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Article Title: A Novel Method of Supplying Nutrients Permits Predictable Shoot Growth and Root : Shoot Ratios of Pre-transplant Bedding Plants

Year of publication: 2007

Link to published version:

<http://dx.doi.org/10.1093/aob/mcl240>

Publisher statement: This is a pre-copy-editing, author-produced PDF of an article accepted for publication in *Annals of Botany* following peer review. The definitive publisher-authenticated version Greenwood, D. et al. (2007.) *A Novel Method of Supplying Nutrients Permits Predictable Shoot Growth and Root : Shoot Ratios of Pre-transplant Bedding Plants*. *Annals of Botany*, Vol 99, pp. 171-182 is available online at: <http://aob.oxfordjournals.org/cgi/content/abstract/99/1/171>

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A novel method of supplying nutrients permits different steady state growth rates and predictable root/shoot ratios of pre-transplant bedding plants

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Optimizing root/shoot ratio and shoot growth by controlling nutrients

ABSTRACT

- *Background and Aims* Growth of bedding plants, in small compost plugs, relies on nutrients in the irrigation solution. The object of the study was to find a way modifying the nutrient supply so that good-quality seedlings can be grown rapidly and yet have the high root/shoot ratios that are essential for efficient transplanting.
- *Methods* A new procedure was devised in which the concentrations of nutrients in the irrigation solution were modified during growth according to changing plant demand, instead of maintaining the same concentrations throughout growth. The new procedure depended on published algorithms for the dependence of growth rate and of critical nutrient concentrations on shoot dry weight W_s (g m^{-2}). It also depended on measuring evapotranspiration rates and shoot dry weights during the growing period. Four independent experiments were carried out in which pansies and petunias were grown with expected optimum and fractions of the optimum concentrations of nutrients and root and shoot weights were measured at intervals.
- *Key results* For each level of nutrient supply W_s increased with time in days, Δt , according to the equation $\Delta W_s/\Delta t = K_2 \cdot W_s/(100+W_s)$ in which K_2 is a growth rate coefficient that remained constant throughout growth. The value of K_2 for the sub-optimum treatment relative to that for the optimum treatment was logarithmically related to the fraction of optimum nutrient supply. The value of K_2 for the optimum treatment was defined by incoming radiation and temperature. A mechanistic model was derived which predicted that, for experiments started in March, April and June, the root/shoot ratio for the sub-optimum treatment as a fraction of that for the optimum treatment should equal the shoot dry weight for the optimum treatment divided that for sub-optimum treatment. Data from the experiments were in good agreement with prediction.
- *Conclusions* The forgoing relationships enabled the effects of nutrient supply, incoming radiation and temperature on shoot growth and root/shoot throughout the growth of both pansies and petunia to be calculated.

Key words: *Viola.tricolor*, *Petunia.hybrida*, pansy, roots, shoot growth, nutrients, nitrogen, phosphate, potassium, evapotranspiration.

INTRODUCTION

Bedding plants, for the retail market, are produced by specialist nurseries as seedlings in small 'plugs' of peat based media (plug plants). These small plugs retain only limited amounts of nutrients so that seedling growth is heavily dependent on the nutrients supplied in the irrigation solution. After 25 to 40 days seedlings are transplanted, often by robots, into larger containers. Such seedlings need to grow quickly (to maximise productivity), show no nutrient deficiency symptoms and have good root systems. High root/shoot ratios are especially important to ensure cohesion of the plugs during transplanting and to ensure good take-off after transplanting (Zandstra and Liptay, 1999). In commercial systems, shoot growth is suppressed by applying plant growth regulators in order to allow time for the root system to develop to an adequate size for successful transplanting. There are however environmental and cost pressures against the use of plant hormones and a promising alternative approach appears to be to modify nutrient supply.

In most experiments on this topic a range of different concentrations of a standard nutrient mix are applied throughout growth despite changing plant needs. Responses are considerable but there is little evidence about their reproducibility so their value for giving practical advice is limited. Salinity can increase with time (van Iersel, 1999; James and van Iersel, 2001) sufficiently to depress growth and occasionally induce quality defects. Attempts to overcome these problems have included the use of slow release fertilizers (van Iersel *et al.*, 1999; Stamps, 2000) and monitoring nutrient concentrations in plant tissue (van Iersel *et al.*, 1999; Stamps, 2000) and plug extracts (Scoggins *et al.*, 2002).

An alternative approach is suggested by experiments, using complex equipment, in which the concentrations of nutrients are increased exponentially (Ingestad and Lund, 1979). The concentration and thus the supply of the limiting nutrient determined growth rate and the relative growth rate equalled the relative addition rate of that nutrient. Another important finding was that nutrient deficiency symptoms only occurred when plant nutrient concentrations fell sharply; thus no deficiency symptoms appeared when the relative addition rates and relative growth rates were small but constant (Ingestad and Lund, 1979; Ericsson and Ingestad, 1988). Increasing root/shoot ratio necessitates reducing the supply of N or P below that required for maximum growth rate (Ericsson, 1995). As bringing about such increases without inducing deficiency symptoms is a requirement of bedding plant producers it seemed that Ingestad and Lund's method could form the basis of method for supplying nutrients in bedding plant production. Ingestad and Lund's method required that the plants were far apart and so could, with optimum nutrients, grow exponentially. Bedding plug plants are, however, grown close together and growth ceases to be exponential before transplanting even when the supply of nutrients is optimal. Nevertheless it seemed possible to overcome this problem by modifying the nutrient supply during growth according to crop nutrient demand.

In commercial practice the choice of nutrient supply depends on financial, management and organisational considerations of the individual production unit as well as requirements of the plants. To aid making this choice, there is a need to obtain a general means of forecasting the effects of nutrient supply on shoot/root ratio and growth rate that applies to widely different conditions. Fortunately a great deal of relevant information is available from work on other plant species. Concise equations relating the rates of crop dry matter growth and their critical nutrient concentrations to plant mass (e.g. Greenwood *et al.*, 1977; Greenwood and Stone, 1998) have been used to define the-time course of nutrient uptake by field crops. Other equations have been developed to relate plant growth with sufficient water and nutrients to temperature and photosynthetically active radiation (e.g. Brewster and Sutherland, 1998). More detailed models have also been developed for the dependence of root/shoot ratio on plant nutrient concentrations (e.g. Agren and Franklin, 2003).

The purpose of the work is to devise a system in which bedding plug plants can be grown with sup-optimum nutrient supplies without inducing deficiency symptoms and to develop and calibrate these models for forecasting the effects of such supplies on root/shoot ratio and growth rate.

THEORY

Definitions of the symbols and the units are given in Appendices 1 and 2.

Growth rate. The rate of shoot dry matter production of many field vegetables when grown, with ample water and nutrients in the UK between April and September, was well defined throughout growth by

$$\Delta W_s / \Delta t = K_2 W_s / (K_1 + W_s) \quad (1)$$

where W_s is shoot dry weight, K_2 is a growth rate coefficient, t is time and K_1 is the value of W_s at which growth rate is half the maximum (Greenwood, *et al.*, 1977). Equation (1) is based on the notion that that intercepted radiation and thus growth rate is first almost proportional to plant mass and then as the canopy closes becomes almost constant. The same equation has been used to interpret results of experiments under more controlled conditions (Smolders and Merckx, 1992; Smolders *et al.*, 1993). All these plants were harvested before the onset of senescence. K_1 and K_2 are highly correlated, and K_1 was always set at 100 g m^{-2} as in the above field experiments. If in eqn (1) $\Delta t \rightarrow 0$ and $K_1 = 100 \text{ g m}^{-2}$, then integration gives

$$K_2(t_e - t_0) = 100 \ln(W_{se}) + (W_{se}) - 100 \ln(W_{s0}) - (W_{s0}) \quad (2)$$

where t_0 is the time in days from an arbitrary reference point when the initial shoot dry weight is W_{s0} and W_{se} is the shoot dry weight at a later date t_e . Equations (1) and (2) would be expected to hold for bedding plants grown without nutrient stress and, as will be shown, they can also hold for the sub-optimum treatments, imposed by the method described in this paper.

Dependence of critical %N, %P and %K on W_s . Critical %N in the dry matter (N_{crit}) declines in commercial populations of plants as they get larger because of an increase in the proportion of structural plus storage material that has a low %N compared with that of the photosynthetic material (Lemaire, 1997). Several different equations give similar graphs for the dependence of N_{crit} on W_s . We have selected the empirical equation

$$N_{crit} = 1.35 [1 + B_n(c) e^{-0.0026 W_s}] \quad (3)$$

where B_n is a coefficient, the value of which varies with the species indicated by c in parenthesis (Greenwood and Stone, 1998). Values of B_n for both pansy and petunia were obtained from preliminary factorial experiments in controlled environment cabinets. There were a range of different levels of nutrients applied by flooding once or twice a day but the different nutrient concentrations did not vary during the growth period. The first experiment tested the effects varying N, P and K concentrations and the second experiment N and P concentrations in the irrigation solution, on dry shoot dry weight and mineral composition. For each experiment, those dry shoot weights that were within 5% of the maximum were identified and the average measured. The averages of the corresponding values of %N and of %K of the first experiment and of %N and of %P in the second experiment were also identified (those of %P of the first experiment were not used because they were

all in the luxury range). These average values of %N, %P and %K were assumed to be best estimates of the critical concentrations. B_n was obtained by substituting the average values of %N for N_{crit} and the average shoot dry weight for W_s in eqn (3) and solving for B_n to give the values in Appendix 1. In addition the ratios of %P/%N and %K/%N were calculated. For pansy they were 0.214 and 1.426 and for petunia 0.153 and 1.708 respectively.

Effect of temperature and radiation on K_2 . When K_2 was measured with the optimum levels of nutrients it was considered that it might be related to temperature and incoming radiation by an adaptation of equations developed by Scaife *et al.*, (1987) and Brewster and Sutherland (1993). It is

$$1/K_2 = ((1/(T_m - T_z) + (f/P_{ar})))g \quad (4)$$

where T_m is the mean daily temperature, T_z is the temperature when growth ceases, P_{ar} is the photosynthetically active radiation, calculated as $0.45 \times$ total solar radiation measured with a (Kipp's solarimeter), f is a coefficient that determines the relative effects of temperature and solar radiation on K_2 and g is a proportionality constant. The parameters f , T_z and g were estimated from the results of a controlled environment experiment kindly provided by Dr A. Langton of Warwick-HRI. The experiments tested the effects of 3 temperatures, 14 °C, 18 °C and 22 °C in factorial combination with two photosynthetically active radiation intensities (1.73 and 3.46 MJ m⁻²) on the shoot dry weights of pansy and petunia at three times during the growth period. The values of the parameters are given in Appendix 1.

Root/shoot ratio Detailed models have been advanced to improve understanding of the effects of various stresses on root/shoot ratios (e.g. Brouwer, 1962; Thornley, 1972; Ericsson, 1995; Tinker and Nye, 2000 p. 266; Agren and Franklin, 2003;). Although they require more inputs than can be readily obtained they provide the basis of a relationship with which to interpret our bedding plant data. It is based on the view that nutrient deficiency of N, or P but not K (Ericsson, 1995) around roots restricts shoot more than root growth and conversely a sub-optimal aerial environment restricts root growth more than shoot growth. We hypothesise that if R is the ratio of root/shoot dry weight and S_n and S_a are the nutrient and aerial stresses then

$$R = \alpha S_n \times \beta S_a \quad (5)$$

where α and β are coefficients.

If we write subscript *sb* to denote sub optimum nutrient supply and subscript *o* to denote optimum nutrient supply then dividing the above equation for the sub optimum treatment by the corresponding equation for the optimum treatment gives

$$[(R)_{sb}]/[(R)_o] = [(S_n)_{sb}]/[(S_n)_o] \times [(S_a)_{sb}]/[(S_a)_o] \quad (6)$$

For a given aerial environment $(S_a)_{sb}/(S_a)_o$ is a constant equal to γ so that eqn (6) can be written as

$$[(R)_{sb}]/[(R)_o] = [(S_n)_{sb}]/[(S_n)_o] \times \gamma \quad (7)$$

A measure of the nutrient stress integrated over time is $(W_s)_o / (W_s)_{sb}$ which may therefore be set equal to $(S_n)_{sb} / (S_n)_o$. As $(S_n)_o$ is by definition equal to 1 it follows from eqn (7) that

$$[(R)_{sb}]/[(R)_o] = [(W_s)_o]/[(W_s)_{sb}] \times \gamma \quad (8)$$

where $\gamma = 1$, if the aerial environment is optimum and less than one when it is sub-optimum.

MATERIALS AND METHODS

Growing system

Seedlings were grown in standard commercially available 360 plug (cell) trays (0.48×0.28 m). Each cell had a volume of about 5 ml, was open its surface but had a drainage hole at its base. Cells were filled with unfertilized sphagnum peat (Bulrush Peat Co Ltd., New Ferry Rd, Bellaghy, Magherafelt, Northern Ireland BT45 8ND) which had a cation exchange capacity of about 100 meq l^{-1} , a bulk density of about 100 kg m^{-3} and initially contained water soluble concentrations that, depending on the experiment, were between 42 and 76 mg l^{-1} of peat for $(\text{NH}_4 + \text{NO}_3)\text{-N}$, between 18 and 29 mg l^{-1} of peat for K and were always less than 0.6 mg l^{-1} of peat for P. A single seed was sown in each cell, the trays were watered, stacked on pallets, wrapped with cling film and incubated in the dark at 16°C for 5 days. Trays were then transferred to a glasshouse in which there was supplementary lighting ([intensity?](#)) with high pressure sodium lamps in the January and March experiments but not those in April and June. Supplementary lighting was set to start at when the light levels dropped below 10 klx and to switch off when they reached 20 klx between 01:00 and 13:00 h. Other environmental conditions are given in Table 1. The trays were on ebb and flood benches (2×0.3 m) with 5 cm sides with 4 holes at their base connected to tubing through which nutrient solution could be pumped. The trays were irrigated each day by raising the level of irrigation solution until the surface of the compost glistened indicating near saturation. After 1 minute, the level of irrigation solution was lowered and the cells drained. For about 10 days the irrigation solution contained no nutrients and seedlings relied on residual nutrients in the peat-based substrate. Thereafter nutrient concentrations were adjusted each week according to plant demand. These were estimated from measurements made during the previous week by assuming that the environmental conditions in both weeks were the same. During the previous week, measurements were made of the average daily evapotranspiration during the week, $E_{vap}(av)$, and of shoot dry weight at the beginning and at the end of the week. Substitution of these weights, W_{so} and W_{se} and the corresponding dates, t_0 and t_e in eqn (2) gives the growth rate coefficient K_2 . Substitution of this value of K_2 and W_{se} at the end of the week in eqn (1) gives the daily increment in Ws and thus enables the dry weight to be calculated for each day during the following week. In addition, the corresponding values critical %N, $N_{crit}(d)$, were calculated from eqn (3) and crop $N_{demand}(d)$ for each day was calculated from $\Delta W_s(d)$ and $N_{crit}(d)$ as follows

$$N_{demand}(d) = \Delta W_s(d) \times N_{crit}(d) / (0.9 \times 100) \quad (9)$$

where (d) indicates a particular day, the 0.9 is included to correct for N in the root and the hundred to correct for N_{crit} being in percentages. The concentration of N required to meet $N_{demand}(d)$ on a particular day is equal to the demand divided by the evapotranspiration for that day. The average evapotranspiration, $E_{vap}(av)$, was assumed to be the same as in the previous week so that the average concentration $N_{conc}(av)$ required in the irrigation solution for the following week was calculated from the average of the 7 predicted values of N_{demand} and the average evapotranspiration as

$$N_{conc}(av) = \sum_{av=1}^7 N_{demand}(d) \times 1000 / (7E_{vap}(av)) \quad (10)$$

where the 1000 is to convert the $N_{conc}(av)$ from g of N l⁻¹ to mg N l⁻¹ and the 7 is to convert from per week to per day. The assumption is that there was no displacement of the existing nutrients from the plugs by the ebb and flow system but rather that the nutrients were only 'recharged' when nutrient solution replaced any water lost by evapotranspiration during growth. The validity of the assumption is supported by the results of the "Preliminary Experiment" that is described below. Evidence exists that the ratios of critical P/N and of K/N do not change appreciably as W_s increases (Ericsson and Ingestad, 1988; Greenwood and Stone, 1998; Belanger and Richards, 1999; Broadley *et al.*, 2004). We therefore maintained the same ratios of P/N and K/N in the irrigation solution throughout growth. On the basis of the P/N and K/N ratios found to give good growth in earlier NPK factorial experiments, a stock solution was made up with ratios, by weight, of P/N of 0.18 and K/N of 1.58 where the N was mostly NO₃-N but also contained NH₄-N. In addition, the solution also contained Mg and Ca ions. The same stock solution was used for both species. It was diluted each week to meet the predicted $N_{conc}(av)$ as defined in eqn (10). An Excel based program to calculate $N_{conc}(av)$ can be downloaded from the Internet at <http://www2.warwick.ac.uk/fac/sci/hri2/research/plantmineralnutrition/bedmod>. Suitable aliquots of a stock solution of minor elements were also added to the irrigation solution to maintain the same concentrations throughout each experiment.

Preliminary experiment

The above method for calculating the amounts of nutrients in the irrigation solution was developed from experiments in which uncropped trays were irrigated daily, with solutions of NaCl, and measurements made of the amounts of Cl⁻ retained in the compost. The irrigation/drainage cycle was carried out for each of 4 days and the concentrations were 100 and 200 mg l⁻¹ of Na as NaCl. It was found that the measured daily increments in the amounts of Cl⁻ retained in the cells were equal to those calculated as the product of the concentration of Cl⁻ in the irrigation solution and the evaporative loss since the last irrigation. There was therefore little or no leaching (Fig.1).

Main Experiments

There were 4 experiments started in January 2004, March 2005, April 2005 and June 2005 subsequently referred to as Jan04, March05, April05 and June05. Details of the experiments, including glasshouse conditions, are given in Table 1. Two bedding plant species were grown in each experiment; *Viola.tricolor* (Pansy *Viola* × *wittrokiana* [cv?](#)) and *Petunia.hybrida* (*Petunia* × [hybrida](#) [cv?](#)). The treatments were nutrient concentrations; they were the optimum as described above and different fractions of the optimum. Shoot and root fresh weights were determined at weekly intervals and dry weights established after drying for 48 h at 80 °C.

RESULTS

Dependence of the growth rate coefficient on nutrient concentration

In every experiment, over the period for which different nutrient regimes were imposed, W_s increased in a curvilinear manner with time and $100\ln W_s + W_s$ was linearly related to time (Fig. 2 and Table 2). The gradients of these relationships are the values of K_2 and had a coefficient of variation of about 4%. They always decreased with decrease in the nutrient supply. The ratios of sub optimum to optimum values of K_2 were related the corresponding ratios of nutrient supply by a single logarithmic relationship that covered all species and experiments (Fig. 3). Increasing the nutrient supply from the optimum to 1.5 × the optimum increased K_2 only slightly from 22.3 to 23 for pansy and from 25.9 to 26.8 for petunia (Table 2). Thus growth of W_s was depressed by restricting nutrient supply below the

optimum but was hardly affected by increasing it. The optimum nutrient regime therefore achieved near maximum growth and values of K_2 for both optimal and sub-optimal regimes were constant for long periods. In addition there were no visual signs of nutrient deficiency until after the transplanting stage.

For each species and for the optimum treatment of each experiment $100\ln W_s + W_s$ was regressed against time and also against cumulative evapotranspiration, from emergence to the final harvest. This latter regression gives the growth rate coefficient, K_{2evap} , expressed in terms of daily evapotranspiration instead of time, as in K_2 . A comparison between K_2 and K_{2evap} for petunia is given in Table 3. The values of r^2 were always between 0.96 and 1.0 but K_2 was generally estimated more accurately than K_{2evap} , the average coefficients of variation were 3.7 % and 7.0% respectively. Values of K_2 for the June05 experiment were higher than for the other experiments but K_2 did not vary greatly between the Jan05, March 04 and April 05 experiments. There was also little variation between values for K_{2evap} for the March04, April 05 and June 05 experiments which were always about $135 \text{ g m}^{-2} \text{ cm}^{-1}$. The values were higher for the Jan05 experiments possibly because of the lower evapotranspiration.

Effect of aerial environment on K_2

The values of K_2 for the optimum nutrient treatment of each experiment on both pansies and petunia were plotted against the values calculated by eqn (4) from the average temperature and radiation over the growth period (Fig. 4). A near proportional relationship existed between the two sets of values and there was little difference between pansy and petunia.

Root/shoot ratio

An example of the effect of reducing the supply of nutrients on root/shoot ratio is given in Table 4. Reducing the nutrient concentrations in the irrigation solution from optimum to 12.5 % of optimum severely depressed shoot growth but had virtually no effect on root growth. The validity of the quantitative relationship (eqn (8)) for the dependence of root/shoot ratio on nutrition was supported by the data from all experiments except the January 05 experiment. Thus $[(R)_{sb}]/[(R)_o]$ was almost proportional to $[(Ws)_o]/[(Ws)_{sb}]$ for the data from the March04 experiment and for the combined data from the March04, April05 and July05 experiments (Fig. 5). The respective gradients and r^2 for the Mar04 experiment were 0.95 and 0.851 (Fig.5A) and, for all 65 observations from the 3 experiments, were 0.91 and 0.64 (Fig. 5B). The petunia data in the January 05 experiment had a gradient of 0.66 and an r^2 of 0.73 but there was no proportional relationship for pansy and only a weak linear one ($r^2 = 0.27$). For these experiments γ of eqn (8) was considerably less than one which according to the theory indicates that the aerial environment limited growth which seems possible from the measurements of the aerial environment given in Table 1.

DISCUSSION

The new method of supplying nutrients

The method described in this paper in which the supply of nutrients is modified during growth according to crop demand appears to be an improvement over the conventional practice of applying the same concentrations throughout growth. The assumption that the variation in the environment from one week to the next would not cause significant error in the estimation of nutrient concentrations in the irrigation solution is supported by the relatively small inter-experiment variation in K_2 when nutrient supply was optimum (Table 2). Our experiments (e.g. Fig. 1) indicate that the amount of nutrient retained in the plugs that is thus available for plant uptake is the product of evapotranspiration

and concentration of nutrients in the irrigation solution; a finding that was confirmed for a commercial overhead irrigation system (unpublished data) which implies that the method described in this paper could apply to this system as well as the Ebb and Flood experimental system. Evidence that with the optimum nutrient level, the new procedure gives near maximum growth rates is provided by the fact that values of K_2 were reduced by lowering nutrient concentrations below the optima but only slightly increased by increasing them above the optima (Table 2). Additional evidence is provided by the values of B_n being well within the range of values expected from the literature (Appendix 1 and Table 5). The ratios of P/N and K/N used for estimating P and K concentrations in the irrigation solution are rather higher than the published means values for other species (Appendix 1 and Table 5) which suggests that there is luxury consumption of these nutrients and that the concentrations of P and K could be reduced without any restriction in growth. Plant growth appeared to be insensitive to substantial increasing the nutrient supply above the optimum (Table 2) which implies that the method will be insensitive to considerable variation in the amounts of nutrients in the peat substrate. The average value of K_2 with the optimum nutrient supply (Table 2), though varying with the aerial environment is within the range of those found for field vegetables grown, with adequate nutrients and water, in the UK between April and September (Table 5). The values of K_{2evap} , calculated by replacing time with cumulative evapotranspiration are, however, only about half those for field vegetables (Greenwood *et al.*, 1977) which indicates a much greater water use efficiency in the glasshouse than in the field.

A major feature of the new method of supplying nutrients is that it allowed K_2 to be maintained at a given sub-optimum value for a long period by maintaining the supply at a lower but fixed proportion of the optimum supply (Fig. 2 and Table 2). Moreover this was done without the appearance of any deficiency symptoms for long periods and always before transplanting, which supports the view that over this period, the system did not lead to appreciable fluctuations in nutrient supply as such symptoms generally only occur when optimum nutrition is followed by sub-optimum nutrition (Ingestad and Lund, 1979). This could be important in the horticulture industry because it may enable plants to be grown with high root/shoot ratios without showing deficiency symptoms.

Relationship between shoot/root ratio, nutrient supply and time

The extent to which sub-optimal nutrition increases root/shoot ratio is of considerable importance in horticulture for the reasons discussed in the introduction. Interpretation of studies on this topic is complicated by the root/shoot ratio changing with increase in plant mass. Ideally graphs are needed of root/shoot ratio and shoot dry weight plotted against time of grown for each of several different rates of nutrient supply. Our approach was based on the constancy, over long periods, of nutrient-supply dependent values of K_2 , as this enabled the shoot dry weight for each day for each nutrient regime to be calculated.

A simulation model was programmed on the basis of calibrated versions of eqns (1), (4) and (8). The increment in dry weight was calculated for each day by eqn (1). The value of K_2 in this equation was calculated from the mean temperature and P_{ar} by eqn (4), with the values of f and g given in Appendix 1; a correction was made for the deviations from eqn (4) by the regression given in Fig. 4. These values of K_2 for optimum nutrient supplies were corrected to give the value for any suboptimum nutrient supply by the relationship given in Fig.3. The value of $[(R)_{sb}]/[(R)_o]$ was calculated from the ratio of W_s for the sub-optimum nutrient supply to that for the optimum supply by the proportional relationship obtained in Fig.5B. They show (Fig. 6A) that root/shoot ratio was only appreciably increased when the nutrient supply was less than $0.6 \times$ the optimum and then it increased in a diminishing manner to a maximum with increase in time. With a nutrient supply of $0.4 \times$ the optimum, root/shoot ratio increased by a factor of 1.4 after 25 days when W_s was equal to 100 g m^{-2} . However, it took 5 days longer to reach this weight than when nutrient supply was the optimum (Fig. 6B). The

effects of other reductions in nutrient supply on root/shoot ratio and duration of growth required to meet a given shoot dry weight were similarly estimated (Fig. 6).

Short-cut method for optimising optimum nutrient concentrations in the irrigation solution

The optimum nutrient concentration in the irrigation solution depends both on the nutrient demand of the seedlings and on evapotranspiration. Increased evapotranspiration increases the volume of nutrient solution supplied (Fig. 1), and thus the quantities of nutrients available for plant uptake. On the other hand increased evapotranspiration is also associated with increased plant growth and thus increased plant demand for nutrients. It seemed therefore that these opposite effects may counterbalance one another in some growing systems so that it may be possible to assess nutrient concentrations without having to make more detailed measurements of evapotranspiration rates. This possibility was tested for each of the four experiments. Daily increments in shoot dry weights were calculated from a starting shoot dry weight by substituting the appropriate value of K_2 , for the given experiment, in eqn (1) and repeating the calculation for each day and updating W accordingly. The corresponding critical %N was calculated for each day by substituting the value of W in eqn (3) and crop N demand was obtained by substituting both W and critical %N in eqn (9). Division of N demand by evapotranspiration for the given day (by analogy with eqn (10)) gave the N-concentration required in the irrigation water to meet crop N-demand for that day.

Graphs, prepared in this way (Fig. 7) of N-concentration against W_s for the Mar04, April05, and July05 experiments, using smoothed evapotranspiration data, were almost coincident until the shoot dry weight exceeded about 50g m^{-2} . Higher concentrations of N were required throughout growth for the Jan05 experiments because transpiration frequently fell to low values. For the Mar04 and April 05 experiments graphs of N-concentration against W_s were coincident throughout the entire range. It appears therefore that for some growth conditions, N- concentrations could be adjusted during much of the growth period to meet crop demand by measuring W_s alone at intervals and omitting the detailed transpiration measurements required for the procedure described in this paper. This would reduce the costs of estimating N-concentrations required to support optimum growth.

CONCLUSIONS

- A new method of was developed that consisted of adjusting nutrient supply according to crop demand rather than maintaining a constant supply as in conventional practice. It depended on measuring evapotranspiration and W_s each week from which estimates were made of nutrient requirements for the following week
- The new method of nutrient supply enabled growth to be maintained for long periods at different values of K_2 without the appearance of any nutrient deficiency symptoms even when nutrients were severely limiting growth.
- The ratio of K_2 for a sub optimum rate of supply relative to that with the optimum rate was logarithmically related to the nutrient supply as a fraction of the optimum. The value of K_2 for the optimum nutrient supply was well defined by a modification of a previously published equation in terms of average temperature and incoming radiation.
- A mechanistic model was derived which showed that with an optimal aerial environment root/shoot ratio for the sub optimum nutrient supply divided by that for the optimum nutrient supply was proportional to the ratio of shoot dry weight for the optimum supply relative to that for the optimum supply. All the experimental data from the March April and June experiments were in good agreement with that expectation.

- A simulation model derived from the forgoing relationships enabled the effects of nutrient supply, mean temperature and incoming radiation on growth, and root/shoot ratio to be calculated for both pansy and petunia.
- A simplification of the new procedure, for some growing situations, enables the concentrations of nutrients in the irrigation solution to be estimated from measurements of W_s alone, without measurements of evapotranspiration, at intervals during growth.

ACKNOWLEDGEMENTS

We thank the UK Department of Environment and Rural Affairs for supporting this work with grant HH1413 SMU, Findons limited, of Stratford-upon-Avon for sowing and germinating the seedlings, Bulrush Peat for supplying the peat and carrying out chemical analyses, Mrs Marion Evers for help in this work and for advice, Dr Allen Langton for providing data and Mr Neil Bragg and Mr Stuart Coutts for support and advice.

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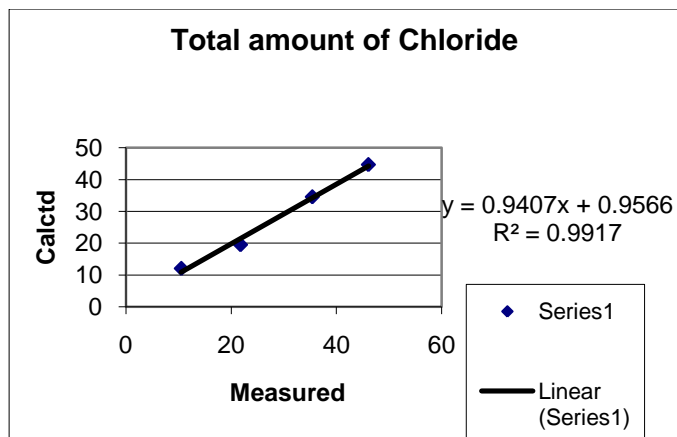
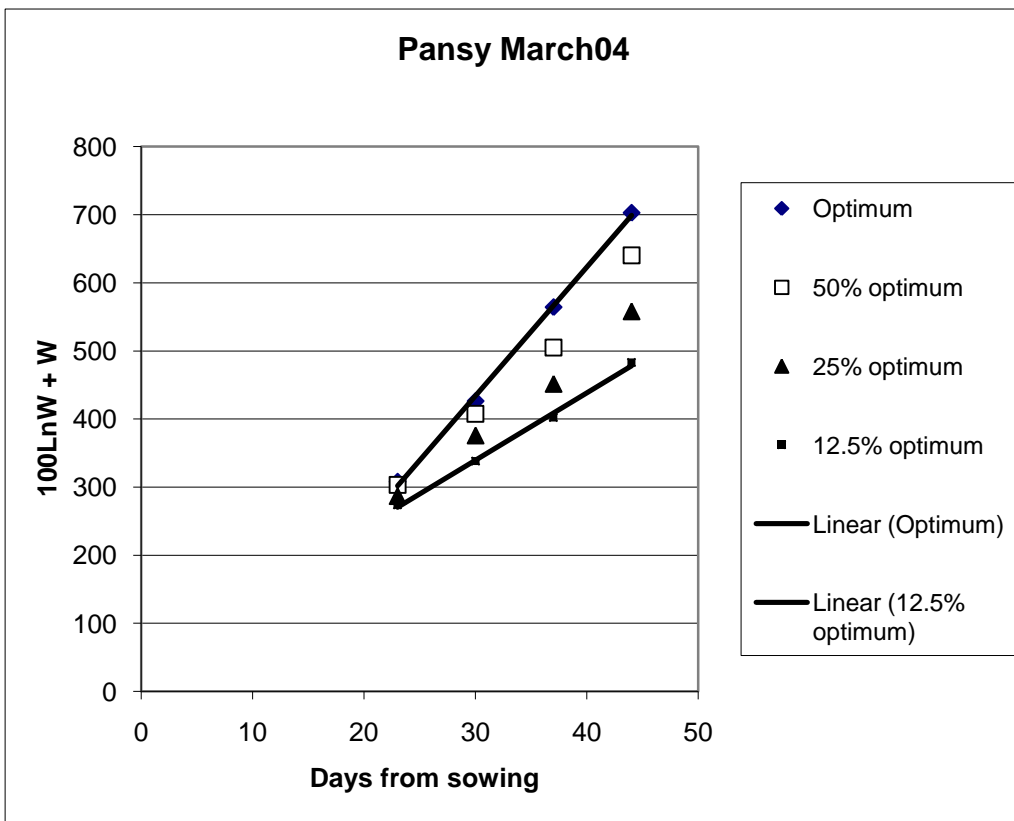
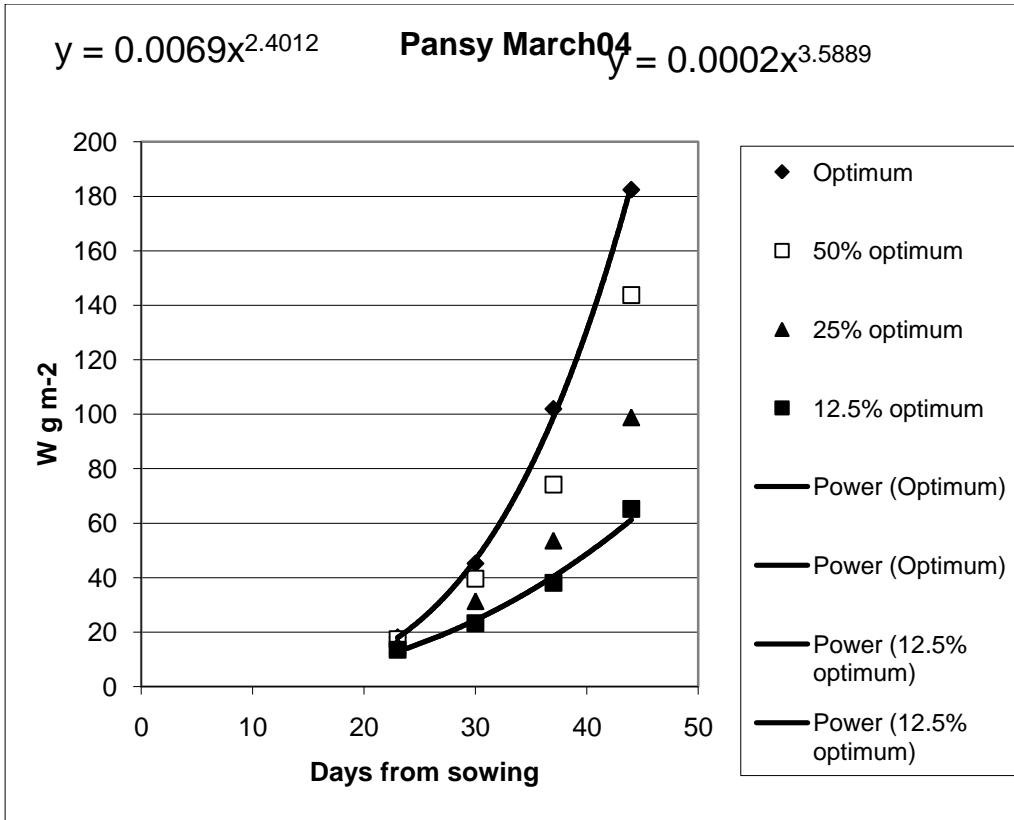


Fig.1 Original data in Spa\Barry - DJGEbb&FloodNaCl.xls.



From Barry\Mar04\Harv.xls\dry wt details n258
 Fig.2

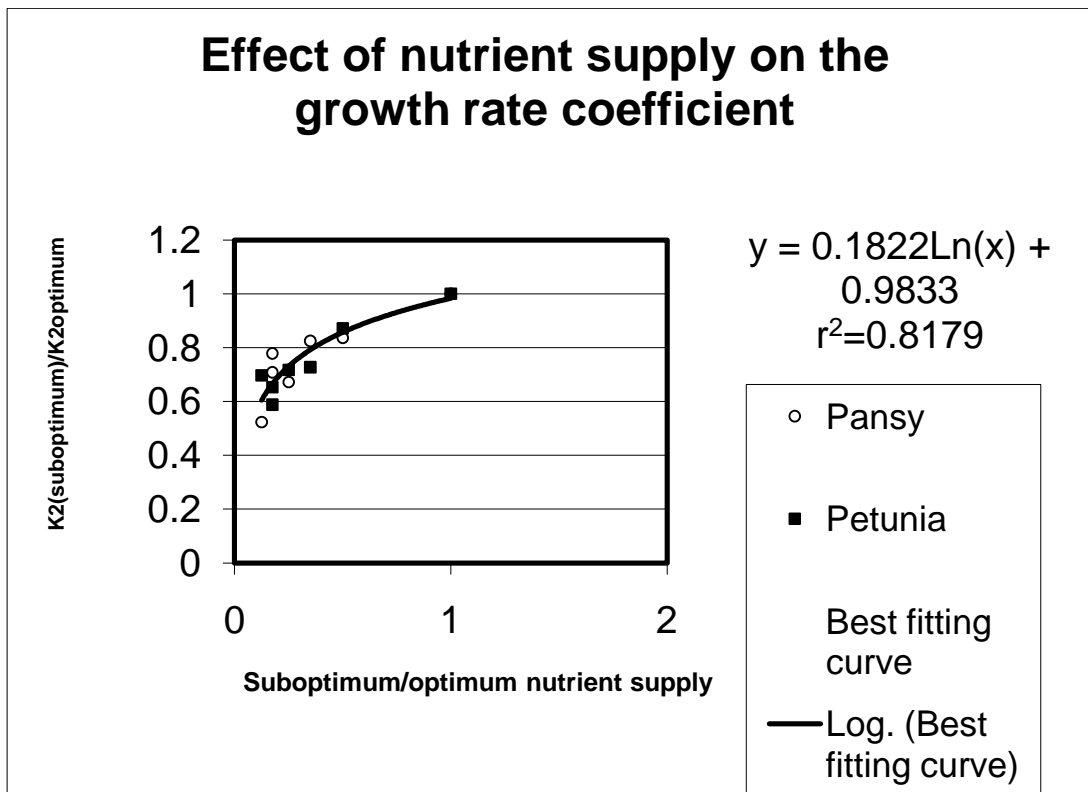
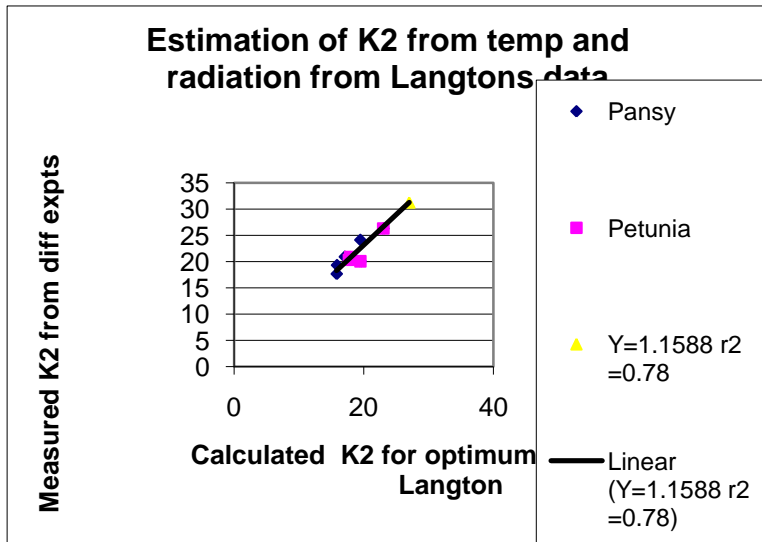
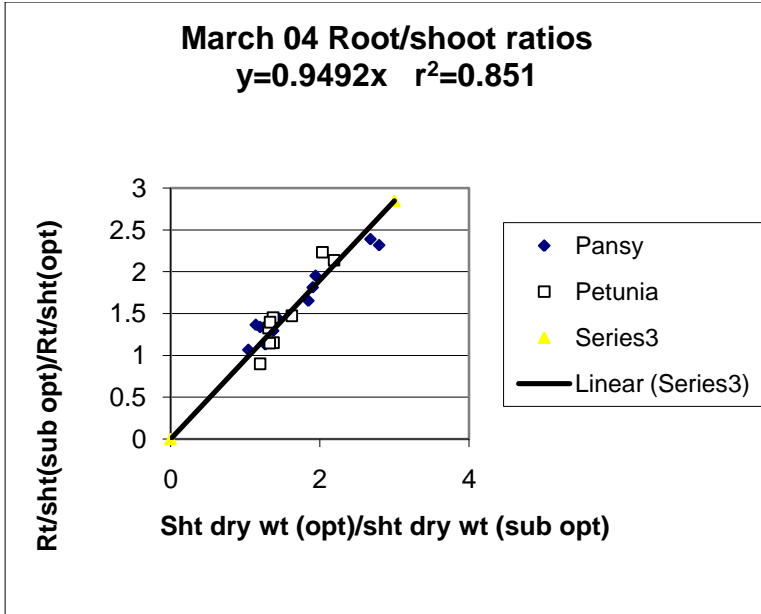


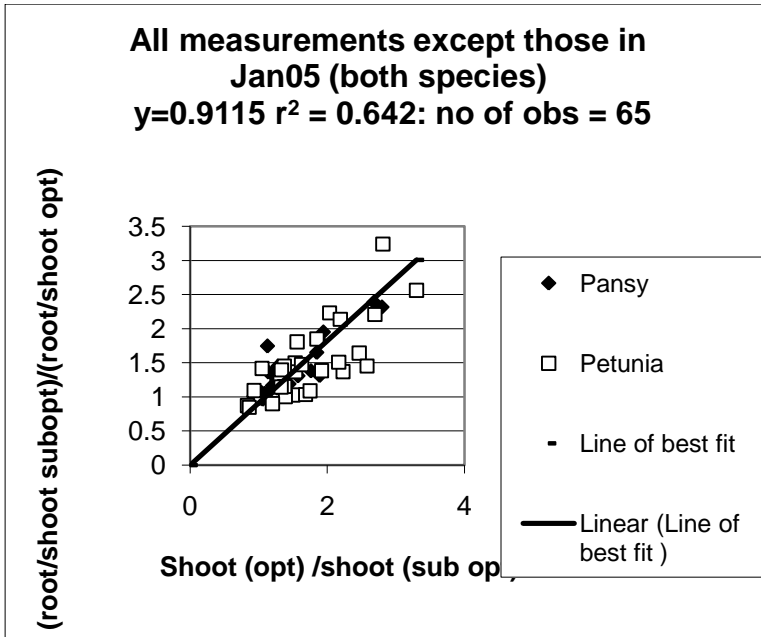
Fig. 3
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From Barry\Dshared area\ yr2005\Joint Rt -St\All RT -st05.xls at D94





From Barry\Dshared area\yr2005\Joint Rt-St\All Rt-st05.xls\ suboptrtsht2 K246



From Yr2005\joint RT-st\ All Rt-st05.xls suboptrtsht2 t13 & f224
Fig.4

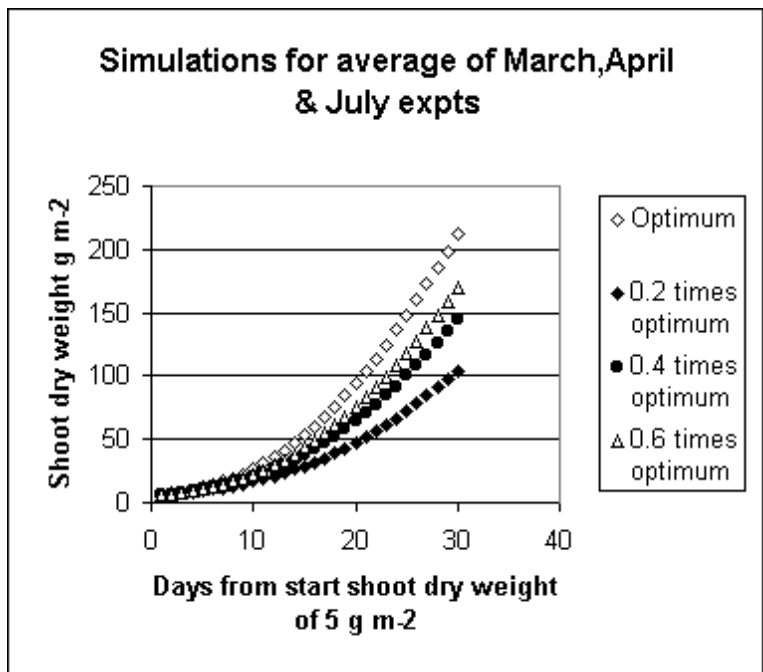
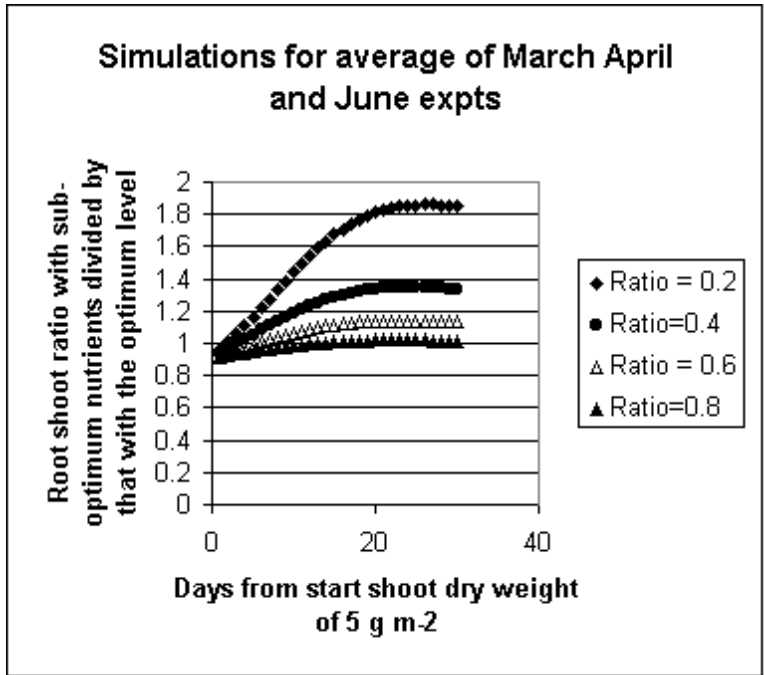
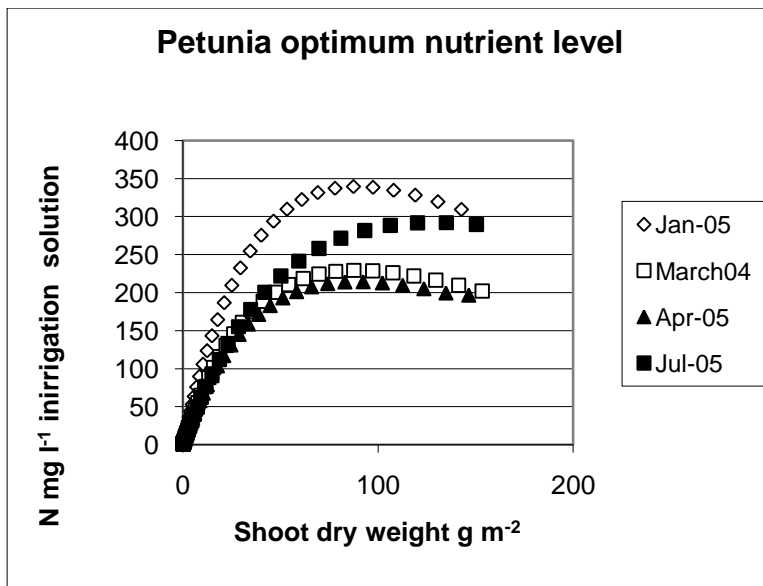
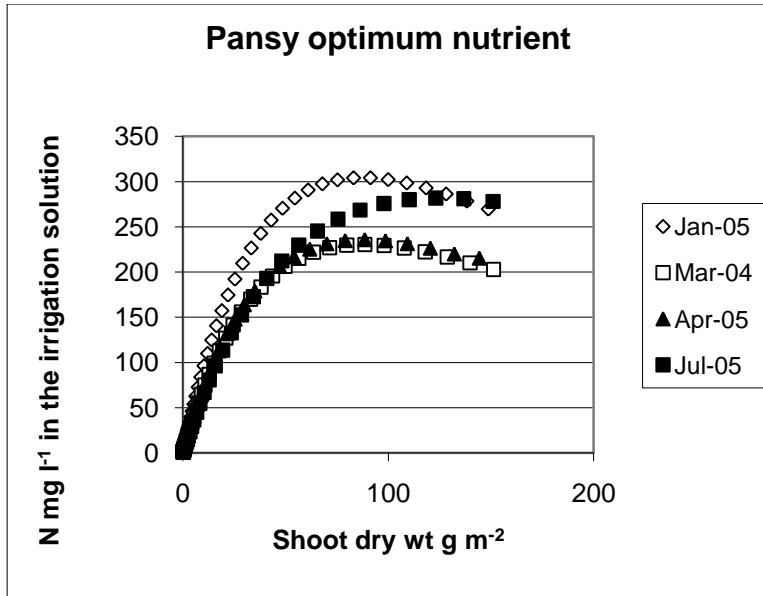


Fig 5. From spa\barry\rtsht.xls



From Barry\comb2.xls Q60 &R16

Fig. 6

APPENDIX 1. *Definition of symbols with default values*

Symbol	Definition	Value		Unit
		Pansy	Petunia	
B_n	Coefficient for dependence of critical %N on plant mass	3.05	2.809	Dimensionless
f	Coefficient defining the relative effects of mean °C & P_{ar} on K_2	0.0404	0.0644	MJ m ⁻² d ⁻¹ °C ⁻¹
g	Coefficient determining relating K_2 to the combined effects of mean °C and P_{ar} on K_2	0.784	0.525	d °C g ⁻¹ m ²
K/N	Ratio of K/N by mass in the irrigation solution	1.58	1.58	Dimensionless
P/N	Ratio of P/N by mass in the irrigation solution	0.18	0.18	Dimensionless
T_z	Temperature at which growth ceases	0	3	°C

APPENDIX 2. *Definition of symbols without default values*

Symbol	Definition	Units
E_{vap}	Evapotranspiration	mm d ⁻¹
γ	Ratio of suboptimum to optimum aerial stress	dimensionless

K_2	Coefficient for the dependence of growth rate on W_s	$\text{g m}^{-2} \text{d}^{-1}$
K_{2evap}	Coefficient for the dependence of growth rate on Evap	$\text{g m}^{-2} \text{cm}^{-1}$
N_{demand}	Daily uptake of N required to permit maximum growth rate	$\text{g m}^{-2} \text{d}^{-1}$
N_{crit}	The minimum %N needed to permit maximum growth rate	% in dry matter
N_{conc}	Daily Nconc required in irrigation solution to meet N_{demand}	g l^{-1}
P_{ar}	Photosynthetically active radiation	$\text{MJ m}^{-2} \text{d}^{-1}$
Parenthesis av	Values averaged over a week	dimensionless
Parenthesis c	Value refers to the specific crop species	dimensionless
Parenthesis d	Indicates the value on day d	dimensionless
R	Ratio of root dry weight to shoot dry weight	dimensionless
S_a	A measure of aerial stress on root/shoot ratio	dimensionless
S_n	A measure of nutrient stress on root/shoot ratio	dimensionless
t	Time	days
t_e	Time of harvest	days
T_0	Start time in simulations	days
T_m	Mean daily air temperature	$^{\circ}\text{C}$
W_s	Shoot dry weight	G m^{-2}

TABLE 1. *Experimental details*

Property	Experiment			
	Jan05	March04	April 05	June05
Nutrient supply proportion of the optimum	1,0.25,0.125	1, 0.5,0.25,0.125	1,0.35,0.175	1,0.75,1.5
Maximum W_s pansy (g m^{-2})	118.4	182.4	188.4	286.2
Maximum W_s petunia (g m^{-2})	60.29	79.1	158.1	253.5
No of replicates	2	3	2	2
Duration of growth (d)	21	28	27	26
Average daily ¹ evapotranspiration	1113	1507	1602	1743
Average photosynthetically active radiation ($\text{MJ m}^{-2} \text{d}^{-1}$)	1.71 ²	1.51	1.84	2.2
Average temperature °C	17.5	18.4	18.9	21.4

¹Averaged over values for pansy and petunia

²Averaged over last 9 days only

TABLE 2 *Effect of nutrient supply on K_2* ¹

Experiment			Optimum nutrient supply	Fraction of optimum nutrient supply			
Species	Name	No of measurements ²	K_2 (s.e.) g m ⁻² d ⁻¹	r^2	Fraction	K_2 (s.e.) g m ⁻² d ⁻¹	r^2
Pansy	Jan05	4	17.08(0.377)	0.999	0.25	13.42 (0.241)	0.999
	Mar04	5	18.91(0.495)	0.999	0.5	15.85(0.844)	0.994
	April05	4	21.29(0.140)	1.000	0.35	17.57(0.551)	0.998
	June05	3	22.25((1.02)	0.998	1.5	22.96(0.537)	0.999
Petunia	Jan05	4	20.75(1.44)	0.991	0.25	16.94(1.39)	0.987
	Mar04	4	17.24(1.03)	0.993	0.5	15.03(1.01)	0.991
	April05	4	20.92(1.16)	0.994	0.35	15.22(0.938)	0.993
	June05	4	25.87(0.126)	1.0	1.5	26.83(0.881)	0.998

¹Estimates of K_2 are for the period during which different nutrient regimes were imposed.

²No of measurements for each of the values of K_2

TABLE 3 Comparison between K_2 ¹ and K_{2evap} ¹ for petunia grown with the optimum nutrient supply

Experiment	No ² of measurements for each K_2	K_2 (s.e.) (g m ⁻² d ⁻¹)	r^2	K_{2evap} (s.e.) (g m ⁻² cm ⁻¹)	r^2
Jan05	4	20.89(1.43)	0.991	182(1.68)	0.965
Mar04	5	20.34(1.88)	0.975	136(22.3)	0.960
April05	5	20.08(0.83)	0.995	123(7.57)	0.989
June05	5	26.32(0.28)	1.000	153((2.92)	0.999

¹Estimates of K_2 and K_{2evap} calculated from measurements made from emergence to final harvest .

²No of measurements for each estimate of K_2 and K_{2evap}

TABLE 4. *Effect of suboptimum nutrient supply on shoot and root growth of petunia*

Days from sowing	Shoot dry weight g m ⁻²			Root dry weight g m ⁻²		
	Optimum	Optimum × 0.125	s.e.d.	Optimum	Optimum × 0.125	s.e.d.
28	15.6	11.7	3.02	4.6	4.0	0.71
36	32.6	20.1	3.36	12.0	10.9	1.63
42	79.1	36.1	8.08	21.7	21.2	0.73

d.f in all comparisons =3

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TABLE 5 *Independently measured parameter values*

Parameter	Plant type	Mean value of parameter	Range values of parameter	Reference
B_n	C3 field vegetables	2.61	1.26-3.49	Greenwood and Draycott (1989)
f	Pansy	0.0332	-	Brewster and Sutherland (1993)
f	C3 flower and vegetables	0.0824	0.0276-0.146	Brewster and Sutherland (1993)
f	C3 flower and vegetables	0.0725	0-0.11	Scaife <i>et al.</i> (1987)
K_2	Non-leguminous C3 field vegetables	20.0	15.4-25.4	Greenwood <i>et al.</i> (1977)
K_{2evap}	Non-leguminous C3 field vegetables	74	59-95	Greenwood <i>et al.</i> (1977)
T_z	Pansy	-3.4	-	Brewster and Sutherland (1993)
T_z	C3 flower and vegetables	+3.2	-7-9.8	Brewster and Sutherland (1993)
T_z	C3 flower and vegetables	0.37	-1-4.0	Scaife <i>et al.</i> (1987)
K/N (mass)	Non-leguminous C3 field vegetables	0.94	0.57-1.36	Greenwood <i>et al.</i> (1980a,b)
K/N (mass)	Malipighales order ¹	0.82	-	Broadley <i>et al.</i> (2004)
K/N (mass)	Solanales order ²	1.197	-	Broadley <i>et al.</i> (2004)
P/N (mass)	Malipighales order ¹	0.16	-	Broadley <i>et al.</i> (2004)
P/N (mass)	Solanales order ²	0.12	-	Broadley <i>et al.</i> (2004)
P/N (mass)	28 different species field crops	0.16	0.05-0.43	A Boldrini (personal communication)
P/N (mass)	C3 vegetable seedlings grown with optimum nutrients	0.11	0.08-0.127	D J Greenwood (unpublished data)
P/N (mass)	Ocean particulate matter (Redfield ratio)	0.14		Sterner and Elser (2002) p. 29

FIG. 1. Relationships between measured amounts of chloride in cell substrate and those calculated as the product of chloride concentration in the irrigation solution and loss of water by evapotranspiration. The regression is $y = 1.039x$, $r^2 = 0.991$.

FIG. 2. (A) Relationships between shoot dry weight (W_s) and the number of days from sowing for pansies grown in the March04 experiment with $1 \times$, $0.5 \times$, $0.25 \times$ and $0.125 \times$ optimum supply of nutrients denoted by \circ , \bullet , \square , \blacksquare respectively. The fitted curves are $y = 0.0002 x^{3.59}$ and $y = 0.0069x^{2.40}$. The s.e.d.'s of W_s after 23, 30, 37 and 44 days from sowing were 0.63, 5.2, 1.64 and 6.0 respectively with 3 df in each case. (B) Linear relationships between $100 \ln W_s + W_s$ and time for the data in (A); the gradients, K_2 obtained with the optimum supply and 0.5, 0.25, and $0.125 \times$ the optimum supply were 18.9, 15.8, 12.7, and 9.9 and the corresponding s.e.'s were 0.49, 0.84, 0.59, and 0.42

FIG. 3. The ratios of sub optimum to the optimum values of K_2 , and the corresponding ratios of nutrient supply for pansy - \circ - and for petunia - \bullet -, grown in each experiment. $Y = 0.182 \ln x + 0.9833$ $r^2 = 0.82$.

FIG. 4. Relationship between values, measured in the 4 glasshouse experiments, of the measured values of K_2 with the optimum supply of nutrients and the values calculated from the average values of P_{ar} and temperature from emergence to final harvest using eqn (4) calibrated with data from independent controlled environment experiments. Data for pansy denoted by - \circ - and for petunia by - \bullet - ; $y = 1.159x$, $r^2 = 0.78$; $T_z = 0$ for pansy and $+3^\circ\text{C}$ for petunia.

FIG. 5. Proportional relationship between $[(R)_{sb}] / [(R)_{o}]_o$ and $(W_s)_o / (W_s)_{sib}$ for (A) the March04 experiment and for (B) the combined data from the March04, April05 and June05 experiments. Data for pansy denoted by - \circ - and for petunia by - \bullet - ; regressions for the data for both species is $y = 0.949x$, $r^2 = 0.851$ for (A) and $y = 0.912x$, $r^2 = 0.64$ for (B)

FIG. 6. (A). Calculated dependence of $[(R)_{sb}] / [(R)_{o}]_o$ on time for pansy seedlings grown with different proportions (0.2, 0.4, 0.6, 0.8) of the optimum nutrient supply. (B) The corresponding relationships between W_s and time. Calculations are with the mean temperatures and P_{ar} for the March04, April05 and June05 experiments.

FIG. 7. Relationships between the calculated optimum N concentrations required in the irrigation solution and shoot dry weight during growth of (A) pansy and (B) petunia in each of the four experiments.