

## Effects of kelp (*Macrocystis integrifolia* and *Ecklonia maxima*) foliar applications on bean crop growth and nitrogen nutrition under varying soil moisture regimes

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### Abstract

A greenhouse experiment was designed to test the effects of two kelp (*Macrocystis integrifolia* and *Ecklonia maxima*) concentrates, when prepared as foliar sprays, upon bean (*Phaseolus vulgaris*) growth and N nutrition under three soil moisture regimes. Plant growth and developmental responses in this greenhouse experiment have demonstrated the effectiveness of the two kelp foliar sprays as plant growth regulating substances. Bean growth and developmental responses to the kelp foliar spray treatments were dependent upon the soil moisture regime to which they have been subjected. Although the two kelp foliar sprays had varying and sometimes contrasting effects on bean growth and N nutrition, which were dependent on the soil moisture treatment, their developmental effects upon the number of nodes, shoot/root ratio, leaf area ratio and specific leaf area were quite similar. A soybean callus bioassay demonstrated the presence of cytokinin-like substances and a callus growth antagonist in the kelp concentrate. Increasing dilution of the kelp concentrate disproportionately reduced the callus growth antagonist relative to the growth promoting or cytokinin-like activity.

### Introduction

Recent field plot trials have demonstrated that the South African kelp (*E. maxima* (Osbeck) Papenfuss) concentrate "Kelpak 66" and the British Columbia kelp (*M. integrifolia* Bory) concentrate, when diluted with water prior to foliar application, were effective in increasing bean (*P. vulgaris* L.) yields (Temple and Bomke, 1989). According to Abetz (1980) kelp foliar sprays may be effective in increasing marketable yields of various crops under environmental stress conditions. However, we are unaware of any documented research which supports the claim that kelp foliar sprays are most effective under water stress conditions.

The cytokinin phytohormones have been postulated as the active constituents of kelp foliar

treatments (Finnie and van Staden, 1985; Sander-son and Jameson, 1986; Tay *et al.*, 1985). Foliar applied cytokinins have been shown to be effective in alleviating some of the plant symptoms associated with drought and waterlogging stress (Levitt, 1980). Environmental factors such as drought and waterlogging decrease yields, increase plant elemental concentrations and reduce total uptake (Datta, 1985; Gerakis *et al.*, 1975; Mengel and Vonbraunshweig, 1972; Marais and Wiersma, 1975; Mattison, 1973; Nambiar, 1976). Interactive effects between the environment and plant may be important factors which determine the efficacy of kelp foliar sprays and the types of plant growth and nutritional responses recorded with their use.

The objectives of this greenhouse investigation were to determine the effect of the kelp foliar sprays on bean (*Phaseolus vulgaris* L.) growth, develop-

ment and N nutrition under varying soil moisture conditions.

### Materials and methods

Bush beans (*P. vulgaris* cv. Galamor) were grown in the greenhouse for 62 days between May 30 and July 31, 1984. Treatments consisted of three foliar sprays and three soil moisture regimes in a 3 × 3 factorial experiment. There were two blocks with three replicates within each of the blocks. Each of the 108 pots in the experiment was initially planted with five seeds and then selectively thinned to two plants per pot on Day 12. Prior to planting, all the seeds were placed on a sieve, wetted and inoculated with *Rhizobium leguminosarum* biovar *phaseoli*. Plants were harvested on Days 37 (onset of flowering) and 62 (maturity). The equivalent of 1.95 kg of dry sterilized sandy loam soil was added to each of the sterilized 15 cm high, 2300 cm<sup>3</sup> pots and packed to a bulk density of 850 kg m<sup>-3</sup> with a total porosity of 0.68 m<sup>3</sup> m<sup>-3</sup>. A soil water retention curve was constructed for this soil using the porous plate extraction method (Richards, 1965).

The soils were analysed for total nitrogen (%N), total carbon (%C), pH and available P, K, Ca, Mg, Fe, Cu, Mn and Zn using the methods described by Temple and Bomke (1988). The soil had a pH of 6.6 and total %N and %C concentrations of 0.41 and 6.6, respectively. Available P (Bray 1) was 200 mg kg<sup>-1</sup>, and the available Ca, K and Mg concentrations (Morgan's Extraction Solution) were 3600, 525 and 550 mg kg<sup>-1</sup>, respectively. The 0.1M HCl extractable Fe, Cu, Mn and Zn concentrations were 55, 5, 130, 40 mg kg<sup>-1</sup>, respectively. 145 mg of 0-0-60 (150 kg ha<sup>-1</sup> equivalent) and 290 mg of 11-55-0 (300 kg ha<sup>-1</sup> equivalent) fertilizer was added to each of the pots and mixed thoroughly prior to potting.

The soil moisture potentials used in the experiment were field capacity (FC; -30 to -50 kPa), dry (D; -120 to -150 kPa) and wet W; 0 to -10 kPa). For the field capacity and dry soils, the soil moisture retention curve was used to calculate the weight of soil equivalent to their respective soil water potentials, and pots were weighed each day and twice on sunny days to maintain the soils at the upper end of the desired water potential range. The lower water potential values for the field capacity and dry soil treatments relate to the average loss of

soil water due to evapotranspiration. The wet soil water treatment was maintained by keeping the pots in a 0.06-m high dish filled with water. The wet soil water potential range represents the soil moisture content from the top of soil (-10 kPa) to the water table (0 kPa).

All pots were maintained at field capacity from seeding until Day 17. On day 17, dry and wet soil moisture treatment were initiated. Wet soils had their pans filled with water and dry soils were allowed to lose water to their defined water potentials, while field capacity soils were maintained at their water potential during the entire experiment. The plants (Day 17) had fully developed primary leaves, and the first trifoliates were beginning to expand.

At the onset of flowering (Day 37) the dry and wet soil moisture period was ended and half of the pots were harvested. The remaining pots were re-randomized with the dry and wet soils returned to field capacity. The wet soils did not have their pans refilled and were not watered until their soil water potential had fallen below field capacity. All remaining pots were maintained at field capacity until harvest (Day 62).

The foliar sprays consisted of the control (C) sprayed with water, the commercial South African kelp (*E. maxima*) concentrate "Kelpak 66" (K), and the *M. integrifolia* experimental kelp concentrate (S) both diluted 1:250 with distilled water. The *E. maxima* and *M. integrifolia* experimental concentrates were described by Temple and Bomke (1989). All sprays were applied with a hand held atomizer until the foliage dripped. Spraying occurred on Days 13, 21, 39 and 49.

On each of the respective harvest dates (Days 37 and 62) the plant height, number of nodes, leaf area and shoot fresh weight were recorded. The roots were excavated the next day from each pot by careful washing of the roots. Prior to drying the roots, nodulation was rated on a scale of 1 to 3 by five independent observers (1 = light, 2 = medium and 3 = heavy). The plant leaves, stems, beans (greater than 6 cm in length, final harvest only) and roots were oven dried at 70°C. On the final harvest (Day 62) the number of marketable beans for each pot was recorded. Calculations for each pot included fresh/dry weight ratios of the shoot, dry shoot/root ratios, specific leaf area (SLA) and leaf area ratio (LAR).

Dry plant samples were ground through a stain-

less steel Wiley mill (1-mm screen) with a 1.000 g sample used for N analysis. Digestion procedures and determination of N concentration have been described by Temple and Bomke, 1988.

Plant growth parameters and N concentration variables were subjected to analysis of variance for each of the two harvests. Foliar treatment means were separated using single degree of freedom contrasts into C vs (K + S) and K vs S, and soil moisture treatments separated into FC vs (D + W) and D vs W. The interactions were separated into C vs (K + S) \* FC vs (D + W), C vs (K + S) \* D vs W, K vs S \* FC vs (D + W) and K vs S \* D vs W. Statistical significance was determined at the 5% level and coefficients of variation (CV) given.

Cytokinins were extracted and purified according to Taylor *et al.* (1982). All solvents were of the highest purity grade available and were glass-distilled before use. Three separate extractions of 1.0, 10.0 and 40.0 g fresh weight of the kelp (*M. integrifolia*) concentrate were made. The kelp was stirred in cold 80% methanol (1:4 w:v) for 1 h at 4°C and filtered through Whatman #3 filter paper in a Buchner funnel. The residue was re-extracted for 4 h in 80% methanol (1:5 original w:v), filtered and reextracted in 80% methanol a third time overnight. The combined filtrates were rotary evaporated under vacuum (< 30°C) to the aqueous phase, adjusted to pH 8.0 with NH<sub>4</sub>OH and centrifuged at 1000 × g for 0.5 h. The supernatant was adjusted to pH 3.0 with acetic acid, and applied to a cellulose phosphate column (bed volume 50 mL). The column was then washed with 6 column volumes of degassed distilled water, the first three of which were adjusted to pH 3.0. Cytokinins were eluted from the column with six column volumes 0.3 M NH<sub>4</sub>OH. The eluate was reduced in volume by rotary evaporation, adjusted to pH 8.0 with 1 M HCl and partitioned four times against equal volumes of water saturated n-butanol. The butanolic phase was rotary evaporated to near dryness and the residue taken up in a minimum volume of methanol which was divided in half, with each half streaked onto a strip of Whatman 3 mm chromatography paper. Descending chromatograms were run in isopropanol:ammonia:water (10:1:1 v:v:v). Developed strips were air-dried and cut into 10 equal strips (R<sub>f</sub> 1 to 10). Strips were placed into 125-mL erlenmyer flasks for inclusion in the bioassay medium.

The bioassay of Miller (1968) was used to determine the cytokinin-like activity of the extract. Soybean (*Glycine max* (Merr) L. cv Acme) seeds were surface sterilized in 10% bleach for 10 minutes and then rinsed with distilled water. Sterilized seeds were then placed on phytohormone-free culture medium in 500-mL erlenmyer flasks and grown for two weeks at 28°C under constant fluorescent light. The cotyledons of healthy seedlings were aseptically removed, cut into blocks, placed on growth media containing 2.5 mg L<sup>-1</sup> kinetin and 2 mg L<sup>-1</sup> naphthalene acetic acid (NAA). The resulting callus was maintained in the dark at 30°C and sub-cultured to provide uniform bioassay material.

Twenty mL of cytokinin-free culture media were placed in each of the 125-mL erlenmyer flasks containing the chromatogram strips, stoppered with cotton and autoclaved (20 minutes at 100 kPa). Four pieces of healthy white callus (2mm × 2mm) were placed in each flask upon the solidified culture media and incubated in the dark for two weeks at 30°C. Total callus weights per flask were determined and compared to a known standard of isotopentenyl adenine in serial dilution to allow estimation of cytokinin-like activity in each test solution. A standard line equation was established and mean responses different from the no cytokinin standard were substituted into the equation to yield estimates of the relative cytokinin-like activity.

## Results

Ambient greenhouse temperatures ranged from a night time low of 19°C to an average day time high of 23°C. The relative humidity ranged from an average night time high of 80% to a day time low of 63%.

Harvest I: Figure 1 depicts the significant growth and development effects for this harvest. The dry plant, root and leaf weights of the controls (C) were greatest upon the field capacity (FC) soil treatment as compared to dry (D) and wet (W) soil moisture treatments. Both the *E. maxima* (K) and *M. integrifolia* (S) kelp foliar treatments increased each of these variables on the dry and wet soil moisture treatments with the greater increases occurring on wet soil. Root weights were increased by the *E. maxima* and *M. integrifolia* treatments regardless of soil moisture treatment. The *E. maxima* foliar treatment increased root growth more on wet soils,

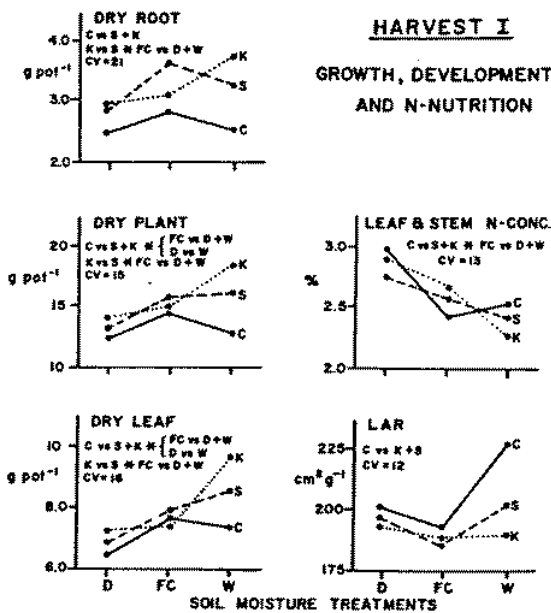


Fig. 1. Harvest I, Day 37: Foliar treatments include control (C) and the *M. integrifolia* (S) and *E. maxima* (K) kelp concentrates. Soil moisture treatments include dry (D), field capacity (FC) and wet (W). Significant contrasts and coefficients of variation (CV) are given.

while the *M. integrifolia* treatment increased plant root growth more on the field capacity soil. LAR was reduced by both the *M. integrifolia* and *E. maxima* kelp foliar spray treatments regardless of soil moisture treatments.

Control plants had higher N concentrations on dry and wet soils relative to the field capacity soil (Fig. 1). Relative to the control both the *E. maxima* and *M. integrifolia* foliar treated plants had lower N concentrations on the dry and wet soils and increased N concentration on field capacity soils.

Harvest II: Significant growth and developmental responses for this harvest are depicted in Figures 2, 3 and 4. Control plants of field capacity soils had higher total, leaf, leaf and stem, bean pod and shoot weights and greater leaf area, number of beans and shoot/root ratios relative to the dry and wet soils. Control root weights, unlike in the first harvest, were greatest on the dry and wet soils, relative to field capacity soils. Control LAR, SLA, nodulation rating and node numbers increased as soil moisture treatments went from dry through field capacity to wet.

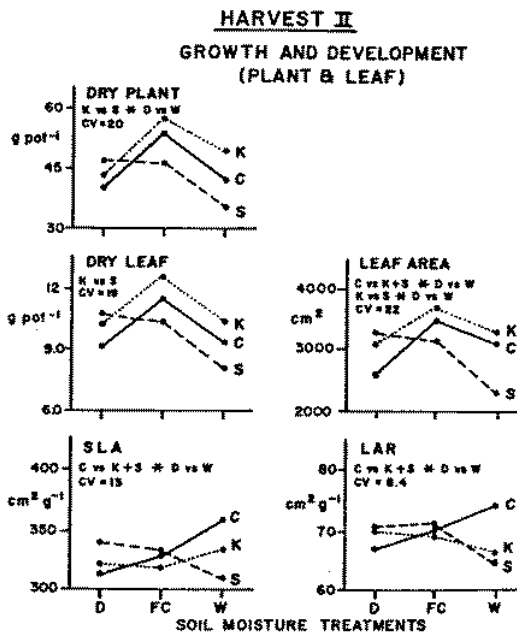


Fig. 2. Harvest II (plant and leaf), Day 62: Foliar treatments include control (C) and the *M. integrifolia* (S) and *E. maxima* (K) kelp concentrates. Soil moisture treatments include dry (D), field capacity (FC) and wet (W). Significant contrasts and coefficients of variation (CV) are given.

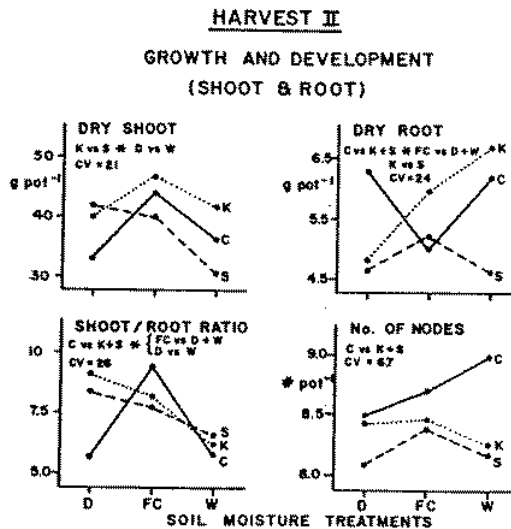


Fig. 3. Harvest II (shoot and root), Day 62: Foliar treatments include control (C) and the *M. integrifolia* (S) and *E. maxima* (K) kelp concentrates. Soil moisture treatments include dry (D), field capacity (FC) and wet (W). Significant contrasts and coefficients of variation (CV) are given.

HARVEST II

GROWTH, DEVELOPMENT AND N-NUTRITION

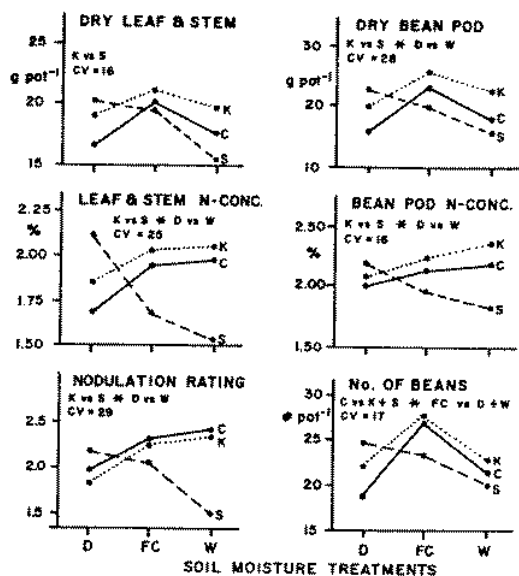


Fig. 4. Harvest II, Day 62: Foliar treatments include control (C) and the *M. integrifolia* (S) and *E. maxima*(K) kelp concentrates. Soil moisture treatments include dry (D), field capacity (FC) and wet (W). Significant contrasts and coefficients of variation (CV) are given.

Plants which were treated with the *E. maxima* kelp concentrate were greener or less senescent than the controls or *M. integrifolia* foliar treated plants for each of dry, field capacity and wet soil moisture treatments, although this greening effect was not as apparent with dry soils. Relative to the controls, plants which were foliar sprayed with the *M. integrifolia* kelp concentrate were greener on dry soils only and were very chlorotic or more senesced on wet soils.

At second harvest the *E. maxima* treated plants, relative to the control, had the greater total, leaf, shoot, combined leaf and stem and bean weights and leaf areas and bean numbers on dry, field capacity and wet soils. In contrast the *M. integrifolia* foliar treatment increased these variables on the dry soil, but its effect on the field capacity soil was similar to that of the controls and less than the control on the wet soil treatment.

Relative to the controls, both the *E. maxima* and *M. integrifolia* kelp foliar treatments increased the LAR and SLA on dry soil and decreased these

variables on wet soil. Shoot/root ratios of kelp treated plants were highest on dry soil but declined through field capacity to wet soil moisture treatments. Both kelp foliar sprays reduced the number of nodes, regardless of the soil moisture treatments. The *E. maxima* treated plants increased root growth from dry through field capacity to wet soil moisture treatments, whereas, the *M. integrifolia* treated plants had the highest root growth on field capacity soils and lowest on dry and wet soil treatments.

Combined leaf and stem and bean pod N concentrations closely followed nodulation ratings. For both the control and *E. maxima* treated plants, nodulation and N concentrations were lowest on dry soils and highest on field capacity and wet soil moisture treatments, whereas *M. integrifolia* treated plants were highest on dry soils and declined through field capacity to wet soils. Combined leaf and stem and bean pod yields and bean numbers for *M. integrifolia* treated plants closely followed the same trends as for N concentrations and nodulation rating.

Figure 5 displays the cytokinin-like activity detected in each of the chromatogram strips ( $R_f$  1 to 10) for each of the kelp concentrates. The calculated total cytokinin-like activity (isopentenyl adenine equivalent) for each 40.0, 10.0 and 1.0 g of kelp extracted material was estimated at 84, 120 and 1680  $\mu\text{g kg}^{-1}$  respectively.

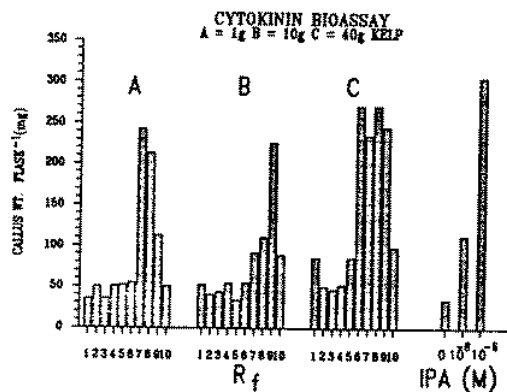


Fig. 5. Soybean callus bioassay activities for each of the 10 eluted chromatograph sections ( $R_f$ ): (A), 1 g; (B) 10 g and (C) 40 g of kelp (*M. integrifolia*) concentrate extracted and chromatographed prior to bioassaying. IPA (isopentenyl adenine) standards activity are given. The total cytokinin-like bioassay (IPA equivalence) activity for A, B and C was 1680, 120 and 84  $\mu\text{g kg}^{-1}$  respectively.

### Discussion

Both the *M. integrifolia* (S) and *E. maxima* (K) kelp foliar sprays were effective in altering bean growth, development and nutrition, however, major differences existed in the efficacy of the two kelp sprays under varying soil moisture regimes.

At flowering (Harvest I) both of the kelp treatments, relative to the controls, were effective in increasing the plant and leaf weights of those plants which were subjected to dry and wet soil moisture treatments. The lower LAR with kelp-treated plants, regardless of the soil moisture treatments, suggests greater dry matter accumulation or net productivity per unit leaf area. The kelp treated plants showed increased root growth independent of the soil moisture, which could reflect a greater supply of shoot photosynthates to enhance root growth.

According to Martin and Matocha (1973) the mineral composition of any plant is a result of the interaction of nutrient supply and plant growth. Any factor which limits growth, be it light, moisture, temperature or some nutrient may cause other nutrients to accumulate. In this investigation the higher elemental shoot N concentrations at first harvest with control plants subjected to the dry and wet soil moisture regimes, relative to the field capacity soil moisture regime, suggest that these elements accumulated as yields declined. Shoot N concentrations of kelp treated plants were lower than that of the controls on the dry and wet soil moisture treatments as yields were enhanced; the kelp-treated plants may have undergone a so called "dilution effect" showing greater tolerance to soil moisture stress as dry matter yields were enhanced. Other researchers (Blunden *et al.*, 1979; Featonby-Smith and van Staden, 1987; Nelson and van Staden, 1984a) have also reported a reduction in elemental N concentration with plants treated with kelp foliar sprays.

At maturation (Harvest II) the *E. maxima* foliar treatment, relative to the controls, promoted growth on both the dry and wet soil moisture treatments. In contrast, the *M. integrifolia* treatment was stimulatory upon the dry soil treatment, yet inhibitory upon the wet soil treatment. Relative to the control, the *M. integrifolia* treated plants, subjected to the wet soil moisture treatment, experienced rapid or accelerated senescence shortly after the third spraying.

Nelson and van Staden (1984) have also observed an initial inhibition of greenhouse cucumber during fruit set with *E. maxima* treatment. They suggested that inappropriate foliar applications during fruit set could have been responsible for the observed response, therefore, kelp foliar treatments should be timed to coincide with particular growth stages, rather than as a regular treatment throughout the growing period. Application of various known growth regulating substances at various stages and/or in combination at various stages of plant development is known to cause conflicting and opposite results and is a factor also controlling the effectiveness of these compounds (Kannan, 1980; Mishra and Gaur, 1985).

Such contrasting effects between kelp treatments could have also been related to the water dilution chosen (1:250) for this investigation. The 1:250 water dilution of the concentrate may have been more optimal for the *E. maxima* concentrate than for the *M. integrifolia* concentrate. The differing growth responses between the kelp concentrate treatments may be related to varying levels of active constituent(s) or inhibitor(s). Finnie and van Staden (1985) have demonstrated that the water dilution ratio of the *E. maxima* kelp concentrate prior to application is an important factor controlling its efficacy. Low dilution ratios (1:100 kelp concentrate:water) were found to have an inhibitory effect upon root growth, whereas higher dilution ratios (1:400 to 1:600) were stimulatory. Such kelp concentrate dilution effects upon root growth could be attributed to growth inhibitors in the concentrate which, upon increasing dilution, become less effective than the growth promoting substances. The results of this investigation could also suggest that optimal dilution ratios of the concentrate may be dependent on the particular soil moisture regime or environmental conditions to which the plants are subjected. Furthermore, the inhibition of bean root growth with the *M. integrifolia* foliar treatment upon the wet soil treatment could also account for the loss of nodulation and the lowering of plant N concentration, as the supply of shoot photosynthates to support active root nutrient uptake and N fixation may have diminished.

Phytohormones, in particular cytokinins, have been postulated as the active constituents of kelp treatments (Featonby-Smith and van Staden,

1983a; 1983b; Sanderson and Jameson, 1986; Tay *et al.*, 1985). However, it has yet to be demonstrated that the cytokinin-like substances which have been detected are indeed physiologically active under field or greenhouse conditions. Table 1 summarizes the data for cytokinin and cytokinin-like substances which have been recorded for the various kelp extracts or concentrates used as foliar sprays. The activities in the *M. integrifolia* concentrates decreased with an increase in the fresh weight of the kelp concentrate extracted and chromatographed prior to the callus bioassay. The reason for this may be related to growth inhibitors present in the extracts which, upon increasing dilution (higher extraction ratio), become less effective than the growth promoting substances. Alternatively, it may also be related to a higher recovery of the active substances at higher extraction ratios. Both of these conjectures need further investigation. Nevertheless, such bioassay results demonstrate the inadequacies of using a bioassay as a means of quantification because the values obtained are dependent on the method of analysis.

Although shoot and root yield responses to *E. maxima* and *M. integrifolia* foliar treatments differed markedly among soil moisture treatments, their effects on plant shoot/root ratio, number of nodes, SLA and LAR were similar. Shoot/root ratios of both the *E. maxima* and *M. integrifolia* foliar treated plants declined from dry through field capacity to wet soil moisture treatments, whereas SLA and LAR remained relatively constant. Both

the kelp foliar sprays were also effective in reducing the number of nodes, regardless of the soil moisture regimes. Although shoot and root yield responses between the two kelp foliar sprays were quite different, the partitioning of photosynthates for dry matter accumulation and development is similar.

These growth, developmental and N nutritional responses establish that, although there are some similarities between the two kelp foliar sprays, there are also some very apparent effective differences in relation to soil moisture environments. Finnie and van Staden (1985) demonstrated that more than one active constituent was present within the kelp concentrate, each of which can elicit different growth responses. Therefore, both qualitative and quantitative compositional differences with respect to suspected active components, such as cytokinins or other yet unidentified compounds, provide a plausible explanation for the different growth regulating effects of the two kelp foliar concentrates of this investigation. Active constituent differences may be related to the different types of kelp utilized and/or the particular time or physiological age at which they were harvested and processed for subsequent use as a foliar spray.

In this investigation the endogenous levels of phytohormones may have been altered differently by the various treatments. The ability of endogenous and exogenous phytohormones to regulate growth, photosynthate partitioning, long distance ion transport, mobilization of particular nutrients, and elemental concentration in plants is well

Table 1. Summary of cytokinin or cytokinin-like concentrations of various kelp extracts and concentrates

Trade name	Type of kelp	Cytokinin/ cytokinin-like concentration	Method of analysis	Reference
Seasol or Agrikelp	<i>Durvillea potatorum</i>	63 $\mu\text{g L}^{-1}$ ( $10^{-7}$ M)*	GC/MS	Tay <i>et al.</i> , 1985
Maxicrop	<i>Ascophyllum nodosum</i>	1300 $\mu\text{g L}^{-1}$ ( $10^{-6}$ M)	Tobacco callus bioassay	Sanderson and Jameson, 1986
Kelpak 66	<i>Ecklonia maxima</i>	26 $\mu\text{g L}^{-1}$ ** ( $10^7$ M)	Soybean callus bioassay	Featonby- Smith and van Staden, 1983
SeaSpray	<i>Macrocystis integrifolia</i>	84-1680 $\mu\text{g L}^{-1}$ ( $10^{-7}$ to $10^{-6}$ M)	Soybean callus bioassay	This paper

\* Approximate molar concentrations in brackets ( $219 \text{ g mole}^{-1}$ ).

\*\*Calculations based on 1000 g of kelp concentrate litre<sup>-1</sup>.

documented (Adedipe *et al.*, 1971; Castro and Malavolta, 1983; Fletcher *et al.*, 1970; Marschner, 1982; Neumann and Stein, 1984; Salisbury and Ross, 1978). Therefore, the type of plant growth, developmental and nutritional responses to a kelp foliar treatment may be expected to interact with the endogenous levels of plant growth regulators, soil nutrient supply, weather conditions and with the concentration and/or timing of the kelp foliar treatment itself. Such parameters exemplify the need for increased knowledge of the complex interactions between plant growth and developmental responses to the environment and how plant growth regulating substances, such as those contained in kelp, could be used to benefit crop productivity.

### Conclusions

The plant growth, developmental and N nutritional responses in this greenhouse experiment have demonstrated the effectiveness of two kelp, *M. integrifolia* and *E. maxima*, foliar sprays as plant growth regulating substances. Bean growth and mineral nutritional responses to the kelp, *M. integrifolia* and *E. maxima*, foliar spray treatments were also dependent upon the particular soil moisture regime or environment to which they had been subjected. Although the two kelp foliar sprays had varying and sometimes contrasting effects on bean growth and N nutritional responses, which were dependent upon the soil moisture treatment, their developmental effects upon the number of nodes, shoot/root ratios, LAR and SLA were quite similar.

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