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CRITICAL POTASSIUM POTENTIALS FOR ~~THE YIELD AND NUTRIENT UPTAKE OF SOME~~ CROPS ~~GROWN IN SOILS~~ IN A CONSTANT ENVIRONMENT

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ABSTRACT

The quantity/potential relations of potassium in soils from six series were evaluated. A linear relationship was observed between $\Delta G_{K,Ca+Mg}$ and log(exchangeable K) for each soil. The effects of the clay content and mineralogy and CEC of the soils on this relationship are discussed.

Pot experiments were conducted in a constant environment to obtain yield responses of perennial ryegrass and creeping red fescue to the mean K potential ($\Delta G_{K,Ca+Mg}$) during growth on the six soils. 'Exhaustion' and 'optimum' K potentials (ΔG_{exh} and ΔG_{opt} respectively) for both grasses were derived from second degree polynomials fitted to the response curves on five of the soils. The micaceous Worcester series soil produced little yield response because of its high rate of release of non-exchangeable K.

These critical K potentials varied with soil type. For both species, ΔG_{opt} increased with decreasing CEC of the soil. This may, however, be an artifact produced by the large 'crop:soil' ratio used, which caused large changes in soil K potential during cropping and thus accentuated the importance of the amount of soil K available to the plant.

Wheat, sweet corn, leafless peas, field beans, sugar beet and clover were grown for 4 weeks on a Newport series soil in pots in a constant environment. The yield response curves were divided into 3 linear sections, for positive, zero and negative response, by a numerical iterative method, and from these, exhaustion, optimum and toxicity (ΔG_{tox}) K potentials were derived.

Values of ΔG_{exh} were similar for all crops. The ΔG_{opt} values increased in the order legumes<cereals<sugar beet. Potassium potentials which produced decreases in yield were far greater than any likely to be encountered in a natural system. It is suggested that yield reductions at high K potentials were caused by inhibition of the uptake of other cations rather than by toxic levels of K in the plant tissue.

The influence of the K contents of the seeds on the critical K potentials is discussed.

An ancillary experiment showed that the light energy input to perennial ryegrass did not affect the work output of the plant in K uptake, as measured by the critical K potentials.

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1. INTRODUCTION

1.1 Chemical potentials and soil potassium

The chemical potential of a component in a system is defined (Moore, 1972) as the change in the Gibbs free energy of the phase with a change in the number of moles of the component, the temperature, pressure and number of moles of all other components being kept constant, ie.:

$$\mu_i = (\partial G/\partial n_i)_{T,P,n_j} \qquad .....(1.1)$$

where μ_i = chemical potential of component i
G = Gibbs free energy
n_i = number of moles of component i
T = temperature
P = pressure
n_j = number of moles of other ions.

Because absolute free energies are not easily measured, chemical potentials in solution are usually referred to the standard state of unit activity. Then,

$$\mu_i = RT \ln a_i \qquad .....(1.2)$$

where a_i = activity of i in mol l^{-1}
R = gas constant = 8.314 J deg^{-1} mol^{-1}
T = temperature
μ_i = chemical potential of i referred to the standard state.

In a multiphase system, in equilibrium, the energy status of a component in the most mobile phase defines its energy status in the system. Thus, the chemical potential of a species in the soil solution or vapour phase defines its free energy throughout the whole soil system, if the system is in equilibrium. Talibudeen (1974) described this equilibrium,

$$\begin{array}{c}\text{Nutrient in}\\ \text{soil matrix}\end{array} \rightleftharpoons \begin{array}{c}\text{Nutrient in}\\ \text{surface phase}\end{array} \rightleftharpoons \begin{array}{c}\text{Nutrient in solution}\\ \text{or vapour phase}\end{array}$$

The matrix - surface reaction is generally very slow, whereas that between surface and solution/vapour is relatively fast. Therefore the surface and solution phases are generally taken to represent the labile pool of a mineral nutrient in the soil, and its chemical potential in these two phases is that which is most important in the short term nutrient supply.

Arnold (1962) describes potassium equilibria in soil thus:-

$$\begin{array}{c}\text{Non-}\\ \text{exchange-}\\ \text{able}\\ \text{potassium}\end{array} \overset{\text{(slow)}}{\rightleftharpoons} \begin{array}{c}\text{Difficultly}\\ \text{Exchange-}\\ \text{able}\\ \text{potassium}\end{array} \overset{\text{(slow)}}{\rightleftharpoons} \begin{array}{c}\text{Readily}\\ \text{Exchange-}\\ \text{able}\\ \text{potassium}\end{array} \overset{\text{(fast)}}{\rightleftharpoons} \begin{array}{c}\text{Water}\\ \text{soluble}\\ \text{potassium}\end{array}$$

Kinetic studies of K release from soil (Talibudeen *et al.*, 1978) suggest three categories of soil K,

a) *matrix K* is that which forms part of crystal lattices of soil minerals,

b) *peripheral K* is held more loosely on sites in the weathered periphery of the clay particles,

c) *surface K* is associated with negative charges surrounding soil particles and is in instantaneous equilibrium with surrounding solution.

Arnold's representation could, therefore, be better expressed:

$$\underset{\text{K}}{\text{Matrix}} \overset{\text{slow}}{\rightleftharpoons} \underset{\text{K}}{\text{Peripheral}} \overset{\text{slow}}{\rightleftharpoons} \underset{\text{K}}{\text{Surface}} \overset{\text{fast}}{\rightleftharpoons} \underset{\text{K}}{\text{Solution}}$$

So when the soil is in equilibrium, the chemical potential of potassium in the soil solution defines the free energy of K throughout the soil. However, chemical potentials of the K^+ ion cannot be determined because activity coefficients can only be measured for pairs of oppositely charged ions, not for single ions. Mean ionic activity coefficients (Everett, 1959) denoted f±, for cation and anion pairs are defined thus:-

$$f\pm = (f+^{v+},\ f-^{v-})^{1/(v^{+}+v^{-})} \qquad \text{.....(1.3)}$$

where f+, v+, f- and v- are activity coefficients and valencies of cation and anion respectively. This has led to the use of ion activity products of oppositely charged ions, or ratios of ions of the same charge, in the presence of a common counter ion, to measure the chemical potentials of nutrient ions relative to that of another ion predominant in the system.

1.2 The Ratio Law

Following up the theory advanced by Terasvuori (1930) and work carried out by Talibudeen (1947) on jute fibre, Schofield (1947) proposed and confirmed the 'Ratio Law' pertaining to cations in solution in equilibrium with exchangeable cations on soil. This was stated as follows:-

> "When cations in a solution are in equilibrium with a larger number of exchangeable ions, a change in the concentration of the solution will not disturb the equilibrium if the concentrations of all the monovalent ions are changed in one ratio, those of all the divalent ions in the square of that ratio and those of all the trivalent ions in the cube of that ratio."

Thus $(H^+)/(K^+)$, $(H^+)/(Ca^{++})^{\frac{1}{2}}$ and $(H^+)/(Al^{+++})^{1/3}$ are constant in any solutions in equilibrium with a given soil. This rule was found to hold for soils with a predominantly negative surface charge in electrolyte concentrations up to 0.01 M.

Aslyng (1950) further confirmed the Ratio Law for Rothamsted soils by showing that their 'lime potential', pH - ½pCa (where p = negative logarithm and H and Ca are activities), measured in dilute solutions of Ca salts, was independent of the calcium concentration in the equilibrium solution. The lime potential was derived by combining the ion product of H^+ and OH^- in water with the potential of calcium hydroxide.

Similarly Schofield and Taylor (1955a) demonstrated how the chemical potentials of bases in soils could be determined by measurement of the activities of the base chloride and hydrochloric acid in solutions in equilibrium with the soil, eg.,

$$a_{Ca}^{\frac{1}{2}}/a_H = (a_{Ca}^{\frac{1}{2}}.a_{Cl})/(a_H.a_{Cl}) = (a_{Ca}^{\frac{1}{2}}.a_{OH})/(a_H.a_{OH}) \qquad .....(1.4)$$

$a_H \times a_{OH}$ is a constant so

$$pH - \tfrac{1}{2}pCa = p(HCl) - \tfrac{1}{2}p(CaCl_2) = \tfrac{1}{2}\log a_{Ca(OH)_2} + 14.2 \qquad .....(1.5)$$

The chemical potential (μ) of $Ca(OH)_2$ is given by:

$$\mu = \mu_o + 2.303\ RT \log a_{Ca(OH)_2} \qquad .....(1.6)$$

(where μ_o is the chemical potential of the standard state). Thus (pH - ½pCa) is directly related to the chemical potential of calcium hydroxide in the soil.

This was also applied to the equilibrium of H^+ ions and K^+, Na^+ or Al^{+++} ions in soil. The ratio $(a_M)^{1/z}/a_H$ was found to be constant in chloride solutions up to 0.1 M for K^+, 0.04 M for Na^+, 0.02 M for Ca^{++} and 0.002 M for Al^{+++} where z is the valency of the cation M. This complied with the findings of Talibudeen (1947) working on jute fibre.

Schofield and Taylor (1955b) proceeded to employ this theory to the measurement of soil pH. pH measurements on various soils made in constant calcium concentrations, are directly proportional to their lime potentials and hence can be meaningfully compared with one another. A 0.01 M $CaCl_2$ solution was found to provide a suitable medium in which to make the measurement. It is sufficiently concentrated not to be significantly altered by soil electrolytes but sufficiently dilute for anions not to penetrate the electrical double layer at soil surfaces. This work showed that such determinations are independent of soil:solution ratio. The concentration of Mg^{++} was included in the expression for the lime potential, ie. $pH - \frac{1}{2}p(Ca + Mg)$, because some soils contain appreciable amounts of Mg and exchange of Mg for Ca has little effect on the measurements.

Taylor (1958) determined the negative logarithms of the equilibrium activity ratio, $a_K/(a_{Ca})^{\frac{1}{2}}$, (ie. $pK - \frac{1}{2}pCa$) in some Rothamsted soils by an interpolation method. Soils were equilibrated with solutions of $CaCl_2$ containing various amounts of K to give a series of activity ratios larger and smaller than that of the soil. The amount of K gained or lost by the solution after equilibration was plotted against the final activity ratio in the solution. The activity ratio of a solution from which no K would be gained or lost on equilibration with the soil was then interpolated, to give the true activity ratio of the soil.

Beckett (1964a) used a similar technique to show that a Lower Greensand soil had the same equilibrium activity ratio ($a_K/(a_{Ca+Mg})^{\frac{1}{2}}$) in KCl + $CaCl_2$ solutions up to 0.06 M.

1.3 Free energies of cation exchange

The free energy of exchange ($\Delta G_{exch.}$) of two ions in a solution is defined as the net free energy change when a chemical equivalent of one ion (A) is transferred from the standard state (unit molarity) to the solution, in which its activity is a_A mol l^{-1}, and one chemical equivalent of another ion (B) of like charge, is transferred from the solution, where its activity is a_B mol l^{-1}, to the standard state (Woodruff, 1955a). So for A, the free energy change per equivalent is given as:-

$$\Delta G_A = (RT \ln a_A)/z_A \qquad .....(1.7)$$

and for B

$$\Delta G_B = -(RT \ln a_B)/z_B \qquad .....(1.8)$$

where z_A and z_B are valencies of A and B respectively. The exchange energy is therefore:-

$$\begin{aligned} \Delta G_{exch.} &= (RT \ln a_A)/z_A - (RT \ln a_B)/z_B \\ &= RT \ln ((a_A)^{1/z_A}/(a_B)^{1/z_B}) \qquad .....(1.9) \end{aligned}$$

The free energy of exchange of two ions in a solution is in fact equal to the difference in their chemical potentials.

This is a hypothetical exchange in which the transferences do not alter the activities of either ion in either the solution or the standard state. But in finite volumes of solution, one must consider exchanges of infinitely small quantities, extrapolated to chemical equivalents, so that existing activities are not altered.

When a soil or clay is in equilibrium with a solution, the partial molar Gibbs free energy ($\overline{G}$) of any diffusable species is constant throughout the system (Arnold, 1962). Therefore, in a soil suspension in equilibrium, $\Delta G_{exch.}$ of two cations, measured in the solution, is equal to the free energy of exchange of the cations on the clay or soil. A dilute electrolyte solution can therefore be used as a tool to measure cation exchange energies on soils and clays (Woodruff, 1955a). The problem of measuring the activities of cations is overcome by using a common anion. Arnold (1962) derived the free energy for potassium-calcium exchange in soil:-

$$(\overline{G}_{KCl})_{soil} = (\overline{G}_{KCl})_{solution} \qquad .....(1.10)$$

$$(\overline{G}_{CaCl_2})_{soil} = (\overline{G}_{CaCl_2})_{solution} \qquad .....(1.11)$$

$$(\overline{G}_{K^+} + \overline{G}_{Cl^-})_{soil} = (\overline{G}_{K^+} + \overline{G}_{Cl^-})_{solution} \qquad .....(1.12)$$

$$(\overline{G}_{Ca^{++}} + 2\overline{G}_{Cl^-})_{soil} = (\overline{G}_{Ca^{++}} + 2\overline{G}_{Cl^-})_{solution} \qquad .....(1.13)$$

combining (1.12) and (1.13) gives the difference in the partial molar free energies of K^+ and Ca^{++} ie. their exchange energy in the soil:

$$\begin{aligned}\Delta\overline{G}_{K,Ca} &= (\overline{G}_{K^+} - \tfrac{1}{2}\overline{G}_{Ca^{++}})_{soil} \\ &= (\overline{G}_{K^+} - \tfrac{1}{2}\overline{G}_{Ca^{++}})_{solution} \qquad .....(1.14)\end{aligned}$$

$$\overline{G}_{K^+} = G_o + RT \ln a_{K^+} \qquad .....(1.15)$$

and $\overline{G}_{Ca^{++}} = G_o + RT \ln a_{Ca^{++}}$ .....(1.16)

Where G_o is the free energy of the standard state. Therefore,

$$\Delta G_{K,Ca} = RT \ln(a_{K^+}/(a_{Ca^{++}})^{\frac{1}{2}}) \qquad .....(1.17)$$

This is a characteristic of a soil which is constant as long as the amounts of K and Ca in the surface phase remain constant. The Ratio Law dictates that it will not be altered by soil to solution ratio or anion concentration of the equilibrium solution, provided cations are not exchanged.

Woodruff (1955a) showed that for Putman Clay, $\Delta G_{K,Ca}$ was less negative the higher the %K saturation and the lower the total base saturation (Figure 1.1). Negative values indicate that K^+ is held on the clay surface preferentially to Ca^{++}. Therefore the lower the %K saturation the greater was the average selectivity of the exchange sites for K^+. As base saturation decreases protons and aluminium ions occupy otherwise K^+-selective sites.

1.4 Quantity/intensity relationships of soil potassium

A quantity/intensity (Q/I) 'curve' relates the change in intensity (or potential) of an ion in an equilibrium reaction in solution, or an adsorption reaction, to the addition or removal of the ion which produced the change. Perhaps the best known example is a pH buffer curve, defining the relationship between the volume of acid or alkali added to a solution and the resulting change in its pH.

Q/I curves are used to study the ion exchange properties of soils, particularly in relation to the supply and availability of potassium to plants. They relate changes in the exchangeable potassium to the free energy of exchange of K^+ for the predominant cation on the exchange complex (usually Ca^{++} in neutral or calcareous soils).

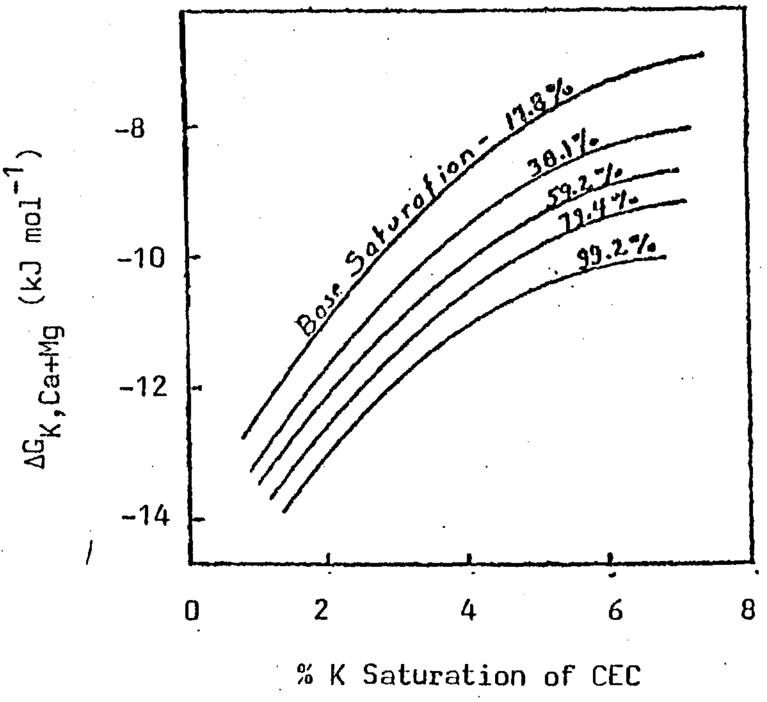


Figure 1.1 Changes in the free energy of Ca→K exchange with % K saturation at various base saturation of the CEC on Putnam Clay (from Woodruff, 1955a).

The activity ratio (AR), $a_K/(a_{Ca + Mg})^{\frac{1}{2}}$, in a solution equilibrated with the soil, has frequently been taken as the intensity factor in the Q/I relationship, as it is closely related to the K-(Ca + Mg) exchange energy ($\Delta G_{K,Ca} = RT \ln AR$). Matthews and Beckett (1962) developed a rapid technique for determining the K-Q/I relationship of soils. They equilibrated soil samples with chloride solutions, containing a range of K:Ca ratios, initially for one hour. The final activity ratios, $a_K/(a_{Ca + Mg})^{\frac{1}{2}}$ in the equilibrium solutions were plotted against amounts of K^+ adsorbed or desorbed by the soil, ΔK (ie. lost or gained by the solution). The shape and position of the resulting curves (eg. Figure 1.2) were independent of soil:solution ratio and total chloride concentration up to 0.06 M, as predicted by Schofield's Ratio Law. The true AR value of each soil, $(AR)_o$, was interpolated from the curve as the AR of a solution whose K concentration would remain unchanged on equilibrium with the soil (cf. Taylor, 1958; Beckett, 1964a). The method involves no absolute measurement of exchangeable K.

For many soils, Beckett (1964b) has interpreted the type of K-Q/I curve shown in Figure 1.2 as consisting of a linear part and a curved part, asymptotic to the y axis, at high and low activity ratios respectively. He suggested that the linear part describes K-(Ca + Mg) exchange on sites not specific for K^+ in accordance with a Gapon-type equation:-

$$\text{Exchangeable K/Exchangeable (Ca + Mg)} = k\, a_K/(a_{Ca + Mg})^{\frac{1}{2}} \quad \ldots\ldots(1.18)$$

where k is a constant dependent on surface charge density (Beckett, 1964b).

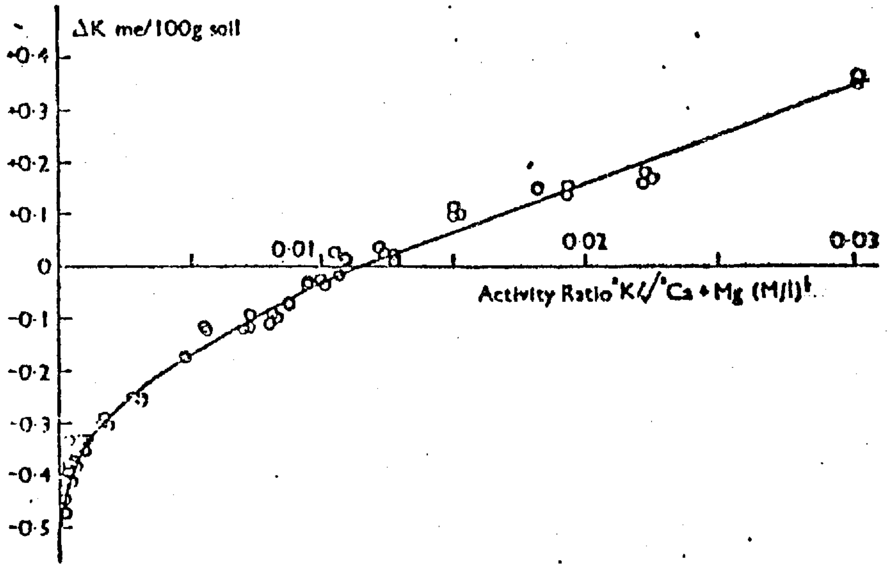


Figure 1.2 The immediate potassium Q/I relationship of a Lower Greensand Soil, (from Beckett, 1964b).

Beckett (1964c) suggests that these unspecific exchange sites are on the planar surfaces of the clay particles and that extrapolation of this linear relationship to AR = 0 gives a value for the size of the labile pool of potassium. The K - Q/I relation of some soils has no linear part; indeed it has been contended that Q/I curves do not have truly linear sections (Addiscott, 1970c).

The curved section of the relationship, according to Beckett (1964c), describes exchange on K-selective sites, possibly at the edges of the clay plates.

Other workers have presented semi-logarithmic Q/I curves: Q/log(AR) or $Q/\Delta G_{K,Ca+Mg}$ (Addiscott, 1970a; Ehlers et al., 1969). These present an expanded view of the relationship at low AR values and, since an AR value of zero is, in practice, unattainable, perhaps a more precise one. The Gibbs free energy of the K - (Ca+Mg) exchange reaction, $\Delta G_{K,Ca+Mg}$, is a true measure of the selectivity of exchange sites for K relative to Ca+Mg (and log(AR) is directly proportional to this).

1.5 Potassium buffer capacity

The K buffering capacity of a soil is the amount of K that must be added to, or removed from, the soil to produce unit change in K intensity ie. it is the slope of the K - Q/I curve.

Beckett (1964b) defined K 'Potential Buffering Capacity' thus

$$PBC = dQ/dI = dK/d(AR) \text{ in meq } \underline{M}^{-\frac{1}{2}} \text{ kg}^{-1} \qquad .....(1.19)$$

Later (1967, 1971) he applied this term specifically to the slope of the linear part of the K:AR relationship and called it 'Linear Buffering Capacity'. However, Addiscott and Talibudeen (1969) suggested that it was incorrect to assume that the greater part of the Q/I curve was linear, quoting theoretical treatments which predicted that it was curvilinear (Deist, 1966). Also Addiscott (1970c) showed that, on three soil types, each given several long-term K manurial treatments, the K buffer capacity decreased continuously with %K saturation of the CEC, indicating that the Q/I curves for these soils were not linear. Talibudeen and Dey (1968a and b) used the buffer capacity $(dQ/dI)_o$ at $(AR)_o$ in comparing K supply from a range of contrasting soils. It seems unlikely that the buffer capacity would change much from $(dQ/dI)_o$ during a growing season in the field.

Addiscott and Talibudeen (1969) suggested that the term PBC is inaccurate when referred to the ΔK:AR relationship because the true thermodynamic K potential is related but <u>not equal</u> to AR. Talibudeen and Dey (1968b) suggested that "the only sound theoretical basis for defining the K buffering capacity of a soil is the amount of K released per unit change in the <u>partial molar free energy</u> of soil K". This idea is supported by evidence concerning the variation of activity coefficients of adsorbed K with %K saturation of the CEC (Deist and Talibudeen, 1967).

Several workers have shown that the K buffering capacity of a soil is not altered by changes in exchangeable K. Beckett et al. (1966) found that K depletion of various soils by cropping for three months in small pots, with beans, barley or cauliflower, displaced their Q/I curves down the Q axis, thus decreasing $(AR)_o$, but did not alter the slopes. Similarly, Addiscott (1970c) showed that some Rothamsted and Woburn soils, from the same sites but given different K manuring for many years, had superimposable Q/I curves but displaced along the Q axis by amounts equal to the difference in exchangeable K of the soils (see also Moss, 1967, on West Indian Volcanic soils). These results imply that for a soil, a single curve relates exchangeable K to AR or $\Delta G_{K,Ca+Mg}$ regardless of K manuring or cropping history.

However, more extreme K depletion by more than 100 years cropping in the field with winter wheat, as in the 'No K' plot of the Broadbalk experiment, increases the slope of the Q/I and also displaces it along the Q axis as in short term cropping (Matthews and Beckett, 1962).

1.6 The significance of the exchange energy, $\Delta G_{K,Ca+Mg}$, to plant potassium uptake

Schofield (1955) proffered 'nutrient potentials' (the chemical potentials of nutrients in soil) as measures of the work the plant has to do to remove nutrients from soil.

He observed that the concept of phosphate potential (monocalcium phosphate potential = $\frac{1}{2}pCa^{++} + pH_2PO_4^-$, Aslyng, 1950) was similar to that of water potential. As with water, additions or removals of phosphate from the adsorbed pool raise or lower the chemical potential of the whole pool. Schofield quoted the pF value of water, (pF = -log (water potential)), above which it is unavailable to plants, as being 4.2. The concept of such a limiting potential for phosphate would be unrealistic as it would take many years for field crops to remove all the available P in the soil. But the phosphate potential gives a measure of the 'level' or intensity of phosphate in the soil.

For reasons discussed in Section 1.3, the thermodynamic potential of potassium in soil is taken as its partial free energy referred to that of calcium + magnesium, this being expressed as the free energy of K-(Ca+Mg) exchange,

$$\Delta G_{K,Ca+Mg} = RT\ \ln(a_K/(a_{Ca+Mg})^{\frac{1}{2}}) \qquad \text{.....(1.20)}$$

To justify any importance of this to plant K uptake, an attempt must be made to explain the significance of $(a_{Ca+Mg})^{\frac{1}{2}}$.

Woodruff (1955b) suggested that a low exchange energy for Ca->K exchange (-14.6 kJ mol^{-1}), and thus a low activity ratio, would cause K deficiency in plants, due to antagonism from an excess of Ca^{++} ions and conversely a high exchange energy would cause Ca deficiency. Certainly low exchange energies cause K deficiency, because they result from low chemical potentials of potassium, but there is little evidence to suggest that excess Ca suppresses K uptake. In fact, evidence from solution culture showed that, whilst yield and K uptake of flax and ryegrass both increased with the K concentration of the solution, neither were affected by the K:Ca ratio in the solution (Wild, et al.,1971).

The free energy of K-(Ca+Mg) exchange is a difference of two chemical potentials,

$$\Delta G_{K,Ca+Mg} = \mu_K - \mu_{Ca+Mg} \qquad \text{.....(1.21)}$$

and is therefore the chemical potential of K referred to that of Ca+Mg. The significance of μ_{Ca+Mg} is as a reference potential, valid where Ca+Mg dominate the exchange complex. In very acid soils, Al^{+++} or a combination of Al^{+++} and $Ca^{++}+Mg^{++}$ have been used as reference ions (Singh and Talibudeen, 1969; Tinker, 1964a and b).

Nutrient uptake by plant roots is a kinetic process. However, kinetic models require knowledge of the nutrient concentration at the root surface, which can only be readily gained in flowing culture solutions. A simpler approach is to consider that the root reduces the nutrient concentration at its surface to a small constant value that is an average for the whole root system and dependent on the average absorbing ability of the roots. It can then be assumed that the rate of uptake will be dependent on the rate of transport of the nutrient ions to the root surface, which in turn will depend largely on the nutrient concentration in the bulk soil solution.

Nye (1977) described the radial flow rate of a nutrient toward a root in the axis of a cylinder of soil, thus:

$$I_r = 2\ \pi r D_I \theta f_I dC_I/dr + 2\ \pi r v C_I \qquad \text{.....(1.22)}$$

where I_r = amount of a nutrient crossing a radial boundary in unit time (mol cm^{-1} s^{-1}),

r = radius of soil cylinder,

D_I = diffusion coefficient in free solution (cm^2 s^{-1}),

θ = volumetric moisture fraction in the soil,

f_I = diffusion impedance factor,

v = flux of water towards the root (cm s^{-1}),

and C_I = concentration of nutrient in solution (mol cm^{-3}).

If the nutrient concentration at the root surface is constant, the diffusion rate varies with the bulk soil solution concentration. The mass flow contribution also varies with the bulk soil solution concentration. So, the principal soil factor controlling uptake of nutrient ions, by plant roots, is the concentration of the ions in the soil solution. The equilibrium concentration of K^+ in the soil solution is determined by two factors: a) the partial molar free energy of K^+ in the labile pool of soil K in equilibrium with the soil solution, and b) the total anion concentration in the soil solution. The latter varies with soil moisture content, leaching, cropping etc; so a measurement of solution K concentration at any instant in time does not have great significance to the continuing supply of K to the plant root. Also, because it varies with anion concentration, and therefore with soil:solution ratio, in the manner defined by the Ratio Law, meaningful estimates of K concentration are difficult to make.

The activity ratio, $a_K/(a_{Ca+Mg})^{1/2}$, does remain constant as the soil solution is diluted, provided no anions are removed from or added to the suspension. Thus AR can be viewed in two ways, a) as RT $\ln(a_K/(a_{Ca+Mg})^{1/2})$, a fundamental thermodynamic parameter and b) as a readily measurable entity related to K concentration in the soil solution.

The force which drives diffusion is the change in the chemical potential of the ion with distance in the direction of diffusion (Barrow, 1966). Thus, according to Stout and Baker (1978) the diffusion of K in soil can be defined by the equation given by Mokody and Low (1966) for clays:

$$J_K = -ABC_K\lambda_K(dG_K/dx) \qquad \text{.....(1.23)}$$

where J_K = diffusive flux

A = cross sectional area of diffusion path

B = Tortuosity factor

C_K = the concentration of exchangeable K

λ_K = the average mobility of K

and (dG_K/dx) = the change in relative partial molar free energy with distance in the direction of diffusion.

The K concentration, and therefore the K potential, to which a plant root can reduce the soil solution in part determines the diffusive flux towards the root at any given K potential in the bulk soil. This depleted rhizosphere K potential is a measure of the root's absorbing power and, assuming it is constant during any particular phase of the plant's growth, rate of K uptake will be related to K potential in the bulk soil.

1.7 Quantity vs. intensity measurements as indices of soil potassium status

Measurements of exchangeable K are inadequate as indications of K supply to plants because the quantity measured depends on the extracting electrolyte chosen and also, although they measure the size of a labile pool, they do not determine how labile it is.

Arnold (1962) obtained a good positive correlation ($r = 0.88$) between exchangeable K content and K uptake by ryegrass during 36 days cropping in 64 soils, whose exchangeable K contents ranged between 0 and 400 mg kg^{-1} (approximately 0-10 meq kg^{-1}). But over the range 100-200 mg kg^{-1} exchangeable K, which included 36 of the soils, the correlation was poor ($r = 0.35$). However the correlation coefficient between K uptake and $\Delta G_{K,Ca+Mg}$ values for 32 of those 36 soils was 0.87.

Jancovič and Németh (1974) gave a more extreme example of the limitations of exchangeable K content as a measure of the relative availability of soil K to plants. They obtained a negative correlation between yields of sunflower seeds and exchangeable K on five soils, in field trials with 3 K treatments on each soil. However there was a positive correlation ($r = 0.59$) between yield and the K concentration in the soil solutions (related to $\Delta G_{K,Ca}$).

Feigenbaum and Hagin (1967) investigated the relationship between $\Delta G_{K,Ca}$ values of six soils, given six K treatments, and K uptake of wheat in a pot experiment. When the results from the sandy loams (CEC-s 95 and 136 meq kg^{-1}) were treated separately from those of the four heavier soils (CEC-s 330 to 470 meq kg^{-1}), good correlations between $\Delta G_{K,Ca}$ and K uptake were obtained for each group of soils.

The regression coefficient was numerically greater for the heavier soils because of their greater buffering capacity.

Sandy loams $r = 0.959$; K uptake $= -0.03\ \Delta G_{K,Ca} + 123$

Silty loam - clay $r = 0.894$; K uptake $= -0.04\ \Delta G_{K,Ca} + 210$

Plotting K uptake against exchangeable K showed a very poor correlation.

McConaghy and Smillie (1965) obtained a linear correlation ($r = 0.92$) between $(AR)_0$ values, up to 2.2×10^{-3}, of some basaltic soils and %K in the first cut of ryegrass in pots. Differences in $(AR)_0$ values accounted for difference in K uptake from soils with similar amounts of exchangeable K. Fergus et. al. (1972) observed a highly significant correlation between the initial K potential (expressed as $\frac{1}{2}p(Ca+Mg)-pK$) of 10 soils and %K in the first cut of ryegrass (in pots). They also showed that, when McConaghy's and Smillie's $(AR)_0$ values were converted to this logarithmic form, a linear correlation with %K in ryegrass was obtained over the whole range of values. The regression lines for these two sets of data were very close to one another and also to that obtained by Arnold et al. (1968) between %K in potato leaves and K potential.

$\Delta G_{K,Ca+Mg}$ values and exchangeable K content of soils correlated equally well with K uptake of wheat (Hagin and Bazelet, 1964). Hagin and Kayumjisky (1966) found that %K in peanut plants, grown in the field, correlated better with $\Delta G_{K,Ca+Mg}$ values than with %K saturation of the CEC or K concentrations in 0.01 M $CaCl_2$ and water extracts of the soil.

On several Indian soils, Ramamoorthy and Paliwal (1965a) obtained correlations between crop responses of paddy and "potassium adsorption ratio" ($=(AR)_o$). Halevy (1977) found that yield responses of cotton correlated equally well with $\Delta G_{K,Ca+Mg}$ values and exchangeable K.

Soil K potential decreases as K is removed by a crop, and so, can only be expected to be related to the initial uptake of K. As described in Section 1.5, K buffering capacity (dQ/dI) defines the quantity of K that can be removed per unit change in intensity and thus the degree to which the intensity changes as K is removed. Therefore its use as an index of the K supplying power of a soil has been investigated by several workers. Singh and Talibudeen (1969) measured the K buffering capacity of 8 Malaysian soils, taken as the slope of the linear part of the $\Delta K : a_K/(a_{Al})^{1/3}$ relationships. They found that this was significantly correlated with K uptake by the legume Pueraria phaseoloides.

Talibudeen and Dey (1968b) suggested that "if the clay fraction of British soils governs their cation exchange properties, PBC (potential buffering capacity) per unit of clay in the soil should be more meaningful as an intrinsic soil property in K exchange" than PBC of the whole soil. However they obtained a negative correlation between this and cumulative K uptake by ryegrass, from soils from 25 British soil series, after 16 and 60 weeks cropping in pots. Neither was K uptake related to the PBC of the whole soil, but a positive, though not significant, correlation was obtained between K uptake and the buffer capacity, $dK/d(\log(AR)_0)$. In this type of exhaustive cropping experiment, it is perhaps not surprising that intensity parameters of the soil, measured before cropping, do not describe K supply very well because release of K from the peripheries of the clay crystal lattices may contribute significantly.

Using regression analysis, Barrow (1966) demonstrated that the importance of $\Delta G_{K,Ca}$ in accounting for K uptake by subterranean clover (Trifolium subterraneum L.) decreased, whilst that of buffer capacity increased, with time of cropping. A multiple regression containing buffer capacity and $\Delta G_{K,Ca}$ terms accounted for up to 89% of the variation in K uptake.

Similarly, Moss and Herlihy (1970) used multiple regression analysis to evaluate the importance of quantity and intensity parameters in the supply of K to ryegrass. After 51 days growth a combination of buffer capacity + exchangeable K accounted for more of the variation in K uptake than did $(AR)_0$ + buffer capacity. The buffer capacity was taken as the slope of a chord joining the intercepts of the Q/I curve with the ΔK and AR axes. With prolonged cropping (up to 977 days) regressions involving the release coefficient (= the slope of the K release:time relationship) accounted for progressively more of the variation in K uptake whilst the importance of other parameters decreased.

Zandstra and MacKenzie (1968) suggested using the product of exchangeable potassium (K_0, obtained by extrapolating the linear part of the Q/I curve to AR = 0; see Figure 1.2) and the linear buffering capacity as a measure of K supply to plants. This complex function they misleadingly named "K potential" and suggested that it is a measure of labile K and its ease of release. It correlated well ($p = 0.001$) with the logarithm of yield responses of oats and barley, although not with that of corn. However, 'available K' extracted with 0.1 $\underline{M}$ NH_4OAc + 0.5 $\underline{M}$ H_2SO_4 correlated equally well with log(yield response).

Nye (1966) derived a mathematical model to describe potassium movement to plant roots in soil by diffusion and plant uptake. This predicted that plant uptake is proportional to the product of the concentration of K in the soil solution and the square root of K buffering capacity:

$$M_t \propto C_{l_i}(\Delta C/\Delta C_l)^{\frac{1}{2}} \qquad .....(1.24)$$

where M_t = amount of nutrient absorbed per unit area of root surface after time (t) since the surface was produced.

C_l = concentration of nutrient in the soil solution.

C = total concentration of mobile nutrient ions (exchangeable K)

C_{l_i} = initial concentration of nutrient in the soil solution.

Bradfield (1972) suggested that "in soils of comparable calcium status" this relationship could be expressed thus:-

$$\text{K uptake} \propto (AR)_o(BC)_o^{\frac{1}{2}} \qquad .....(1.25)$$

where $(BC)_o$ is the buffer capacity at $(AR)_o$. He related cumulative K uptake per unit of dry matter, in ryegrass, grown on 9 soils in pots, to the negative logarithm of this function, ie. $p((AR)_o(BC)_o^{\frac{1}{2}})$. Correlation coefficients for 28, 56 and 84 days cropping were -0.91, -0.80 and -0.75 respectively. A single linear relationship was also observed between $p((AR)_o(BC)_o^{\frac{1}{2}})$ and % K in strawberry leaves grown on five different soils.

To summarize, intensity measurements are less ambiguous in defining the status of labile K in soils and, under certain circumstances, correlate better with crop uptake than quantity measurements. Because soil K potential changes as K is removed, a single measurement can only be related to short term depletion by crops. Buffer capacity describes the degree to which a soil can resist changes in K potential as K is removed and so, as long as it remains constant, it is directly related to K uptake. However, for many soils, buffer capacity varies with exchangeable K. Thus, intensity parameters have not been accepted as reliable indices of soil K status for practical agriculture.

1.8 The concept of critical potassium potentials for crops

The relationship between the supply of a nutrient and crop yield can be expressed schematically as shown in Figure 1.3 (Russell, 1950). This suggests exponential crop response to increasing nutrient at very low levels of supply, diminishing response as the nutrient level approaches an optimum, no response where the nutrient is not limiting and negative response where it is present at such a high level as to be toxic. The problem arises of how to quantify nutrient supply so that the response curve becomes a characteristic of the crop and independent of the soil, given that other environmental factors remain constant. As discussed in the previous section, the concentration of

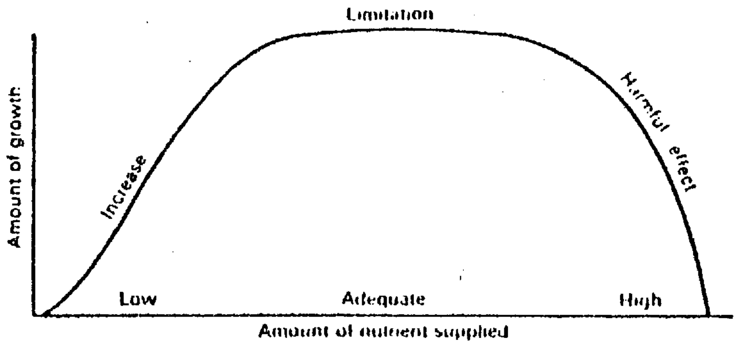


Figure 1.3 A general relationship between the amount of a plant nutrient supplied and plant growth (from Russell, 1973).

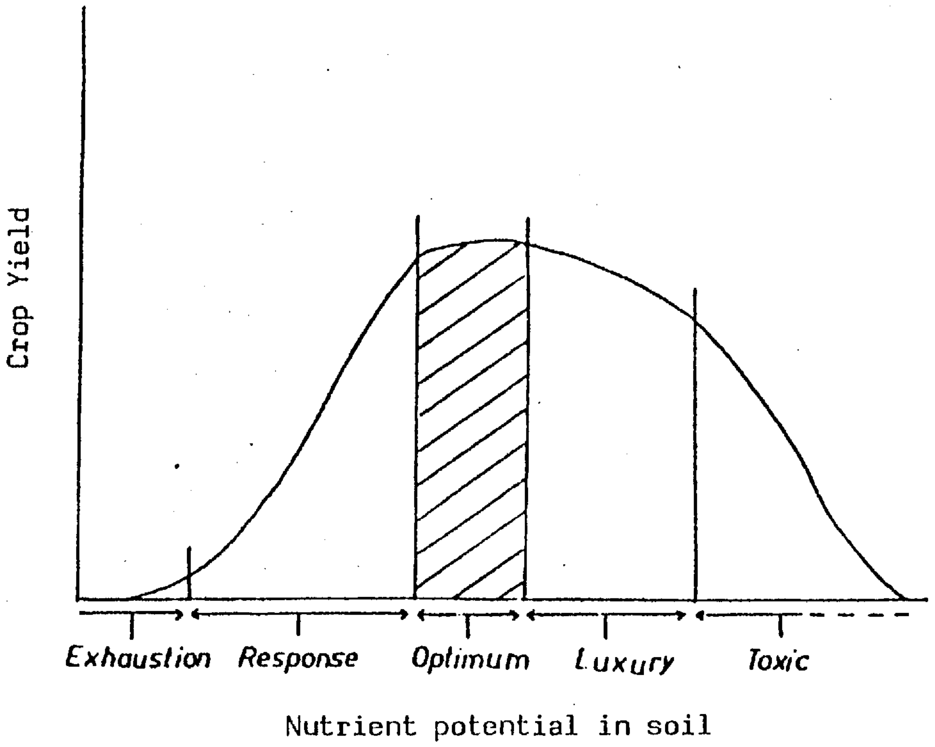


Figure 1.4 A diagrammatic representation of the effect of soil nutrient potential on crop performance, (from Talibudeen, 1974).

the nutrient ion in the soil solution is probably most relevant to plant uptake, but its chemical potential has more meaning in relation to K supply from the exchange surfaces in the soil.

Talibudeen (1974) gives a schematic plant response curve, to a nutrient potential, similar to that shown in Figure 1.4. However he used a "Plant efficiency index" instead of plant yield, which is preferred here. Ideally the nutrient potential should be averaged over the period of growth (Talibudeen and Dey, 1968a; Addiscott and Talibudeen, 1969; Beckett, 1972). From this curve, critical nutrient potentials can be evaluated that are characteristic of a plant taxon during a particular phase of growth, under the prevailing environmental conditions (Talibudeen, 1974; Talibudeen and Page, 1978). These are:-

1. Exhaustion Potential: The nutrient potential below which the plant is unable to take up nutrient. Deficiency symptoms appear and dry matter production ceases.
2. Response Potential: Plant yield increases rapidly with nutrient potential. This perhaps better describes a range of potential values rather than a single one.
3. Optimum Potential: Yield is maximum, but not total nutrient uptake.
4. Luxury Uptake Potential: The nutrient supply is greater than that required for maximum yield but is not at the level which is toxic to the plant, so that nutrient uptake increases but there is no change in yield. Like 'response potential' this region extends over a range of potential values.
5. Toxicity Potential: The potential above which plant yield decreases.

For any plant taxon, these critical potentials may be different at different development stages. Also, the maximum growth of some part of a plant, in the earlier stages, may not result in maximum yield of the harvested part. For instance, excessive top growth in some root crops results in poor root yields and, in cereals, too much spring nitrogen can lead to excess tillering, which reduces grain yield.

Exhaustion and optimum K potentials have been reported for several crops and will be discussed later. Response potentials are less well defined and have received little mention in the literature. Potassium toxicity does not seem to have been recorded.

Critical K concentrations in solution were determined for several plants in flowing culture solutions (Asher and Ozanne, 1967; Wild, et al., 1974). Solutions of constant concentration continually circulated around the roots, so a depletion zone cannot develop close to the root surface, and there is no adsorbing surface in the medium to restrain ions. Therefore, rate of uptake depends only on the plant and the solution concentration. This can be expressed (Wild, et al., 1974),

$$F = \alpha [K] \qquad \text{.....(1.26)}$$

where F = flux into the plant (g K atom $cm^{-2}s^{-1}$)

α = root absorbing "power" (cm s^{-1})

$[K]$ = K concentration in the circulating solution.

These authors found that α varied with plant species and with $[K]$. However its units are those of 'linear velocity' not 'power', the latter being meaningless in this context. Expressed fully, the units of α are: mols of nutrient absorbed per unit concentration at the root surface per unit of root surface area per second. It is therefore the rate of nutrient absorption per unit of root surface per unit concentration. If α was constant the rate of uptake per unit of root surface would vary linearly with concentration, which seems unlikely. A negative exponential relationship, with a vertical asymptote at the concentration at which all the uptake sites (whatever their nature) are permanently occupied, seems more probable.

Table 1.1 gives K concentrations which gave maximum yields for various crops and also the corresponding chemical potential transforms,

$$\mu_K = RT \ln a_K = RT \ln[K] \qquad \text{.....(1.27)}$$

assuming [K] approximates to a_K. These concentrations are considerably lower than would be expected in soil solution, certainly for maximum yield (cf. Nair and Talibudeen, 1973), because rate of uptake from a flowing culture solution does not depend on transport processes in the soil. Wild et al. (1974) showed that, even in sand culture, a considerably greater K concentration was required in the solution than in flowing solution culture for maximum yield. The chemical potential of K in culture solutions cannot be compared to $\Delta G_{K,Ca}$ measured in soil, because the latter is K potential referred to Ca potential. A measurement of $RT \ln(a_K/a_{Ca}^{\frac{1}{2}})$ in a solution culture would have little relevance to K supply in the absence of an exchange surface.

1.9 The exhaustion potassium potential

Talibudeen (1974) described this as the chemical potential of a nutrient in the soil (or any growth medium) which allows very little

TABLE 1.1 Potassium concentrations and equivalent chemical potentials for maximum yield of crops grown in flowing culture solution.

CROP	OPTIMUM CONCENTRATION $\underline{M} \times 10^6$	OPTIMUM POTENTIAL (RT ln[K] at 27°C) kJ mol^{-1}	REFERENCE
Silver grass (*Festuca myuros*)	24	26.5	Asher and Ozanne (1967)
Rye grass (*Lolium rigidum*)	24	26.5	
Brome grass (*Bromus rigidus*)	24	26.5	
Veldt grass (*Ehrharta longifolia*)	24	26.5	
Cock's-foot (*Dactylis glomerata*)	33	25.7	Wild, *et al.* (1974)
Sweet vernal grass (*Anthoxanthum odoratum*)	33	25.7	
Oats (*Avena sativa*)	1000	17.2	Asher and Ozanne (1967)
Barley (*Hordeum vulgare*)	1000	17.2	
Vetch (*Vicia sativa*)	95	23.1	
Subterranean clover (*Trifolium subterraneum*)	95	23.1	
Rose clover (*Trifolium lirtum*)	95	23.1	
Barrel medic (*Medicago tribuloides*)	24	26.5	
Field pea (*Pisum arvense*)	24	26.5	
Red clover (*Trifolium pratense*)	10	28.7	Wild, *et al.* (1974)
Trefoil (*Medicago lupulina*)	3	3.17	

dry matter production in the plant and leads to its eventual death. Addiscott (1970b), discussing K potential, distinguished between 'uptake potential' which corresponds to cessation of K uptake, and 'exhaustion potential', which corresponds to cessation of growth. In relation to crop production, there seems little point in attempting to make this distinction, even assuming that there is a difference.

In the exhaustion situation, the rate of diffusion of the nutrient to the plant root is very low and, if the concentration gradient is the main factor limiting diffusion, the concentration in the bulk solution approaches that at the root surface. The nutrient concentration to which the roots can reduce the solution at their interface depends on the root absorbing 'power'. Root absorbing 'power' therefore determines the concentration to which the nutrient in the bulk solution must be reduced before diffusion to the root surface is halted. Therefore, root absorbing 'power', at least partly, determines the exhaustion potential of a plant.

However, critical nutrient concentrations for plants are generally lower in flowing culture solution than in the soil solution (see Section 1.8) so the nutrient concentration in the bulk soil solution is probably never as low as that at the root surface. Factors other than the concentration gradient eg. tortuosity are also important in limiting diffusion rate in the soil.

Potassium exhaustion potentials ($\Delta G_{exh.}$) for crops are difficult to measure in soils, because, as the soil is stressed, K is released from initially non-exchangeable sources. Quite large amounts of K have to be removed before the supply is reduced to an exhaustion level. Fergus, Martin, Little and Haydock, (1972) exhaustively cropped 10 soils with setaria (Setaria sphacelata, a millet) in pots. Potassium removed by the plants varied between 0.79 and 81.0 meq per pot (1920 cm^3 soil per pot) in from 3 to 16 cuts before growth ceased. The resulting exhaustion potentials of the 10 soils ranged between -17 and -29 kJ mol^{-1} and had a mean value of -18.8 kJ mol^{-1}. Fergus, et al., (ibid) suggested that despite the range, this mean value "can be taken as the practical limit for seteria."

Martin and Fergus (1973) carried out similar experiments with 4 crops on 5 soils. The resulting exhaustion potentials varied more with soil type than with the crop. They suggested that this may have been because of different solubilities of K in different clay minerals, hence different rates of release from different mineral assemblages.

Talibudeen and Dey (1968a and b) cropped a variety of soils with perennial ryegrass, taking cuts until dry matter production was reduced to 0.05 g per 200 g soil per 4 weeks. Soils from the 'Rothamsted Classical Experiments' had final $(AR)_0$ values of between 2.8 and 10.2 x 10^{-4} $\underline{M}^{\frac{1}{2}}$ (-20.4 and -17.2 kJ mol^{-1}) with a mean of 5.8 x 10^{-4} $\underline{M}^{\frac{1}{2}}$ (-18.6 kJ mol^{-1}). Perennial ryegrass reduced the $(AR)_0$ values of 25 other British soils to between 3 and 12 x 10^{-4} $\underline{M}^{\frac{1}{2}}$ (-19.3 and -16.8 kJ mol^{-1}) giving a mean exhaustion value of 5.7 x 10^{-4} $\underline{M}^{\frac{1}{2}}$ (-18.6 kJ mol^{-1}), very close to the mean value for Rothamsted soils. In similar experiments, Islam and Bolton (1970) obtained exhaustion values for perennial ryegrass on Rothamsted and Woburn soils. These were 1.5 - 3 x 10^{-5} $\underline{M}^{\frac{1}{2}}$ and 2.8 - 3.8 x 10^{-5} $\underline{M}^{\frac{1}{2}}$ (-27.7 to -26.0 and -26 to -25.4 kJ mol^{-1}) for Rothamsted and Woburn soils respectively; considerably lower than the figures of Talibudeen and Dey for Rothamsted soil. Although the soils used came from different fields, they were not very different mineralogically, so they were probably more exhaustively cropped in the latter work.

Addiscott and Johnston (1975) determined K potentials of 5 Rothamsted and 1 Woburn soil after exhaustive cropping with ryegrass. To ensure that the K supply was exhausted, the soils were sown with a second crop of grass after the first had died. The mean exhaustion K potential for the Rothamsted soils was -23.3 kJ mol^{-1} and for the Woburn soil -21.8 kJ mol^{-1}. The value on Rothamsted soil agreed well with Addiscott's (1970a) calculated 'uptake potential' for perennial ryegrass (23.4 kJ mol^{-1}). The derivation of the latter was based on the assumption that K uptake was best correlated to the amount of labile K that could be removed before this limiting potential was attained. Then, for each soil, the K removals (ΔK) required to reduce its K potential to each of a series of arbitrary values were calculated. Correlation coefficients were obtained between these sets of ΔK values and K uptake by ryegrass from the soils. The 'uptake potential' was evaluated graphically, as the K potential giving rise to the maximum correlation. This method gave different values for Rothamsted and Woburn soils. The values on Woburn soils increased with time, indicating rapid K release, but those on Rothamsted soils were fairly constant at about -23 kJ mol^{-1}.

Addiscott and Mitchell (1970) used the same technique to determine the 'uptake potential' for potatoes on Rothamsted soils a) after 27 days growth and b) when the tops senesced, ie. when the soil K reached exhaustion level. They obtained values of -17.4 and -20.5 kJ mol^{-1} respectively. After the final harvest they also measured K potential in the exhausted soils of -19.7 kJ mol^{-1}. They suggested that this 'exhaustion potential' was numerically close enough to the 'uptake potential' to be considered the same entity.

Barrow, et al. (1967) measured the K potential of soils which subterranean clover (Trifolium subterraneum) had exhausted after several cuts. The plants remained alive but there was no net increase in dry weight; fresh growth and K uptake were only facilitated by K release from senescing leaves. The resulting exhaustion potentials decreased with increasing K buffering capacity, with an asymptotic minimum value of approximately -25.1 kJ mol^{-1}. This variation, they suggested, could have been caused by K release from broken roots remaining in the soil, which would have the greatest effect on the K potentials of the soils with the lowest K buffering capacity.

From field experiments in Israel, Hagin and Dovrat (1963) reported a limiting K potential (corresponding to severe deficiency symptoms and very low yield) of -20.1 kJ mol^{-1} for vetch and Dovrat (1966) obtained a limiting value of -17.8 kJ mol^{-1} for a berseem-vetch mixture.

Exhaustion K potentials can also be derived by extrapolating yield : K potential curves to zero yield, although this does not take into account the possibility that the response curve may be sigmoid and therefore not easy to extrapolate. Alternatively, one could extrapolate K uptake or concentration : K potential curves to obtain an exhaustion potential, but the same problem arises. Koch, et al., (1970) obtained K potential values of -17.2 and -15.5 kJ mol^{-1} for zero % K in corn leaves, by extrapolation. Similarly fitted lines to % K : K potential relationships gave exhaustion potentials of about -17 kJ mol^{-1} for setaria (Fergus, et al, 1972) and potatoes (Arnold, et al., 1968) and -20.7 kJ mol^{-1} for ryegrass (McConaghy and Smillie, 1965).

Table 1.2 summarizes K exhaustion potential data discussed here. It can be seen that it is a difficult parameter to measure for a crop, in soil, and that it varies with soil type. With the Q/I relationship, the exhaustion potential can be used to delineate the quantity of potassium in a soil, initially available to a crop (Addiscott, 1970b; Beckett, 1972; Beckett and Clement, 1973). It can be used to compare the ability of crops to remove K from soils.

1.10 The optimum potassium potential

The optimum K potential ($\Delta G_{opt.}$), for any crop can be loosely defined as that which gives maximum yield. How rigorously it can be defined depends on the shape of the yield response curve of the crop to K potential in the growth medium. If yield increases with K potential to a maximum and then decreases at higher K potentials, $\Delta G_{opt.}$ is easily interpolated. If however yield rises to an asymptotic maximum, a more arbitrary value of $\Delta G_{opt.}$ must be chosen such as that which gives 95% maximum yield. (cf. Arnold, *et al.*, 1968; Tinker, 1964b; Singh and Jones, 1975).

The K potential of a soil generally decreases as K is removed. So, for maximum yield, the optimum K potential must be passed through during growth and has to be estimated as a mean value for the period of growth under investigation. It is defined by yield response, not uptake and therefore must be sensitive to other environmental factors which affect yield. For instance, increased light intensity may produce a larger plant. The K uptake resulting in maximum yield, will then be greater, and therefore the optimum K potential will also increase.

TABLE 1.2 Potassium exhaustion potentials.

CROP	NO. OF SOILS	$-\Delta G$ EXHAUSTION (kJ mol^{-1})	REFERENCE
Setaria	10	29 - 17	Fergus, *et al.* (1972)
Rhodes grass	5	17.5 - 10.4	Martin and Fergus (1973)
Siratro	5	17.8 - 10.3	
Lucerne	5	16.1 - 9.1	
Perennial ryegrass	31	20.4 - 17.2	Talibudeen and Dey (1968a)
" "	25	19.3 - 16.8	" " (1968b)
" "	12	25.4 - 27.7	Islam and Bolton (1970)
" "	1	23	Addiscott (1970)
" "	6	23.7 - 21.8	Addiscott and Johnston (1975)
" "	4	20.7	McConaghy and Smillie (1965)
Vetch	1	20.1	Hagin and Dovrat (1963)
Berseem and Vetch	1	17.8	Dovrat (1966)
Subterranean clover	22	25.1	Barrow, *et al.* (1967)
Corn	1	17.2 - 15.5	Koch, *et al.* (1970)
Potatoes	2	17	Arnold, *et al.* (1968)
Potatoes (after 27 days)	1	17.4	Addiscott and Mitchell (1970)
" (top senescence)	1	20.5	

Data on optimum K potentials for different crops are scarce and most values offered are the results of single measurements ie. not mean values for a cropping period. Scheffer, Ulrich and Lisanti (1962) gave K potential values, in the soil before cropping, for the optimum supply of K for several crops in field experiments. These were, for wheat and barley, sugar beet, potatoes and grapes, -14.4, -12.6, -10.2 and -7.5 kJ mol^{-1} respectively.

On 20 Indian soils, Ramamoorthy and Paliwal (1965b) found that $\Delta G_{K,Ca+Mg}$ values of between -12.8 and -11.8 kJ mol^{-1} corresponded to yield responses of paddy, in field experiments, of 5% or less. Hagin and Koyumdjisky (1966) failed to obtain any yield response of peanuts to K fertiliser on soils in which the lowest K potential initially was -14.2 kJ mol^{-1}.

Singh and Jones (1975) determined optimum K potentials for beans, celery, tomatoes and potatoes, using a sorption isotherm technique. Solutions containing a range of K concentrations and 0.01 M with respect to $CaCl_2$, were equilibrated (24 hours) with samples of a silt loam to obtain a K adsorption isotherm (ie. K adsorbed vs. K concentration in the equilibrium solution). Equilibrium $\Delta G_{K,Ca+Mg}$ values were also calculated. The isotherm was then used to calculate the $\Delta G_{K,Ca+Mg}$ values of 2 kg samples of the soil, with a range of KCl additions. The crops were grown on these soils, in pots, and $\Delta G_{opt.}$ determined as those values which gave 95% of maximum yield: for beans, tomatoes, celery and potatoes (tops) -10.5, -10.4, -9.9 and -9.6 kJ mol^{-1} respectively.

Arnold, et al., (1968) related yields of potato tubers, grown on two field sites, with 4 levels of K fertiliser, to both initial and final $(AR)_0$ values of the soils. The initial and final values corresponding to maximum yield were approximately 0.005 and 0.0016 $\underline{M}^{\frac{1}{2}}$ ($\Delta G_{K,Ca+Mg}$ = -13.2 and -16.1 kJ mol^{-1}). The $\Delta G_{opt.}$, as measured before cropping, is thus considerably lower than values obtained by other workers. This demonstrates the limitation of using this single measurement to make comparisons between soils. A more valuable measurement would perhaps have been the mean of the initial and final $\Delta G_{K,Ca+Mg}$ values which corresponded to maximum yield ie. $\Delta G_{opt.}$ = -14.6 kJ mol^{-1}.

Tinker's (1964b) yield response curve of oil palms, grown in several acid soils, to AR_u ($= a_K/((a_{Ca+Mg})^{\frac{1}{2}} + P(a_{Al})^{1/3})$, unified activity ratio) shows that an AR_u value of approximately 0.006 gave 95% maximum yield. This transformed to energy units, gives a $\Delta G_{K,Ca+Mg+Al}$ value of -12.8 kJ mol^{-1}. Although not directly comparable with $\Delta G_{K,Ca+Mg}$ values, exchange energies involving aluminium are useful indices of K potential in acid soils.

1.11 The present work

The aim of this work was to determine thermodynamic K potentials ($\Delta G_{K,Ca+Mg}$) in the growth medium, corresponding with critical levels of dry matter yield for different crops, and examine the factors which affect them. The first objective then, was to obtain precise yield response curves to a wide range of soil K potentials in a constant environment. A constant environment obviates the major factors influencing yield response curves in the field, ie. the climatic environment, and also the water regime in the soil.

Critical K potentials for crops, quoted in earlier work (Beckett, 1972; Talibudeen and Page, 1978), have been determined in glasshous and field experiments by single measurements before and/or after cropping. The K potential changes as K is removed from the soil to an extent determined by the K buffering capacity of the soil. In this work, therefore, estimates were made of average soil K potentials during limited periods of growth and yield responses were related to these.

The critical K potentials determined previously have been mainly $\Delta G_{exh.}$ and $\Delta G_{opt.}$, corresponding respectively with minimum yield and/or zero K uptake and with maximum yield but not necessarily optimum K uptake. The toxicity level of K, $\Delta G_{tox.}$, has not received any attention previously because it is of little practical importance. However, it was considered worthwhile in this work to determine $\Delta G_{tox.}$ for various crops, in an attempt to show that toxic K potential thresholds do exist, for reasons that are not clearly defined.

Pot experiments were thus designed to obtain yield response data from which exhaustion, optimum and toxicity K potentials could be derived by curve fitting procedures. The supply of other nutrients and also the total anion concentration of the soil had to be balanced for all K treatments.

Critical K potentials are measures of the work capability of the plant in K uptake and should be independent of soil type. However, evidence reviewed earlier (Sections 1.7 and 1.9) suggested that yield responses of some crops to soil K potential vary with soil type. It was therefore necessary to see how K uptake varied with K potential on contrasting soils and to ascertain whether or not critical K potentials vary with soil properties, particularly texture and cation exchange capacity, which control soil K potential. If, for any crop : soil combination, these 'critical' values vary between soils, it becomes important to determine which critical potentials are most crop specific, and what experimental factors affect them.

Growing crops in a limited volume of soil leads to substantial depletion of the exchangeable K and large changes in K potential. So, for this type of work, the 'soil : plant ratio' should ideally be very large. However, the spatial limitation of working in constant environment cabinets necessitated working with small pots and did not allow investigations of the effect of larger soil volumes. The relationship between crop specificity of critical K potentials and 'soil : plant ratio' provides another possible line of research.

The moisture content of the soil was also recognised as an important controlling factor in the supply of K to plant roots, especially in a small volume of soil where it changes rapidly.

The principal environmental factors which might affect critical K potentials for crops are light intensity and temperature. The amount and quality of light regulates the energy input to the plant for photosynthesis and this study is concerned with energy output by the plant for K uptake. An experiment was designed to see if there was an interaction between the two.

So experiments were conducted to 1) determine and compare critical K potentials for some cereal and broadleaf crops in their early stages of growth; 2) determine and compare critical K potentials for two grasses on contrasting soil types; 3) examine the effect of light intensity on the yield - K uptake - soil K potential relationship and on critical K potentials for ryegrass.

In the long term, this work is aimed towards defining crop nutrient requirements (in this case, K) in terms of the chemical potentials of nutrient ions in the soil : water system so that the nutrient can be maintained at the correct level for the crop in the soil during a specified growth period.

2. GENERAL METHODS

2.1 Selection of soils

Soils were chosen for, a) low organic matter contents (<2.6 % organic C) e.g. soils in arable cropping in recent years, (comparisons between soils of high organic matter content are difficult in nutrition studies because of unequal mineralisation of N, P and S during pot experiments);

b) a low total N content (all but one are 0.2% or less) for the same reason;

c) low exchangeable K or %K saturation of the CEC (all but one have less than 4% K saturation) so that good crop responses to K could be obtained, and also so that the labile K could be reduced to an exhaustion level in a short time, by cropping in pots without added K;

d) a range of CEC-s and therefore buffer capacities;

and e) availability and accessibility of soil already sampled or of the site for sampling.

Soils from Rothamsted and ADAS experiments met most of these requirements.

2.2 Soil Analysis

Air dry soil with < 2 mm crumb size was used in this work unless otherwise stated. Details of all routine soil analyses are given in the Rothamsted manual, Analysis of Crops, Soils and Fertilisers.

The International Pipette method was used for mechanical analyses. Water holding capacities were measured by the method of Gasser (1962). Exchangeable cations were extracted from the soils by leaching with $\underline{M}$ NH_4OAc at pH 7 and assayed by atomic absorption spectrophotometry. Cation exchange capacities were determined by steam distillation of the NH_4^+ saturated soils with MgO.

Soil pH was measured in water and in 0.01 M $CaCl_2$ (1:2.5, soil: solution ratio). Carbonate contents of the soils were determined by measuring the CO_2 pressure produced when reacted with hydrochloric acid. Available phosphate was estimated as that soluble in 0.5 M $NaHCO_3$ solution (Olsen method).

Total soil N was determined by Kjeldahl digestion and estimation of NH_4-N by colorimetry in the Technicon AutoAnalyser. The nitrogen mineralizable over a three month period was estimated, with and without added $Ca(NO_3)_2$, by an incubation method (Gasser, 1961). Organic C was determined by the method of Tinsley (1950).

2.3 Soil preparation for pot experiments

The soils were adjusted to a range of exchangeable K levels (c. 1-70 meq kg^{-1}) by adding K (as KNO_3 and K_2SO_4) and also, for some experiments, by leaching K^+ out with $CaCl_2$ solutions (see below). Several kilograms of soil were leached (1 kg per vessel) in the apparatus shown in Figure 2.1.

To test the process, Batcombe and Newport series soils were leached with 0.1, 0.5 or 1.0 M $CaCl_2$. The leaching was started by saturating the soils with 500 ml of solution, before turning on the peristaltic pump. Initially the pump was adjusted to deliver about 2 l per day. However, after 24-48 hours when the soil had settled down, this flow rate was found to be faster than the percolation rate, and so it was decreased to approximately 1.5 l per day.

Table 2.1 shows that, for both soils, only small quantities of K were extracted from the soils daily after 72 hours leaching. Also, leaching the soil for 72 hours with 0.1 M $CaCl_2$ extracted at least 80% of the total amount of K removed by any of the solutions in 144 hours and so this procedure was adopted to prepare 'low K' soils for pot experiments. The soils thus leached were further washed with

Figure 2.1 A leaching apparatus for preparing 'low K' soils for pot experiments.

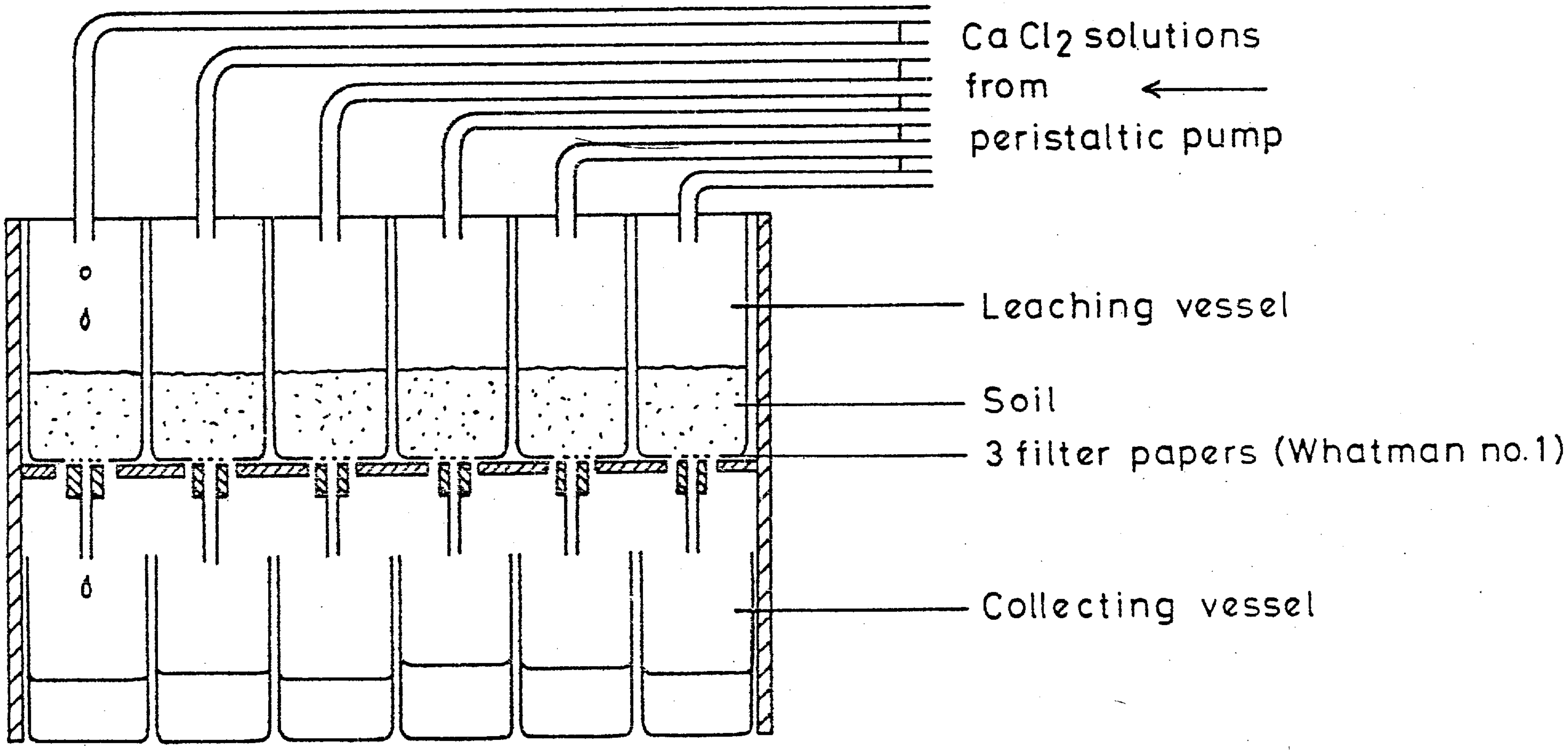


Table 2.1. Cumulative potassium leached from soils in preparation for pot experiments

Soil Series	$CaCl_2$ concentration (M)	Leaching Time (HRS):-						Total solution volume (l)
		24	48	72	96	120	144	
		K leached (meq kg^{-1})						
Batcombe	0.1	0.51	0.91	1.17	1.25	1.29	1.32	9.9
	0.5	0.68	1.05	1.24	1.37	1.40	1.42	10.4
	1.0	0.70	1.05	1.27	1.39	1.45	1.47	8.3
Newport	0.1	2.28	2.85	3.03	3.14	3.21	3.24	9.9
	0.5	2.79	3.38	3.49	3.54	3.62	3.65	10.4
	1.0	2.42	2.81	3.25	3.32	3.34	3.35	10.8

0.005 M $CaCl_2$ solution containing 0.0005 M $MgCl_2$ to reduce the salt concentration and to ensure that the exchangeable magnesium was not seriously depleted. The chloride concentration in this leachate was measured by colorimetry in the Technicon AutoAnalyzer every few hours for 24-48 hours until it was 0.0055 M. More dilute solutions were not used because they dispersed soil crumbs and made it impermeable. The soils were allowed to drain in the vessels for 24 hours and then tipped onto trays to air-dry before being broken up and sieved to < 2 mm.

Potassium was added to soils in mixed solutions of KNO_3, $Ca(NO_3)_2$, $Mg(NO_3)_2$ and K_2SO_4, to give a range of K^+ concentrations at constant NO_3^- and Mg^{++} concentrations. Details of these treatment solutions are given later in descriptions of individual experiments. Appropriate volumes of solution were added to the soils to bring them to 10% moisture content.

After 24 hours, a trace element mixture (0.32 g kg^{-1} soil, of fritted trace elements, type 253A made by Ferro Ltd. and containing 2% boron, 2% copper, 12% iron, 5% manganese, 13% molybdenum and 4% zinc), monocalcium phosphate (0.488 g kg^{-1} soil) and calcium sulphate (0.84 g kg^{-1} soil) were thoroughly mixed into the damp soils with a Kenwood mixer.

The 'high K' levels were obtained by adding K_2SO_4. Calcium sulphate was added to the 'low K' treatments to balance, in part, their sulphate levels with those of the 'high K' treatments. It was thought that the amount of sulphur added (4.9×10^{-3} moles kg^{-1}) would be much more than that required by the plants.

The soils, thus prepared, were left for 7 days sealed in polythene bags to equilibrate. They were then divided between replicate pots and sub-sampled for subsequent analysis. In the pots, the soil was compressed gently and seeds were sown, or seedlings planted.

2.4 Q/I Analysis of the soils (See Figure 2.2)

Sub-samples (4.4 g) of the damp prepared soils were weighed into previously weighed 50 ml centrifuge tubes. Ten ml of 0.01 M $CaCl_2$ was added to each. The tubes were weighed, shaken vigorously to disperse the soil, then put on a 'Rolamix' for 24 hours in a constant temperature room. The air temperature was maintained at 21°C, but the heat created by the machine quickly raised the temperature of the mixture in the tubes to a constant 27°C, which was therefore recorded as the 'isotherm' temperature.

The tubes were then centrifuged and the supernatants analysed for K, Ca and Mg by atomic absorption spectrophotometry.

Although Beckett (1964b) recommends 1 hour for 'instantaneous' cation exchange equilibria, other work (Matthews and Beckett, 1962; Le Roux and Sumner, 1968) suggests that extending the time to 24 hours does not displace the K-Q/I relationship significantly. Moss (1967) and Islam and Bolton (1970) used 16 hour and 24 hour equilibrium periods respectively. Indeed, Beckett (1964b) allowed his suspensions to settle overnight after 1 hour's mixing, so the soil was in contact with the solution much longer then 1 hour.

After sampling the supernatant, the tubes were weighed again (to evaluate the residual volume of solution) and then the soils were shaken with six successive 30 ml aliquots of M NH_4OAc at pH 7, for 16 hours with the first aliquot, then for 1 hour with each of the remaining aliquots. Whatman No.42 15 cm filter papers were dried at 80°C and weighed. After every wash, the tubes were centrifuged and the extracts poured off through the filter papers and accumulated in

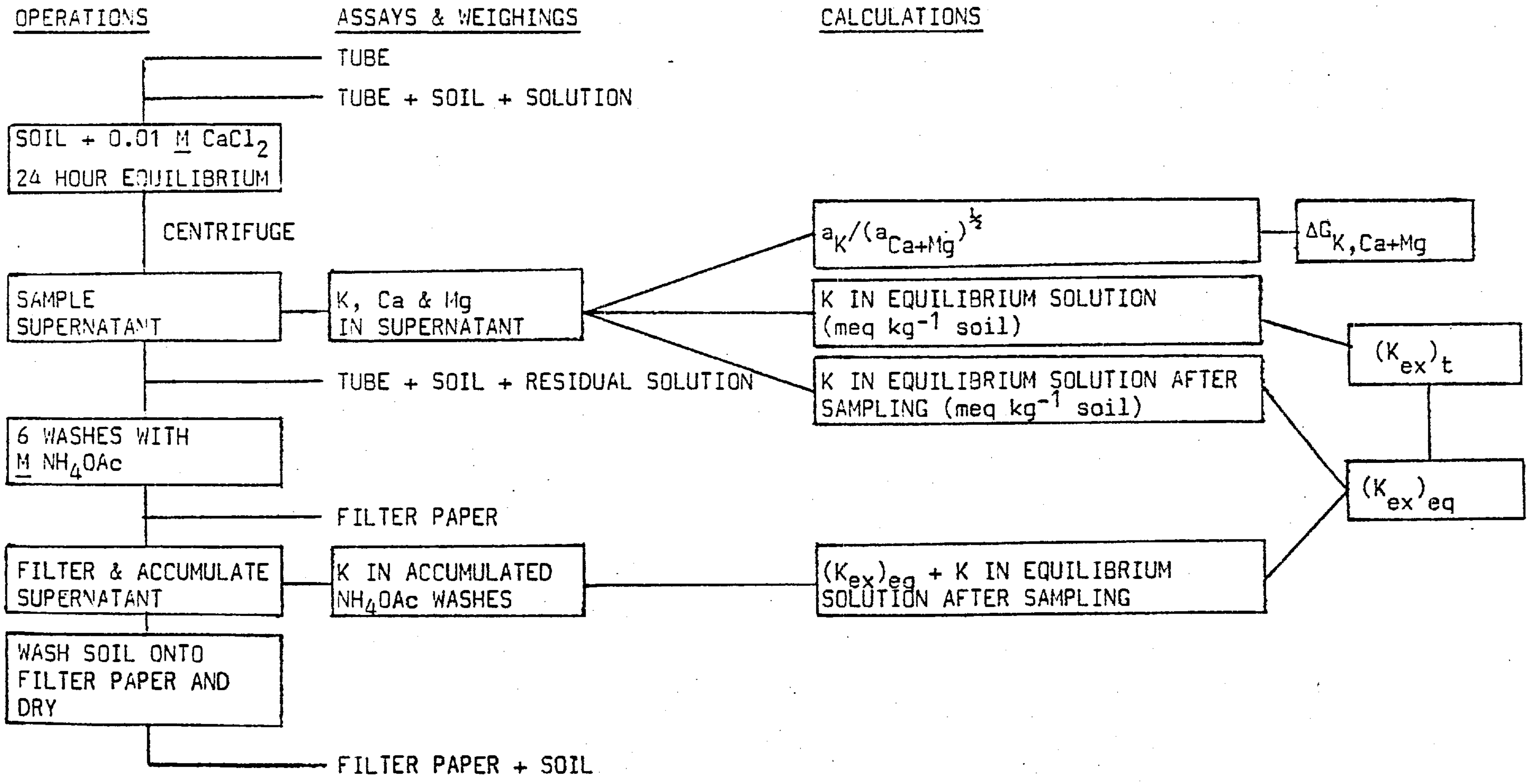


Figure 2.2 Evaluation of the Q/I relationships of soil prepared for pot experiments

250 ml volumetric flasks. After the last extraction, the soils were also washed onto the filter paper. When the NH_4OAc had drained off the soils were rinsed with water to wash any remaining K into the flasks. Finally, the flasks were made up to volume with water and K was determined in the resulting solutions by flame photometry (using standards made up in 0.72 $\underline{M}$ NH_4OAc). The filter papers and soil were dried at 80°C and weighed, and the dry soil weight obtained by subtraction.

Assuming a density of 1, the volumes of the $CaCl_2$ equilibrium solution before and after sampling were calculated;

$$\text{Solution Volume} = \text{Wt of (tube + soil + solution)} - \text{soil wt.} - \text{tube wt.} \qquad .....(2.1)$$

From these 'residual volumes' and the equilibrium K concentrations, the amounts of K contained in the residual solutions were calculated as meq kg^{-1} soil.

The equilibrium exchangeable K ($(K_{ex})_{eq}$) was calculated thus: $(K_{ex})_{eq}$ = K in NH_4OAc extract - K in residual $CaCl_2$ solution.

The total exchangeable K ($(K_{ex})_t$) was calculated as the sum of $(K_{ex})_{eq}$ and the K in the $CaCl_2$ - equilibrium solution,

$$\text{i.e.} \quad (K_{ex})_t = (K_{ex})_{eq} + K_s \qquad .....(2.2)$$

The activity ratio, $a_K/(a_{Ca+Mg})^{\frac{1}{2}}$, in the equilibrium solution was calculated from the K, Ca and Mg concentrations and the Debye-Hückel empirical formula for estimating activity coefficients (Beckett, 1965). Plotting the log/log transformations of the $(K_{ex})_{eq}$: AR relationships gave straight lines (see later). These were used to interpolate or extrapolate the true AR ($(AR)_o$) values of the soils. Because the 0.01 M $CaCl_2$ desorbs K from the soil, the AR value measured is lower than $(AR)_o$. $(AR)_o$ was therefore interpolated from the curve as the AR value corresponding to $(K_{ex})_t$.

To compare the exchange characteristics of the soil, K-(Ca+Mg) exchange energies,

$$\Delta G_{K,\ Ca+Mg} = RT \ln (AR) = 5.744 \log(AR) \text{ kJ mol}^{-1} \qquad .....(2.3)$$

were plotted against the equilibrium %K saturation of the CEC (= $(K_{ex})_{eq}$ x 100/CEC).

To enable interpolation of low AR values (of cropped soils), K desorption isotherms were obtained for the soils prepared with no added K. The soil was equilibrated for 24 hours with 0.01 M $CaCl_2$ at soil:solution ratios from 1:5 to 1:400. The final activity ratios in the equilibrium solutions and the K desorbed were obtained as described above. K desorbed (ΔK) was plotted against log(AR).

Quantity/intensity curves, of the form described by Beckett (1964b), were obtained for Batcombe and Newport series soils. Soils were 'rollermixed' for 24 hours at 27°C with KCl + $CaCl_2$ solutions, 0.02 M with respect to Cl^-, with K:Ca ratios from 0 to infinity at a 1:7.5 soil to solution ratio, and also with 0.01 M $CaCl_2$ solutions at soil to solution ratios down to 1:400. Activity ratios and K desorbed were calculated as before and K desorbed plotted against log(AR).

2.5 Sampling and analysis of soils after cropping

After every harvest soils were sampled with a No.4 cork borer taking 2 or 3 cores from each pot and bulking those from replicate treatments (cf. Talibudeen and Dey, 1968 a). The samples were put in previously weighed 50 ml centrifuge tubes, 15 ml of 0.01 $CaCl_2$ added and the tubes weighed again. They were then equilibrated for 24 hours at 27°C and activity ratios determined in the supernatant as before. Dry soil weights, solution volumes and K desorbed were obtained as described previously.

$(AR)_o$ was evaluated from the exchange isotherms by double interpolation thus: a 'quantity' value was interpolated corresponding to the measured AR and added to the desorbed K; $(AR)_o$ was interpolated as the AR value corresponding to this total.

The mean AR for a growth period $(\overline{AR})$ was calculated from the $(AR)_o$ values at the beginning and the end of the growth period and hence the corresponding K potential or exchange energy,

$$\overline{\Delta G} = 5.744 \log(\overline{AR}) \text{ kJ mol}^{-1} \quad .... \ (2.4) \ .$$

2.6 Cropping conditions

Plants were grown in 250 g of soil (sieved < 2 mm) in 3½" plastic pots. The soil surface was covered with 30 g of black alkathene beads, to minimise evaporation of water from the soil surface.

Experiments were carried out in Saxcil constant environment cabinets (1.3 x 1.3 x 1.5 m high) with a 16 hour light period. Illumination in the cabinets was supplied by Phillips Warm White (No.29) fluorescent tubes, which give energy peaks in the violet and yellow parts of the spectrum (440 and 590 nm respectively) and a minimum in the blue-green (460 - 520 nm). For further details of the illumination of this type of cabinet see Carpenter and Moulsley, 1960.

For the grasses, light intensity was maintained at 17,000 lx (1 lx = 1 lux = 1 lumen m^2) unless otherwise stated. A preliminary experiment with ryegrass, on the Batcombe series soil, showed that, over a range of soil exchangeable K levels (0-40 meq kg^{-1}), a higher light intensity did not increase yields, (mean yields for 17,000 and 28,000 lx were 6.43 and 6.35 g and the standard error of the difference was 0.10). The same basal treatments were given as in later experiments. For other crops, on advice from the growth cabinet operators, the light intensity was increased to full capacity, 28,000 lx.

The temperature was maintained at 20 and 15°C and the relative humidity at 70 and 90% during day and night periods respectively.

Air was circulated in the cabinets at a linear velocity of 15 cm s^{-1}. The pots were watered to weight daily to bring the soil to 30% moisture content (dry soil basis).

2.7 Harvesting

The plant shoots were cut, dried and weighed, then ground to pass a 1 mm sieve. They were analysed for P, K, Ca and Mg by dry ashing, solution in 0.6 M HCl then assay of P by colormetry on the Technicon AutoAnalyzer and the cations by atomic absorption spectrophotometry.

3. SOIL PROPERTIES

3.1 Description and composition of the soils

Table 3.1 gives the location, parent material, texture, clay mineralogy and recent K manurial history of the soils, Table 3.2 the results of mechanical analysis and water holding capacity and Table 3.3 relevant chemical analysis.

The soils will be referred to by the name of the soil series to which they belong (Table 3.1 column 1).

The Andover, Hanslope and Newport(2) soils were taken from 'no K' plots of the ADAS long term (1951 to 1964) experiments investigating the residual effects of K and P fertiliser on crop yields, in an arable rotation, at Experimental Husbandry Farms (E.H.F.-s). The treatments were maintained for several years after 1964 on one of the replicate blocks at each site to provide a 'museum' of soils. (Russell and Batey, 1971).

The treatments were 0, 21, 42 and 63 kg K ha^{-1} annually, or 63 and 125 kg K ha^{-1} every three years. At Bridget's, the rates were 0, 42, 63 and 84 kg K ha^{-1} annually or 125 and 188 kg K ha^{-1} triennially. Soils were taken from the 'no K' plots of these experiments at Bridget's, Boxworth and Gleadthorpe E.H.F.-s to obtain a range of textures and CEC's and low total N contents (Table 3.3).

The Andover soil is a rendzina derived from the Upper Chalk. It was under permanent pasture until ploughed for the residual K experiment in 1951, hence its higher 'total N' content than the other soils. It had a low K status (index 2 in 1951 reduced to index 1 during the experiment; M.A.F.F. Bulletin 209) and this was reflected in substantial yield responses of all the rotation crops

Table 3.1 Soil description and potassium fertiliser history

Soil Series	Source	Parent Material	Texture	Clay Mineralogy	Date Collected	Potassium Fertiliser
Andover	Bridget's E.H.F.*, Hants.	Upper Chalk	silty loam (rendzina)	smectite > mica, kaolinite	1969	nil since 1953
Batcombe	Delharding field, Rothamsted, Herts.	Clay with flints	silty loam	interstratified illite and smectite > mica, kaolinite	Nov. 1976	nil since 1956
Bromyard	Rosemaund E.H.F., Hereford.	Old Red Sandstone	silty loam	mica > chlorite > interstratified mica and smectite	1969	nil since 1951
Hanslope	Boxworth E.H.F., Cambs.	Chalky boulder clay	silty clay loam	smectite > mica, kaolinite	1969	nil since 1965
Newport (1)	Gleadthorpe E.H.F., Notts.	Bunter Pebble Beds	sandy loam	kaolinite > vermiculite > mica	1969	nil since 1965
Newport (2)			loamy sand		Mar. 1979	nil 1951-72 570 kg ha^{-1} since 1972
Worcester	Brackenhurst Agricultural College Notts.	Keuper Marl	clay loam	mica > chlorite, interstratified mica and chlorite	1969	nil since 1965

* Experimental Husbandry Farm

Table 3.2 Mechanical analysis and water holding capacity of the soils

Soil Series	Coarse Sand (2000-200 µm)	Fine Sand (200-20 µm)	Silt (20-2 µm)	Clay (<2 µm)	Loss on Solution (HCl and H_2O_2)	Air Dried Moisture	Water Holding Capacity (Dry soil basis)
			%				
Andover	2.4	27.3	15.0	19.5	35.2	2.6	50
Batcombe	6.2	43.4	20.4	26.2	4.4	2.2	49
Bromyard	0.6	37.4	33.4	23.0	3.6	1.9	55
Hanslope	14.1	26.3	14.8	36.0	5.9	3.5	52
Newport(1)	42.5	32.2	10.7	9.9	4.7	1.1	46
Newport(2)	45	—— 47	——	8.0	-	-	39
Worcester	3.3	31.3	24.4	31.6	9.2	2.1	54

Table 3.3 Chemical analyses of the soils

Soil Series	CEC per unit clay	Exchangeable Cations				Base saturation	pH		CaCO$_3$	HCO$_3^-$-soluble P	Total N	Organic C
		CEC	K	Ca	Mg		Water	0.01 M CaCl$_2$				
	meq kg^{-1}					%			%	ppm	%	%
Andover	862	168	2.9	-	5.7	100	7.9	7.3	31.6	27.8	0.37	2.62
Batcombe	530	139	1.9	100	4.7	77	5.5	5.0	0.0	5.6	0.17	1.68
Bromyard	696	160	2.6	133	18.3	96	6.3	5.4	0.0	13.3	0.17	1.32
Hanslope	608	219	4.9	-	9.9	100	8.0	7.1	0.4	18.2	0.21	1.61
Newport(1)	899	89	3.4	50	11.8	73	6.2	5.4	0.0	51.7	0.15	1.64
Newport(2)	812	65	2.2	48	9.9	92	7.0	6.4	0.0	35.0	0.09	1.11
Worcester	389	123	8.5	-	117.0	100	7.9	7.5	9.0	10.2	0.19	1.36

(potatoes, barley, kale and spring wheat) to K fertiliser. The large CEC of this soil (168 meq kg^{-1}) in relation to its moderate clay content (19.5 %; thus 861 meq CEC per kg clay in the soil) can be attributed to the predominance of smectite (montmorillonite, 40-60 %) in the clay fraction.

The Hanslope soil (Boxworth E.H.F.) is a heavy arable soil (36 % clay) derived from Chalky Boulder clay. The clay minerals are also predominantly smectitic and the CEC of the soil 219 meq kg^{-1} (608 meq kg^{-1} of clay). It has a good K status (index 3 in 1951) and the rotation crops (potatoes, barley, mangolds and beans) did not respond to K fertiliser.

The Newport(2) soil is a loamy sand derived from the Bunter Sandstone. It's K status was low (index 1) in 1952 and all rotation crops (potatoes, barley, swedes and clover) responded to K fertiliser.

The Andover and Hanslope soils were collected from the 'museum' blocks of the experiments in 1969, when the treatments were still maintained. The Newport(2) soil was collected in 1979, 7 years after the treatments were abandoned on the 'museum' block. In 1973 a crop of potatoes was grown on the block to test the residual effects of the K treatments and then, between 1974 and 1979, a total of 570 kg K ha^{-1} was applied for four crops of barley, one of sugar beet and one of potatoes. In addition, 30 tonnes ha^{-1} of battery hen manure, supplying a further 100-150 kg K ha^{-1}, was applied to the sugar beet in 1975. However, the exchangeable K level in the 'no K' plots was still only 2.2 meq kg^{-1} when the soil was collected in 1979.

The Newport(1) and Worcester series soils were also taken from two ADAS experiments sited at Gleadthorpe E.H.F. and Nottinghamshire College of Agriculture, Brackenhurst respectively. The experiments were investigating the direct and residual effects of K fertiliser on barley yields. The treatments were started in 1966 and soils for the present work were collected in 1969 from the 'no K' plots.

The Newport(1) soil had a higher clay content, CEC and exchangeable K content than the Newport(2) soil. It had been cropped without added K for only four years, so it was not as K-depleted as Newport(2), and was also more acid.

Barley grain and straw showed little or no yield response to K fertiliser during the first four years of the experiments on the Newport(1) and Worcester soils. The latter soil is derived from Keuper marl, a fairly heavy soil (32 % clay) but with a low CEC (123 meq kg^{-1}, thus 384 meq CEC per kg clay content of the soil) because the dominant clay mineral is mica. The high mica content means that the soil is rich in 'nonexchangeable' forms of potassium. It contains 9 % $CaCO_3$ and has a considerable amount of exchangeable magnesium derived from magnesium-rich minerals, sepiolite and palygorskite (Avery & Bullock, 1977).

The Bromyard soil was from the long term manurial reference plots at Rosemaund E.H.F., Hereford. This experiment was started in 1951 to measure crop responses from fertiliser treatments applied annually to a six course rotation (potatoes, wheat, kale, barley, ley 1 and ley 2). There were six blocks so that each crop was grown every year. The soil used in the pot experiments was a mixture of samples taken from the N + P plots (no K) of each block. It is a silty loam with a micaceous clay fraction. The exchangeable K content of the bulked samples was only 2.6 meq kg^{-1}. However only potatoes and the second ley gave consistent responses to K fertiliser in the last complete rotation (6 years) before the soil was sampled in 1969. This suggests that K was released at a significant rate from the micaceous clay.

The Batcombe soil from Delharding field, Rothamsted, is an acid silty loam which did not receive any P or K fertiliser after 1955. Between 1958 and 1976 (when sampled) cereals were grown for 10 years, potatoes one year, field beans one year and grass two years. Thus the levels of P and K in the soil were low.

3.2 Quantity/potential relations of potassium in the soils - results and discussion

(See General Methods, Section 2.4)

3.2.1 $\Delta G_{K,Ca+Mg}$ related to % K saturation of the CEC

Figure 3.1 shows the relationship between soil K potential, expressed as the free energy of K-(Ca+Mg) exchange ($\Delta G_{K,Ca+Mg}$), and % K saturation of the CEC in the experimental soils. Curves of the form,

$$\Delta G_{K,Ca+Mg} = b \log(\% \text{ K saturation}) - a \qquad .....(3.1)$$

(where a and b are constants) were fitted to this relationship for each soil by the 'least squares' method of the Maximum Likelihood Program (Ross 1978). For all soils, $\Delta G_{K,Ca+Mg}$ increased (i.e. became less negative) with log(% K saturation) over the range investigated. The fitted parameters (a and b) are given in Table 3.4.

Because these curvilinear relationships are independent of differences in CEC, they enable us to compare the effects of major soil components on the K selectivities of the exchange sites in the soils. The cation exchange properties of soils, poor in organic matter, are determined mainly by the mineralogy of their clay fractions and the degree to which their exchange sites are saturated with bases (Woodruff 1955a).

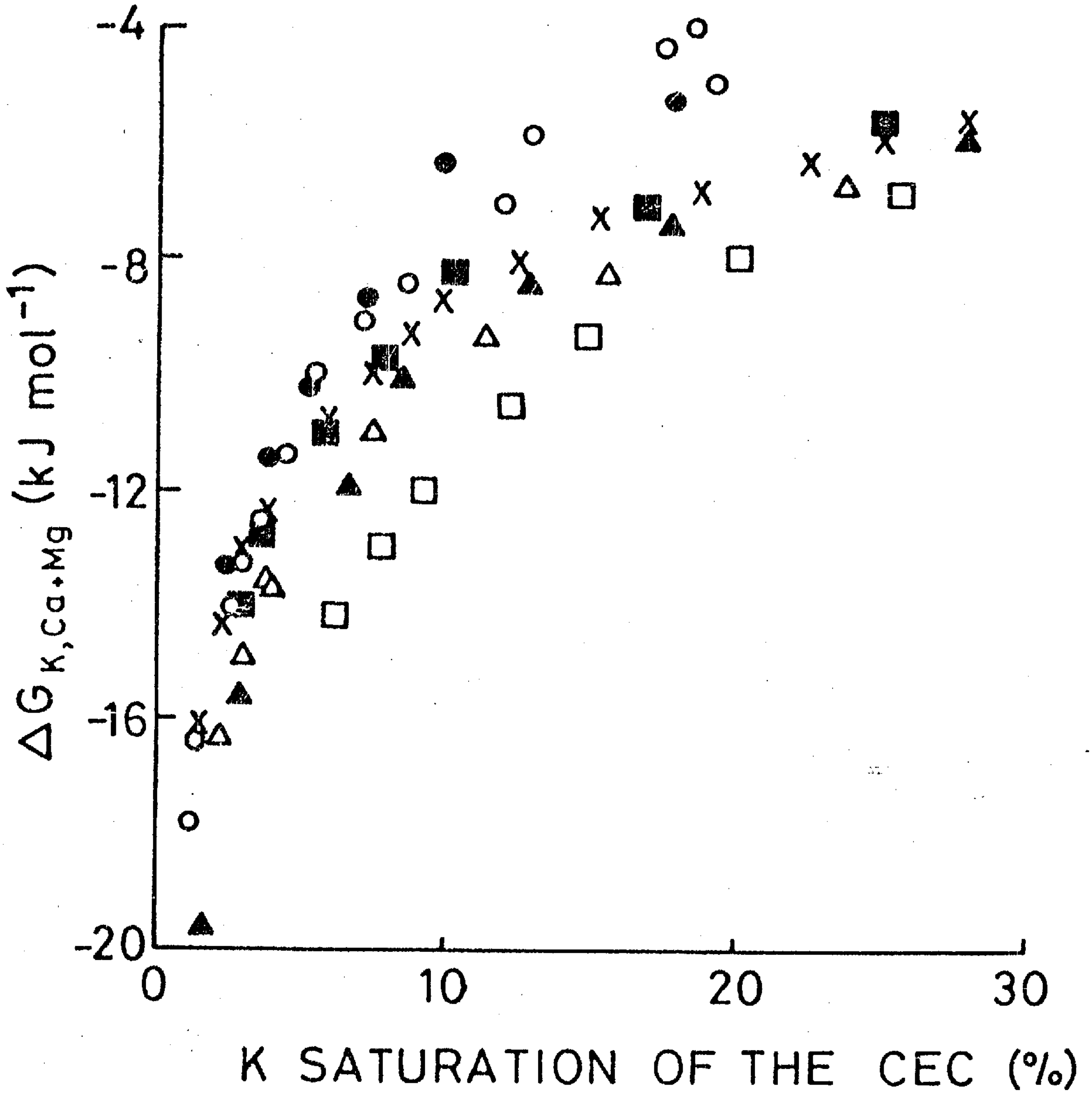


Figure 3.1 The relationship between the free energy of (Ca+Mg)->K exchange ($\Delta G_{K,Ca+Mg}$) and %K saturation of the CEC for the soils (▲ Andover; X Batcombe; ■ Bromyard; △ Hanslope; ● Newport(1); ○ Newport(2); □ Worcester).

Table 3.4 Fitted parameters for the relationship :

$$\Delta G_{K,Ca+Mg} = b \log (\%K \text{ saturation}) - a = b \log K_{ex} + b \log(100/CEC) - a$$

Soil Series	Intercept (a)	±S.E.	Regression Coefficient (b)	±S.E.	% Variance accounted for	[b log(100/CEC) - a]	Buffer capacity coefficient (2.303/b)
Andover	20.8	0.24	10.90	0.63	97.7	-23.26	0.211
Batcombe	16.9	0.05	7.96	0.13	99.6	-18.04	0.289
Bromyard	17.6	0.05	8.65	0.13	99.8	-19.37	0.266
Hanslope	19.2	0.07	9.25	0.21	99.6	-22.35	0.249
Newport (1)	16.7	0.24	9.49	0.76	95.6	-16.22	0.243
Newport (2)	18.1	0.08	10.72	0.21	98.4	-16.13	0.215
Worcester	23.2	0.06	11.66	0.24	99.7	-24.25	0.197

The isotherms suggest (Figure 3.1) that the Worcester soil had the greatest concentration of K-selective exchange sites per unit weight of soil and the Newport soil the smallest. This observation suggests that the very K-selective exchange sites on the hydrous micas in the clay fraction dominate the cation exchange properties of the Worcester soil. By contrast, the Newport soils contain mainly kaolinitic minerals in the clay fraction and therefore have a very low concentration of K-selective sites. The position of the Andover, Batcombe and Hanslope isotherms, relative to those of the Worcester and Newport soils suggests that the smectite minerals, which predominate in their clay fractions, are responsible for their intermediate K selectivity. The Bromyard soil is also micaceous but had less negative $\Delta G_{K,Ca+Mg}$ values than the Worcester soil over the whole isotherm. This may result from its much lower pH, 5.4 compared with 7.5 for the Worcester soil (Table 3.3).

The two Newport soils had very similar isotherms despite their different pH-s. The isotherm of the Batcombe soil was only slightly displaced from those of the Andover and Hanslope soils, with similar mineralogies, despite a much lower pH. However, in the clay minerals of these five soils, there are few sites for which Al^{+++} (present at low pH-s) and K^{+} ions compete than in the two micaceous soils (Worcester and Bromyard).

3.2.2 $\Delta G_{K,Ca+Mg}$ related to K_{ex}

The relationship between $\Delta G_{K,Ca+Mg}$ and % K saturation of the CEC gives fundamental information concerning the soil components and their K-(Ca+Mg) exchange properties. However, the relationship between $\Delta G_{K,Ca+Mg}$ and K_{ex} is of more practical use because it relates changes in amounts of K per kg soil to changes in potential. Equations describing this relationship for the seven soils were derived thus:

$$\begin{aligned}\Delta G_{K,Ca+Mg} &= b\log(\%\ K\ \text{saturation}) - a\\ &= b\log(K_{ex} \times 100/CEC) - a\\ &= b\log K_{ex} + b\log(100/CEC) - a \qquad \text{.....}(3.2)\end{aligned}$$

From this, an expression for the K buffering capacities of the soils was derived:

$$d(\Delta G_{K,Ca+Mg})/d(K_{ex}) = b/2.303\ K_{ex} \qquad \text{.....}(3.3)$$

therefore $$dK_{ex}/d(\Delta G_{K,Ca+Mg}) = 2.303\ K_{ex}/b \qquad \text{.....}(3.4)$$

The LHS of equation 3.4 is the K buffering capacity described by Talibudeen and Dey (1968b) as having a "sound theoretical basis".

So the K buffering capacity of each soil varied linearly with K_{ex} over the range investigated. The constants, b/log(100/CEC) – a, and the buffer capacity coefficients 2.303/b are also given in Table 3.4.

The relationship between $\Delta G_{K,Ca+Mg}$ and % K saturation (Figure 3.1) of the CEC is determined by the relative selectivity of the exchange sites in the soil for K and Ca+Mg. However the relationship between $\Delta G_{K,Ca+Mg}$ and K_{ex} (Figure 3.2) is affected by the CEC of the soil as well as the selectivity of the exchange sites. The greater the concentration of negative sites the lower is the K potential of any given value of K_{ex}. Thus the Hanslope soil (largest CEC, intermediate K selectivity) had the lowest (most negative) $\Delta G_{K,Ca+Mg}$

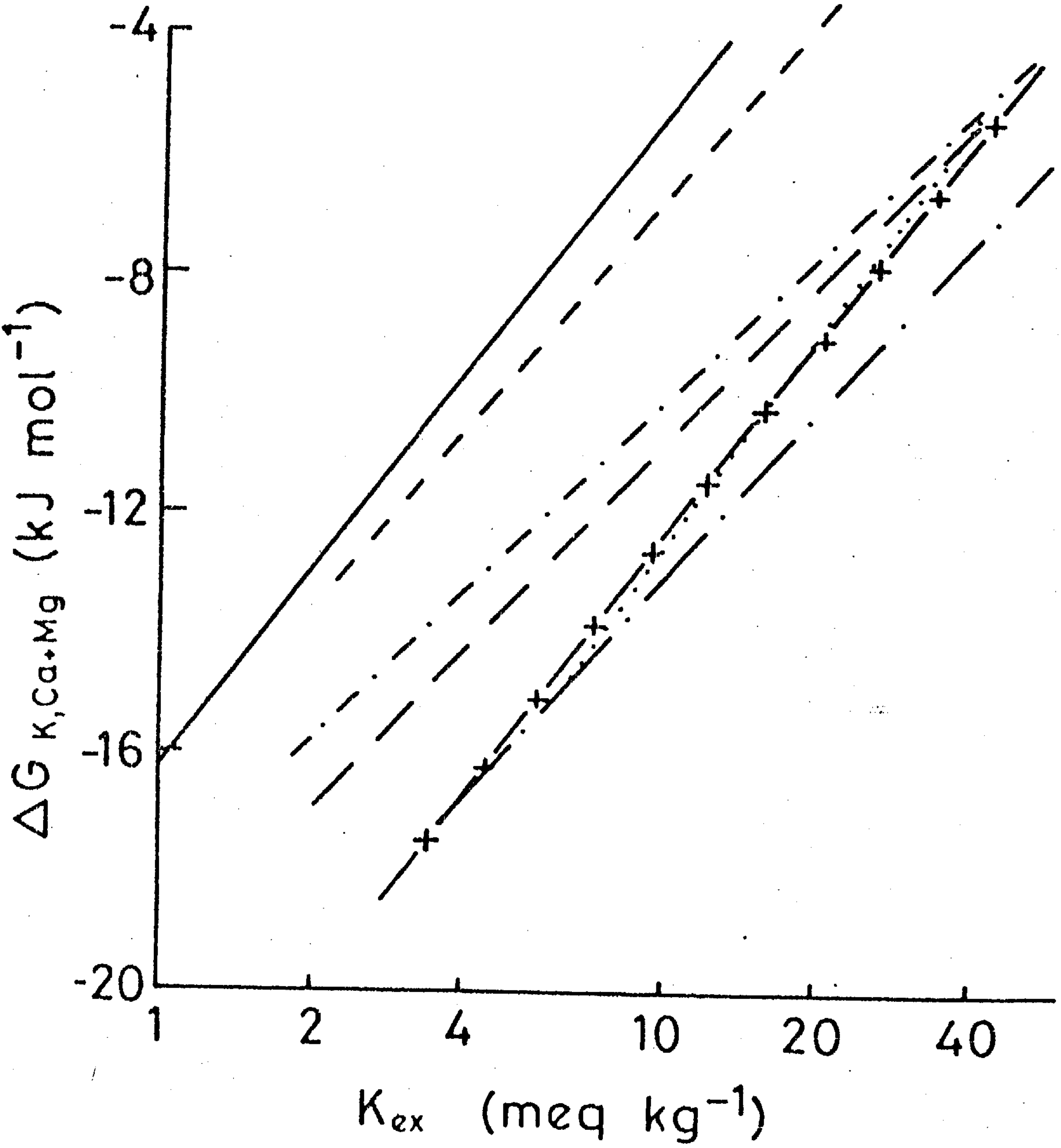


Figure 3.2 Fitted linear relationships between $\Delta G_{K,Ca+Mg}$ and log K_{ex} for the soils (X——X Andover; ·—·—· Batcombe; —— ——Bromyard; •———•Hanslope; ——— Newport(1); — — — Newport(2); ······ Worcester).

value for any given level of K_{ex}, whereas the Worcester soil gave the lowest $\Delta G_{K,Ca+Mg}$ value for any percentage K saturation of the CEC. The Newport soils (smallest CEC and lowest K selectivity) had the highest $\Delta G_{K,Ca+Mg}$ values for any value of K_{ex} or % K saturation.

Quantity/Intensity curves (where Q = ΔK and I = log(AR)) for the Batcombe and Newport(1) soils are plotted in Figure 3.3. $(AR)_o$ values were interpolated as described in Section 1.2. These Q/I curves were compared with the $\Delta G_{K,Ca+Mg}:K_{ex}$ isotherms by a) converting AR to $\Delta G_{K,Ca+Mg}$ values, so $\Delta G_o = RT \ln(AR)_o$, b) equating $\Delta K = 0$ with the K_{ex} value corresponding to ΔG_o and c) equating changes in ΔK to changes in K_{ex}. Figure 3.4 shows the points of the Q/I curve plotted in this manner and the fitted curves for the $\Delta G_{K,Ca+Mg}:K_{ex}$ relationship (as shown in Table 3.4) and that for each soil they coincided at K_{ex} values >2 meq kg^{-1}. At lower levels of K_{ex}, calcium chloride releases more K than ammonium acetate for the same $\Delta G_{K,Ca+Mg}$ value, probably because the calcium ion opens up interlayer spaces at the edges of the 2:1 clay minerals.

3.2.3 Potassium desorption isotherms

Figure 3.5 shows K desorption isotherms for Andover, Bromyard, Hanslope, Newport and Worcester soils. The curves for all but the Newport soil were divided (by eye) into two linear parts with different slopes defining two buffering capacities. Thus when $\Delta G_{K,Ca+Mg}$ decreased below a certain value, the K buffering capacity of the soil increased sharply, i.e. a large amount of K was released for a small change in $\Delta G_{K,Ca+Mg}$. Ehlers et. al. (1967) also observed this in loess soils.

The general accepted model of soil K equilibria, presented by Talibudeen (1972), suggests critical soil solution concentrations of

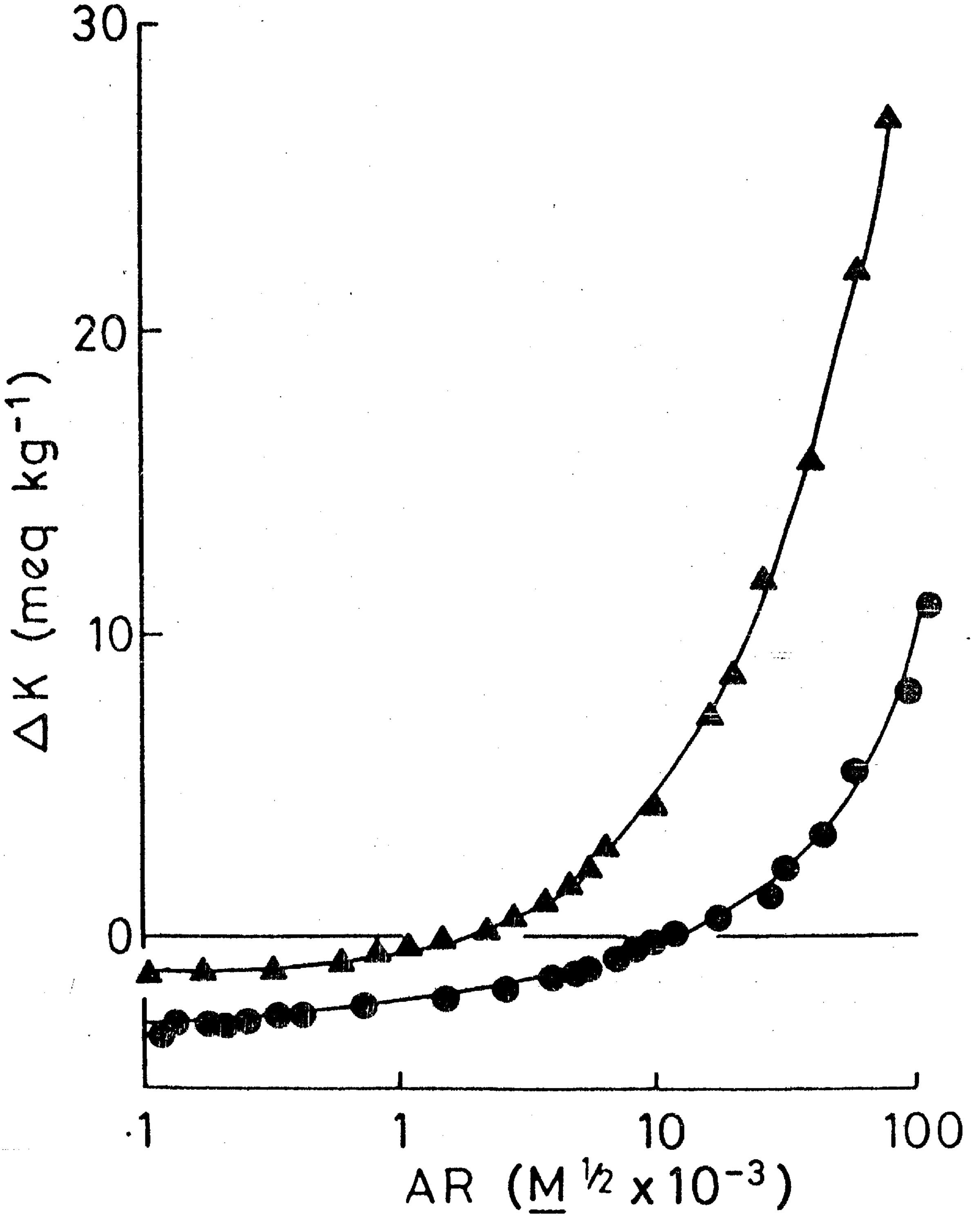


Figure 3.3 ΔK:(log AR) curves for Batcombe and Newport soils

(▲ Batcombe; ● Newport(1)).

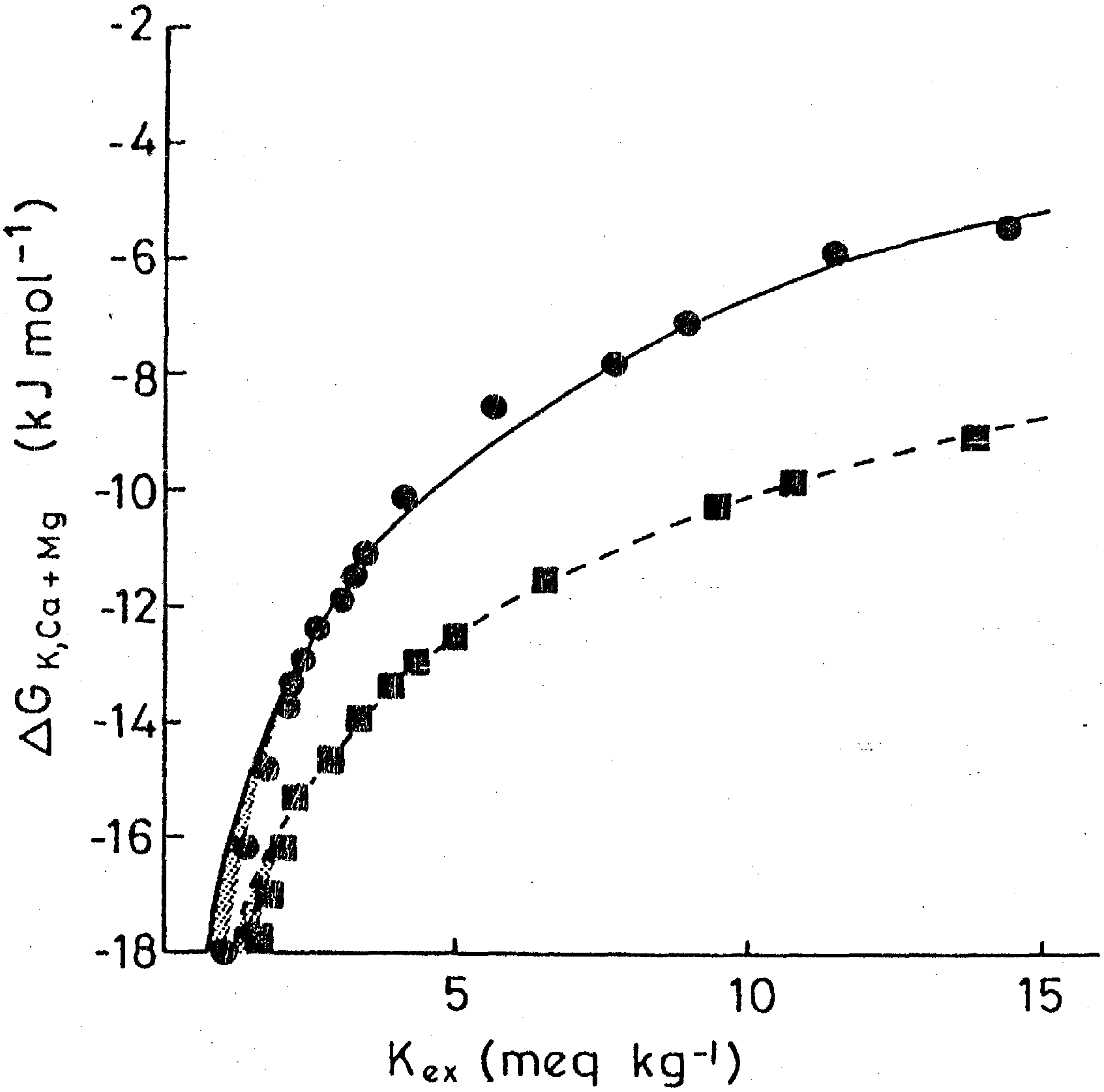


Figure 3.4 A comparison of $\Delta K : \Delta G_{K,Ca+Mg}$ and $K_{ex} : \Delta G_{K,Ca+Mg}$ curves for Batcombe and Newport soils (■ Batcombe; ● Newport(1)).

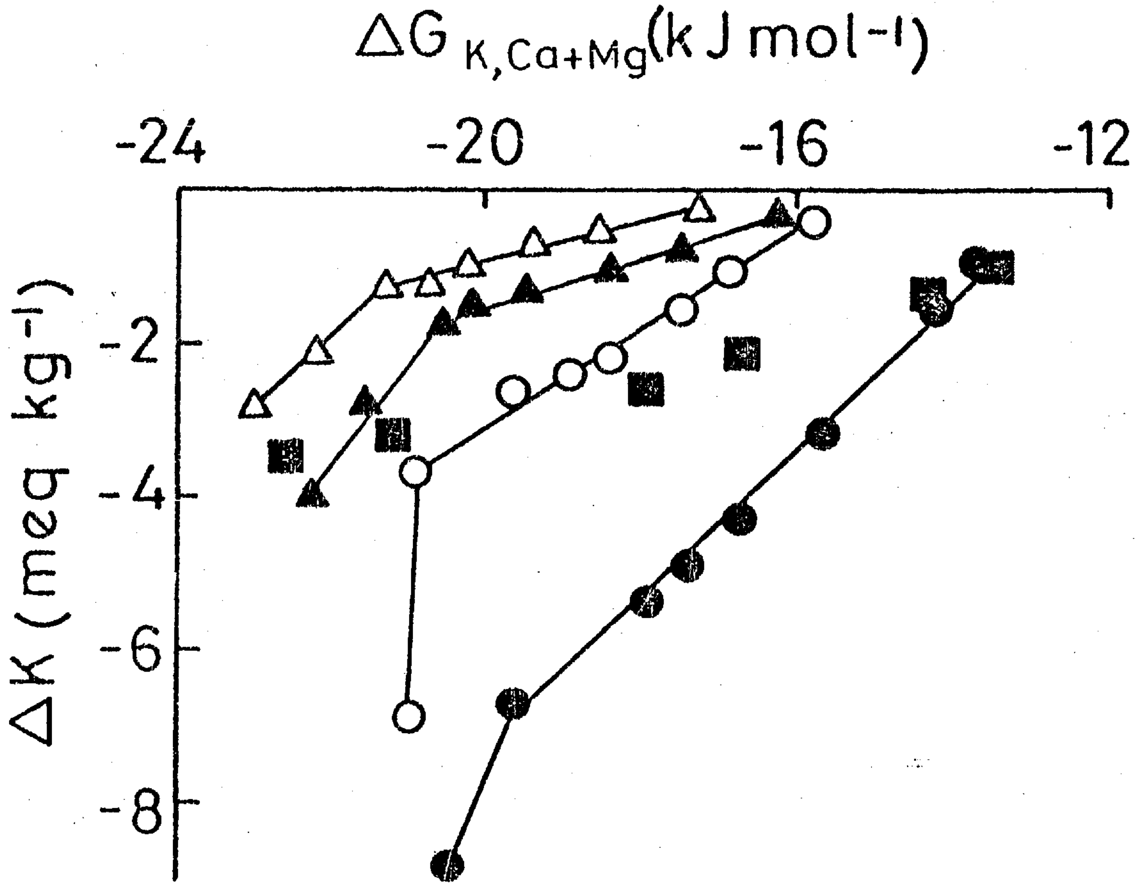


Figure 3.5 Potassium desorption isotherms for the soils (Δ Andover; ▲ Bromyard; ○ Hanslope; ■ Newport(1); ● Worcester).

K which induce transfer of K between phases (Figure 3.6). This implies that, below a threshold potential of the surface (rapidly exchanging) K, or above a threshold potential of the peripheral or slowly exchanging K, a potential gradient exists so that K diffuses out into the surface phase. Thus a minimum K saturation of the surface exchange sites and a minimum potential of the surface K are maintained.

Applying this concept to the present results suggests that the observed abrupt increase in buffer capacity is caused by the release of peripheral K and that the $\Delta G_{K,Ca+Mg}$ value at which the increase occurs is the threshold K potential discussed above. For the Andover, Bromyard, Hanslope and Worcester soils the observed threshold $\Delta G_{K,Ca+Mg}$ values were -21.4, -20.6, -20.9 and -19.7 kJ mol^{-1} respectively; that for the Newport soil must be below the range measured.

3.2.4 Summary of K-(Ca+Mg) exchange properties of the soils

The Worcester soil is calcareous, highly micaceous and therefore very K selective. However at K_{ex} values >6 meq kg^{-1} it does not have the lowest $\Delta G_{K,Ca+Mg}$ of the soils because of its low CEC. The Bromyard soil is also micaceous but is acid so it's K selective sites are occupied by Al ions and only less K selective sites are available for K-(Ca+Mg) exchange. The K-(Ca+Mg) exchange properties of the Bromyard soil are therefore similar to those of the Hanslope, Batcombe and Andover soils whose predominantly smectitic clay fractions have fewer K-selective sites. The high CEC of the Hanslope soil gives it the lowest $\Delta G_{K,Ca+Mg}$ values over most of the $\Delta G_{K,Ca+Mg}:K_{ex}$ isotherm. The Newport soils have low clay contents, dominated by kaolinitic minerals which have few K-selective sites, and low CEC-s. They therefore

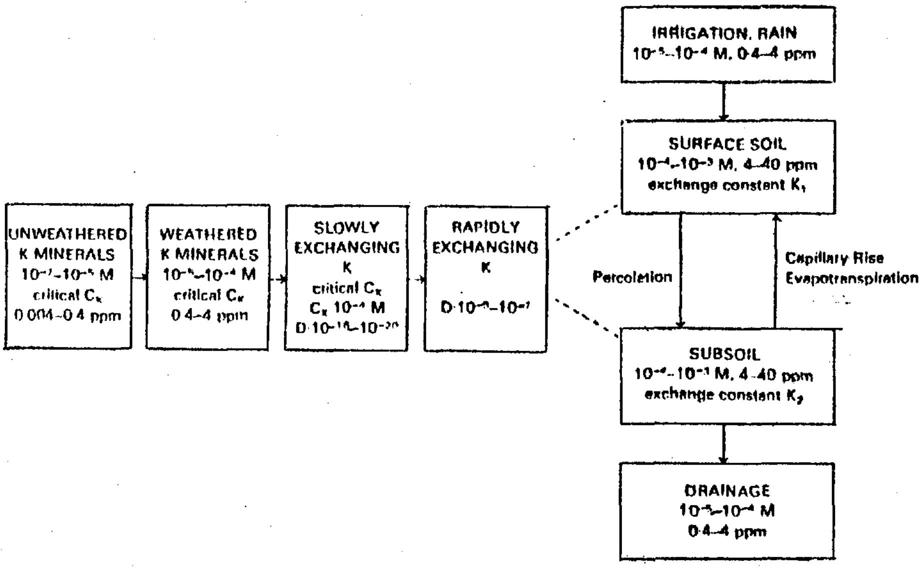


Figure 3.6 Equilibria and transport of potassium in soil (from Talibudeen, 1972).

have the highest $\Delta G_{K,Ca+Mg}$ values of all the soils for any given % K saturation or K_{ex} value.

3.3 The mineralisation of nitrogen - results and discussion (see General Methods, Section 2.2)

The incubation test was conducted to measure the amount of nitrogen likely to be mineralised during crop growth in the pot experiments, and investigate the variation between the soils in amounts mineralised compared to the amount added as basal fertiliser.

Table 3.5 shows the total inorganic N ($NO_3^- + NO_2^- + NH_4^+$) in the soils initially and after 83 days incubation, with and without 314 ppm of N added as $Ca(NO_3)_2$. The latter treatment was included to ascertain whether $Ca(NO_3)_2$-N added as fertiliser affects the mineralisation of native N. The results show that the addition did not have any consistent effect on the quantity of N mineralised.

With the Andover soil, the soil weight used was 10 g (compared with 15 g for the other soils) because enough soil was not available. However, the volumes of water and $Ca(NO_3)_2$ solution added were not reduced proportionally, so that the soil moisture content was near water holding capacity, hence the soil was probably anaerobic during part of the incubation period. So although the Andover soil had the highest total N the initial inorganic N contents, the nett accumulation of mineral N was lower in the treated and untreated soil, than in the other soils with the exception of the NO_3^--treated Newport soil, where mineral N was inexplicably lost.

Figure 3.7 shows the progression of N mineralisation, with time, without added $Ca(NO_3)_2$. The rate of mineralisation declined with time. In all soils the NH_4^+ concentration rose to a maximum during the first

Table 3.5 The mineralisation of N during 83 days incubation at 20°C

N added as $Ca(NO_3)_2$ (ppm):			0			314		
Soil Series	Initial Total N		Inorganic N (ppm)			Inorganic N (ppm)		
	(%)	(ppm)	Initial	Final	Released	Initial	Final	Released
Andover	0.37	3700	96	136	40	567*	614	47
Batcombe	0.17	1700	20	88	68	334	420	86
Bromyard	0.17	1700	48	138	90	362	455	92
Hanslope	0.21	2100	13	96	83	327	425	98
Newport(1)	0.15	1500	12	67	56	326	299	-27
Worcester	0.19	1900	18	107	89	332	436	104

* 471 ppm N added

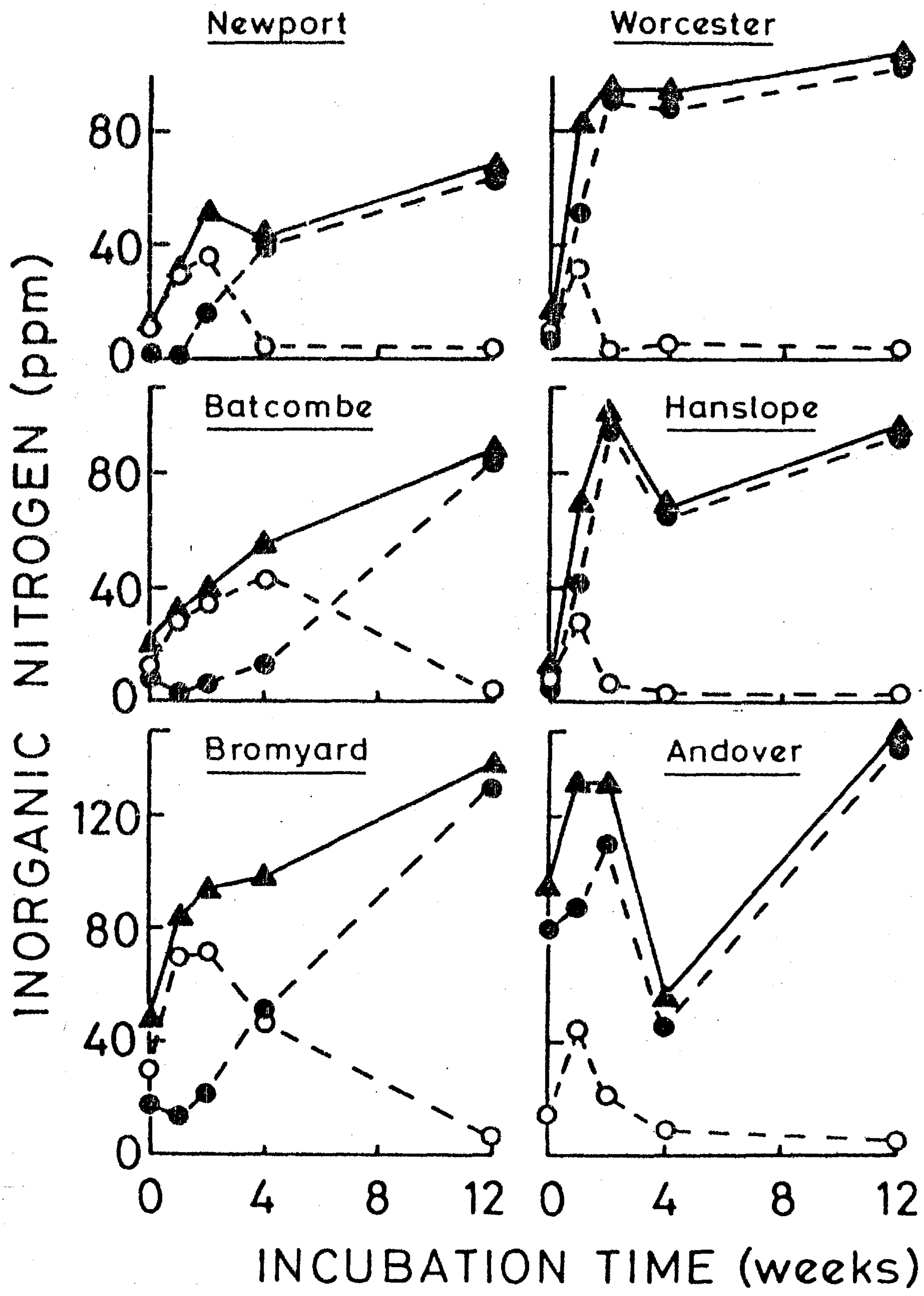


Figure 3.7 The dynamics of N mineralisation in the soils

(○ NH_4^+-N; ● NO_3^--N; ▲ (NO_3^- + NH_4^+)-N).

four weeks and then declined as it was nitrified, so most of the mineral N measured after 12 weeks incubation was nitrate. The initial accumulation of NH_4-N was greater than that of NO_3-N in the acid soils but not in the neutral and calcareous soils. This confirms the findings of other workers that nitrification is rate-limited by low pH.

It was concluded that differences in the amounts of N likely to be mineralised in the soils, during crop growth in pots would be small compared to the amount to be added as fertiliser before (314 ppm) and during (150 ppm weekly after the second week) the experiments.

4. CRITICAL POTASSIUM POTENTIALS FOR RYEGRASS AND FESCUE ON CONTRASTING SOILS

4.1 Introduction

In flowing solution culture, K concentration governs the supply of K to the plant roots and for a given set of environmental conditions, there must be a single specific relationship between yield and the K concentration of the solution at a given stage of growth of a particular crop. This relationship would enable exhaustion, optimum and toxic K concentrations to be defined for the crop at any stage of development. Conversion of these to energy units (Equation 1.27) gives the corresponding unique critical K potentials for the crop. For reasons already discussed (Section 1.3), the potential of K in soils is generally taken as $\Delta G_{K,Ca+Mg}$. If $\Delta G_{K,Ca+Mg}$ has the same relevance to the plant in soil as does RT ln a_{K+} in solution culture, critical values as described above should be obtainable for any plant and, given equal levels of other nutrients and other edaphic limiting factors, these should be independent of soil type.

The following experiments were designed to evaluate critical K potentials for two grasses, perennial ryegrass (Lolium perenne var. S.23) and creeping red fescue (Festuca rubra genuina) on contrasting soils and thus test this hypothesis under controlled conditions.

4.2 Methods

Pot experiments of design A and B were conducted with ryegrass and fescue. Soils were prepared, as described in Section 2.3, in Experiment A to give eight K levels on six soil series (Andover, Batcombe, Bromyard, Hanslope, Newport(1) and Worcester) and in Experiment B to give twenty K levels on two soil series (Batcombe and Newport(1)). Details of the amounts of KNO_3, K_2SO_4, $Ca(NO_3)_2$, $Mg(NO_3)_2$ and $CaSO_4$ added to the soils are given in Appendix 1. The treatments were in duplicate. In each case individual experiments for each of the two grasses were conducted sequentially because of limited space in the constant environment cabinets.

After preparation of the soil, 350 mg of ryegrass seed or 300 mg of fescue seed was sown in each pot, giving approximately 250 seeds per pot. The soil surface was covered with 30 g of black alkathene beads. Water was added to saucers to bring the soil to 25% moisture. The duplicate pots were divided between two Saxcil Growth Cabinets, randomised in each and allowed to germinate in darkness at 20°C. This took about 5 days, after which the cabinets were set to the conditions described in Section 2. After two weeks, 15 ml of a solution containing ammonium nitrate (0.25% N), diammonium phosphate (0.0083% P) and magnesium nitrate (0.0083% Mg), was added to each pot weekly. This supplied 150 mg N, 5 mg P and 5 mg Mg per kg soil per week.

The grass was cut, 1 cm above the soil surface, 30, 58 and 86 days after germination in Experiment A, and 14 and 40 days after germination in Experiment B. The smaller growth period in Experiment B was designed to avoid effects produced by shortages of basal nutrients, particularly P and S (see later). Also, the 2 week period for the first cut was chosen to lessen its effect on cumulative yield because of anomalies sometimes produced by uneven germination. The clippings were dried, weighed and analysed for K and P, and Ca and Mg in Experiment B.

To determine K in the plants from the seed, the K content of seeds, dried at 80°C, was also determined.

The soil pH from alternate K treatments (K levels nos. 1, 3, 5, and 7) of the ryegrass part of Experiment A was measured in the 0.01 M $CaCl_2$ equilibrates of soil samples taken before and after cropping.

4.3 Results

4.3.1 Calculation of mean potassium potential values ($\overline{\Delta G}_{K,Ca+Mg}$) for periods of growth

For each K treatment, mean AR values were calculated for the growth periods, from germination to the first cut ($\overline{AR}_1$), to the second cut ($\overline{AR}_2$) and, in Experiment A, to the third cut ($\overline{AR}_3$).

In Experiment A, the 3 periods of growth were of approximately equal length, therefore the mean AR values for each period were weighted equally, thus:

$$\overline{AR}_1 = (AR' + AR'')/2 \qquad \text{.....(4.1)}$$

$$\overline{AR}_2 = ((AR' + AR'')/2 + (AR'' + AR''')/2)/2 \qquad \text{.....(4.2)}$$

$$\overline{AR}_3 = ((AR' + AR'')/2 + (AR'' + AR''')/2 + (AR''' + AR'''')/2)/3 \qquad \text{.....(4.3)}$$

where AR', AR'', AR''' and AR'''' are the AR values before sowing and after the 1st, 2nd and 3rd cuts respectively. Corresponding mean free energy values were calculated from these:

$$\overline{\Delta G}_{K,Ca+Mg} = RT \ln \overline{AR} \qquad .....(4.4)$$

In Experiment B, the mean AR value for the total period of growth ($\overline{AR}_2$) was calculated from the mean values for the individual growth periods weighted for their respective durations. Thus,

$$\overline{AR}_2 = 14(AR' + AR'')/40 + 26(AR'' + AR''')/40 \qquad .....(4.5)$$

The corresponding value of $\overline{\Delta G}_{K,Ca+Mg}$ was calculated using Equation 4.4.

4.3.2 Grass yields on 6 soils (Experiment A)

4.3.2.1 Relationship with potassium uptake

Cumulative yields and K uptakes were determined at each harvest. Coefficients of variation (=100 x (residual mean square)$^{\frac{1}{2}}$/ grand mean) for these data are given in Table 4.1. These are low and demonstrate the precision of pot experiments carried out in a controlled environment. For both species they are highest after the first cut, due to slightly uneven germination.

Table 4.2 gives cumulative yields after the final cut. Without added K (K level 1) yields vary greatly between soils (12-46 g in ryegrass and 14-40 g in fescue). However, at a high level of added K, e.g. K level 6, there is little variation in yield between soils (41-48 g in ryegrass and 41-49 g in fescue). Therefore most of the variation in yield between soils without added K was due to differences in their levels of native K_{ex}.

Similarly Figures 4.1 and 4.2 suggest that a single relationship between dry matter yield and K uptake for each species describes the

Table 4.1 Coefficients of variation (%) of the cumulative yield and K uptake data of perennial ryegrass and creeping red fescue on six soils.

	Ryegrass			Fescue		
	weeks after germination					
	4	8	12	4	8	12
	%					
Yield	4.2	3.3	3.4	5.5	4.0	3.4
K uptake	5.3	3.7	3.4	6.6	3.6	4.4

Table 4.2 Final cumulative yields of perennial ryegrass and creeping red fescue on six soils.

soil	K level: 1	2	3	4	5	6	7	8
	Yield (g kg^{-1} soil)							
Ryegrass								
Andover	11.6	24.0	31.7	38.2	43.3	47.1	57.8	61.3
Batcombe	12.8	26.4	29.3	33.7	38.4	41.1	47.8	53.9
Bromyard	25.2	39.7	38.8	42.8	42.9	46.1	54.1	58.4
Hanslope	35.7	39.4	41.0	43.4	43.7	46.7	52.8	58.9
Newport	22.0	29.6	36.9	43.9	45.3	46.9	55.5	58.2
Worcester	46.0	45.1	46.0	46.7	46.2	48.2	54.4	54.5
				S.E.D. = 1.43				
Fescue								
Andover	14.4	26.3	31.7	37.8	40.6	44.4	51.1	55.4
Batcombe	16.5	27.1	31.6	35.0	37.4	40.6	45.2	49.7
Bromyard	23.9	33.1	37.7	39.6	41.4	44.2	49.4	51.6
Hanslope	34.9	39.5	40.9	41.3	43.0	43.8	49.4	54.5
Newport	24.2	32.8	37.3	41.9	46.2	48.9	55.7	52.9
Worcester	39.5	41.6	43.6	42.6	44.1	44.0	50.2	52.7
				S.E.D. = 1.37				

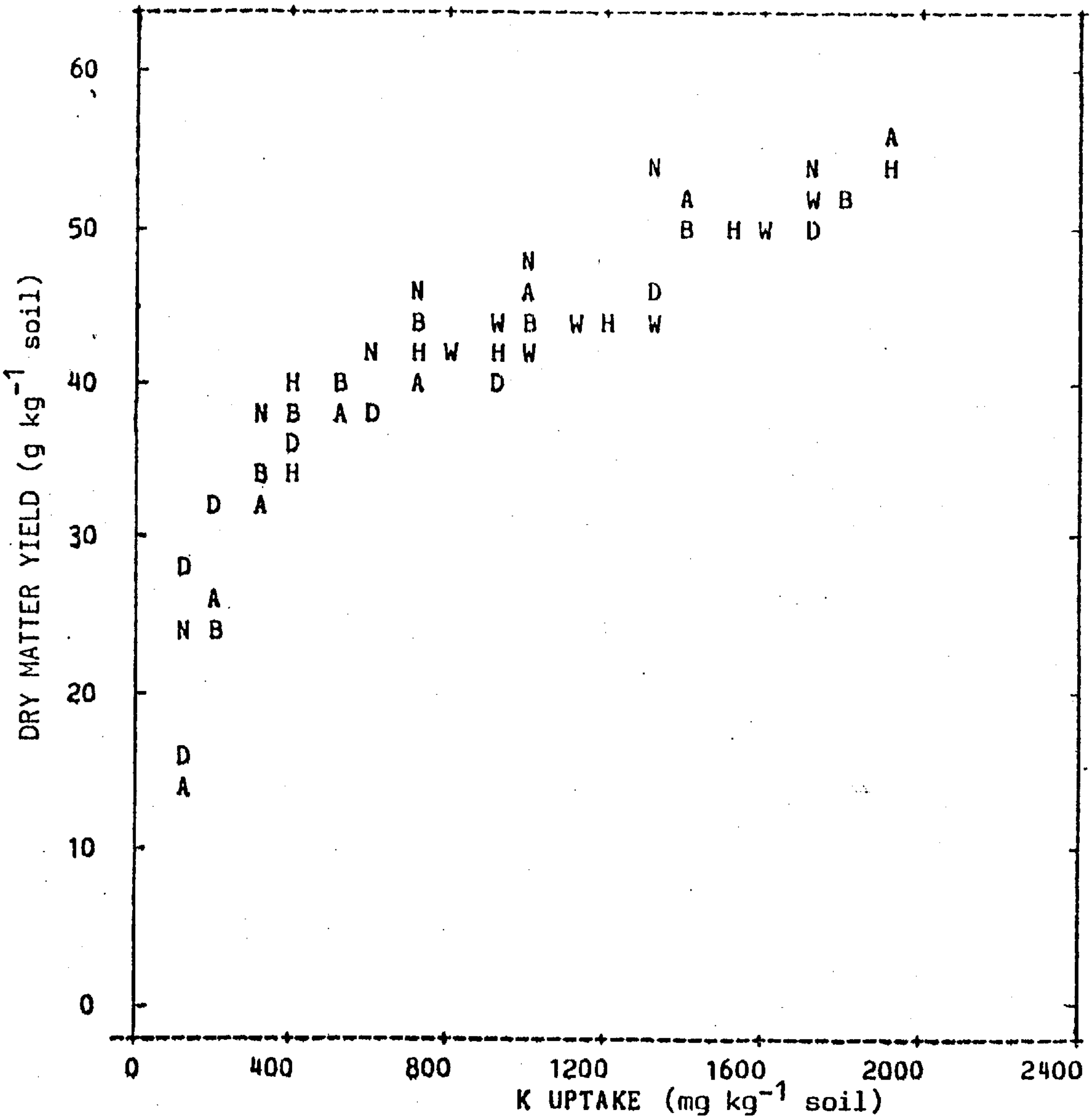


Figure 4.1 The relationship between cumulative dry matter yield and K uptake of perennial ryegrass after 12 weeks' growth (3 cuts) on 6 soils (A Andover; D Batcombe; B Bromyard; H Hanslope; N Newport(1); W Worcester).

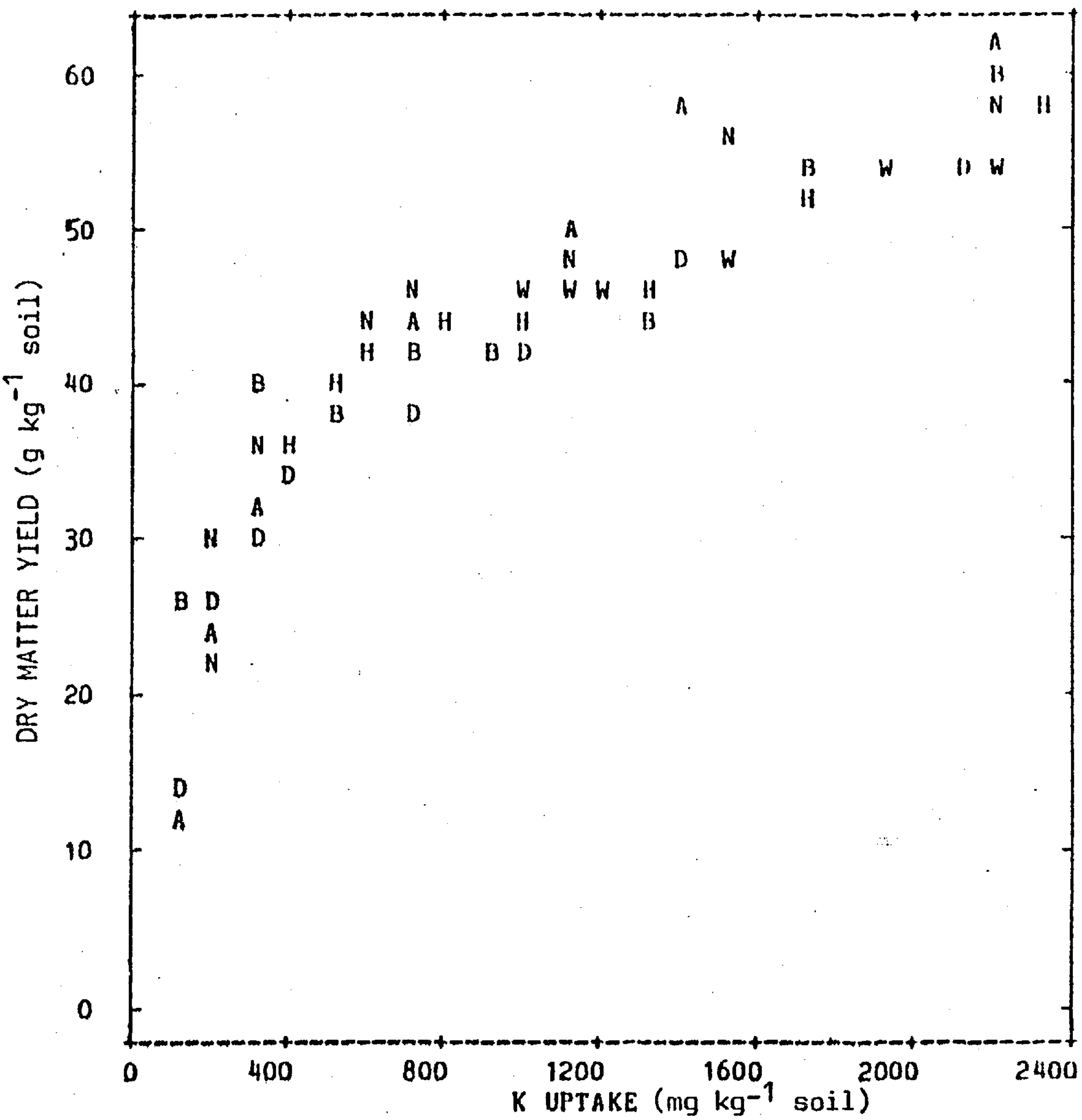


Figure 4.2 The relationship between cumulative dry matter yield and K uptake of creeping red fescue after 12 weeks' growth (3 cuts) on 6 soils (key: as for Figure 4.1).

results for the 6 soils adequately. However, these plots show that, on each soil, the yields increased with K uptake toward an asymptotic maximum corresponding to a K uptake of between 1200 and 1600 mg kg^{-1} soil.

4.3.2.2 Effect of the sulphate status of the soil

At the two highest K levels, yields responded further, very markedly, to increased K uptake. This effect can perhaps be seen best in the case of the Worcester soil which gave no significant yield response to K except at these two highest K levels. The additional K at these two high levels was given as K_2SO_4 and the extra sulphate was not completely balanced in the lower K treatments with $CaSO_4$ (see Appendix 1). So it is possible that the larger yields were responses to S.

Because this effect was most pronounced with the Worcester and Hanslope soils, the third cut of ryegrass on these soils was analysed for S. The results are given in Table 4.3 and show that the grass from the two high K treatments on both soils was considerably richer in S than was that from lower K treatments.

McNaught and Chrisstoffels (1961) found optimum sulphur contents of 0.26 and 0.30% for two mixtures of grasses, both including ryegrass. This suggests that, in the last period of growth, the grass in the lower K treatments was S deficient, although there were no visible symptoms to indicate this. The effect was less marked on the yields of fescue, which is therefore perhaps less demanding of S than is ryegrass. Also the response mainly occurred after at least 8 weeks growth. As a result of these findings the two highest K treatments were disregarded in subsequent analyses of the yield data.

Table 4.3 % S in the third cut of ryegrass grown on Hanslope and Worcester series soils (mean values of duplicates).

K Treatment	Hanslope	Worcester
	% S	
1	.127	.043
2	.104	.048
3	.071	.045
4	.058	.049
5	.084	.041
6	.055	.040
7	.279	.156
8	.550	.376

4.3.3 Critical $\Delta G_{K,Ca+Mg}$ values for dry matter yields of perennial ryegrass and creeping red fescue on 6 soils (Experiment A)

4.3.3.1 Evaluation

Figures 4.3 and 4.4 show cumulative yield response curves, of ryegrass and fescue respectively, to increasing mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for each growth period. Responses vary from soil to soil. Little or no response was obtained for ryegrass or fescue on the Worcester soil (Figure 4.3f). This suggests that the rate of release from the peripheral K in the soil (Talibudeen, et al., 1978), and thus it's rate of supply to the roots was adequate because maximum yield was attained at very low soil K potentials.

Second degree polynomials were fitted to the data from the other five soils. The corresponding coefficients and the percentage of the variance that they accounted for are given in Table 4.4. The $\overline{\Delta G}_{K,Ca+Mg}$ value corresponding to the yield maximum is taken as the optimum K potential (ΔG_{opt}) for each growth period on each soil. Potassium exhaustion potentials (ΔG_{exh}) were derived by extrapolating the fitted response curves to zero yield.

4.3.3.2 ΔG_{opt} and the interaction with soil type

The ΔG_{opt} values are given with the corresponding yields, calculated from the fitted equations, in Table 4.5. For the various cuts of each species, maximum yields were similar, except those of the fescue on the Newport soil which were higher throughout, possibly because of its higher phosphate status.

Table 4.5 shows that in these small pots containing 200 g soil, ΔG_{opt} varied more with soil type than with species. With ryegrass,

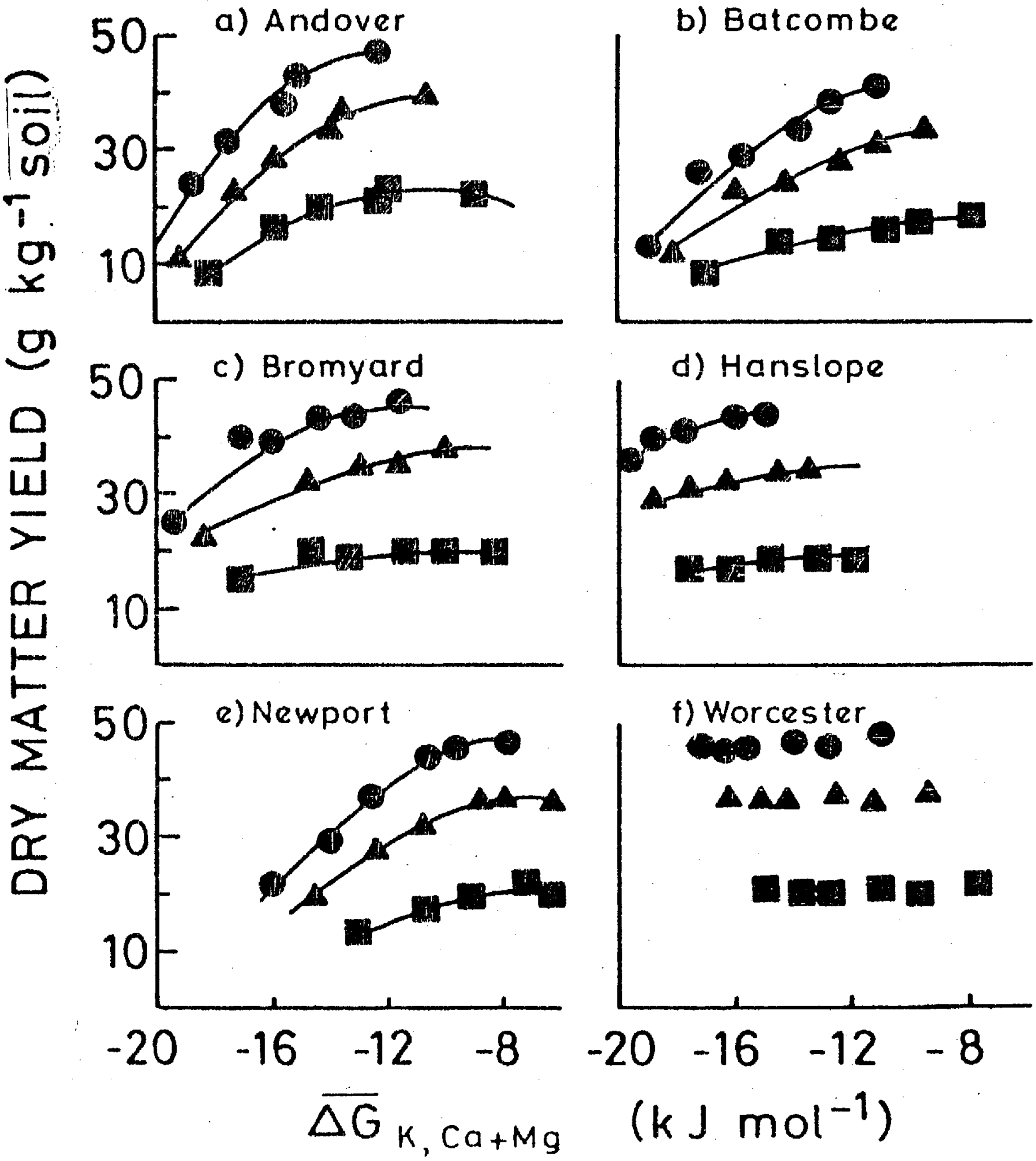


Figure 4.3 The relationship between dry matter yield of perennial ryegrass and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4, 8 and 12 weeks' growth on 6 soils (■ 4 weeks'; ▲ 8 weeks'; ● 12 weeks').

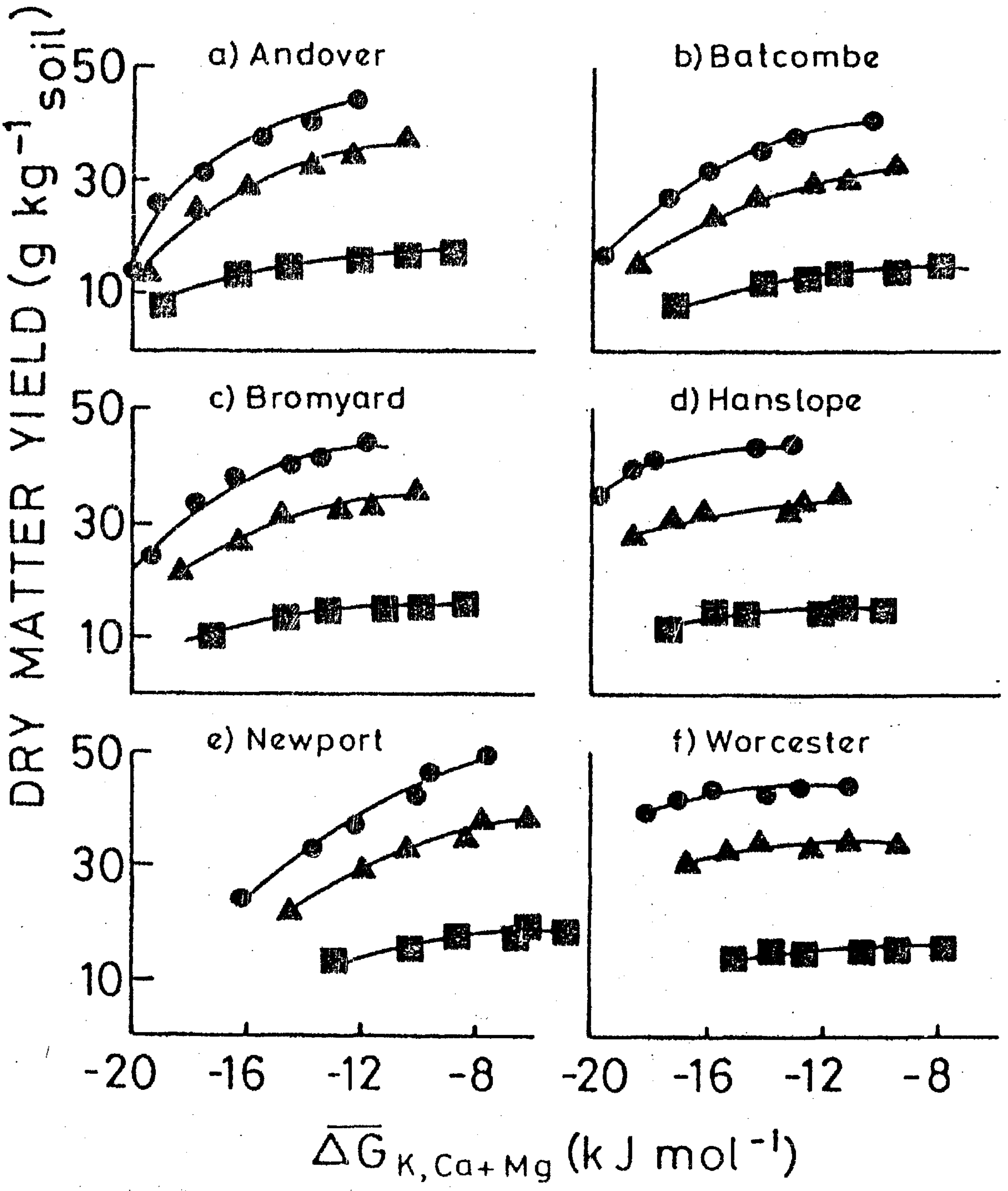


Figure 4.4 The relationship between dry matter yield of creeping red fescue and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4, 8 and 12 weeks' growth on 6 soils (key: as for Figure 4.3).

Table 4.4 Second degree polynomial coefficients relating cumulative yields of perennial ryegrass and creeping red fescue to mean soil K potentials ($\overline{\Delta G}_{K,Ca+Mg}$) for respective periods of growth ($y = a + bx + cx^2$).

Soil Series	Cut No.	Ryegrass				Fescue			
		a	b	c	% Variance accounted for	a	b	c	% Variance accounted for
Andover	1	-5.45	-5.38	-0.254	98.1	8.13	-1.89	-0.098	94.4
"	2	2.28	-7.21	-0.349	98.4	4.95	-5.74	-0.266	95.2
"	3	-34.22	-13.30	-0.545	98.1	-8.15	-8.69	-0.366	96.4
Batcombe	1	17.65	-0.63	-0.066	93.9	11.65	-0.90	-0.064	98.1
"	2	33.53	-1.23	-0.133	99.4	27.95	-1.65	-0.124	98.2
"	3	21.04	-4.93	-0.281	98.6	18.65	-4.58	-0.238	98.7
Bromyard	1	16.63	-0.95	-0.060	95.8	10.68	-1.22	-0.071	96.5
"	2	25.44	-2.76	-0.157	96.0	20.62	-3.05	-0.163	94.8
"	3	14.13	-5.85	-0.270	98.2	-3.85	-7.87	-0.329	94.6
Hanslope	1	7.69	-1.77	-0.071	59.3	-2.72	-2.99	-0.123	78.8
"	2	15.37	-3.22	-0.133	98.6	26.58	-1.54	-0.077	74.8
"	3	-65.11	-14.02	-0.452	94.6	-18.68	-8.44	-0.288	76.7
Newport	1	11.66	-2.68	-0.196	95.0	14.70	-1.32	-0.114	89.7
"	2	25.63	-3.49	-0.267	98.9	34.65	-1.60	-0.171	95.9
"	3	38.76	-3.29	-0.274	98.5	53.89	-0.47	-0.146	97.4

Table 4.5 Maximum yields of perennial ryegrass and creeping red fescue and corresponding optimum K potentials (ΔG_{opt}) derived from second degree polynomials.

Soil Series	ΔG_{opt} (kJ mol^{-1})			Maximum Yield (of kg^{-1} soil)		
No. of weeks growth	4	8	12	4	8	12
Ryegrass						
Andover	-10.59	-10.32	-12.20	23.0	39.5	47.0
Batcombe	-4.72	-7.28	-8.75	19.2	36.4	42.6
Bromyard	-7.96	-8.79	-10.81	20.4	37.6	45.7
Hanslope	-12.47	-12.05	-15.52	18.7	34.8	43.7
Newport	-6.82	-6.50	-5.99	21.1	37.0	48.6
Fescue						
Andover	-9.59	-10.79	-11.87	17.2	35.9	43.4
Batcombe	-7.05	-6.67	-9.62	14.8	33.4	40.7
Bromyard	-8.62	-9.38	-11.95	16.0	34.9	43.2
Hanslope	-12.41	-9.98	-14.65	15.4	34.3	43.2
Newport	-5.78	-4.69	-5.13	18.8	39.3	55.1

for all the soils except Batcombe, ΔG_{opt} values were similar for 4 and 8 weeks growth and generally lower (more negative) for 12 weeks. The former observation was less true for fescue, but again the ΔG_{opt} values for the 6 soils were lowest after 12 weeks. This was probably because yields were limited and their K requirements reduced, by depleted supplies of some basal nutrients in the third period of growth.

ΔG_{opt} decreased with increasing CEC of the soils; the correlation coefficients for ryegrass and fescue were 0.86 and 0.88 respectively ($P<0.001$ in both cases). The regressions fitted to the relationships were similar for both grasses (Figure 4.5); for ryegrass,

$$\Delta G_{opt} = -0.11(\pm 1.60) - 0.059(\pm 0.010)\ \mathrm{CEC} \qquad \text{.....(4.6)}$$

and for fescue,

$$\Delta G_{opt} = 1.03(\pm 1.59) - 0.065(\pm 0.010)\ \mathrm{CEC} \qquad \text{.....(4.7)}$$

So, with the 'crop:soil ratio' used here, the smaller the CEC the greater was the K potential required for maximum yield. Earlier (Section 3.2.2) it was also observed that the smaller the CEC, the greater was the K potential corresponding to any given level of K_{ex}. These relationships suggest that, at these crop: soil ratios yield is controlled more by the level of K_{ex} than the free energy of K-(Ca+Mg) exchange of the soil.

An alternative explanation for the variation in ΔG_{opt} between soils is that it was produced by different rates of release of

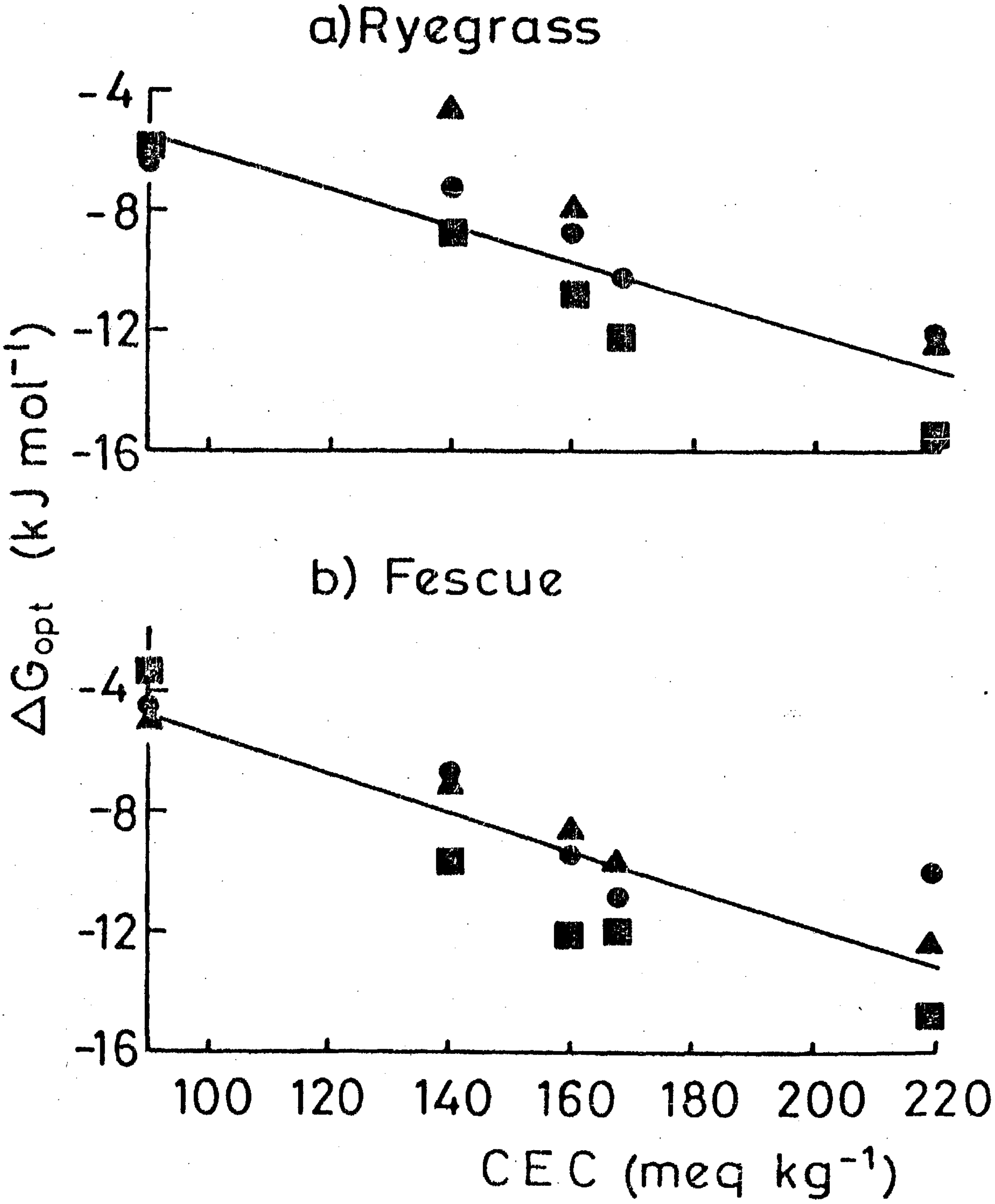


Figure 4.5 The effect of the CEC of the soil on the optimum K potential ($\Delta G_{opt.}$) for a) perennial ryegrass and b) creeping red fescue (key: as for Figure 4.3).

non-exchangeable K from the soils. These would be controlled largely by the amounts of 2:1 layer silicates in the soils. Only data for the mineralogy of the clay fraction is available, but expressing the 2:1 mineral content of the clay fraction as a percentage in the whole soil (Table 4.6) provides a basis for comparisons. ΔG_{opt} correlated better with the CEC than with this 2:1 mineral percentage (in the latter correlation $r = -0.69$ and -0.76 for ryegrass and fescue respectively).

4.3.3.3 ΔG_{exh}

The ΔG_{exh} values, obtained by extrapolation, are given in Table 4.7. Although difficult to determine experimentally, they provide a basis for comparisons between soils. For both grasses, they varied considerably between the 5 soils. The mean values for the soils decreased in the order Newport > Batcombe and Andover > Bromyard > Hanslope in both cases.

For the Andover and Batcombe soils, ΔG_{exh} values were very similar and did not change significantly with the period of growth. Those for fescue were lower than those for ryegrass. ΔG_{exh} values on the Bromyard soil also varied little with time or species, except for the lower value for the 4 weeks' growth of ryegrass. With the Newport soil, ΔG_{exh} decreased with time. The very low ΔG_{exh} values for the three growth periods of both grasses on the Hanslope soil suggest a significant rate of release of non-exchangeable K.

The range of ΔG_{exh} values obtained (-17.5 to -28.2 and -18.5 to -31.0 kJ mol^{-1} for ryegrass and fescue respectively) was of a similar order to that obtained by Fergus <u>et al</u>. (1972) for setaria

Table 4.6 The 2:1 layer silicate mineral content of the clay fraction expressed as a percentage of the whole soil.

Soil Series	2:1 silicates (%)
Andover	14
Batcombe	16
Bromyard	23
Hanslope	29
Newport	7
Worcester	32

Table 4.7 Exhaustion K potentials (ΔG_{exh}) extrapolated from yield response curves for perennial ryegrass and creeping red fescue, on six soils.

Soil Series	No. of weeks growth			
	4	8	12	Mean
	ΔG_{exh} kJ mol^{-1}			
Ryegrass				
Andover	-20.1	-21.0	-21.5	-20.9
Batcombe	-21.6	-21.1	-21.1	-21.3
Bromyard	-26.4	-24.3	-23.9	-24.9
Hanslope	-28.7	-28.2	-25.3	-27.4
Newport	-17.5	-18.9	-20.1	-18.8
Mean	-22.9	-22.7	-22.4	-22.7
Fescue				
Andover	-22.8	-22.4	-22.8	-22.7
Batcombe	-22.3	-23.1	-22.7	-22.7
Bromyard	-23.9	-24.0	-23.4	-23.8
Hanslope	-24.2	-31.0	-26.9	-27.4
Newport	-18.5	-19.7	-21.0	-19.7
Mean	-22.3	-24.0	-23.4	-23.3

by exhaustive cropping of 10 soils (-17 to -29 kJ mol^{-1}), although their soils ranged from 3 to 63% clay, a greater range than examined here.

The constant ΔG_{exh} values for the three growth periods of ryegrass on the Batcombe soil were higher (mean -21.3 kJ mol^{-1}) than that derived by Addiscott (-23.4 kJ mol^{-1}; 1970a) and that determined by exhaustive cropping (-23.3 kJ mol^{-1}; Addiscott and Johnston, 1975). These, however, refer to 'zero' K uptake rather than to zero yield. It is possible that, at very low K potentials, the yield response curve becomes asymptotic to the $\overline{\Delta G}_{K,Ca+Mg}$ axis so that extrapolation of the quadratic response curve over-estimates ΔG_{exh}. For reasonable yield production though, and for maximum response to increasing K potential, the values presented here are meaningful.

4.3.4 Derivation of critical $\Delta G_{K,Ca+Mg}$ values for perennial ryegrass and creeping red fescue on 2 soils (Experiment B)

More extensive data were obtained in this experiment than in Experiment A, which made it possible to fit more precise response curves. Yields from the first cut (2 weeks after germination) were not considered separately but only as part of the cumulative yield, so as to minimise the variation produced by uneven germination. Coefficients of variation for cumulative yields of ryegrass and fescue were 3.4 and 7.7% respectively.

The yield response curves to the mean K potential for the two growth periods (see Section 4.3.1), are shown in Figure 4.6. The third degree polynomials (as shown) fitted the data better than

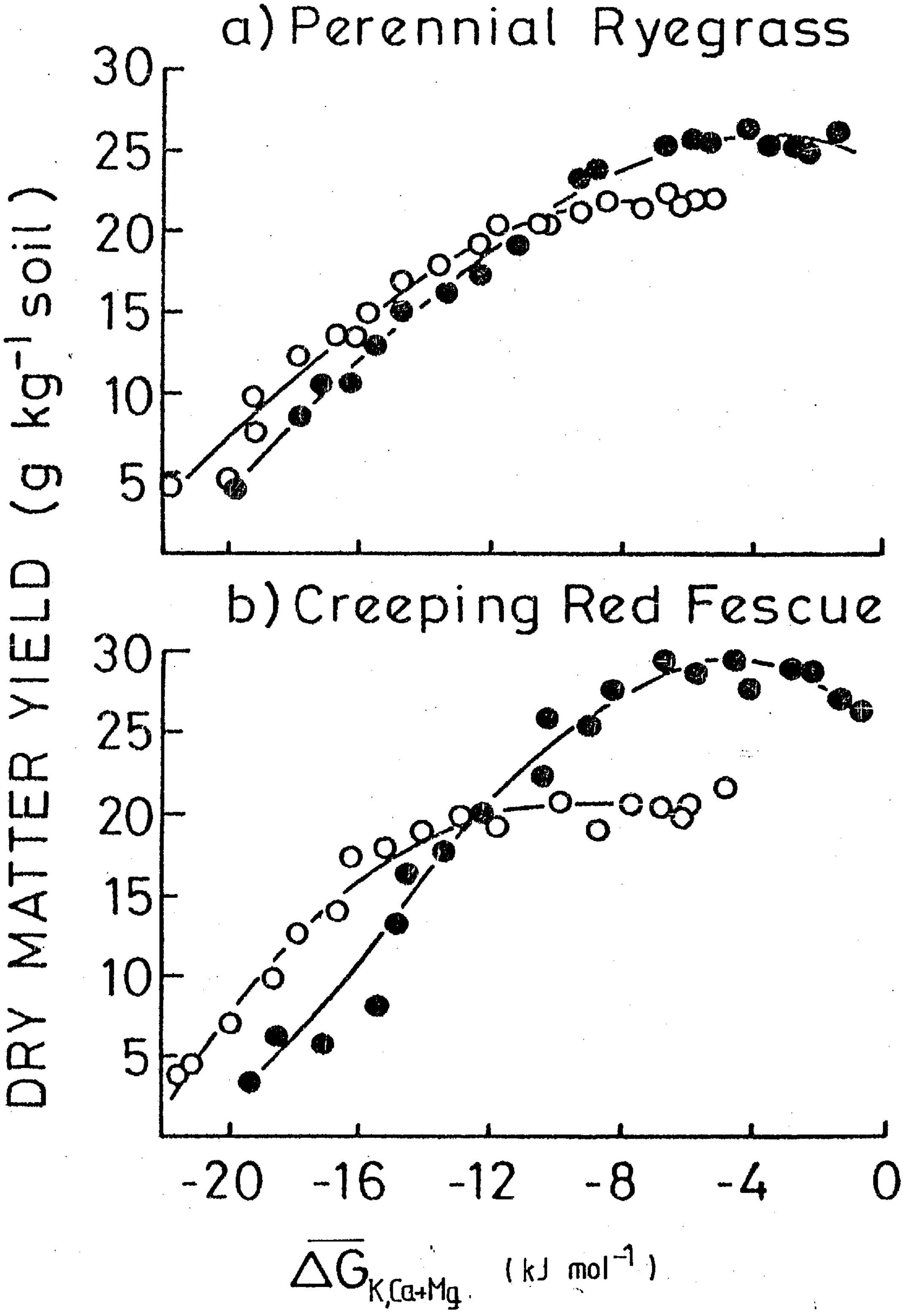


Figure 4.6 The relationship between dry matter yields of a) perennial ryegrass and b) creeping red fescue and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 6 weeks' growth on Batcombe and Newport soils (○ Batcombe; ● Newport).

second degree polynomials, so the former were used to derive ΔG_{opt} values as described in Section 4.3.2. However, to avoid possible anomalies caused by extrapolating 'third degree' polynomials (i.e. tendency to a minimum at low $\overline{\Delta G}_{K,Ca+Mg}$ values), ΔG_{exh} values were derived from the second degree polynomials as in Experiment A. Polynomial coefficients are given in Table 4.8 and ΔG_{opt} and ΔG_{exh} values in Table 4.9.

As in Experiment A, there was a greater difference in ΔG_{opt} between soils than between species, the light-textured Newport soil giving less negative values than the heavier-textured Batcombe soil. The fescue had more negative ΔG_{opt} values than the ryegrass on both soils, suggesting that the fescue has a lower K requirement. There was less variation between soils in the ΔG_{exh} values obtained than in ΔG_{opt} although, as with ΔG_{opt} those from the Batcombe soil gave the lowest and almost equal values for the two species. Ryegrass gave only a slightly lower ΔG_{exh} value than fescue on the Newport soil so it can be concluded that the two grasses have approximately equal minimum K potential requirements for yield production.

In 2 of the 4 cases (ryegrass on Batcombe and fescue on Newport soil) ΔG_{opt} values from Experiment B were the same as those from Experiment A after two cuts. However the total growth period after two cuts was 2 weeks longer in Experiment A and the yield much greater. Also, because of the more extensive data, values obtained in Experiment B must be considered more reliable.

Table 4.8 Second and Third degree polynomial coefficients relating cumulative yields of perennial ryegrass and creeping red fescue to mean soil K potentials($\overline{\Delta G}_{K,Ca+Mg}$) for the period of growth on Batcombe and Newport series soils.

	Species	Soil	a	b	c	d	% Variance accounted for
Degree 2, $y = a+bx + cx^2$							
	Perennial ryegrass	Batcombe	18.8	-1.01	-0.081	-	97.6
	"	Newport	25.7	-0.27	-0.070	-	98.7
	Creeping red fescue	Batcombe	14.0	-1.75	-0.103	-	96.5
	"	Newport	27.1	-0.85	-0.114	-	95.0
Degree 3, $y = a + bx + ox^2 + dx^3$							
	Perennial ryegrass	Batcombe	15.7	-1.89	-0.152	-0.0018	97.5
	"	Newport	24.0	-1.08	-0.162	-0.0029	99.0
	Creeping red fescue	Batcombe	15.1	-1.13	-0.037	-0.0019	98.3
	"	Newport	24.3	-2.40	-0.299	-0.0061	97.8

Table 4.9 Maximum yields, optimum K potentials (ΔG_{opt}) and exhaustion K potentials (ΔG_{exh}) of perennial ryegrass and creeping red fescue on Batcombe and Newport series soils, as derived from third degree polynomials.

Species	Soil	Maximum yield	ΔG_{opt}	ΔG_{exh}
		(g kg^{-1} soil)	—— (kJ mol^{-1})	——
Ryegrass	Batcombe	22.1	-7.09	-22.8
	Newport	26.0	-3.68	-21.2
Fescue	Batcombe	20.9	-9.03	-22.9
	Newport	29.6	-4.68	-19.6

4.3.5 Potassium uptake

The contribution of seed K was small, 5.6 and 4.2 meq kg^{-1} of soil for ryegrass and fescue respectively, <20% of the smallest cumulative uptakes.

Figures 4.7 and 4.8 show that the relationship between cumulative K uptake and $\overline{\Delta G}_{K,Ca+Mg}$ for ryegrass and fescue varied with soil type. Much of this variation can be explained by the differences in Q/I relations of the soils, because K uptake was much better correlated with exchangeable K (Figures 4.9 and 4.10).

Considerably more K was taken up from the Worcester soil, by both grasses, than was initially exchangeable to NH_4OAc when the latter was less than 30 meq kg^{-1}. This demonstrates the high rate of release of peripheral K from this micaceous soil.

Figures 4.7 and 4.8 suggest that curvilinear relationships exist between K uptake and $\overline{\Delta G}_{K,Ca+Mg}$ for each soil. The more extensive data obtained in Experiment B confirmed this (Figure 4.11). K uptake increased exponentially with $\overline{\Delta G}_{K,Ca+Mg}$ to a point where the slope of the curve is maximum. At higher values of $\overline{\Delta G}_{K,Ca+Mg}$ the slope decreases and in the case of fescue tends to zero.

The $\overline{\Delta G}_{K,Ca+Mg}$ values for maximum K uptake in fescue, estimated from the curves, were approximately -5 and -2.5 kJ mol^{-1} on the Batcombe and Newport soils respectively. Data for the ryegrass did not extend to high enough $\overline{\Delta G}_{K,Ca+Mg}$ values to obtain maximum K uptakes. So ryegrass will take up more K than fescue.

Because the K uptake:$\overline{\Delta G}_{K,Ca+Mg}$ curves tend to be asymptotic to the $\overline{\Delta G}_{K,Ca+Mg}$ axis it is difficult to extrapolate $\overline{\Delta G}_{K,Ca+Mg}$ values

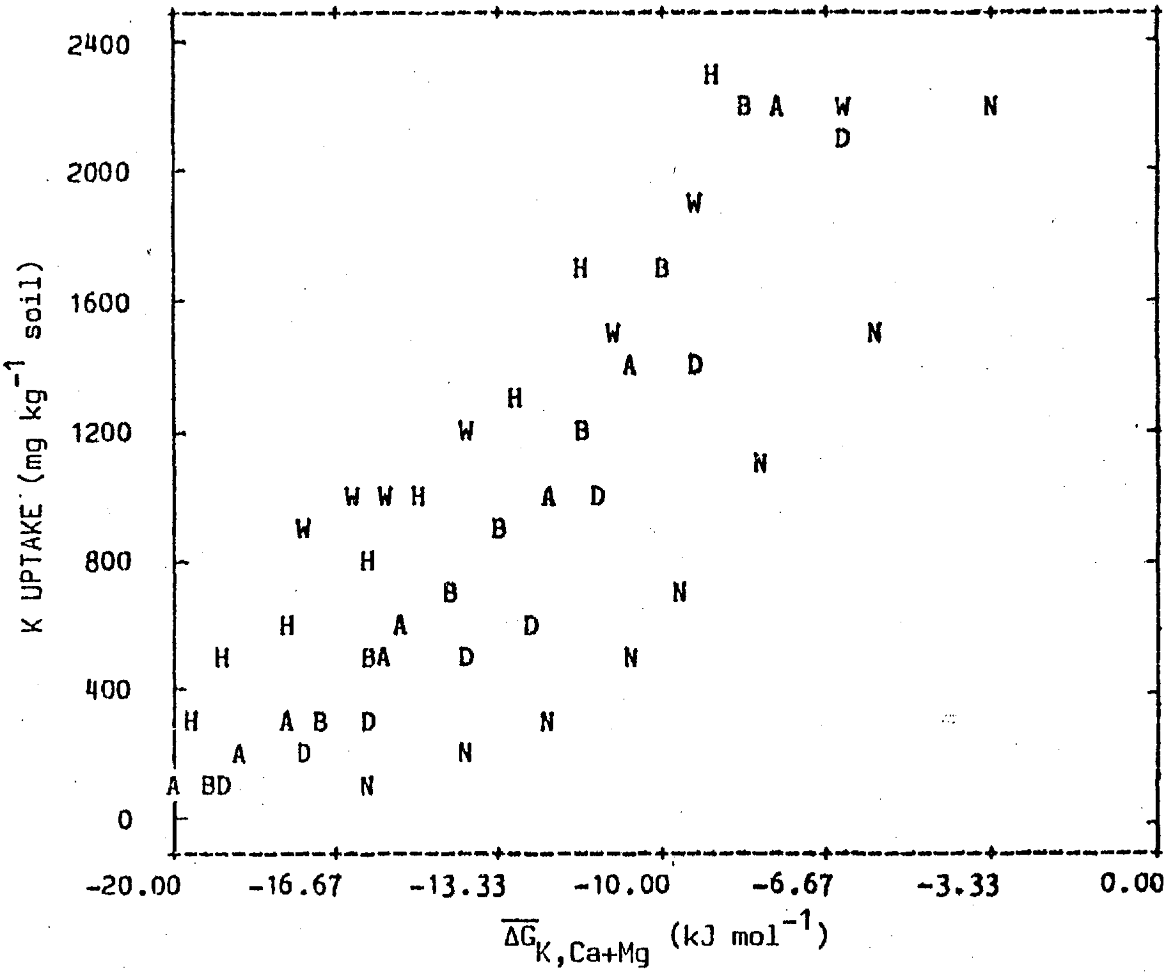


Figure 4.7 The relationship between the cumulative K uptake of perennial ryegrass and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 12 weeks' growth on 6 soils (key: as for Figure 4.1).

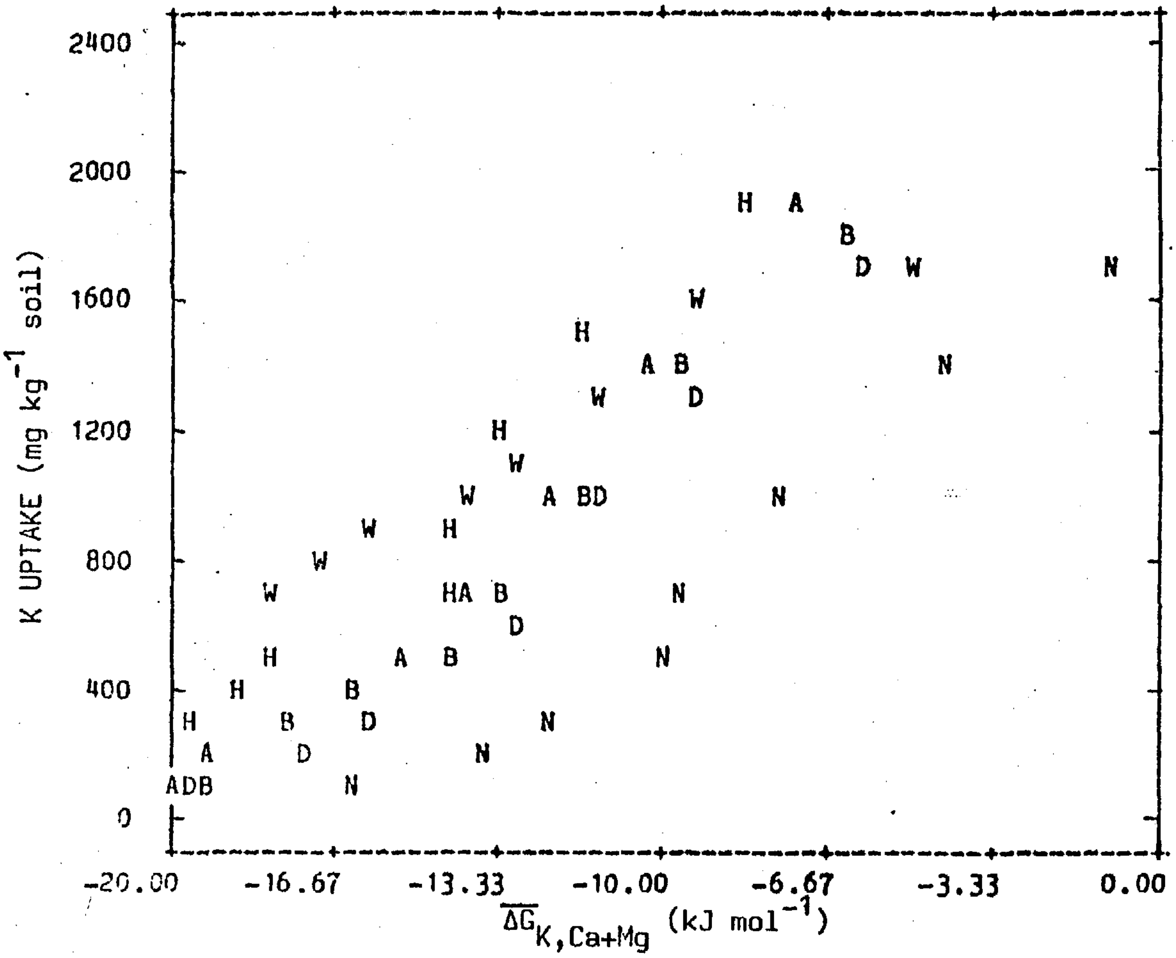


Figure 4.8 The relationship between the cumulative K uptake of creeping red fescue and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 12 weeks' growth on 6 soils (key: as for Figure 4.1).

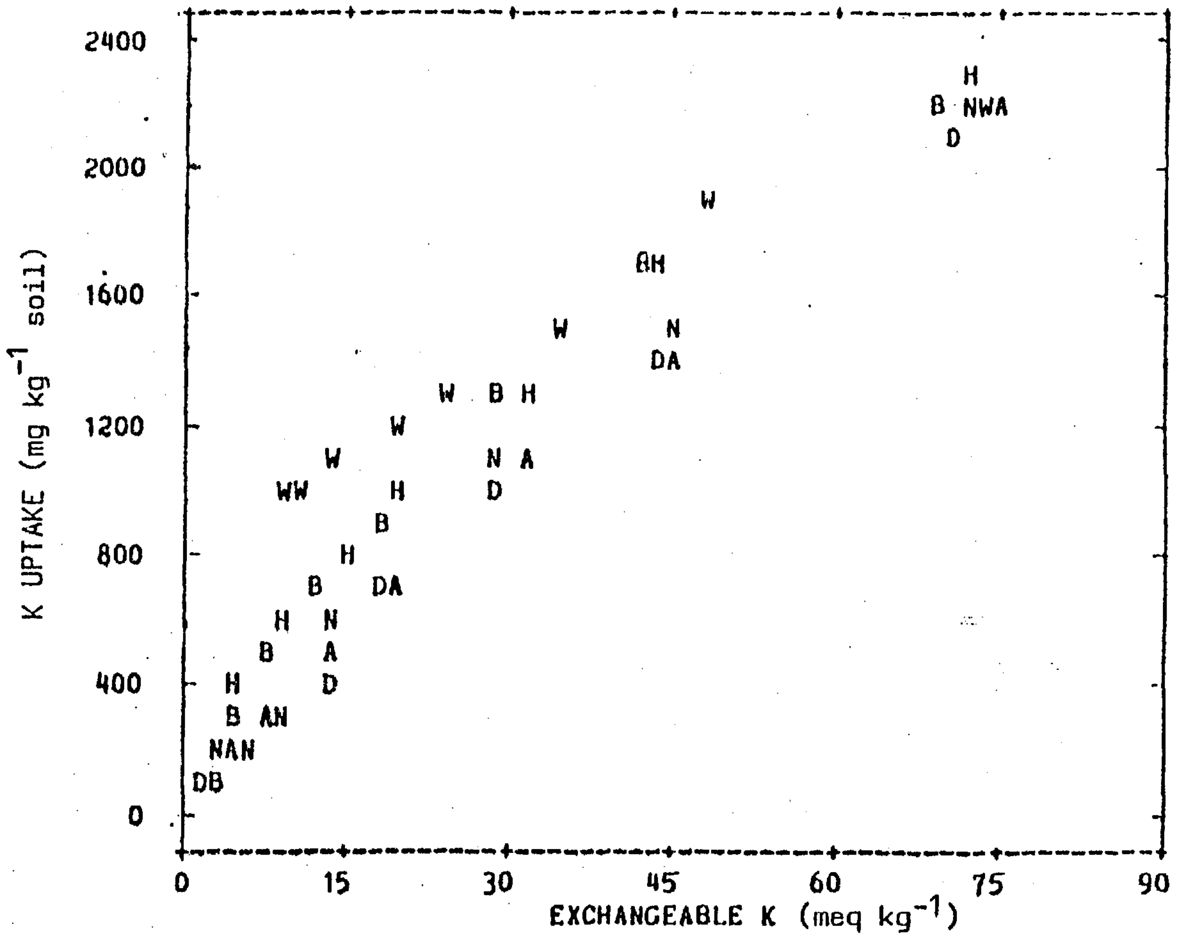


Figure 4.9 The relationship between the cumulative K uptake of perennial ryegrass during 12 weeks' growth and the initial exchangeable K in 6 soils (key: as for Figure 4.1).

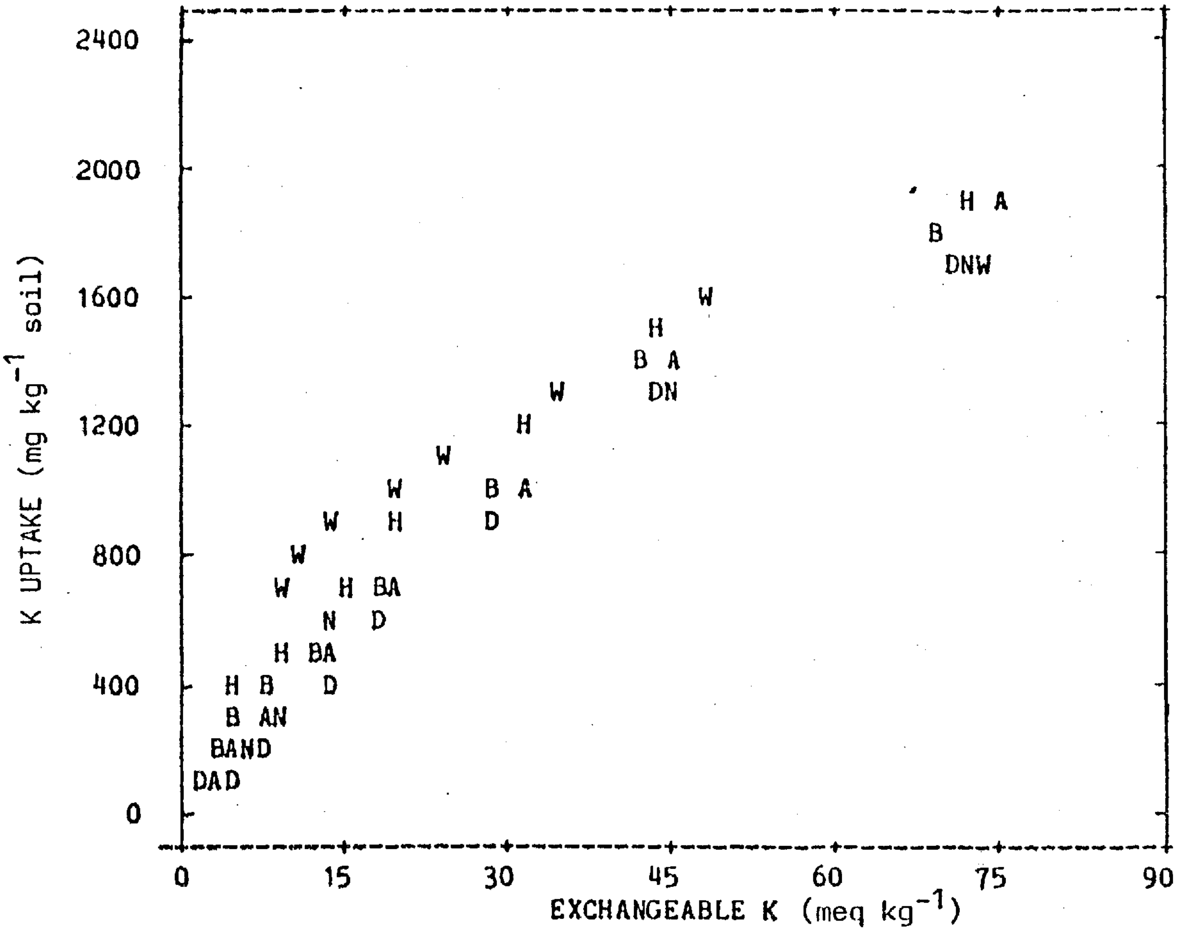


Figure 4.10 The relationship between the cumulative K uptake of creeping red fescue during 12 weeks' growth and the initial exchangeable K in 6 soils (key: as for Figure 4.1).

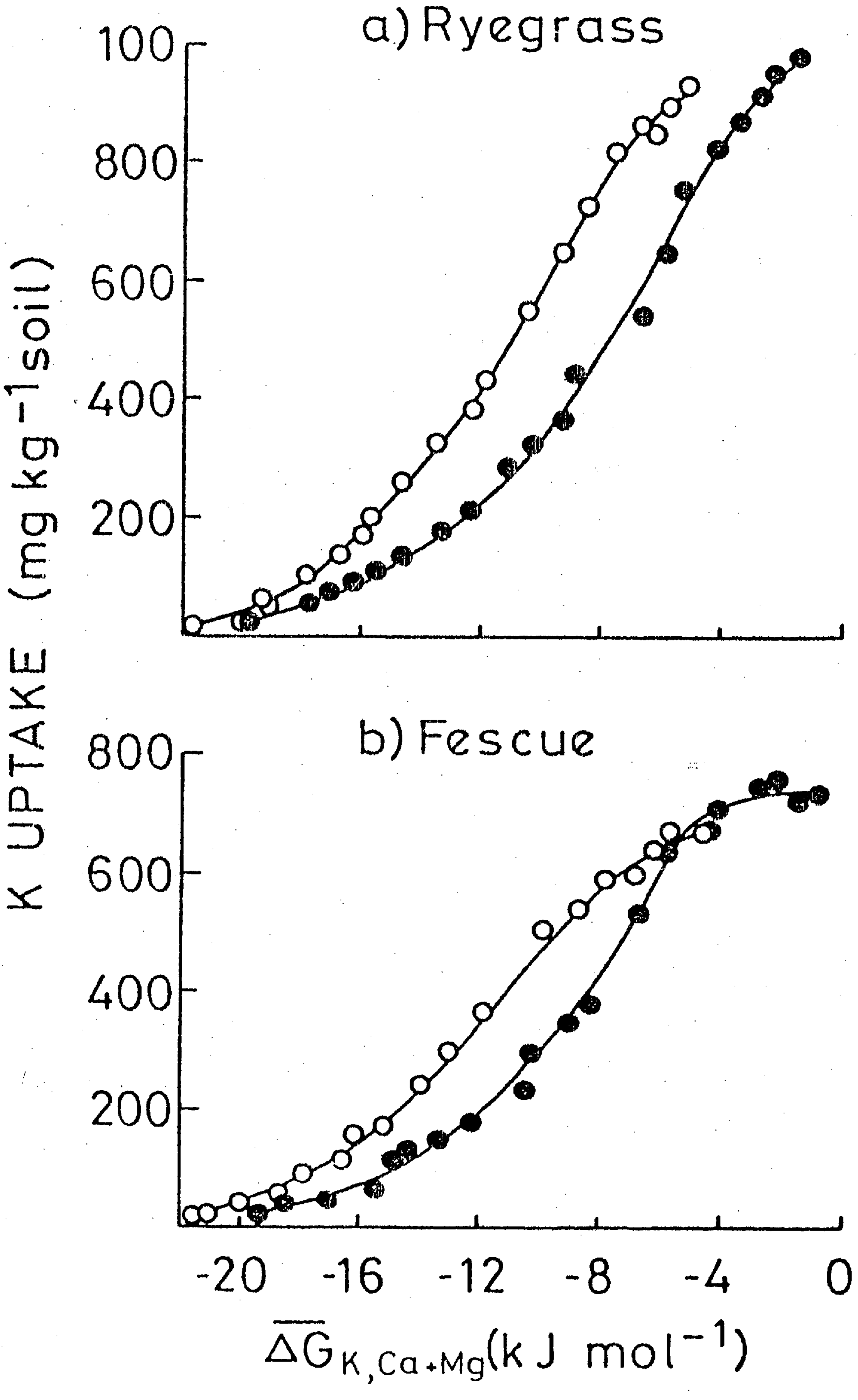


Figure 4.11 The relationship between the cumulative K uptakes of a) perennial ryegrass and b) creeping red fescue and the mean soil K potential for 6 weeks' growth on Batcombe and Newport soils (○ Batcombe; ● Newport).

for zero K uptake (i.e. the ΔG_{exh} value with respect to K uptake). However, it can be seen that these $\overline{\Delta G}_{K,Ca+Mg}$ values are less than -20 kJ mol^{-1} and may well be as low as values estimated by Addiscott (-23 kJ mol^{-1} for ryegrass on Batcombe soils; 1970a).

'Cumulative' %K in the dry grass from Experiment A was calculated as,

$$\%K = \text{cumulative K uptake/cumulative yield} \qquad .....(4.8)$$

at each harvest. Figures 4.12 and 4.13 show the relationship between %K and $\overline{\Delta G}_{K,Ca+Mg}$ for ryegrass and fescue respectively. The curves for all the soils except for Worcester were of an exponential type, tending to be asymptotic to the $\overline{\Delta G}_{K,Ca+Mg}$ axis at low values. The relationship was independent of the duration of the growth period; on each soil the same relationship held at all three harvests. For both grasses, the curves for the Andover, Batcombe and Bromyard soils (similar exchange isotherms) were very close to one another, but the curves for the other three soils were displaced individually from these. On each soil the relationship was almost identical for the two grasses.

So, K uptake per unit of dry matter was constant for each $\overline{\Delta G}_{K,Ca+Mg}$ value on any given soil, but the different cation exchange properties of the soil produced different relationships. The K concentration in the plant (%K) increases with soil K potential, and this relationship is independent of the duration of the growth period.

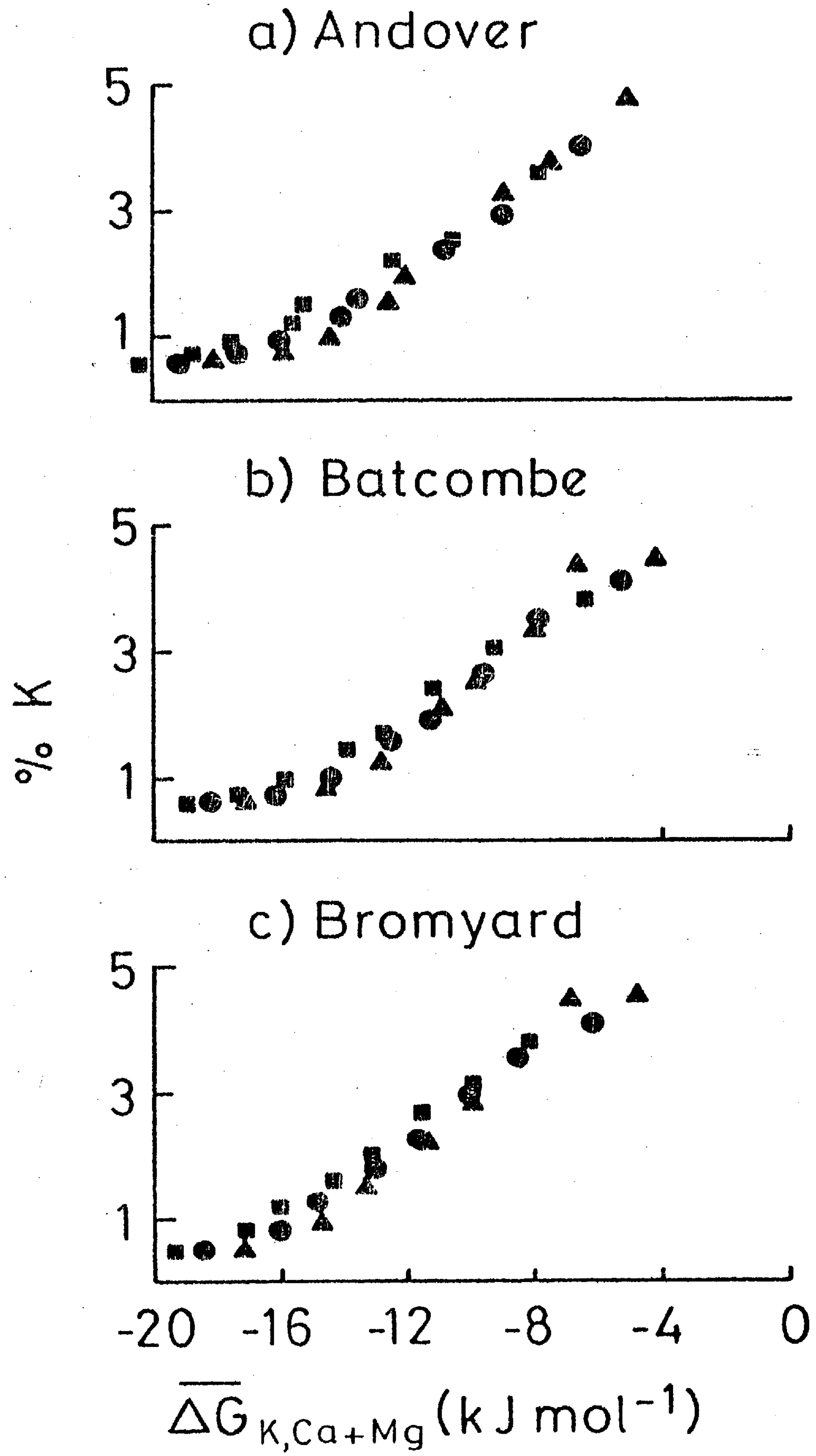


Figure 4.12 The relationship between cumulative K uptake per unit dry matter (%K) of perennial ryegrass and mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4, 8 and 12 weeks' growth on 6 soils. (■ 4 weeks'; ▲ 8 weeks'; ● 12 weeks').

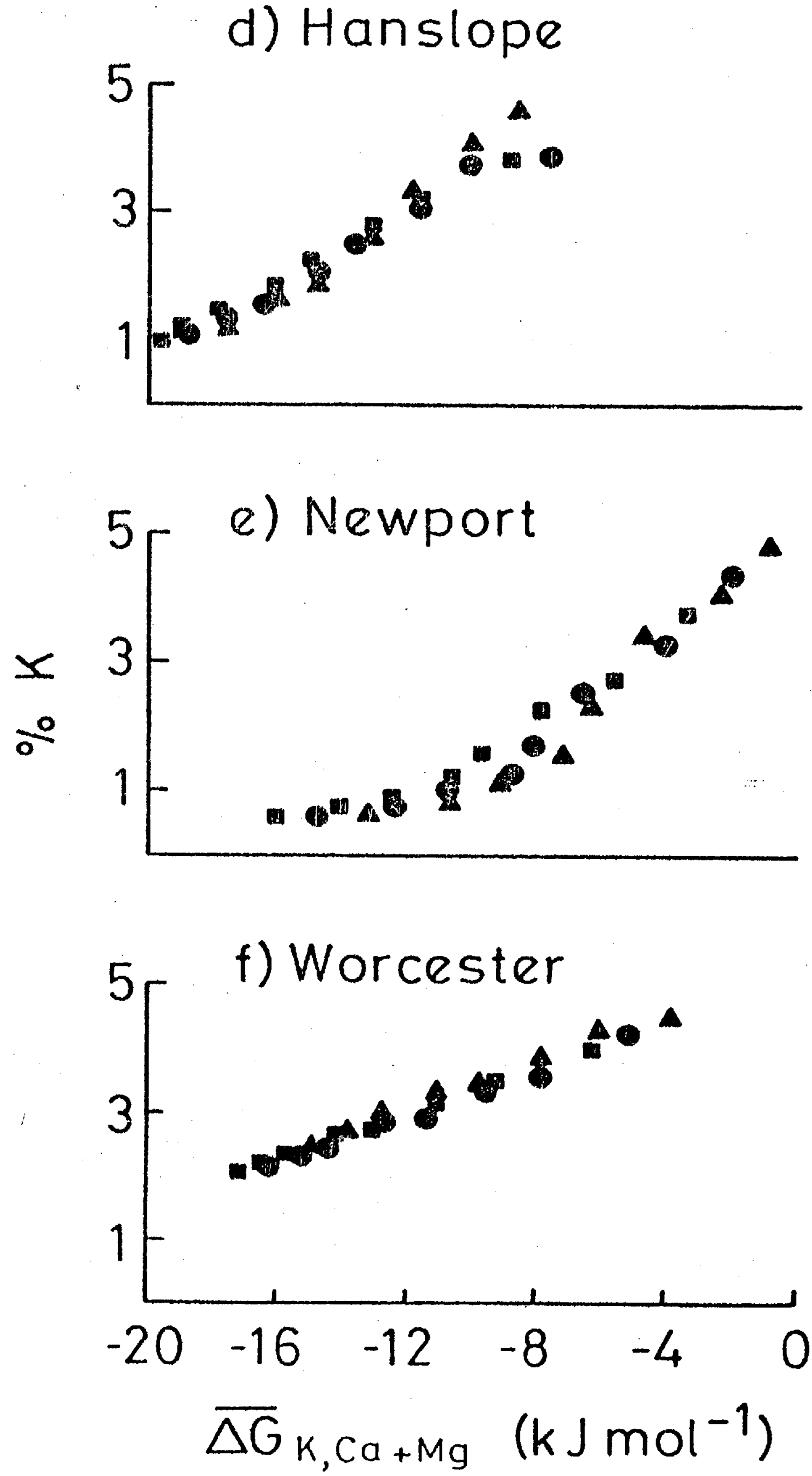


Figure 4.12 Continued.

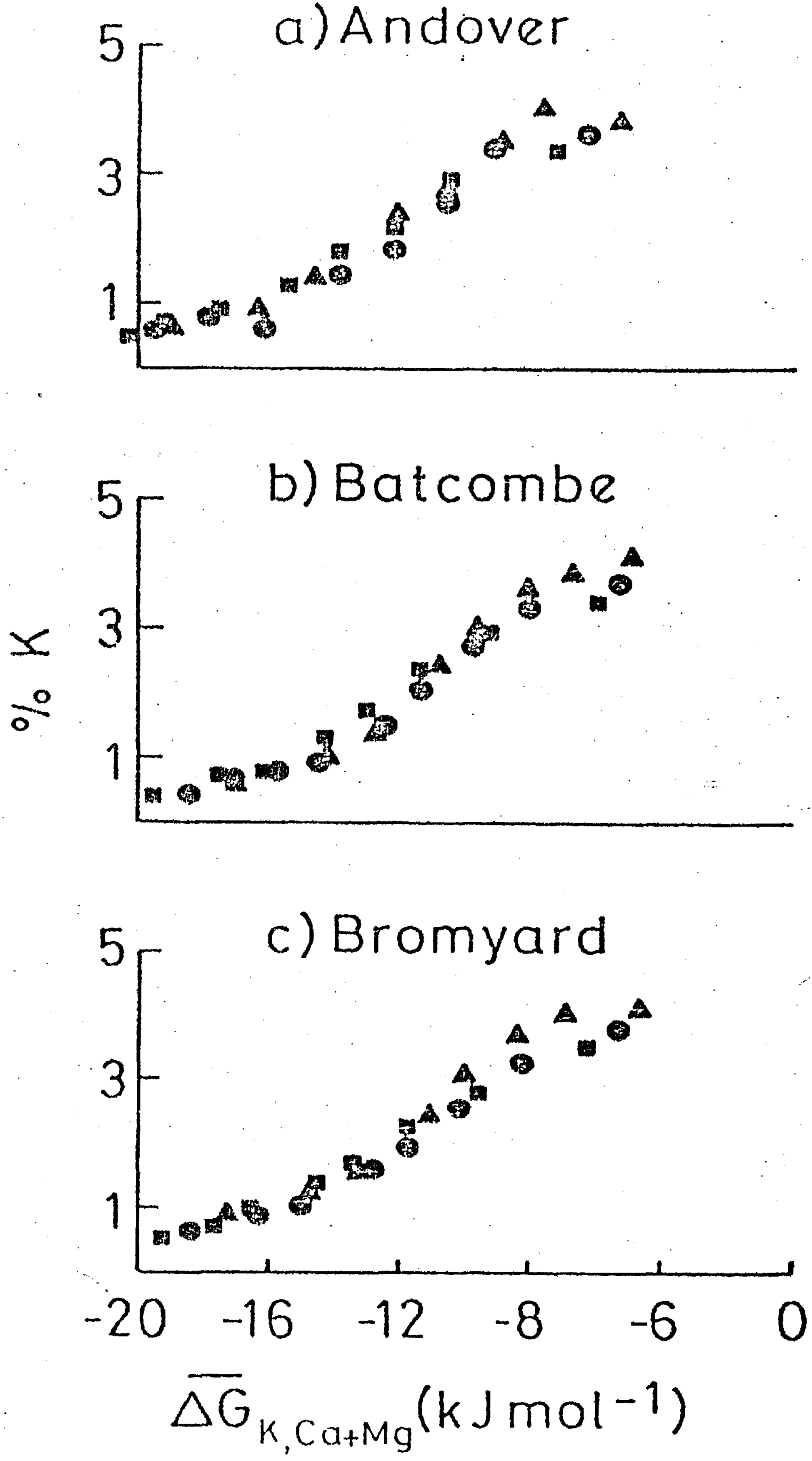


Figure 4.13 The relationship between cumulative K uptake per unit dry matter (%K) of creeping red fescue and mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4, 8 and 12 weeks' growth on 6 soils (■ 4 weeks'; ▲ 8 weeks'; ● 12 weeks').

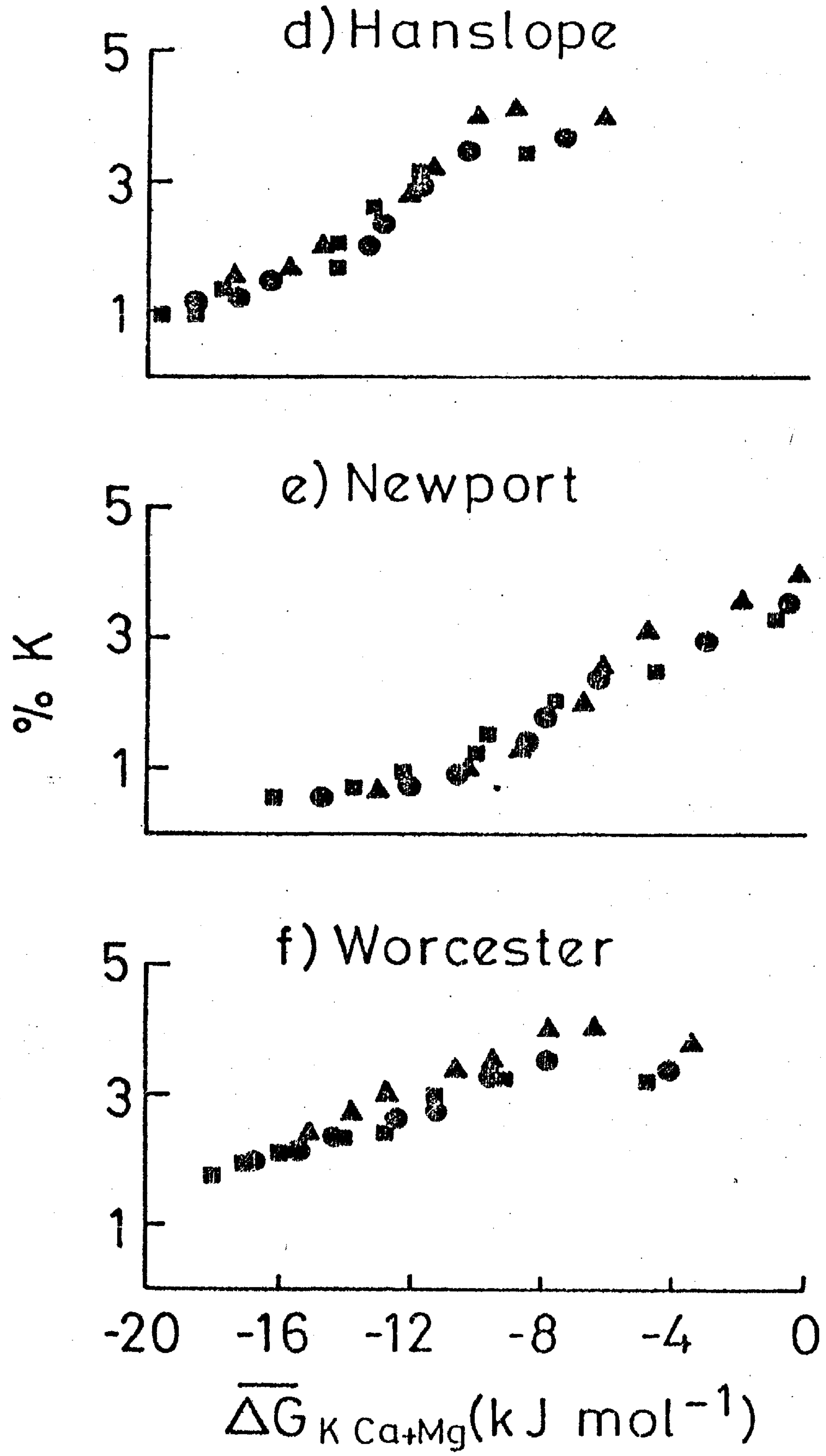


Figure 4.13 Continued.

4.3.6 Calcium and Magnesium uptake in Experiment B

Figures 4.14 and 4.15 show how the Ca and Mg uptakes of the grasses varied with $\overline{\Delta G}_{K,Ca+Mg}$ on the Batcombe and Newport soils. Both increased to a maximum at between -15 and -18 kJ mol^{-1} on the Batcombe soil and between -11 and -16 kJ mol^{-1} on the Newport soil. At higher $\overline{\Delta G}_{K,Ca+Mg}$ values, both Ca and Mg uptakes decreased, probably because K is selectively absorbed by the plant and at high concentrations inhibits uptake of Ca and Mg (Woodruff, 1955b). The decrease in Ca uptake is more marked than that of Mg uptake, probably because less Ca was added to the soils at the higher K levels (Appendix 1) whereas the amount of Mg added was constant. Also Mg is actively taken up by the plant whereas Ca uptake is passive.

Native Ca levels in the soils were high so it is unlikely that the soil Ca level alone limited Ca uptake.

4.3.7 Soil pH

The pH values of the soils from Experiment A, on which ryegrass was grown, were measured before and after cropping to ascertain whether or not they were significantly affected by a) the added nutrient solutions b) intensive cropping. The latter is a particularly important consideration when growing plants in small pots. The results are given in Table 4.10.

The most noticeable effects of the treatment solutions were on the acid soils (Batcombe, Bromyard and Newport) whose pH values were raised slightly (0.2-0.6 pH units), probably because their base saturations were increased by the added K and Ca. This was a

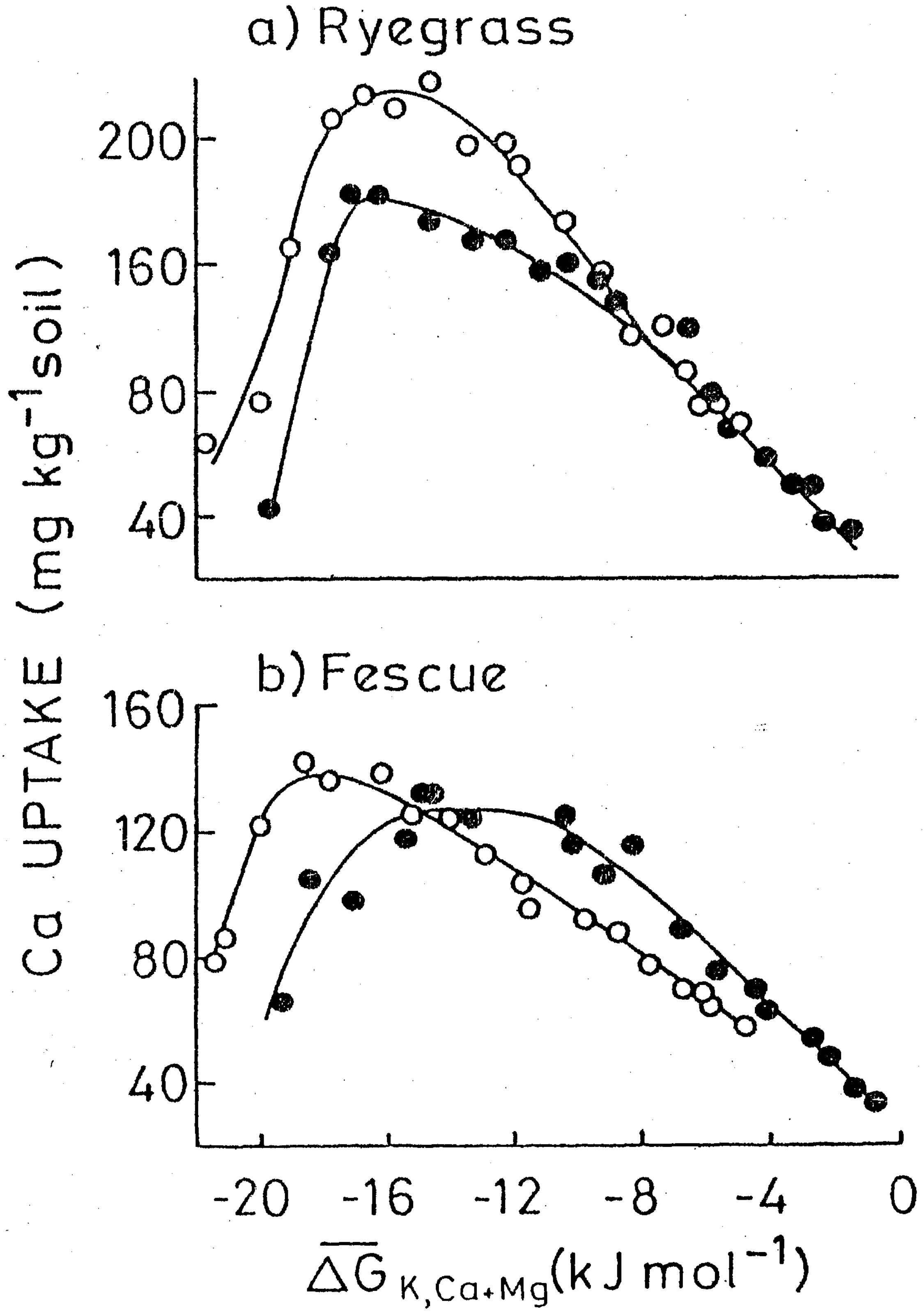


Figure 4.14 The relationships between Ca uptakes of a) perennial ryegrass and b) creeping red fescue and mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 6 weeks' growth on Batcombe and Newport(1) soils (key: as for Figure 4.11).

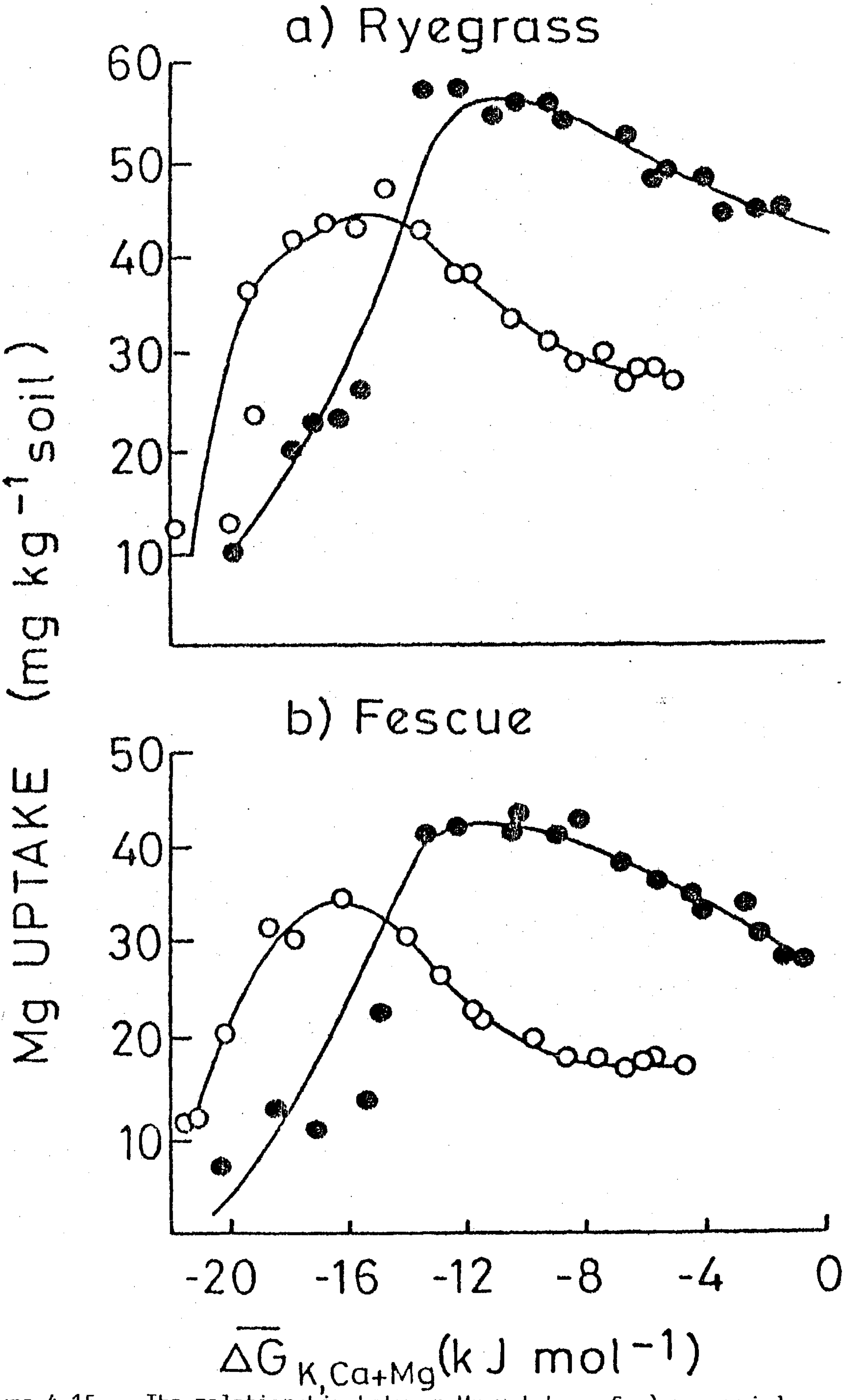


Figure 4.15 The relationship between Mg uptakes of a) perennial ryegrass and b) creeping red fescue and mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 6 weeks' growth on Batcombe and Newport(1) soils (key: as for Figure 4.11).

Table 4.10 The pH of soils before and after 12 weeks cropping with ryegrass.

Soil Series	K level	pH		
		Without added nutrients	Prepared soil before cropping	After cropping
Andover	1	7.3	7.2	7.2
"	3		7.2	7.5
"	5		7.4	7.5
"	7		7.3	7.5
Batcombe	1	4.8	5.2	4.8
"	3		5.1	4.9
"	5		5.1	4.8
"	7		5.0	4.5
Bromyard	1	5.4	5.8	5.1
"	3		5.9	5.4
"	5		6.0	5.1
"	7		6.0	5.2
Hanslope	1	7.1	7.4	7.2
"	3		7.0	7.2
"	5		7.0	7.0
"	7		7.2	7.2
Newport(1)	1	5.4	5.7	5.5
"	3		5.8	5.0
"	5		5.7	5.3
"	7		5.8	5.1
Worcester	1	7.5	7.2	7.5
"	3		7.3	7.7
"	5		7.2	7.6
"	7		7.2	7.4

temporary effect because the pH in these soils decreased during cropping to a value similar to, or slightly less than, that before treatment. On average the pH values of the Andover and Hanslope soils were not affected significantly by the nutrient treatments or cropping. The pH of the Worcester soil was decreased by the treatments but reverted during cropping to its pre-treatment value. The amount of K added to the soil did not affect its pH.

5. CRITICAL POTASSIUM POTENTIALS FOR SOME CROPS IN THEIR EARLY GROWTH ON A NEWPORT SERIES SOIL

5.1 Introduction

Previous workers have used a variety of techniques to determine either optimum or exhaustion K potentials for crops (see Section 1). In this Section, experiments are described which were designed to derive critical K potentials for some commonly grown crop plants in their first 4 weeks of growth. Yield responses of spring wheat, sweet corn, leafless peas, field beans, sugar beet and clover to a wide range of soil K potential were measured, from which exhaustion, optimum and toxicity K potentials were derived.

The experiments described in Section 4 showed that critical K potentials for ryegrass and fescue varied with soil type. This may also be so with the other crops, but the time and facilities available in controlled environments during this work made such experimentation impracticable. So, in these experiments, only the Newport(2) soil was used.

5.2 The crops

These plants are all grown as field crops in Britain, with the exception of the sweet corn which is a horticultural cultivar of maize, in this case an F1 hybrid called 'First of All'. The spring wheat 'Highbury', was a semi dwarf variety, recently introduced as a commercially grown crop. Field beans are a long-established grain legume grown for animal feed. The variety used in this work was 'Minden'. Leafless peas (variety 'Filby') have been introduced recently as a possible substitute for field beans because of their greater suitability for combine harvesting. The sugar beet variety was 'Bush', and the white clover a New Zealand variety, 'Huia'.

The A.D.A.S. fertiliser recommendations (Ministry of Agriculture, Fisheries and Food, Bulletin 209, 1973) indicate the relative K requirements of the crops. The recommended annual K additions for each crop on, for instance, index 1 soils (61-120 ppm K by volume, extracted with M NH_4NO_3) increase in the order wheat and beans (30) < peas (40) < clover (80) < sweet corn (100) < sugar beet (150 kg K ha^{-1}), i.e. wheat and the legumes have very similar K requirements and maize is slightly higher. For sugar beet, it is nearly 3 times greater than the others. The recommendation for clover is only for seed crops not for swards.

However the relative K requirements for maximum growth in the early stages may be different from those for maximum yield of the harvested part at maturity. Concentrations of K in the plant as high as 4% have been reported for young wheat and maize plants (Page, et al., 1978; Berger, 1962, respectively). This concentration drops throughout growth. Draycott (1972) quotes K concentrations in young sugar beet leaves of over 6% dropping to around 3% at harvest.

Except for clover, these crops are all quite tall at maturity. So, to make best use of the constant environment cabinets, and the time available the crops were grown for only 4 weeks in small pots on the Newport(2) soil. The highest concentrations of K in plant tissue are found in the early stages of growth (e.g. Page, et al., 1978; Draycott, 1972). The root system is less extensive at this time; so, for an optimum K concentration in the plant, quite a high K intensity (or K potential) in the soil may be necessary.

5.3 Methods

For each crop, the Newport(2) soil was adjusted to 24 K levels in the manner described in Section 2.3. Details of the solutions used for this are given in Appendix 1. Treatments were duplicated. Two crops were grown in each experiment and duplicate pots of each divided between 2 Saxcil Growth Cabinets.

The peas, beans, wheat and sweet corn were germinated on dampened filter paper. Two or three days after germination, the seedlings were planted in the prepared soil, 4 to a pot. The soil surface was covered with black plastic chips. The pots were placed in the Saxcil cabinets and water was added to their saucers to bring the soil to 20% moisture content.

The beet, because of its small seeds and seedlings, was germinated in the potted soil directly. Initially, ten seeds were sown in each pot then the soil was brought to 20% moisture content and covered with black plastic chips. On emergence, the seedlings were thinned to four per pot and the pots were put in the Saxcil cabinets.

The clover was grown in much the same way as the grass (Section 4). 0.18 mg of seed was sown on the prepared soil, watered and covered with black plastic chips as above. The germinated seedlings were allowed to grow for 4 weeks in the Saxcil cabinets.

For all the crops, the cabinets were set to give maximum light intensity, 28000 lx. All crops were grown for 4 weeks after germination then the tops were cut at soil level and dried, weighed, ground and analysed for K.

One hundred seeds of each crop were weighed, dried and weighed again, then ground and analysed for K.

5.4 Yields and critical potassium potentials of wheat, sweet corn, field beans, peas and sugar beet

5.4.1 Growth

These crops all grew satisfactorily over this short period. The wheat tillered, except at the 3 lowest K levels, but stems did not start to extend. Brown specks developed on the wheat leaves at the two lowest K levels, indicative of K deficiency.

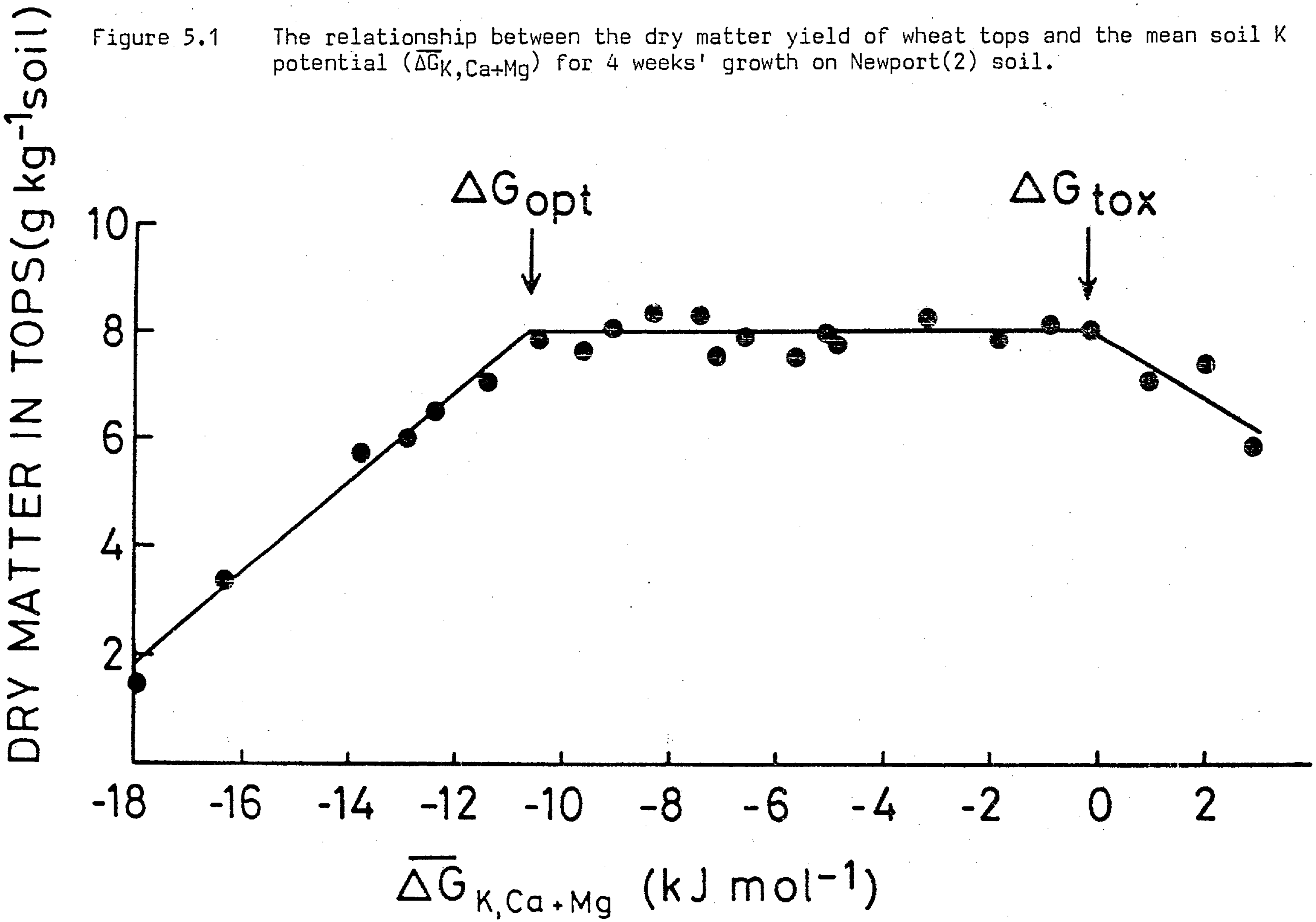
The sweet corn leaves developed a slight purple tinge towards the end of the growth period, indicating the beginings of P deficiency. However growth was not impeded so this was not considered to be a serious problem.

The beans grew well at all levels of K. However, at low levels of K the bean plants tended to be taller and spindlier whereas, at the higher K levels, the plants were shorter but with thicker stems and larger leaves. The leafless peas grew quite prolifically and care had to be taken so that plants from adjacent pots did not intertwine. Sugar beet also grew well but, at low K levels, developed brown patches on the leaves, probably indicative of K deficiency.

5.4.2 Determining critical potassium potentials

Mean soil K potentials ($\overline{\Delta G}_{K,Ca+Mg}$) for the period of growth were calculated as described in Section 4.3.1. Figures 5.1-5.5 show dry matter yields of the plant tops plotted against $\overline{\Delta G}_{K,Ca+Mg}$. These responses were interpreted as having three parts corresponding to positive, zero and negative response. At low $\overline{\Delta G}_{K,Ca+Mg}$ values, yield increased with increasing $\overline{\Delta G}_{K,Ca+Mg}$ to a maximum. The

Figure 5.1 The relationship between the dry matter yield of wheat tops and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.



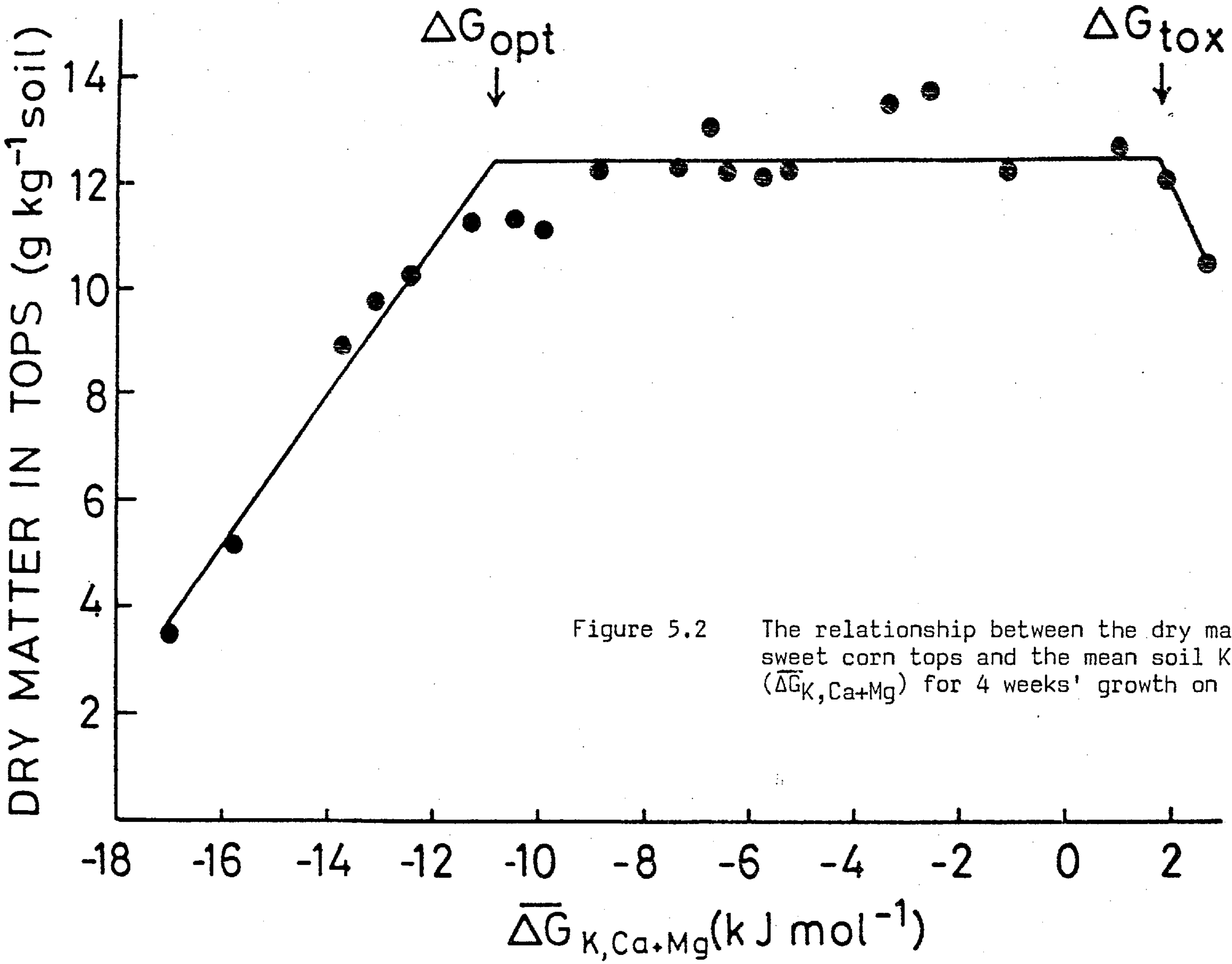


Figure 5.2 The relationship between the dry matter yield of sweet corn tops and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

Figure 5.3 The relationship between the dry matter yield of leafless pea tops and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

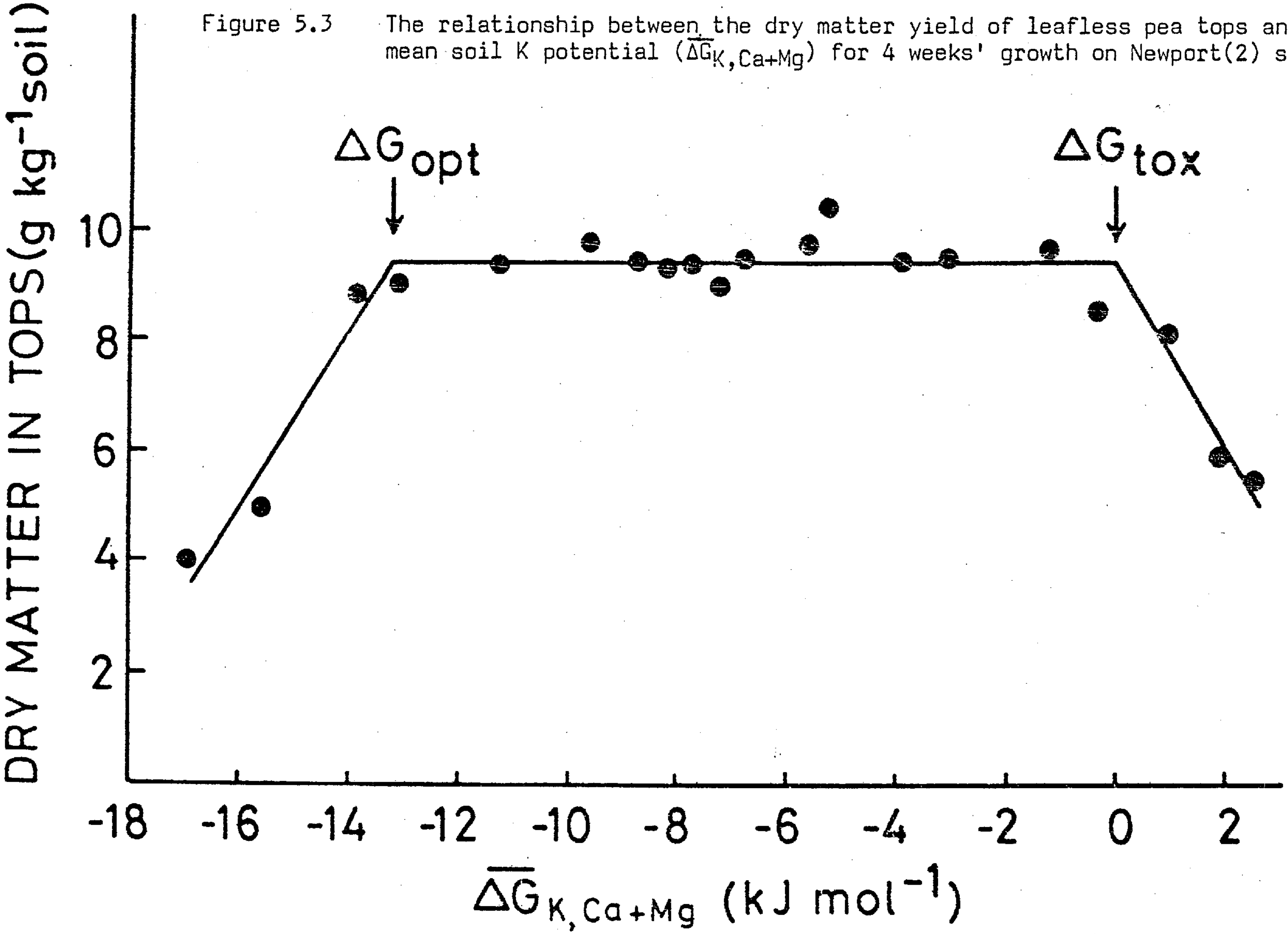
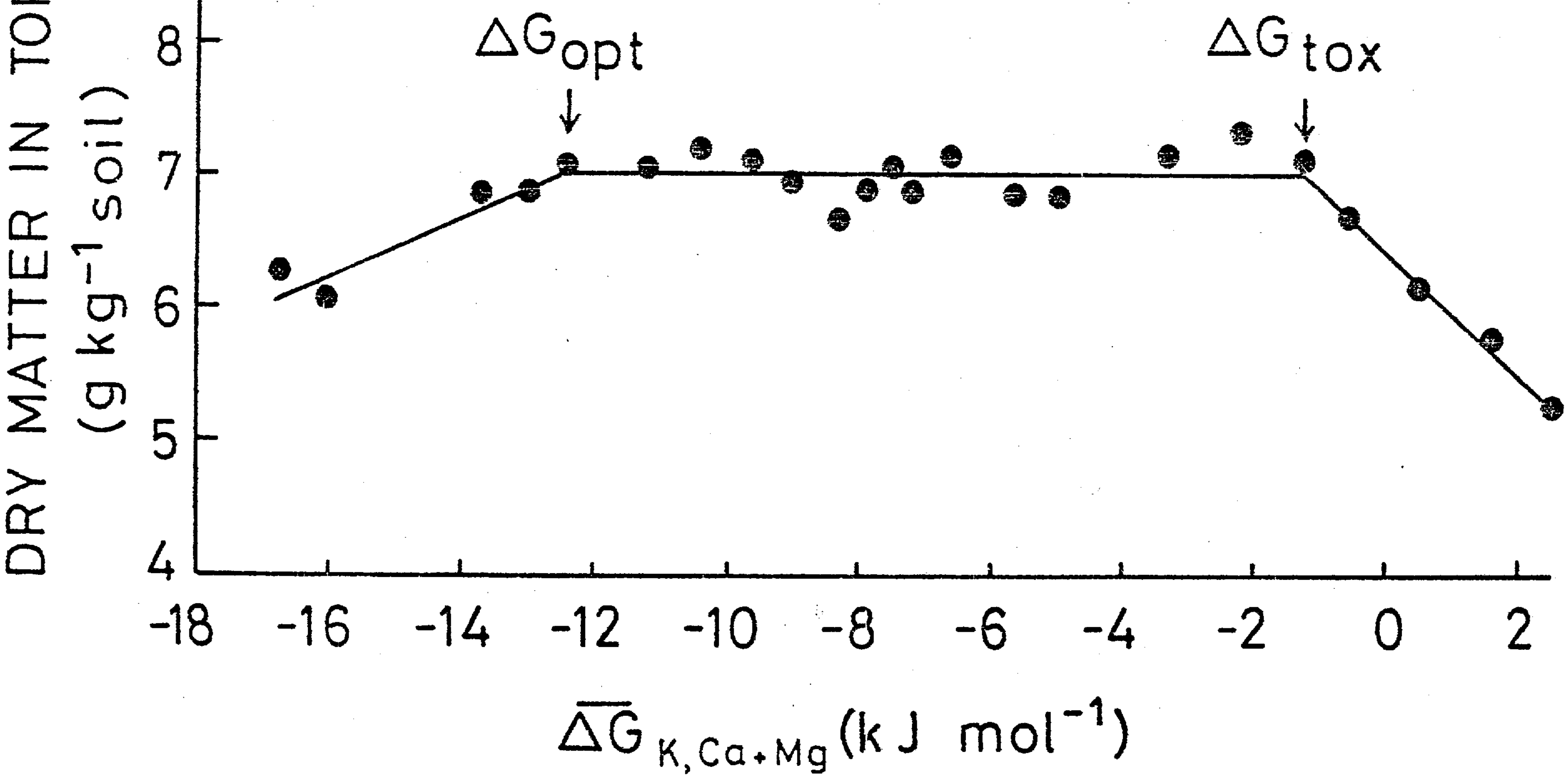


Figure 5.4 The relationship between the dry matter yield of field bean tops and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.



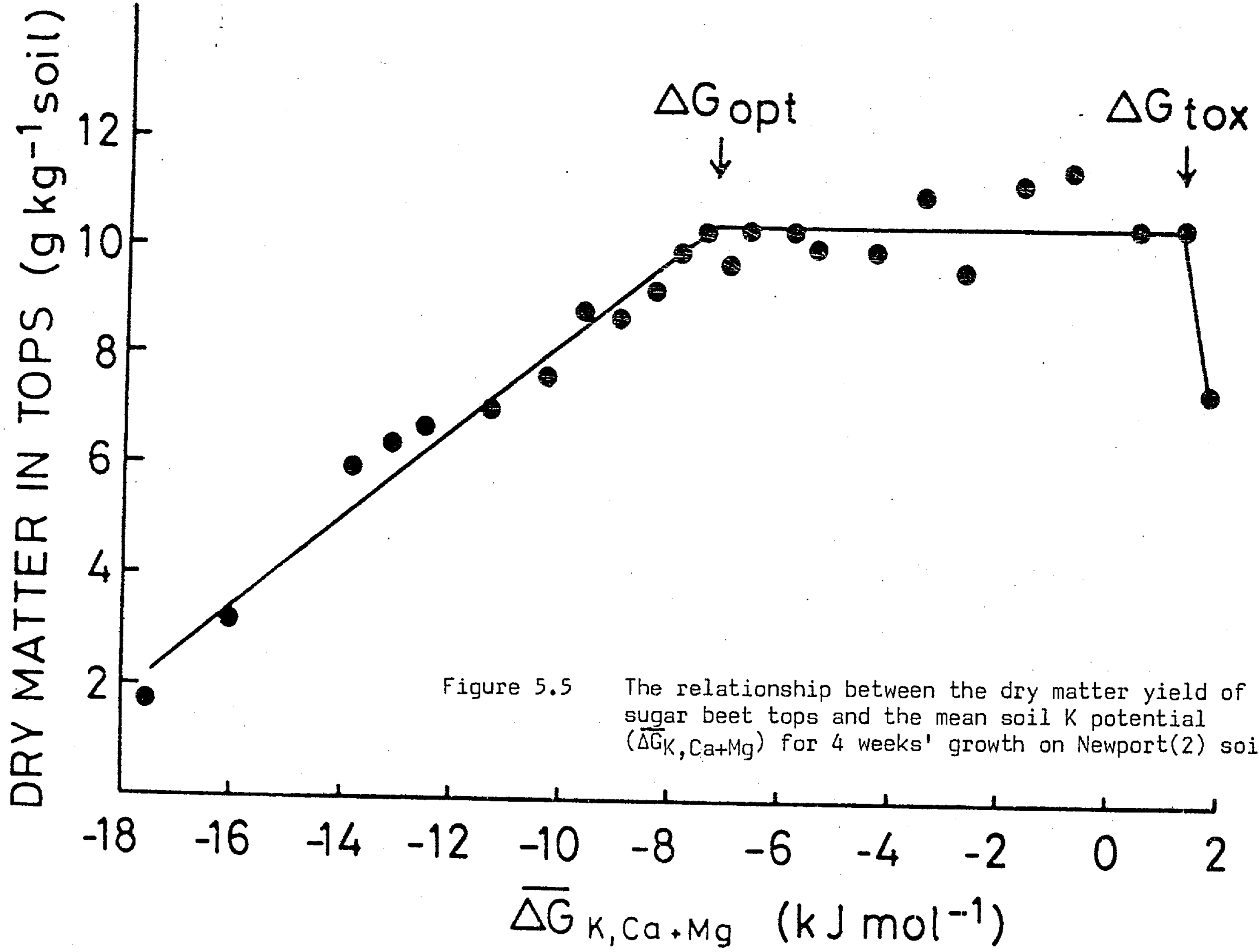


Figure 5.5 The relationship between the dry matter yield of sugar beet tops and the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

$\overline{\Delta G}_{K,Ca+Mg}$ value corresponding to the attainment of maximum yield is referred to as ΔG_{opt}. As $\overline{\Delta G}_{K,Ca+Mg}$ increased further, yield did not change but K uptake increased (see later). This is referred to as 'luxury uptake'. At higher $\overline{\Delta G}_{K,Ca+Mg}$ values, a point was reached where yield actually decreased, called here ΔG_{tox}.

These points were estimated by fitting three linear portions to the data, for positive, zero and negative response, using an iterative, least squares method from the Rothamsted 'GENSTAT' computer program (Rothamsted, 1977). Thus the intersections of the three lines gave ΔG_{opt} and ΔG_{tox}. Exhaustion potentials, ΔG_{exh}, were determined by extrapolating the line for positive response to 'zero' yield. Table 5.1 gives slopes and intersections of the fitted lines together with their standard errors. The latter are not available for sugar beet because too few data for the negative response slope prevented the fitting procedure from being finalised.

5.4.3 Yields and ΔG_{opt}

Sweet corn gave the highest yield and, perhaps surprisingly, beans the lowest. The peas and beans had the lowest ΔG_{opt} values, suggesting that these grain legumes have a low K requirement, or that they have a great ability to remove K from soil. The K contents of their seeds were the highest of all (Table 5.2) so perhaps this reduced their K requirement in this early stage of growth.

The ΔG_{opt} values for the two cereals were very similar to one another, which is surprising since sweet corn is usually regarded as having a higher K requirement than wheat. However a difference may manifest itself in later stages of growth particularly

Table 5.1 Fitted parameters for crop yield responses to the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport series soil.

Crop	Response slopes				Maximum		Intersections				
	+ve	SE	-ve	SE	Yield	SE	ΔG_{opt}	SE	ΔG_{tox}	SE	ΔG_{exh}
					(g kg^{-1} soil)		(kJ mol^{-1})				
Wheat	0.85	0.07	0.59	0.21	7.98	0.10	-10.58	0.35	-0.12	0.75	-20.0
Sweet Corn	1.42	0.12	2.21	1.46	12.41	0.21	-10.82	0.32	1.76	0.44	-19.5
Field Beans	0.21	0.05	0.47	0.05	7.04	0.05	-12.37	0.63	-1.25	0.19	(-40.3)
Peas	1.59	0.22	1.71	0.42	9.40	0.13	-13.21	0.36	0.01	0.46	-19.1
Sugar Beet	0.79	-	8.46	-	10.38	-	-7.25	-	1.29	-	-20.4
Clover	1.01	0.05	-	-	-	-	-	-	-	-	-20.8

Table 5.2 Potassium concentration in the seeds.

Crop	K concentration	
	(% of dry matter)	(mg kg^{-1} soil)
Wheat	0.37	2.2
Sweet corn	0.47	14.6
Field Beans	1.28	99.2
Leafless peas	1.04	38.7
Sugar Beet	0.18	0.5
Clover	1.24	8.9

as corn a) has considerably more seed K and b) grows to be a larger plant than wheat.

Sugar beet gave the highest $\overline{\Delta G}_{opt}$ value, approaching that of the grasses on this soil. Thus it requires more K and/or has a low ability to take up K. It has very little seed K and high concentrations of K in the tops (Draycott, 1972) so the former is probably true.

5.4.4 $\underline{\Delta G}_{exh}$

Values of ΔG_{exh} were similar for all crops except the beans (Table 5.1). The very low value for the beans (corresponding to a soil solution K concentration of about 10^{-9} $\underline{M}$) results mostly from too few data for the positive response slope and also the very large amount of K in the bean seeds. However the ΔG_{exh} values of the other crops correlate approximately and positively with the seed K i.e. the greater the seed K the more positive is ΔG_{exh}. This suggests that a greater ability to extract K at low potentials has evolved with a small seed K content. Although this argument is the opposite of that put forward in the case of the beans, i.e. that a large K content of the seed enables the plant to live at lower K potentials, it seems to operate for the other four crops and the data for the beans is not reliable enough to refute it.

5.4.5 $\underline{\Delta G}_{tox}$

ΔG_{tox} values ranged between -1.25 and +1.76 kJ mol^{-1}. A positive exchange energy means that energy is released when Ca replaces K on the exchange sites, i.e. calcium is held preferentially to K. So the plant does not have to work to remove K from the system. It does however, have to do work then to take up Ca and Mg, which it may not have the capacity to do. The plant may therefore suffer from lack of one or other of these nutrients.

So, whether it is because of a toxic concentration of K in the plant, induced Ca or Mg deficiency or other nutrient imbalance, very high soil K potentials cause decreases in yield so that a ΔG_{tox} value can be defined.

The high ΔG_{tox} value for sweet corn is perhaps congruous with its reputation of having a high K requirement. Sugar beet also has a high toxicity threshold for K. It has a high K requirement and therefore a high tolerance. Field beans, the opposite extreme, apparently have a low K requirement and a low K tolerance.

5.5 Content and concentration of potassium in dry matter

Figures 5.6-5.10 show the relationships between $\overline{\Delta G}_{K,Ca+Mg}$ and a) K uptake (i.e. K content) and b) K concentrations %K in the plant tops.

The amount of seed K is indicated on the K uptake graphs. It made a relatively small contribution to the K taken up in the sugar beet and wheat even at the lowest $\overline{\Delta G}_{K,Ca+Mg}$ values. In peas and sweet corn it approximated to the K in the tops at the lowest soil K level; but that in bean seeds exceeded that in the tops at the lowest soil K level by two-fold.

It is not possible to calculate how much of the K in the shoots was taken up from the soil and how much was transferred from the seed. Not all of the K from the seed gets into the shoot;

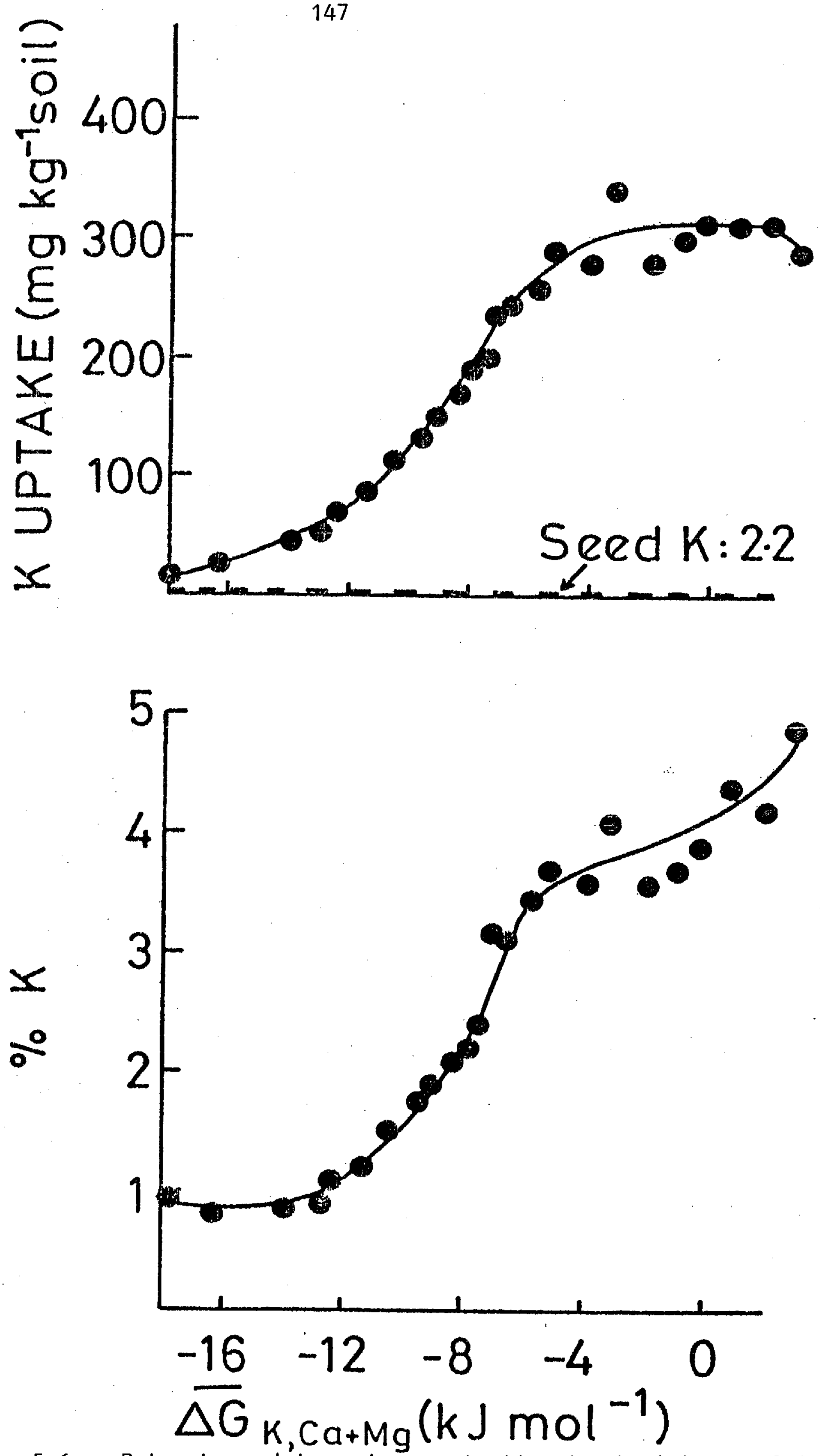


Figure 5.6 Potassium uptake and concentration in wheat tops related to the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

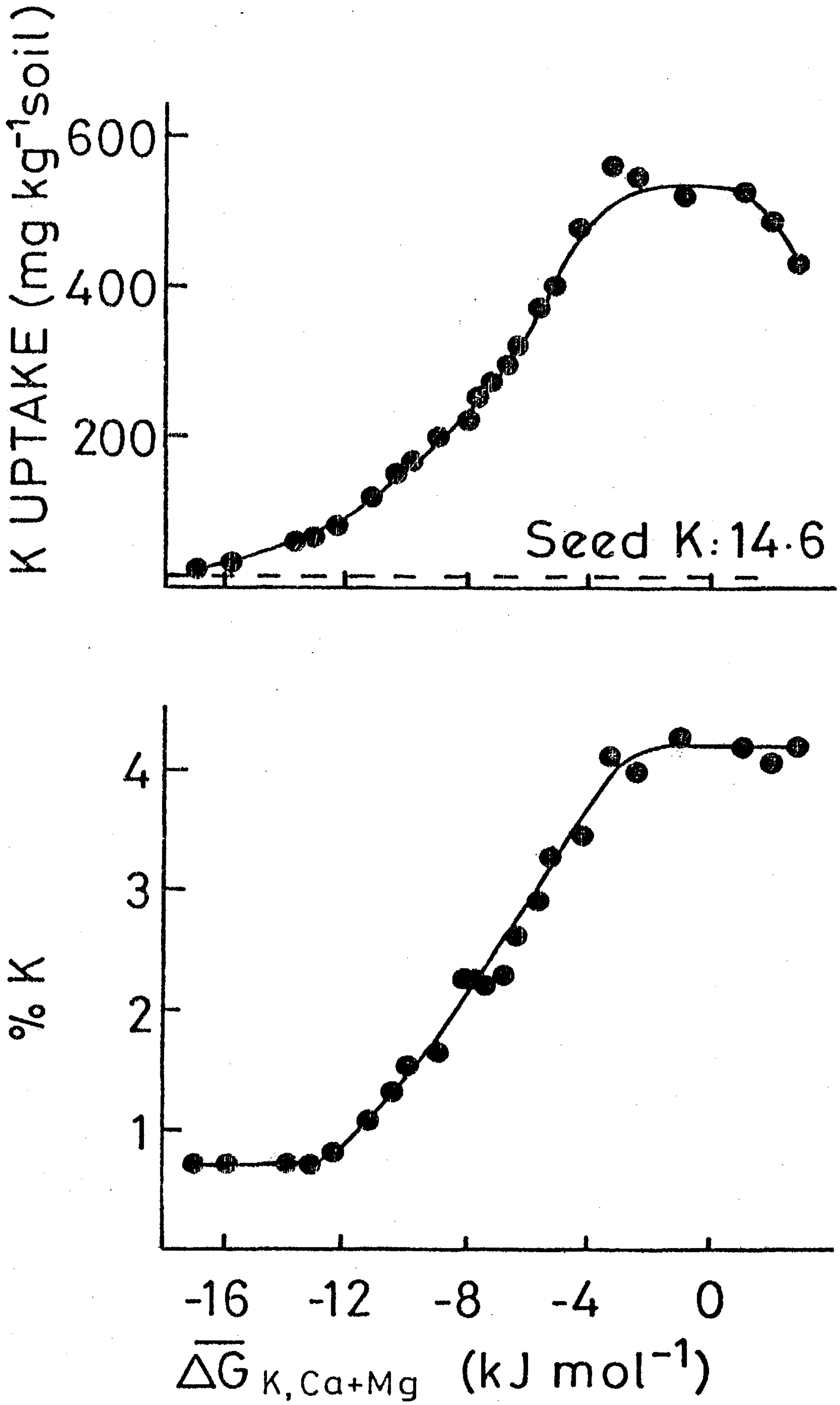


Figure 5.7 Potassium uptake and concentration in maize tops related to the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

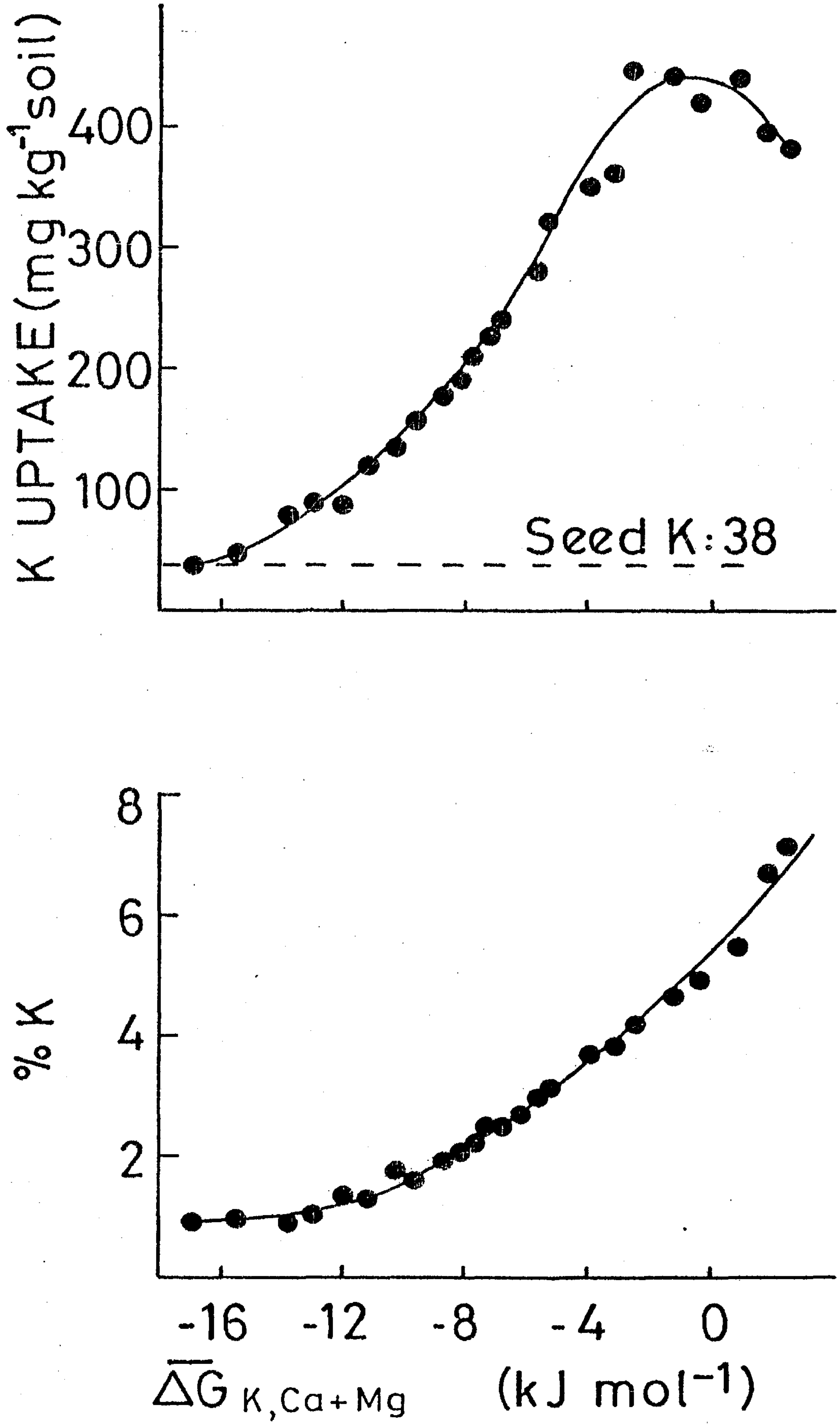


Figure 5.8 Potassium uptake and concentration in leafless pea tops related to the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

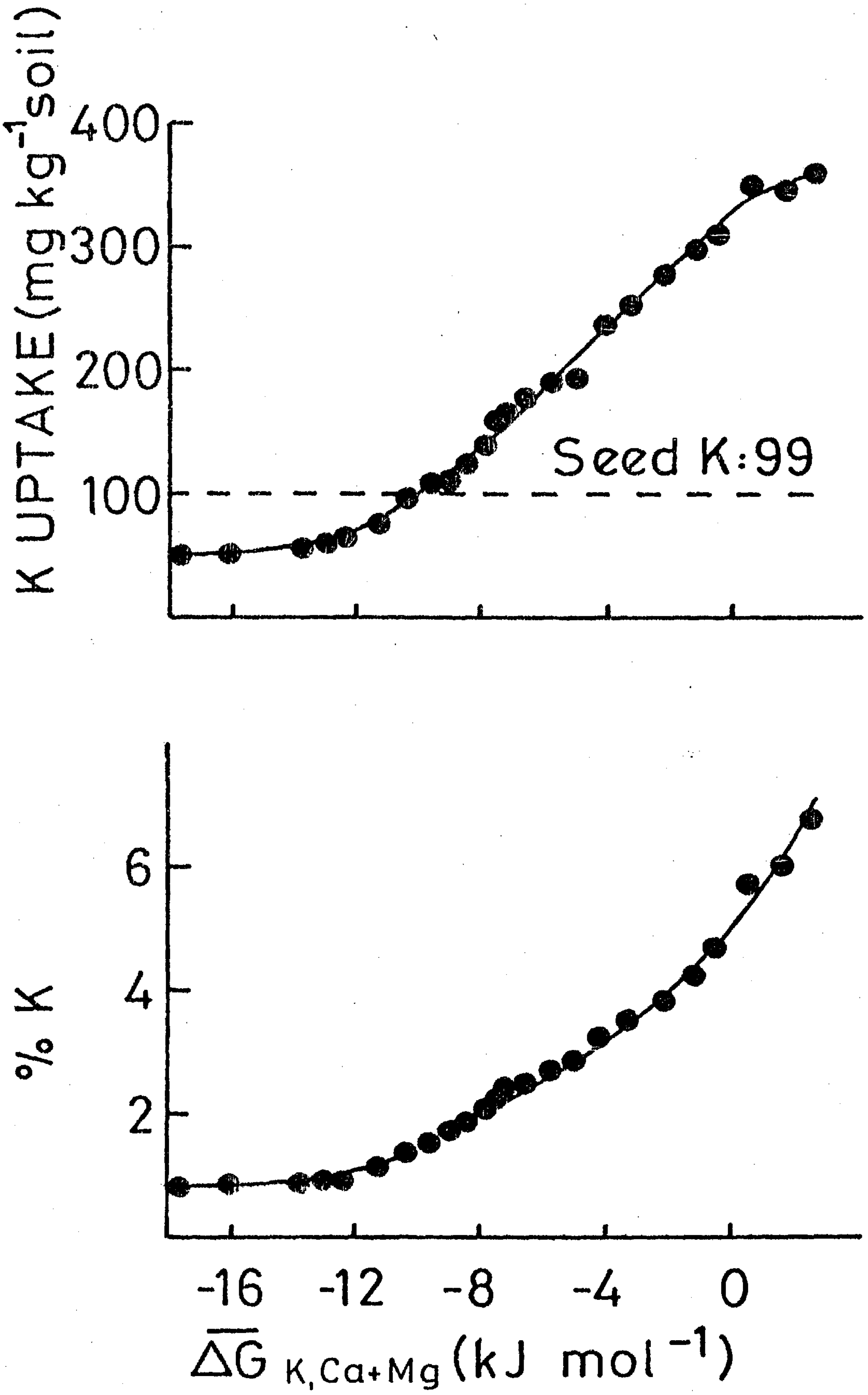


Figure 5.9 Potassium uptake and concentration in field bean tops related to the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

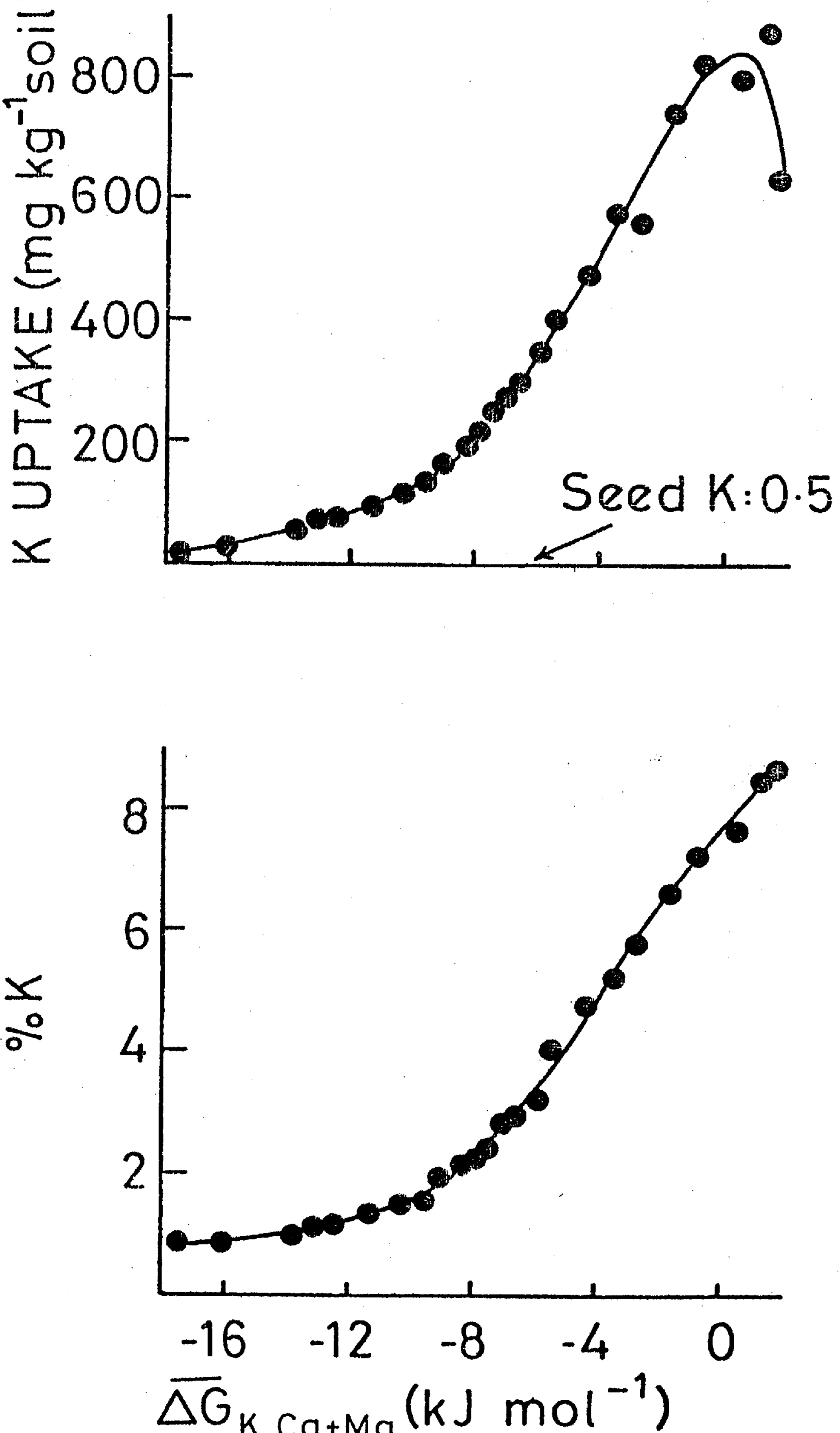


Figure 5.10 Potassium uptake and concentration in sugar beet tops related to the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

some must also be translocated to the roots. It is also possible that some K is released into the soil as the seed decomposes.

However, as suggested earlier; high seed K levels must play a role in determining the critical K potentials of a crop, particularly ΔG_{exh} and ΔG_{opt} in the early stages of growth.

The form of the K uptake curves was similar for all five crops (Figures 5.6-5.10), having a characteristic exponential rise in K uptake at low $\overline{\Delta G}_{K,Ca+Mg}$ values, as also observed for the two grasses (Section 4.3.5). At high $\overline{\Delta G}_{K,Ca+Mg}$ values K uptakes reached a maximum. Approximate $\overline{\Delta G}_{K,Ca+Mg}$ values corresponding to maximum K uptake were -6, -3, -2, -1 and 0 kJ mol^{-1} for wheat, sweet corn, peas, sugar beet and beans respectively. This implies that wheat had the lowest uptake capacity per unit volume of soil and beans the most. At values of $\overline{\Delta G}_{K,Ca+Mg}$ greater than ΔG_{tox}, K uptake decreased in all crops except beans, probably as a result of the corresponding decrease in dry matter production.

At low $\overline{\Delta G}_{K,Ca+Mg}$ values, %K in all crops did not increase until a certain threshold was reached (Figures 5.6-5.10; i.e. yield and K uptake increased by the same factor for the same increase in $\overline{\Delta G}_{K,Ca+Mg}$). Above this threshold, K uptake increased proportionately more than did yield for the same change in $\overline{\Delta G}_{K,Ca+Mg}$. Threshold values were similar for wheat, sweet corn, peas and beans (approximately -14, -13, -14 and -14 kJ mol^{-1} respectively), but that for sugar beet was slightly more negative -16 kJ mol^{-1}.

With increases in $\overline{\Delta G}_{K,Ca+Mg}$ above these values, for peas and beans, %K increased exponentially over the whole range measured and, in sugar beet, to a point where the slope of the curve began to decrease slightly (-4 kJ mol^{-1}). For sweet corn, after an initial exponential rise, %K reached a maximum of about 4.2% at -2 kJ mol^{-1}. With wheat, %K increased with $\overline{\Delta G}_{K,Ca+Mg}$ to a plateau corresponding with maximum K uptake and then, at higher $\overline{\Delta G}_{K,Ca+Mg}$ values, increased further as yield decreased.

The decrease in yield at ΔG_{tox} could be caused by inhibition of uptake of other nutrients by excess K in the soil or to toxic levels of K in the plant. With sweet corn, the latter cannot be the case because the concentration in the plant was maximum at $\overline{\Delta G}_{K,Ca+Mg}$ values lower than ΔG_{tox}. For the other four crops, one or both factors could be responsible.

Table 5.3 gives ΔG_{opt} and ΔG_{tox} values together with corresponding plant K concentrations for the five arable crops and also for ryegrass and fescue in Experment A (ΔG_{opt} only; see Section 4). The two legumes required the lowest %K for maximum yield, followed closely by the cereals. The optimum %K for the grasses was considerably higher but sugar beet had the largest requirement of 2.6% K for maximum yield.

Toxicity values were not obtained for the grasses. As already stated, for sweet corn the %K in the crop at ΔG_{tox} cannot be considered toxic, but for the other crops, it is possible that these values are toxicity thresholds. Sugar beet was clearly the most tolerant; wheat, beans and peas were considerably less so.

5.6 Clover

The clover germinated very unevenly, giving very variable yield data. Figure 5.11 shows the yields of clover plotted against $\overline{\Delta G}_{K,Ca+Mg}$. ΔG_{opt} and ΔG_{tox} could not be derived as they were for the grasses (Section 4) or the other crops (Section 5.4).

Table 5.3 Optimum and toxic K potentials (ΔG_{opt} and ΔG_{tox}) and corresponding tissue K concentrations for several crops after 4 weeks' growth on Newport series soil.

Crop	ΔG_{opt} (kJ mol^{-1})	% K at $\overline{\Delta G}_{opt}$	ΔG_{tox} (kJ mol^{-1})	% K at ΔG_{tox}
Wheat	-10.6	1.4	-0.1	4.0
Sweet Corn	-10.8	1.2	1.8	4.2
Field Beans	-12.4	1.0	-1.3	4.4
Peas	-13.2	1.0	0.0	5.3
Sugar Beet	-7.3	2.6	1.3	8.3
Perennial Ryegrass	-6.8	2.0	-	-
Creeping Red Fescue	-5.8	2.3	-	-

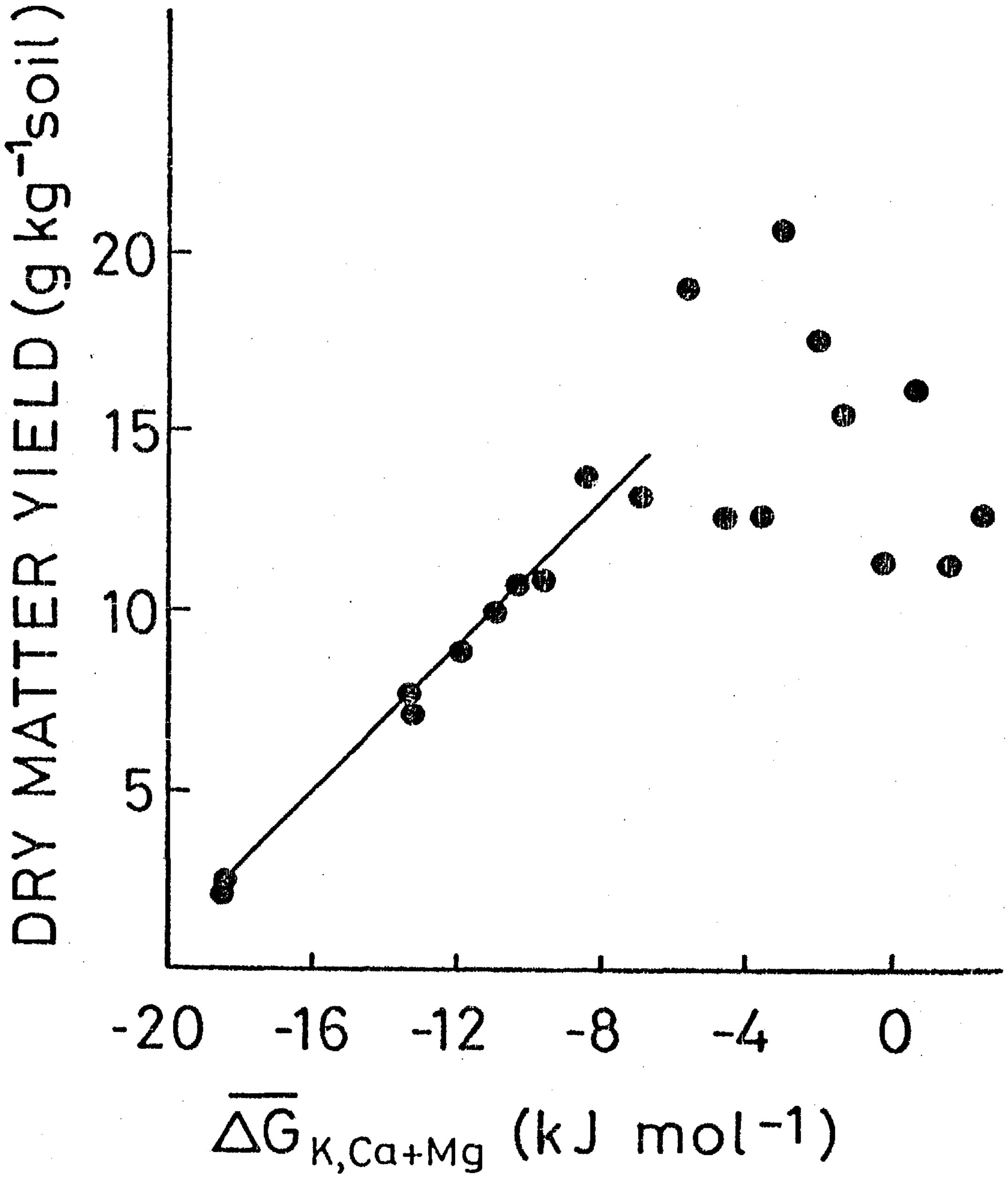


Figure 5.11 Dry matter yield of clover related to the mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Newport(2) soil.

However, at low values of $\overline{\Delta G}_{K,Ca+Mg}$, yield increased linearly with ΔG_{opt}, so that a linear regression could be fitted over the range -19 to -7 kJ mol^{-1}. From this, a ΔG_{exh} value of -20.8 kJ mol^{-1} was obtained by extrapolation, similar to the values obtained for the other crops except for field beans (Table 6.1). It is a much more positive value than that obtained by Barrow, *et al.* (1967) for subterranean clover (-25 kJ mol^{-1}). However, they obtained their value by cropping the soil until the clover took up no more K (see Section 1), i.e. for zero K uptake rather than zero yield.

6. THE EFFECT OF LIGHT INTENSITY ON CRITICAL POTASSIUM POTENTIALS FOR PERENNIAL RYEGRASS ON BATCOMBE SOIL

6.1 Introduction

A soil nutrient potential defines the work (or energy output) required of the plant to remove the nutrient from the soil. Critical nutrient potentials at specific levels of such plant performance at each development stage are determined by the plant's requirement and ability to extract the nutrient from the soil. Both of these factors may be affected by the energy input to the plant as radiation utilised in photosynthesis. If the quality and the intensity of radiation is limiting, improving it gives a bigger plant with a larger nutrient requirement and possibly a greater ability, in the form of a more extensive root system and a greater uptake capacity per unit of root surface, to remove the nutrient.

Thus critical K potentials for plants may vary with light intensity and quality. Interactions between the K status of the plant and photosynthetic rate have been reported by several workers. Haeder and Mengel (1976) found that increasing the K concentration of a culture solution ten-fold in part compensated for a reduced light intensity in the yield production, at anthesis, and also doubled the rate of $^{14}CO_2$ assimilation in spring wheat. Smid and Peaslee (1977) found that the CO_2 assimilation rate in maize increased with K concentration in the plant. Tanaka and Hara (1972) observed that the photosynthetic rate of young maize leaves increased with K concentration of the tissue up to 1.5% on a dry matter basis.

It therefore seems that the K requirement of the plant, in terms of concentration in the tissue, increases with decreasing light intensity. However, the total requirement may decrease with decreasing light intensity, as the size of the plant is reduced. Therefore it is difficult to predict the effect of changes in light intensity on critical K potentials for crops. The following experiment investigated the effect of reducing the intensity of light on the optimum K potential for perennial ryegrass.

6.2 Methods

Batcombe soil was prepared as described in Section 2 to give 16 K levels, each replicated 6 times. Details of the treatment solutions are given in Appendix 1.

Ryegrass seed was sown and germinated in the pots in the manner described for Experiments A and B in Section 4.2. The pots were randomised in 3 replicate blocks in each of two Saxcil growth cabinets. After germination, the light intensity in one of the cabinets was set to 17000 lx and the other to 8500 lx. Nutrient solution was added to the pots during growth as described in Section 4.2. The grass was cut 40 days after germination. The clippings were dried and weighed and analysed for K.

Soil samples were taken and analysed as described in Section 2.

6.3 Results

Table 6.1 gives the mean yields for each treatment. The coefficient of variation of the yields was 3.8%. Yields were significantly larger under the higher light intensity for each K level.

Table 6.1 Dry matter yields of perennial ryegrass grown under 2 light intensities on Batcombe soil given 16 K levels. (Coefficient of variation = 3.8% : S.E.D. = 0.4)

K level	Light Intensity (lx) 8500	Light Intensity (lx) 17000
	— Yield (g kg^{-1} soil) —	
1	9.6	11.1
2	10.7	12.6
3	11.1	13.4
4	11.8	13.8
5	11.9	14.9
6	12.3	14.8
7	13.0	14.6
8	12.9	14.8
9	13.4	15.8
10	13.0	15.9
11	13.8	16.3
12	13.9	16.8
13	14.1	16.4
14	14.5	16.3
15	14.2	16.3
16	14.2	16.6

Mean soil K potentials for the growth period, ($\overline{\Delta G}_{K,Ca+Mg}$) were calculated as described in Section 4.3. Figure 6.1 shows the mean yields plotted against $\overline{\Delta G}_{K,Ca+Mg}$. Third degree polynomials were fitted to these response curves for each light intensity, the parameters of which are given in Table 6.2.

Although yields were higher at the higher light intensity, the maxima of the 2 curves occurred at similar values of $\overline{\Delta G}_{K,Ca+Mg}$, i.e., ΔG_{opt} values for the ryegrass under the 2 light intensities were not significantly different. This observation can be explained by the fact that K uptakes were the same under the 2 light intensities at any given value of $\overline{\Delta G}_{K,Ca+Mg}$ (Figure 6.2). It follows that K concentrations in the grass were greater under the lower light intensity, as is demonstrated in Figure 6.3. So the K concentration in the plant at ΔG_{opt}, i.e. that required for maximum yield, is higher under 8,500 lx than under 17,000 lx.

The ability of the plant to remove K from the growth medium is not reduced by a decreased light intensity, but its K requirement, in terms of tissue concentration, for maximum yield is increased. This can be explained by the observation that K increases CO_2 assimilation rate, as discussed in the Introduction to this Section. This allows greater efficiency of light utilisation in photosynthesis and yield production and therefore compensates partly for the potential loss in yield due to the reduced light intensity.

However, the energy input to the plant had no direct effect on its energy output in the uptake of K.

The ΔG_{opt} value (-4.8 kJ mol^{-1}) obtained for ryegrass under 17,000 lx in this experiment did not coincide with the value obtained

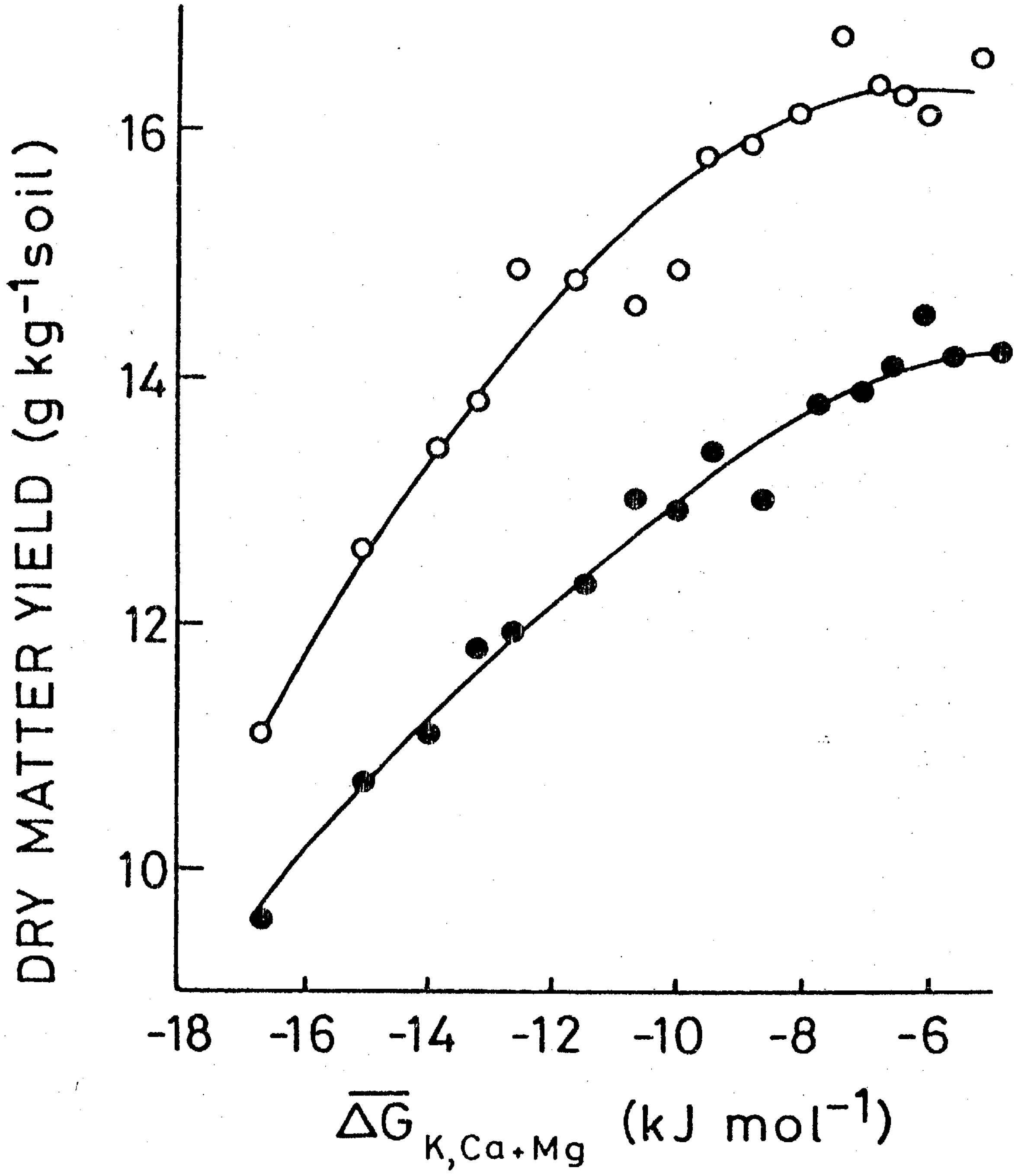


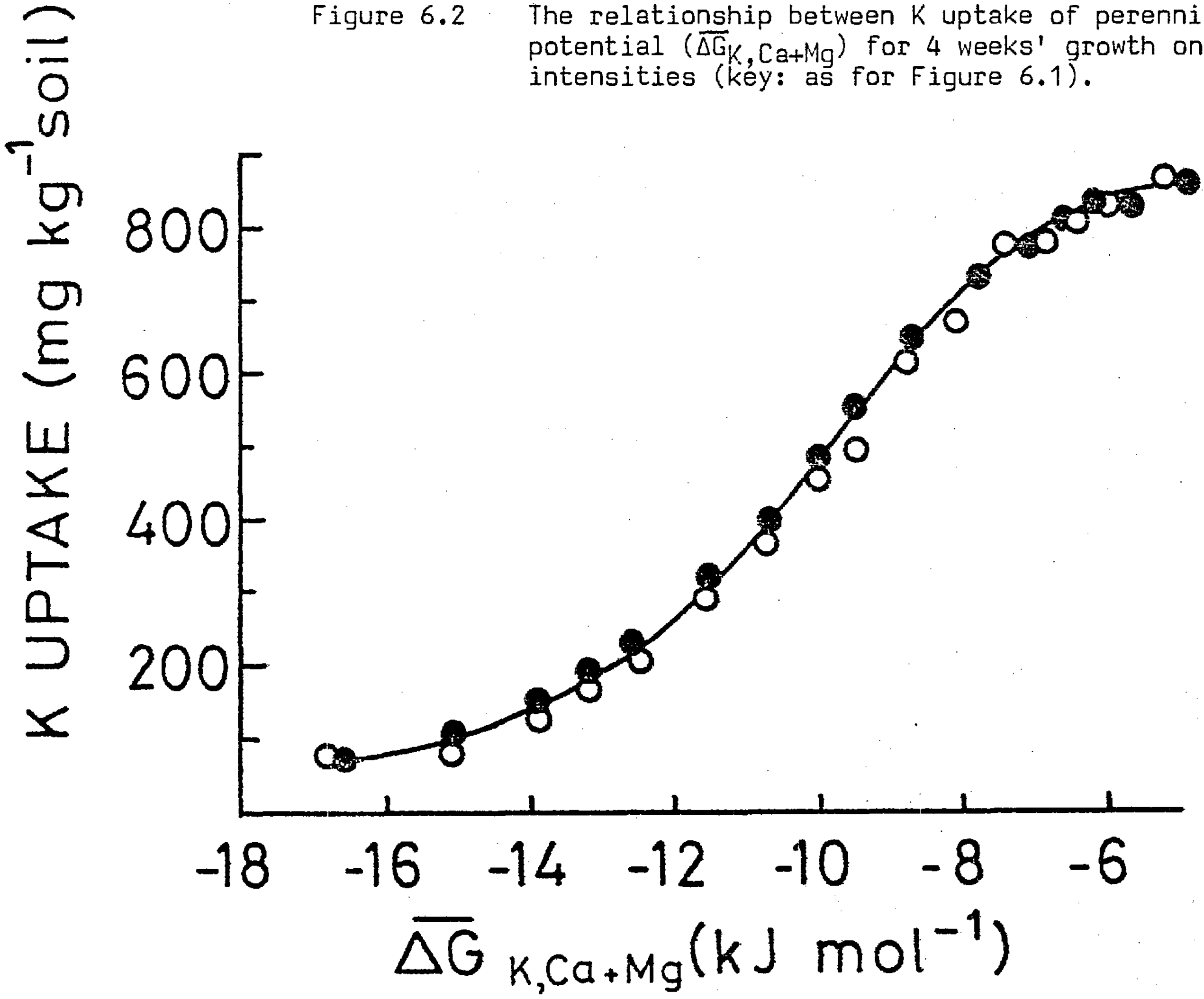
Figure 6.1 The relationship between yield of perennial ryegrass and mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Batcombe soil under 2 light intensities.

(○ 28,000 lx; ● 17,000 lx).

Table 6.2 Third degree polynomial coefficients relating dry matter yields of perennial ryegrass to mean soil K potential over 4 weeks' growth, and derived ΔG_{opt} values and maximum yields ($y = a + bx + cx^2 + dx^3$).

Light Intensity (lx)	a	b	c	d	% Variance Accounted for	ΔG_{opt} (kJ mol^{-1})	Maximum Yield (g kg^{-1} soil)
17000	16.0	-0.19	-0.013	0.00095	98.7	-4.8	16.5
8500	13.4	-0.40	-0.051	-0.00083	99.1	-4.4	14.2

Figure 6.2 The relationship between K uptake of perennial ryegrass and mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Batcombe soil under 2 light intensities (key: as for Figure 6.1).



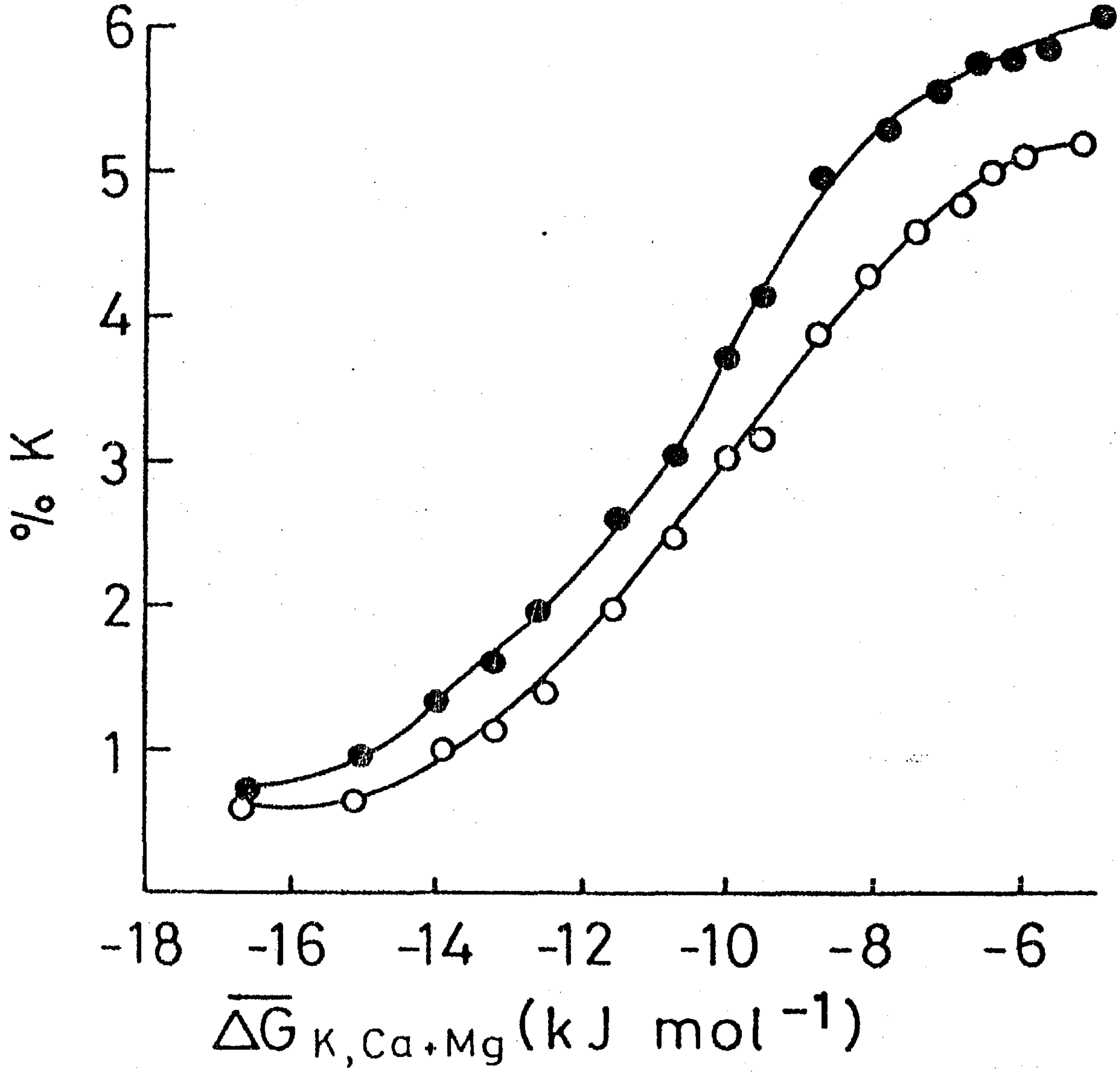


Figure 6.3 The relationship between K concentration in perennial ryegrass and mean soil K potential ($\overline{\Delta G}_{K,Ca+Mg}$) for 4 weeks' growth on Batcombe soil under 2 light intensities (key: as for Figure 6.1).

on the same soil and under the same light intensity in Experiment B (Section 4, -6.3 kJ mol^{-1}). Although the 2 values result from similar total growth periods, that from Experiment B was derived from 2 cuts. After the first cut, the plants required K mainly for growth of the tops and not for establishment of a root system. So usage of K in yield production in Experiment B was more efficient and ΔG_{opt} for the total growth period was less than in the experiment reported here. The ΔG_{opt} value obtained in Experiment A for 4 weeks growth of ryegrass (-4.7 kJ mol^{-1}) was not significantly different from that obtained in this experiment, despite the shorter growth period.

Exhaustion K potentials were not extrapolated from this data because the degree of extrapolation would have been too great to give the results any meaning, particularly since the fitted curves were third degree polynomials.

7. GENERAL DISCUSSION AND CONCLUSIONS

7.1 Comments on experimental techniques

The techniques used in this work for soil and plant analysis and initiating the pot experiments are well established and therefore require no further discussion.

The use of constant environment facilities for the pot experiments was most important in this work. It gave a very satisfactory level of precision, demonstrated by low coefficients of variation and the ability to fit curves to the data which accounted for nearly all the variance. The small pots, chosen for this work to make the best use of the constant environment space available, influenced the results in several ways:-

a) they restricted the size of crop that could be grown and hence the duration of the growth period of the crop;

b) the basal nutrients in the small volume of soil were quickly depleted. This was successfully allowed for by applying large amounts in most cases (N, Mg, P and trace elements) but, after 8 weeks' growth of grass, S became limiting (see Section 4.3.2.2);

c) exchangeable potassium was also depleted rapidly in the small volume of soil. This accentuated the effects on grass yields of differences in rates of release of non-exchangeable K between soils. It also caused changes in K potential much greater than would be seen in the field and necessitated calculations of mean values of $\Delta G_{K,Ca+Mg}$ for a growth period, which would be questioned if the K uptake:time curve is non-linear (as would be expected during exponential growth). However, it is hoped that the short growth periods reduced any errors of this nature.

7.2 The derivation of critical potassium potentials

Response curves are a common feature of agronomic research but they have not often been used to obtain critical nutrient potentials for crops. The two types of 'fitted curves' used in this work (polynomials for grasses and intersecting straight lines for other crops) to derive critical $\Delta G_{K,Ca+Mg}$ values gave results which cannot be directly compared with one another. Because they result from more extensive data, the intersecting straight lines probably gave more meaningful results.

Other workers have obtained crop response curves to either K concentration in culture solution (e.g. Asher and Ozanne, 1967; Wild, et al., 1974) or AR_0 values in soil (e.g. Arnold, et al., 1968; Tinker, 1964b). These curves tend to asymptotic maxima, from which it is difficult to interpolate optimum concentrations or AR_0 values. The use of the more fundamentally based logarithmic function of K potential in this work has allowed ΔG_{opt} to be precisely interpolated, and also the large range of soil K potential used enabled the derivation of ΔG_{tox} values for some crops.

The extrapolation of the response curves back to zero yield perhaps gives more definitive values of ΔG_{exh} than the more direct methods involving exhaustive cropping (Addiscott and Johnston, 1975; Barrow, et al., 1967; Islam and Bolton, 1970; Martin and Fergus, 1973; Sinclair, 1979; Talibudeen and Dey, 1968). The ΔG_{exh} values obtained from the latter (discussed in Section 1) are generally more negative than those obtained by extrapolation in this work. This indicates that the initial yield response to increasing K potential probably increases exponentially, whereas the extrapolated values of ΔG_{exh} define the $\Delta G_{K,Ca+Mg}$ values where responses become significant. They provide, therefore, an index which can be used to compare the tolerances of crops to low K levels more reliably than those observed when crop yield is negligible.

7.3 The critical $\Delta G_{K,Ca+Mg}$ values obtained

The similar ΔG_{exh} values obtained in this work for wheat, sweet corn, peas, clover and sugar beet suggest that these crops do not differ significantly in their tolerance to low K levels on any one soil. The ΔG_{exh} values for 4 weeks' growth of the grasses on the Newport(1) soil were more positive, indicating that they require a higher K level for survival than the other crops, i.e., they have a lesser ability to remove K from the soil at low K levels. The ΔG_{exh} value obtained for field beans was extremely low (-40 kJ mol^{-1}), but the data for positive yield response from which it was extrapolated was limited so it could well be erroneous.

ΔG_{opt} values decreased in the order grasses>sugar beet>wheat and sweet corn>field beans>peas, for 4 weeks' growth on Newport series soils (Newport(1) for the grasses and Newport(2) for the other crops). Values for the grasses, derived from polynomials, are not strictly comparable with those for the other crops, but this is unlikely to affect the order given above.

The seed K contents differed considerably between the various crops (Table 5.2) and when large, as in the peas and beans, made large contributions to the total K uptake over the short growth period. At the lowest soil K level, the seed K content of the beans was more than that of the tops. The beans and peas had the most negative ΔG_{opt} values, and sugar beet and the grasses, with the lowest contributions of K from their seeds, had the highest ΔG_{opt} values. The level of seed K was therefore important in determining critical $\Delta G_{K,Ca+Mg}$ values for the crops.

In a mature crop, K contributed by the seed would only represent a tiny fraction of the total in the plant and thus not have a direct influence on the soil K level required for optimum growth. However, the seed K content may affect the establishment of the seedlings, a high content enabling the development of an extensive root system (by interaction with N and P) which in turn might enable the plant to survive on a soil of low K potential. Thus seed K content could be a factor to be considered when selecting crops for any particular soil, especially where K fertiliser is expensive or in short supply.

The results also showed that very high soil K potentials reduce crop yields. Because K concentrations in the plants were maximum at K potentials lower than ΔG_{tox}, it is unlikely that this was caused by toxic effects of K in the plant. The yield reduction could be attributed though to the observed inhibition of Ca and/or Mg uptake at high soil K potentials. However, values of ΔG_{tox} were far higher than any $\Delta G_{K,Ca+Mg}$ values likely to be encountered in normal soils.

7.4 Implications of this work to the value of $\Delta G_{K,Ca+Mg}$ in agronomy

This work has shown that the critical K potentials, ΔG_{exh}, ΔG_{opt} and ΔG_{tox}, can be determined for crops for a specified period of growth in a soil medium.

The experiments with grasses on different soils (Section 4) showed that ΔG_{opt} and ΔG_{exh} for both grasses varied considerably between soils, in small pots with high crop densities. This was probably because of the large change in $\Delta G_{K,Ca+Mg}$ over the cropping period (Table 7.1). Under these conditions, ΔG_{opt} correlated with the CEC-s of the soils - the greater the CEC, the more negative was ΔG_{opt}, which suggests that the quantity of K available to the plant in the soil, rather than the K potential, controlled K uptake. It is possible that, with a smaller 'crop:soil' ratio, i.e. less intense cropping and smaller K removals, this effect would be lessened and that critical K potentials would be independent of soil type, which would simulate field conditions better.

Similarly, as stated above, the rate of release of 'peripheral' K affected K uptake from these small volumes of soil. The experiments showed that there was little or no yield response to increasing K potential on the micaceous Worcester soil, presumably because of a high rate of release of 'peripheral' K.

So, these experiments have not produced conclusive evidence to show that critical K potentials can be determined for all crops independent of soil type, but the question remains open, because of the experimental conditions of abnormal 'crop:soil' ratios in this work. It has been shown though that such measurements allow comparisons between crops of a) their ability to survive at low K potentials; b) the optimum K potentials for yield production; c) their tolerance of high K potentials.

The characteristics of a plant which determine its critical K potentials include the extent of the root system, the rate of uptake per unit surface area of the root and the amount of K required by the crop. Thus, a fast growing crop will need much K which it can obtain from a low soil K potential only if it has an

Table 7.1 Changes in soil K potential corresponding to ΔG_{opt} during 4 weeks' growth of some crops

Crop	Soil	$\Delta G_{K,Ca+Mg}$ (kJ mol^{-1})	
		Before cropping	After cropping
Ryegrass	Andover	-7.3	-19.3
	Batcombe	-8.0	-10.1
	Bromyard	-6.7	-15.7
	Hanslope	-10.4	-17.9
	Newport(1)	-4.6	-16.2
Fescue	Andover	-7.2	-15.7
	Batcombe	-6.4	-15.2
	Bromyard	-6.7	-20.5
	Hanslope	-10.0	-14.8
	Newport(1)	-3.6	-7.5
Spring wheat	Newport(2)	-8.7	-17.8
Sweet corn	Newport(2)	-8.7	-19.8
Field beans	Newport(2)	-10.7	-20.3
Leafless peas	Newport(2)	-11.6	-17.4
Sugar beet	Newport(2)	-5.8	-14.6

efficient root system i.e., one which is extensive and also has a high uptake rate. The critical $\Delta G_{K,Ca+Mg}$ values derived in this work, because of the restrictive soil volume did not reflect differences in the extents of the root systems of the crops. Also, the short growth period probably minimised differences in the total K demands of the crops. Therefore, the observed differences between the critical K potentials for the crops mainly reflected differences in the uptake rates of the roots of the plants, and also in the K contents of the seeds (as already suggested) to a greater extent than might be expected in the field.

7.5 Energy input and output

Light intensity during growth did not affect ΔG_{opt} for ryegrass or the relationship between $\Delta G_{K,Ca+Mg}$ and K uptake by the plant. Uptake of K is known to be an active process, i.e., it requires energy. Talibudeen (1974) suggested that $\Delta G_{K,Ca+Mg}$ is a measure of the work output of the plant in K uptake. This being the case, the results obtained in this work suggest that there is no relationship between the energy input in photosynthesis and work output in K uptake.

7.6 Suggestions for future work

Two obvious questions that this work leaves unanswered are, a) do critical K potentials for other crops vary with soil type in the same way as do those for the grasses? b) is the variation from soil to soil an artifact produced by experimentation in small pots? To answer (a), the experiments conducted in this work on wheat, sweet corn, field beans, peas, sugar beet and clover should be repeated on contrasting soils. Experiments in larger pots or in the field would be required to answer (b). For larger pots, more extensive constant environment facilities would be required. In the field the precision of the controlled environment is lost and also it is difficult to create a large range of soil K potential, because of the high K buffering capacity of large volumes of soil undergoing natural wetting and drying cycles. Experiments with larger volumes of soil would have the additional advantage though of allowing determination of critical K potentials for later stages of development of the crops. This is an important consideration in the continuation of this work.

Projecting more generally, it may be of value to search for ways in which critical K potentials relate to and can be used in conjunction with measurements of rates of release and transport of soil K.

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APPENDIX

Experimental nutrient treatments

(Applied to the soil in mixed solutions to give 10:1 soil:solution ratio, except CaS04 which was added as a powder.)

1. For ryegrass and fescue on six soils (Experiment A; see Section 4).

K Level	KNO_3	K_2SO_4	$Ca(NO_3)_2$	$Mg(NO_3)_2$	$CaSO_4$	Total K^+
			meq kg^{-1} soil			
1	0	0	18.2	4.2	9.8	0
2	2.8	0	15.4	4.2	9.8	2.8
3	5.6	0	12.6	4.2	9.8	5.6
4	11.2	0	7.0	4.2	9.8	11.2
5	16.8	0	1.4	4.2	9.8	16.8
6	18.2	9.8	0	4.2	0	28.0
7	18.2	23.8	0	4.2	0	42.0
8	18.2	51.8	0	4.2	0	70.0

APPENDIX (continued)

2. For ryegrass and fescue on two soils (Experiment B; see Section 4) :

K Level	KNO_3	K_2SO_4	$Ca(NO_3)_2$	$Mg(NO_3)_2$	$CaSO_4$	Total K^+
			meq kg^{-1} soil			
			Leached soil			
1	0	0	18.2	4.2	9.8	0
2	0.7	0	17.5	4.2	9.8	0
3	1.4	0	16.8	4.2	9.8	1.4
4	2.1	0	16.1	4.2	9.8	2.1
5	2.8	0	15.4	4.2	9.8	2.8
			Unleached soil			
6	0	0	18.2	4.2	9.8	0
7	1.4	0	16.8	4.2	9.8	1.4
8	4.2	0	14.0	4.2	9.8	4.2
9	5.6	0	12.6	4.2	9.8	5.6
10	8.4	0	9.8	4.2	9.8	8.4
11	11.2	0	7.0	4.2	9.8	11.2
12	16.8	0	1.4	4.2	9.8	16.8
13	18.2	4.2	0	4.2	9.8	22.4
14	18.2	9.8	0	4.2	0	28.0
15	18.2	16.8	0	4.2	0	35.0
16	18.2	23.8	0	4.2	0	42.0
17	18.2	30.8	0	4.2	0	49.0
18	18.2	37.8	0	4.2	0	56.0
19	18.2	44.8	0	4.2	0	63.0
20	18.2	51.8	0	4.2	0	70.0

APPENDIX (continued)

3. For wheat, sweet corn, field beans, peas, sugar beet, and clover on Newport(2) soil.

K Level	KNO_3	K_2SO_4	$Ca(NO_3)_2$	$Mg(NO_3)_2$	$CaSO_4$	Total K^+
			meq kg^{-1} Soil			
			Leached soil			
1	0	0	18	2	8	0
2	0.5	0	17.5	2	8	0.5
			Unleached soil			
3	0	0	18	2	8	0
4	0.5	0	17.5	2	8	0.5
5	1	0	17	2	8	1
6	2	0	16	2	8	2
7	3	0	15	2	8	3
8	4	0	14	2	8	4
9	5	0	13	2	8	5
10	6	0	12	2	8	6
11	7	0	11	2	8	7
12	8	0	10	2	8	8
13	9	0	9	2	8	9
14	10	0	8	2	8	10
15	12	0	6	2	8	12
16	14	0	4	2	8	14
17	18	0	0	2	8	18
18	18	4	0	2	4	22
19	18	8	0	2	0	26
20	18	16	0	2	0	34
21	18	22	0	2	0	40
22	18	32	0	2	0	50
23	18	42	0	2	0	60
24	18	52	0	2	0	70

APPENDIX (continued)

4. For ryegrass under 2 light intensities on Batcombe soil (see Section 6).

K Level	KNO_3	K_2SO_4	$Ca(NO_3)_2$	$Mg(NO_3)_2$	$CaSO_4$	Total K^+
			Meq Kg^{-1} soil			
1	0	0	18.2	4.2	9.8	0
2	1.4	0	16.8	4.2	9.8	1.4
3	2.8	0	15.4	4.2	9.8	2.8
4	4.2	0	14.0	4.2	9.8	4.2
5	5.6	0	12.6	4.2	9.8	5.6
6	8.4	0	9.8	4.2	9.8	8.4
7	11.2	0	7.0	4.2	9.8	11.2
8	14.0	0	4.2	4.2	9.8	14.0
9	16.8	0	1.4	4.2	9.8	16.8
10	18.2	4.2	0	4.2	5.6	22.4
11	18.2	9.8	0	4.2	0	28.0
12	18.2	16.8	0	4.2	0	35.0
13	18.2	23.8	0	4.2	0	42.0
14	18.2	30.8	0	4.2	0	49.0
15	18.2	37.8	0	4.2	0	56.0
16	18.2	51.8	0	4.2	0	70.0

M.B. Page

Ph.D. Thesis 1980 (London)

ERRATA

Page	Line	
22	Equation 1.3 should read:	$f_\pm = (f_+^{v+} . f_-^{v-})^{1/(v++v-)}$
23	Equation 1.5 should be qualified:	the dissociation constant of water is 14.2 at 20°C.
24	21	', (ie. pK - ½pCa)' should read: ', ie. -(pK - ½pCa),'.
31	1	'unspecific' should read 'non-specific'.
41	10	Commas missing; should read: 'in soil by diffusion, and plant uptake.'
47	last	'3.17' should read '31.7'.
55	last	'e' missing from glasshouse.
69	19	'colormetry' should read 'colorimetry'.
79	20	'few' should read 'fewer'.
89	10	Inorganic N released for Newport(1) should be 55 ppm.

ERRATA (cont'd.)

Page	Line	
106	3	Left heading should read: 'Maximum Yield (g kg^{-1} soil)'
112	10	'a symptotic' should read 'asymptotic'.
116	3	Should read: ',as derived from second and third degree polynomials.'
153	6	Should read: 'or by toxic'.
	13	'Experment' should read 'Experiment'.
161)) 15)	4)) 16)	The key to Figure 6.1 should read: (O 17,000 lx; ● 8,500 lx).
187	18	'Shore' should read 'Shone'.

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PLANT CHEMISTRY, SOIL MICROBIOLOGY AND
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NITRATE CONCENTRATIONS UNDER WINTER WHEAT AND IN FALLOW SOIL DURING SUMMER AT ROTHAMSTED

by M. B. PAGE and O. TALIBUDEEN

Rothamsted Experimental Station, Harpenden, Herts

SUMMARY

Soil nitrate measurements were made on Broadbalk, under winter wheat and in adjacent fallow soil, during April–August in the years 1972 to 1975 with a nitrate ion selective electrode. The results are presented as pNO_3 values ($= -\log_{10}[NO_3^-]$).

For a given level of manurial N, annual mean pNO_3 values correlate with total rainfall for the period of measurement but not with percolation rate. On the N_2PKNaMg plot, a sharp decrease in nitrate concentration was consistently observed during May in fallow and cropped soil. During long dry periods, nitrate concentrations increased in the 5–25 cm zone in July and August, and on the FYM plot rose to maxima in July.

Grain yield and annual mean pNO_3 values were very poorly correlated although the high pNO_3 ('Nil' and PKNaMg) plots gave much smaller yields than the low pNO_3 plots given N manures.

The annual mean difference between $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ correlated with grain yield on the N_2PKNaMg plot. In 1972, 1974 and 1975, minima in this difference were observed at Feekes' stages of development 6, 10 and 11.1 on this plot, representing depletion of soil nitrate by the crop. Quadratic curves, fitted to the effect of the period of cropping on this difference for the N_2PKNaMg and N_4PKNaMg plots during 1972–74, show maximum depletion of nitrate during June and July. Similar highly replicated measurements made on a commercial field of winter wheat (Long Hoos III at Rothamsted) in 1975 demonstrated well the depletions of nitrate in cropped soil at these stages of crop development.

INTRODUCTION

In aerobic soil environments, nitrogen is taken up by cereals mainly as nitrate. Ammonia or ammonium-N is quickly transformed to nitrate-N by nitrification or adsorbed by soil minerals. Knowledge of its availability in the soil to the crop and also of the crop's needs throughout its development are important.

Jansson[7] considers nitrate to be a 'passive' fraction of soil nitrogen because, once formed, it does not readily enter into the continuous 'immobilisation-mineralisation' processes. This is based on the observation[6] that microbes prefer ammonium to nitrate as a source of mineral nitrogen. Evidence reviewed[2] suggests that under aerobic conditions, nitrate is not appreciably reduced to N_2 and N_2O by denitrifying bacteria. Also, only small amounts of nitrate are formed in the soil by mineralisation of organic matter in a continuously cropped arable soil receiving only mineral N fertiliser.

Data from Rothamsted's drain gauges[12] show that fallow soil, containing 0.15% N, released initially (1877) 45 kg NO_3-N ha^{-1} $year^{-1}$ in drainage water which dropped to 23.5 kg NO_3-N ha^{-1} $year^{-1}$ after 50 years. However, as much as 78 kg NO_3-N ha^{-1} was recorded in the top 18 in of the unmanured fallow plots on Broadbalk during May and June in this period. The soil serving the drain gauges was kept free of vegetation so that plant residues could not accumulate. When small amounts of sucrose were added, nitrate in the drainage waters decreased to 9 kg ha^{-1} $year^{-1}$ because heterotrophic bacteria, given an energy source, were much more efficient than Nitrosomonas in competing for freshly mineralised ammonium. In a cropped soil, organic matter added annually as roots and stubble probably accentuates this effect, although the residues are eventually broken down and are not built up from year to year[8]. Similar effects in the rhizosphere were reported[2 4], *i.e.* residues from root hairs, cap cells and exudates continuously supplied fresh organic matter. Hence, under crops on old arable soils, nitrification is not likely to contribute significantly to the pool of available nitrate.

The main factors affecting levels of nitrate in the plough layer of an arable soil under a cereal crop, fertilised with mineral nitrogen, are therefore rainfall, rate of evaporation and crop uptake. Climate causes big variations in the distribution of nitrate down a soil profile from year to year. Russell and Richards[12] showed, from a mean of 38 years' results, that in the summer months nitrate in drainage waters, from fallow soil, is more closely related to percolation (the net effect of rainfall and evaporation) than to total rainfall; however in the winter months the reverse is true.

In soils fertilised with FYM, rates of mineralisation and nitrification are prime factors in determining the levels of nitrate available to the plant. These depend very much on soil temperature and moisture content. Therefore variations in climate can cause even greater changes in patterns of nitrate distribution from year to year.

This paper presents results of four years' nitrate measurements made on Broadbalk in the summer months and of one years' measurements made on a commercial field. Trends in them are sought which are consistent from year to year. Also these results will be compared with the results of other workers using different methods. Methods and results of the first year's work have already been published[9].

METHODS

The system of measurement and instrumentation described earlier[9] was used throughout with only slight modifications to suit very dry conditions. All measurements on Broadbalk were made on Section I (continuous wheat, last fallowed 1966). The plots chosen were changed from year to year (Table 1). In 1973 and 1974, holes were maintained at 5, 15 and 25 cm (5, 12.5 and 20 cm in 1972) on two opposite corners of each plot, between the rows of crop and in the path 40 cm from the crop. Holes were lined with plastic tubing, 4 cm in diameter, and corked in between measurements, which were made at regular intervals between April and August.

In 1975 measurements were made at 15 and 50 cm depths only. Also, on plot 07, holes were put in on all four corners, in duplicate, at 15 cm depths in the crop and adjacent headland as before. Additional measurements were made on a commercial field of winter wheat, Long Hoos III. Here ten, 2 m square, fallow sites were arranged in a strip 150 metres long across the field. Four holes, 15 cm deep were sunk in each of these, 50 cm from the crop and four adjacently in the crop. One hole was also put in the centre of each fallow plot *i.e.* 100 cm from the crop.

TABLE 1

Measurement sites on Rothamsted Farm

Plots	Broadbalk					Long Hoos III
	2/2	03	05	07	09	
Manuring regime*	FYM 35 tonnes ha^{-1}	Nil	PKNaMg	96 kg N ha^{-1} + PKNaMg	192 kg N ha^{-1} + PKNaMg	134 kg N ha^{-1} + PK
Measurements made	1973 1974 1975	1973	1974	1972 1973 1974 1975	1972 1973 1974	

* P 35 kg ha^{-1}; K 90 kg ha^{-1}. (On Long Hoos III, P = 27 kg ha^{-1}, K = 52 kg ha^{-1}); Mg 35 kg ha^{-1} every 3 years; Na 15 kg ha^{-1} (discontinued in 1974); All N as 'Nitro-Chalk' in mid-April.

Measurements were made by first wetting the soil at the bottom of the holes with 5 mls of water. In 1973 and 1974 the procedure was to wait 10–15 minutes to allow the soil and water to come to equilibrium so that the soil was locally at about water holding capacity. In very dry conditions, cracks and fissures presented problems with this method so in 1975 the soil was mixed with the water to a paste and then left only 3–4 minutes before the measurement was made.

Statistical evidence from the more highly replicated 1975 results shows that the data is best fitted by a log-normal distribution. Therefore all measurements have been presented as pNO_3 values ($= -\log_{10}[NO_3^-]$, where $[NO_3^-]$ is in moles litre^{-1}). Results from the years 1972–74 have been summarised by taking profile means. These were calculated as

$$\text{Profile Mean} = \tfrac{1}{2}\left(\frac{a+b}{2} + \frac{b+c}{2}\right) = \frac{a+2b+c}{4}$$

where a, b and c are 5, 15 (or 12.5) and 25 (or 20) cm measurements respectively. This was considered to be the best estimate possible from the data.

RESULTS AND DISCUSSION

pNO_3 values related to rainfall, percolation and nitrogen manuring during 1972–75

On Broadbalk, Plot 07 is taken as the standard with which other plots are compared because its fertiliser regime is closest to that used commercially on similar soils. Here, overall pNO_3 levels vary considerably from year to year (Table 2). (Strictly, because the 1975 measurements were only made at one depth, the 'means' cannot be compared with those of previous years.) The large differences between the means of the years 1972–74 can be explained to some extent by rainfall (Table 3). Higher rainfall in 1973 gave rise to higher pNO_3 values (*i.e.* lower nitrate concentrations), whilst in 1972 lower rainfall gave lower pNO_3 values. Percolation through 50 cm of soil does not relate better than rainfall to the pNO_3 value in the 5–25 cm zone of the soil. Similar relationships exist for Plot 09 but here, because twice as much fertiliser-N is given annually, pNO_3 values were lower (Table 4).

TABLE 2

Yearly mean pNO_3 (May 1st – August 10th) on Broadbalk Plot 07 ($N_2PKNaMg$)

	1972	1973 (5–25 cms)	1974	1975 (15 cm depth only)
Fallow	2.65	3.71	3.16	3.07
Crop	3.45	4.50	3.93	3.52
Difference (Fallow-crop)	−0.80	−0.79	−0.77	−0.45
Mean of fallow and crop	3.05	4.11	3.55	3.30

TABLE 3

Monthly rainfall (and percolation through 50 cm of soil) in mm*

	1972	1973	1974	1975
May	44 (3.3)	55 (18.0)	26 (–)	68 (28.8)
June	37 (–)	83 (44.3)	77 (11.9)	25 (–)
July	29 (–)	55 (17.0)	30 (–)	21 (–)
Aug 1–10	36 (12.0)	30 (9.9)	34 (0.4)	11 (–)
Total	146 (15.3)	223 (89.2)	167 (12.3)	125 (28.8)

* Data from Rothamsted Physics Department meteorological records

TABLE 4

Yearly mean pNO_3 (May 1st – August 10th) on Broadbalk Plot 09 ($N_4PKNaMg$)

	1972	1973	1974
Fallow	2.60	3.64	3.03
Crop	3.39	4.18	3.54
Fallow-crop	−0.79	−0.54	−0.51
Mean of fallow and crop	3.0	3.91	3.29

TABLE 5

Yearly mean pNO_3 (May 1st – August 10th) on Broadbalk Plots 03 (Nil) and 05 (PKNaMg)

	Plot 03	Plot 05
	1973	1974
Fallow	4.46	3.96
Crop	4.71	4.20
Fallow-crop	−0.25	−0.24
Mean of fallow and crop	4.59	4.08

Mean pNO_3 values for Plots 03 and 05 (no fertiliser nitrogen) in 1973 and 1974 respectively (Table 5) were higher than those on other plots in the same years, particularly in the fallow soil. Only in the cropped soil was the pNO_3 value close to that of Plot 07. The means for Plot 03 in 1973 were higher than those for Plot 05 in 1974, again probably because of the higher rainfall in 1973. Plot 2/2 (FYM) gave much higher pNO_3 values in 1973 than in 1974 and they were also generally slightly higher than on Plot 07. The evidence *very tentatively* suggests that the relationship between the mean pNO_3 value

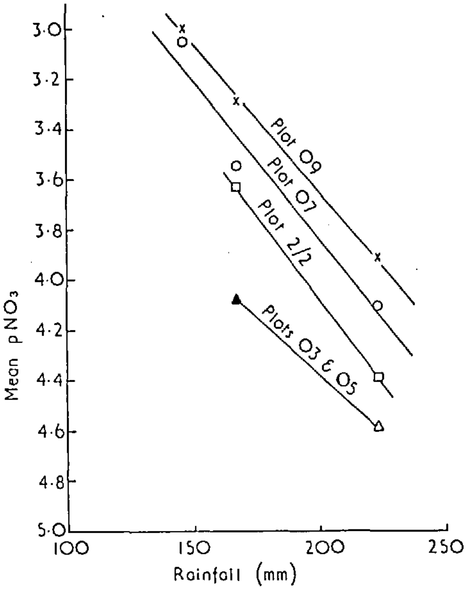


Fig. 1. Mean pNO_3 of cropped and fallow soil *vs* rainfall for the period May 1st to April 10th during 1972–74 on Broadbalk Section I. (□ Plot 2/2; △ Plot 03; ▲ Plot 05; ○ Plot 07; × Plot 09).

and the rainfall for the period is linear for a given level of manurial N (Fig. 1).

The pattern of change in pNO_3 varies greatly from year to year but some consistencies do exist. On Plot 07 and on Long Hoos III, a definite increase in pNO_3 (*i.e.* a drop in nitrate concentration) occurs always during May, in cropped and fallow soil, to give a minimum nitrate concentration in early June (Figs. 2 and 3). This change is usually greater in the cropped than in the fallow soil. The extent of this increase varies from year to year and correlates loosely with total rainfall for April and May, *e.g.* it was most in 1973 when rainfall was highest and least in 1974 when rainfall was lowest. Similar drops in nitrate concentration were observed[3] at Rothamsted in fallow soil and soil under winter wheat fertilised with calcium nitrate. Then soil samples were taken from the 0–6 in layer and extracted with acidified potassium sulphate.

Subsequent changes in pNO_3 (June to August) are less consistent and harder to explain. Generally during dry periods pNO_3 values decreased, evaporation at the surface causing upward movement of

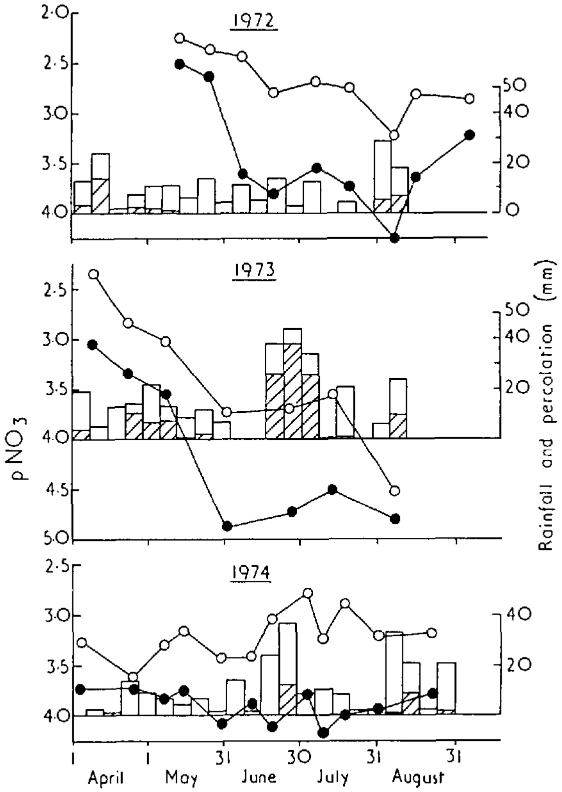
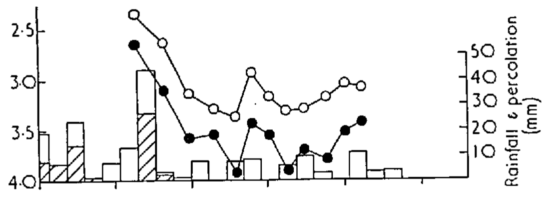


Fig. 2. Change of $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ in the 5–25 cm zone with time, on Broadbalk Section I, Plot 07, and weekly rainfall and percolation through 50 cm of soil at Rothamsted, for April to August 1972–74. (○ Fallow soil; ● cropped soil; histograms give rainfall and percolation (shaded)).

soil solution from the lower depths. This is well demonstrated by the measurements of July 1975 from Broadbalk Plot 07 and Long Hoos III. After a dry period, rainfall initially decreases pNO_3 in the 5–25 cm zone (as in June 1974), or at least maintains it at a steady level, as long as there is nitrate to be washed down from the surface. After this has all been removed, further heavy rainfall leaches the 5–25 cm zone of nitrate (as in July of 1972, 1973 and 1974). Measurements made in 50 cm holes on Plot 07 in 1975 (Fig. 4) show that a week's heavy rain in May brought nitrate down to that depth but during the dry weeks that followed, pNO_3 increased rapidly (*i.e.* NO_3–N concentration decreased) and, from mid-June onwards through July,

(a) Broadbalk



(b) Long Hoos III

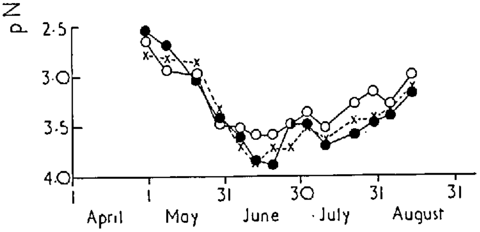


Fig. 3. Change of $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ at 15 cm depth with time on Broadbalk Section I, Plot 07 and Long Hoos III, and weekly rainfall and percolation through 50 cm of soil at Rothamsted for April to August 1975. (● Cropped soil; o fallow soil 50 cm from crop; × fallow soil 100 cm from crop; histograms give rainfall and percolation (shaded)).

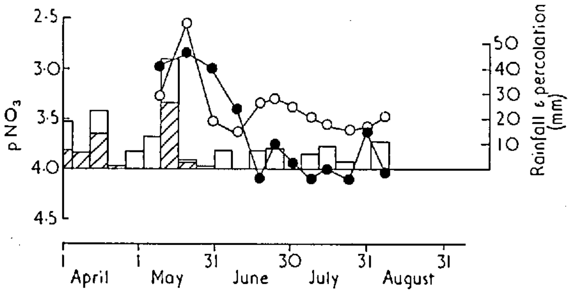


Fig. 4. Change of $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ at 50 cm depth with time on Broadbalk Section I, Plot 07 and weekly rainfall and percolation through 50 cm of soil at Rothamsted for April to August 1975. (● Cropped soil; o fallow soil; histograms give rainfall and percolation (shaded)).

continued to increase slowly as nitrate moved up slowly from the 50 cm zone towards the surface.

On Plot 09, patterns of change in pNO_3 were similar to those on Plot 07 in each year. On Plot 2/2 (FYM), fallow soil consistently

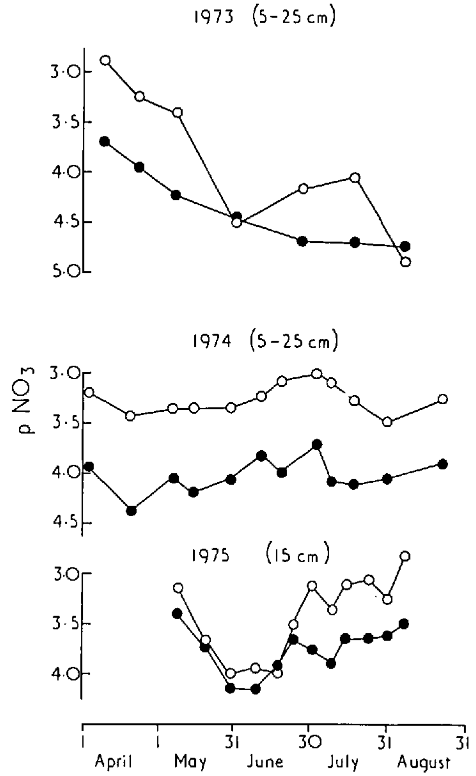


Fig. 5. Change of $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ with time on Broadbalk Section I, Plot 2/2, April to August 1973–75. (● Cropped soil; ○ fallow soil).

gave well defined maxima of nitrate concentration (*i.e.* pNO_3 minima) in early July (Fig. 5), caused by rising temperatures increasing mineralisation. In cropped soil this effect is altered by plant uptake. Early work on Broadbalk[11] showed that nitrate concentrations (samples taken at 15 cm) in a dunged fallow plot reach a maximum in September, with a minor peak in July. If our measurements had been continued through August, September and October, similar results might have been obtained.

pNO_3 values and grain yields on Broadbalk

Grain yields (Table 6) only reflect soil nitrate concentrations in that the 'no N' plots (03 and 05) had higher mean pNO_3 values and gave lower yields than plots given N manures. Yearly changes in

TABLE 6

Grain yields, Broadbalk, Section I 1972–75[10] in tonnes ha^{-1}

Plot	1972	1973	1974	1975
2/2	6.82	6.22	6.43	3.79
03	1.76	1.87	1.95	1.21
05	1.68	1.81	1.70	1.49
07	5.30	5.43	5.37	3.72
09	5.86	5.26	6.25	5.75

pNO_3 on each plot did not produce corresponding variations, except on Plot 09 in 1973 where a low yield agrees with a high mean pNO_3 value. This suggests that other factors are more important in determining yield; high rainfall in 1973 may have physically damaged the crop as well as decreased the nitrate concentration. Yields for 1975 are very poor, except on Plot 09. This could be in part due to the very wet winter causing bad soil structure and the dry summer following making nitrate less accessible to the crop, reflected in the mean difference in pNO_3 between the fallow soil and the cropped soil (taken as a measure of crop uptake). Table 2 shows that the differences are remarkably constant for the years 1972–74 but for 1975 the difference is much less. The profile means (5–25 cm) for 1972–74 are compared here with measurements from 15 cm depths only in 1975, however the contrast remains if the 1975 differences are compared with those for the 15 (or 12.5) cm depths from 1972–74 (Table 7).

During June and July, nitrate is taken up by roots from quite small concentrations but the evidence suggests that these must drop below a pNO_3 value of 4 before yields are affected.

Changes in pNO_3 related to stages of development of the crop

Large differences between $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ occurred during June and July on Plots 07 and 09 in the years 1972–74 showing the period of maximum nitrate uptake, evident from the quadratic curves fitted to the data. The 1972 measurements indicated that at Feekes' stages of development 6, 10 and 11.1 (early stem extension, boot and milk) the crop took up more nitrate than at others, inferred from differences in nitrate concentrations, rather than differences in pNO_3 between fallow and cropped soil. From the

TABLE 7

Yearly mean differences between $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ at 15 (or 12.5) cm depth on Broadbalk, Section 1, Plot 07, and Long Hoos III

	Broadbalk				Long Hoos III
	1972 12.5 cm	1973 15 cm	1974 15 cm	1975 15 cm	1975 15 cm
$(pNO_3)_{fallow}$ — $(pNO_3)_{crop}$	−0.92	−0.80	−0.84	−0.45	−0.15

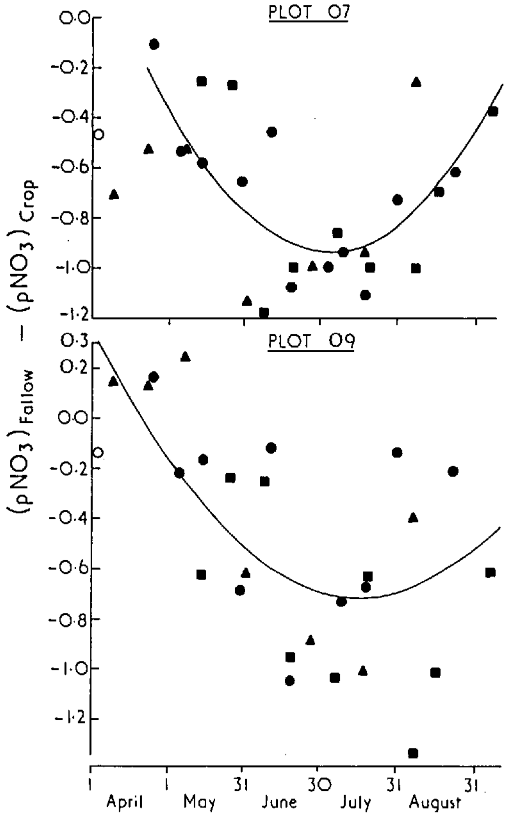


Fig. 6. The quadratic relationship of the change in $(pNO_3)_{crop} - (pNO_3)_{fallow}$ with time in the 5–25 cm zone on Broadbalk Section I, April to August 1972–74. *Plot 07*: $100y = 1.47\ (\pm\ 0.33\ x^2 - 2.74\ (\pm\ 0.12)x + 0.33\ (\pm\ 0.04)$ Variance accounted for = 45%. Residual mean square = 0.056. *Plot 09*: $100y = 0.95\ (\pm\ 0.40)x^2 - 2.01\ (\pm\ 0.17)x + 0.35\ (\pm\ 0.07)$. Variance accounted for = 34%. Residual mean square = 0.136 (■ 1972; ▲ 1973; ● 1974).

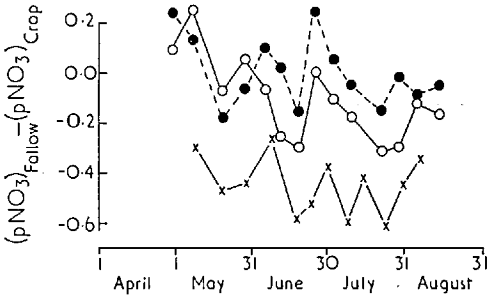


Fig. 7. Change in $(pNO_3)_{fallow}$ — $(pNO_3)_{crop}$ at 15 cm depth with time on Broadbalk Section I, Plot 07 and on Long Hoos III in 1975 (×——× Broadbalk; o—o Long Hoos III fallow soil 50 cm from crop; ●- - - -● Long Hoos III fallow soil 100 cm from crop).

quadratic curve of the differences in pNO_3, these 'depletion minima' appear less pronounced. Such minima also occurred in 1974, but the 1973 measurements were too few to pinpoint them. However, in 1975 although the overall difference between $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ was smaller than in previous years, well-defined minima did occur on Broadbalk Plot 07 and on Long Hoos III at Feekes' scale stages 6, 10 and 11.1. In general, the differences are greater on Broadbalk Plot 07 than on Long Hoos III, probably because more fertiliser N was given to the latter (Table 1). Inexplicably, measure-

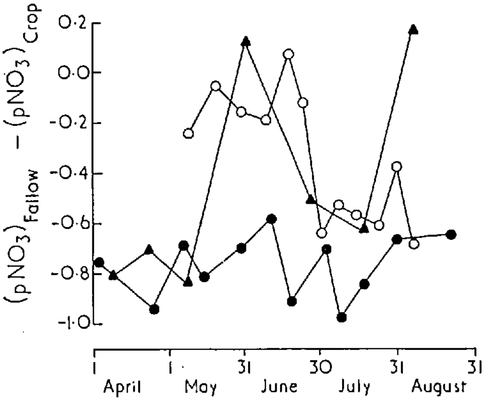


Fig. 8. Change in $(pNO_3)_{fallow}$ — $(pNO_3)_{crop}$ with time on Broadbalk Section I, Plot 2/2 in the 5–25 cm zone in 1973 and 1974 and at 15 cm in 1975. (▲ 1973; ● 1974; o 1975).

ments taken 100 cm from the crop gave higher pNO_3 values (*i.e.* lower nitrate concentration) than those only 50 cm away, although they gave the same depletion pattern (Fig. 7).

On Long Hoos III, S.E.'s of the means from the fallow soil ranged from 0.06 to 0.09 pNO_3 units and from the cropped soil from 0.03 to 0.12 pNO_3 units (40 replicates). With 8 replicates on Broadbalk Plot 07 in 1975, the corresponding S.E.'s were 0.09 to 0.24 and 0.06 to 0.25 pNO_3 units.

Depletion minima occurred on Plot 2/2 in July 1973 and 1975 (during stage 11.1, grain filling). In 1974 $(pNO_3)_{crop}$ was consistently much higher than $(pNO_3)_{fallow}$ (Fig. 8).

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PLANT CHEMISTRY, SOIL MICROBIOLOGY AND
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THE HAGUE
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THE GROWTH AND NUTRIENT UPTAKE OF WINTER WHEAT

by M. B. PAGE, JEAN L. SMALLEY and O. TALIBUDEEN

Rothamsted Experimental Station, Harpenden, Herts, England

SUMMARY

Measurements with an ion selective electrode under winter wheat and in adjacent fallow soil, from April to July 1976, showed that nitrate concentrations were high in the 0–25 cm zone and correspondingly lower at 50 cm, because of the extreme drying conditions. Maximum differences in nitrate concentrations between cropped and fallow soil occurred at Feekes' stages 6, 10, and 11.1 indicating periods of maximum uptake by the crop (*cf* Ref.[4]).

Dry matter weight of wheat, sampled biweekly, was maximum 15 days before maturity. The foliage senesced and lost weight from Feekes' stage 10.1 onwards. Nutrient concentrations in the foliage decreased from Feekes' stage 4, but N, P and Mg concentrations in the ears increased during Feekes' stage 11. N, P and Mg accumulated in the ears at the expense of the foliage during stage 11, maximum uptake occurring at stages 11.3, 11.1 and 11.2 respectively. In contrast, K and Ca uptake ceased at stages 10.1 and 10.5 respectively and then both were lost from the foliage in heavy showers.

Rates of N uptake and soil nitrate depletion correlated significantly, enabling N uptake to be deduced approximately from these *in situ* soil nitrate measurements.

INTRODUCTION

In previous work (1972–75), soil nitrate levels in the root zone of winter wheat and in adjacent fallow soil were monitored during April-August with a nitrate ion selective electrode[3 4]. These measurements showed from year to year that rainfall systematically affected the mean pNO_3 values ($pNO_3 = -\log[NO_3^-]$, where $[NO_3^-]$ is in moles litre^{-1}) down the profile to a depth of 50 cm. More important, the pattern of nitrate uptake by the crop could be deduced from the difference in nitrate concentration between fallow and cropped soil integrated over the depth 0–25 cm, although N uptake was not directly measured. In this way periods of maximum uptake were consistently identified corresponding to Feekes' scale[2] stages 6, 10 and 11.1 (early stem extension, boot and milk).

For wheat grown in a controlled environment, van de Sande-Bakhuyzen[6] showed that (1) the total dry weight of the plants increased until maturity, and (2) the rate of N uptake was maximum during stem extension and grain filling but ceased temporarily during anthesis. A glasshouse experiment at Rothamsted[5] with spring wheat gave a similar growth curve but N uptake did not cease during anthesis. The N concentration in the shoots decreased to a minimum at the end of anthesis then increased as N accumulated in the ears.

In field experiments, 1971–73, with winter wheat, Widdowson and Welbank (private communication) found that shoot dry weight reached a maximum about fifteen days before maturity and than decreased slightly. From tillering onwards, the rate of N uptake progressively decreased until maturity without a break at anthesis and % N decreased to a minimum at maturity. These experiments also showed that % K in the shoots decreased steadily after attaining a maximum at Feekes' stage 5 (late tillering) whereas % P decreased linearly throughout. P uptake followed a similar pattern to that of N but K was taken up until anthesis and then lost quite rapidly until maturity.

Gasser and Thorburn[1] found similar patterns of growth, changes in nutrient concentration and uptakes in field experiments with spring wheat. Particularly, they showed that the total amounts of N, P and Mg were maximum in the crop at maturity but that K and Ca uptake ceased at Feekes' stages 10.1 and 10.5 respectively, decreasing thereafter by about 15% only, much less than observed by Widdowson and Welbank (ibid) and in this work.

This paper describes soil nitrate measurements made in 1976 in conjunction with regular crop sampling, correlates N uptake with soil nitrate depletion and compares it with the uptake of other nutrients.

METHODS

Winter wheat (var. Cappelle Desprez) was grown on a flinty silt loam top-dressed uniformly with 100 kg N ha^{-1} as 'Nitro-Chalk' in early April. Ten 2 m square plots, 7 m apart, were fallowed. Weekly nitrate measurements were made as before[2] in ten-fold replication, with a nitrate ion selective electrode on the surface and at 12.5, 25 and 50 cm depths under the crop and in fallow soil. The measurements are presented here as pNO_3 values but some are converted to mg l^{-1} NO_3–N in the soil solution where relevant. Mean profile values have been calculated as:

$$\text{Profile mean (0–25 cm)} = \frac{a + 2b + c}{4}$$

$$\text{Profile mean (0–50 cm)} = \frac{a + 2b + 3c + 2d}{8}$$

where a, b, c and d are measurements made at 0, 12.5, 25 and 50 cm depths respectively.

The crop was harvested from five 0.25 m^2 squares, randomly selected every 3–4 days. The samples were dried, weighed, ground and then analysed for dry weight, N, P, K, Ca and Mg. After Feekes' stage 10.1 (ear emergence), the ears were removed and analysed separately.

From these analyses, weekly N uptake was calculated and correlated with the weekly depletion of soil nitrate expressed as the difference in (1) pNO_3 and (2) NO_3–N concentration in mg l^{-1} of soil water between cropped and fallow soil.

RESULTS AND DISCUSSION

Soil nitrate

Low rainfall in 1976 (95 mm for April–July compared to a ten year average for that period of 239 mm) resulted in higher and less variable nitrate concentrations in the 0–25 cm zone than in previous years, with no comparable large decreases in May (Fig. 1a). At 50 cm the pattern was similar although nitrate concentration decreased during May in fallow and cropped soil, probably because of the upward capillary movement of soil solution caused by surface evaporation (Fig. 1b) under the extreme drying conditions during May and June (Fig. 1c).

As in previous years[2], periods of maximum differences between $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ and between $[NO_3^-]_{fallow}$ and $[NO_3^-]_{crop}$ (where $[NO_3]$ is expressed in mg l^{-1} NO_3^-–N) occurred at Feekes' stages 6, 10 and 11.1 indicating periods of maximum uptake by the crop. This pattern was best seen at the 25 cm depth (Fig. 2).

Dry matter yield

The dry weight of winter wheat increased to a maximum 15 days before maturity (Fig. 3; *cf* Widdowson and Welbank, ibid). Dry

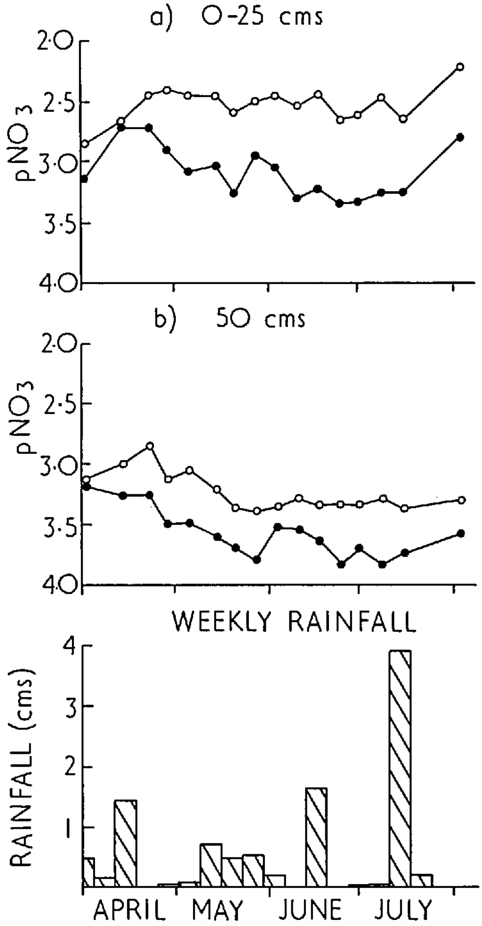

Fig. 1. Changes in $(pNO_3)_{fallow}$ and $(pNO_3)_{crop}$ with time, (**a**) in the 0–25 cm zone, and (**b**) at 50 cm. (● cropped soil; ○ fallow soil) and (**c**) rainfall during April–July 1976.

matter accumulation slowed down after ear emergence because ear weight increased but the foliage senesced and lost weight. In contrast, spring wheat [1] [5] did not lose dry weight before maturity because its straw weight decreased less than that of winter wheat.

Nutrient concentrations and uptake

N. Between Feekes' stages 4 and 10.5 (anthesis), % N in the shoots decreased rapidly as growth rate exceeded rate of N uptake (Fig.

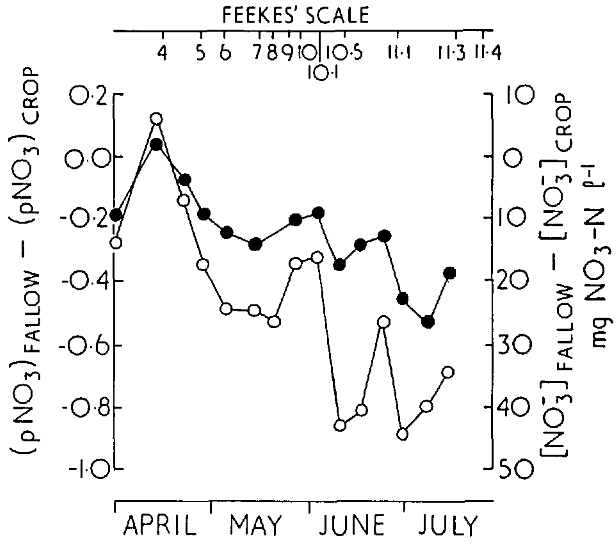

Fig. 2. Depletion of soil nitrate under winter wheat, as $(pNO_3)_{fallow}-(pNO_3)_{crop}$ and as $[NO_3^-]_{fallow}-[NO_3^-]_{crop}$, with time during April-July at 25 cm. (○ $(pNO_3)_{fallow}-p(NO_3)_{crop}$; ● $[NO_3^-]_{fallow}-[NO_3^-]_{crop}$)

4a). During grain filling % N in the foliage decreased sharply as that in the ears increased. The N concentration in spring wheat shoots grown in pots[5] also decreased until Feekes' stage 10.5, but % N in the ears increased much more than in those of the winter wheat grown in the field.

N uptake in winter wheat increased until Feekes' stage 8 (flag leaf emergence), ceased during anthesis, then increased to a maximum 15 days before maturity (Fig. 4b). This final N uptake, with N translocated from the foliage, resulted in a four-fold increase of N in the ears (*cf* controlled environment experiments[4]).

P, Mg, K and Ca. The concentrations of these nutrients in the shoots decreased from a maximum at the end of April until maturity, except perhaps for Mg which reached a minimum at Feekes' stage 10.5 (Fig. 5–8). % P in the ears decreased to a minimum at stage 11.2 (grain 'mealy' ripe) then increased until maturity, that in the foliage decreasing from ear emergence onwards (Fig. 5a). % Mg in the ears increased to an asymptotic maximum at Feekes' stage 11.3, that in the foliage decreasing throughout (Fig. 6a). Thus P and Mg uptakes in the shoots followed similar patterns, continuing to maxima at

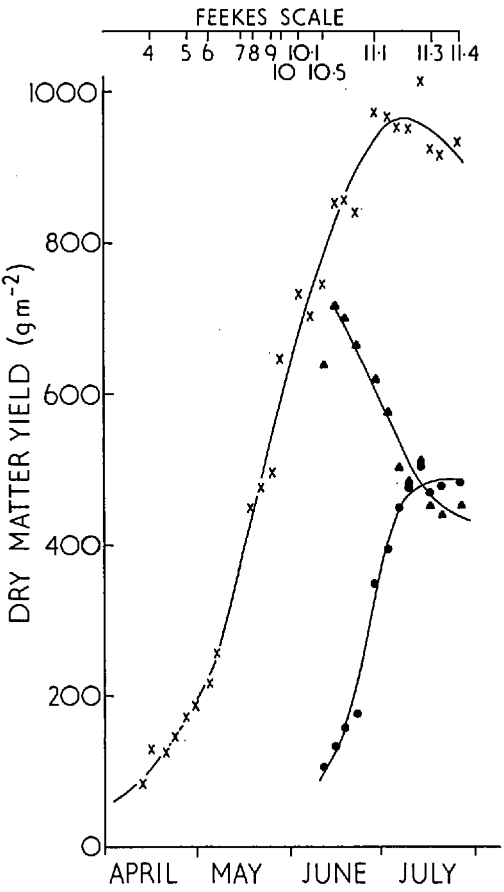

Fig. 3. Accumulation of dry matter by winter wheat between Feekes stage 4 and maturity. (× total tops; ● ears; ▲ foliage)

Feekes' stages 11.1 and 11.2 respectively (Figs. 5b and 6b). Both accumulate in the ears during anthesis and grain filling, P to be incorporated as nucleotides, sugar phosphates, *etc.*, and Mg, presumably as Mg phosphates and phytates, to facilitate the synthesis of chlorophyll during seedling growth.

Unlike N, P and Mg, % K and % Ca did not increase in the ears (Figs 7a and 8a). % Ca increased in the foliage during grain filling when foliage dry weight decreased faster than Ca was lost. K and Ca uptake ceased at Feekes' stages 10.1 and 10.5 respectively (*cf*

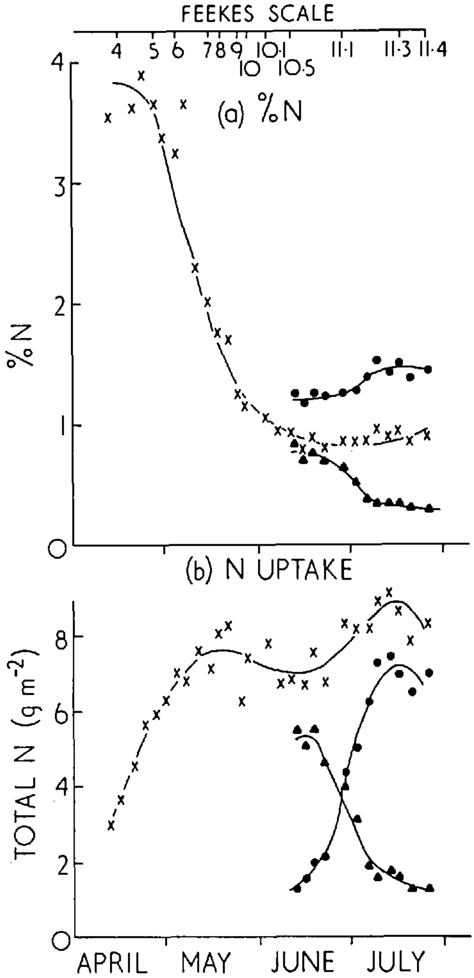

Fig. 4. (**a**) Changes in N concentration and (**b**) the pattern of N uptake, with time, of winter wheat between Feekes stage 4 and maturity.
(× total tops; ● ears; ▲ foliage)

Gasser and Thorburn[1]), but then both were rapidly lost, being leached from the foliage. Sharp changes coincided with heavy showers (Figs. 7b, 7c and 8b).

Table 1 summarises the changes described above, between anthesis and maturity and illustrates well the difference between N, P and Mg which accumulates in the ears and K and Ca which do not.

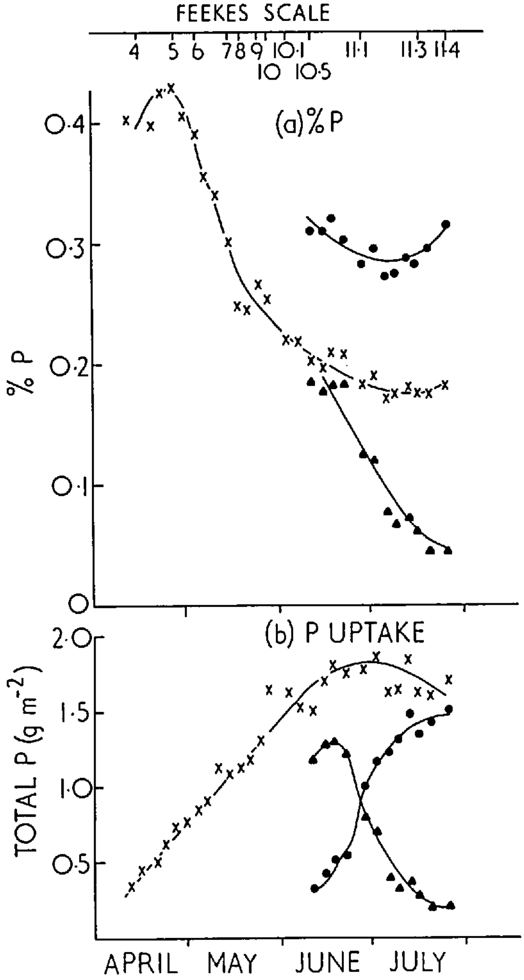

Fig. 5. (**a**) Changes in P concentration, and (**b**) the pattern of P uptake, with time, of winter wheat between Feekes stage 4 and maturity.
(× total tops; ● ears; ▲foliage)

TABLE 1

Nutrient uptake and its change between anthesis and maturity in the whole plant and the distribution of this change between ears and foliage

	Ears		Foliage		Whole Plant		Total in plant at maturity kg ha^{-1}
	Change kg ha^{-1}	Change %	Change kg ha^{-1}	Change %	Change kg ha^{-1}	Change %	
N	+57	+441	−42	−77	+15	+22	83
P	+12	+370	−10	−83	+ 2.1	+14	17
K	+ 9.1	+ 89	−70	−59	−61	−47	68
Ca	+ 1.4	+140	− 7.6	−37	− 6.2	−29	15
Mg	+ 3.7	+438	− 2.5	−56	+ 1.2	+23	6.5

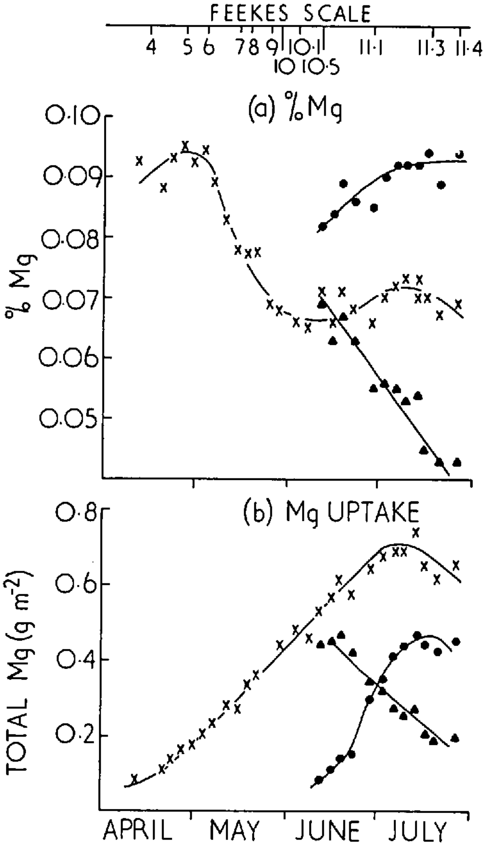

Fig. 6. (**a**) The change in Mg concentration, and (**b**) the pattern of Mg uptake, with time, of winter wheat between Feekes stage 4 and maturity. (× total tops; ● ears; ▲ foliage)

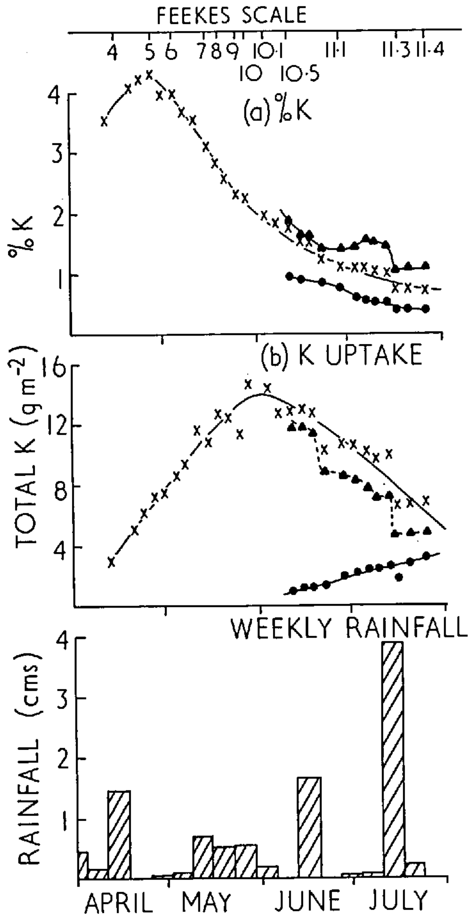

Fig. 7. (**a**) Changes in K concentration, and (**b**) the pattern of K uptake, with time, of winter wheat, and (**c**) rainfall between Feekes stage 4 and maturity.
(× total tops; ● ears; ▲ foliage; *histogram* gives rainfall).

Correlation of soil nitrate depletion and crop N uptake

Weekly crop N uptake was significantly correlated with weekly changes in $[(pNO_3)_{fallow}-(pNO_3)_{crop}]$ at 12.5 cm and 25 cm, and in the 0–25 and 0–50 cm profiles (Table 2), but much less so with weekly soil nitrate depletions, $([NO_3-N]_{fallow}-[NO_3-N]_{crop})$, expressed in mg l^{-1}. The linear relationship between soil nitrate depletion (y)

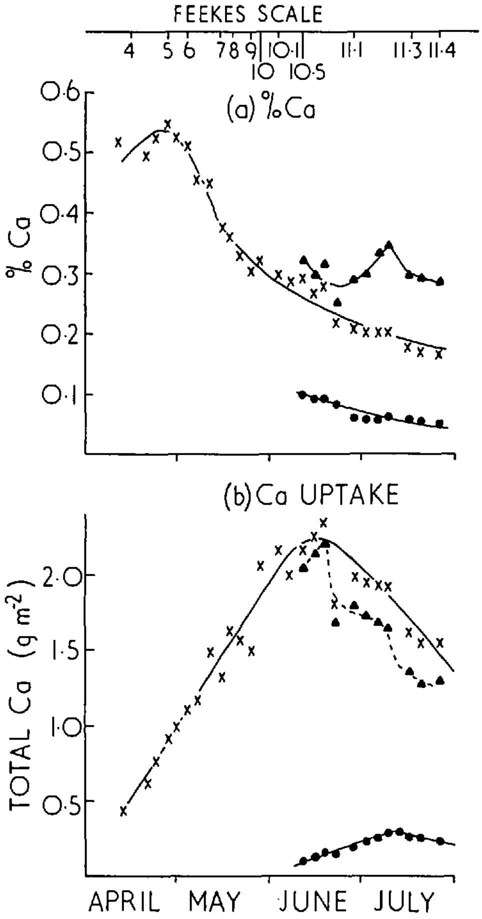

Fig. 8. (**a**)The change in Ca concentration, and (**b**) the pattern of Ca uptake, with time, of winter wheat between Feekes stage 4 and maturity.
(× total tops; ● ears; ▲ foliage)

and crop uptake in kg N ha^{-1} (x), for the 0–50 cm profile, is given by the equation:

$$y = 0.56\ (\pm\ 0.15)x - 2.07\ (\pm\ 1.23)$$

This shows that a soil nitrate depletion of 54 mg l^{-1} corresponds to an N uptake of 100 kg ha^{-1}. For a '50 cm depth' hectare containing about 7×10^6 kg soil with a 40% water-holding capacity, a soil

TABLE 2

The correlation of weekly soil nitrate depletions, as $(pNO_3)_{fallow}-(pNO_3)_{crop}$ and ppm NO_3-N with weekly crop N uptake (P = 0.05*; .01**; .001***)

Depth (cms)	Correlation coefficient	
	pNO_3	ppm NO_3-N
0	−0.09	0.33
12.5	−0.63*	0.11
25	−0.80**	0.66*
50	−0.40	0.35
0–25	−0.79**	0.51
0–50	−0.89***	0.77**

nitrate depletion of 54 mg l^{-1} is equivalent to a removal of 150 kg N ha^{-1}. This disparity between observed and calculated values is not unreasonable considering the assumptions made and that the nitrogen in the roots is not taken into account.

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Paper 10

CROP PERFORMANCE AND SOIL NUTRIENT POTENTIAL

O. Talibudeen and M.B. Page

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1. SOIL NUTRIENT POTENTIAL

A review (Talibudeen 1974) of the definition of the chemical potential of a plant nutrient in the soil, soil nutrient potential (SNP), showed that for all practical purposes it can be represented by the activity (or concentration in dilute solutions) in the soil water in equilibrium with the soil (static or dynamic). It is also convenient when comparing crop/soil environments to consider this equilibrium activity or concentration in energy units (i.e. $\Delta Gi = -RT\ln A_i$ in solution culture and $\Delta Gi = -RT\ln AR_o$ in soil culture, where AR_o is the equilibrium activity ratio (Beckett 1972)) Because it (a) facilitates the use of the 'activity-ratio' or '-product' concept where nutrient ions are involved in exchange/adsorption/precipitation processes in the soil, (b) enables a more rigorous comparison to be made of soil nutrient status under various environmental conditions (e.g. various competing or interacting ions, chelating molecules and temperatures), (c) makes it feasible to put the nutrient extracting abilities of various crops and chemical extractants on a common energy scale, and (d) allows the needs of the growing plant to be assessed on a common scale through its various development stages under changing environmental conditions. (The units of concentration, activity ratio and energy are conventionally molarity, $(\text{molarity})^{1/2}$ and calories per mole or joules per mole.)

2. SOIL NUTRIENT POTENTIAL AND CROP PERFORMANCE

2.1 A Concept

Ideally a SNP should be the average value in the root zone under the environmental conditions prevailing in the soil. These 'environmental conditions' integrate the effects on SNP of pH, temperature, the partial pressures of oxygen, carbon dioxide and water (and in the context of modern agriculture, perhaps ammonia) and the various chemical components of the soil complex. To relate SNP to crop performance, measurements would need to be averaged over a particular stage of development.

In relating SNP to crop growth, the most common yardsticks used to define plant performance are dry matter yield (PY)(of a particular plant part) and nutrient uptake (NU) into the shoots. In recent years, a more fundamental plant index of root absorbing power (RAP) has been suggested and measured in the laboratory for a few plants with root systems of ideal shape, e.g. cylinders with no root hairs (Fried and Shapiro 1960, Nye 1966, Fried and Broeshart 1967). RAP has been shown, as one would expect and predict, to be related to the development stage of the plant, plant species and root age. To project this concept to the field requires simplifying assumptions and laborious measurements of roots. The latter do not include all active root components.

The effects of a wide range of SNP values, on PY and NU shown in Figure 17 allow the identification of mean values of several critical crop energy parameters for a particular development stage that can be derived experimentally by measuring the mean SNP over that stage:

i. The 'exhaustion' (or 'threshold' or 'uptake') potential, when PY and nutrient concentration (NC) in the plant increase slowly with SNP;

ii. the 'response' (or 'deficiency') potential, when PY and NC increase rapidly with SNP;

iii. the 'optimum' (or 'adequate supply') potential, when PY is maximum:

and

iv. the 'luxury-toxic uptake' potential, when PY decreases and NC increases with increasing SNP.

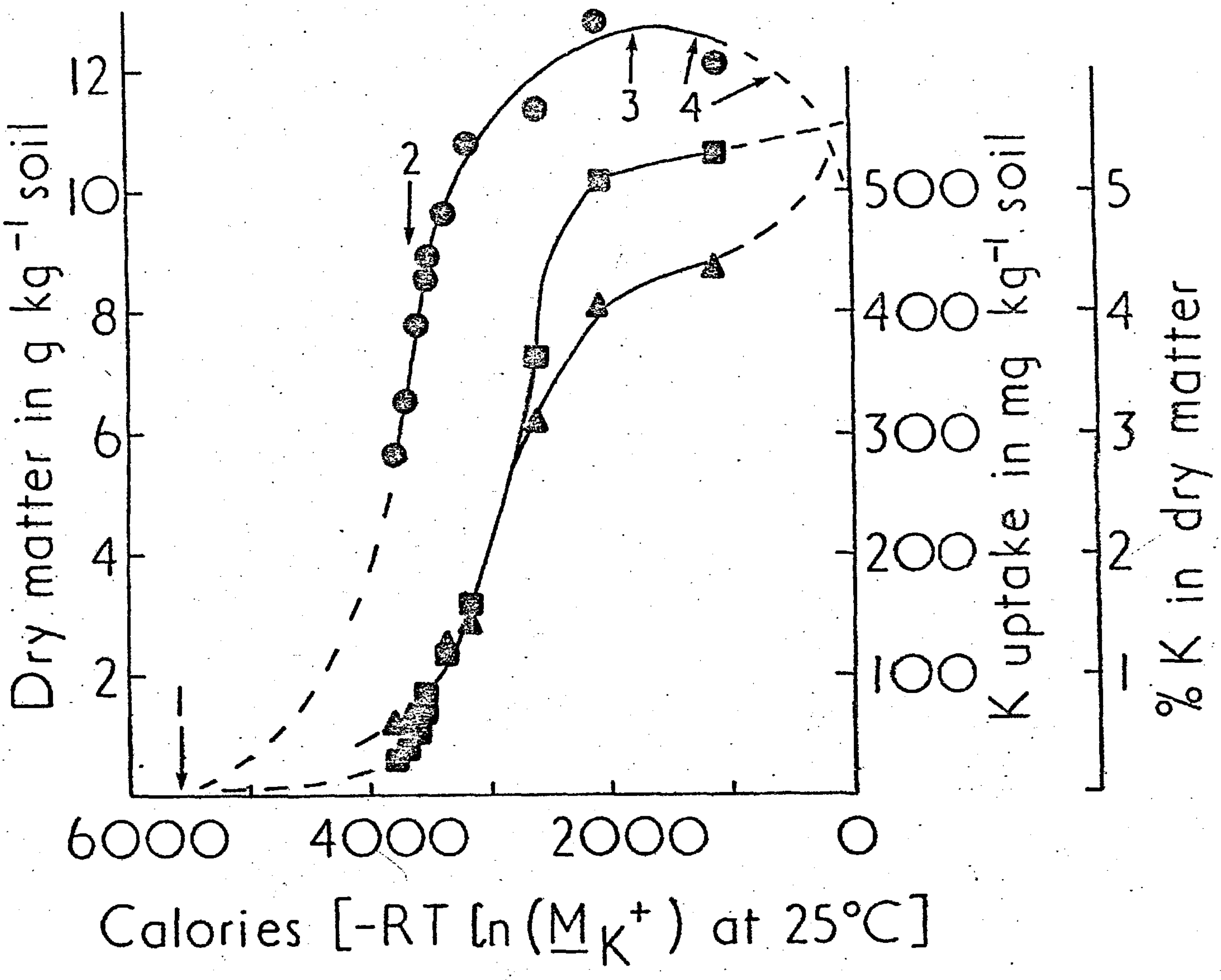

Fig. 17 Effect of soil potassium potential (cal/mole) on the growth characteristics of perennial ryegrass (S23) in a controlled environment. (1 exhaustion, 2 response, 3 optimum, 4 luxury and toxic potentials)

Dry matter ●—●; K uptake ■—■; % K in dry matter ▲—▲

2.2 Some Difficulties

The concept described above is undeniably an oversimplification but attempts to bridge the gap between the older ad hoc agronomic experimentation and the more recent sophisticated, fundamentally based models being developed and investigated in the laboratory. (The basic tenets of the latter are not yet of practical use to the agronomist.) Some difficulties in designing experiments for investigating this concept are now discussed.

The transitions between development stages are not likely to be distinct but could be evaluated by analysing the observed PY : SNP and NU : SNP curves at each stage. At various development stages, the SNP values giving maximum dry matter yields (ΔG_{opt}) may be different. Furthermore, the maximum growth of some part of a plant in the earlier stages may not result in maximum yield of the harvested part. For instance, excessive vegetative growth in some root crops results in poor root yields. Similarly, with wheat too much N in spring can lead to excessive tillering which reduces grain yield. In contrast, more N given during grain filling (when 'available' N in the soil is usually at a low level) often increases grain yield and invariably increases N concentration in the grain, suggesting particularly the need to maintain an optimum SNP during grain filling. So, to obtain maximum benefit at final harvest from native and applied nutrients in the soil, the SNP at each development stage should be such that the yield at final harvest is maximum and not necessarily ΔG_{opt} for that stage.

To take account of recognized nutrient interactions for a particular crop (e.g. N:K, N:P, K:Mg, Ca:P; pH (Al):P,K,Ca,Mg; trace element interactions), initial experiments would need to use 'optimum' basal levels of such interacting nutrients (other than the tested nutrient) based on previous experience. Subsequently, their effect could be investigated by factorially combining a few levels of an interacting nutrient into the main experiment set up to study the crop performance:SNP relationships. Such ideas develop naturally from the basic concepts of soil nutrient potential originally proposed by Schofield (1963) and his collaborators at Rothamsted during 1934-55, starting with soil water and concluding with P, K and lime potentials.

2.3 Procedures Used Hitherto

The methods used so far to derive one or more of these critical potentials are briefly described below:

2.3.1 Empirical approach A

The nutrient status of the soil (before growing the crop but after equilibrium with various levels of added fertilizer) is assessed by calculating the SNP from the composition of the equilibrium soil water (Schofield 1947). The yield response of the crop at final harvest is measured and, combined with SNP values, is used to assess the exhaustion, response and optimum potentials but not, so far, luxury-toxic potentials of the crop (Woodruff 1965). At best such estimates can only be approximate. By far the largest body of data for various crops (Beckett 1972) concerns SNP values covering a range between crop exhaustion and response. Such values, at least for higher plants, must be regarded only as average and approximate because SNP in the dynamic equilibrium between plant and soil changes during growth and also the critical values may not be the same for the various development stages. (The former reason is less true for nutrients involved in exchange/adsorption/precipitation reactions in the soil.) However, for a particular soil, they indicate the level to which SNP must be brought to produce a stated level of performance by a particular crop, given normal environmental conditions (Table 12).

Table 12 CRITICAL SNP VALUES FOR THE GROWTH OF VARIOUS CROPS AT 25°C (cal/mole)

Crop	Exhaustion	Response	Optimum	Reference
		(a)	Potassium	
Grass and hay (unspecified)	–	–4500 (pH 7)	–	Schaffer et al 1962
Ryegrass	–4600, –5600 and –5400	–	–	Arnold 1962, Talibudeen and Dey 1968, Addiscott 1970
Wheat	–4700 and –4200	–3200 and –3700	–3400	Scheffer et al 1962, Feigenbaum and Hagin 1967
Winter rye and spring barley	–	–	–3400	Schaffer et al 1962
Oats	–3800	–	–	Acquaye et al 1967
Maize and Sorghum	–4300	–3800	–	Acquaye et al 1967
Rice	–	–3700	–3000	Ramamoorthy and Paliwal 1965
Vetch and clover	–5000	–	–4400	Hagin and Dovrat 1963
Subterranean clover	–6200	–	–4600	Barrow 1966, Barrow et al 1977
Soyabean	–	–4010	–	Woodruff and McIntosh 1961
Alfalfa	–	–3900	–	Levin et al 1969
Potato	–4900	–3900 and –4200	–2500 and –2400	Schaffer et al 1962, Arnold et al 1968, Addiscott and Mitchell 1970.
Sugarbeet	–	–	–3000	Scheffer et al 1962
Oil palm	–	–3900	–3000	Tinker 1964
Cacao	–	–	–3900	Moss 1964
Banana	–	–	–3200	Moss 1964
Strawberry	–4000	–	–	Bradfield 1969
		(b)	Magnesium	
Sugarbeet	–	–2300	–	Tinker 1967
Coconut	–2700	–	–	Nethsinghe 1962
		(c)	Phosphate	
Unspecified crop (wheat)	–	–7600	–6900	Aslyng 1964

Table 13 CRITICAL CONCENTRATIONS AND THE EQUIVALENT CHEMICAL POTENTIALS (IN PARENTHESES) FOR THE GROWTH OF VARIOUS CROPS IN FLOWING NUTRIENT CULTURE SOLUTIONS

Crop	Exhaustion	Response	Optimum	Luxury	Reference
	(a) Potassium $\underline{M} \times 10^6$ (and $-RT\ln(\underline{M})$ at 25°C				
Ryegrass, Bromgrass	1 (8200)	8 (7000)	24 (6300)	1000 (4100)	Asher and Ozanne 1967
Oats, barley	1 (8200)	24 (6300)	1000 (4100)	-	
Subterranean clover, vetch	1 (8200)	8 (7000)	100 (5500)	1000 (4100)	
	(b) Phosphate $\underline{M} \times 10^6$ (and $-RT\ln(\underline{M})$ at 25°C)				
Bromgrass, clover	0.04 (10200)	0.2 (9200)	5 (7300)	25 (6300)	Asher and Loneragan 1967
Lupin	-	1 (8200)	5 (7300)	25 (6300)	
Potato	1 (8200)	-	40 (6000)	-	Houghland 1947
Wheat	1 (8200)	5 (7300)	10 (6900)	-	Sommer 1936, Teakle 1929
Barley	1 (8200)	2 (7800)	5 (7300)	-	Bingham 1951
Soyabean	1 (8200)	3 (7600)	5 (7300)	-	Parker 1927
Pea	2 (7800)	-	30 (6200)	-	Sommer 1936

2.3.2 Empirical approach B

Several workers have reported critical nutrient concentrations for the growth of various crops by maintaining their roots in flowing and aerated culture solutions containing the tested nutrient in a wide range of concentrations (up to one thousandfold). Critical concentrations of the nutrient are converted to energy units (i.e. chemical potentials) by calculating ionic activities by conventional methods for comparison with the corresponding SNP values (Table 13). These critical potentials seem to be smaller by at least 1-2 kcal/mole than those derived from SNP experiments. Perhaps this results from the better root systems developed in solution culture, although nutrient potentials in soil and solution culture are not strictly comparable.

2.3.3 Quantitative approach

For determining the exhaustion potential of a crop, this approach utilizes the relationship between the quantity (Q) of (exchangeable) nutrient ion in the soil and its 'potential' (I) to calculate the amounts of K required to be removed from it to decrease its potential to various predetermined values. Nutrient uptakes from the soil, maintained at various nutrient levels, are correlated with each of these calculated nutrient removals. Plotting these correlation coefficients against SNP for each soil treatment at various times gives a maximum r value at the exhaustion potential of the crop (Addiscott 1970a,b, Addiscott and Mitchell 1970) this potential being independent of the period of growth and the soil used, provided "non-exchangeable" forms of the nutrient are not substantially released. Values for the exhaustion potential for various crops can be derived in this way with a mean standard error of about ±10%. In addition to the degree of precision is the advantage that the extracting power of the crop can be equated to that of an appropriate conventional laboratory extractant by interpolating its SNP value on the quantity:potential curve for a soil (in a neutral electrolyte) corresponding with the amount of nutrient ion it can extract from the soil (Addiscott and Mitchell 1970).

Such a procedure, coupling soil nutrient availability to a particular crop to a specific extractant, is of value to the agricultural chemist.

2.4 Illustrative Results

The results described here are intended to illustrate the nature of the information available so far and are in no way exhaustive. Those on potassium are taken from an earlier review (Beckett 1972) and are grouped for various crops after converting activity ratio units into energy units, assuming a uniform soil temperature of 25°C.

2.4.1 Potassium

For the Gramineae, an optimum SNP of -3000 to -3400 cal/mole is observed for wheat, rye and paddy rice grown under quite different environments. Exhaustion potentials vary from -5500 cal/mole for ryegrass, -4300 for wheat, maize and sorghum to -3800 for oats. Response potentials are also reasonably uniform at about -3750 for wheat, maize, sorghum and rice, but those for grass and hay crops are lower at -4500 cal/mole at pH 7.

Legumes can grow at lower K potentials than the Gramineae, critical exhaustion and response potentials being -5600 (mean) and -4500 to -4000 cal/mole respectively.

The exhaustion and response potentials for potatoes are similar to those for the Gramineae although the optimum potential is higher at -2400 cal/mole. The optimum value for sugarbeet is -3000 although in the absence of sodium, this could be higher.

The requirements of tree crops in the tropics for optimum nutrition do not seem to differ much from the Gramineae on the energy scale, values of -4000 to -3000 cal/mole being obtained. However, observations are scarce.

2.4.2 Magnesium and phosphorus

See Table 12; there is too little published information for relevant comment.

3. IMPLICATION OF SOIL NUTRIENT POTENTIAL IN THE SUPPLY OF NUTRIENTS TO PLANTS

3.1 Equilibrium Conditions

The quantity (q) : potential (p) (or intensity or concentration) relationship of a soil is well-recognized and has been briefly referred to in relation to its importance in predicting nutrient supply by a soil. The adsorption isotherm is conventionally expressed as the amounts of nutrient in unit volumes of soil and equilibrium solution for which linear and curvilinear relationships are observed depending on the nature of the soil:nutrient interaction.

When linear, the slope, or buffering capacity, $b = dq/dc$, is constant and the amount of nutrient supplied over a concentration range c_1 to c_2 is easily calculated. When the q:c relationship is nonlinear, b can be calculated in several ways: (a) by the function $b = d\,(Rc^n)/dc$ where R and n are constants (Olsen <u>et al</u> 1962); (b) by deriving the buffer capacity parameter from a single Langmuir process equation of the type:

$$q = K_1c/(K_2 + c)$$

giving $b = K_2q^2/K_1c^2$ where K_1 and K_2 are constants, from which a 'supply parameter' $(K_1K_2)^{-1/4}(qc)^{\frac{1}{2}}$ is derived and which is shown to be highly significantly correlated with phosphate uptake by cotton (Khasawneh and Copeland 1973) with zinc uptake by wheat from four contrasting Indian soils (Sidhu <u>et al</u> 1977), and with zinc desorption by several extractants from an Indian soil (Sinha <u>et al</u> 1975); (c) by calculating a 'maximum buffering' capacity (MBC) for phosphate adsorption on soils by fitting high and low bonding energy Langmuir processes (Holford and Mattingly 1976a, Dalal and Hallsworth 1976) on the q:c relationship. The equilibrium buffering capacity (EBC) can then be obtained as before by differentiation:

$$EBC = k_1q'/(1+k_1c)^2 + k_2q''/(1+k_2c)^2$$

from which MBC is easily obtained for the condition $c \Rightarrow 0$). Highly significant correlations are obtained between phosphate uptake by ryegrass and EBC or MBC, especially the latter. As expected, this shows that the higher the buffer capacity, the lower the concentration c necessary and the larger the amount q required for a certain amount of phosphate uptake (Holford and Mattingly 1976b).

3.2 <u>Dynamic Conditions</u>

3.2.1 <u>Nutrient flow through soil</u>

Diffusive and mass flow are the mechanisms of the movement of nutrients to roots. The physical and chemical characteristics of the soil complex that affect diffusive flux are well known and identifiable quantitatively. This is achieved by studying the modification (by each soil complex) of the diffusion coefficient of the nutrient in free solution (Olsen <u>et al</u> 1965

$$D_{soil} = D_{soln}.f.\ \theta/b$$

where F is the tortuosity factor (i.e. the pore space for nutrient movement and its layout in the soil complex), θ the fractional volume of the pore space occupied by soil water and b (=dq/dc) the nutrient buffer capacity determined from the amounts of 'available' nutrient in unit volume of soil, q, and soil water, c, the latter being exponentially related to SNP. f and θ are interactive factors so that the tortuosity factor f decreases much more with decreasing θ, less so at lower θ values.

Clearly, measurements of such soil parameters can only be made with any acceptable precision in the laboratory and we are faced, for the foreseeable future, with considerable approximations in applying laboratory f and θ values in the field. However, for a similar transformation, a b value, averaged across the rhizosphere, is unlikely to change much if soil pH does not change. Little is known about the effects of changes in other soil factors, e.g. water content of the soil, on the factor b.

We also recognize that the mass flow component of nutrient flux through the soil must be affected to some extent by a tortuosity factor not too different to that for diffusive flux and that the buffer capacity of water in the soil is given by the water characteristic of the soil, i.e. the water 'content:potential' relationship. The gradients in the water SNP are created by evapotranspiration.

3.2.2 The root:soil interaction in nutrient flow

Within the last decade, efforts have been made to determine experimentally nutrient absorption rates by roots (Loneragen et al 1968, Wild et al 1974). This was foreshadowed by the postulation of carrier sites in roots (Epstein 1956) whose number depends partly on the nutrient concentration in the bathing solution (Hagen and Hopkins 1955, Wild et al 1974). It has also been demonstrated that the roots of various species have different concentrations of carrier sites (Noggle and Fried 1960). From the sophisticated, complex, experimental and mathematical models developed recently (Noggle and Fried 1960, Brewster and Tinker 1970, Baldwin et al 1973, Nye et al 1975) some conclusions can be derived which show an understandable similarity to work of twenty years earlier (Hagen and Hopkins 1955, Wild et al 1974):-

i. The unit absorption rate (UAR) of the nutrient by the root (in amount g/sec) decreases with the period of growth at low nutrient concentration in the bathing solution but is relatively constant at higher concentrations;

ii. UAR varies with species;

iii. Uptake is given by $(2 a\alpha l) c$, where a is root radius, α root absorption coefficient, l total active root length of the plant and c the nutrient concentration in the bathing solution, again related to SNP (Nye et al 1975);

iv. When these root characteristics are related to diffusive flux in the soil, we are presented with an "uptake-supply balance" index $(\alpha a/D_{soil}.b)$ for each plant:soil combination, also varying with development stages of the plant. These models have been and are being elaborated for mass flux, transpiration, competition between parallel and random roots, interferences with root hairs etc. Modifications by soil temperature, mycorrhizal hyphae, changes by the roots of environmental conditions in the rhizosphere, e.g. pH, chelation of ions etc. by exudates and decomposition products, would have to be introduced later.

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