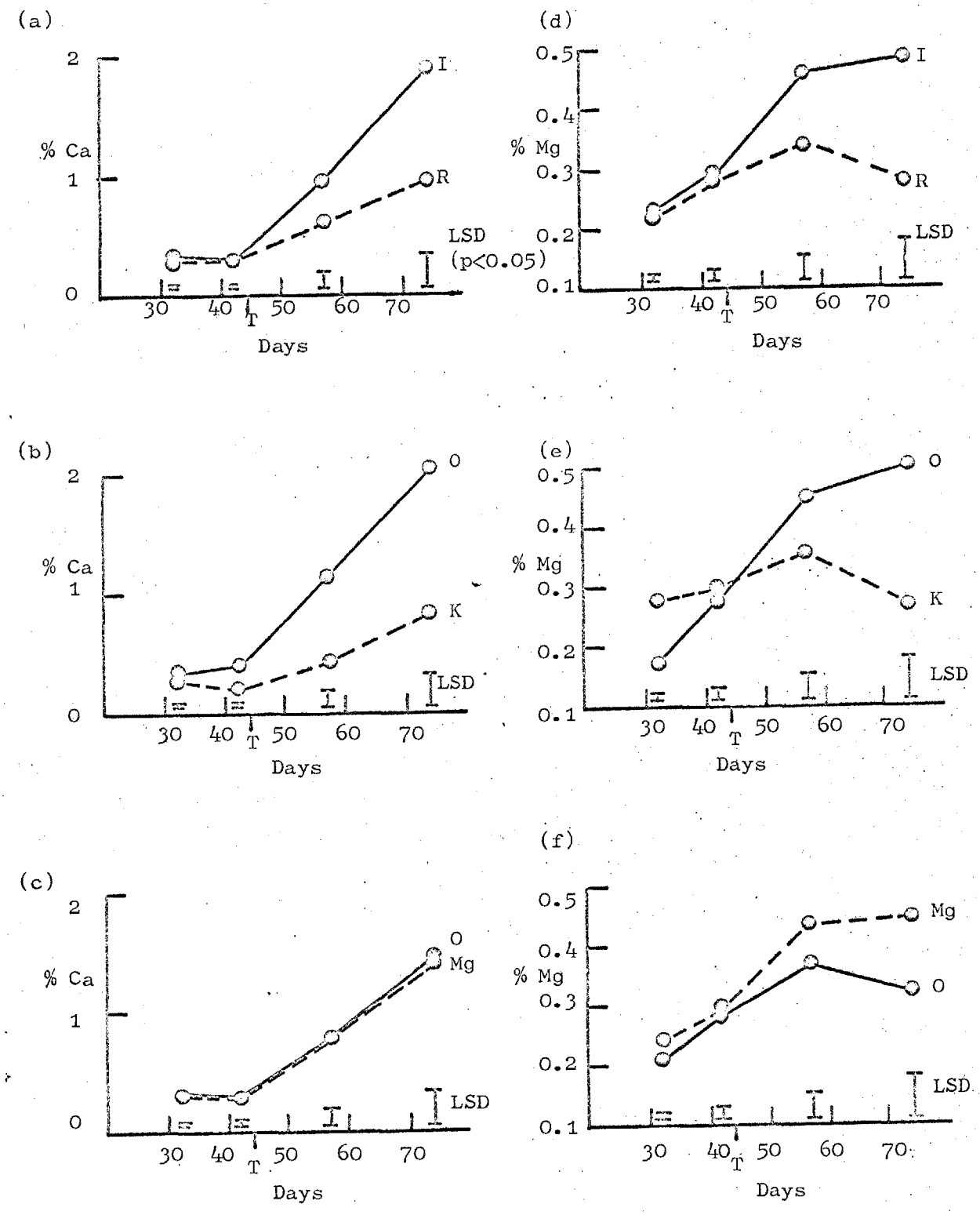
The effects of (a) Removing tubers, (b) Giving K, and (c) Giving Mg on changes in the sum of the leaf cation concentrations*(K+Ca+Mg). (I = Plant intact; R = Tubers removed ; 0 = No added nutrient; T = Tubers formed)



* dry weight basis.

Fig. 6/4

The effects of (a, d) Removing tubers, (b, e) Giving K, and (c, f) Giving Mg on (a,b,c) % Ca and (d,e,f) % Mg in the leaf dry wt. Legend as Fig. 6/3



Effects on the growth of the plants

Water use. Before the tubers formed there were no significant effects on water use. Between tuber formation (44 days) and the death of the first plant (81 days), giving K increased the amount of water used, probably because it increased the size of the plants, whereas giving Mg had no effect. Removing the tubers decreased the amount of water used in this period, by about 1.8 litres, much more than the amount of water that would have been in the tubers had they formed (probably 0.15-0.18 litre). Thus water flow in the xylem was presumably decreased, and this may have been a contributory factor in the effects of tuber removal on Ca and Mg concentrations in the leaves (Table 6/3).

Stem growth. Plants which had their tubers removed developed thick starchy bases to their stems, especially when given K. Table 6/4, giving the dry weights of the dead stems shows the magnitude of these effects. Plants with their tubers removed or given K had larger quantities of K and P in their stems; quantities of Ca and Mg were not much affected, except that giving K and leaving the tubers intact significantly decreased the amount of Mg in the stem, c.f. Chapters 4 and 5 (Appendix IV).

Number and weight of tubers. Giving K significantly increased the number and fresh weight of tubers formed but decreased their % dry matter (Table 6/5). In this soil, which contained more Mg than that used in the previous experiment, giving Mg did not significantly affect the number, weight or % dry matter of the tubers.

Numbers of tubers removed. Very large numbers of tubers were removed, 437 from one plant. Giving Mg significantly increased the number produced (Table 6/6).

Abnormal growths. Plants whose tubers were removed developed growths from their axillary buds. These were either horizonally - growing stolon-like

TABLE 6/4

Weights of dead stems

	Dry weight (g)		
	0	K	Mean
Plants intact	10.7	14.0	12.4
Tubers removed	15.7	34.3	25.0
Mean	13.2	24.2	18.7

S.E.'s*	Means	1.07
	Within table	1.51

Above are means of treatments with and without added Mg, which had no effect

* there were 13 degrees of freedom

TABLE 6/5

Effects of added K and Mg on (a) number, (b) fresh weight and (c) % dry matter of tubers on intact plants

		0	K	Mean
(a)			Number	
	0	13	15	14
	Mg	9	18	14
	Mean	11	17	14
	S.E.'s*	Means		1.3
		Within table		1.9
(b)			Fresh weight (g)	
	0	147	288	218
	Mg	141	271	206
	Mean	144	280	212
	S.E.'s*	Means		14.1
		Within table		20.0
(c)			% Dry matter	
	0	22.9	22.0	22.4
	Mg	24.1	20.8	22.4
	Mean	23.5	21.4	22.4
	S.E.'s*	Means		0.30
		Within table		0.43

* there were 6 degrees of freedom

TABLE 6/6

The effects of giving K and Mg on the numbers of small tubers cut off

	Number		
	0	K	Mean
0	273	258	266
Mg	361	336	349
Mean	317	297	307

S.E.'s* Means 22.2
Within table 31.5

* there were 5 degrees of freedom

Fig. 6/5 (a,b)

Abnormal growths on plants with tubers removed

(a)

(b)

growths (Fig. 6/5a) or objects resembling cherries with very small leaves (Fig. 6/5b). The first type grew at the top of the plant and appeared on all tuberless plants; the second grew near the base of the plants and came mainly on tuberless plants given K.

Discussion

Sinks. The enhancing effect of K on Mg concentration has now been observed in tubers grown in soils varying in pH and exchangeable Mg content and also in leaves from the apical meristem; it was found too in tubers from potatoes grown in the field (Bolton, 1971). It thus seems fairly definitely related to sink function, and a possible mechanism for this is discussed in Chapters 7, 8 and 9.

Innate development programme v. shoot:tuber competition. Three factors suggest that the movements of ions are better described in terms of the 'innate development programme' than 'competition':

(a) Removing the tubers only slightly delayed the decreases after tuber formation in the P concentration of the young leaves and their K concentration when no K was added; these changes were certainly not prevented.

(b) The change in the ratio

$$\frac{\%\ \text{Mg when K added}}{\%\ \text{Mg when no K added}}$$

was affected as little as the changes in the P and K concentrations.

(c) The ratio seemed to change in a smooth progression; the change appeared to start before the tubers formed and the ratio passed through the value 1.0 almost exactly at the time tuber formation started.

(d) Formation of abnormal growths in tuber-inducing [illegible]

Effects related to senescence. Removing the tubers and adding K both had the following effects:

(a) Increased longevity of the plants.

(b) Decreased Ca, and to a lesser extent Mg, concentrations in the leaf dry matter.

(c) Decreased sum of cation concentrations in the leaf dry matter.

Removing the tubers also decreased water use; giving K increased the water used in this experiment, but probably because it increased the size and leaf area of the plants. Other results (Blanchet, Maertens & Bosc, 1970; Addiscott & Talibudeen, 1971) suggest that the water used per gram of dry matter formed could have been decreased. Thus removing the tubers probably decreased the flow of water in the xylem and giving K may have done so.

Giving K probably decreased the Ca concentration in the xylem sap (Chapter 3).

A further, more hypothetical, effect needs to be considered. K deficiency in leaves causes photo-respiration to increase (Jackson & Volk, 1968) and so probably increases the concentrations in the leaves of the tri-carboxylic acids involved in the respiratory cycle. The anions of some of these acids, notably cis-aconitic and oxaloacetic acids, are likely to form neutral non-ionic chelate complexes with Ca and Mg; should oxaloacetic acid break down to oxalic acid, insoluble Ca oxalate will be formed, and has been found in leaves (Joy, 1964; Al-Rais, Myers & Watson, 1971). Improving the K supply may thus decrease the complexing of Ca and Mg in leaves.

The accumulation of Ca complexes and even Ca oxalate crystals in leaves may disrupt their photosynthetic activity or even physically alter the cells.

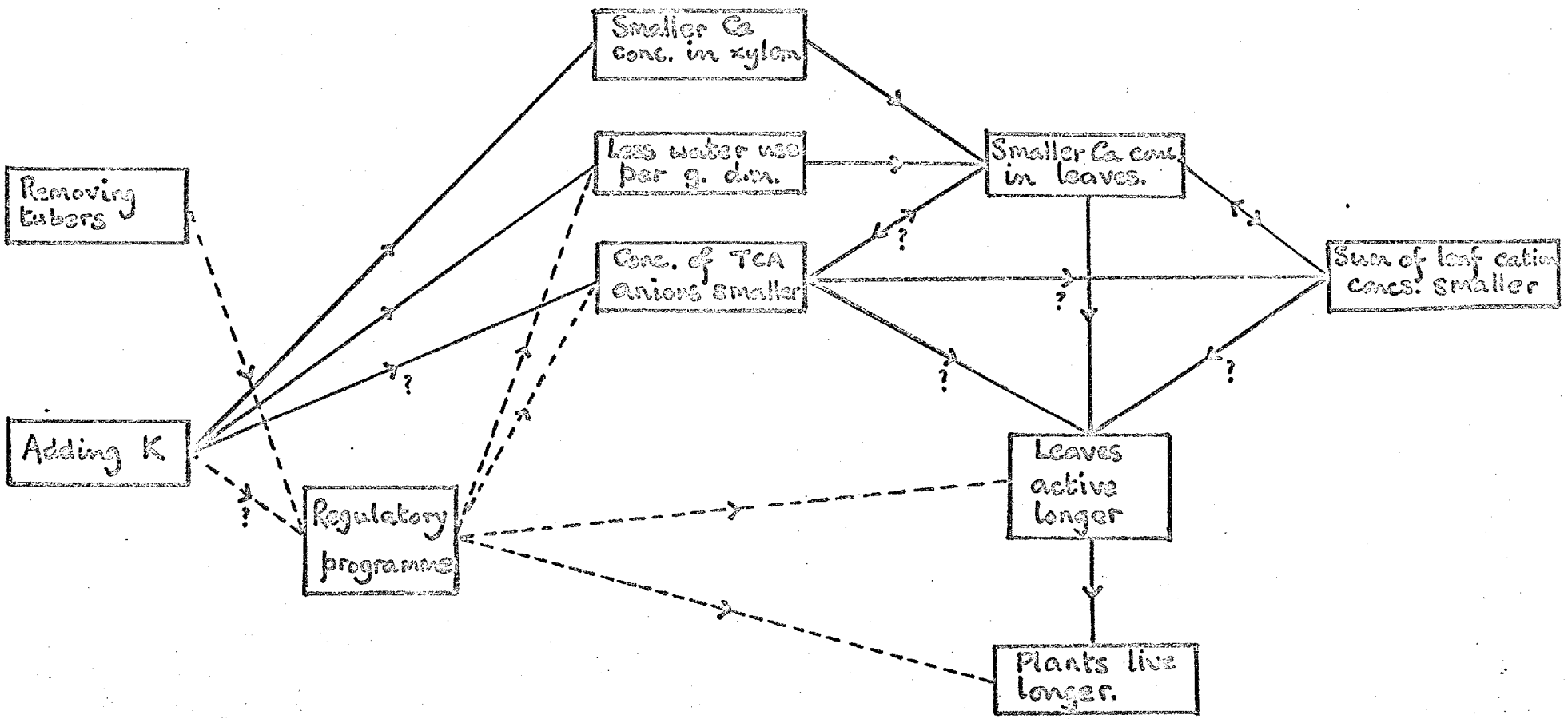
Lessening of photosynthesis in the leaves would cause utilisation of carbohydrate reserves (except in storage organs) followed by rapid senescence.

Senescence thus involves a whole syndrome of possible effects. Possible connections between the effects discussed are shown by solid lines in Fig. 6/6.

The concept of an 'innate development programme', discussed before, implies that the 'programme' is responsible for senescence. However it is not clear at present whether the 'programme' directly regulates all the effects discussed (broken lines in Fig. 6/6), or whether the programme is directly responsible only for the shift of activity from shoot formation to tuber formation, which, in turn, leads to the syndrome of senescence effects.

Fig. 6/6

Possible inter-relationships between the various effects of removing tubers and giving K



CHAPTER 7

THE EFFECTS OF SHORT-TERM ADDITIONS OF POTASSIUM AND MAGNESIUM ON TRANSLOCATION OF ^{14}C-LABELLED ASSIMILATE AND IONS INTO THE TUBERS

Introduction

The previous chapters showed that giving the plants K increased the Mg concentrations in the 'sinks'; the effect seemed definitely related to 'sink' function. It could have arisen because giving K increased some 'sequestrating' effect of the tubers for Mg, or as a consequence of the nature of the translocation of assimilate and ions to the 'sinks'; the former case implies specific control of the phenomenon by the 'sinks', the latter none.

Work on potato plants by Moorby (1968) showed that when ^{14}C-labelled photosynthetic assimilates were exported from leaves to tubers, the label was very unevenly distributed between tubers, and the amount of ^{14}C a tuber received was not related to its size; this suggests the largest tubers were not necessarily growing faster than the smallest. No experiments seem to have been made on the accumulation of nutrients by different tubers on the same plant.

If the K-Mg effect arises because K stimulates the tubers to 'sequestrate' Mg in some way, it should be greatest in the most actively-growing tubers. This was tested by growing potato-plants in solution until they formed tubers and exposing the tops to ^{14}C-labelled CO_2 immediately after the plants had been subjected to a ten-fold increase in K and/or Mg concentration in solution or sprayed with K and/or Mg; ^{14}C-activity and

water-soluble K, Mg and P (thought best to represent recently acquired nutrients) were determined in individual tubers on the same plant. In the larger tubers, their distributions within tubers were measured as well.

The 'sequestration' hypothesis was also tested by measuring how much Mg and ^{14}C-labelled sucrose fresh potato tuber discs absorbed when shaken in solutions containing Mg, ^{14}C-labelled sucrose and varying K concentrations. If the hypothesis is correct, active (^{14}C absorbing) discs may be stimulated by added K to absorb extra Mg.

The effects of adding K and/or Mg on the total translocation of ^{14}C, K, Mg and P were also examined in relation to theories of phloem transport.

Methods

Twelve potato plants were grown in solution in the apparatus shown in Fig. 7/1, which was based on that of Houghland (1950). Five litres of solution was contained in a large stone jar sealed with bituminous paint and was aerated 2 hours a day through the capillary tube. The plant supports were made from PVC piping with $\frac{1}{8}$ inch nylon gauze on the bottom supported by PVC wire*.

Viable eyes, cut from seed as in the previous experiment, were incubated until they formed good roots and then transferred to the supports. The roots were passed through the gauze into the solution and the segment was covered in moist peat, which was built up round the plant as it grew. The polythene sheet kept the moisture in the peat.

The technique produced healthy plants about 80 cm high, which produced up to about 300 g of fresh tubers each before they were harvested (well before they died off).

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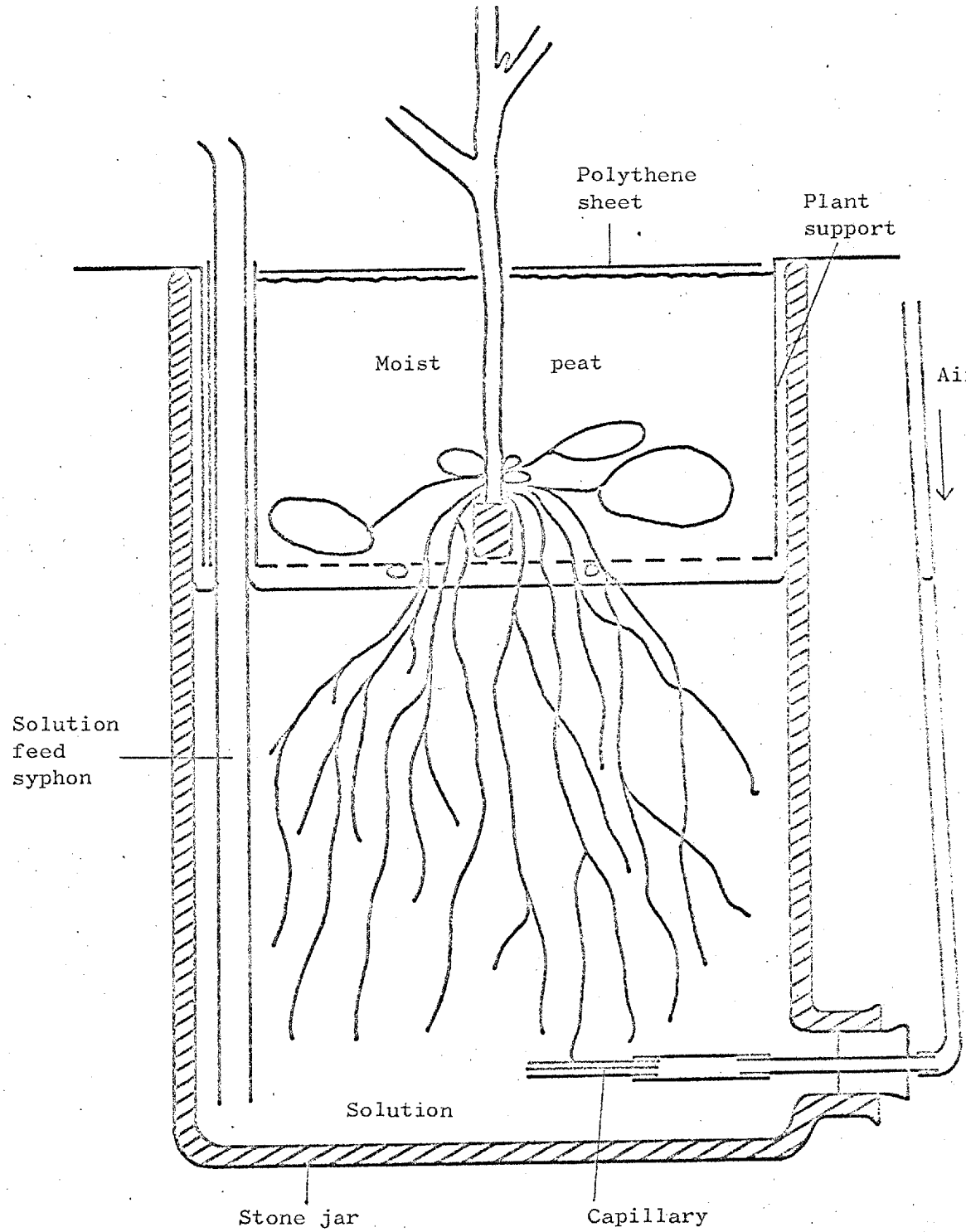
* These were kindly made by Mr. K. Smith

Fig. 7/1

The apparatus used to grow plants in solution



The solution initially contained:

$Ca(NO_3)_2$	5	m-equiv/l	H_3BO_3	0.025	m-equiv/l
$NH_4H_2PO_4$	1	"	$MnSO_4$	0.0025	"
KCl	0.5	"	$CuSO_4$	0.0015	"
$MgSO_4$	1	"	$ZnSO_4$	0.0015	"
			Fe EDTA	0.16	m-equiv/l

and had a pH of 4.9. They were replenished from a central syphon and changed weekly. The $Ca(NO_3)_2$ concentration was decreased to 1 m-equiv/l after 35 days and those of $NH_4H_2PO_4$, KCl and $MgSO_4$ to 0.5, 0.1 and 0.2 m-equiv/l after 56 days. (The pH barely altered, to 5.0). All plants had the same solutions until the experimental period started.

Final experiments

At 73 days, 4 plants were transferred to different solutions:

'Control' : As growth solution, 0.1 and 0.2 m-equiv/l of K and Mg.

'Extra K' : As control, but 1 m-equiv/l of extra K given as K_2SO_4.

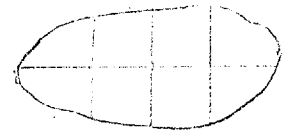
'Extra Mg' : As control, but 2 m-equiv/l of extra Mg given as $MgSO_4$.

'Extra K+Mg' : As control, but extra K and Mg given at above rates.

The plants were then enclosed in covers made from heavy transparent polythene sheet, and 30 minutes after the transfer, they were each exposed for 5 hours to 50 μC of $^{14}CO_2$ generated by acidifying $Ba^{14}CO_3$. Twenty-three hours after the transfer, the plants were taken from the solutions and analysed.

The leaves, stems and roots were analysed by the standard procedures in Chapter 2.

The tubers were halved longitudinally and each half separated (if large enough) into nearly equal segments (see text figure) normally weighing 8-10 g (fresh). The segments from one half were dried and retained



Each segment from the other half was immediately macerated in 40 ml of distilled water in a MSE homogeniser and an aliquot of the resulting suspension counted by liquid scintillation (see Appendix VI for the technique) for ^{14}C activity. The remaining suspension was centrifuged and the supernatant liquid sampled for analysis for water-soluble K, Mg and P.

At 87 days an identical experiment was made except that instead of the extra K and/or Mg being given in the solution, it was sprayed on the tops at the rates of 2.5 m-equiv of K and/or 5.0 m-equiv of Mg per plant.

The experiment on the absorption of Mg and ^{14}C-labelled sucrose by tuber discs

Tubers were taken from growing plants of the same variety (King Edward) in the field and were used within 30 minutes. Discs 1 mm thick and 17.5 mm in diameter were cut from the rose* ends using a cork borer and a razor blade. Ten discs per tube were rapidly weighed into 50 ml stoppered polypropylene tubes and shaken for 1 or 3 hours in solutions containing 0.1 M sucrose, 0.008 μC/ml of ^{14}C as sucrose, 0.0075 N $MgSO_4$ and 0-0.40 N K_2SO_4, with two replicates of each K treatment. After shaking, the discs were drained, washed with distilled water and homogenised and analysed as previously described.

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* The 'heel' end of a tuber is that at which it is attached to the plant. The other is the 'rose' end.

Results

Appendix V gives details of the weights and the concentrations of ^{14}C activity, K, Mg and P in all the tubers harvested.

The distribution of ^{14}C activity and nutrients between tubers

Carbon-14 activity. Large variations were found in the quantity and the concentration of activity in different tubers on the same plant. The quantity was sometimes broadly related to tuber fresh weight (e.g. Fig. 7/2a) such that larger tubers tended to contain more activity, and sometimes unrelated (e.g. Fig. 7/2c). The concentration of activity was not related to tuber weight (Fig. 7/2b, d).

These results support Moorby's (1968) observations.

Potassium. The concentrations of water-soluble K (fresh weight basis) varied very little between tubers (Appendix V).

Magnesium. The concentrations of water-soluble Mg (fresh weight basis) varied more between tubers than those of water-soluble K. To see if the variations were related to growth activity, the regression of Mg concentration on that of ^{14}C activity was calculated at each harvest for each plant separately and for all four taken together, and, because the Mg concentration tended to decrease as the tuber fresh weight increased, multiple regressions on the concentration of ^{14}C activity and the weight were also calculated Table 7/1). Only in the multiple regression for the control in the first harvest was the water-soluble Mg concentration related to that of ^{14}C activity and it was concluded that Mg accumulation by individual tubers was not specifically related to growth activity.

Phosphate. Water-soluble P concentration (also on fresh weight basis) varied more between tubers than those of water-soluble K and Mg. It also

Fig. 7/2

(a,c) Quantity and (b,d) the concentration of ^{14}C activity in the tubers of a plant plotted against their fresh weight. (a,c) K treatment, (b,d) K, Mg treatment, both 73 day harvest.

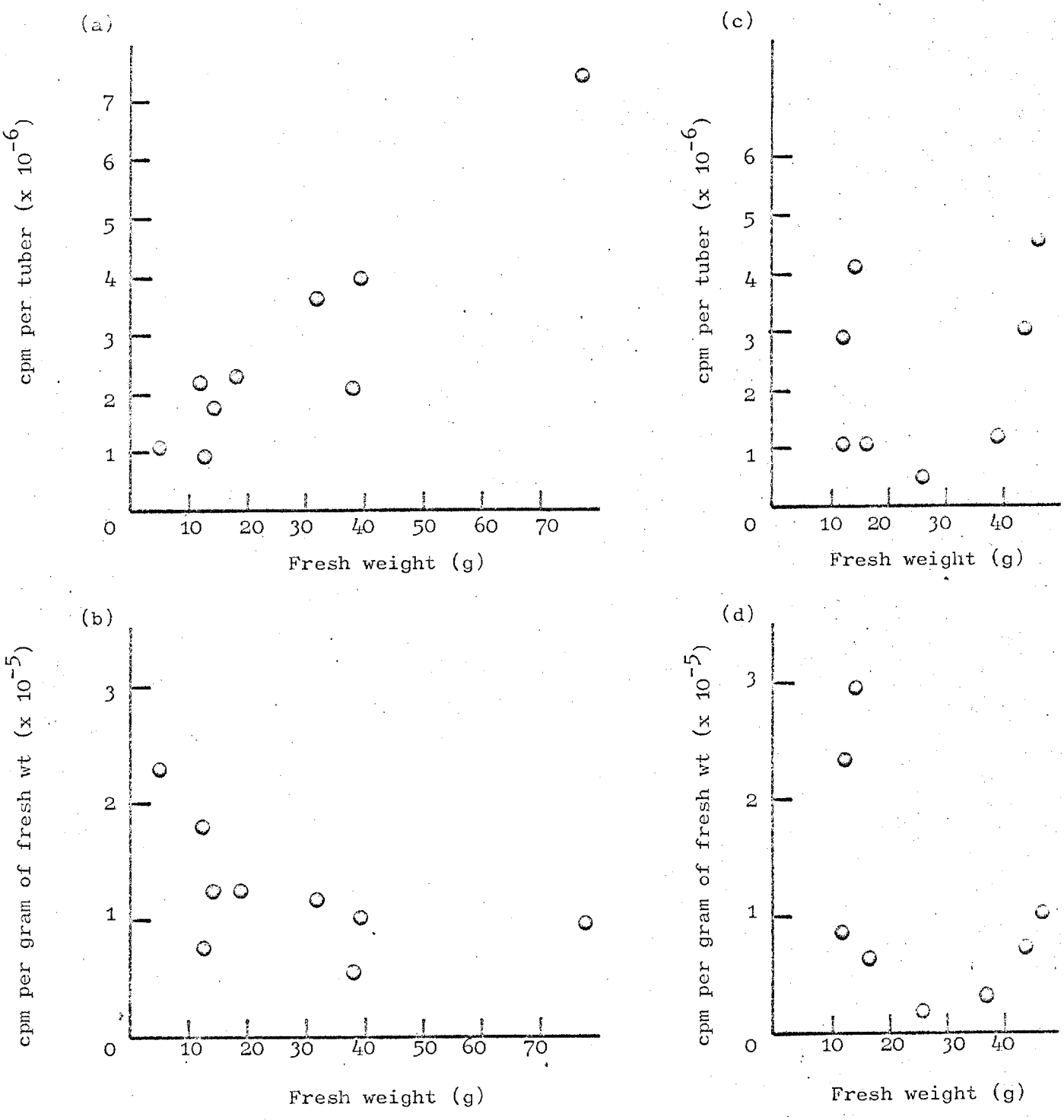


TABLE 7/1

Percentages of variation in the concentrations of water-soluble Mg and P in tuber fresh matter accounted for by single and multiple regressions on ^{14}C concentration (S) and tuber fresh weight (W)

	Percentage of variation accounted for by		
	Single regression on S	Single regression on W	Multiple regression on S + W
73-day harvest			
Mg concentration			
Control	NS	NS	68(++)
K tr.	NS	NS	NS
Mg tr.	NS	NS	NS
K+Mg tr.	NS	NS	NS
All together	NS	NS	NS
P concentration			
Control	NS	NS	NS
K tr.	61(+)	NS	61(+:NS)
Mg tr.	NS	49(-)	74(NS:-)
K+Mg tr.	65(+)	63(-)	89(+:-)
All together	24(+)	27(-)	40(+:-)
87-day harvest			
Mg concentration			
Control	NS	NS	NS
K tr.	NS	NS	NS
Mg tr.	NS	NS	NS
K+Mg tr.	NS	27(-)	NS
All together	NS	NS	NS
P concentration			
Control	NS	NS	NS
K tr.	66(+)	NS	62(+:NS)
Mg tr.	28(+)	NS	62(+:-)
K+Mg tr.	NS	NS	NS
All together	NS	NS	9(NS:-)

Notes: NS means Not Significant ($p < 0.05$).

+ , - or NS after a figure means that the regression coefficient was positive, negative or (in the multiple regressions) not significant.

In the multiple regression column, the signs of the regression coefficients are in the order (S : W).

tended to decrease as the tuber's weight increased, and so both single regressions on the concentration of ^{14}C activity and multiple regressions on that and fresh weight were calculated for water-soluble P. Table 7/1 shows that at the 73 day harvest (nutrients given in solution), the water-soluble P concentration was positively related to the concentration of ^{14}C activity in tubers on plants given K or K+Mg and when all the plants were taken together. At the 87 day harvest (nutrients sprayed), the relationship appeared only for the plants given K or Mg. Thus the concentration of water-soluble P seemed better related to growth activity than that of K or Mg.

Distribution of ^{14}C activity and nutrients within individual tubers

Table 7/2 gives examples of the variations in the concentrations of ^{14}C activity and water-soluble K, Mg and P. Both the ^{14}C and K concentrations increased from the heel to the rose ends, presumably reflecting growth activity, except that in two tubers the penultimate segment (3) had a slightly larger ^{14}C activity concentration than the end segment (4) (see final example). The concentrations of water-soluble Mg and P were mostly smaller in the middle than at the ends. The distributions of ^{14}C activity and K accord with those found by Badenhuisen and Dutton (1956) and Johnston, Hoffman and Petrasovits (1968).

Effect of the treatments on translocation

Only one replicate of each nutrient treatment was used because the experiment was intended primarily to study differences between tubers on the same plant, and more replicates would have made the amount of work at each harvest impossibly large. However, certain inferences about the translocation of carbohydrate and nutrients could be drawn.

TABLE 7/2

Examples of gradients of activity and water-soluble nutrient concentrations in tubers

			Segment number*			
			1	2	3	4
Largest on control. Harvest 1	cpm/g x 10^{-5}		0	0	0	-
	µ-equiv/g	K	40	50	80	-
		Mg	3.8	4.2	6.1	-
		P	6.3	5.6	6.7	-
Largest on Mg-treated plant. Harvest 1	cpm/g x 10^{-5}		0.58	2.03	3.70	-
	µ-equiv/g	K	45	56	74	-
		Mg	6.2	5.5	6.0	-
		P	9.4	9.3	10.7	-
Largest on K-treated plant. Harvest 2	cpm/g x 10^{-5}		0.07	0.41	1.14	2.42
	µ-equiv/g	K	42	48	57	79
		Mg	6.4	5.6	6.2	7.2
		P	7.1	6.7	7.5	10.6
Largest on K+Mg-treated plant. Harvest 2	cpm/g x 10^{-5}		0.03	0.30	1.19	1.08
	µ-equiv/g	K	31	42	58	76
		Mg	6.5	5.3	6.7	6.9
		P	11.5	10.2	10.3	11.6

* Segment 1 was always that nearest the plant (heel end).

Translocation effects were examined in the light of the treatments themselves and their effects on the quantities of K and Mg in the leaves and stems (Table 7/3). In the 73 day harvest when the nutrients were given in solution, giving Mg (as $MgSO_4$) seemed to increase the amount of K in the plant as much as giving K and more than giving both (though these effects have no statistical backing). The 'effect of Mg' on the amounts of K in the leaves and stems was probably due to the extra sulphate ions stimulating K uptake. No treatment much affected the quantity of Mg in the leaves or stems. In the 87 day harvest, spraying K seemed to increase its amount in the leaves, and spraying Mg its amount in both stems and leaves.

Carbohydrates. Table 7/4 shows that at the 73 day harvest the extra K, Mg or K+Mg all seemed to increase the total quantity and mean concentration of ^{14}C activity in the tubers, although the observation that giving extra $MgSO_4$ increased the amount of K in the plant but not that of Mg suggests that all the effects could have been attributable to extra K uptake. Plotting the total ^{14}C activity in the tubers against the quantities of K in the leaves or stems (Fig. 7/3a, b) showed it was not very well related to K in the leaves but closely related to K in the stems such that the relationship's intercept was almost zero, implying a constant tuber activity : stem K ratio.

In the 87 day harvest, spraying K seemed to have far more effect on the amount of ^{14}C activity in the tubers than spraying Mg or K+Mg. The amount of activity was not well related to the amount of K in the leaves and that in the stems varied little.

Potassium. Neither extra K nor extra Mg altered the concentration of water-soluble K in the tubers (Table 7/4). i.e. It varied neither between tubers nor between plants, but only within individual tubers in this experiment.

TABLE 7/3

Quantites of K and Mg in the leaves, stems and roots

		Plants given			
		0	K	Mg	K+Mg
Harvest 1 (73 days)					
m-equiv. K	(Leaves	1.75	2.26	2.72	2.43
	(Stems	0.751	1.46	1.56	1.19
	(Roots	0.230	0.470	0.287	0.333
m-equiv. Mg	(Leaves	6.30	5.04	5.44	5.22
	(Stems	1.85	1.96	1.41	1.49
	(Roots	0.250	0.296	0.255	0.202
Harvest 2 (87 days)					
m-equiv. K	(Leaves	0.96	1.99	1.21	2.27
	(Stems	0.412	0.371	0.339	0.475
	(Roots	0.133	0.115	0.180	0.174
m-equiv. Mg	(Leaves	5.33	6.33	7.43	9.22
	(Stems	1.44	1.35	1.74	1.91
	(Roots	0.159	0.171	0.197	0.253

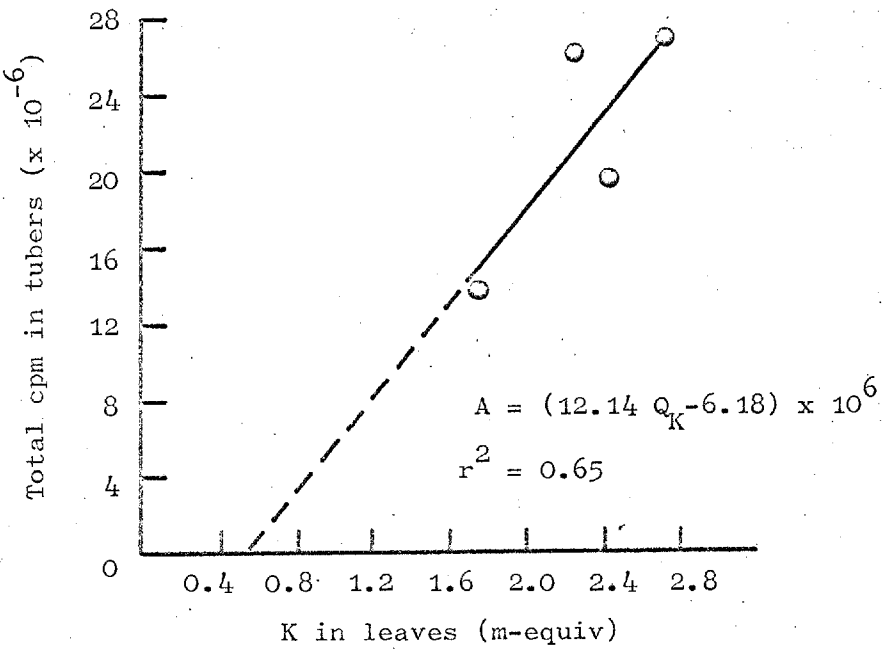
TABLE 7/4

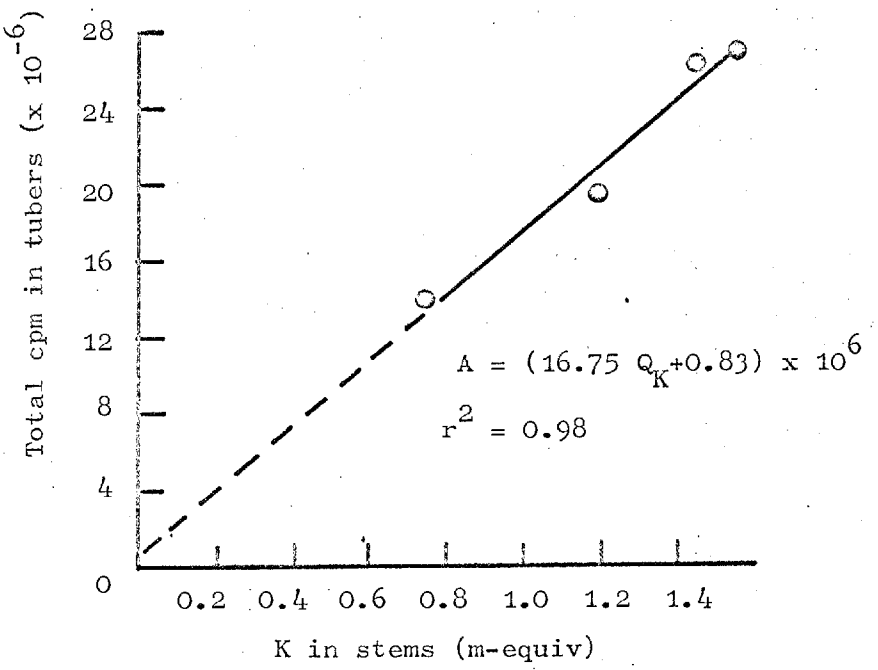
Total quantities and mean concentrations of ^{14}C activity and water-soluble K, Mg and P; (concentrations on fresh weight basis)

	Plants given			
	0	K	Mg	K+Mg
Harvest 1 (73 days)				
Fresh wt. of tubers (g)	291	257	191	213
Total activity (cpm x 10^{-6})	13.88	26.15	26.93	19.52
Conc. of activity (cpm/g x 10^{-5})	0.476	1.016	1.414	0.918
Total K (m-equiv)	16.34	14.44	10.90	11.61
K conc. (μ-equiv/g)	56.1	56.1	57.2	54.6
Total Mg (m-equiv)	1.283	1.451	1.161	1.429
Mg con. (μ-equiv/g)	4.40	5.64	6.09	6.72
Total P (m-equiv)	2.225	2.291	2.054	2.501
P conc. (μ-equiv/g)	7.64	8.90	10.78	11.76
Harvest 2 (87 days)				
Fresh wt. of tubers (g)	290	294	284	283
Total activity (cpm x 10^{-6})	15.78	33.77	20.09	20.15
Conc. of activity (cpm/g x 10^{-5})	0.545	1.147	0.707	0.713
Total K (m-equiv)	15.56	15.58	15.71	15.52
K conc. (μ-equiv/g)	53.7	52.9	55.3	54.9
Total Mg (m-equiv)	1.485	1.673	2.082	1.824
Mg conc. (μ-equiv/g)	5.13	5.68	7.33	6.46
Total P (m-equiv)	2.338	2.924	3.251	3.281
P conc. (μ-equiv/g)	8.07	9.93	11.44	11.61

Fig. 7/3

The total quantity of ^{14}C in the tubers of each plant plotted against the amounts of K in (a) the leaves, (b) the stems.





Magnesium and phosphate. Giving extra K, Mg or K+Mg seemed to increase the concentrations of water-soluble Mg and P. By pooling the residual sums of squares of the concentrations in tubers after those accounted for by the regressions had been taken out, it could be shown whether it was likely that differences between the means for plants were attributable to experimental error, but this technique obviously did not eliminate the possibility of variation between plants.

The increases in the concentration of water-soluble Mg caused by giving Mg or K+Mg were significant ($p < 0.05$ or < 0.01) and that caused by extra K given in solution was almost so ($p \simeq 0.07$); all the increases in P concentration were significant ($p < 0.05$ or < 0.01). All of these observations are subject to the proviso that variation between plants could have been responsible, although the uniformity of the mean K concentration between plants and the repetition of the effects found in the first harvest at the second harvest suggest that the effects are genuine.

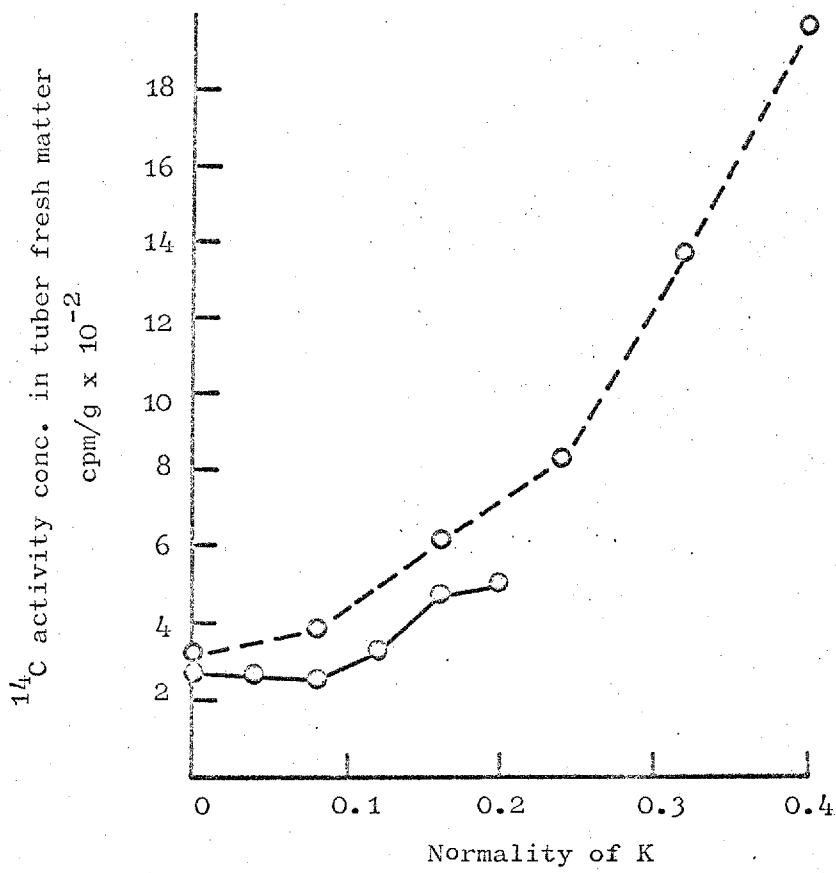
In the first harvest, differences in the concentrations of water-soluble Mg and P could be attributed to variations in the weight of tubers formed because the quantities were not very much changed (Table 7/4), but the differences appeared again in the second harvest when tuber weights were more uniform, and so are probably genuine.

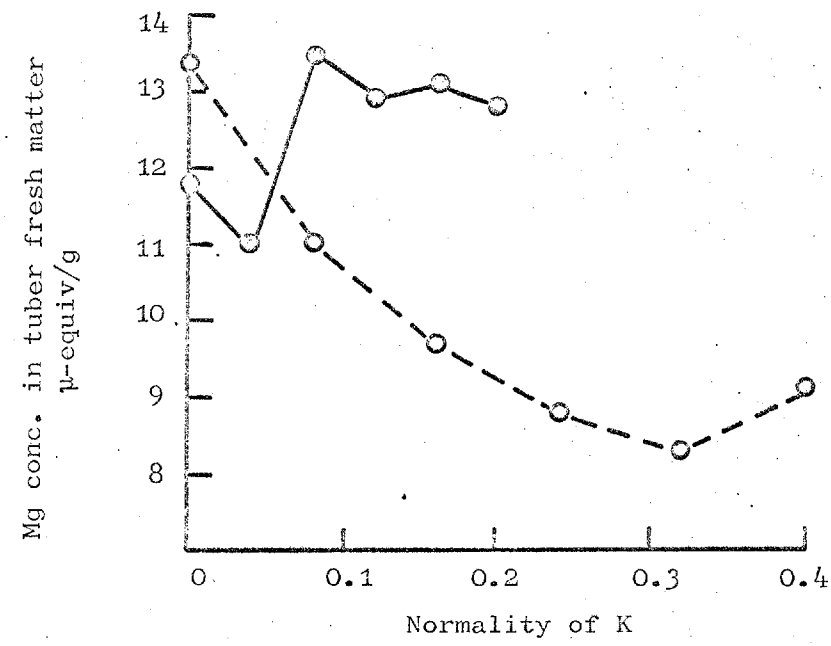
The absorption of ^{14}C-labelled sucrose and Mg by discs of tuber shaken in varying K concentrations

Fig. 7/4 (a, b) shows the results of shaking the tuber discs in solutions containing labelled sucrose, $MgSO_4$ and varying concentrations of K_2SO_4. Increasing the external K concentration seemed to increase the

Fig. 7/4

The concentrations of (a) ^{14}C activity, (b) Mg (water-sol.) in the fresh matter of the tuber discs shaken in solutions containing varying K concentrations, o——o 1 hr, o- - -o 3 hr





concentration of ^{14}C activity in the discs, especially after 3 hours shaking (Fig. 7/4a), perhaps because the K stimulated starch synthetase activity (c.f. Murata & Akazaura, 1968; Nitsos & Evans, 1969), so that more sucrose was incorporated. This showed the discs remained active, but the increased K concentration did not stimulate Mg absorption and seemed to have decreased it after 3 hours (Fig. 7/3b).

Discussion

Do the tubers 'sequestrate' Mg?

It was suggested that the increase in the Mg concentration in tubers caused by adding K could arise because giving K increased some 'sequestrating' effect of the tubers for Mg or because of the nature of the translocation process. If the 'sequestrating' effect was responsible, the effect seemed likely to be most apparent in the most vigorously-growing tubers. However, although giving K slightly increased the concentration of water-soluble Mg in the tubers in this experiment, there was no relationship between Mg concentration and growth activity, as measured by the concentration of ^{14}C activity. Furthermore, increasing the external K concentration did not stimulate the tuber discs to absorb Mg. Thus, there was no evidence for any sequestrating effect.

Phosphate behaved differently from Mg; there was a positive relationship between the water-soluble P concentration and growth activity as measured by the concentration of ^{14}C activity. Growth in potato tubers involves the synthesis of starch and other macro-molecules. Energy (from respiration) used for this purpose is probably transferred via adenosine triphosphate and other high-energy phosphate compounds and its use involves the liberation of

inorganic phosphate. It was probably this phosphate that was measured.

Effects due to the translocatory process

If, as now seems likely, the K-Mg relationship in the tuber 'sinks' did not arise from a 'sequestrating' of Mg by the tubers, the effect possibly arose from the nature of the translocation process.

According to Munch (1926) translocation is caused by a pressure . Giving K could perhaps increase photosynthesis and thereby increase the osmotic pressure of sucrose at the source. Giving K seems unlikely to increase the peristalsis postulated by Thaine (1969), except perhaps by increasing photosynthesis and so providing more respirable carbohydrate. Both these possible effects would therefore arise because giving K increased photosynthesis of carbohydrate, and translocation should depend on the total leaf area and on the K concentration of the leaves, i.e. broadly on the quantity of K in the leaves. However, the amount of ^{14}C activity in the tubers was not very well related to the quantity of leaf K at the 73 day harvest (Fig. 7/3a) or the 87 day harvest.

In general terms, the Spanner* hypothesis suggests that giving K should increase phloem translocation by increasing the K concentration in the phloem. Translocation should then be dependent on the volume of the phloem and the K concentration in its solution, i.e. on the quantity of K in the phloem. Assuming K is consistently distributed in the stems, translocation should be almost as well related to the quantity of K in the stems. At the 73 day harvest, the quantity of ^{14}C activity in the tubers was very well related to the quantity of K in the stems (Fig. 7/3b), and the ratio 'tuber ^{14}C activity : quantity of stem K' seemed almost constant.

No very conclusive evidence on the mechanism of phloem transport came from the experiment in which the nutrients were sprayed on the tops. Only

* Spanner, 1958

when K was sprayed alone was the quantity of ^{14}C activity in the tubers very much increased. Sprayed K falling on the leaves or stem epidermis would probably find its way quite rapidly into the phloem, where it would act as described.

The two chapters following present a fairly detailed non-equilibrium thermodynamic analysis of ion and solution fluxes in the phloem sieve-tubes aimed at showing how the interactions described occur and which of the theories of phloem transport they best fit.

CHAPTER 8

ANALYSIS OF TWO THEORIES OF PHLOEM TRANSPORT BY THE METHODS OF STEADY-STATE THERMODYNAMICS

Introduction

The theories of phloem transport suggesting that phloem translocation is caused by osmotic pressure differences (Munch, 1926), electro-osmosis (Spanner, 1958) or peristalsis in transcellular tubules (Thaine, 1969) were discussed in Chapter 1. In this chapter and the following one, the Munch and Spanner theories are analysed by the methods of steady-state thermodynamics to see how the effects they predict compare with those found in the preceding chapters. Thaine's theory was not amenable to this approach, although it may be noted that Aikman and Anderson (1971) showed that such a mechanism would use a feasible amount of energy.

For the present purpose, the essential difference between the Munch and Spanner theories is that in the former the flow of water drives the flow of ions, whilst in the latter the flow of K^+ ions across each sieve plate drives the flow of water. In an alternative electro-osmotic theory, that of Fensom (1957), the longitudinal flow of ions in a length of phloem drives the flow of water.

In this chapter, the consequences of the theories for K^+ movements are discussed, and in the next, those for ion interactions in the sinks and in the rest of the plant.

Conditions and assumptions for the calculations

The system discussed consists of one sieve plate and one lumen channel in series. Four working conditions are assumed.

1) The system is in a steady-state when conducting.

2) Because no-one has ever found an appreciable electrical potential difference over a length of phloem (see, for example, Tyree and Fensom, 1970), it is assumed that any potential difference across the sieve-plate is approximately balanced by one of opposite sign across the lumen. This seems justified by Bowling's (1969) measurements of potential difference in Vitis vinifera.

3) The flux of water through the sieve-pores is assumed equal to that through the lumen.

4) The sieve-pores and any fibrils they contain are assumed to be negatively charged, as are the lumen walls. If they are pH-dependent, the charges may vary with the K^+ concentration, because altering the concentration of K^+ but not those of inorganic anions may increase the pH of the sieve-tube solution.

Four simplifying approximations are also made:

1) It is assumed that because the sieve-pores are negatively charged, the concentration of anions therein is negligible compared with that of K^+ ions. (c.f. Dainty, Croghan & Fensom, 1963; Spanner, 1970).

2) K^+ ions are assumed to be the dominant carriers of current in the sieve-pores.

3) K^+ ions are assumed not to interact directly with any other ions.

4) The sieve-tube solution is taken to be dilute enough for $\frac{\text{volume}}{\text{flux}}$ of water to be considered equivalent to $\frac{\text{total volume}}{\text{flux}}$.

The velocities of K^+ ions and water in the sieve-pores

In a typical sieve-pore solution, there may be 500-1000 water molecules to each K^+ ion. In the Munch theory, the water propels the K^+ ions and with about 500 molecules to one ion, variations in the K^+ concentration should have little effect on the relative velocities of water and ions. The ratio (α) of the velocity of water (v_w) to that of K^+ ions (v_1) will be equal to or exceed unity ($\alpha = v_w/v_1$).

However Spanner's theory suggests that the K^+ ions impel the water so that α will be less than unity; furthermore, with one K^+ ion tending to propel about 500 water molecules, the more ions there are per volume of water, the more effectively they will move it. i.e. α should increase with the K^+ concentration.

The overall velocity of an ion in the phloem

The velocities of species i in the sieve-pores (length l) and the lumen (length l') are v_i and u_i. Thus its mean overall velocity is:

$$\frac{u_i v_i (l + l')}{l u_i + l' v_i}$$

However, since l' may be about 400 times l, this term is equal to u_i to such a good approximation that even if $v_i = 10u_i$ the error is only 0.25%. i.e. The overall velocity of a species can be taken as undistinguishable from its velocity in the lumen.

Glossary of symbols

v_i and u_i are the velocity of i in the sieve-pores and the lumen, f_{ij} and g_{ij} are the frictional coefficients, p_{ij} and q_{ij} the 'reduced' frictional coefficients and γ_j and γ'_j the volume fractions of j (see next section).

J_i and c_i are the flux and concentration of i in the sieve-pores (moles/unit time and moles/unit volume) (J'_i and c'_i in the lumen); z_i is its valency (if relevant).

l, A, ΔP and ΔE are respectively the length, aggregate cross-section, pressure difference and electrical potential difference of the sieve-pores (ΔP and ΔE in the direction of the length), whilst l', A', $\Delta P'$ and $\Delta E'$ are the corresponding quantities in the lumen.

$\mathcal{F}$ is the Faraday.

Subscripts. $K^+ = 1$; water = w; pore or lumen wall = m; V = volume.

Signs. Conventional. i.e. Water and current flow respectively in the direction of negative ΔP and ΔE.

Theoretical Approach

The Onsager relationships

The Onsager equations are used in the 'resistance' form, relating potential differences to fluxes. Pressure (ΔP) and electric potential (ΔE) differences are related to fluxes of volume (J_V) and current (I) as follows:

$$\Delta P = R_{PP} J_V + R_{PE} I \qquad (1)$$

$$\Delta E = R_{EP} J_V + R_{EE} I \qquad (2)$$

where R_{PP} and R_{EE} are the 'resistance coefficients' relating J_V to ΔP and I to ΔE, and R_{PE} and R_{EP} are the 'cross coefficients' allowing for the influence of I on ΔP and J_V on ΔE. Onsager's reciprocal relationship (Onsager, 1931) requires that $R_{PE} = R_{EP}$.

Spiegler's frictional model

Spiegler (1958) based his model on the law of friction stating that the frictional force on a species i gliding on a species j is proportional

to their relative velocity $(v_i - v_j)$. The force on one mole of i can be written

$$-F_i = f_{ij} (v_i - v_j) \qquad (3)$$

and that on one mole of j

$$-F_j = f_{ji} (v_j - v_i) \qquad (4)$$

where the frictional coefficients are not equal but are related by

$$c_i f_{ij} = c_j f_{ji} \qquad (5)$$

(The negative signs indicate that the forces on i and j act in the opposite directions to their velocities.)

f_{ij} relates to the frictional interaction of one mole of species i with particles of j in its vicinity. For comparing systems having different membrane densities and/or solution concentrations, Spiegler suggested the use of 'reduced' frictional coefficients obtained by dividing f_{ij} by either the molar concentration or volume fraction of j and referring to unit amounts of both kinds of particle. This is relevant for considering the effects of varying the K^+ concentration and 'reduced' coefficients, obtained by dividing f_{ij} by the volume fraction of j, such that $p_{ij} = f_{ij}/\gamma_j$, are used where appropriate.

Spiegler's model has previously been used in this context by Dainty, Croghan and Fensom (1963) and Spanner (1970).

In practice, the coefficients do not seem to be exactly constant, but they vary relatively little (Spiegler, 1958; Mackay & Meares, 1959).

Setting up the frictional equations for the sieve-pores

Consider first the water. The frictional force on one mole of water caused by K^+ ions and the pore walls,

$$-F_w = f_{w1}(v_w - v_1) + f_{wm}(v_w - v_m), \qquad (6)$$

though since the pores are static, $v_m = 0$.

In the steady-state, the frictional force is balanced by the pressure gradient in the pores;

$$\text{i.e.} \quad -F_w = (-\Delta P)/l\mathcal{C}_\omega.$$

Whence, by rearranging,

$$(-\Delta P)/l\mathcal{C}_\omega = v_w(f_{w1} + f_{wm}) - v_1 f_{w1} \qquad (7)$$

Consider next the K^+ ions. The frictional force on one mole of K^+ ions caused by the water and the pore walls,

$$-F_1 = f_{1w}(v_1 - v_w) + f_{1m}(v_1 - v_m) \qquad (8)$$

and again $v_m = 0$.

In the steady-state, this frictional force is balanced by the electrochemical potential gradient across the pores, and if the contribution of the K^+ activity gradient can be neglected, this can be equated with the electric potential gradient;

$$\text{i.e.} \quad -F_1 = z_i \mathcal{F}(-\Delta E)/l$$

and

$$-z_i \mathcal{F} \Delta E/l = v_1(f_{1w} + f_{1m}) - v_w f_{1w} \qquad (9)$$

These equations have the same form whether the translocation mechanism is that of Munch or that of Spanner, but whereas in the former case v_w exceeds or equals v_1, in the latter v_1 exceeds v_w. Moreover, since the presence of fibrillar protein in the sieve pores is an impossibility for Munch flow but almost essential for Spanner's mechanism, the coefficients f_{1m} and f_{wm} must have much the smaller values for Munch flow.

Calculating the Onsager coefficients

The fluxes, J_w and J_1, of water and K^+ ions in the pores have the values $Ac_w v_w$ and $Ac_1 v_1$; thus $v_w = J_w/Ac_w$ and $v_1 = J_1/Ac_1$. The current $I = z_1 \mathcal{F} J_1$ since K^+ ions are the predominant current carriers, so $J_1 = I/z_1\mathcal{F}$.

From equation (5), $f_{w1} = f_{1w} \cdot \frac{c_1}{c_w}$.

Making all these substitutions in equation (7), we have

$$\Delta P = J_w \left\{ \frac{-l(f_{1w}c_1 + f_{wm}c_w)}{Ac_w} \right\} + I \left\{ \frac{lf_{1w}}{Az_1\mathcal{F}} \right\} \qquad (10)$$

Making similar substitutions (except that for f_{w1}) in equation (9), we have

$$\Delta E = J_w \left\{ \frac{lf_{1w}}{Az_1\mathcal{F}c_w} \right\} + I \left\{ \frac{-l(f_{1w} + f_{1m})}{Az_1^2\mathcal{F}^2c_1} \right\} \qquad (11)$$

Comparing equations (10) and (11) with (1) and (2), we see, as $J_w \simeq J_V c_\omega$,

$$R_{PP} = \frac{-l(f_{1w}c_1 + f_{wm}c_w)}{Ac_w}; \quad R_{PE} = \frac{lf_{1w}}{Az_1\mathcal{F}};$$

$$R_{EP} = \frac{lf_{1w}}{Az_1\mathcal{F}}; \quad R_{EE} = \frac{-l(f_{1w} + f_{1m})}{Az_1^2\mathcal{F}^2c_1}$$

As required by the Onsager reciprocal relationship, $R_{PE} = R_{EP}$. Allowing for differences in formulation, these results agree with those of Spanner (1970).

The electro-osmotic efficiency

The ratio of the efficiency of an electro-osmotic mechanism to that of a pressure-flow mechanism (the electro-osmotic efficiency index) was shown by Dainty, Croghan and Fensom (1963) to be equal to $R_{PE}^2/R_{PP}.R_{EE}$ $(=\eta)$. Putting in the values found for R_{PE}, R_{PP} and R_{EE} and putting $f_{ij} = p_{ij} . \gamma_j$, we find (see also Spanner, 1970)

$$\eta = \left\{ \left(1 + \frac{p_{1m}\gamma_m}{p_{1w}\gamma_m}\right) \left(1 + \frac{p_{wm}\gamma_m}{p_{1w}\gamma_w} \cdot \frac{c_w}{c_1}\right) \right\}^{-1} \qquad (12)$$

The concentration of K^+ ions is unlikely much to exceed 0.1 M and variations in it at this level should affect γ_w and γ_m little, so that η increases with the K^+ concentration. This increase implies less wastage of free energy against friction, and since at any one rate of flow frictional effects at the pore walls are nearly constant, there must be less frictional loss of energy in the solution. In the light of the basic law of friction discussed earlier, this suggests that the difference between the velocities of K^+ ions and water must be lessened, so that the assumption made that the ratio of the velocities (α) increases with the K concentration in the electro-osmotic (Spanner) system seems to concur with the expression derived for η.

Deductions from the Theory

Theoretical effects of varying the K^+ concentration on the values of ΔP and ΔE across the sieve-plate

Using the identities $v_w = \alpha v_1$ and $f_{ij} = p_{ij} \gamma_j$ and equations (5), (7) and (9) gives

$$-\Delta P = v_1 l \left\{ p_{1w} \cdot \frac{c_1}{c_w} \cdot \gamma_w (\alpha - 1) + \alpha p_{wm} \gamma_m \right\} \quad (13)$$

$$-\Delta E = \frac{v_1 l}{z_1 \mathcal{F}} \left\{ p_{1w} \cdot \gamma_w (1 - \alpha) + p_{1m} \gamma_m \right\} \quad (14)$$

Munch theory. With the water molecules propelling the K^+ ions, α is greater than or equal to unity and probably varies little with the K^+ concentration. p_{1w}, p_{1m} and p_{wm} are approximately constant and γ_w and γ_m should be little affected by changes in the K^+ concentration. Thus from equation (13) ΔP will always be negative in the direction of flow and, unless $\alpha = 1$, will increase with c_1/c_w; i.e. the fall in pressure across the sieve-plate will tend to increase with the K^+ concentration. Equation (14) shows ΔE may be positive, zero or negative according to the values of the terms and should be little affected by the K^+ concentration.

Spanner theory. With the K^+ ions propelling the water molecules, α is expected to be less than unity and to increase with the K^+ concentration. ΔP may therefore be positive, zero or negative according to the values of the terms in equation (13). ΔE will always be negative in the direction of flow, as originally described by Spanner (1958), but should become less so as the K^+ concentration increases.

In the special, but quite feasible, case of $\Delta P = 0$, α can be evaluated from equation (13) and

$$\alpha_{\Delta P = 0} = \frac{p_{1w} \gamma_w c_1}{p_{1w} \gamma_w c_1 + p_{wm} \gamma_m c_w} \cdot \quad (15)$$

$\alpha_{\Delta P = 0}$ is less than unity and increases (non-linearly) with the K^+ concentration. This value is relevant only to Spanner's theory because ΔP cannot be zero in the Munch system.

Flow in the lumen

The sieve pores and the lumen channel are, in effect, in series. However, Kedem and Katchalsky (1963) showed that treating the resistances addititively leads to problems, so the calculations that follow are developed simply from two of the assumed working conditions, (a) that the electric potential difference across the lumen ($\Delta E'$) is opposite in sign and about equal in magnitude to that across the sieve-plate (ΔE), and (b) that the fluxes of water in the lumen and the sieve pores are the same.

Equations relating the pressure and electric potential differences ($\Delta P'$ and $\Delta E'$) across the lumen to the velocities (u_i) and frictional coefficients ($g_{ij} = q_{ij} \cdot \gamma'_j$) can be developed in the same way as for the sieve pores, giving

$$-\Delta P'/l' = u_w(g_{w1} + g_{wm}) - u_1 g_{w1} \qquad (16)$$

$$-z\mathcal{F}(\Delta E')/l' = u_1(g_{1w} + g_{1m}) - u_w g_{1w} \qquad (17)$$

The velocities of water and K^+ ions in the lumen. The fluxes of water in the sieve-pores and the lumen are assumed equal;

$$\text{i.e. } v_w c_w A = u_w c'_w A'$$

But to a close approximation $c_w = c'_w$, so

$$u_w = v_w \cdot \frac{A}{A'} = B\, v_w \quad \text{(say)} \qquad (18)$$

The velocity (u_1) of K^+ ions in the lumen is calculated from the assumption that the potential differences across the sieve-plate and lumen are opposite and about equal, i.e. $\Delta E' = -\beta \cdot \Delta E$ where $\beta \simeq 1$; by using this identity and also $u_w = Bv_w = B\alpha v_1$, and substituting in equations

(9) and (17), we have

$$u_1 = v_1 \left\{ \frac{\alpha(1'Bg_{1w} + 1\beta f_{1w}) - 1\beta(f_{1w} + f_{1m})}{1'(g_{1w} + g_{1m})} \right\}$$

or, in terms of reduced coefficients,

$$u_1 = v_1 \left\{ \frac{\alpha(1'Bq_{1w}\gamma'_w + 1\beta p_{1w}\gamma_w) - 1\beta(p_{1w}\gamma_w + p_{1m}\gamma_m)}{1'(q_{1w}\gamma'_w + q_{1m}\gamma'_m)} \right\}$$

However 1' is several hundred times 1 and g_{1w} is much larger than g_{1m} (Spanner, 1970) and so u_1 does not differ greatly from $B\alpha v_1$, i.e. from u_w. Thus the ostensibly reasonable assumptions abouts the fluxes and potentials in the sieve-plate and lumen lead to the equally reasonable conclusion that, regardless of the translocation mechanism, water and K^+ ions move in the lumen with rather similar velocities.

The pressure difference across the lumen. From equation (16) we see that because u_w and u_1 are fairly similar and g_{w1} is greater than g_{wm} (Spanner, 1970), $\Delta P'$ should be relatively small in magnitude.

Discussion

The movement of K^+ ions

The overall velocity of a particle in the sieve-tubes is determined to a very large extent by its velocity in the lumen, because the lumen is several hundred times longer than the sieve-pores. Thus the conclusions of the previous section suggest that the overall velocity of K^+ ions does not differ much from that of the solution as a whole.

Some support for this deduction is found by considering the movement of K^+ and carbohydrate in the phloem to a 'sink'. The uncharged and

hydrogen-bonded sucrose molecule probably moves with the same velocity as the water and therefore about the same as the K^+ ions. This implies that the ratio of K^+ to carbohydrate should be roughly the same in a 'sink' as in the phloem solution; K^+ and sucrose are usually about 0.05 M and 0.3 M in the solution, corresponding to about 2% of K in sink dry matter (assumed predominantly carbohydrate), about that usually found in potato tubers. This agreement suggests the velocities cannot differ greatly.

If the conclusion about the velocities is correct, it implies that K^+ ions remain in the tubers, which might therefore be called a 'terminal sink' for K^+ ions, as opposed to a 'sink' such as the roots from which they seem to be recirculated (Dijkshoorn, 1962).

Implications for the Munch and Spanner theories

The movement of K^+ ions in the sieve tubes implied by the foregoing discussion is essentially what might be expected from the Munch theory. It is also quite feasible in relation to Spanner's theory, but it would be necessary to postulate two components of K^+ flow, (a) a component of K^+ flow moving down the sieve tubes as described and (b) a 'propelling' component circulating as Spanner envisaged through the sieve plates and companion cells. However, an alternative approach embodying the essential features of Spanner's theory but describing a simpler type of flow involving both components is shown in Chapter 10.

Pressure and potential effects

Pressure differences in normally-functioning phloem never seem to have been measured. (It would be most difficult.) That Spanner's mechanism involves a smaller pressure fall across each sieve-tube seems to stand in its favour. Further, equation (13) suggests that in the conditions of Munch flow, increasing the K^+ concentration may increase the pressure

difference across each sieve-plate, or, if the pressure difference does not vary, decrease the rate of flow, a result at variance with Hartt's (1969) observations on sucrose movement in sugar-cane.

The two types of flow lead to different hypothetical values for the potential difference across each sieve-plate and these can be compared with the measured values of Bowling (1968, 1969) for Vitis vinifera.

Taking the overall velocity of water ($\simeq u_w$) as 50 cm/hr and A/A' as 0.5 gives v_w = 100 cm/hr. The values of f_{1w} and f_{1m} quoted by Spanner (1970) from Mackay and Meares (1959) are taken and l put at 1μ (10^{-4} cm). For Munch flow, α (v_w/v_1) exceeds unity but probably not by much (say α = 1.2), but for Spanner-type flow, α may only be about 0.5 (say). Putting these values in equation (9) gives values of -3 mV and -23 mV respectively for Munch and Spanner-type flow, of which the latter is closer to Bowling's measured value of 19 mV (direction not specified). However, much clearly depends on the reasonableness of the arbitrary values taken.

Although the above discussion favoured Spanner's theory, two problems must be noted: (a) the large ion current densities involved, of the order of 1 amp/sq cm in the sieve pores; (b) the large charge density needed in the pores, calculated by Spanner (1970) to be about 4.7 charge units per Å of fibril length. Both these problems arise basically from the large K^+ concentration in the sieve tubes.

Fensom's theory. (Fensom, 1957)

Fensom's variant of the electro-osmotic theory envisaged that flow was maintained in the sieve tubes by a flow of ions maintained over a length of phloem. This implies a substantial poential difference over the length of phloem, and Tyree and Fensom (1970) found no such potential difference and so discounted this variant of the theory.

CHAPTER 9

INTERACTIONS BETWEEN POTASSIUM AND OTHER IONS EXAMINED IN THE LIGHT OF PHLOEM TRANSPORT MECHANISMS

Introduction

A feature of the anatomy of vascular plants is the close proximity of xylem and phloem elements in the stems. For potato plants, Artschwager (1918) showed they are arranged in vascular bundles, each containing xylem elements separated by only a few cambial cells from the external phloem and a few parenchyma cells from the internal phloem. This arrangement suggests that ions and other solutes may be transferred between the xylem and the phloem in the stem, as suspected by Mason, Maskell and Phillis (1936) who worked on cotton plants.

If such transference takes place, increasing the flux of an ion moving in the phloem to a sink should increase the rate of transfer and decrease the flux of that ion in the xylem, so that less reaches the leaves. Such a mechanism could explain many of the effects found in Chapters 4 and 5, especially those on the distribution of Mg.

In this chapter, a theoretical analysis of K effects on ion movements through the sieve-tube walls is combined with one of the effects on ion velocities along the sieve-tubes using the methods of the previous chapter, to see how well the translocation mechanisms account for the effects of K nutrition on concentrations of ions in 'sink' dry matter and on their distribution in the plants.

Assumptions etc

The working conditions taken for the system and the approximations made are the same as for the previous chapter. The symbols and subscripts are the same, but with the addition that any ion other than K^+ has the subscript 2.

The assumptions concerning the fluxes and potential are again made. Where a second ion is concerned, it is assumed that there are no appreciable direct interactions with K^+, and that compared with K^+ the second ion does not carry an appreciable amount of current. (K^+ seems to be much the most concentrated ion in the phloem solution - Table 1/1.)

No allowance is made for the flux of water radially through the walls; this is probably very small throughout most of the phloem.*

Theoretical approach

Radial fluxes of ions into the sieve tubes

The possibility of ions being transferred from the xylem to the phloem suggests radial movements of ions into the sieve-tube lumens may occur, probably because of differences in chemical and electrical potential between the inside and outside. A short length (h) of lumen of internal and external radii a and b is considered. The total inward flux (ϕ) of an ion is related to the concentration (c) and electrical potential (E) gradients along the radius r (between a and b) as follows

$$D.\frac{dc}{dr} + mc.\frac{dE}{dr} = \frac{\phi}{2\pi rh} \qquad (1)$$

where D, the diffusion coefficient, and m, the mobility of the ion, are related by the Nernst-Einstein relationship $m = Dz_i\mathcal{F}/RT$ where R and T are

* otherwise translocation would not be very efficient.

the universal gas constant and the absolute temperature respectively.

If E_x is made the potential difference between the outside and inside, and k the dielectric constant of the sieve tube wall,

the electric field at r, $\frac{dE}{dr} = -\frac{kE_x}{r \ln(b/a)}$ (2)

By making substitutions and integrating, we find

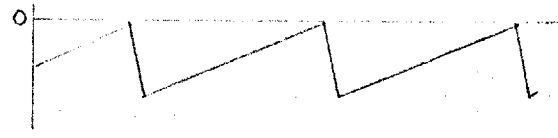
$$\phi = \frac{2\pi Dh\,(a^{\theta} c_o - b^{\theta} c_i)}{b^{\theta} - a^{\theta}} \qquad (3)$$

where $$\theta = \frac{z_i \mathfrak{F}}{RT} \cdot \frac{kE}{\ln(b/a)} \qquad (4)$$

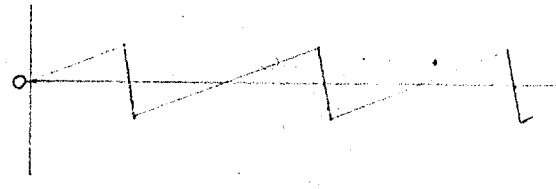
Variation of the electrical potential difference. It is assumed that $\Delta E' = -\Delta E$, i.e. there is no overall potential difference along a length of phloem. This is necessary for the following calculations.

The potential difference between the inside and outside of the lumen varies along its length and the potential difference 'profile' can be fixed only if assumptions are made. Two are considered:

(a) that the solution immediately on the 'upstream' side of each sieve-plate is at zero potential relative to the outside; because the potential falls across the sieve plate, the potential difference profile would be as follows



(b) that the potential of the solution is zero relative to the outside at the mid-point of the lumen (and of the sieve-plate).



The potential difference of the inside relative to the outside at distance x from the 'upstream' sieve-plate (E_x) is given in these cases by

$$\text{(a)}\quad E_x = \Delta E(1'-x)/1' \qquad \text{(b)}\quad E_x = \Delta E(\tfrac{1}{2}1'-x)/1' \tag{5}$$

The relationship between E_x and x is assumed linear (i.e. the gradient constant so that the ions travel at constant velocity in the lumen).

Using the equations

Ion movements can be examined in two cases:

(i) When the concentration of an ion builds up along the length of a sieve-tube, as that of K^+ might if it is 'pumped out' below each sieve-plate.

(ii) When there is no net change in an ion's concentration between one end of the lumen and the other, e.g. where an ion that is not 'pumped out' has reached flux equilibrium with the zone through which it is being transferred.

(i) Concentration builds up. We consider a short length of lumen δx at distance x from the 'upstream' sieve-plate. The ion moves longitudinally with velocity u_i. The concentration of the ion varies along the length and is c_x at x increasing to $(c_x + \delta c_x)$ at $(x + \delta x)$. The radial flux into δx is given by putting $h = \delta x$ and $c_i = c_x$ in equation (3). The radial flux causes an increment in the longitudinal flux of $Au_i \delta c_x$ (A' = cross section). In the steady state, the radial flux and the longitudinal flux increment balance each other and

$$A'u_i \delta c_x = \frac{2\pi D\,(a^\theta c_o - b^\theta c_x)\theta}{b^\theta - a^\theta} \cdot \delta x \tag{6}$$

where $\theta = \frac{z_i \mathcal{F}}{RT} \cdot \frac{kE_x}{\ln(b/a)}$ and E_x is given by 5(a) or 5(b). $A' = \pi a^2$.

c_x is not easily evaluated from these equations, but for the potential difference profile (a), E_x is always negative and so θ for a cation is negative and also quite large. This means $(b/a)^{\theta}$ can be neglected by comparison with 1, and since c_x is mostly smaller than c_o, $(b/a)^{\theta} \cdot c_x$ by comparison with c_o. Thus, by dividing the top and bottom by a^{θ} in (6) and simplifying, we have

$$\frac{dc_x}{dx} = -\frac{2D\theta}{a^2 u_i} \cdot c_o = -\frac{2D}{a^2 u_i \ln(b/a)} \cdot \frac{z_i \mathcal{F}}{RT} \cdot kc_o \frac{\Delta E(l'-x)}{l'} \qquad (7)$$

Integrating and putting $c_x = c_x^{\,o}$ at $x = 0$ gives

$$c_x = c_x^{\,o} - \frac{2 \cdot D}{a^2 u_i \ln(b/a)} \cdot \frac{z_i \mathcal{F}}{RT} \cdot c_o \Delta E \cdot \frac{2l'x-x^2}{2l'} \qquad (8)$$

For the potential difference profile (b), the relationship is not continuous. From $x = 0$ to $\frac{1}{2}l'$ the concentration is determined by an equation similar to (8) but with the final term $(l'x-x^2)/2l'$. By a similar approach it can be shown that between $x = \frac{1}{2}l'$ and $x = l'$, the concentration is governed by the equation

$$c_x = c_x^{\frac{1}{2}l'} \exp\left\{ \frac{2D}{a^2 u_i \ln(b/a)} \cdot \frac{z_i \mathcal{F}}{RT} \cdot k\Delta E \frac{(l'x-x^2)}{2l'} \right\} \qquad (9)$$

(ii) No overall change in concentration. This implies that the net radial flux of an ion into the lumen is zero. The flux $\delta\phi$ into a short length of lumen (δx) is given from equation (3) as

$$\delta\phi = \frac{2\pi D\,(a^{\theta} c_o - b^{\theta} c_m)\theta \int x}{b^{\theta} - a^{\theta}} \qquad (10)$$

where θ is as before and c_m is the mean concentration of the ion in the lumen. (c_x should not vary much from c_m if there is no overall change.)

For the potential difference profile (a), θ is always negative for a cation, so that $(b/a)^{\theta}$ can be neglected by comparison with 1, but c_m may be larger than c_o, so $(b/a)^{\theta}.\ c_m$ cannot this time be neglected by comparison with c_o. θ is given by (4) and E_x by 5(a); combining these gives a term Q such at $\theta = Q\,(l' - x)$,

where $$Q = \frac{z_i \mathcal{F}}{RT} \cdot \frac{k\Delta E}{\ln(b/a)} \cdot \frac{1}{l'} \qquad (11)$$

and the condition for no net flux is

$$-2\pi DQ \int_0^{l'} \left\{ [c_o - (b/a)^{Q(l'-x)} c_m](l'-x) \right\} dx = 0 \qquad (12)$$

which gives

$$c_m \left\{ \frac{1}{Q\ln(b/a)} - \frac{(b/a)^{Ql'}}{Q\ln(b/a)} + l'(b/a)^{Ql'} \right\} = \frac{c_o\, Q\ln(b/a).(l')^2}{2} \qquad (13)$$

For a cation, Ql' is large and negative and terms containing $(b/a)^{Ql'}$ can be neglected, giving

$$c_m = \frac{c_o}{2}[Ql'.\ln(b/a)]^2 = \frac{c_o}{2}\left[-\frac{z_i \mathcal{F}}{RT} \cdot k\Delta E\right]^2 \qquad (14)$$

The value of ΔE is given by equation (9) in the previous chapter, so that applying equation (14) to the ion subscripted 2 gives

$$c_2' = \frac{c_o}{2}\left\{\frac{z_2}{z_1} \cdot \frac{kv_1 l}{RT}\left[f_{1w}(1-\alpha) + f_{1m}\right]\right\}^2 \qquad (15)$$

For potential profile (b), the effect of the electrical potential difference in one half of the lumen is countered by an opposite effect in the other half. By integrating equations similar to (3) between 0 and $\frac{1}{2}l'$ and between $\frac{1}{2}l'$ and l', remembering that for a cation θ is negative in the first half and positive in the second, it can be shown that to a good approximation the condition for no net flux is

$$c_m = c_o$$

$$\text{i.e. } c_2' = c_o \qquad (16)$$

The value of c_o for each cation can be approximated from its concentrations in the 'stem water' measured in the first experiment (Appendix II). Comparing these with concentrations measured in phloem solutions by others (Table 1/1) suggests c_o tends to be larger than c_m for Ca^{++} and Mg^{++} and roughly the same for K^+, but none of these is a reliable guide, because K^+ may be 'pumped out' of the phloem and Ca^{++} and Mg^{++} complexed so that their movement is restricted. Equation (14), from the potential difference profile (a), suggests c_m is larger than c_o, rather than the other way round, so profile (b) may be nearer the real situation. It could be inferred from the behaviour of Ca^{++} and Mg^{++} that the potential difference between the inside and the outside is zero immediately below the sieve plate, but this seems unlikely if the ions are 'pumped' at this point (see Spanner, 1970).

The effects of varying the K^+ concentration on ion velocities in the sieve plate and the lumen

Whichever the translocation mechanism, the velocity of K^+, the dominant mobile ion in the sieve tubes, influences the electric potential differences across the sieve-pores and the lumen, which in turn affect the velocities of other ions. The velocity of the water flow in the sieve-tubes also influences the velocities of other ions both directly and through its effect on the potential differences. Since the velocities of K^+ ions and water are inter-related, the velocities of other ions can be related to either.

The velocity of the second ion (subscripted 2) is again related to the potential difference (which depends on the flux of K^+) using Spiegler's frictional formulation.

Sieve-plate. We obtain for the second ion a relationship analogous to equation (9) in the previous chapter

$$\frac{-z_2 \mathcal{F} \Delta E}{l} = v_2(f_{2w} + f_{2m}) - v_w f_{2w} \qquad (17)$$

Equating the values of ΔE from equation (12) and equation (9) in the previous chapter, and remembering that $v_w = \alpha v_1$, we get

$$v_2 = v_1 \left\{ \frac{\alpha(z_1 f_{2w} - z_2 f_{1w}) + z_2 (f_{1w} + f_{1m})}{z_1(f_{2w} + f_{2m})} \right\}$$

or $$v_2 = v_w \left\{ \frac{(z_1 f_{2w} - z_2 f_{1w}) + (1/\alpha) z_2 (f_{1w} + f_{1m})}{z_1(f_{2w} + f_{2m})} \right\} \qquad (18)$$

Lumen. For the second ion in the lumen we obtain the relationship

$$\frac{-z_2 \mathcal{F} \Delta E'}{l'} = u_2(g_{2w} + g_{2m}) - u_w g_{2w} \qquad (19)$$

Whence, remembering that $\Delta E' = -\beta \Delta E$ and $u_w = B\alpha v_1$ (see Chapter 8), we have

$$u_2 = v_1 \left\{ \frac{\alpha(Bg_{2w}l'z_1 + \beta f_{1w} l z_2) - \beta l z_2 (f_{1w} + f_{1m})}{l' z_1 (g_{2w} + g_{2m})} \right\} \qquad (20)$$

or

$$u_2 = u_w \left\{ \frac{(Bg_{2w}l'z_1 + \beta f_{1w} l z_2) - (1/\alpha) \beta l z_2 (f_{1w} + f_{1m})}{Bl' z_1 (g_{2w} + g_{2m})} \right\} \qquad (21)$$

(Note that β was in a previous section taken as unity.)

Deductions

Evaluation of the overall effects of varying the phloem K^+ concentration on ion concentrations in the sinks

We are interested ultimately in the effects on the concentrations of other ions in 'sink' dry matter. The latter is formed mainly from carbohydrate carried as uncharged sucrose molecules which undergo considerable hydrogen bonding and so probably travel at the same velocity as the water. The concentration of an ion in the 'sink' dry matter depends on the ratio of its flux in the phloem to that of carbohydrate. Assuming the concentration of the carbohydrate does not much change, the concentration of the ion in the 'sink' will be influenced by (a) its concentration in the phloem solution and (b) the ratio of its velocity to that of the solution as a whole. Since the mean velocity of a species in the phloem as a whole is very close to that in the lumen, for (b) we may use the ratio of the lumen velocities u_2/u_w.

Effects on the concentrations and relative velocities. The effect of varying the K^+ concentration can be seen by differentiating c_2', the concentration of the second ion in the lumen solution, and u_2/u_w, the ratio of the velocities, with respect to c_1, the K^+ concentration in the sieve pores; c_1, which should be closely related to the K^+ concentration in the lumen, is used because α depends on c_1, so we may use the identities

$$\frac{dc_2'}{dc_1} = \frac{dc_2'}{d\alpha} \cdot \frac{d\alpha}{dc_1} \quad \text{and} \quad \frac{d(u_2/u_w)}{dc_1} = \frac{d(u_2/u_w)}{d\alpha} \cdot \frac{d\alpha}{dc_1}$$

From equations (15) and (16) for the potential difference profiles (a) and (b) we get

$$\frac{dc_2'}{d\alpha} = -c_o \left[\frac{z_2}{z_1} \cdot \frac{kv_1 l}{RT}\right]^2 \cdot f_{1w}\left\{ f_{1w}(1-\alpha) + f_{1m}\right\} \quad \text{for (a)} \qquad (22)$$

and $$\frac{dc_2'}{d\alpha} = 0 \quad \text{for (b)} \qquad (23)$$

From equation (21) we get

$$\frac{d(u_2/u_w)}{d\alpha} = \frac{1}{\alpha^2} \cdot \frac{\beta l z_2}{Bl' z_1} \cdot \frac{(f_{1w} + f_{1m})}{(g_{2w} + g_{2m})} \qquad (24)$$

(β was earlier put at 1).

Because the K^+ concentration is hypothetically varied, f_{1w} etc should be replaced by $p_{1w}\gamma_w$ etc but the concentrations of K^+ and Mg^{++} are both small enough not to affect the γ terms appreciably, and the substitution is not necessary.

The overall effect on the concentration of the second ion in the sink dry matter, i.e. on the ratio of its flux in the phloem to that of

carbohydrate (J'_2/J'_c), is given by

$$\frac{J'_2}{J'_c} = \frac{u_2}{u_w} \cdot \frac{c'_2}{c'_c} \cdot \frac{A'}{A'} \qquad (A' \text{ cancels})$$

and $$\frac{d(J'_2/J'_c)}{dc_1} = \left\{ \frac{1}{c'_c} \cdot \frac{u_2}{u_w} \cdot \frac{dc'_2}{d\alpha} + \frac{c'_2}{c'_c} \frac{d(u_2/u_w)}{d\alpha} \right\} \frac{d\alpha}{dc_1} \qquad (25)$$

where c'_c the carbohydrate concentration in the phloem solution, is assumed constant.

Overall effects

Munch theory. Where the water impels the K^+ ions, α should vary little with the K^+ concentration; thus $d\alpha/dc_1 \simeq 0$ and the concentration of a second ion in sink dry matter should be little affected if the K^+ concentration in the sieve-tubes varies.

Spanner theory. Here, K^+ ions impel the solution, α should increase with c_1 and effects on the concentration of the second ion in the sink dry matter are to be expected. The overall effect was evaluated by taking Mg^{++} as the second ion and giving the following values:

$c_1 = 0.05$ M; $c_w = 55$ M; $c_o(Mg) = 0.01$ M; $c'_c = 0.3$ M

$v_1 = 200$ cm/hr (1/18 cm/sec)

$l = 10^{-4}$ cm; $l' = 1.4 \times 10^{-2}$ cm

$B = 0.5$; $\beta = 1$

$R = 8.31$ J deg c^{-1} mole^{-1}; $T = 293$ ^oA

$k = 10$

$f_{1w} = 4 \times 10^{8}$ J sec cm^{-2} $mole^{-1}$ (Spanner, 1970)

$f_{1m} = 2 \times 10^{8}$ " (")

$f_{wm} = 2 \times 10^{5}$ " (")

$g_{2w} = 16 \times 10^{8}$ "

$g_{2m} = 32 \times 10^{3}$ "

The values of g_{2w} and g_{2m} were taken by assuming that the frictional coefficients are proportional to the surface area of the hydrated ion, i.e. to the square of the hydrated radius. Mg^{++}, having twice the hydrated radius of K^{+}, was assumed to have frictional coefficients four times larger than those given by Spanner (1970) for K^{+}.

For α and $d\alpha/dc_1$, the values at $\Delta P = 0$ were used from equation (15) in the previous chapter. This will overestimate α if, as is probable, ΔP is positive.

Putting these values in the equation (24) for $d(J_2'/J_c')/dc_1$ gave the following values; for potential profile (a), -43; for profile (b), 0.4×10^{-2}. The discussion in a previous section suggested (b) was probably nearer the real situation.

The data in Appendix II shows that the % Mg in tuber dry matter changed by about 0.035% when the K^{+} concentration in the 'stem water' changed by about 0.09 M. If the latter is a reasonable measure of c_1, $d(J_2'/J_c')/dc_1$ should be about 5×10^{-2}. Thus the second value may be as close as could be expected in view of the many estimates involved. As required, its sign is positive implying that the flux of Mg in the sieve tubes is increased

relative to that of carbohydrate so its concentration in the sink dry matter will be larger.

The reverse effect may be expected for a bivalent anion having similar frictional characteristics.

Discussion

The behaviour of magnesium. The increase in the concentration of Mg in sinks suggested by calculations based on Spanner's theory corresponds with the observations described in Chapters 4, 5 and 6, and these effects on Mg therefore seem to constitute evidence in favour of Spanner's theory.

The extra Mg that went to the tubers when K was given seemed to be that prevented from reaching the leaves rather than remobilised from the leaves; this is what would be expected were Mg^{++} ions to move out of the xylem and through surrounding cells into the phloem as described at the beginning of this chapter.

Thus Mg behaviour seems fairly satisfactorily explicable in terms of these two concepts.

This sink effect also casts light on the behaviour of Mg^{++} ions in the sap exuded from the detopped plants discussed in Chapter 3. The roots act as a sink, especially before the tubers form. Giving K may therefore have two effects on the Mg^{++} concentration of the xylem exudate: (a) it may decrease the concentration of absorbed Mg^{++}, perhaps because of the electrical effects discussed in Chapter 3, but (b) it may increase the amount of Mg^{++} translocated to the roots in the phloem. The combination of these two effects may account for the shape of the curve obtained by plotting the Mg^{++} concentration in the sap against K added to the soil

(Fig. 3/1c). If so, Mg^{++} is evidently recirculated from the roots; however, a calculation similar to that performed for K^{+} in the last chapter suggests that Mg^{++} is not recirculated from the tubers.

The behaviour of calcium

Calcium ions did not behave like Mg^{++} ions. Giving K did not increase the % Ca in sinks and the concentration of Ca in the tubers was very small compared with that in the rest of the plant. Giving K also decreased the overall uptake of Ca but not that of Mg.

The tuber concentrations suggest differences in phloem translocation between Ca^{++} and Mg^{++}. Biddulph, Cory and Biddulph (1959) and Ringeot, Sauer and Gielink (1968) noted very little phloem movement of Ca^{++}, but attributed this to strong retention by the leaves rather than any fundamental inability to enter or move in the phloem.

The hypothetical transference of ions from the xylem to the phloem would be much affected by the reactions of the ions with such compounds as pectin, lignin, hemicellulose and organic acids which they would encounter. Pectin complexes Ca^{++} but not Mg^{++}, and lignin, hemicellulose and several organic acids complex Ca^{++} more than Mg^{++} (Molloy & Richards, 1971). Ca oxalate is considerably more insoluble than Mg oxalate, and whereas Ca oxalate crystals are common in the stems of the Solanaceae (Metcalfe & Chalk, 1950), Mg oxalate is not reported. Only unbound Ca ions can move into the phloem as described and all these factors seem likely to make the concentration of free Ca ions in the vascular bundles small so that little Ca enters the phloem.

Even were an appreciable concentration of Ca^{++} ions to enter the phloem, it would probably be precipitated by the tartrate and oxalate ions

reported by Peel and Weatherley (1959). (Mg^{++} ions would not.) Effects on the velocity of Ca^{++} may therefore be irrelevant because so little is there.

The behaviour of phosphate

At the phloem pH (about 8) phosphate should be present as $HPO_4^{=}$ and $PO_4^{\equiv}$. The previous discussion suggests that giving K should somewhat slow down these ions and decrease their concentration in sink dry matter. However the measurements of Gardner and Peel (1972) suggest that much of the P in the sieve tubes is present as adenosine tri-phosphate (ATP). This ion has four negative charges, but it is also very large and has a number of sites where hydrogen bonding could occur, so that its frictional interaction with water (g_{2w} in equation (24)) may be very large and the effects of the K^+ concentration much decreased. This could explain why giving K had little effect on P concentrations in tubers.

CHAPTER 10

AN ALTERNATIVE APPROACH TO SPANNER'S ELECTRO-OSMOTIC THEORY OF PHLOEM TRANSPORT

The essential feature of Spanner's theory is that K^+ ions propel the phloem solution through the sieve-pores as a result of the electro-osmotic drag caused by their movement. The ions move through the pores because they are 'pumped' out of the sieve-tubes on the 'downstream' side of each sieve-plate.

One problem in the theory is how the K^+ ions are recirculated after they have been pumped out. Spanner originally (1958) suggested that the ions returned via the companion cells, but later (1970) he thought it more likely that they are recirculated by means of 'weaker' sieve tubes.

The calculation made at the end of Chapter 8 suggests that a large proportion of the K^+ in the phloem moved to the tuber 'sinks' at a velocity not very different from that of the whole solution, in what is essentially bulk flow.

These considerations imply two components of K^+ flow, the recirculated 'propelling' component and the bulk-flow component. Both these components must move across the sieve-plates, giving rise to two components of the ion current therein. Spanner (1970) thought the size of the ion current from what was essentially the 'propelling' component constituted a problem in the theory, so the implied two components do so doubly.

These problems can be avoided by assuming that when K^+ ions are 'pumped out' they are not specifically recirculated but simply go into a 'pool' of K^+ in the surrounding tissues which is maintained partly from the trans-

ference from the xylem and partly by the 'pumping out'. From this pool the ions move through the sieve-tube walls back into the lumen due to electrochemical potential gradients. That an appreciable 'pool' of K exists in the stems can be seen from the quantity and concentration of water-soluble K found in the stems and petioles (Chapter 4 & Appendix II).

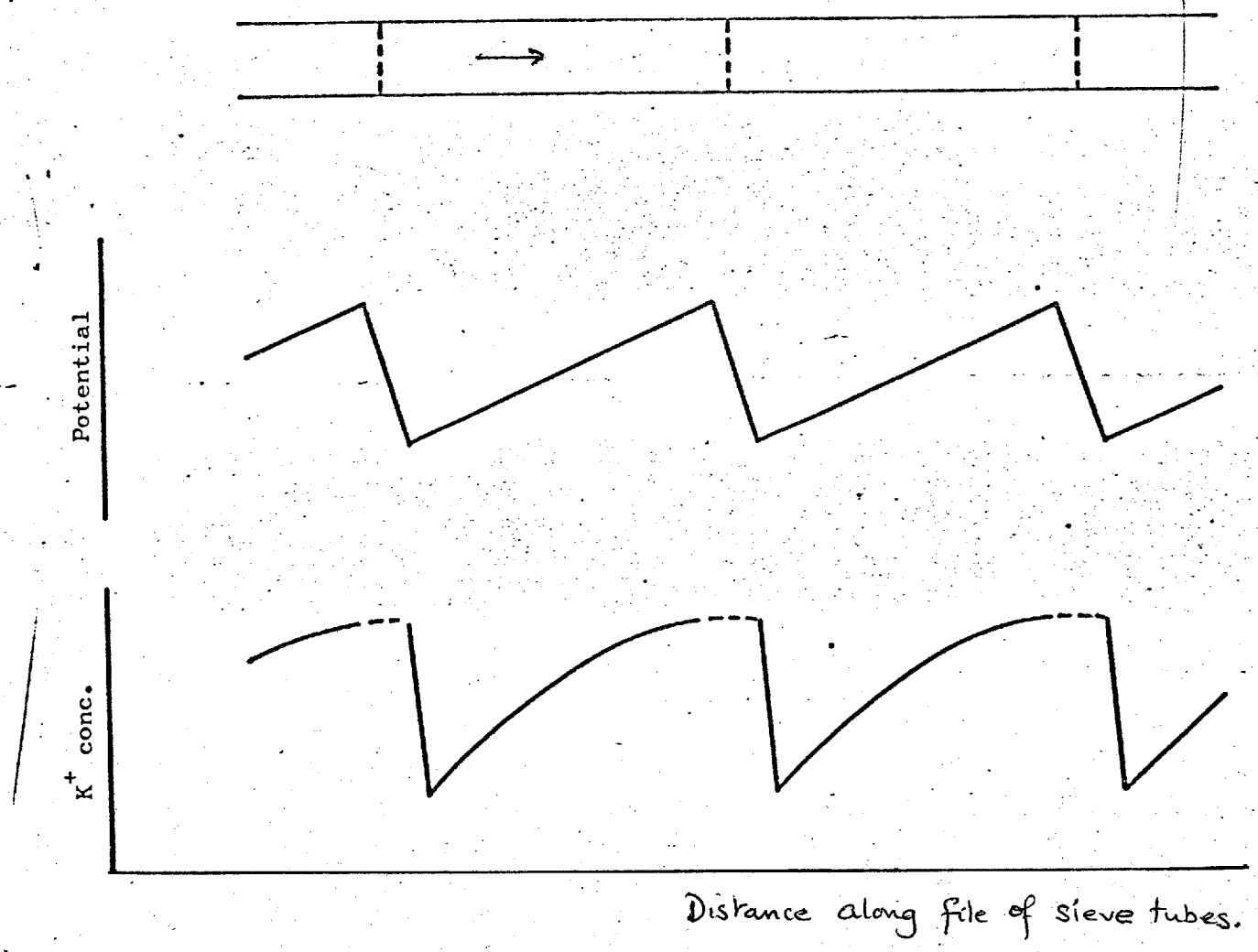
The 'pumping out' leaves the solution immediately 'downstream' of the 'pump' at a smaller K^+ concentration than the surrounding tissues. Furthermore, the solution here is likely to be at a lower electrical potential than the surrounding tissues. (If, as was assumed in Chapter 9, the solution is at zero potential relative to the surroundings on the 'upstream' side of the sieve plate or at the mid-point of the lumen, it must be at a negative potential on the 'downstream side'.) Thus K^+ ions should move back into the sieve tube initially under the influence of both chemical and electrical potential gradients, and their concentration should build-up along each lumen in a way described by the equations derived in Chapter 9. Fig. 10/1 shows hypothetical profiles of electrical potential and K^+ concentration.

Such a system could exist in a steady-state when conducting. It would give rise to an overall flux of K^+ ions corresponding to the largest K^+ concentration in the sieve-tubes, but although there would be a constant flux of K^+ ions along the phloem, no one K^+ ion would probably be moving all the time. Other ions, except probably phosphate, and uncharged molecules should move in simple fashion straight along a series of sieve-tubes.

The mechanism involves only one component of K^+ flow at the sieve-plates, so that the resulting K^+ ion current should not be seriously greater than that for Munch-type flow, the difference being mainly that due to the differing relative velocities of K^+ ions and water in the two systems.

Fig. 10/1

Hypothetical profiles of potential and K^+ concentration



Two experimental observations can be satisfactorily accounted for by this mechanism:

(a) That when various parts of the plants gave up K during tuber formation, the stem and in particular its soluble fraction gave up clearly the most K (Chapter 4).

(b) That when the roots of plants grown in solution were exposed to an increased K^+ concentration for a short period (23 hours), the concentrations of ^{14}C, Mg and phosphate seemed somewhat enhanced, but that of K did not (Chapter 7). The extra K in the sieve tubes should increase α and thence the velocity of the whole solution (see Chapter 9 for details), but it would itself be delayed from reaching the tubers by being frequently 'pumped out' into the pool.

The 'K pumps'

Recent work on the absorption of ions by roots (e.g. Shone, 1968, 1969; Dunlop & Bowling, 1971 a,b,c) has mostly suggested that K^+ ions can be absorbed by roots against an electrochemical potential gradient. If so, it seems equally likely that K^+ ions can be pumped out of sieve-tubes against such a gradient. The results of Fisher, Hansen and Hodges (1971) for Rb uptake by roots suggest the 'K-pumps' in the sieve-tubes may well be associated with K-stimulated ATP-ase systems, especially in the light of the appreciable ATP concentrations reported in willow phloem by Gardner and Peel (1972).

CHAPTER 11

FINAL DISCUSSION - THE ORGANISATION OF ION MOVEMENTS IN PLANTS

The previous chapters showed evidence that many of the potassium effects described can be explained by reference to the anatomy of the vascular bundles and the nature of phloem transport. There remains the problem of how different parts of the plant come to be 'sinks' - that is, how phloem transport comes to be directed towards them - and why some cease to be 'sinks', in short, how the plant is organised. The results in Chapter 6 suggested fairly definitely that ion movements are controlled by some kind of 'development programme' rather than by competitive effects, but they did not show how the 'programme' is put into action.

One consequence of the suggested transference of ions from the xylem to the phloem (Chapter 9) is that increasing the flux of Mg in the phloem by giving K must decrease the flux of Mg in the xylem. Seen in this light the K-Mg interactions in leaves can be explained in terms of their anatomy and function. Esau (1945) showed that in vegetative shoots of Helianthus and Sambucus the first phloem elements matured before the first xylem elements, as might be expected because such a shoot must import photosynthate. If this is true of the potato plants used in these experiments, young shoots would initially be supplied with nutrient ions through the phloem so that giving K would increase their Mg concentration, as reported in Chapter 6. When the xylem started to function, the shoots might initially be supplied with ions by both the xylem and phloem. A particular leaf gradually produces an increasing proportion of the photosynthate it

needs and eventually becomes a 'nett exporter' producing more than it uses. This implies reversal of flow in the phloem, so that the leaf is then supplied with nutrient ions only through the xylem, so that giving K decreases its Mg concentration, as is usually found in mature leaves. Since little further growth occurs in such a leaf, Ca and Mg brought in by the xylem stream accumulate in an approximately constant weight of leaf tissue so that their concentrations increase with time.

The leaflets sampled right at the tops of the shoots must all have been in the young vegetative state until shoot growth recessed when the tubers formed. Consequently the effect of K on their Mg concentrations changed when the tubers formed (Chapter 6).

A leaf changing from a 'nett importer' to a 'nett exporter' may be associated with a build-up of sugar within the leaf such that the osmotic pressure causes a reversal of flow in the phloem. However, although such effects may account for the direction of phloem transport in leaves and petioles, they do not explain the organisation of phloem transport in the whole plant.

Biddulph and Cory (1965) showed in bean plants that all mature leaves exported to some extent to the shoot meristem, but whilst those near it exported almost exclusively to it, those near the roots exported mostly to the roots; intermediate leaves exported according to their position. Biddulph and Cory investigated the output of the first trifoliate leaf and found it flowed down to the primary leaf node. At this point, where anastomosis occurs, part of the flow continued downwards and part was transferred into cauline bundles in which it ascended. Metabolite from younger leaves just beginning to export left the leaf traces at the node of insertion and ascended in the cauline bundles.

The way in which exported photosynthate moves seems to accord with the concept that shoot and root 'sinks' exert some kind of 'pull' which becomes less effective with distance. In potato plants, the dominant 'pull' exerted by the tubers also accords with this concept. However little is known of the mechanism of the 'pull'. It is almost certainly mediated in some way by the hormones such as indolyl-3-acetic acid, cytokinins and gibberellic acids discussed in Chapter 1, and these have been shown to cause such a 'pull' (Seth & Wareing, 1967). Indeed, as Heslop-Harrison (1969) commented, 'It cannot be fortuitous that compounds having the capacity to provoke cell proliferation in undifferentiated tissues and to induce growth in dormant buds - and also known to be concerned in the growth of seeds and fruits and other storage organs - should also have specific effects on translocation'. No suggestions seem to have been made as how the hormones cause the 'pull'. Any postulated mechanism must be capable of acting on the phloem transport system, so the mode of action of the latter needs to be known for certain before any definite suggestions can be made.

The Munch pressure-flow system depends on osmotic pressure gradients. Cell differentiation promoted by hormones would lower the osmotic pressure in the region of a 'sink' thereby directing flow in its direction, but it is doubtful whether such a mechanism can explain the subtleties of flow described by Biddulph and Cory (1965) or the effects of directly applied hormones showed by Seth and Wareing (1967). Furthermore, Chapter 6 showed that removing the tubers caused the plants to have thickened starchy stem bases, suggesting that phloem translocation was directed downwards in spite of the 'sinks' being removed.

It is also questionable how hormones could direct peristaltic flow in the transcellular tubules suggested by Thaine (1969). Peristalsis would reinforce flow once it was initiated but it is hard to see how a hormone could start flow in a particular direction.

In Spanner's electro-osmotic theory flow is driven ultimately by the 'pumping' of K^+ ions. Movements of K^+ ions can be influenced by hormones; for example, Ilan, Gilad and Reinhold (1971) showed that kinetin could enhance the absorption of K^+ by sunflower cotyledons. Cytokinins have been found in potato tubers (Tizio, 1966) and so may be present in the basal regions and stolons too. By enhancing either the 'pumping' of K or its return to the sieve-tube a cytokinin might locally accelerate or initiate the movement of the solution and thereby 'unbalance' a file of sieve tubes causing flow in its direction especially if the system has the inertial characteristics postulated by Spanner (1958).

Exactly how cytokinins may influence K^+ movements is a matter of hypothesis. However, in the last chapter it was suggested that the K^+ 'pumps' may be associated with K^+-stimulated ATP-ase systems and cytokinins influence enzymes in a variety of ways (Letham, 1967), suggesting that any effect is most likely to be associated with the 'pumps'.

There remains the question of how the cytokinins and other hormones originate, but little seems known and it is beyond the scope of this discussion to review this subject, except to note that these compounds seem to be associated with the nucleic acid metabolism of the plant.

SUMMARY

The work described shows how potassium accumulated and moved in developing potato plants and how its behaviour influenced the absorption and distribution of other nutrients.

The absorption of nutrients was studied by comparing their concentrations in the sap exuded from the xylems of detopped plants with their concentrations in the soil solution. Adding K to the soil increased the concentrations of all the cations in the soil solution, but still decreased the concentration of Ca^{++} in the sap and, over a limited range, that of Mg^{++} too; i.e. effects in the roots over-rode effects in the soil solution. Phosphate absorption seemed slightly enhanced by adding K and nitrate absorption unaffected. The ratios of the concentrations in the sap to those in the soil solution did not change greatly as the plants developed.

Metabolic sinks, such as tubers, are known to influence the distribution of mobile nutrients in the plant. Thus the effects of adding K on the concentrations and quantities of other nutrients in the tubers were measured, and changes in the rest of the plant interpreted in their light. Giving K increased the % Mg in tuber dry matter so that the % Mg was linearly related to the % K. The % Ca in the tubers was very small compared with that in the rest of the plant and was little affected by adding K. The % P was little affected (but tended to be decreased) and the % N seemed to be partly diluted by extra growth. Because giving K also increased the weight of tuber dry matter formed, it increased the quantity of all nutrients, especially Mg. The increase in the quantity of Mg was at the expense of the supply to the rest of the plant; the proportion of the Mg taken up

after tubers formed that went to the leaves and stems was decreased by adding K, and the larger K additions caused the stems to lose Mg. Much of the extra P in the tubers was supplied by increased uptake, but all other parts lost some P when the tubers formed.

Ca continued to accumulate in the leaves while the tubers formed and did not seem to be re-mobilised. Giving K decreased the quantity and concentration of Ca in the leaves, apparently by lessening its concentration in the xylem. Although giving K seemed to lessen the amount of Mg reaching the leaves, once there Mg seemed immobile.

In a young plant the apical meristems of the shoot are an important sink, but as the tubers develop shoot growth recesses. This is attributable either to competition between shoots and tubers with the latter gaining the ascendancy, or to an 'innate development programme'. In the former case, removing the tubers as they form should largely prevent such competition and therefore much reduce the nutrient movements previously described; in the latter (programme) case, removing the tubers should not prevent the nutrient movements, although it may delay them because removing reproductive organs delays senescence.

An experiment was made in which half the plants had their tubers removed and in which the effects of added K and Mg were tested. Young leaves sampled close to the apical meristems showed that giving K initially increased the % Mg in their dry matter; this was the same interaction as in the tubers, suggesting it was a sink characteristic. As the tubers formed, the interaction in the youngest leaves was reversed, added K decreasing their % Mg - the interaction usually found in leaves. This pattern of behaviour was found whether or not the tubers were removed.

Furthermore, movements of P and K from the shoot, as shown by the leaves, were not much affected by removing the tubers. All these effects suggest that the growth of the plant and the nutrient movements were regulated by some kind of 'innate development programme' rather than simply by competition.

The sum of the cation concentrations in the youngest leaves increased sharply when the tubers started to form, mainly because that of Ca increased, but removing the tubers nearly prevented this increase and giving K delayed it. The increase in the cation concentration sum has been associated with senescence by other workers, and this accords with the observation that removing the tubers prolonged the life of the plants by 50 days and giving them K by 27 days.

Removing the tubers also lessened the water used by the plants, by ten times more than the amount that would have been contained in the tubers.

Plants that had their tubers removed developed abnormal growths from their axillary buds.

A final experiment attempted to explain the effect of adding K on the % Mg in sinks. Two kinds of effect were considered, (a) 'sequestrating of Mg' by the sinks that was stimulated by added K, (b) a translocatory effect, arising from the effect of adding K on the system that transports carbohydrate and nutrients to the tubers.

The tubers on a potato plant seem to grow at different rates or to 'take it in turns' to grow; this is shown by the way the amount and concentration of ^{14}C activity vary between the tubers of a plant exposed to $^{14}CO_2$. The 'sequestration' hypothesis implies that the most actively-growing tubers would be stimulated by added K to acquire most Mg.

This was tested by growing plants in uniform solutions until they formed tubers. The plants were given extra K and/or extra Mg for 23 hours, in solution or sprayed on the tops, while for the first 5 hours of this period the tops were exposed to $^{14}CO_2$. Individual tubers were counted for ^{14}C activity and analysed for water-soluble (hoped to be freshly-acquired) K, Mg, and P.

The concentration of water-soluble Mg was slightly increased by giving K or Mg, and varied slightly between tubers on the same plant, but was not related to growth activity as measured by the concentration of ^{14}C activity. Thus it lent no weight to the 'sequestration' hypothesis, and a subsidiary experiment, which showed that increasing the K^+ concentration of a bathing solution did not stimulate discs of potato tuber to absorb Mg, also gave no support to the concept.

The concentration of water-soluble P in the tubers was also increased by giving K or Mg and was in several plants related to the concentration of ^{14}C activity, probably because the most actively-growing tubers had the largest turnover of the energy-storing phosphate compounds involved in starch synthesis. That of water-soluble K did not vary either between tubers on the same plant or between plants given the different treatments.

All the treatments increased the quantity of ^{14}C-activity in the tubers, some substantially, but the treatment effects could not be assessed statistically, although when the extra nutrients were given in solution, the quantity of ^{14}C in the tubers was very well related to the quantity of K in the stems ($r^2 = 0.98$).

It was concluded that the effect of adding K on the % Mg in the dry matter of sinks probably arose from its effect on phloem transport.

The xylem and phloem elements in the stems of potato plants are arranged in vascular bundles, with xylem and phloem often separated by only a few cells. This suggests that ions and other solutes may be transferred from one to the other, implying that where, for example, K increased the flux of an ion in the phloem it might decrease its flux in the xylem. Such transference could explain the way in which giving K caused the tubers to gain Mg and P at the expense of supply to other parts.

To see what effects giving K should have on ion fluxes in the phloem, the phloem transport theories of Munch and Spanner were analysed theoretically by the methods of steady-state thermodynamics, using Spiegler's frictional formulation. The effects of varying the phloem K concentration on the potential differences across the sieve-plate and lumen and thence on the concentrations and velocities of other ions in the sieve-tubes were calculated.

The behaviour of Mg in the plant seemed explicable by reference to the effects predicted from Spanner's theory. That of P could likewise be explained if it was assumed that P moves in the phloem mainly as adenosine tri-phosphate. Ca did not behave like Mg probably because it underwent more complexing by organic constituents of the stem cells.

A slightly revised approach to Spanner's theory was presented; this seemed to account satisfactorily for the behaviour of K itself.

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APPENDIX I

Ion concentrations in the soil extract and the exuded sap

(See Chapter 3)

K added mg/pot	Concentrations (mM) of K^+	Ca^{++}	Mg^{++}	Na^+	PO_4^{---}	NO_3^-
Harvest 1 (28 days)						
(a) In the soil extract						
0	0.023	3.32	0.141	0.222	n.d.	4.87
20	0.022	3.58	0.119	0.142	n.d.	3.42
80	0.135	4.86	0.206	0.227	n.d.	4.71
160	0.352	6.42	0.262	0.260	n.d.	4.38
300	0.948	7.56	0.311	0.293	n.d.	2.70
500	1.874	7.64	0.285	0.233	n.d.	2.24
(b) In the exuded sap						
0	1.85	6.41	1.10	0.409	1.51	16.1
20	1.63	4.92	0.89	0.284	1.17	12.2
80	2.67	4.43	0.76	0.121	1.40	11.8
160	3.82	4.75	0.92	0.374	1.75	14.1
300	5.55	3.74	0.94	0.156	1.85	11.8
500	6.28	2.81	0.93	0.317	2.02	9.9
Harvest 2 (44 days)						
(a) In the soil extract						
0	0.0085	1.34	0.046	0.091	0.027	0.00
20	0.014	2.42	0.080	0.124	0.025	1.35
80	0.017	2.67	0.084	0.089	0.019	0.27
160	0.039	4.34	0.136	0.124	0.017	0.33
300	0.606	7.61	0.228	0.199	0.016	0.32
500	1.613	10.08	0.284	0.245	0.015	0.23
(b) In the exuded sap						
0	1.49	3.71	1.55	0.231	1.18	3.7
20	2.19	6.84	1.58	0.175	1.69	15.8
80	1.50	2.85	0.97	0.374	1.14	2.9
160	1.86	2.31	0.79	0.430	0.89	4.1
300	6.47	2.80	1.27	0.619	1.27	7.0
500	5.45	2.29	1.22	0.521	1.26	3.3

APPENDIX I CONTINUED

K added mg/pot	Concentrations (mM) of K^+	Ca^{++}	Mg^{++}	Na^+	PO_4^{---}	NO_3^-
Harvest 3 (63 days)						
(a) In the soil extract						
0	0.016	6.6	0.178	0.223	0.011	10.1
20	0.0055	3.4	0.074	0.091	0.012	3.9
80	0.013	6.7	0.144	0.188	0.010	7.8
160	0.035	7.1	0.160	0.188	0.008	4.1
300	0.202	11.0	0.233	0.252	0.008	6.0
500	0.656	12.8	0.246	0.293	0.006	5.6
(b) In the exuded sap						
0	1.74	7.90	2.25	0.20	1.63	20.6
20	0.41	9.83	1.40	0.49	0.62	21.7
80	0.72	6.27	1.00	0.53	0.95	8.9
160	2.27	7.11	1.32	0.34	0.82	16.5
300	5.57	6.20	1.22	0.90	1.23	13.3
500	4.17	5.14	1.08	0.64	0.73	12.3
Harvest 4 (80 days)						
(a) In the soil extract						
0	0.0043	1.4	0.029	0.143	0.008	3.4
20	0.0047	4.3	0.032	0.125	0.007	2.4
80	0.0056	3.4	0.034	0.119	0.006	1.7
160	0.014	4.8	0.054	0.126	0.005	1.6
300	0.060	4.9	0.046	0.280	0.005	2.6
500	0.244	5.9	0.102	0.279	0.003	1.3
(b) In the exuded sap						
0	0.16	3.51	0.83	0.55	0.72	6.1
20	0.28	4.17	0.84	0.40	0.45	6.2
80	0.58	3.56	0.75	0.41	0.44	6.4
160	0.66	5.58	1.27	1.25	0.65	8.5
300	0.58	3.96	0.78	0.99	0.90	1.8
500	0.84	3.12	0.83	0.75	0.97	2.4

Note Each figure is the mean of two replicates.
Correlations and regressions shown in the text were calculated using the replicates individually.

APPENDIX II

Quantities and concentrations of nutrients in plant parts, and quantity of dry matter

(See Chapter 4)

K added mg/pot		Harvest			
		28 days	44 days	63 days	80 days
Quantities in m-equiv/pot					
	(a) Leaves				
0	K	0.36	0.46	0.38	0.19
20	K	0.51	0.54	0.36	0.24
80	K	0.66	0.89	0.69	0.43
160	K	0.89	1.18	1.29	0.62
300	K	1.18	1.54	1.77	1.38
500	K	1.40	1.54	2.11	1.73
0	Ca	1.38	2.23	3.40	4.20
20	Ca	1.32	1.73	3.75	4.19
80	Ca	1.07	2.07	2.93	4.41
160	Ca	0.91	1.67	2.83	2.96
300	Ca	1.15	1.23	2.54	2.86
500	Ca	0.98	1.00	1.39	1.81
0	Mg	0.24	0.59	0.60	0.69
20	Mg	0.28	0.37	0.68	0.61
80	Mg	0.20	0.51	0.68	0.59
160	Mg	0.20	0.42	0.54	0.42
300	Mg	0.24	0.34	0.39	0.29
500	Mg	0.23	0.30	0.42	0.31
0	P	0.13	0.15	0.16	0.11
20	P	0.15	0.15	0.11	0.11
80	P	0.14	0.18	0.16	0.11
160	P	0.15	0.17	0.22	0.10
300	P	0.17	0.19	0.20	0.11
500	P	0.16	0.19	0.20	0.12
0	N	2.19	2.82	3.34	2.60
20	N	2.58	2.63	3.36	2.87
80	N	1.61	3.33	3.57	2.73
160	N	2.58	3.44	4.56	2.55
300	N	3.08	3.26	3.87	3.30
500	N	2.98	3.21	4.08	3.47

APPENDIX II CONTINUED

K added mg/pot		Harvest			
		28 days	44 days	63 days	80 days
Quantities in m-equiv/pot					
	(a) Leaves continued				
0	D.M. (g)	0.59	1.3	1.3	1.3
20		0.71	1.0	1.5	1.5
80		0.60	1.5	1.7	1.6
160		0.67	1.5	2.2	1.6
300		0.82	1.8	2.1	1.9
500		0.82	1.6	2.2	1.8
	(b) Stem (soluble fraction)				
0	K	0.34	0.48	0.29	0.07
20		0.48	0.54	0.25	0.10
80		0.51	1.15	0.73	0.12
160		0.73	1.56	1.74	0.34
300		0.91	2.10	1.79	0.93
500		0.99	2.07	2.36	1.67
0	Ca	0.23	0.39	0.42	0.37
20		0.26	0.32	0.44	0.46
80		0.10	0.27	0.38	0.51
160		0.08	0.12	0.28	0.71
300		0.05	0.09	0.18	0.58
500		0.03	0.07	0.10	0.13
0	Mg	0.08	0.28	0.30	0.27
20		0.10	0.22	0.29	0.37
80		0.05	0.22	0.22	0.35
160		0.05	0.15	0.22	0.23
300		0.06	0.18	0.16	0.17
500		0.04	0.17	0.13	0.06
0	P	0.031	0.088	0.054	0.031
20		0.039	0.086	0.038	0.036
80		0.033	0.137	0.071	0.028
160		0.038	0.138	0.153	0.034
300		0.048	0.191	0.093	0.036
500		0.042	0.184	0.119	0.036

APPENDIX II CONTINUED

K added mg/pot		Harvest			
		28 days	44 days	63 days	80 days
Quantities in m-equiv/pot					
	(c) Stem (insoluble fraction)				
0	K	0.024	0.041	0.034	0.011
20	K	0.047	0.063	0.045	0.064
80	K	0.049	0.172	0.094	0.014
160	K	0.094	0.340	0.363	0.150
300	K	0.121	0.381	0.293	0.103
500	K	0.116	0.426	0.743	0.211
0	Ca	0.44	1.09	1.02	0.93
20	Ca	0.63	0.86	1.38	1.29
80	Ca	0.46	1.31	1.54	1.27
160	Ca	0.52	1.22	1.48	1.71
300	Ca	0.50	1.04	1.33	1.55
500	Ca	0.47	1.00	1.37	1.36
0	Mg	0.020	0.106	0.113	0.099
20	Mg	0.034	0.089	0.145	0.139
80	Mg	0.023	0.132	0.139	0.137
160	Mg	0.032	0.143	0.152	0.120
300	Mg	0.042	0.132	0.127	0.078
500	Mg	0.038	0.151	0.141	0.077
0	P	0.017	0.041	0.034	0.019
20	P	0.021	0.041	0.041	0.025
80	P	0.014	0.066	0.053	0.021
160	P	0.020	0.067	0.087	0.032
300	P	0.019	0.065	0.032	0.028
500	P	0.015	0.072	0.076	0.022
0	D.M. (g)	0.25	1.2	1.0	0.8
20	D.M. (g)	0.41	1.0	1.4	1.2
80	D.M. (g)	0.27	1.8	1.9	1.1
160	D.M. (g)	0.33	1.9	2.6	1.5
300	D.M. (g)	0.36	1.9	1.8	1.5
500	D.M. (g)	0.32	2.0	2.8	1.8

APPENDIX II CONTINUED

K added mg/pot		Harvest				
		28 days	44 days	63 days	80 days	Final
Quantities in m-equiv/pot						
	(d) Roots					
0	K	0.16	0.30	0.23	0.11	0.02
20		0.22	0.28	0.17	0.16	0.01
80		0.21	0.47	0.20	0.12	0.02
160		0.26	0.42	0.44	0.18	0.01
300		0.24	0.40	0.60	0.14	0.04
500		0.34	0.61	0.39	0.46	0.03
0	Ca	0.60	0.96	1.44	1.57	0.24
20		0.63	0.72	1.25	1.38	0.37
80		0.52	1.33	1.15	1.47	0.46
160		0.42	1.04	1.24	1.30	0.51
300		0.39	0.70	1.46	0.91	0.43
500		0.52	0.80	1.17	1.64	0.27
0	Mg	0.08	0.19	0.18	0.14	0.02
20		0.13	0.18	0.18	0.17	0.02
80		0.10	0.29	0.19	0.17	0.02
160		0.08	0.22	0.30	0.17	0.03
300		0.09	0.21	0.26	0.18	0.01
500		0.11	0.25	0.21	0.26	0.02
0	P	0.031	0.091	0.079	0.050	0.015
20		0.055	0.083	0.055	0.047	0.010
80		0.042	0.087	0.066	0.033	0.012
160		0.027	0.060	0.064	0.041	0.014
300		0.034	0.049	0.079	0.022	0.011
500		0.041	0.101	0.087	0.079	0.008
0	D.M. (g)	0.41	1.07	1.04	1.00	0.19
20		0.60	0.69	1.01	1.17	0.23
80		0.80	1.13	0.93	1.01	0.31
160		0.83	0.92	1.22	0.95	0.29
300		0.51	0.63	1.26	0.95	0.33
500		0.88	0.85	0.77	1.11	0.19

APPENDIX II CONTINUED

K added mg/pot		Harvest			Final harvest
		63 days	80 days	Final	
Quantities in m-equiv/pot					
	(e) Tubers				(f) Dead Tops
0	K	0.63	1.31	1.38	0.09
20	K	1.26	1.51	2.02	0.14
80	K	1.36	1.98	2.36	0.18
160	K	0.55	3.50	4.06	0.59
300	K	1.46	4.62	5.34	1.22
500	K	2.19	5.34	6.01	2.24
0	Ca	0.22	0.33	0.24	5.63
20	Ca	0.39	0.28	0.51	6.14
80	Ca	0.31	0.34	0.37	7.58
160	Ca	0.13	0.35	0.48	5.79
300	Ca	0.23	0.34	0.61	5.51
500	Ca	0.23	0.35	0.41	3.96
0	Mg	0.10	0.26	0.22	1.08
20	Mg	0.20	0.27	0.37	1.08
80	Mg	0.19	0.31	0.48	1.15
160	Mg	0.08	0.58	0.67	0.64
300	Mg	0.21	0.66	0.85	0.46
500	Mg	0.29	0.69	0.86	0.34
0	P	0.15	0.38	0.40	0.11
20	P	0.22	0.39	0.50	0.10
80	P	0.27	0.42	0.54	0.11
160	P	0.10	0.53	0.65	0.06
300	P	0.20	0.64	0.64	0.04
500	P	0.28	0.59	0.65	0.06
0	N	1.57	4.56	5.31	n.d.
20	N	2.89	4.06	6.01	n.d.
80	N	2.60	5.19	6.83	n.d.
160	N	1.14	6.10	7.35	n.d.
300	N	2.10	5.02	7.38	n.d.
500	N	2.87	5.34	7.52	n.d.
0	D.M. (g)	1.9	4.8	4.6	2.1
20	D.M. (g)	4.0	5.5	6.3	2.4
80	D.M. (g)	3.4	8.4	7.8	3.2
160	D.M. (g)	0.9	8.8	9.4	2.5
300	D.M. (g)	2.5	8.1	9.7	3.1
500	D.M. (g)	3.5	8.4	10.1	3.2

APPENDIX II CONTINUED

K added mg/pot		Harvest			
		28 days	44 days	63 days	80 days
Concentrations as % of dry matter					
	(a) Leaves				
0	K	2.4	1.4	1.2	0.6
20	K	2.8	2.2	0.9	0.6
80	K	4.4	2.3	1.6	1.1
160	K	5.2	3.1	2.3	1.4
300	K	5.6	3.4	3.4	2.8
500	K	6.7	3.7	3.7	3.7
0	Ca	4.7	3.5	5.1	6.7
20	Ca	3.7	3.4	4.9	5.5
80	Ca	3.5	2.8	3.4	5.6
160	Ca	2.7	2.3	2.6	3.7
300	Ca	2.9	1.4	2.5	3.0
500	Ca	2.4	1.2	1.2	2.0
0	Mg	0.50	0.56	0.55	0.67
20	Mg	0.48	0.44	0.54	0.49
80	Mg	0.41	0.41	0.48	0.46
160	Mg	0.37	0.35	0.30	0.32
300	Mg	0.35	0.23	0.23	0.18
500	Mg	0.34	0.22	0.23	0.20
0	P	0.69	0.35	0.38	0.26
20	P	0.63	0.45	0.23	0.21
80	P	0.70	0.37	0.28	0.21
160	P	0.71	0.34	0.31	0.19
300	P	0.64	0.32	0.29	0.18
500	P	0.60	0.36	0.27	0.20
0	N	5.3	3.1	3.6	2.9
20	N	5.1	3.7	3.1	2.6
80	N	5.8	3.1	2.9	2.4
160	N	5.4	3.3	2.9	2.2
300	N	5.3	2.6	2.6	2.4
500	N	5.1	2.8	2.5	2.6

APPENDIX II CONTINUED

K added mg/pot		Harvest			
		28 days	44 days	63 days	80 days
Concentrations					
	(b)	Stem (soluble fraction)		mM in stem water	
0	K	73	50	37	8
20	K	78	70	21	9
80	K	111	95	50	10
160	K	126	113	113	22
300	K	144	163	131	62
500	K	147	160	134	97
0	Ca	49	42	52	46
20	Ca	42	39	36	43
80	Ca	21	22	27	46
160	Ca	15	9	19	48
300	Ca	8	7	13	39
500	Ca	5	5	6	7
0	Mg	17	30	35	33
20	Mg	17	28	24	35
80	Mg	10	18	15	32
160	Mg	8	11	14	15
300	Mg	9	14	12	11
500	Mg	6	14	7	4
0	P	6.6	9.3	6.9	3.8
20	P	6.3	10.9	3.1	3.4
80	P	7.0	11.3	4.8	2.5
160	P	6.8	9.8	9.9	2.2
300	P	7.8	14.7	6.8	2.4
500	P	6.1	14.3	6.8	2.1

APPENDIX II CONTINUED

K added mg/pot		Harvest			
		28 days	44 days	63 days	80 days
Concentrations as % of dry matter					
	(c) Stem (insoluble fraction)				
0	K	0.38	0.14	0.13	0.05
20	K	0.45	0.25	0.12	0.20
80	K	0.75	0.36	0.20	0.05
160	K	1.19	0.66	0.56	0.47
300	K	1.29	0.77	0.63	0.27
500	K	1.43	0.79	1.02	0.50
0	Ca	3.6	1.9	2.0	2.2
20	Ca	3.1	1.7	2.0	2.1
80	Ca	3.4	1.5	1.7	2.2
160	Ca	3.7	1.4	1.2	2.4
300	Ca	2.8	1.1	1.5	2.0
500	Ca	3.0	1.1	1.0	1.6
0	Mg	0.10	0.11	0.13	0.14
20	Mg	0.10	0.11	0.12	0.14
80	Mg	0.11	0.09	0.09	0.14
160	Mg	0.14	0.10	0.07	0.10
300	Mg	0.14	0.08	0.09	0.06
500	Mg	0.15	0.10	0.06	0.05
0	P	0.21	0.11	0.10	0.07
20	P	0.16	0.12	0.09	0.06
80	P	0.16	0.11	0.10	0.06
160	P	0.25	0.11	0.11	0.07
300	P	0.17	0.11	0.06	0.06
500	P	0.15	0.11	0.08	0.04

APPENDIX II CONTINUED

K added mg/pot		Harvest				
		28 days	44 days	63 days	80 days	Final
Concentrations as % of dry matter						
	(d) Roots					
0	K	1.96	1.16	0.97	0.44	0.48
20	K	1.83	1.61	0.69	0.51	0.22
80	K	2.19	1.66	0.85	0.48	0.22
160	K	2.63	1.76	1.60	0.70	0.21
300	K	3.08	2.52	1.91	0.78	0.53
500	K	2.92	2.84	2.02	1.62	0.57
0	Ca	3.9	1.9	3.1	3.3	2.6
20	Ca	2.7	2.1	2.6	3.0	3.6
80	Ca	2.1	2.4	2.6	3.3	3.1
160	Ca	2.6	2.3	2.3	3.2	3.8
300	Ca	2.3	2.2	2.4	3.4	2.7
500	Ca	2.3	1.9	3.1	3.8	3.0
0	Mg	0.32	0.23	0.24	0.19	0.15
20	Mg	0.35	0.32	0.23	0.24	0.13
80	Mg	0.31	0.32	0.26	0.24	0.09
160	Mg	0.30	0.29	0.34	0.25	0.12
300	Mg	0.37	0.42	0.25	0.41	0.16
500	Mg	0.29	0.36	0.35	0.32	0.11
0	P	0.31	0.28	0.26	0.16	0.26
20	P	0.37	0.38	0.18	0.13	0.15
80	P	0.39	0.24	0.23	0.10	0.13
160	P	0.27	0.20	0.19	0.14	0.18
300	P	0.37	0.26	0.20	0.13	0.11
500	P	0.27	0.37	0.19	0.26	0.12

APPENDIX II CONTINUED

K added mg/pot		Harvest 63 days	Harvest 80 days	Harvest Final	Final harvest
Concentrations as % of dry matter					
	(e) Tubers				(f) Dead Tops
0		(1.56	1.06	1.18	0.16
20		(1.22	1.08	1.25	0.22
80	K	(1.57	0.94	1.18	0.22
160		(2.37	1.54	1.68	0.98
300		(2.45	2.23	2.16	1.54
500		(2.46	2.48	2.33	2.76
0		(0.28	0.14	0.13	5.5
20		(0.20	0.10	0.16	5.2
80	Ca	(0.19	0.08	0.09	4.7
160		(0.29	0.08	0.10	4.8
300		(0.20	0.09	0.13	3.6
500		(0.14	0.08	0.08	2.5
0		(0.079	0.066	0.073	0.63
20		(0.061	0.059	0.072	0.55
80	Mg	(0.069	0.046	0.074	0.43
160		(0.104	0.080	0.087	0.32
300		(0.110	0.099	0.108	0.18
500		(0.103	0.100	0.104	0.13
0		(0.32	0.24	0.27	0.17
20		(0.18	0.22	0.25	0.13
80	P	(0.25	0.16	0.21	0.11
160		(0.34	0.18	0.21	0.07
300		(0.28	0.25	0.21	0.04
500		(0.25	0.22	0.20	0.06
0		(1.19	1.33	1.65	n.d.
20		(1.02	1.04	1.33	n.d.
80	N	(1.09	0.88	1.22	n.d.
160		(1.75	0.97	1.09	n.d.
300		(1.18	0.87	1.07	n.d.
500		(1.18	0.88	1.04	n.d.
0		(13.8	19.2	16.2	-
20		(19.1	20.8	19.0	-
80	%	(19.1	23.6	20.3	-
160	D.M.	(12.8	22.7	21.0	-
300		(14.9	20.7	19.5	-
500		(17.7	19.2	18.4	-

APPENDIX II CONTINUED

Regressions quoted in Chapter 4

All are calculated with the replicates separated, giving 12 points.

x is always the quantity of K added in m-equiv/pot.

y is the variate quoted.

Variates from the 80-day harvest

Quantity of K in leaves (m-equiv/pot)

$y = 0.180 + 0.125x$; $r^2 = 0.94$

Quantity of K in stem dry matter (m-equiv/pot)

$y = 0.032 + 0.014x$; $r^2 = 0.31$

Quantity of K in roots (m-equiv/pot)

$y = 0.096 + 0.023x$; $r^2 = 0.42$

Quantity of K in tubers (m-equiv/pot)

$y = 1.500 + 0.315x$; $r^2 = 0.88$

Total K uptake (m-equiv/pot)

$y = 1.768 + 0.610x$; $r^2 = 0.98$

Quantity of Ca in leaves (m-equiv/pot)

$y = 3.833 - 0.165x$; $r^2 = 0.38$

Quantity of Mg in tubers (m-equiv/pot)

$y = 0.290 + 0.036x$; $r^2 = 0.75$

Quantity of P in tubers (m-equiv/pot)

$y = 0.396 + 0.017x$; $r^2 = 0.76$

APPENDIX II CONTINUED

Variates from other harvests

Quantity of Ca in leaves (44 days) (m-equiv/pot)

$y = 2.052 - 0.088x$; $r^2 = 0.74$

Total Ca in plant (44 days) (m-equiv/pot)

$y = 4.795 - 0.167x$; $r^2 = 0.81$

Quantity of Mg in leaves (44 days) (m-equiv/pot)

$y = 0.498 - 0.017x$; $r^2 = 0.46$

Nutrient movements

Gain of Ca by leaves, 44-80 days (m-equiv/pot)

$y = 2.242 - 0.110x$; $r^2 = 0.72$

Loss of P by soluble stem fraction, 44-80 days (m-equiv/pot)

$y = 0.068 + 0.0079x$; $r^2 = 0.76$

APPENDIX III

Quantities and concentrations of nutrients in plant parts, second experiment

(See Chapter 5)

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Quantities							
	(a)	Leaves	K, Mg, Ca and P in m-equiv/pot				
0		0.87	0.87	0.95	0.54	0.75	0.80
1		4.80	4.26	2.25	2.29	2.62	3.24
2.5	K	9.10	7.33	7.56	5.91	5.98	7.18
Mean		4.92	4.15	3.59	2.91	3.12	3.74
		S.E.'s*	Column mean 0.56		Row mean 0.43		
			Within table 0.97				
0		0.96	3.15	2.72	4.76	5.05	3.33
1		0.51	1.69	2.79	3.02	5.83	2.77
2.5	Mg	0.39	0.84	1.97	1.02	6.44	2.13
Mean		0.62	1.89	2.49	2.93	5.77	2.74
		S.E.'s	Column mean 0.17		Row mean 0.13		
			Within table 0.30				
0		14.0	17.1	15.6	11.9	12.0	14.1
1		8.9	13.5	8.6	12.2	7.6	10.1
2.5	Ca	4.8	5.4	4.5	4.3	4.3	4.6
Mean		9.2	12.0	9.5	9.5	8.0	9.6
		S.E.'s	Column mean 0.79		Row mean 0.61		
			Within table 1.37				
0		0.39	0.55	0.44	0.42	0.44	0.45
1		0.40	0.46	0.22	0.34	0.32	0.35
2.5	P	0.61	0.33	0.36	0.30	0.36	0.39
Mean		0.47	0.45	0.34	0.35	0.37	0.40
		S.E.'s	Column mean 0.040		Row mean 0.031		
			Within table 0.069				

* There were 26 degrees of freedom throughout this Appendix

APPENDIX III CONTINUED

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Quantities							
	(b)	Stems	K, Mg, Ca and P in m-equiv/pot				
0	(	0.50	0.39	0.64	0.18	0.52	0.44
1	(	1.90	1.74	1.49	0.62	3.08	1.77
2.5	K (	10.16	5.41	6.15	5.44	6.04	6.64
	(						
Mean	(	4.19	2.51	2.75	2.08	3.21	2.95
		S.E.'s	Column mean 0.27		Row mean 0.21		
			Within table 0.47				
0	(	0.68	1.08	1.04	2.34	1.14	1.26
1	(	0.16	1.65	0.39	2.81	0.85	1.17
2.5	Mg (	0.24	0.32	0.34	0.75	0.47	0.43
	(						
Mean	(	0.36	1.02	0.59	1.97	0.82	0.95
		S.E.'s	Column mean 0.077		Row mean 0.060		
			Within table 0.134				
0	(	7.4	7.6	11.3	6.0	6.4	7.7
1	(	8.8	11.6	10.5	6.8	10.7	9.7
2.5	Ca (	8.6	6.7	9.1	7.1	7.4	7.8
	(						
Mean	(	8.3	8.6	10.3	6.6	8.1	8.4
		S.E.'s	Column mean 0.62		Row mean 0.48		
			Within table 1.07				
0	(	0.41	0.42	0.55	0.45	0.34	0.43
1	(	0.23	0.42	0.25	0.23	0.33	0.29
2.5	P (	0.37	0.20	0.22	0.27	0.19	0.25
	(						
Mean	(	0.34	0.34	0.34	0.32	0.29	0.33
		S.E.'s	Column mean 0.0028		Row mean 0.022		
			Within table 0.049				

APPENDIX III CONTINUED

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Quantities							
	(c)	Roots	K, Mg, Ca and P in m-equiv/pot				
0	(	0.45	0.26	0.16	0.14	0.26	0.25
1	(	0.27	0.36	0.46	0.31	0.89	0.46
2.5	K (	1.05	0.98	0.85	1.43	0.87	1.04
	(						
Mean	(	0.59	0.53	0.49	0.62	0.67	0.58
		S.E.'s	Column mean 0.079		Row mean 0.061		
			Within table 0.136				
0	(	0.35	0.63	0.20	0.30	0.35	0.37
1	(	0.18	0.63	0.37	0.88	0.60	0.53
2.5	Mg (	0.21	0.49	0.23	1.24	0.29	0.49
	(						
Mean	(	0.25	0.58	0.27	0.81	0.41	0.46
		S.E.'s	Column mean 0.049		Row mean 0.038		
			Within table 0.084				
0	(	5.9	5.3	3.7	2.8	3.3	4.2
1	(	5.0	5.7	7.0	5.5	8.7	6.4
2.5	Ca (	3.2	4.5	5.3	6.3	5.1	4.9
	(						
Mean	(	4.7	5.1	5.3	4.9	5.7	5.2
		S.E.'s	Column mean 0.61		Row mean 0.50		
			Within table 1.05				
0	(	0.28	0.15	0.12	0.08	0.12	0.15
1	(	0.07	0.11	0.10	0.09	0.16	0.11
2.5	P (	0.12	0.08	0.08	0.15	0.07	0.10
	(						
Mean	(	0.16	0.11	0.10	0.10	0.12	0.12
		S.E.'s	Column mean 0.016		Row mean 0.013		
			Within table 0.028				

APPENDIX III CONTINUED

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Quantities	(d)	Tubers	K, Mg, Ca and P in m-equiv/pot				
0	(	11.1	10.6	9.1	9.6	10.0	10.1
1	(	21.0	22.2	25.2	27.1	24.5	24.0
2.5	K (	20.9	32.7	30.0	35.2	30.4	29.9
Mean	(	17.7	21.8	21.5	24.0	21.6	21.3
	S.E.'s	Column mean 1.08 Row mean 0.84 Within table 1.88					
0	(	1.34	1.47	1.33	1.58	1.25	1.39
1	(	2.22	3.04	2.87	4.08	2.92	3.03
2.5	Mg (	2.00	4.01	2.91	4.24	3.33	3.30
Mean	(	1.85	2.84	2.37	3.30	2.50	2.57
	S.E.'s	Column mean 0.12 Row mean 0.09 Within table 0.21					
0	(	1.80	1.24	1.88	1.54	1.65	1.63
1	(	1.61	1.39	1.46	2.17	2.10	1.75
2.5	Ca (	1.36	1.46	1.51	1.76	1.22	1.46
Mean	(	1.59	1.37	1.62	1.82	1.66	1.61
	S.E.'s	Column mean 0.19 Row mean 0.15 Within table 0.33					
0	(	3.12	2.98	2.80	2.65	2.76	2.86
1	(	4.06	4.23	4.51	4.79	4.57	4.43
2.5	P (	3.43	4.86	4.15	4.96	4.25	4.33
Mean	(	3.54	4.02	3.82	4.13	3.86	3.88
	S.E.'s	Column mean 0.15 Row mean 0.12 Within table 0.27					

APPENDIX III CONTINUED

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Concentrations							
	(a)	Leaves	% K, % Mg, % Ca, % P in dry matter				
0	(	0.58	0.46	0.59	0.34	0.45	0.48
1	(	3.46	1.63	1.35	1.16	1.63	1.85
2.5	K (	4.17	4.29	4.35	3.44	3.41	3.94
	(						
Mean	(	2.74	2.13	2.10	1.65	1.83	2.09
		S.E.'s	Column mean 0.28		Row mean 0.21		
			Within table 0.48				
0	(	0.20	0.51	0.50	0.95	0.98	0.63
1	(	0.11	0.21	0.53	0.47	1.15	0.49
2.5	Mg (	0.06	0.15	0.37	0.20	1.14	0.38
	(						
Mean	(	0.12	0.29	0.47	0.54	1.09	0.50
		S.E.'s	Column mean 0.021		Row mean 0.016		
			Within table 0.037				
0	(	4.8	4.6	4.6	4.0	3.8	4.4
1	(	3.2	2.7	2.7	3.2	2.2	2.8
2.5	Ca (	1.1	1.6	1.3	1.3	1.3	1.3
	(						
Mean	(	3.0	3.0	2.9	2.8	2.4	2.8
		S.E.'s	Column mean 0.18		Row mean 0.14		
			Within table 0.32				
0	(	0.21	0.23	0.21	0.21	0.22	0.21
1	(	0.22	0.14	0.11	0.14	0.16	0.15
2.5	P (	0.22	0.16	0.16	0.14	0.16	0.17
	(						
Mean	(	0.22	0.17	0.16	0.16	0.18	0.18
		S.E.'s	Column mean 0.015		Row mean 0.011		
			Within table 0.025				

APPENDIX III CONTINUED

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Concentrations							
	(b)	Stems	% K, % Mg, % Ca, % P in dry matter				
0	(	0.28	0.25	0.35	0.12	0.31	0.26
1	(	1.05	0.48	0.69	0.32	1.38	0.78
2.5	K (	4.80	2.76	3.25	2.17	3.43	3.28
	(						
Mean	(	2.04	1.16	1.43	0.87	1.71	1.44
		S.E.'s	Column mean 0.13		Row mean 0.10		
			Within table 0.23				
0	(	0.14	0.21	0.17	0.50	0.26	0.26
1	(	0.03	0.17	0.06	0.49	0.12	0.17
2.5	Mg (	0.04	0.05	0.06	0.09	0.08	0.06
	(						
Mean	(	0.07	0.14	0.10	0.36	0.15	0.16
		S.E.'s	Column mean 0.027		Row mean 0.021		
			Within table 0.047				
0	(	2.2	2.4	3.1	2.1	2.1	2.4
1	(	2.4	2.0	2.5	1.9	2.5	2.3
2.5	Ca (	2.1	1.7	2.4	1.5	2.2	2.0
	(						
Mean	(	2.2	2.0	2.7	1.8	2.2	2.2
		S.E.'s	Column mean 0.14		Row mean 0.12		
			Within table 0.25				
0	(	0.20	0.20	0.23	0.24	0.18	0.21
1	(	0.10	0.10	0.09	0.10	0.11	0.10
2.5	P (	0.14	0.08	0.09	0.09	0.09	0.10
	(						
Mean	(	0.14	0.13	0.14	0.14	0.13	0.14
		S.E.'s	Column mean 0.010		Row mean 0.007		
			Within table 0.017				

APPENDIX III CONTINUED

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Concentrations							
	(c)	Roots	% K, % Mg, % Ca, % P in dry matter				
0	(	0.55	0.32	0.32	0.31	0.46	0.39
1	(	0.49	0.49	0.57	0.45	0.86	0.57
2.5	K (	1.54	1.21	1.34	1.32	1.29	1.34
	(						
Mean	(	0.86	0.67	0.74	0.69	0.87	0.77
		S.E.'s	Column mean 0.062		Row mean 0.048		
			Within table 0.107				
0	(	0.13	0.24	0.12	0.21	0.20	0.18
1	(	0.10	0.26	0.14	0.40	0.19	0.22
2.5	Mg (	0.10	0.19	0.12	0.36	0.13	0.18
	(						
Mean	(	0.11	0.23	0.13	0.33	0.17	0.19
		S.E.'s	Column mean 0.14		Row mean 0.11		
			Within table 0.25				
0	(	3.7	3.5	3.8	3.6	3.1	3.5
1	(	4.6	3.7	4.4	4.1	4.4	4.3
2.5	Ca (	2.5	2.9	4.3	2.9	4.0	3.3
	(						
Mean	(	3.6	3.4	4.2	3.5	3.8	3.7
		S.E.'s	Column mean 0.20		Row mean 0.15		
			Within table 0.34				
0	(	0.27	0.16	0.18	0.16	0.17	0.19
1	(	0.10	0.12	0.10	0.10	0.12	0.11
2.5	P (	0.13	0.08	0.11	0.11	0.09	0.10
	(						
Mean	(	0.17	0.12	0.13	0.12	0.13	0.13
		S.E.'s	Column mean 0.011		Row mean 0.009		
			Within table 0.019				

APPENDIX III CONTINUED

K added (g/pot)		Mg added (mg/pot) 0	120(S)	120(L)	300(S)	300(L)	Mean
Concentrations							
	(d)	Tubers	% K, % Mg, % Ca, % P in dry matter				
0	(	1.59	1.41	1.45	1.54	1.55	1.51
1	(	2.18	1.71	1.99	1.84	2.13	1.97
2.5	K (	3.12	2.54	2.69	2.48	2.75	2.72
	(						
Mean	(	2.30	1.88	2.04	1.95	2.14	2.06
		S.E.'s	Column mean 0.044		Row mean 0.034		
			Within table 0.076				
0	(	0.060	0.061	0.065	0.078	0.061	0.065
1	(	0.072	0.073	0.070	0.086	0.078	0.076
2.5	Mg (	0.093	0.097	0.082	0.092	0.094	0.092
	(						
Mean	(	0.075	0.077	0.072	0.086	0.078	0.077
		S.E.'s	Column mean 0.0013		Row mean 0.0010		
			Within table 0.0021				
0	(	0.14	0.09	0.15	0.13	0.13	0.13
1	(	0.09	0.05	0.06	0.08	0.09	0.07
2.5	Ca (	0.10	0.06	0.07	0.06	0.06	0.07
	(						
Mean	(	0.11	0.07	0.09	0.09	0.09	0.09
		S.E.'s	Column mean 0.011		Row mean 0.008		
			Within table 0.019				
0	(	0.35	0.32	0.35	0.34	0.34	0.34
1	(	0.33	0.26	0.28	0.26	0.31	0.29
2.5	P (	0.41	0.30	0.30	0.28	0.31	0.32
	(						
Mean	(	0.36	0.29	0.31	0.29	0.32	0.32
		S.E.'s	Column mean 0.009		Row mean 0.007		
			Within table 0.016				

APPENDIX IV

Detailed data from the tuber removal experiment

(See Chapter 6)

Nutrient concentrations in young leaves

		Intact plants		Tuberless plants	
		O	K	O	K
First sampling (32 days)	% K, % Mg, % Ca, % P in leaflet dry matter				
O	% K	2.36	4.12	2.18	4.54
Mg	% K	2.37	4.02	2.45	3.70
O	% Mg	0.167	0.263	0.150	0.256
Mg	% Mg	0.181	0.310	0.188	0.281
O	% Ca	0.373	0.291	0.294	0.290
Mg	% Ca	0.307	0.260	0.317	0.256
O	% P	0.721	0.768	0.709	0.872
Mg	% P	0.705	0.869	0.746	0.721
	S.E.'s*	% K 0.128, % Mg 0.0082, % Ca 0.0264, % P 0.0240			
Second sampling (42 days)	% K, % Mg, % Ca, % P in leaflet dry matter				
O	% K	2.31	3.06	2.12	2.91
Mg	% K	2.15	2.97	2.35	2.91
O	% Mg	0.286	0.298	0.275	0.277
Mg	% Mg	0.290	0.306	0.258	0.314
O	% Ca	0.385	0.196	0.402	0.210
Mg	% Ca	0.421	0.177	0.315	0.225
O	% P	0.802	0.801	0.748	0.783
Mg	% P	0.717	0.770	0.774	0.778
	S.E.'s*	% K 0.076, % Mg 0.0138, % Ca 0.0304, % P 0.0190			

* There were 13 degrees of freedom

APPENDIX IV CONTINUED

		Intact plants		Tuberless plants	
		O	K	O	K
Third sampling (57 days)	% K, % Mg, % Ca, % P in leaflet dry matter				
O	% K	1.47	3.63	1.71	3.15
Mg	% K	1.46	3.36	1.78	3.16
O	% Mg	0.452	0.387	0.363	0.270
Mg	% Mg	0.601	0.404	0.378	0.354
O	% Ca	1.372	0.625	0.935	0.234
Mg	% Ca	1.424	0.413	0.848	0.417
O	% P	0.566	0.489	0.648	0.588
Mg	% P	0.519	0.456	0.637	0.552
	S.E.'s*	% K 0.139,	% Mg 0.0278		
		% Ca 0.0956,	% P 0.0292		
Fourth sampling (74 days)	% K, % Mg, % Ca, % P in leaflet dry matter				
O	% K	0.66	3.67	0.92	2.64
Mg	% K	0.68	3.62	1.04	2.81
O	% Mg	0.479	0.316	0.307	0.182
Mg	% Mg	0.814	0.340	0.406	0.226
O	% Ca	2.65	1.35	1.34	0.46
Mg	% Ca	2.61	0.98	1.53	0.55
O	% P	0.355	0.423	0.327	0.316
Mg	% P	0.443	0.385	0.429	0.312
	S.E.'s*	% K 0.139,	% Mg 0.0458		
		% Ca 0.185	% P 0.0226		

* There were 13 degrees of freedom

APPENDIX IV CONTINUED

			Intact plants		Tuberless plants	
			O	K	O	K
Quantities of nutrients in dead stems (m-equiv/pot)						
O	K	(	0.72	12.11	2.68	29.07
Mg		(	0.63	12.66	2.13	27.75
O	Mg	(	3.43	1.86	4.03	4.79
Mg		(	8.99	3.02	6.75	6.61
O	Ca	(	12.0	16.0	14.0	18.6
Mg		(	15.9	11.9	12.0	17.8
O	P	(	0.85	0.67	1.90	3.90
Mg		(	1.45	0.66	1.62	3.44
	S.E.'s* K 1.64, Mg 0.84 Ca 2.14, P 0.32					
Weight of dry stems (g)						
O			9.4	14.6	16.9	32.3
Mg			11.9	13.4	14.4	36.3
	S.E.* 2.14					
Life span of the plants (days)						
O	Days to tuber	(	43.7	44.3	43.0	45.1
Mg	formation	(	42.3	44.3	43.7	42.3
O	Total	(	87	117	139	165
Mg	life	(	93	110	132	169
	S.E.* Time to tuber formation 1.20 Total time 5.6					

* There were 13 degrees of freedom

APPENDIX IV CONTINUED

		Intact plants		Tuberless plants	
		O	K	O	K
Water uptakes by the plants (litres)					
O	Up to	4.62	5.26	4.71	3.92
Mg	44 days	4.31	4.98	3.92	5.01
O	44 to	5.19	8.41	3.13	7.16
Mg	81 days	5.16	8.46	3.70	6.13
	S.E.'s*	0.36,	0.34		

Note 44 days was the start of tuber formation, 81 days marked the death of the first plant. Water use after 81 days depended mainly on the longevity of the plants and is not recorded.

* There were 13 degrees of freedom

APPENDIX IV CONTINUED

Nutrient concentrations in normal and cut tubers

			O	K
Normal tubers				
O	% K	(	1.43	2.18
Mg		(	0.94	2.28
O	% Mg	(	0.080	0.095
Mg		(	0.060	0.110
O	% Ca	(	0.039	0.036
Mg		(	0.042	0.031
O	% P	(	0.375	0.389
Mg		(	0.322	0.399

S.E.'s * % K 0.248, % Mg 0.0083
% Ca 0.0047, % P 0.0183

Cut tubers				
O	% K	(	1.92	3.22
Mg		(	1.95	3.40
O	% Mg	(	0.111	0.138
Mg		(	0.112	0.156
O	% Ca	(	0.065	0.072
Mg		(	0.065	0.067
O	% P	(	0.595	0.609
Mg		(	0.565	0.614

S.E.'s + % K 0.090, % Mg 0.0035
% Ca 0.0048 % P 0.0125

* There were 6 degrees of freedom

\+ " " 5 " " "

APPENDIX V

Weights and mean concentrations of ^{14}C activity and water-soluble K, Mg and P in individual tubers

(See Chapter 7)

All concentrations are per g of tuber fresh weight

	Fresh weight g	Conc of ^{14}C activity cpm/g x 10^{-5}	µ-equiv/g of water-sol. K	Mg	P
73 day Harvest					
Control	65.7	0.00(0)	58	4.8	6.2
	52.6	0.43	60	4.3	7.8
	53.1	1.17	53	5.4	8.0
	43.1	0.32	52	4.0	7.8
	36.8	0.39	54	3.7	8.3
	24.2	0.53	48	3.4	8.9
	11.1	0.78	73	4.0	8.1
	4.7	0.96	83	4.1	8.1
Extra K	77.5	0.96	56	5.7	8.6
	38.0	0.55	59	6.8	8.8
	39.1	1.01	53	5.1	8.2
	31.5	1.16	63	7.3	9.3
	18.3	1.25	55	3.1	8.8
	14.2	1.24	50	4.1	9.5
	12.3	0.76	58	4.4	9.5
	12.2	1.80	59	5.5	9.8
	4.7	2.29	60	4.8	12.1
	9.7*	(0.82)	(44)	(6.9)	(9.2)
Extra Mg	77.3	2.10	58	5.8	9.7
	35.8	0.65	58	5.8	10.6
	28.6	1.77	53	5.8	10.8
	27.9	0.41	57	6.8	11.1
	8.5	1.22	59	7.5	15.0
	7.6	0.03	62	6.9	12.7
	4.8	2.31	57	6.8	17.5

* Collection of small tubers

APPENDIX V CONTINUED

	Fresh weight g	Conc of ^{14}C activity cpm/g x 10^{-5}	µ-equiv/g of water-sol. K	Mg	P
73 day Harvest continued					
Extra K+Mg	45.9	0.99	57	6.8	10.8
	43.5	0.69	54	6.4	11.1
	38.7	0.30	54	6.7	10.7
	25.8	0.18	53	6.7	11.1
	16.1	0.64	56	6.5	11.8
	14.0	2.94	55	8.0	14.8
	12.4	2.33	53	6.4	14.2
	12.0	0.85	51	6.0	13.9
	4.3*	(2.98)	(58)	(10.0)	(19.6)
87 day Harvest					
Control	87.6	0.61	54	4.7	8.0
	68.7	0.65	55	6.5	6.9
	63.9	0.18	54	4.8	8.5
	29.5	0.68	54	4.8	9.0
	27.9	0.60	48	4.0	8.6
	5.4	0.85	57	5.3	9.8
	4.2	0.97	50	4.7	8.5
	2.5	1.27	51	5.9	8.7
Extra K	83.1	0.98	56	6.3	7.9
	57.5	0.72	52	5.7	10.1
	50.8	1.29	52	5.6	11.5
	50.1	2.38	51	5.4	12.2
	21.7	0.46	47	4.4	9.8
	13.9	0.00(1)	59	4.9	8.9
	11.1	1.84	52	6.7	11.2
	2.6	0.00(2)	60	5.6	7.3
	2.5	0.00(1)	55	5.9	7.6
	1.1*	(0.02)	(38)	(7.0)	(2.4)

* Collection of small tubers

APPENDIX V CONTINUED

	Fresh weight g	^{14}C Conc of ^{14}C activity cpm/g x 10^{-5}	µ-equiv/g of water-sol. K	Mg	P
87 day Harvest continued					
Extra Mg	84.6	1.07	54	7.2	11.0
	50.2	0.00(1)	54	7.5	10.4
	36.0	1.25	51	6.8	11.2
	26.6	1.07	59	7.1	13.0
	14.3	0.00(1)	53	6.6	11.4
	13.5	0.31	65	8.0	11.8
	11.0	1.22	59	8.4	13.8
	10.6	0.91	50	6.8	13.2
	9.9	0.59	68	8.6	12.0
	8.9	0.09	56	6.4	11.5
	7.0	0.47	55	6.6	12.1
	4.3	0.00(1)	52	9.5	10.4
	7.3*	(0.00(1))	(59)	(9.5)	(12.2)
Extra K+Mg	82.0	0.65	51	6.3	10.9
	56.8	1.75	49	5.6	11.7
	40.2	0.31	63	6.4	11.1
	28.6	0.18	67	7.3	12.5
	26.0	0.69	50	6.9	12.4
	16.0	0.11	55	7.1	12.9
	9.3	0.89	61	7.3	13.2
	7.0	0.02	55	6.9	11.8
	5.6	0.25	66	7.1	11.6
	5.4	0.01	57	6.5	11.5
	3.1	0.53	49	6.5	10.5
	2.6	0.11	50	8.4	10.6

APPENDIX VI

Counting carbon-14 activity by liquid scintillation

(See Chapter 7)

Principle. The sample is mixed with a toluene-based phosphor. The low-energy β-emission of the ^{14}C causes scintillations in the phosphor of a wavelength characteristic of the type and energy of the emission and these are counted.

Method. A Beckman LS 250 counter was used. Five ml of the suspension of homogenised tuber was mixed with 5 ml of the phosphor and 0.5 g of 'Cab-O-Sil', a thixotropic gelling agent used to keep the solids in suspension during counting, and shaken in a special glass vial. This mixture was counted.

Recovery of added ^{14}C. When ^{14}C was added to tuber homogenate as sucrose, about 90% of the added activity was counted, regardless of the quantity of ^{14}C added (2,000-10,000 cpm).