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GROWTH STUDIES WITH LETTUCE

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(LACTUCA SATIVA L)

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A thesis presented in partial fulfilment  
of the requirements for the degree of  
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Plant Science at  
Massey University.

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ABSTRACT

In a sand culture experiment carried out in a heated glasshouse, the effect of five levels of P (ranging from 7.75 p.p.m. - 124 p.p.m. on the growth of two cultivars of lettuce was examined. Samples were taken at weekly intervals for ten weeks and growth analysis, and chemical analysis of the whole plant were carried out for total N, P and K from the samples.

Significant differences between cultivars were found for net assimilation rate and leaf area ratio, with a slightly higher relative growth rate in young 'Cobham Green' plants. 'Cobham Green' had a greater leaf area ratio but smaller net assimilation rate than 'Webb's Wonderful'. The higher relative growth rate of Cobham Green at the early stages of growth was mainly due to its higher leaf area ratio, but net assimilation rate became an important component during later growth stages, possibly as a result of mutual shading.

Within each cultivar, however, the variation in relative growth rate was based on net assimilation rate rather than in leaf area ratio.

iii.

Both dry weight and the percentage of total P increased with increase in P supply. The percentages of total N and K decreased towards the market maturity but no general trend was observed in the percentage of total P.

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## CHAPTER I

### INTRODUCTION

Since Liebig developed his theories on the mineral nutrition of plants, the determination of the nutrient requirements of crops has been an important subject of physiological and agricultural research.

In the past, the use of chemical analysis has been qualitative (Goodall and Gregory, 1947) in the sense that an analysis of the plant material was performed in order to suggest or confirm a diagnosis of the disorder as due to the deficiency of a nutrient element. In many of the studies aimed at establishing a quantitative relationship between plant response and its chemical composition, the material for analysis was collected at harvest time (Goodall, 1948; Macy, 1936). In recent years interest has shifted from the analysis of plant material at harvest time to the analysis at earlier stages of development, with a view to using the information in improving the growth of these same plants.

Some of the techniques that have been developed for the assessment of the nutrient status or the nutrient requirements of crop plants are:

1. The diagnosis of nutrient deficiencies in plants based on the recognition of symptoms.
2. Chemical analysis of the soil or soil extracts to estimate the nutrient supply in the rhizosphere.
3. Chemical analysis of the plants or plant parts to determine their nutrient status.
4. The measurement of plant responses after the addition of nutrients in field experiments.

Specific symptoms are usually not apparent under moderate deficiency conditions and this restricts the usefulness of method 1. There are also cases where symptoms produced by pests and diseases, or by weather conditions, or even by sprays of hormones may be indistinguishable from mineral deficiency symptoms (Wallace, 1961). Methods 2 and 3 are in general based on the relationship between the concentration of certain nutrient elements in soil or plant extracts and the yield responses resulting from nutrient applications. The success of soil or plant analysis techniques depends on the agreement between the forecast and the yield increases obtained after fertilizer additions. The field experiment (method 4) is the ultimate test to which any diagnostic method must be submitted.

Growth analysis is now commonly used to study plant growth and to explain variations in crop yield. However, growth analysis has not been widely used to study the differences in plant growth between cultivars of lettuce in relation to their response to fertilizer treatment.

Lettuce has been found to respond to phosphorus application (Webster, 1969; Nichols, 1971b). The purpose of the present study was to find out the effects of different levels of phosphorus on the growth of lettuce using growth analysis techniques together with chemical plant analysis.

## CHAPTER II

### REVIEW OF LITERATURE

#### A. NUTRITION OF CROP

Of the sixteen elements known to be essential for the growth of higher plants, carbon is obtained from the atmosphere as carbon dioxide; hydrogen and oxygen as water mainly from the soil; and the others are absorbed mainly in solution from the soil. According to Epstein (1965), an element is essential (a) if, without it, the plant cannot grow normally and complete its life cycle, and (b) if it is part of the molecule of an essential plant constituent or metabolite.

The macronutrients—carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), sulphur (S), potassium (K), calcium (Ca) and magnesium (Mg)—are required in much larger concentrations than the micronutrients such as iron (Fe), manganese (Mn), zinc (Zn), boron (B), copper (Cu), molybdenum (Mo), and chlorine (Cl), though this is no indication of their

relative influence on crop performance. Of these elements, Mg, Ca, S and the micronutrients have specific biochemical roles and a relatively small effect on growth within narrow ranges of supply, forming a group that contrasts with the remaining three elements N, P and K, which have large general effects on growth that vary with the amount supplied over a wide range. Most soils provide too little of these elements to produce maximum yields, hence the grower's chief task in controlling the nutrition of his crops is to make good deficiencies of N, P and K by the use of fertilizers. Soils differ greatly in their capacity to furnish these elements, both inherently and because of their previous treatment, so each season the grower must judge the quantities of fertilizers to be applied to give the best economic return.

The main practical problem of crop nutrition is to control the yield and quality of crops by adjusting the supply of N, P and K, and an important scientific problem is to understand how this control operates.

The selection of the proper application rate of a plant nutrient depends on a knowledge of the nutrient requirement of the crop and the nutrient supplying power of the soil in which the crop is to be grown. When the soil does not furnish adequate quantities of the elements necessary for normal development, it is essential that the required amounts are supplied. This

necessitates finding a method that will permit the determination of the deficient elements.

Pot trials are often a preliminary to field experiments. They have a very obvious advantage in that temperature, water, soil properties, crop stand, cultural practices, and pests and diseases are more easily controlled. Relationships found between a nutrient element and crop yield however may disappear when these trials are repeated in the field.

Crop yield is usually the parameter by which the various treatments are compared, often in combination with soil and plant analyses. Total plant analysis can be a useful guide, but critical levels are very dependent on the levels of the other elements and these vary with yields, soil type, climate, etc.

A vast amount of data on vegetable nutrition is available, and only the nutrition of lettuce, with particular reference to P nutrition, will be reviewed here.

#### 1. Phosphorus Nutrition

The phosphorus nutrition of plants in soil has been studied intensively (Dean and Fried, 1953). The soil solution is the most important immediate source of nutrients for absorption by roots. For rapidly growing vegetable crops such as lettuce which do not substantially deplete the labile pool of P in normal agricultural soils, the intensity of P supply may provide a better

estimate response than the quantity factor (Mattingby, 1965). Ordinarily the P concentration in the soil solution is quite low, of the order of 1 ppm (parts per million) or less, as reported by Stout and Overstreet (1950) and Arnon (1972). Stout and Overstreet (1950) calculated that the soil solution might need to be completely replenished with phosphate ten times a day, during the growing season, to support the growth of most crops. Fried, Hagen, Saiz del Rio and Leggett (1957) have indicated that if the soluble P is continuously removed from the system, the rate of replenishment of P into the soil solution is much greater than its rate of absorption by plants. Olsen and Watanabe (1966) have also shown that the rates of the reactions making additional P available are generally fast enough to meet plant needs.

Phosphorus is absorbed by plants as the phosphate ion. Whether it is absorbed as dihydrogen phosphate ion,  $\text{H}_2\text{PO}_4^-$ , or as the monohydrogen phosphate ion,  $\text{HPO}_4^{--}$ , depends upon the pH of the soil solution. Under normal pH range for plant growth, most of the P absorbed by plants is in the  $\text{H}_2\text{PO}_4^-$  form, and to a much lesser degree, the  $\text{HPO}_4^{--}$  form. Increasing proportion of the latter is absorbed at pH above 7 because it becomes the dominant ion in soil solution (Thompson and Troeh, 1973).

Solubility of the inorganic forms is a more serious problem in P nutrition than in that of any other macromutrient. Calcium phosphates become insoluble under alkaline conditions and iron and aluminium phosphates become insoluble under acid conditions. A pH range of 6.5 to 7.5 is most favourable for P availability (Truog, 1946).

Arnon and Hoagland (1940) showed that excellent and equally high yields of crop plants can be obtained from fertile soil, soil cultures, or sand cultures when grown in the same climatic environment. Studies using culture solutions have shown that plant growth is retarded with solution P concentrations of 0.1 ppm or less. On the other hand, crops appear to grow normally on soils where the concentration of P in the soil is less than 0.1 ppm (Bould and Hewitt, 1963). Similarly, Burd (1947) has shown that most plants need a phosphate concentration of 20 to 30  $\mu\text{M}$  (0.6 - 0.9 ppm) for healthy growth in solution culture yet show no response to phosphatic fertilizers on soils having less than 10  $\mu\text{M}$  (0.3 ppm) in the soil solution. Tidmore (1930) showed that corn, sorghum and tomatoes could secure adequate amounts of phosphate from solutions containing only 0.5 ppm of soluble phosphate. Hoagland (1947) obtained excellent potato growth in the nutrient solutions maintained at a phosphate concentration of 1.5 ppm. Bingham (cited by Asher and Loneragan, 1967) found that a solution concentration of about 0.3 ppm resulted in maximum

growth of lettuce. This figure is different from that given by Smith and Scaife (1973) of about 1 ppm on five different soils. The apparent anomaly could be due to the ability of roots to obtain phosphate directly from the surfaces of soil particles (Islam, 1955). Alternatively, the concentration of phosphate necessary for healthy growth of plants may have been overestimated due to the considerable technical difficulties in maintaining low phosphate concentrations in solution culture. This is supported by the results of Asher and Longergan (1967) in which they were able to produce healthy plants at much lower concentrations of phosphate than was thought possible due to improved techniques.

## 2. Function of Phosphorus

Phosphorus is absorbed in the main as the dihydrogen phosphate ion,  $\text{H}_2\text{PO}_4^-$ . It is one of three quantitatively prominent nutrient elements which are absorbed as complex anions, the other two being N ( $\text{NO}_3^-$ ) and S ( $\text{SO}_4^{2-}$ ) (Epstein, 1971).

Phosphate plays a key role in energy metabolism. It occurs in phospholipids including those of membranes, in sugar phosphates, various nucleotides, coenzymes and nucleic acids. A deficiency, therefore, causes immediate and severe disruption of metabolism and development.

### 3. Interactions Between Nutrients

The response to a particular nutrient element is seldom independent. It is now generally accepted that the concentration of one nutrient element in plant tissue influences yield and growth responses to other nutrients. This is particularly evident between the ion pairs N and P, N and K, N and Mg, P and K, and P and Mg.

Slater and Goodall (1957) showed a synergistic effect between N and P, but an antagonism between N and K in lettuce plants. The percentage of total N in the plant was increased by increasing levels of N or P supply and by K deficiency, and changes in the content of nitrate-nitrogen were similar to those for total N, but were much more marked. In the same series of papers, Grant Lipp and Goodall (1958a) found that the concentration of P in plant dry matter was usually increased by increasing the levels of P supply, but decreased by the additions of other nutrients. In another paper, Grant Lipp and Goodall (1958b) obtained an increase in the concentration of K in the plant dry matter by increased K supply, but a decrease in the concentration of K in the plant dry matter by increased N and in some instances by increased P supply. Haworth and Cleaver (1964) reported an interaction between K and P, and between Ca and Mg in seedlings of eight vegetables in sand culture. They found that increases in the percentage of K content caused a reduction in the percentage of P, Ca and Mg.

#### 4. Nutrient-element Balance and the Growth of Lettuce

Schroeder (1948) stressed that a balanced supply of nutrients is essential for optimal production in lettuce. Lambeth (1953) suggested that an N-K unbalance could be a contributing factor to low lettuce yields. He also suggested an optimum potash saturation level above 8.1 per cent of the exchange capacity. Several investigators have shown that the availability of cations and plant growth in soils is more closely related to the degree of base saturation than to the total supply of exchangeable bases (Allaway, 1945; Mehlich and Colwell, 1943). Harward, Jackson, Lott and Mason (1955) studied the effect of different levels of Al, Fe and Mn upon the growth and composition of Iceberg lettuce. They found that higher levels of Al in solution had a marked effect on reducing the content of K in the leaves.

#### 5. Concentrations and Uptake of Nutrients at Harvest of Lettuce

Lorenz and Minges (1942) reported that at market maturity the plants averaged 2.65% N, 0.37% P, 6.51% potash, 1.67% lime (CaO), on the basis of dry weight determination. Zink and Yamaguchi (1962) gave a range of 3.10 - 6.65% for N, 0.34 to 0.79% P, 4.57 - 9.44% K, 0.91 - 1.60% Ca and 0.32 - 0.84% Mg. Minard (1971) obtained the range for summer crop of 3.3 - 4.2% N, 0.22 - 0.24% P and 5.83 - 6.6% K. The figures for winter crops were slightly lower.

The total amount of various nutrients removed by lettuce crop can be derived from these figures and is summarised in Table I.

#### 6. Concentration and Uptake of Nutrients During Growth

McGeorge, Wharton and Frazier (1940) reporting the analyses of lettuce plants grown in Arizona found that the Ca and P percentage remained approximately constant throughout the growth of the plant, but N and K fluctuated, with N showing a decrease as the plants approached maturity. Lorenz and Minges (1942) noticed a marked decrease in Ca with maturity, and a slight decrease in N, on the dry weight basis, while P and K remained practically constant throughout growth. Zink and Yamaguchi (1962) indicated a trend for total N, P, Mg and Na to decrease as the lettuce crop approached market maturity. The Ca level of the plants remained fairly constant throughout the growth of the crops. The K content fluctuated.

The rate of nutrient uptake has been found to be very slow during the early phase of growth, but when the maximum rate of growth occurs during the twenty-one days before crop maturity it is accompanied by the maximum rate of uptake of nutrients. During this period, over 70% of the N, P, K, Ca and Mg are absorbed (Lorenz and Minges, 1942; Zink and Yamaguchi, 1962).

TABLE I

NUTRIENT ELEMENTS (kg/ha) REMOVED BY LETTUCE CROP

Fresh weight kg/m	Dry weight kg/ha	N	P	K	Ca	Mg	Na	References
34540		51	8	105	23	-	-	Lorenz and Minges, 1942
19360		45	5	48	7	3	-	Hester and Sheldon, 1949
57610		106	13	194	37	13	10	Zink and Yamaguchi, 1962
	6720 <sup>1</sup>	222	15	450	60	25	9	Minard, 1971
	5600 <sup>1</sup>	235	13	392	62	28	28	Minard, 1971
	5040 <sup>2</sup>	252	22	252	71	10	3	Minard, 1971
	5040 <sup>2</sup>	262	24	311	63	10	3	Minard, 1971
45440		112	21	184	-	8	-	Better Crop, 1973

1 = Summer crop

2 = Winter crop

This pattern of nutrient uptake is very similar to that of spinach (Zink, 1965).

Many factors such as cropping history of the soil, fertilizer practices, soil moisture content, soil type and environmental factors all have effects on the nutrient uptake of plants. It is therefore not surprising to find some inconsistencies among these experiments.

#### 7. Effect of Phosphorus on Yield

The failure to supply an essential element to a plant will result in the stunted growth and ultimately in premature death of that plant. The inclusion of increasing quantities of the element should mean more and more growth, until a point will be reached where further increases could produce no extra growth, and, in fact, might even have adverse effects.

Early studies on nutrition of lettuce by Woodman (1939, 1940, 1942), either in soil or in sand cultures, have indicated a response of lettuce to N and P as regard to the yield and earliness of maturity, while K has little effect. Detailed studies conducted in Australia (Goodall, Grant Lipp and Slater, 1955) have shown marked effects of P on the growth of lettuce. N supply gives an optimum-type curve, with a tendency for the optimum level to shift upwards with increasing P supply, but

the plants are less sensitive to K supply. The highest N supply level had a clearly adverse effect on growth. This adverse effect of N was later confirmed by Cleaver (1971) who was able to show a complete 'overturning' response curve with high levels of N. Similar results were found by Scaife and Johns (1969) on other vegetables. Webster (1969) on a Levin silt loam showed that the yields of lettuce were increased with increases of P up to 3560 kg/ha of serpentine superphosphate, but had very little response to N or K. Nichols (1971b) using up to 5000 kg/ha of serpentine superphosphate, also obtained a P response in lettuce. Minard (1971) considered that the P requirement of lettuce on Levin silt loam to be as high as 3800 kg/ha of serpentine superphosphate.

Smith and Scaife (1973) investigated five soils in pot experiments and showed that the amounts of P requirement for maximum lettuce growth varied from 120 ppm on a sandy soil to 300 ppm on a moss peat. They attributed these differences in P requirement to the P adsorption by the soil.

Goodall and Gregory (1947) have shown that, with different levels of P supply, large differences in plant P concentration are found soon after the seed reserves are exhausted, which gradually give place to large differences in yield and a much

smaller range of P concentration. This was demonstrated in lettuce crop by Grant Lipp and Goodall (1958) who analysed seedlings of 11 days old and obtained an optimal plant P concentration of at least 0.50%. The concentration in completely P - starved plants was about 0.1%. Smith and Scaife (1973) gave an optimum for lettuce seedling of 0.60%. Thus there is fair arrangement as to the optimal leaf P concentration.

In order to understand the influence of nutrition on the growth of young lettuce seedling, Berry (1971a) grew plants in a modified Hoagland's solution with nine treatments of phosphate. The critical levels in the conductive, lamina and root tissue were respectively 780, 600 and 580 ppm soluble phosphate -P on a dry weight basis. For diagnostic purposes, a value of 1000 ppm phosphate -P was suggested for determining the nutrient status of P in the tops of seedling lettuce. In this conjunction, it may be noteworthy that a critical level for the tops of seeding of 2% K was proposed by Berry and Carey (1971). For Zn, a critical value of 9 ppm was best defined in the matured petiole (Berry, 1971b).

Grant Lipp and Goodall (1958a) obtained the following critical levels for P content in the tops of lettuce of 0.471% at 29 days and 0.365% at 37 days and 44 days.

## B. ENVIRONMENTAL FACTORS AFFECTING GROWTH AND DEVELOPMENT OF LETTUCE.

One of the most outstanding characters of living matter is growth. It is commonly conceived as increase in size and may be measured in a variety of ways (length, weight, volume etc). Increase in size, however, although the most obvious aspect, is only one feature of growth. Basically the growth of a multicellular plant involves both increase in cell number by cell division, and increase in cell size. Many authors (e.g. Wareing and Phillips, 1970) distinguish sharply between growth, development and differentiation. In their opinion, growth only implies cell division and cell enlargement processes, while the consequence of structural and functional changes that occur during the life cycle of an organism is regarded as a process in which the organism passes an orderly stage of development through time, and the intervals necessary to encompass the various critical stages, or events, are the units by which the course of growth may be recorded. Whether development is regarded as a separate phenomenon or as an aspect of growth, the course of development can be altered by environmental factors. However, changes such as from juvenility to maturity,

in plants showing heteroblastic development, are better explained by some internal mechanism of the plant (Wareing and Phillips, 1970).

The major environmental factors affecting plant growth and development of crops can be grouped as follows (de Vries, 1963):

I. Above Ground Factors

1. Radiation, including light
2. Temperature
3. Wind
4. Cloudiness
5. Precipitation
6. Composition of the atmosphere
7. Humidity

II. Below Ground Factors

1. Soil temperature
2. Soil moisture
3. Composition of the soil atmosphere
4. Nutrients
5. Soil reaction
6. Soil texture and structure

I. ABOVE GROUND FACTORS

1. Radiation

Three important aspects of radiation are: (a) intensity, (b) quality, and (c) duration (daylength).

(a) Intensity

Milthorpe (1945) found that shading decreased dry weight, leaf area, height and net assimilation rate of flax plant. Similar result has been obtained by Wagenaar (1954), working with spinach, who showed a dry matter and leaf area increase with increasing light intensity.

Foley (1965) examining the effect of solar radiation on vegetable crops found that the response of each of the tested crops to the irradiance was conditioned by whether or not the growing point was protected by leaves from direct irradiance. The upright growth habit of leaves of Romaine lettuce protects the growing point of the plant while the growing point of leaf lettuce is exposed. As a result of this difference, growth of Romaine lettuce was found to grow better under full sunlight while that of leaf lettuce in reduced light. Mattei, Sebastiani and Gibson (1973) obtained a significant decrease in the growth of two lettuce cultivars with reduced light levels. Fresh and dry weights were reduced when daylight was reduced by 70%. At the same time growth rate and dry matter also decreased with high radiation levels and it was found that the optimum light levels lay between 100 and 200 cal cm<sup>-2</sup> day<sup>-1</sup>.

Bensink (1960, 1971) studied the morphogenetic effects of light intensity on lettuce leaf growth. Under the conditions of low light intensity long and narrow leaves were formed, but

short, broad leaves were produced under high light intensity. This phenomenon was also found by Verkerk and Spitters (1973).

There appears to be no objection to supplying continuous light to lettuce seedlings (Lanckow and Heissner, 1960; van Steen, 1953). However, Seidel (1950) recommended that supplementary light should be applied at night, either from 4.00pm. to midnight or from midnight to 8.00am. Sheard (1961) showed that supplementary illumination in the propagation stage advanced the maturity of glasshouse lettuce by nine days, but the plants were lighter in weight and more susceptible to botrytis and tipburn than the controls. Lanckow (1962) showed that extension of light period by illumination at night had a greater effect on seedling growth than supplementary light during the day. Lanckow and Heissner (1965) grew lettuce seedlings with supplementary light from fluorescent lamps for eight hours from 4.00pm. to midnight and obtained improved quality and earlier maturity. Dullforce (1971) concluded that only during the early propagation stages was the use of artificial light likely to be economic. However, it has been found that lettuce plant is able to use the weaker light more efficiently than the stronger light (Brouwer and Huyskes, 1968; Dullforce, 1971; Verkerk and Spitters, 1973). In view of this, low light intensity can be given as an extension of daylight ( $4 \text{ cal cm}^{-2} \text{ day}^{-1}$  by Dullforce, 1971; Lanckow, 1962; Seidel, 1950).

A low light intensity of  $4 \text{ cal cm}^{-2} \text{ day}^{-1}$  is not below the compensation point of the photosynthetic curve for lettuce since some plants have been shown to have much lower light compensation point. For instance, Hughes (1966) recorded a value of  $0.3 \text{ cal cm}^{-2} \text{ day}^{-1}$  for the compensation point for Impatiens parviflora. Dullforce (1971) suggested a value of  $2 \text{ cal cm}^{-2} \text{ day}^{-1}$  or less for the winter lettuce cultivar 'Cheshunt 5B'. Heath and Meidner's (1967) results with the cultivar 'Grand Rapids' also indicated that the lettuce plant was able to gain dry weight in very low light conditions.

Apart from the beneficial effect of supplementary light during the seedling stage, light has effects on the growth and development of lettuce plant. Yield differences of lettuce between different glasshouses has been attributed by Ameeru (1962) to differences in light intensity. Lettuces planted in mid-November matured earlier and weighed more per head under a 9-meter-span house with a  $30^\circ$  roof slope than under a 3-meter-span house with a  $20^\circ$  roof slope. However, such increased light intensity in the 9-meter-span house would necessarily involve higher temperature, and so the environmental conditions between these two types of glasshouse would be different. Brouwer and Huyskes (1968) showed that growth rates of two varieties of lettuce were increased with increasing

light intensities. Dennis (1971) obtained significant increases in total dry weight and total leaf area of lettuce when irradiance of  $181 \text{ J M}^{-2} \text{ min}^{-1}$  was applied at night or during the day. However, the effect of night application was more pronounced than application coincidentally with daylength. This may be due to the internal factors in the plant affecting the rate of photosynthesis or respiration. The supplement at this irradiance resulted initially in significantly higher relative growth rates which could be attributed to the significant increased net assimilation rates, since leaf area ratios were significantly reduced by the supplements thus acting against increases in relative growth rate. The investigations of Blackman, Black and Kemp (1955), Black (1955) and Hodgson (1967) covered Helianthus annuus, Trifolium subterraneum and Vicia faba showed many common trends. In every case increasing solar radiation enhanced the net assimilation rate and relative growth rate, but depressed the leaf area ratio. Bierhuizen, Ebbens and Koomen (1973) reported that the time of harvest of cultivar 'Noran' depended on the total radiation after the plants had attained 100% soil cover.

High light intensity could cause lettuce tipburn. Lam and Hafen (1967) showed that the disorder was more severe when plants were grown under high light intensity while little or

no damage from tipburn appeared on plants grown under low light intensity. Tibbitts and Rao (1968) suggested that the effects of light in influencing tipburn appeared to be an indirect effect of an increase in photosynthetic activity with resultant increases both in the growth rate and the dry matter accumulation of the plants which led to rupture of laticifers and injury.

(b) Quality

The effects of light quality on plant life are manifold. Examples of some of its effects on various phases of growth and development are: seed germination, elongation of stems and development and shape of leaves.

The early work of Flint and McAlister (1935) on photobiological effect of near infrared irradiation on lettuce seed germination has been widely cited. They found that germination of lettuce seed was promoted by red and inhibited by near infrared radiation, with a maximum activity at about 730 nm. This finding has since been variously confirmed by Borthwick, Hendricks, Toole and Toole (1954), and Hagen, Borthwick and Hendrick (1954).

Mohr and Wehrung (1960) mentioned that hypocotyl lengthening in lettuce seedlings under the reversible red-infrared system was negligible, whereas white, blue and far red light strongly

inhibited it. They also showed that the control of hypocotyl growth was by the blue-far red reaction system.

Bensink (1961) grew lettuce plants under light of different spectral regions and found that elongation of leaves and stems was much more obvious in the yellow-red part of the spectrum than it was in the blue-violet. De Lint (1961) showed that the blue light alone at low intensity caused little or no elongation. When near infrared light was added to blue light, lettuce plants elongated. Near infrared alone, at low intensity, induced elongation of the stems, internodes and leaves when this treatment followed a daily basic period in strong white light.

Dunn (1958) found that red or blue light caused greater dry weight increases in lettuce than other colours or combinations of colours of lights.

(c) Duration

Olson (1968) looked at the effects of long and short photoperiods on growth of lettuce leaves. Leaf initiation was more rapid and leaf width greater with 16-hour than 8-hour photoperiods, the increased leaf width resulted from a greater number of cell divisions. A low irradiance of  $18 \text{ J M}^{-2} \text{ min}^{-1}$  in the middle of the night increased the mean leaf size of lettuce plants. According to Dennis (1971), this increase may be photoperiodic in nature.

From their extensive work, Garner and Allard (1920) have shown that flowering in many plant species is controlled mainly by the relative length of day and night. Since then a considerable amount of information has been amassed on the effects of daylength on the growth and development of plants. Andrew (1953) found a consistent promotion of seedstalk development and flowering when lettuce plants were grown under long days. Milthorpe and Horowitz (1943) reported an acceleration of flowering in vernalized lettuce grown with long days and high temperatures. Likewise Rappaport and Wittwer (1956a) showed that a 16-hour day promoted, and a 9-hour day delayed seedstalk development of head lettuce in an environment suitable for seedstalk formation. In a similar study, Rappaport and Wittwer (1956b) suggested that flower induction in Bibb cultivar was governed by photoperiod, but that both photoperiod and temperature influenced the rate of subsequent seedstalk development. On the other hand, photoperiod as well as temperature might both control induction and seedstalk elongation in Grand Rapids. Dennis (1971) found that increased stem and subsequent rapid bolting of lettuce plants could occur when low irradiance supplement was given at night.

Brouwer and Huyskes (1968) found that the variety Rapide and its hybrid both made better use of available light energy in long days than in short days.

## 2. Temperature

Temperature plays a major role in plant growth, because of the dependence of the biochemical processes on temperature. For crop production, a suitable temperature range lies between  $10^{\circ}$  -  $40^{\circ}\text{C}$ . Species differ in their temperature requirements and for lettuce, the range is narrower, a mean temperature in the range of  $10$  -  $20^{\circ}\text{C}$  is considered as suitable (Zink and Yamaguchi, 1962).

Bensink (1961) showed that a high night temperature promoted the development of narrow leaves whereas low night temperature had the effect of promoting the formation of broad leaves.

Thompson and Knott (1933) reported that higher temperatures hastened bolting of many lettuce varieties. Lettuce growth and heading were poor above  $21^{\circ}\text{C}$ . Andrew (1953) used lettuce variety Imperial 456 in his work along with variety Great Lakes. He observed that there was no significant difference in seed-stalk development between plants grown at  $10^{\circ}$  night temperature and those grown at  $15^{\circ}\text{C}$  night temperature. There was an indication, however, that higher temperature was more effective in further increasing seedstalk development on plants subjected

to vernalization. Rappaport and Wittwer (1956a) found that a night temperature above  $18^{\circ}\text{C}$  subsequent to vernalization accelerated flowering and resulted in seedstalks without preceding head formation. Below  $18^{\circ}\text{C}$ , vernalized plants first produced a high percentage of firm, vegetative heads and then flowered. Non-vernalized plants flowered only at night temperatures above  $18^{\circ}\text{C}$ . Raleigh (1959) showed that night temperatures were more important in controlling the seedstalk in variety Imperial 456. The lower the night temperature the shorter the length of seedstalk.

Madariaga and Knott (1951) and Zink and Yanaguchi (1962) studied the possibility of using heat unit method to predict the maturity date of lettuce. The remainder-index system was used for accumulating temperature. A base temperature of  $4.2^{\circ}\text{C}$  was considered to be physiologically justified. In both experiments it was found that lettuce did not require the same number of heat units to reach maturity when planted at different times of the year.

One might expect that a radiation summation might be a better approach than a heat unit system because photosynthesis is more dependent on light intensity than in temperature. In fact Nichols (1971b) found that solar radiation provided a better time scale than heat units for lettuce. He also suggested that

a single set of parameters would not adequately describe the growth of lettuce, over a number of sowing dates. Bierhuizen and Feddes (1973) obtained a linear relation between total radiation and fresh or dry weight yield of lettuce cultivated in spring and autumn.

Bierhuizen, Ebbens and Koomen (1973) distinguished the growth cycle up to heading, of lettuce into three periods: a period of germination, a period from germination till 100% soil cover by the leaves and subsequently a period until harvest. They showed that the time for closed leaf surface depended on a specific heat unit, whereas time of harvest depended on the subsequent total radiation.

Went (1950) has emphasised that the effect of temperature is a complex one and cannot be expressed just as heat units. The assumption that the relationship between temperature and growth is a direct one throughout the range at which plants grow is clearly suspect.

(a) Interaction between light and temperature

Bensink (1971) showed that the effects of temperature on leaf width depended greatly on the prevailing light intensity: a negative response observed at low light intensity changed into a positive one at high light intensity. It further appeared that light intensity effects on leaf width

were especially manifest at high temperature, whereas for leaf length they were more pronounced at low temperature.

Light and temperature may exert a compensatory influence on heading as was found for the length to width ratio developed by the leaves. Both high light intensity and low temperature tended to decrease to length/width ratio (Bensink, 1960, 1961). Heading may occur at high temperature ( $21^{\circ}\text{C}$ ) provided light intensity is sufficiently high.

Verkerk and Spitters (1973) showed that the higher the light energy, the less critical the temperature and the smaller the beneficial effect of different day and night temperatures.

According to Rappaport and Wittwer (1956b), the minimum night temperature moved from  $15.5^{\circ}\text{C}$  to  $18.5^{\circ}\text{C}$  when plants were grown at a daylength of sixteen hours. A combination of high air and root temperatures and daylengths appeared to promote flowering in seedlings.

### 3. Wind

The effects of wind on crop are variable. Canopy ventilation is necessary for satisfactory plant function. Wind speeds between 0.5 m per second and 3 m per second are reported to be suitable for this purpose. Lack of canopy ventilation favours pests and diseases. Wind carries  $\text{CO}_2$  to the leaf surface, removes water vapour, transfer heat

momentum vertically and horizontally. The extent to which it exercises these functions is related to its velocity. Strong winds cause physical damage to plants and persistent winds of lesser intensity induce morphological changes (Nixon-Smith, 1969).

Winter (1965) has shown that the growth of lettuce and cabbage could be adversely affected by wind of moderate intensity and that there was a possibility that yield might be increased by suitable sheltering.

Shelters are best placed normal to the path of the prevailing wind. A shelter with 50% permeability provides effective protection on the leeward side of up to 16 or 20 times its height (Nixon-Smith, 1969).

Stahfelt (1955) has demonstrated that the rapid removal of water from the leaf by wind would be expected to cause the stomata to close even in daylight. This closure of stomata in response to wind would not only reduce water loss, but would also interfere with gas exchange, photosynthesis and ultimately, growth.

#### 4. Cloudiness

Cloudiness affects plant growth indirectly because light intensity is reduced. At night, long wave radiation losses from the earth are reduced, hence the earth cools down slower.

## 5. Precipitation

Precipitation is important mainly in relation to its effect on soil moisture. In this respect rain is the most important form of precipitation. However, under certain conditions, precipitation in the form of heavy rain, snow or hail may physically damage the plants. Rain also causes leaching of minerals and other substances from the leaves (Tukey and Morgan, 1962; Tukey, 1970).

Condensation of water vapour in the air in the form of cloud, mist or fog reduces light intensity, and also tends to reduce the rate at which the ambient temperature changes.

## 6. Composition of the Atmosphere

Four-fifths of the atmosphere consists of nitrogen. Almost all the rest of the atmosphere consists of oxygen. Carbon dioxide, of which the air contains only about 0.03% or 300 ppm, is an essential raw material for the process of photosynthesis.

Gaastra (1966) has discussed the physiological basis of CO<sub>2</sub> effects on crop productivity through enhanced rates of photosynthesis. For most parts of photosynthetic curve of the lettuce leaves the photosynthetic rate of chloroplasts in the leaf becomes limited by the supply of CO<sub>2</sub> and is

determined by the capacity of the  $\text{CO}_2$  transport process from the external air towards the chloroplasts. Thus artificially increased  $\text{CO}_2$  concentration can result in enhanced photosynthetic rates at a large range of light intensities. Heath and Meidner (1967) studied the relationship between the compensation points for light and  $\text{CO}_2$  at  $15^\circ\text{C}$  and  $25^\circ\text{C}$  and found that there was a fall in the light compensation point with increasing  $\text{CO}_2$  concentration. They argued that the apparent beneficial effects of  $\text{CO}_2$  enrichment of the glasshouse atmosphere with lettuce or other crops at light intensities that might be expected to be severely limiting, must be in part due to the reduction of the light compensation point at high  $\text{CO}_2$  concentration.

Hartmann (1966) summarised the effects of raising  $\text{CO}_2$  concentration to 1000 ppm on head lettuce: 1). the  $\text{CO}_2$  treatment increased the weight of the lettuce heads, 2). the  $\text{CO}_2$  treatment permitted earlier harvest of lettuce, and 3). none of the cultivars examined responded in a more than proportional way to  $\text{CO}_2$  treatment. Gardner (1966) obtained a 34% increase in the weight of lettuce at the Lee Valley Station with supplementary  $\text{CO}_2$ . Wittwer (1966), Sturm, Gugenhan and Deiser (1969) reported that supplementary  $\text{CO}_2$  had a favourable effect on earliness and generally increased head weight.

Supplementary CO<sub>2</sub> can have beneficial effect on the quality of lettuce as well, as was found by Klougart (1964) and Nillar (1968). A reduction in botrytis and mildew infection on lettuce was reported by Hartmann and Zischka (1964) and Miller (1968).

Some accounts of the effects of air pollutants such as sulphur dioxide and ozone on crops are given by Dugger and Ting (1970) and Hand (1973), who cited lettuce as more susceptible to sulphur dioxide than many other plant species. Hill, Pack, Treshow, Downs and Transtrum (1961) observed wide differences in sensitivity to ozone between different species within the same family and lettuce was one of the few among the thirty four different species investigated to be considered as resistant to ozone. In addition to the differential sensitivity between species to ozone, Reinert, Tingey and Carter (1972) also found similar differences between cultivars within certain species. The symptoms of ozone injury in lettuce agrees with that found by Hill et al. (1961) as chlorotic and necrotic lesions on the upper leaf surface, with bifacial necrotic spots at any advanced injury stage.

## 7. Humidity

Atmospheric moisture conditions can be expressed in terms of relative humidity, vapour pressure deficit and few other terms. Under certain conditions when stomata are opened and at a constant temperature, the rate of transpiration depends on the steepness of the vapour pressure gradient from plant tissue to air, hence the greater the vapour pressure deficit in the air, the higher the transpiration rate. An increase in temperature or wind speed produces a steeper vapour pressure gradient. Under high temperature or strong wind, the rate of transpiration can be high. If the transpiration rate exceeds that of plant water supply, then stomatal aperture will be reduced or even closed, resulting in a reduction in the rate of photosynthesis (Kramer, 1959).

The humidity of the atmosphere affects more than the water economy of plants. In terms of dry matter production, a humid atmosphere can give rise to a more efficient use of soil water. Humidity also affects growth and development, often in very different and even opposite ways. Seedlings usually emerge earlier and grow better from soils exposed to a more humid atmosphere (Heydecker, 1962; Heydecker, Pareek and Sivanayagam, 1970). Under high humidity, leaf area is

often reduced, vegetative storage organs are formed later or not at all. On the other hand, the growth rate of sunflowers and sweetcorn is speeded up (Heydecker and Pareek, 1969).

Humidity can be important in relation to pathogens. Many plant pathogens especially fungi can only survive or complete their life cycles at certain degree of air moisture. In lettuce, fungus diseases such as Sclerotinia, Botrytis and downy mildew and bacterial leaf spot require high humidity at certain stages of their life cycle for successful growth and infection (Brien, Dye, Fry, Harrison, Jacks and Newhook, 1957).

## II. BELOW GROUND FACTORS

### 1. Soil Temperature

The temperature of soil at any particular time and depth is the result of heat being gained at the surface by day and lost again from the surface by night. The movement of heat in soil is slow if the soil surface is loose and friable, or covered with an insulating layer of long grass, but is much more rapid if the surface is firm, moist and bare.

Soil temperature is important in terms of seed germination, root growth and uptake of water and ions. An extensive review of the effects of soil temperature on plant growth has been presented by Hagan (1952).

Lettuce seed planted when soil temperatures are above 25°C may fail to germinate, with resulting poor stands (Heydecker, 1959). The failure of lettuce seed to germinate well at temperatures above 25°C is not fully understood. Borthwick and Robbins (1928) suggests this is due to a semi-permeable integumentary membrane which retards gas exchange or that it might be due to an accumulation of metabolic products. Heydecker, Orphanos and Chetram (1969) considered that reduced metabolic demand at low temperatures enabled diffusion process to supply sufficient O<sub>2</sub> to the sites of embryonic respiration.

A number of chemicals have been tested for their effects on lettuce seed germination (Haber and Luippold, 1960; Kahn, 1960; Leff, 1964) but only kinetin and thiourea are effective in overcoming high temperature dormancy. Thompson and Kosar (1939) and Thompson and Horn (1944) showed that germination of lettuce seed at temperatures above 25°C could be enhanced by treating the seed with thiourea before planting while soaking the seeds in 10-100 mg/litre kinetin solution for three minutes was effective (Smith, Yen and Lyons, 1968; Odegbaro and Smith, 1969).

Seeds of certain species or varieties raised in different years often behave differently when germinated under identical conditions. Correlations between preharvest environments and the subsequent germination behaviour of lettuce seed have been observed by Harrington and Thompson (1952) who established significant positive correlations between the germination percentages and the temperatures during seed maturation in the field. They found that lettuce seeds which had matured at high air temperatures germinated well at high soil temperatures. Koller (1962) also found that maturation of lettuce seeds under high temperatures or in continuous light increased the high temperature tolerance of seed germination both in continuous dark and after a short light-break. According to Evenari (1965), the effect of the maturation temperatures on the germinability of the seeds is twofold: (1) the higher the temperature the more pronounced is the promoting effect of continuous red light and (2) the shorter is the time needed for after ripening, i.e. needed for the development of photosensitivity.

In addition, germination temperatures have been associated with the growth and development of pea (Highkin and Lang, 1966) and barley (Laude and Cobb, 1969) after germination. Zink (1967) showed that earlier maturity and heavier yields of

lettuce was obtained from those grown on the warmest side of the bed. In the soil warming experiments by Boxall (1971), lettuce receiving the warmer treatments matured earlier than the unheated plants.

## 2. Soil Moisture

Soil moisture is a factor of the utmost importance to plants, often determining whether or not plants grow and even whether or not they survive. Soil moisture occurs in a continuous range of conditions from waterlogging, field capacity, wilting point and death point. Somewhere between field capacity and wilting point is a stage where plant growth is slowed down and plants die at death point.

The root system of the different groups of lettuce differ. Most of the roots will be in the top 25 to 30 cm of soil (Sweet, 1943). Many factors which interfere with the growth of plants as a whole will affect root growth not only in total but also in distribution, of which one is soil moisture (Evans, 1973). Rowse (1973) found that irrigation increased root growth near the soil surface, but root distribution below 0.1 m were not affected.

Plant growth and yield are often affected long before plants have extracted more than a small proportion of the available water from a soil. Salter (1959) found that the

yield of summer lettuce was reduced if the soil moisture deficit reached more than 13 mm at any time during growth. Also Salter (1957) obtained highest yields from plots in which the soil had been restored to field capacity daily from sowing until harvest.

Hudson, Salter and Majmudar (1955) showed that tomatoes responded markedly to different water regimes, lettuces grew equally well under a variety of water regimes. The lettuce was little affected by different water regimes as far as the weight of the head was concerned, although the roots under drier regimes tended to spread rather more deeply in the soil than in those in the wetter regimes. They suggested that provided the soil was deep and moist enough on planting, there may be little response to further irrigation. The reason between the differences in response of tomatoes and lettuces was that lettuce roots were still growing strongly into fresh moist soil regions when the plants were ready for harvest. Whereas tomato roots had fully occupied the available soil by half way through their growing season. Majmudar and Hudson (1957) stated that in early stages of establishment of an annual crop (e.g. lettuce) there may be no response to irrigation so long as the roots were growing strongly into fresh, moist areas of soil, even though the surface layers

had dried out almost to wilting point. At a later stage, when all the available rooting zone had been occupied, or when the roots were no longer growing strongly, plants might respond to irrigation at relatively low tensions. However Veihmeyer and Holland (1949) and Sale (1966b) showed that there was some response to irrigation even when the plants were very small. This small response to irrigation in the early stages of growth of lettuce indicates that the growth of lettuce decreases when quite small soil moisture deficit has been built up, as was found by Salter (1957). This response, however, must not be taken as a physiological moisture-sensitive stage of growth of lettuce, similar to that found for some other crops, e.g. peas (Salter, 1963). According to Sale (1966b) the response of lettuce to irrigation was due to the rapid increase in soil moisture deficits during later growth. Sale (1966a, b) has shown that the greatest growth response of lettuce to irrigation is one week before the harvest. Such an irrigation would be expected to increase both the mean fresh weight and the quality of lettuce. Dunkel (1956) grew lettuce in a glasshouse with overhead sprinklers so that the soil moisture in four treatments did not fall below 50, 60, 70 or 80% of field capacity. Results of several years of trials showed that for short-day lettuce cultivars the most favourable soil moisture content lay between 50 and 80% of field capacity.

Robinson and McCoy (1965) found that with irrigation, the seeding rates of lettuce could be reduced resulting in lower thinning cost and earlier maturity of crop. At the same time, higher yields could be obtained by increasing the plant population in irrigated land (Robinson, 1970).

### 3. Soil Atmosphere

The soil atmosphere consists of four-fifths of N, but its CO<sub>2</sub> and O<sub>2</sub> contents vary because the plant roots and soil organisms remove O<sub>2</sub> from it and respire CO<sub>2</sub> into it. An average figure of 0.15 - 0.65% CO<sub>2</sub> has been given by Vilenskii (1957), but he cited a figure as high as 1.88% under forest conditions.

Most crops can only make vigorous growth if the CO<sub>2</sub> concentration around their roots is not too high, nor the O<sub>2</sub> concentration too low. Thus good soil aeration is necessary to prevent accumulation of CO<sub>2</sub> which can harm the plant roots at excessively high concentration.

The composition of the soil atmosphere depends on the relative rates of two opposing processes: the rate of production of CO<sub>2</sub> in the soil and its rate of removal. Both the CO<sub>2</sub> and O<sub>2</sub> concentrations in the soil atmosphere are continuously fluctuating and differ in different soil depths.

High CO<sub>2</sub> concentration may inhibit germination or harm the very young root system of the seedling. However, at

germination, seeds are more susceptible to low  $O_2$  rather than high  $CO_2$  concentration. Later growth is more affected by high  $CO_2$  in the soil atmosphere (Heydecker, 1962).

#### 4. Soil Nutrients

Soil is the principal source of essential elements for plant growth. The amount of a particular element in the soil depends on soil type. Many soils are never plentifully supplied with all essential elements of plants.

Plants take in nutrients from the soil mostly in the form of ions. For maximum production, crop plants usually require greater amounts of nutrients than the soil solution contains at any one time. As plants remove nutrient ions from the soil solution, the soil solution is being replenished with ions from soil minerals and organic matter.

Plant development will depend not only upon the presence of essential elements, but their relative proportions and their overall total.

Liebig postulated the law of limiting factors which states that the growth of any plant is regulated by the plant nutrient element present in the least amount (Epstein, 1971).

## 5. Soil Reaction

Soils may be acid, neutral or alkaline in reaction, but most soils have pH between 4 and 8. The reaction of soils is significant in crop production and management practices. There is evidence that pH has little or no direct effect on plant growth and that it acts mainly through indirect effects. A soil of pH 4 probably has enough soluble  $Al^{+++}$  to be very detrimental to most plants (Cate and Sukhai, 1964; Foy, Arminger, Briggie and Reid, 1965). Another way in which pH is related to plant growth is through the physical condition of the soil. Soil pH values above 8.5 indicate the presence of considerable  $Na^+$  and the likelihood of dispersed soil colloids. Plant growth is markedly reduced where colloids are dispersed. High soil pH values are usually associated with saline soil. The main problem with saline soil is a shortage of water available to the plants (Thompson and Troeh, 1973).

The most universal effect of pH on plant growth is nutritional. The pH value of the soil influences the rate of plant nutrient release by weathering, the solubility of all materials in the soil, and the amounts of nutrient ions stored on the cation-exchange sites. In other words, each degree of soil reaction affects plant growth in a certain way owing to either a depressed solubility of some elements or to

an increased solubility of others. A pH between 6.5 and 7.5 is usually best for P availability. Iron and aluminium phosphates precipitate at low pH and calcium phosphates precipitate at high pH (Truog, 1946). The chemical conditions which accompany the different degrees of soil reaction, therefore, may be favourable to the growth of some crops, unfavourable to others, and in still some other cases they have little effect.

A pH value near neutral is best for most plants. The availability of all the plant nutrients is at least reasonably satisfactory at pH between 6.5 to 7.5 (Truog, 1946). Lettuce will not thrive on very acid soils. The optimum pH range seems to be from pH 6 to 8. Hardenburg (1928) obtained best top yields of lettuce on muck soil with pH range of 5 to 6.5. However, for Hartman and Stair (1938), a pH range of 7.1 - 7.4 seemed to give higher yields than pH 6.6.

## 6. Soil Structure

The structure of the soil is one of the most important features and qualities of soil. Soil structure depends on the way in which the individual fine particles are aggregated into small crumbs or clouds. The most desirable size for the surface crumbs to have, from the point of view of plant growth, lies in the range of 1-3 mm (Kononova, 1966).

Soil with good structure provides the best conditions for supplying water and nutrients to the plants. Plant roots grow better and make better use of soil water in a relatively loose, well-aerated soil. Cereals and cotton have been shown to make better and earlier growth, gave higher yields when grown on well-structured soil. However, this would be expected with other crops as well. For lettuce, a well-drained soil ranging from a sandy loam to a clay loam is preferred to those that are coarser or finer. A good content of organic matter is also desirable. Besides being a source of nutrients for the plant, and the most important factor in soil structure formation, organic matter has also a fundamental effect on water-holding capacity and greatly influences the exchange capacity and buffering properties of the soil (Kononova, 1955).

### C. GROWTH ANALYSIS

Since the introduction of such concepts as net assimilation rate (NAR) and relative growth rate (RGR) by Gregory (1917) and by Blackman (1919), many researchers have applied them in the quantitative analysis of plant growth. Watson (1952) used the term 'growth analysis' to describe these techniques, which in simple terms, may be defined as the study of the changes in the whole plant during its ontogeny. It has its faults and has been criticised (Evans and Hughes, 1962; Milthorpe, 1963; Williams, 1946), nevertheless, it has proved to be a useful means of assessing the integrated effect of environment on plant growth.

Growth analysis techniques study plant responses to environment in terms of the rate of increase in total dry matter over intervals of one or two weeks. The method presumes that dry matter increase is the result of net photosynthetic activity. Almost all the dry matter increase of a plant is attributable to the net result of gains due to photosynthesis and losses due to respiration of the whole plant (Friend, 1966; Richards, 1959).

The Relative Growth Rate (RGR) is defined as the change in dry weight per unit of dry weight per unit of time, or

$$\text{RGR} = \frac{1}{W} \cdot \frac{dW}{dt}$$

where W is the total dry weight.

Net assimilation rate (NAR) is defined as the change in dry weight per unit of leaf area, per unit of time, or

$$\text{NAR} = \frac{1}{A} \cdot \frac{dW}{dt}$$

where A is the total leaf area.

The leaf area ratio (LAR) is the ratio of the leaf area to the total dry weight of the plant, or

$$\text{LAR} = \frac{A}{W}$$

At any instant, these three expressions are related as follows (Radford, 1957):

$$\frac{1}{W} \cdot \frac{dW}{dt} = \frac{1}{A} \cdot \frac{dW}{dt} \times \frac{A}{W}$$

$$\text{i.e. } \text{RGR} = \text{NAR} \times \text{LAR}$$

The traditional use of these formulae involves the calculation of mean RGRs, NARs and LARs over approximately weekly time periods using the formulae:

$$\text{RGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \quad . \quad . \quad . \quad . \quad . \quad (1)$$

$$\text{NAR} = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{\log_e A_2 - \log_e A_1}{A_2 - A_1} \quad . \quad . \quad . \quad (2)$$

$$\text{LAR} = \frac{A_2 - A_1}{W_2 - W_1} \times \frac{\log_e W_2 - \log_e W_1}{\log_e A_2 - \log_e A_1} \quad . \quad . \quad . \quad (3)$$

Where  $W_1$  and  $W_2$  are the plant dry weights at the times of the two sampling occasions  $t_1$  and  $t_2$ , and  $A_1$  and  $A_2$  are the corresponding leaf areas.

An alternative approach involving the fitting of smooth curves to the  $\log_e$  of the dry weights and leaf areas against time has been used by Hughes and Freeman (1967). With this method, the work load of large samples necessary with the classical method can be spread out by more frequent sampling of smaller samples. Other advantages of this approach has been discussed by Radford (1967).

The RGR is a measure of the efficiency of the plant as a producer of new material and was originally termed the "efficiency index" by Blackman (1919). It is usually expressed in g/g/day.

The concept of NAR was first introduced and used by Gregory (1917) in an attempt to obtain an estimate of the assimilatory efficiency of leaves from simple growth measurements. It is an expression of performance of the photosynthetic system and can be estimated from successive determinations of dry weight and leaf area at short intervals throughout the growth period.

In 1920, West, Briggs and Kidd, assuming that the leaf areas were changing exponentially, proposed the use of formula (2) for calculating NAR. This equation is only an approximation

since it assumes that changes in weight are linearly related to changes of leaf area. Indeed, Williams (1946) has stated that under some conditions this method of computation may lead to substantial errors. Radford (1967) also has indicated that the condition of linearity between leaf area and plant weight is not necessarily implied by exponential growth. However, with short inter-sampling periods the error is reduced and this formula can be used with fair accuracy.

The early concept of NAR was that it was independent of internal factors, at least during vegetative growth, but was controlled by external factors such as light and temperature (Gregory, 1926, Heath and Gregory, 1938; Watson, 1952). However, Milthorpe, (1959), Thorne, (1950, 1961) and Williams, (1946) found appreciable variations in NAR unassociated with external factors, which appear to be due to a reduction in photosynthetic capacity, and an increase in respiration, together with the ageing and the mutual shading of the lower leaves) (Milthorpe, 1963).<sup>x</sup>

All the dry weight of a plant is not active in photosynthesis, and since all dry matter increase, except for a small amount of mineral uptake, is caused by photosynthesis, a better estimate of plant efficiency might be based on leaf area. However, other leaf attributes such as leaf weight and leaf protein have been used (Williams, 1946).

The difficulty in interpreting the effects of external factors on NAR lies in the fact that the rate is largely the balance between the gains due to assimilation by the leaves and the respiration losses of the whole plant. Under field conditions respiration can result in losses up to about 40% of gross photosynthesis (Gaastra, 1962; Monteith, 1966). NAR, being expressed per unit leaf surface, any treatment which affects the LAR would alter the NAR (Richards, 1969). In fact, Blackman and Wilson (1951a) have shown that an increase in LAR, an increase in shoot : root ratio, and a reduction in light intensity will all affect the NAR.

In shading experiments with a number of plant species, Blackman and co-workers (1948, 1951a, b) established that during the early vegetative phase both the changes in NAR and LAR, over a wide range of illumination, were linearly related to the logarithm of light intensity, but under heavy shade these relationships no longer held (Blackman, 1959a, b). They found that during the active growth phase, variations in the light level did not significantly affect the leaf weight but had a marked effect on the leaf area. Hence, a reduction in light intensity invariably leads to an increase in LAR, and this allows the plants to compensate for decreasing NAR and thus maintain RGR.

Significant differences of NAR has been found to occur between species grown in the same environment and even between varieties of the same species (Watson, 1947a). This is in contrast with the view of Heath and Gregory (1938) who concluded that the mean NAR during the vegetative phase is approximately constant for a wide range of species and environments. It is now regarded that NAR can vary from species to species. However, Blackman and Wilson (1951a) believed that when conditions for growth were optimal, the NARs were of the same between species. Many determinations of NAR seem to have values between  $0.4 - 0.7 \text{ g/dm}^2/\text{week}$  (Heath and Gregory, 1938).

Variation in nutrient supply over a wide range have little or no effect on NAR (Watson, 1947b). Blackman and Wilson (1951b) found that nutrient supply had little effect on NAR in low light intensities, but with increasing light intensities the NAR increased with improved nutrient supply.

Net assimilation rate is generally regarded as less variable than the LAR and hence differences in RGR and in the yield of crop plants are determined mainly by differences in LAR (Heath and Gregory, 1938; Watson, 1956).

These considerations show that the main opportunity for increasing yield lies in the increase of leaf area. In some conditions, a deficient water supply decreases NAR, but

decreases LAR even more (Watson, 1952), so irrigation is one way of improving crop yield! Fertilizers increase LAR (Watson, 1947b; Blackman and Wilson, 1951b), but the major elements differ in the time when they are most effective. For example, Watson (1955) has shown that N increases leaf area throughout the growth period of barley and potato; P increases leaf areas particularly in the early stages of growth, but later it hastens senescence of the leaves and eventually may decrease leaf area; K, on the other hand, is most effective in the later stages of growth and tends to delay senescence of the leaves. Watson (1952) found that in general the fertilizer responses (mainly of cereals) were due to increase in LAR. In recent years, fertilizers trials on vegetables seem to show that the increase in RGR is due to increasing NAR (Austin, 1963; Nichols, 1971a, b). Austin argued that there was a delay in sampling in Watson's works which could have missed the earlier small differences in NAR. According to him this small percentage variation in NAR had as much effect on yields as a considerably greater percentage variation in leaf area ratio. Nichols, using radish and lettuce on the Manawatu silt loam, showed that the response to P fertilizer was due to a higher NAR.

Briggs, Kidd and West (1920) were able to show for certain annual plants that the LAR exhibited an ontogenetic drift essentially similar to that of the RGR and that consequently the NAR changed relatively little during a large part of the life cycle of the plants.

As discussed earlier a reduction in radiation level almost invariably results in a rise in the LAR and this allows the plant to compensate for decreasing NAR and thus maintain the RGR. Dullforce (1956) found that LAR was affected positively by temperature.

Leaf area ratio can be considered as being made up of two components, the leaf weight ratio (LWR) and specific leaf area (SLA) (Evans and Hughes, 1961). Hence

$$\begin{aligned} \text{LAR} &= \text{LWR} \times \text{SLA} \\ &= \frac{L}{W} \times \frac{A}{L} \end{aligned}$$

where L is leaf weight. This concept enables differences in LAR to be attributed to either (a) the differential distribution of photosynthetic products between leaf growth and other plant growth, or (b) the differences in leaf thickness (Radford, 1967).

Blackman (1956) has clearly demonstrated in shading experiments that the change in LAR is largely dependent on

the change in SLA, and that LWR remains relatively constant. In another series of experiments Blackman (1956) found that temperature had a positive effect on LAR and SLA, but had little effect on LWR. Evans and Hughes (1961) also obtained the same effects of light and temperature on LAR and SLA. In young plants of Impatiens parviflora, they were able to show a marked ontogenetic drift in SLA while the LWR remained almost linear.

"Dullforce (1959) found that a SLA value of  $10 \text{ dm}^2/\text{g}$  was associated with heading in winter lettuce. She also considered a LAR value of  $9 \text{ dm}^2/\text{g}$  as a critical value for heading in lettuce." This can be considered as an instance of constancy of LWR.

The relative growth rate will respond to light intensity owing to a morphological component, LAR, and a physiological component, NAR (Hughes, 1962). At rather low light intensities the effect of LAR is most important whereas at the higher light intensities RGR increases mainly as a consequence of increasing NAR (Butt, 1968; Brouwer, 1973), although frequently RGRs do not increase above  $100 \text{ cal}/\text{cm}^2/\text{day}$  (Hughes, 1962).

"Growth analysis shows that both NAR and LAR are affected by temperature. A striking similarity has been found with onions and wheat by Butt (1968) and Friend (1966). At low temperatures, the initial rise in RGR is due mainly to an

increasing NAR, but at higher temperatures, the RGR reaches an optimum as a consequence of a rising LAR together with a decreasing NAR, thereafter, the decrease in RGR is only due to a decrease in LAR. From these experiments a lower optimum temperature for NAR and a higher optimum temperature for LAR resulted in a frequently broad optimum temperature for RGR somewhere in between.

A second approach in growth analysis is through the crop growth rate which has been defined as the rate of increase of dry weight per unit area of land (Watson, 1956). The CGR is partitioned into the components which reflect the efficiency and the size of the leaf surface (Watson, 1958). The components are related to the growth rate as follows:

$$\text{CGR} = \text{NAR} \times \text{LAI}$$

Where LAI, or leaf area index, is the area of leaf per unit area of ground surface occupied by the crop.

"Another useful concept introduced by Watson (1947a) is the leaf area duration or the integral of LAI itself over the whole growth period of a crop and hence its capacity for assimilation. Thus if NAR were constant the dry matter produced would be proportional to the leaf area duration.<sup>1)</sup>

Crops grown from seeds have an initial period when LAI is very small but this increases, slowly at first and then more rapidly to a maximum. During a large part of the life of a crop the LAI is less than one and this is one reason for the low efficiency of annual crop in utilizing solar energy. Factors such as seed size, number of seeds per unit area of land and time of sowing influence LAI, particularly during the initial period. Plants with a high relative leaf growth rate (rate of change of total leaf area) are advantageous and the effect of phosphate fertilizer on early leaf growth may have special value in this connection (Watson, 1956). For lettuce, the rate at which the crop covers the ground is determined mainly by temperature during its early stages of growth and hence high temperature may be useful in shortening the time for plants to reach a LAI of one.

Maximum rates of dry matter production can be expected to occur when optimal value of LAI coincides with maximum value of NAR (Watson, 1956).

## D. PLANT ANALYSIS

### 1. Introduction

Plant analysis as a tool for assessing the nutritional requirement or status of plants has received much attention since the review of Ulrich (1952). However, the idea of plant analysis as a diagnostic tool in mineral nutrition is not new. Such a concept was expressed a century ago by Hellriegel (quoted by Smith, 1962) who in 1869 stated "if the necessary foundations are first laid by field trials, crop analysis will provide a portion of plant nutrients present and available in the soil". The emphasis in current research has changed from the soil to the plant. However, both of these techniques are useful and one method may at times supply the information that the other will not. For many crops, plant analysis is more generally useful than soil analysis as is illustrated by the extensive comparison of the two by Titus and Boynton (1953) and Heeney and Hill (1961).

Plant analysis may be viewed as a study of the relationship of the nutrient content of the plant to its growth. It is based on the concept that the concentration of a nutrient within the plant at any particular time is an integrated value of all

the factors that have influenced the nutrient concentration up to the time the plant sample is taken.

There are two main approaches to plant analysis: tissue analysis and leaf analysis.

Tissue analysis involves a measurement of plant nutrients contained in the extracts of, usually, the stems or petioles of plants.

As a research tool, leaf analysis has become more widely used in recent years than ever before. Leaf analysis is concerned with the concentration of total nutrients in leaves, at specific growth stages, in relation to plant performance. It is based on the contention that the leaf is the principal site of metabolism, that changes in nutrient supply are reflected in nutrient composition of the leaf and that the nutrient concentrations in the leaf at specific growth stages are related to the performance of the crop (Bould, 1968). The leaf is not the only tissue that will reflect the nutrient status of the plant, but it is usually the best for most nutrients (Rogers, Batjer and Billingsley, 1955; Smith, Reuther, Specht and Hrnciar, 1954).

## 2. The Shape of Nutrient Response Curves

The application of plant analysis to the nutrition of plants revolves around the critical concentration of a nutrient

or nutrient function within the plant, (or some plant part) and its determination from a nutrient response curve. The concept of critical concentration is based on a predictable functional relationship between nutrient concentration and yield (Goodall and Gregory, 1947), and Ulrich and Hills (1967) selected the critical level as that which produces 90% of the maximum yield. A typical plant nutrient response curve is presented schematically in Figure 1A. This shows the zone of deficiency where yield increases sharply as more nutrient is absorbed by the plant, but there is little change in concentration of the nutrient in the plant part analysed. Within the transition zone both nutrient concentration and growth increase as more nutrient is absorbed by the plant. The adequate region is that region of the curve where there are changes in nutrient concentration as more of the deficient element is absorbed but there are no further changes in growth (Ulrich, 1961). The critical concentration is estimated within the transition zone.

Frequently a second type of response curve, called the "Steenbjerg effect" or "C-shape" curve (Figure 1B) is encountered in literature (Steenbjerg 1951, 1963). With this C-shaped curve, a plant which contains a very low

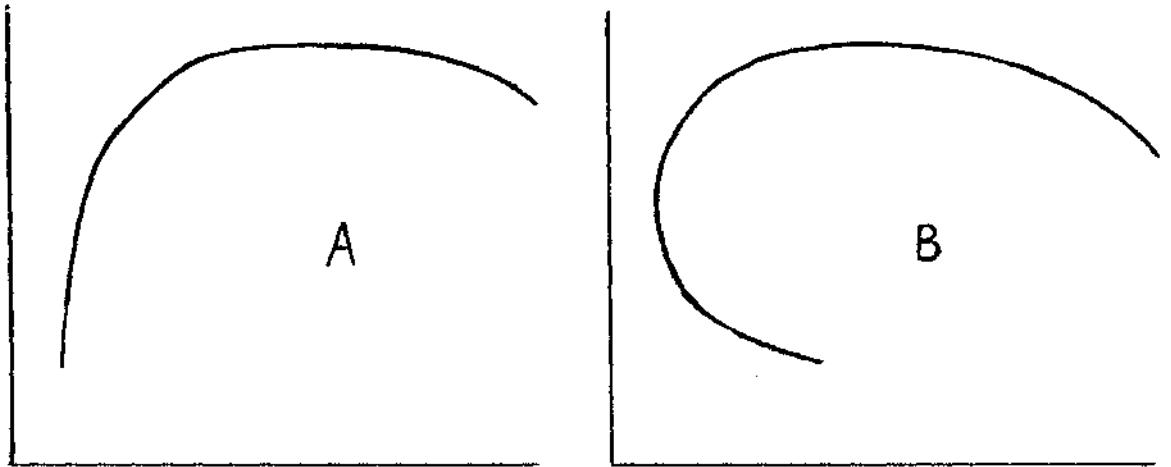


Figure 1 Generalized nutrient response curves of yield as a function of nutrient concentration. (Oates, 1977).

concentration of nutrient would be expected to respond to increased nutrient supply with increased yield in a similar manner as with curve 1A. However, with this curve, there is a decrease in plant nutrient content with the initial increase in yield. Hence, a somewhat higher concentration of nutrient in the plant may signify either an extremely deficient or an adequate supply of nutrient. For meaningful plant analysis, this situation is to be avoided.

The most useful nutrient response curve is one in which the transition zone is sharp, i.e. there is a narrow range in nutrient concentration between plants that are deficient and those that are well supplied with the nutrient in question.

### 3. Factors Affecting Leaf Nutrient Concentration

Leaf analysis is used as a means of:

1. detecting plant response to various cultural treatments,
2. identifying the nutrient element associated with apparent nutrient disorders, and
3. determining the fertilizer requirements of crops.

The main problem of leaf analysis is in the interpretation of data, for while the nutrient composition of leaves is

primarily controlled by nutrient supply (Steenbjerg and Jakobson, 1963) it may be influenced by many internal and external factors (Smith, 1962; Bates, 1971).

Smith (1962) states that, "next to the supply of elements the physiological age of tissue is probably the most important factor affecting the mineral composition of a given species." The pattern of nutrient content with age varies with the species (Guha and Mitchell, 1966), and with the nutrient (Howlett, 1961; Mason and Whitefield, 1960). The concentrations of N, P, K, Ca and Zn are greater in young tissues than in old while the reverse tends to be true for Ca, Mg, Mn and Fe (Smith, 1962). It is therefore important that the physiological age of the tissue sampled be the same for a meaningful interpretation of plant analysis.

Many tissues have been used in plant analysis (Goodall and Gregory, 1947), but leaves are usually the most satisfactory plant part (Bould, Bradfield and Clarke, 1960; Emmert, 1959; Smith, 1962). Occasionally tissues other than leaves are more suitable for certain crops and particular nutrients (Clements, 1964; Emmert, 1959).

The total quantity of a nutrient element is more frequently measured in plant analysis, but soluble fractions are also used.

Most work done on soluble fractions employs acetate buffer solution. Nicholas (1956) compared various soluble fractions of a number of nutrients with the total concentration and in general found that they are closely correlated except in the range of luxury consumption. In certain cases, some advantage has been demonstrated with sulphate - sulphur (Ulrich, 1968) and nitrate - nitrogen over total concentrations (Burham and Babiker, 1968).

Critical concentrations vary from species to species (Chapman, 1966), however, the problem still exists whether different cultivars of a single species vary in critical concentration of any one plant nutrient. Reuther and Smith (1966) have suggested that although nutrient uptake varies widely among cultivars, the critical concentrations probably do not. On the other hand, works of Kessler (1961) on apple cultivars and that of Shea, Gabelman and Gerloff (1967) on snap bean cultivars seem to have found marked differences in critical Zn and K concentrations respectively.

An important but complex situation of ion-interactions has been discussed for a wide range of crops and reviewed by Brown (1963). A shift in concentration of one nutrient element is almost always accompanied by secondary changes

in tissue content of other elements. Another important aspect of ion-interactions is that one nutrient may affect the critical levels of another nutrient (Bates, 1971). Examples of multi-element effects have been cited by Smith (1952), who found that increased N caused a change in the leaf concentration in eight elements and leaf K affected nine other elements.

Environment may strongly influence the tissue content of minerals and consequently the interaction of tissue analysis. Weather is considered as a major cause in the year-to-year variation in nutrient content in uniformly fertilized plants (Emmert, 1959; Heeney and Hill, 1961).

Low soil moisture has been shown to reduce plant concentrations of P, K, B, Mo and Zn but to increase that of N, Mg and Mn (Bates, 1971; Emmert, 1959).

Soil aeration, which is frequently a function of soil moisture, can have a large effect on nutrient uptake and concentration in leaves (Grable, 1966).

Soil temperature, air temperature and both the duration and intensity of light are also reported to influence the concentrations of nutrients in plants (Burr, 1961; Ketcheson, 1968; Lange, Ehrler and Hamner, 1959; Zurbicki, 1961).

#### 4. Sampling

Plants are not homogenous in their nutrient element make up, since leaves, stems, petioles, etc., as well as similar plant parts at different locations on the plant, will differ in composition. Therefore, it is essential to select a specific plant part at a definite location on the plant when sampling. In making a choice of possible tissues, one must be guided by such physiological and practical considerations as the accuracy of the analytical technique and the homogeneity and accessibility of the plant material.

Frequently no one specific time for sampling or no one plant part is suitable for all elements. Various portions of the plant have been used. In general, leaves are the most appropriate plant part to sample. Only in the leaf are the ontogenetic drifts in the major nutrients known to resemble those in the whole plant (Petrie, 1934). Sharper nutrient response curves are usually given by matured leaves (Ulrich and Berry, 1961). The petiole is usually used for nitrate - nitrogen, phosphate - phosphorus and chlorine while the blade is more satisfactory for the other essential mineral nutrients (Ulrich and Hill, 1967). Plants with

symptoms suspected to be a nutrient element deficiency should be sampled when the visual symptoms first appear.

With many leaf nutrient elements, there is usually an initial period of rapid and characteristic change during growth and development of young leaves, than a period of minimum change in the fully developed leaves, and finally a period of more rapid change as senescence approaches and mobile elements are withdrawn. The period of minimum change is normally chosen for sampling leaves.

Consistency of sampling is of prime importance both in regard to comparable tissue and time of sampling for quantitative comparison between plants of same species. Steyn (1961) was able to show a distinct advantage in using rigid selection for age, position and number of leaves in a sample of citrus and pineapple.

For each crop careful research is needed to determine which part of the plant is most indicative of the nutrient status of the plant. What field sampling is best, and how often during the season analyses should be made. The precision and cost of the analytical survey are also factors to be considered.

## 5. Analysis

The general attitude toward plant analysis for diagnostic purposes is to have the samples analysed for as many nutrients as possible. Without complete analysis, it is not possible to properly consider nutrient inter-relationships and nutrient-element balance. When more complete analyses become possible, there is a tendency to collect more samples. Thus there is a need to analyse a large number of samples for several elements. To accomplish this, instrumentation or automation or both is necessary. This has been made possible by the use of photo-electric spectrometers and other instruments. At present, rapid analysis of plant material can be made for all elements except N.

N analysis is the most time-consuming determination and is determined by Kjeldahl method; K is determined by flame photometry and all other elements are determined by the emission photo-electric spectrometer.

## 6. Establishment of Standards

Much interest has been shown in recent years to establish leaf nutrient standards for different crops (Bould, 1961, 1968; Goodall and Gregory, 1947; Kenworthy, 1961; Reuther, Embleton and Jones, 1958). Leaf standard values may be described as deficient, low, optimum, high and excess (Jones, 1967).

Most investigators use dry rather than fresh plant material for analysis. Concentrations determined in dry material tend to be less variable. It is common to express the nutrient concentration of macronutrients as percent dry weight and microelements as part per million, although milliequivalents and microequivalents have been used.

#### 7. Usefulness and Limitations

The general usefulness of plant analysis as a research tool is widely recognised. On the practical side, it has made a major contribution to agriculture by revealing nutritional problems and the prevention of deficiencies. Some of the more important factors affecting tissue composition have been discussed. A good knowledge of the factors involved in plant growth is required for meaningful and accurate interpretation of plant analysis. Another limitation of plant analysis is the sampling method which has yet to be perfected and standardised.

Plant analysis of annual crops can rarely be made early enough in the season to serve as a guide for correcting the condition in the current growing season with fertilizer treatments. The results may, of course, be very helpful in planning treatments in future years. On the other hand, analyses of perennial plants such as fruit trees can be immediately useful in correcting deficiencies.

## CHAPTER III

### MATERIALS AND METHODS

#### A. GENERAL

The experiment was carried out in a glasshouse sited at Massey University's Agriculture and Horticulture Plant Growth Facilities. The glasshouse is 5.2 X 5.2 metres and is made up of a light aluminium frame with a concrete floor.

Throughout the experiment the air temperature in the glasshouse was kept between 15<sup>o</sup> and 24<sup>o</sup>C. This was done by using a hot-water heater mounted with a fan to help dissipate the heat and circulate the hot air, together with a ventilation system comprising louvres and two ventilation fans operated automatically by hydraulic rams, all controlled by a thermostatically actuated switch.

The plants were grown in black plastic bags of 10 X 10 X 15 cm. These containers were filled with fine sand to about 12 cm. deep

and placed on a three centimetre thick sand bed on top of the trolleys.

The trolleys were lined with black plastic film, perforated to allow free drainage. Ten trolleys were used, five on each side of the glasshouse, and each carried one hundred and sixty two bags

#### B. PLANT MATERIAL AND PROPAGATION

The two cultivars used in the experiment were "Cobham Green" (a butterhead lettuce), hereafter called "Cobham" and "Webb's Wonderful" (a crisphead lettuce), hereafter called "Webb's". The seeds were obtained from Harrison's Seeds, Leicester, England.

The seeds were sown on 18 September, 1972 (for sowing rates, see Table II) into bags filled with a well-watered sand medium and then covered with another centimeter of sand. The bags were again watered and then covered with moist newspapers to reduce evaporation.

The seeds germinated in four to five days and thinning was carried out to give one plant per bag, except for the first-harvest plots where all the seedlings were used for the analysis and second-harvest plots where five plants were retained. Thinning was carried out with the aim of giving a more uniform population.

## C. METHOD

### 1. Experimental Design

The experimental design was a split plot with two replications (blocks). The five main treatments were the levels of phosphorus and the split plot treatments, factorially arranged, were the cultivars and harvest dates.

### 2. Sampling Method

Samples of plants of each of the two cultivars were taken from each treatment and replicate, every seven days after emergence, for ten weeks. The first and the last harvests each consisted of one single sample, but two samples were taken at each of the other eight intermediate harvests. The number of plants in each sample varied with harvest (Table II).

### 3. Nutrient Solution and Feeding

Five treatments of P based on that given by Bollard (Hewitt, 1966) were used (Appendix I). Various combinations of reagents were used to give quarter ( $P_1$ ), half ( $P_2$ ), unit ( $P_3$ ), 2-fold ( $P_4$ ) and 4-fold ( $P_5$ ) levels of P with relatively limited differences only in sulphate concentration. Nitrogen

TABLE II

NUMBER OF SEEDS SOWN PER POT, AND THE TOTAL NUMBER OF PLANTS  
HARVESTED PER SAMPLE FOR THE TWO CULTIVARS USED IN  
THE EXPERIMENT

---

Harvest number	Number of pots	Number of seeds/pot	Number of plants/pot	Total number of plants harvested
1	11	18	9	99
2	5	10	5	25
3	7	5	1	7
4	5	5	1	5
5	4	5	1	4
6	3	5	1	3
7	3	5	1	3
8	3	5	1	3
9	3	5	1	3
10	4	5	1	4

---

was given in equal parts as ammonium and nitrate. The micronutrients were added according to the Long Ashton formulation (Hewitt, 1966). Iron in chelated form with ethylenediamine tetra acetic acid (EDTA) is now the preferred and usual source of iron used in sand cultures.

Each level of nutrient solution was prepared from stock solutions and stored in inert covered containers. Tap water was used since only the major elements in plant tissue were to be analysed. The pH of the five nutrient solutions was adjusted by adding dilute sulphuric acid until all the solutions gave a value of 6.5 when freshly prepared.

Throughout the experiment the nutrients were supplied at the equivalent of:

Macronutrients	parts per million	Micronutrients	parts per million
N	224	Fe	2.80
K	156	Mn	.55
Mg	48	Cu	.064
Ca	80	Zn	.065
S	160-176	B	.33
		Mo	.048

For P, the amounts supplied were:

Treatments	P <sub>1</sub>	P <sub>2</sub>	P <sub>3</sub>	P <sub>4</sub>	P <sub>5</sub>
Parts per million	7.75	15.5	31	62	124

Nutrient feeding was carried out in the morning with a watering can at the beginning of the experiment, when the plants were small, followed by minimum water sprays to wash down nutrient solution from the leaves. At the later stage of plant life, each plant was given a generous amount of solution by hand to provide some drainage loss. This, together with flooding of the sand bed with a large quantity of water at 14-day intervals was to avoid the build up of excessive soluble salts.

#### 4. Growth Measurements

Growth changes over the period of the experiment were described by estimates of total leaf area and dry weights obtained at 7-day intervals. Harvesting was carried out every seven days by first cutting the tops off the plants at sand levels and tipping the sand out of the bag after soaking in the water. Roots were carefully washed free from sand particles, using a fine brush to remove any sand particles which were held tightly by the roots.

(a) Dry Weight

For the estimation of dry weight the plants of each sample were separated into leaves, stems and roots except in the first harvest when the plant was divided into only cotyledons and roots. These plant parts were then put into glass bottles, which had been sprayed with a silicon aerosol to prevent the plant material sticking to the glass and dried in a forced draught oven at 80°C for 24 hours. When the plant parts became too bulky for the bottles, paper bags were used. The containers were then cooled in a desiccator and the dry weights of the plant parts determined.

(b) Leaf Area

The area of the leaf is the principle factor governing the ability of the plant to intercept light energy. Thus the measurement of leaf area is of direct importance in plant growth and productivity studies.

The more widely used methods of measuring leaf area were reviewed by Frear (1935) and by a series of papers presented at the Third Easter School in Agricultural Science, University of Nottingham (1956).

Three methods were used in this experiment.

i. Air-flow planimeter

This method is slow and only suitable for small leaves.

ii. Automatic area meter

The machine used was by Hayashi Denko Co., Tokyo. The leaves were placed between two rotating belts and the leaf area was recorded automatically. This method is easy to use and faster than the planimeter method, but is not very satisfactory for lettuce leaves because of the folding and crinkling nature of the lamina.

iii. The 'punch' method

One again, the method ii. was too slow for the large leaf area of the last three harvests and punch method was used. This method only gives an approximate value, but its advantage is speed.

Using a 'punch' of known area, thirty complete leaf cores were taken by random pushing the punch into the leaves and their fresh weight taken. The total leaf area of the plant sample was then computed by simple proportioning.

5. Ground Cover

During harvesting time, plant samples for each treatment were arranged so that their leaves did not overlap. Together with necessary information such as treatment level, replication

number, sample number and a half-inch ruler, a photograph was taken of the plants perpendicularly from the top.

The images of the plants from the negative were then projected on to a white screen. In order to obtain the exact size of the plant, the half-inch ruler and its image on the screen must be coincided. When this happened, the outlines of the individual plant were traced on the paper and then cut out before putting the paper cuttings through the automatic area meter.

#### 6. Chemical Analysis

For chemical analysis of total N, P and K the dried plant parts of each sample were bulked together and ground into fine powder. The plant material was re-dried at 80°C before chemical analysis was carried out.

A rapid method for the determination of N, P and K proposed by Cavell (1954) was adopted.

A small sample of the dried plant material was digested with concentrated sulphuric acid and sodium sulphate, using copper sulphate as a catalyst until the solution turned from dark brown into a light blue colour. The digestion was continued for another two hours after the colour change.

When the digestion had finished and cooled down, distilled water was used to make the digested solution to 250 cc.

(solution A). From this solution, total N, P and K were determined.

The weight of the sample to be digested varied according to the amount of dry matter available. All the samples from the first three harvests and some samples from the fourth and fifth harvests had less than two grams of dry matter and suitable dry weights were used in digestion. Otherwise two grams of plant material were used in the digestion.

(a) Nitrogen determination

A 10 ml. aliquot of solution A was distilled in a Markham distillation apparatus with 10 ml. 10N NaOH. About 25 ml. distillate were collected in 10 ml. 2% boric acid and titrated with 0.1 N HCl using Bromcresol green/methyl red as indicator.

$$\text{Total N(\% dry wt.)} = \frac{14 \times \text{net titre} \times \text{normality acid}}{\text{dry wt. (g)}}$$

(b) Phosphorus determination

In a 100-ml. graduated flask, a suitable amount of 2.6 N NaOH was added to 50 ml. solution A, cooled and diluted to 100 ml. To a 5 ml. aliquot of this solution, 5 ml. of

ammonium molybdate/ammonium vanadate mixture were added. Colour development was read at 480 m $\mu$  using a spectrophotometer, after half an hour, against a distilled water blank and P calculated from a standard curve where:

$$P (\% \text{ dry wt.}) = \frac{\text{Soluble P (p.p.m.)}}{20}$$

(c) Potassium determination

25 ml. of solution A were made alkaline with ammonium hydroxide (methyl red as indicator) and diluted to 100 ml. with distilled water. Readings were taken on a Callenkemp flame-photometer and K determined from a standard curve and where:

$$K (\% \text{ dry wt.}) = \frac{\text{Soluble K (p.p.m.)}}{20}$$

## CHAPTER IV

### RESULTS

#### A. GENERAL OBSERVATIONS

Throughout the experiment the characteristic reddish tints usually associated with P deficiency (Wallace, 1961) were not observed but differences in size were apparent between the phosphate levels a fortnight after plant emergence. After 3-4 weeks the plants which had received  $P_1$  and  $P_2$  treatments were smaller and had small leaves, which were harder and tougher than the softer and thinner leaves of the plants receiving higher P ( $P_3$ ,  $P_4$  and  $P_5$ ).

The roots of the plants of the  $P_3$  -  $P_5$  treatments were larger and had more branches than those of  $P_1$  and  $P_2$  treatments.

The  $P_3$  -  $P_5$  treated plants were the largest throughout the experiment and began to head about 42 days after emergence. The  $P_1$  and  $P_2$  plants were stunted in growth and showed no sign of heading even by the end of the experiment.

Some of the plants of P<sub>4</sub> and P<sub>5</sub> had tipburn disorder when the tissue collapsed and necrosis occurred in the marginal tissue of young leaves. Tipburn injury readily occurs in lettuce which have been growing rapidly under certain environmental conditions (Tibbitts, Struckmeyer and Rao, 1965).

Cobham suffered relatively more in this experiment from the tipburn disorder than Webb's.

Some plants of Cobham in P<sub>5</sub> showed signs of bolting in the final harvest. These plants had elongated stems and longer internodes with small leaves.

#### B. DRY WEIGHT

For all the treatments, the total plant dry weights increased throughout the experiment (Figures 2A and B, and Appendix II).

For both cultivars, increased in P concentration resulted in an increase in the dry weight in every harvest, apart from the last two harvests of Cobham where P<sub>3</sub> treatment had higher dry weights. This was in part due to severe tipburn disorder.

The growth of both cultivars showed a typical logistic growth pattern. The plant dry weight increased very slowly initially, and much of the dry matter was produced in the last three harvests.

$\text{Log}_e \text{d.w. (mg)/plant}$

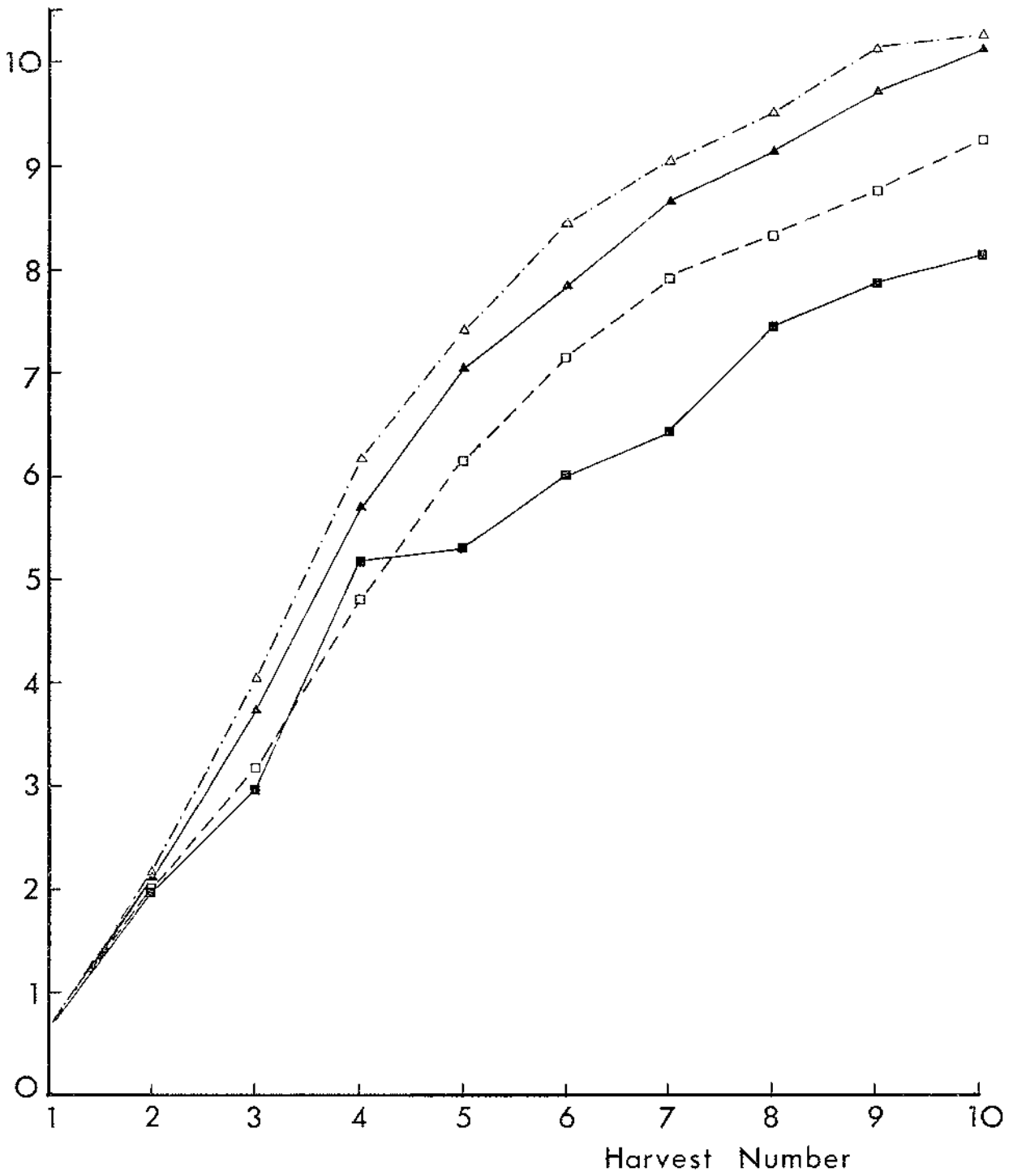


Fig. 2A. The effect of phosphorus fertilizer on total plant weight of Cobham Green  
■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

$\text{Log}_e \text{ d.w. (mg) / plant}$

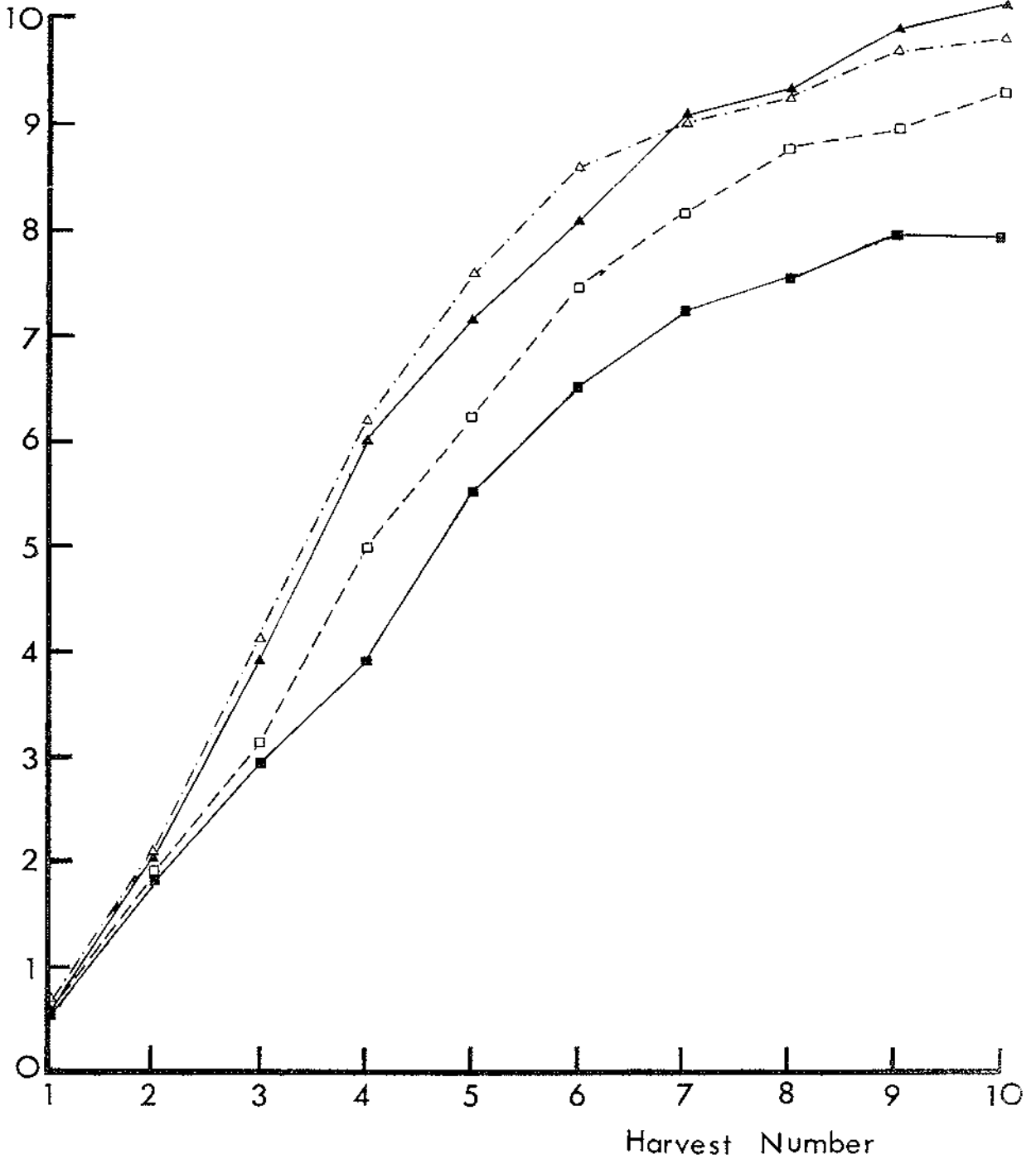


Fig. 2B. The effect of phosphorus fertilizer on total plant weight of Webb's Wonderful.  
■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

### C. RELATIVE GROWTH RATES

Relative growth rates were calculated for all the treatments for the entire period of the experiment and are presented in Appendix III. For this purpose, dry weights of the whole plant were used. These growth rates were subjected to analysis of variance (Appendix IV).

Increase in P supply from  $P_1$  to  $P_3$  appeared to have increased the relative growth rate for both cultivars, although the effect did not reach significant level.

There was a highly significant harvest effect. The growth rate rose from first harvest interval to interval three followed by a sharp fall for the next 14 days before levelling off.

Significant interactions between harvest and P treatments (Table III) and between harvest and cultivars (Table IV) were observed.

### D. NET ASSIMILATION RATES

The data for net assimilation rates are presented in Appendix V and their statistical analyses are shown in Appendix VI.

For the first three harvest intervals, there was no consistent trend in both cultivars. After this initial

TABLE III

EFFECT OF LEVELS OF PHOSPHORUS AND HARVEST DATE ON RELATIVE GROWTH RATE

(g/g/DAY)

Treatment	Days from sowing									Treatment mean
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63	63-70	
P <sub>1</sub>	.1984	.1401	.1266	.2295	.1489	.1014	.1080	.0150	-.0040	.1182
P <sub>2</sub>	.2011	.1670	.2557	.2062	.1364	.0645	.0630	.0441	.0604	.1332
P <sub>3</sub>	.2284	.2446	.3083	.1754	.1176	.1306	-.0216	.0708	.0500	.1449
P <sub>4</sub>	.2319	.2860	.2941	.1758	.1222	.0779	.0478	.0871	.0288	.1502
P <sub>5</sub>	.2417	.2774	.2603	.1575	.0971	.0857	.0471	.0615	.0403	.1410
Interval mean	.2203	.2230	.2490	.1889	.1244	.0920	.0849	.0557	.0351	

TABLE IV

EFFECT OF HARVEST DATE AND CULTIVAR ON RELATIVE GROWTH RATE (g/g/DAY)

Cultivar	Days from sowing									Cultivar mean
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63	63-70	
Cobham	.2219	.2278	.2515	.1991	.1433	.0987	.0130	.0277	.0155	.1332
Webb's	.2186	.2182	.2465	.1787	.1056	.0860	.0847	.0837	.0547	.1418

period, the rate dropped from  $P_1$  to  $P_5$  for most of the growth stages of the crop.

The effects of fertilizer treatment was highly significant and throughout the experiment Webb's had a significantly ( $P < 0.01$ ) higher net assimilation rate than Cobham in all the treatments (Table V).

There was also a highly significant harvest effect. Apart from a few discrepancies, the general trend was for the net assimilation to fall with ontogeny.

The only significant interaction was between harvest and P treatment (Table VI).

#### E. LEAF AREA RATIOS

This growth function expresses the relationship between leaf area and dry weight of the entire plant between two harvests.

The leaf area ratio increased consistently with increasing P levels from  $P_1$  to  $P_4$  (Appendix VII) and the difference reached significant level (Appendix VIII).

There was a significant difference between the leaf area ratio of the two cultivars. Cobham had a higher leaf area ratio for all the five P treatments throughout the experiment than Webb's.

TABLE V

EFFECT OF CULTIVAR ON NET ASSIMILATION RATE

Cultivar	Cobham	Webb's
N.A.R. (g/dm <sup>2</sup> /day)	.05023	.06395

TABLE VI

EFFECT OF LEVELS OF PHOSPHORUS AND HARVEST DATE ON NET ASSIMILATION RATE (g/dm<sup>2</sup>/DAY)

Treatment	Days from sowing									Treatment mean
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63	63-70	
P <sub>1</sub>	.1320	.1019	.0826	.1005	.0677	.0528	.0566	.0096	-.0024	.0668
P <sub>2</sub>	.1175	.0908	.1246	.0825	.0477	.0231	.0249	.0201	.0234	.0616
P <sub>3</sub>	.1381	.1045	.1112	.0543	.0287	.0349	.0079	.0198	.0152	.0572
P <sub>4</sub>	.1218	.0996	.0963	.0477	.0275	.0189	.0095	.0252	.0093	.0506
P <sub>5</sub>	.1220	.0991	.0931	.0475	.0201	.0245	.0106	.0146	.0119	.0493
Interval mean	.1263	.0992	.1016	.0665	.0383	.0307	.0219	.0179	.0115	

Once again, there was a marked time trend and for Cobham leaf area ratio increased with age, in the case of  $P_1$  and  $P_2$ , up to 42 days and then decreased for the remaining period of the experiment. For  $P_3$ ,  $P_4$  and  $P_5$ , the peaks occurred in the 56 days after emergence. A similar pattern was observed in Webb's.

The interactions between harvest and P treatments and between P treatments and cultivars were also significant and are presented in Tables VII and VIII respectively.

#### F. TOTAL LEAF AREA

The estimates of leaf area per plant at each harvest are presented in Appendix IX and shown in Figures 3A and B. These indicate that the leaf area per plant increased with increasing P supply. In all the treatments, the increase in leaf area per plant tended to follow the logistic pattern. It is doubtful whether the falling off in leaf area in the last harvest from  $P_3$  to  $P_5$  was a true indication of the growth patterns of the two cultivars, since both had rotted leaves under higher P supply.

Throughout the experiment, Cobham had a larger leaf area per plant than Webb's for all the treatments. Discrepancies towards the end of the experiments was due to more severe rotting of the leaves of Cobham compared to Webb's.

TABLE VII

EFFECT OF LEVELS OF PHOSPHORUS AND HARVEST DATE ON LEAF AREA RATIO ( $\text{dm}^2/\text{g}$ )

Treatment	Days from sowing								Treatment mean	
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63		63-70
P <sub>1</sub>	1.52	1.43	2.36	2.25	2.26	2.00	1.95	1.62	1.66	1.83
P <sub>2</sub>	1.75	1.88	2.05	2.49	2.89	2.77	2.29	2.38	2.63	2.35
P <sub>3</sub>	1.69	2.36	2.77	3.32	4.09	3.87	4.17	3.68	3.36	3.26
P <sub>4</sub>	1.91	2.89	3.10	3.74	4.44	4.56	5.01	4.08	3.65	3.71
P <sub>5</sub>	2.04	2.97	2.81	3.36	4.92	3.90	5.05	4.63	3.38	3.67
Interval mean	1.78	2.31	2.62	3.03	3.72	3.42	3.69	3.28	2.94	

TABLE VIII

EFFECT OF LEVELS OF PHOSPHORUS AND CULTIVAR ON  
LEAF AREA RATIO (dm<sup>2</sup>/g)

Treatment	Cultivar		Treatment mean
	Cobham	Webb's	
P <sub>1</sub>	2.00	1.66	1.83
P <sub>2</sub>	2.45	2.24	2.35
P <sub>3</sub>	3.51	3.01	3.26
P <sub>4</sub>	4.24	3.18	3.71
P <sub>5</sub>	4.28	3.06	3.67
Cultivar mean	3.30	2.63	

$\text{Log}_e$  leaf area ( $\text{cm}^2$ )/plant

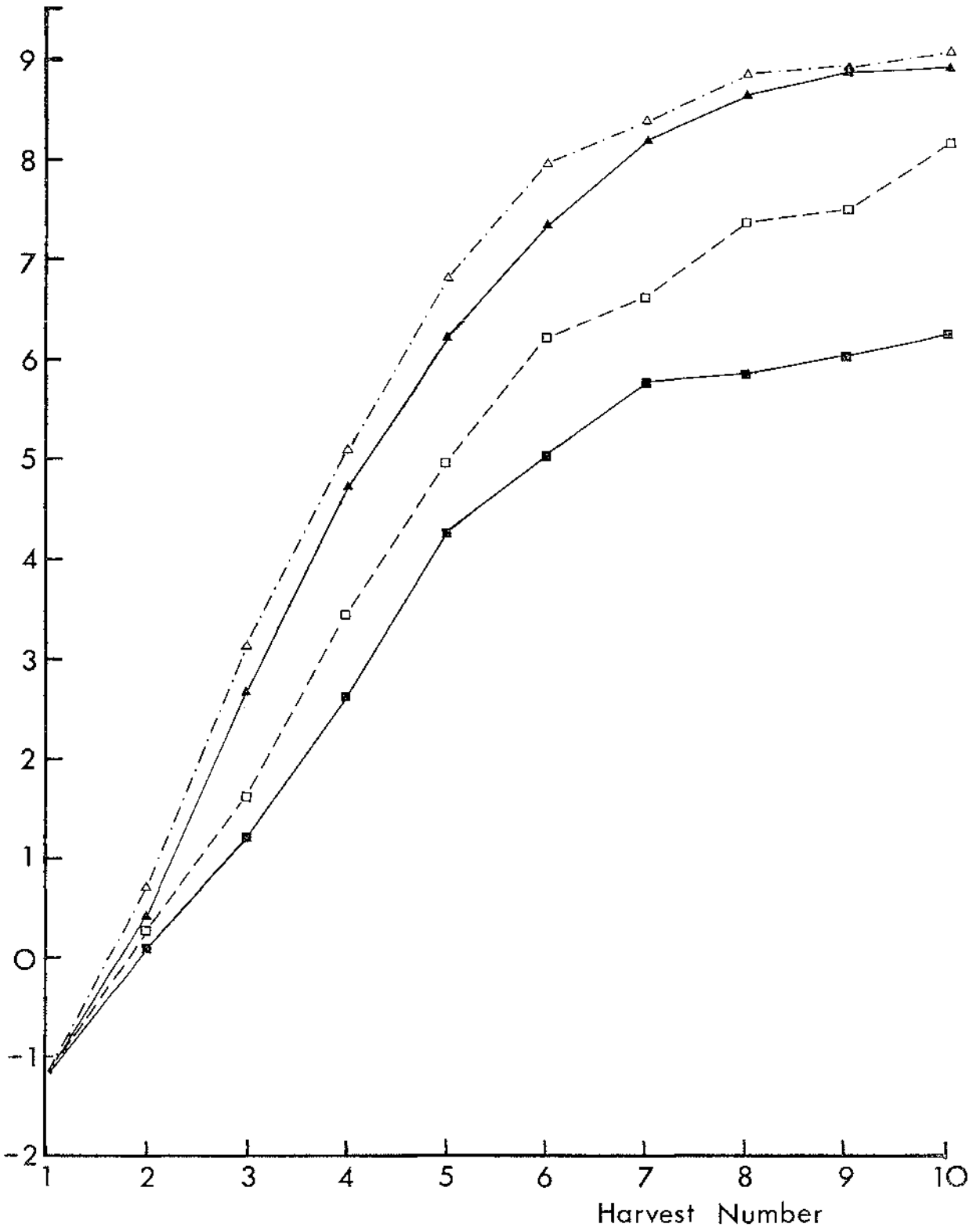


Fig. 3A. The effect of phosphorus fertilizer on leaf area per plant of Cobham Green.

■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

$\text{Log}_e$  leaf area( $\text{cm}^2$ )/plant

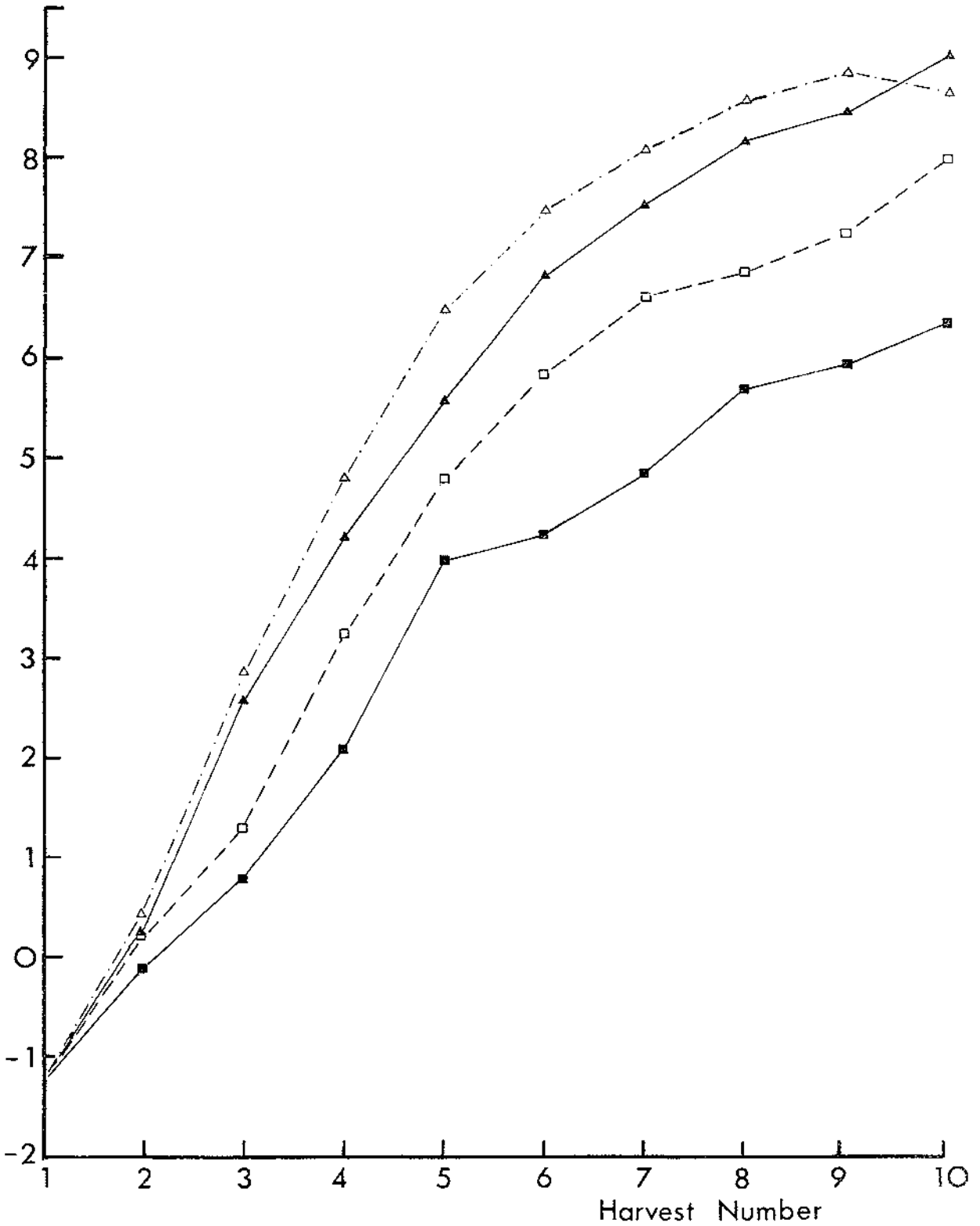


Fig. 3B. The effect of phosphorus fertilizer on leaf area per plant of Webb's Wonderful.  
■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

#### G. GROUND COVER

The data for the mean ground cover per plant for Cobham and Webb's are presented in Appendix X.

In general, the ground cover per plant for both the cultivars increased from  $P_1$  through to  $P_5$  (Figures 4A and B) and increased from the first to the final harvest.

Differences between the two cultivars were apparent with Cobham having higher mean values in all treatments at all harvests except for those under higher P treatments near the end of the experiment.

#### H. LEAF AREA/GROUND COVER RATIO

The data and the statistical analysis are presented in Appendices XI and XII respectively.

Phosphorus treatments reached significant level with higher P supply having higher leaf area/ground cover ratio, while Cobham had significantly higher ratio than Webb's in all the treatments.

There was a significant harvest effect too with the ratio increased throughout the experimental period. Two harvest interactions with fertilizer and cultivar were also highly significant (Tables IX and X). In addition, fertilizer and cultivar interactions also reached significant level (Table XI).

$\text{Log}_e$  ground cover( $\text{cm}^2$ )/plant

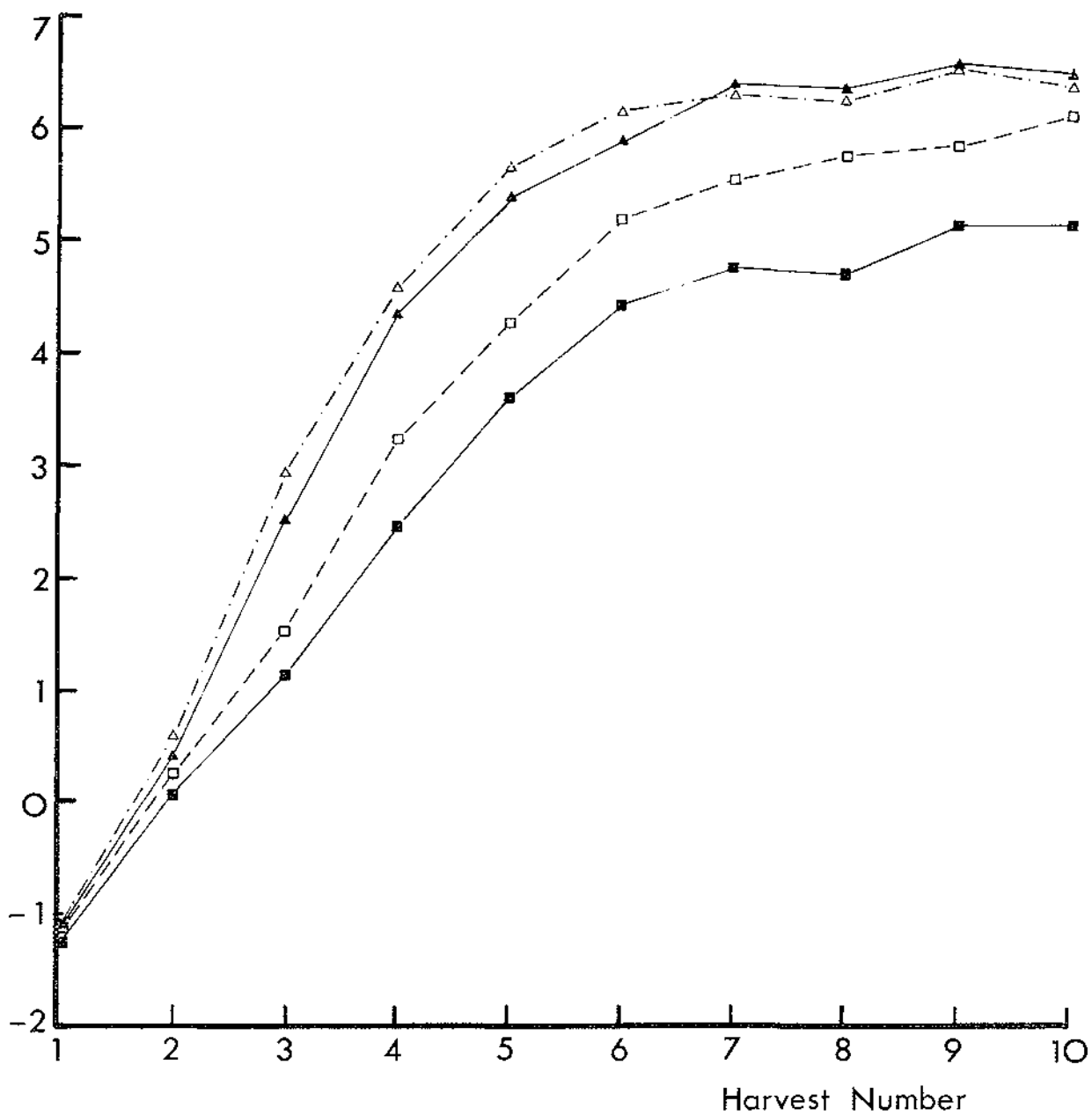


Fig. 4A. The effect of phosphorus fertilizer on ground cover per plant of Cobham Green.  
■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

$\text{Log}_e$  ground cover( $\text{cm}^2$ )/plant

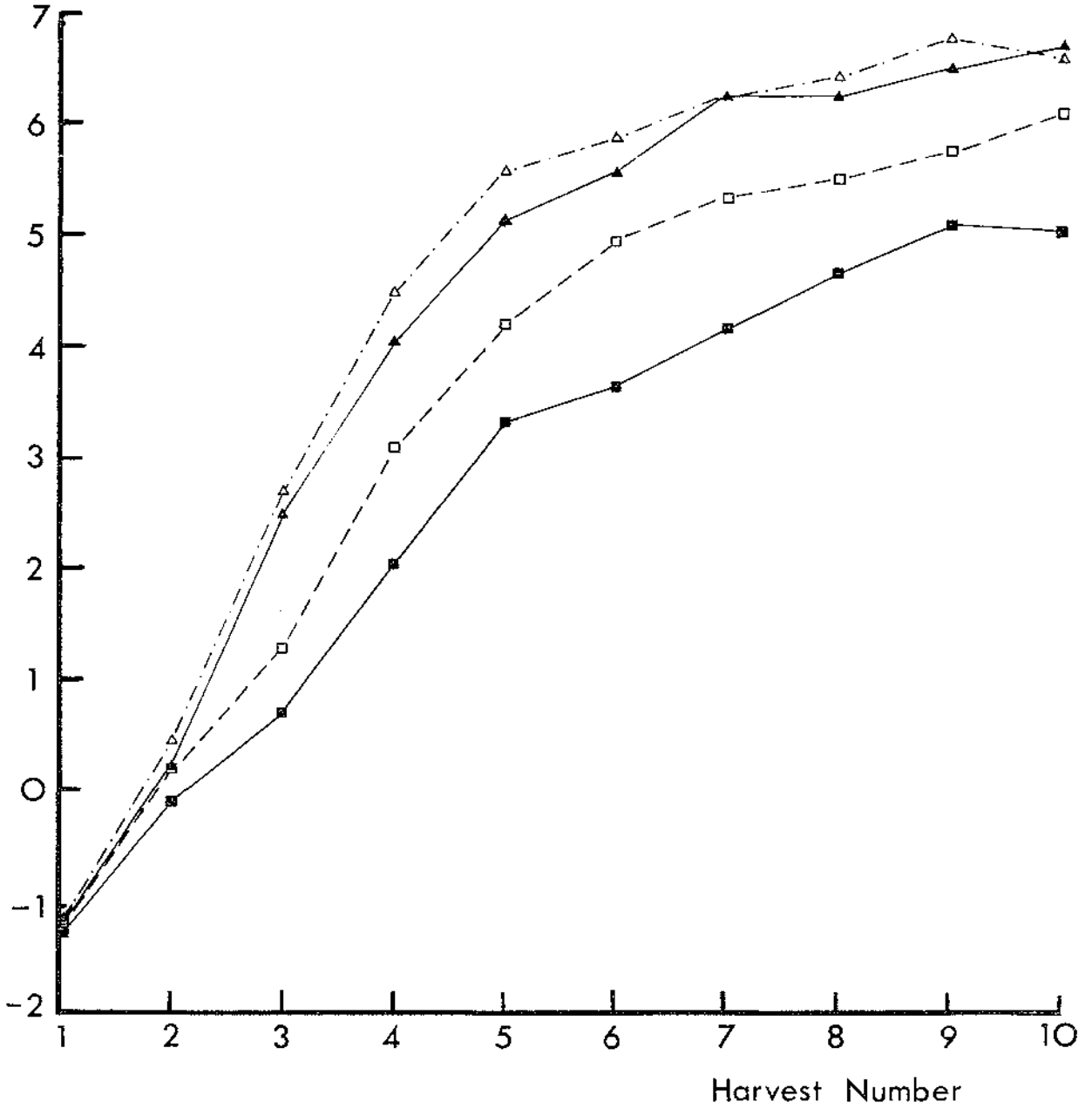


Fig. 4B. The effect of phosphorus fertilizer on ground cover per plant of Webb's Wonderful.  
■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

TABLE IX

EFFECT OF LEVELS OF PHOSPHORUS AND HARVEST DATE ON LEAF AREA/GROUND COVER RATIO

Treatment	2	3	4	Harvest number		7	8	9	10	Treatment mean
				5	6					
P <sub>1</sub>	1.00	1.05	1.11	1.96	1.80	2.37	3.12	2.45	3.37	1.82
P <sub>2</sub>	1.00	1.05	1.20	1.95	2.51	3.18	4.41	4.85	7.29	2.74
P <sub>3</sub>	1.01	1.11	1.30	2.28	3.93	4.90	8.52	8.79	10.77	4.26
P <sub>4</sub>	1.02	1.15	1.70	2.94	5.51	7.15	11.60	9.13	11.84	5.20
P <sub>5</sub>	1.02	1.18	1.52	3.36	5.48	6.41	11.95	10.20	12.99	5.41
Harvest mean	1.01	1.11	1.37	2.50	3.85	4.80	7.92	7.08	9.25	

TABLE X

EFFECT OF HARVEST DATE AND CULTIVAR ON LEAF  
AREA/GROUND COVER RATIO

Harvest number	Cultivar		Harvest mean
	Cobham	Webb's	
2	1.01	1.01	1.01
3	1.12	1.10	1.10
4	1.42	1.31	1.36
5	2.68	2.31	2.50
6	4.12	3.57	3.85
7	5.27	4.33	4.80
8	8.85	6.99	7.92
9	7.67	6.50	7.08
10	9.99	8.51	9.25
Cultivar mean	4.68	3.96	

TABLE XI

EFFECT OF LEVELS OF PHOSPHORUS AND CULTIVAR ON  
LEAF AREA/GROUND COVER RATIO

Treatment	Cultivar		Treatment mean
	Cobham	Webb's	
P <sub>1</sub>	2.01	2.04	2.03
P <sub>2</sub>	3.17	2.92	3.05
P <sub>3</sub>	5.24	4.23	4.74
P <sub>4</sub>	6.45	5.12	5.79
P <sub>5</sub>	6.53	5.49	6.01
Cultivar mean	4.68	3.96	

## I. CHEMICAL ANALYSES

### 1. Total nitrogen, phosphorus and potassium contents of plants

The values of the analyses for the total N, P and K contents of the entire plants, as per cent of dry weight, are presented in Appendices XIII, XIV and XV respectively and their respective analyses of variance in Appendices XVI, XVII and XVIII.

#### (a) Total nitrogen

Total N fluctuated somewhat throughout the growth of the plant. However, for both Cobham and Webb's there was a tendency for total N to increase from day 7 to day 28 or 35 and then to decrease as the plant approached market maturity under all treatment conditions (Appendix XIII).

The range of total N was from 3.95% to 7.11% for Cobham and from 3.86% to 5.81% for Webb's.

Phosphorus supply significantly increased N content in both cultivars.

Interactions between fertilizer and harvest (Table XII) and between harvest and cultivars (Table XIII) were also significant. These are illustrated in Figures 5 and 6.

TABLE XII

EFFECT OF LEVELS OF PHOSPHORUS AND HARVEST DATE ON TOTAL NITROGEN (% DRY WEIGHT)

Treatment	Harvest number										Treatment mean
	1	2	3	4	5	6	7	8	9	10	
P <sub>1</sub>	4.68	3.96	4.80	5.41	5.78	4.85	4.92	4.02	4.18	5.08	4.77
P <sub>2</sub>	5.58	4.64	5.68	5.52	5.19	5.20	4.85	4.20	4.48	4.88	5.02
P <sub>3</sub>	5.47	4.45	5.09	5.17	5.08	5.33	4.88	4.79	4.31	4.57	4.91
P <sub>4</sub>	5.51	5.00	6.38	5.84	5.38	5.18	5.21	4.84	4.69	4.82	5.29
P <sub>5</sub>	5.60	5.00	6.36	5.46	5.41	5.40	5.19	4.93	4.69	4.75	5.28
Harvest mean	5.37	4.61	5.66	5.48	5.37	5.19	5.01	4.56	4.47	4.82	

TABLE XIII

EFFECT OF LEVELS OF PHOSPHORUS AND CULTIVAR ON TOTAL N  
(% DRY WEIGHT)

Harvest number	Cobham	Cultivar Webb's	Harvest mean
1	4.78	5.95	5.37
2	4.84	4.37	4.61
3	6.23	5.10	5.67
4	5.47	5.49	5.48
5	5.48	5.30	5.39
6	5.14	5.24	5.19
7	5.08	4.94	5.01
8	4.60	4.51	4.56
9	4.68	4.26	4.47
10	5.01	4.63	4.82
Cultivar mean	5.13	4.98	

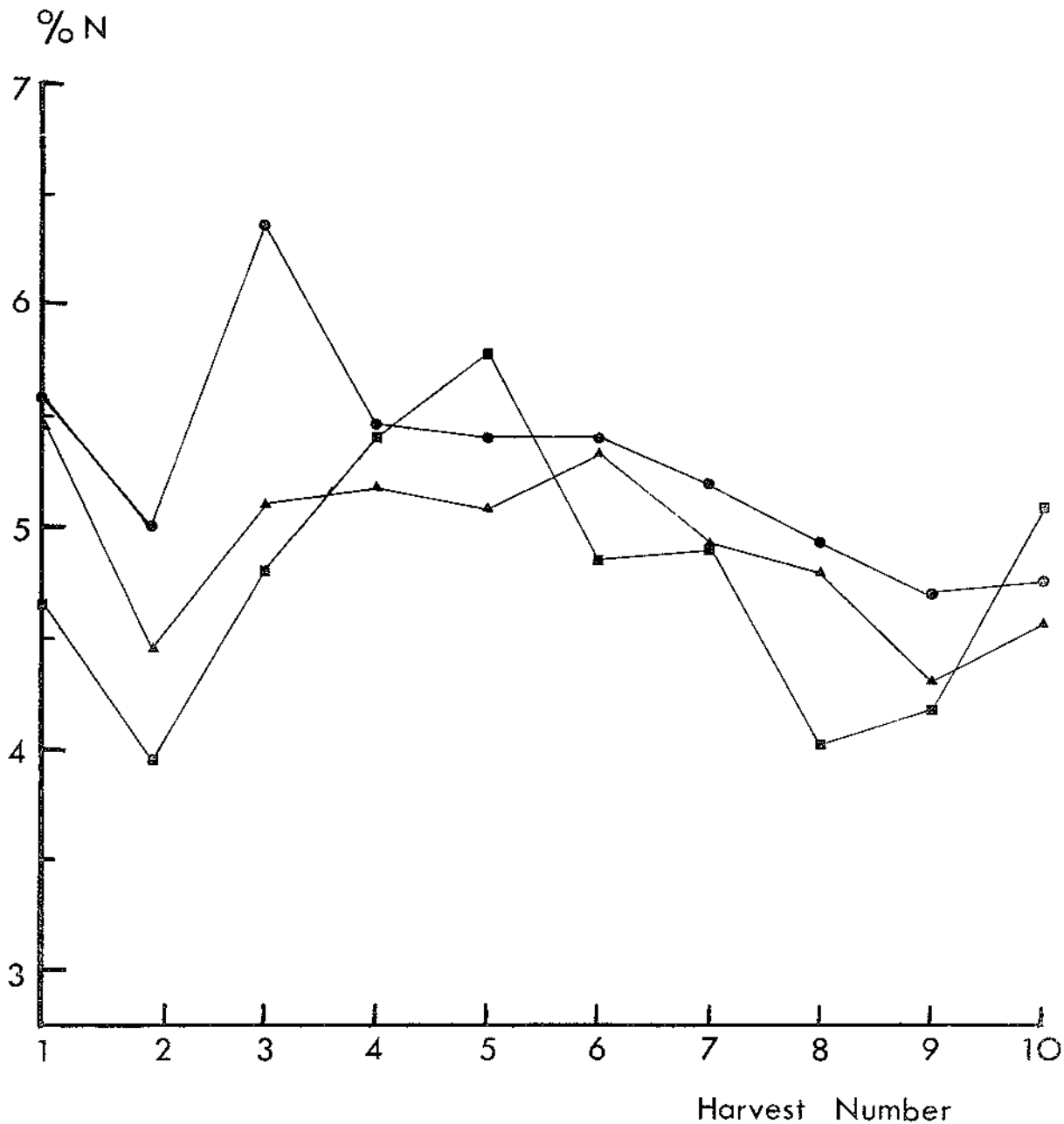


Fig. 5 The effect of phosphorus fertilizer on total plant nitrogen (dry weight basis) for combined Cobham/Webb's. ■—■ : P<sub>1</sub> level, ▲—▲ : P<sub>3</sub> level, ●—● : P<sub>5</sub> level.

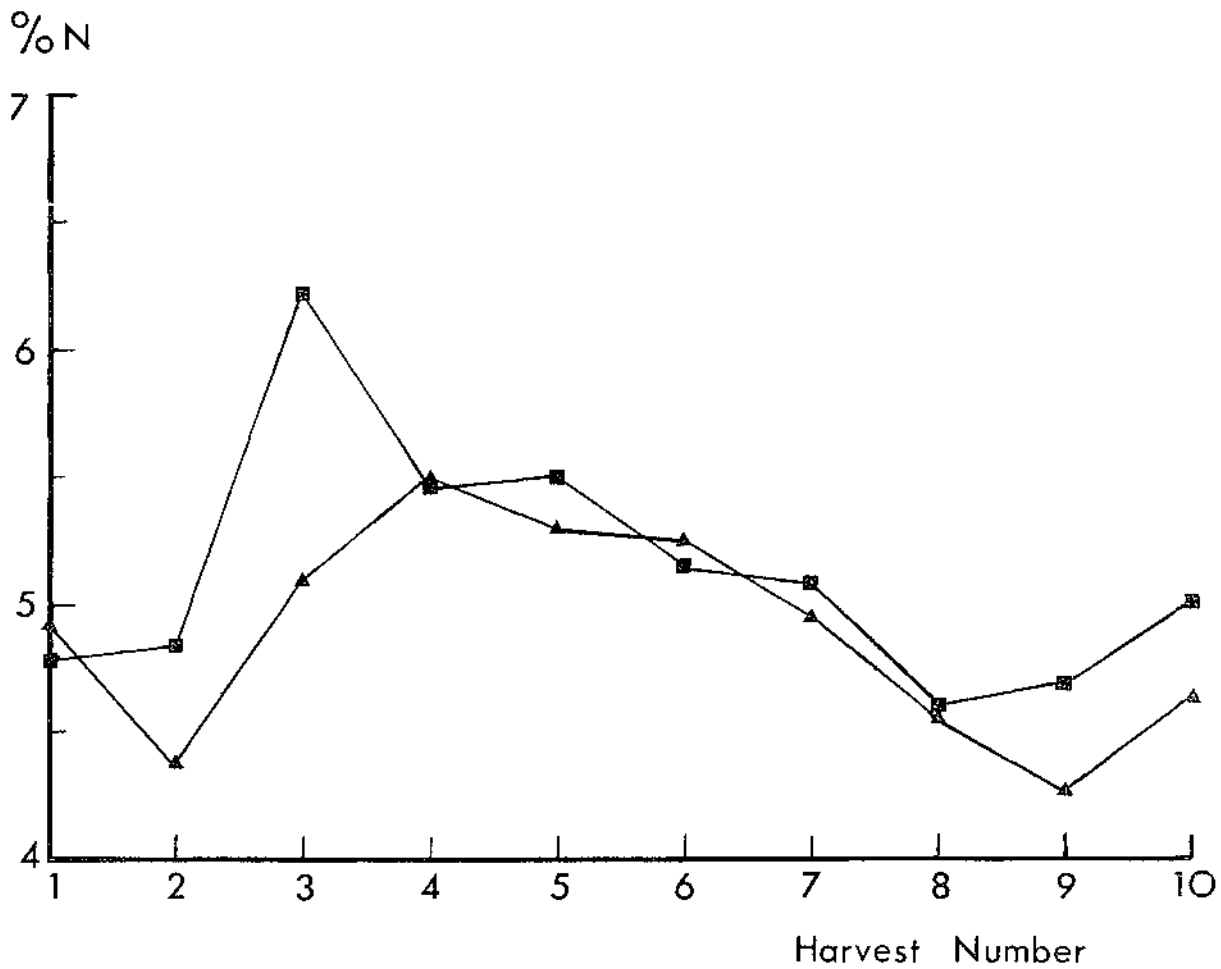


Fig. 6 The effect of phosphorus fertilizer on total plant nitrogen (dry weight basis) of Cobham Green and Webb's Wonderful. ■—■ : Cobham Green, ▲—▲ : Webb's Wonderful.

(b) Total phosphorus

The P content fluctuated throughout the growth in all treatments for both cultivars. However, in  $P_1$  to  $P_3$  treatments, there was a rapid decrease in P content from harvest 1 to 2, then a rise in P content up to harvest 4 (Webb's) or 5 (Cobham) followed by another decline in the content. For  $P_4$  and  $P_5$  treatments, there was a tendency for the P content to increase and then decrease as plants approached market maturity. The P content of the whole plant ranged from a high of 1.17% ( $P_5$ ) to a low of 0.06% ( $P_1$ ) in Cobham and 0.96% ( $P_5$ ) to 0.14% ( $P_1$ ) in Webb's.

The effect of P treatment on P content was highly significant. With few exceptions, both cultivars had their P content increased at least 3-fold from  $P_1$  to  $P_5$  in most harvests. These facts were clearly demonstrated in Figure 7 and in Tables XIV and XV, even though the results of both cultivars were combined regardless of the significant difference between the cultivars.

A significant harvest and cultivar interaction was observed (Figure 8 and Table XVI).

(c) Total potassium

The plant K content throughout the growth of the plant followed a similar course to that of total N. That is, the

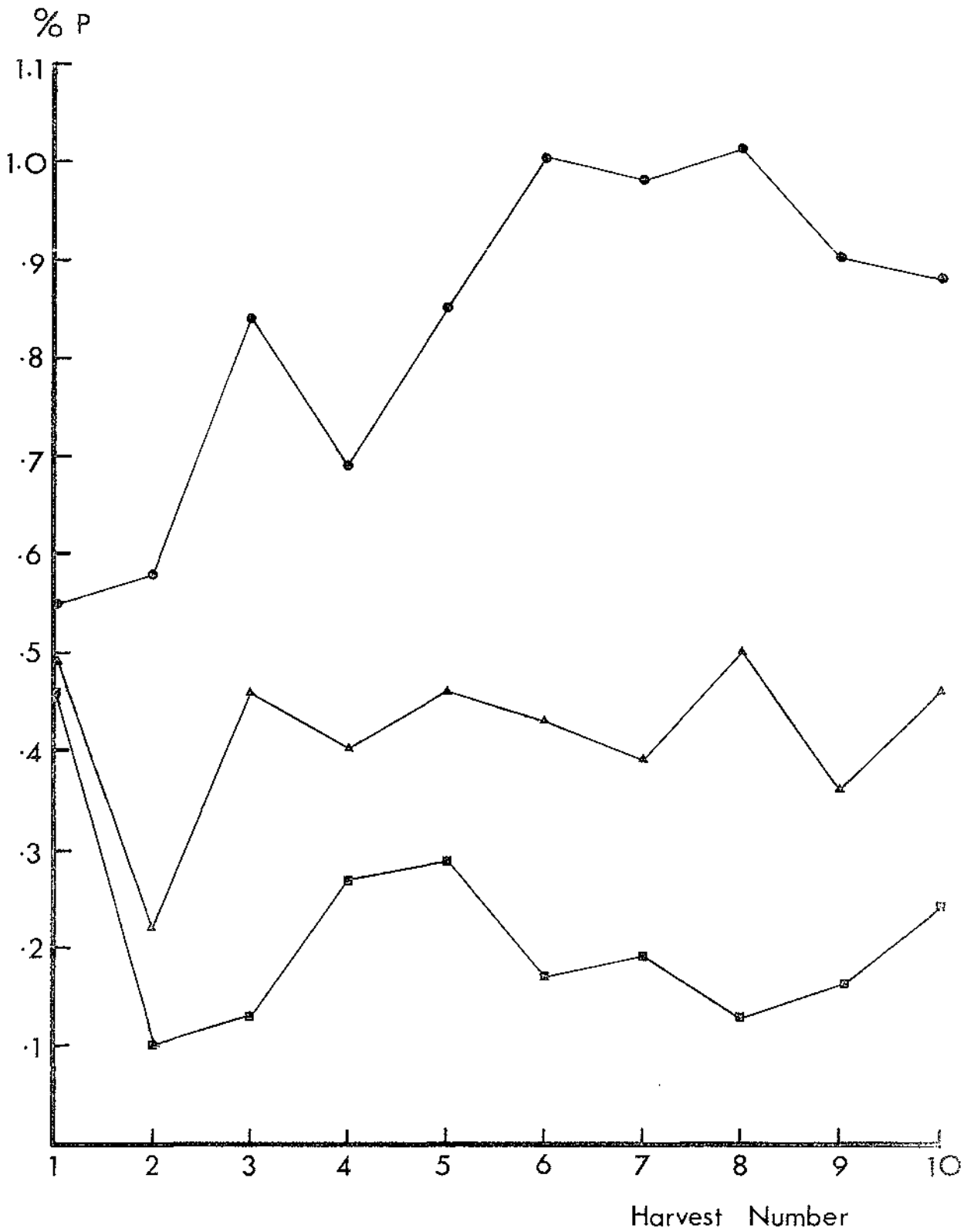


Fig. 7 The effect of phosphorus fertilizer on total plant phosphorus (dry weight basis) for combined Cobham/Webb's. ■—■ : P<sub>1</sub> level, ▲—▲ : P<sub>3</sub> level, ●—● : P<sub>5</sub> level.

TABLE XIV

EFFECT OF LEVELS OF PHOSPHORUS AND HARVEST DATE ON TOTAL PHOSPHORUS (% DRY WEIGHT)

Treatment	Harvest number										Treatment mean
	1	2	3	4	5	6	7	8	9	10	
P <sub>1</sub>	.47	.10	.13	.27	.29	.17	.19	.13	.16	.24	.22
P <sub>2</sub>	.54	.15	.21	.36	.34	.32	.25	.18	.21	.34	.29
P <sub>3</sub>	.50	.22	.46	.40	.46	.43	.39	.50	.36	.46	.42
P <sub>4</sub>	.53	.42	.72	.63	.71	.76	.75	.72	.65	.79	.67
P <sub>5</sub>	.55	.58	.84	.69	.85	1.02	.98	1.01	.90	.88	.83
Harvest mean	.52	.29	.47	.47	.53	.54	.51	.51	.46	.54	

TABLE XV

EFFECT OF LEVELS OF PHOSPHORUS AND CULTIVAR ON  
TOTAL PHOSPHORUS (% DRY WEIGHT)

Treatment	Cultivar		Treatment mean
	Cobham	Webb's	
P <sub>1</sub>	.194	.234	.214
P <sub>2</sub>	.266	.313	.290
P <sub>3</sub>	.447	.384	.416
P <sub>4</sub>	.719	.615	.667
P <sub>5</sub>	.923	.736	.830
Cultivar mean	.510	.456	

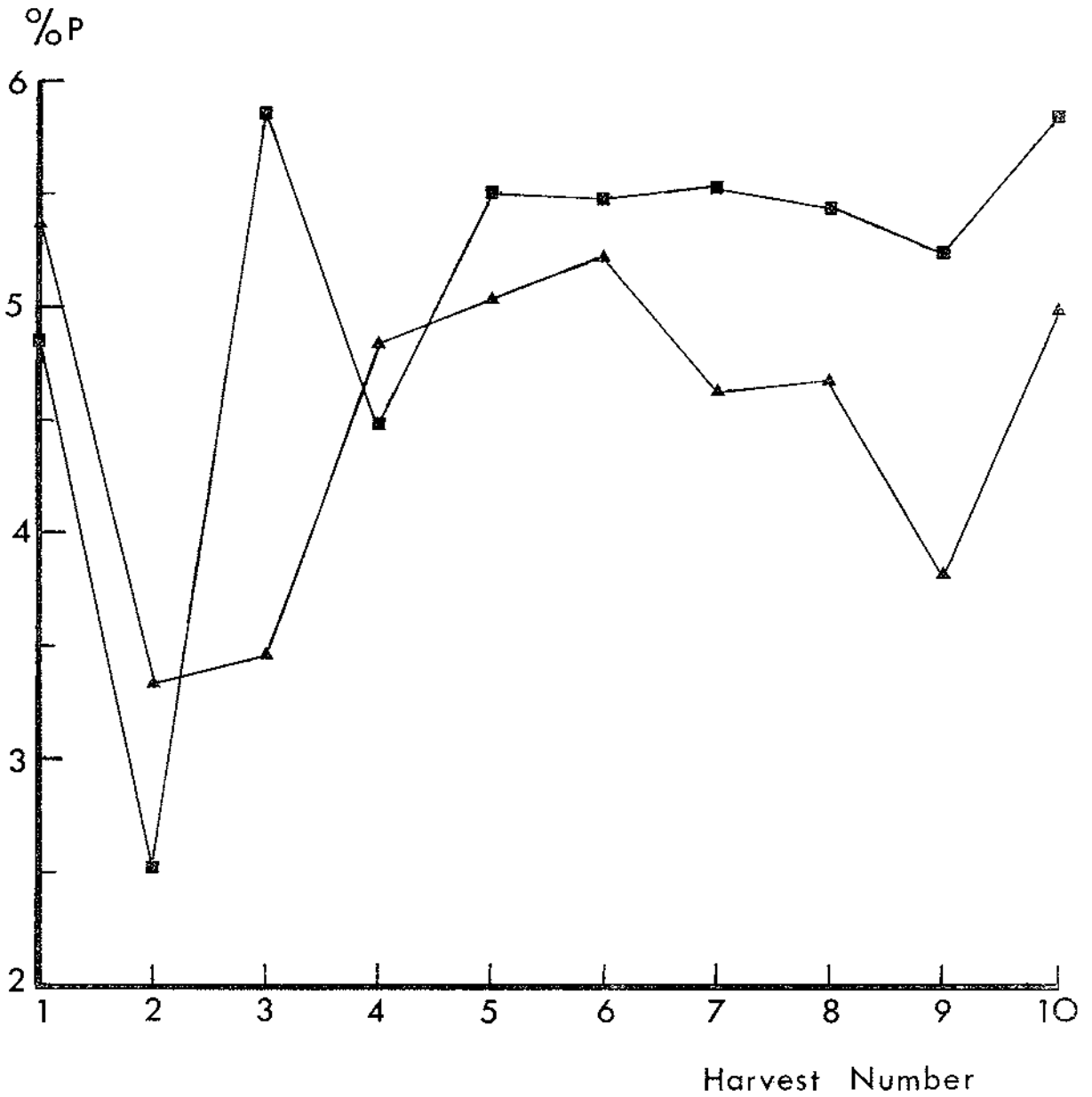


Fig. 8 The effect of phosphorus fertilizer on total plant phosphorus (dry weight basis) of Cobham Green and Webb's Wonderful.  $\blacksquare$ — $\blacksquare$  : Cobham Green,  $\blacktriangle$ — $\blacktriangle$  : Webb's Wonderful.

TABLE XVI

EFFECT OF HARVEST DATE AND CULTIVAR ON TOTAL PHOSPHORUS  
(% DRY WEIGHT)

Harvest number	Cultivar		Harvest mean
	Cobham	Webb's	
1	.489	.546	.518
2	.256	.335	.296
3	.590	.348	.469
4	.451	.486	.469
5	.554	.507	.531
6	.549	.524	.537
7	.554	.464	.509
8	.546	.469	.508
9	.524	.382	.453
10	.585	.499	.542
Cultivar mean	.510	.456	

K content of the tissue increased during the first five weeks of plant growth, thereafter it declined as the plant approached market maturity. The range in the mean K content was from 6.65% to 1.97% in Cobham and a high of 7.18% to a low 1.33% in Webb's.

P supply had a significant effect on the K content of the whole plant.

Three significant interactions are presented in Tables XVII, XVIII and XIX, and illustrated in Figures 9 and 10.

## 2. Nutrient uptake

Figures 11, 12 and 13 show the cumulative N, P and K uptake respectively for the whole plant of the two cultivars of lettuce crop. The mean values of the nutrient uptake by the plant are presented in Appendices XIX, XX and XXI.

### (a) Nitrogen uptake

As can be seen in Figure 11A, N uptake by Cobham was very slow in the early phase of plant growth and then increased more and more to the end of the experiment, particularly in the  $P_3 - P_5$  treatments.

TABLE XVII

EFFECT OF LEVELS OF PHOSPHORUS AND HARVEST DATE ON TOTAL POTASSIUM (% DRY WEIGHT)

Treatment	Harvest number										Treatment mean
	1	2	3	4	5	6	7	8	9	10	
P <sub>1</sub>	1.82	3.50	3.21	5.07	6.23	5.62	5.14	4.23	4.12	4.52	4.35
P <sub>2</sub>	2.35	4.26	5.12	5.89	6.31	5.95	5.78	4.60	4.69	5.36	5.03
P <sub>3</sub>	2.06	4.20	7.13	5.69	6.80	5.78	5.40	5.06	4.76	4.69	5.16
P <sub>4</sub>	1.83	4.59	6.89	5.73	6.46	5.41	5.06	4.91	4.23	4.73	4.98
P <sub>5</sub>	1.93	4.58	7.85	5.34	5.68	5.69	4.66	4.60	4.38	4.23	4.89
Harvest mean	2.00	4.23	6.04	5.54	6.30	5.69	5.21	4.68	4.44	4.71	

TABLE XVIII

EFFECT OF HARVEST DATE AND CULTIVAR ON TOTAL POTASSIUM  
(% DRY WEIGHT)

Harvest number	Cultivar		Harvest mean
	Cobham	Webb's	
1	2.26	1.73	2.00
2	4.54	3.91	4.23
3	6.50	5.58	6.04
4	5.52	5.56	5.54
5	6.16	6.44	6.30
6	5.45	5.93	5.69
7	5.08	5.33	5.21
8	4.69	4.67	4.68
9	4.46	4.41	4.44
10	4.72	4.70	4.71
Cultivar mean	4.94	4.83	

TABLE XIX

EFFECT OF LEVELS OF PHOSPHORUS AND CULTIVAR ON TOTAL  
POTASSIUM (% DRY WEIGHT)

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Treatment	Cultivar		Treatment mean
	Cobham	Webb's	
P <sub>1</sub>	4.34	4.35	4.35
P <sub>2</sub>	4.95	5.11	5.03
P <sub>3</sub>	5.12	5.19	5.16
P <sub>4</sub>	5.15	4.82	4.99
P <sub>5</sub>	5.13	4.66	4.90

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Cultivar mean	4.94	4.83	
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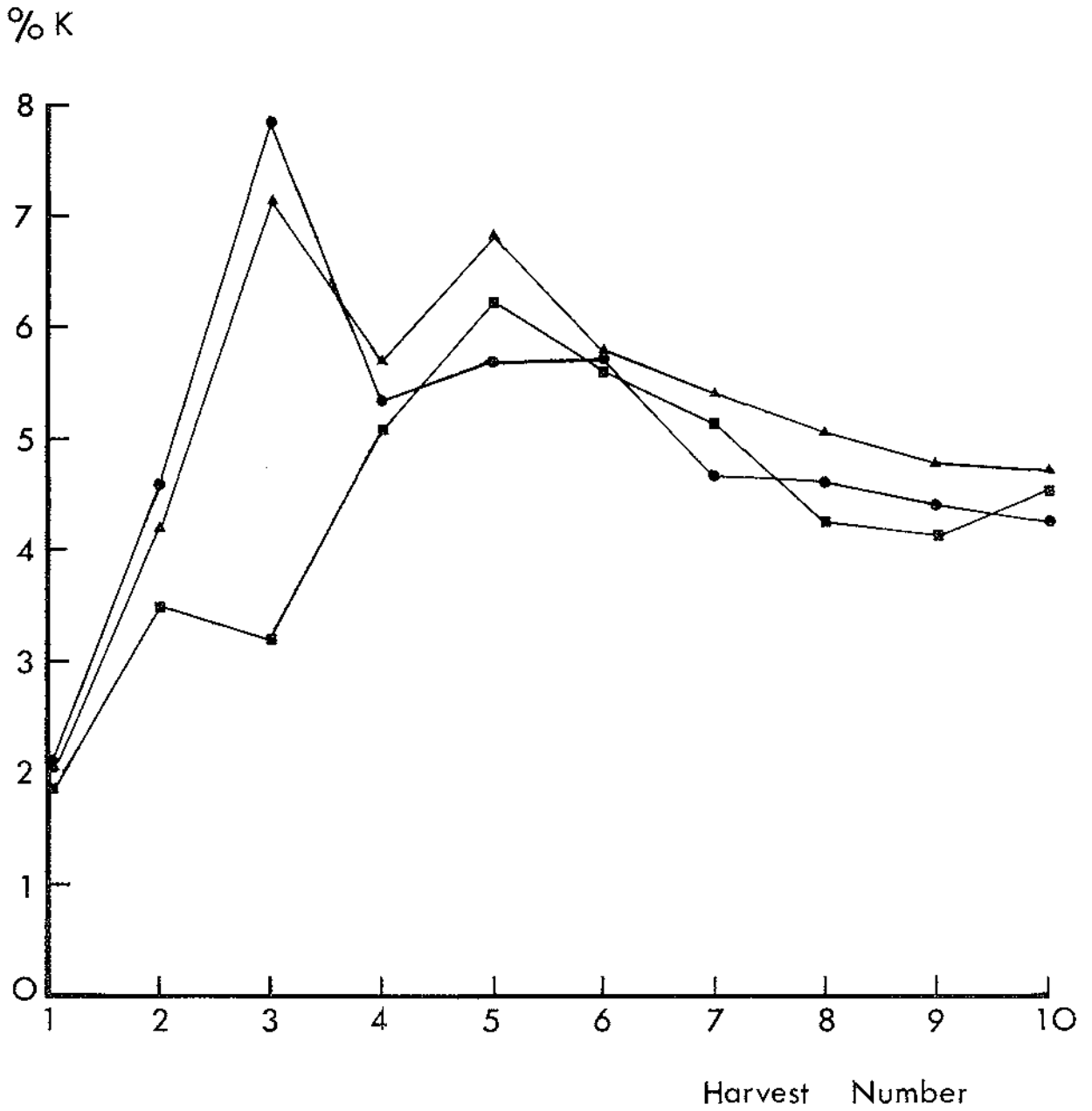


Fig. 9 The effect of phosphorus fertilizer on total plant potassium (dry weight basis) for combined Cobham/Webb's. ■—■ : P<sub>1</sub> level, ▲—▲ : P<sub>3</sub> level, ●—● : P<sub>5</sub> level.

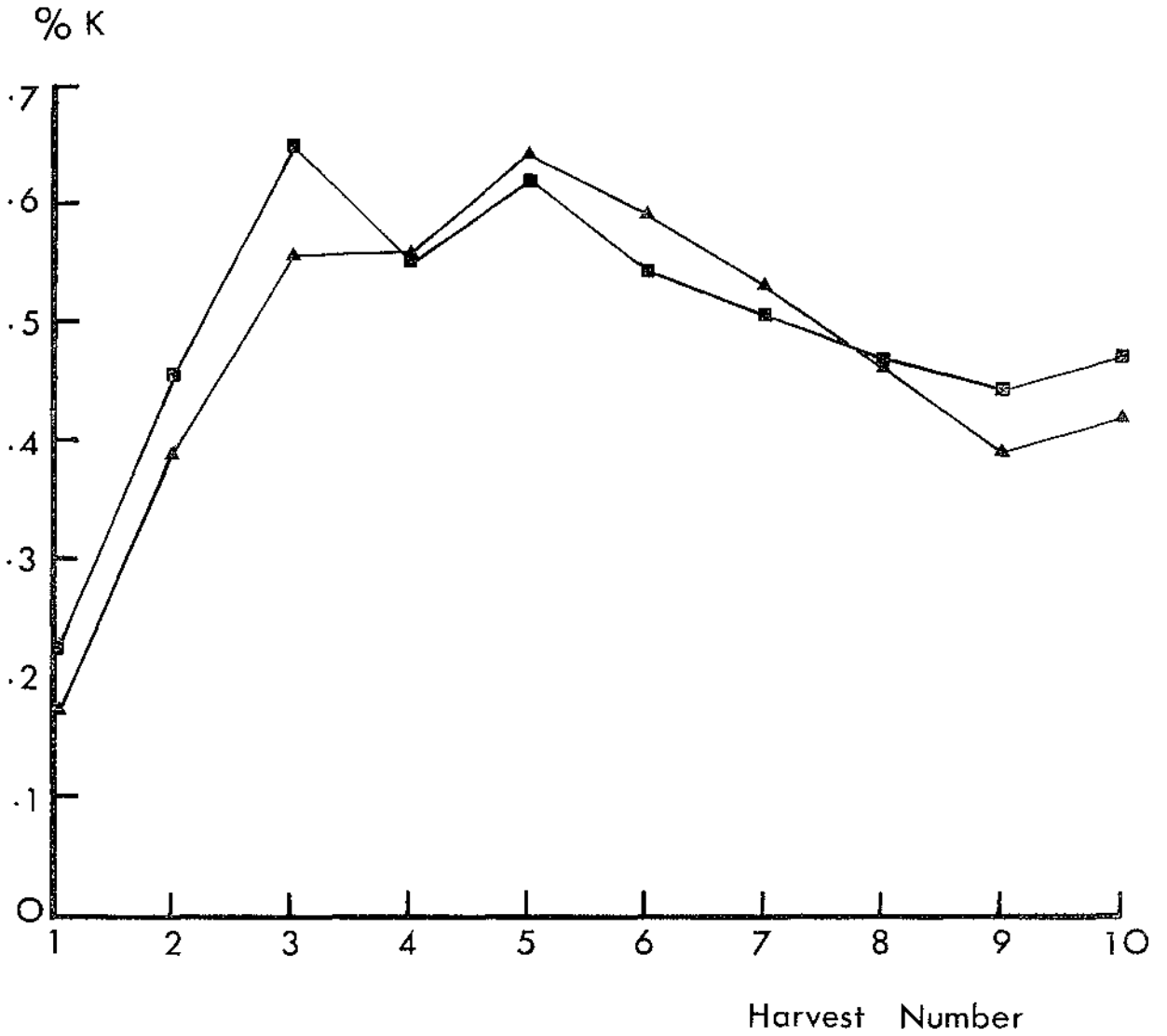


Fig. 10 The effect of phosphorus fertilizer on total plant potassium (dry weight basis) of Cobham Green and Webb's Wonderful. ■—■ : Cobham Green, ▲—▲ : Webb's Wonderful.

$\text{Log}_e$  N uptake (mg) / plant

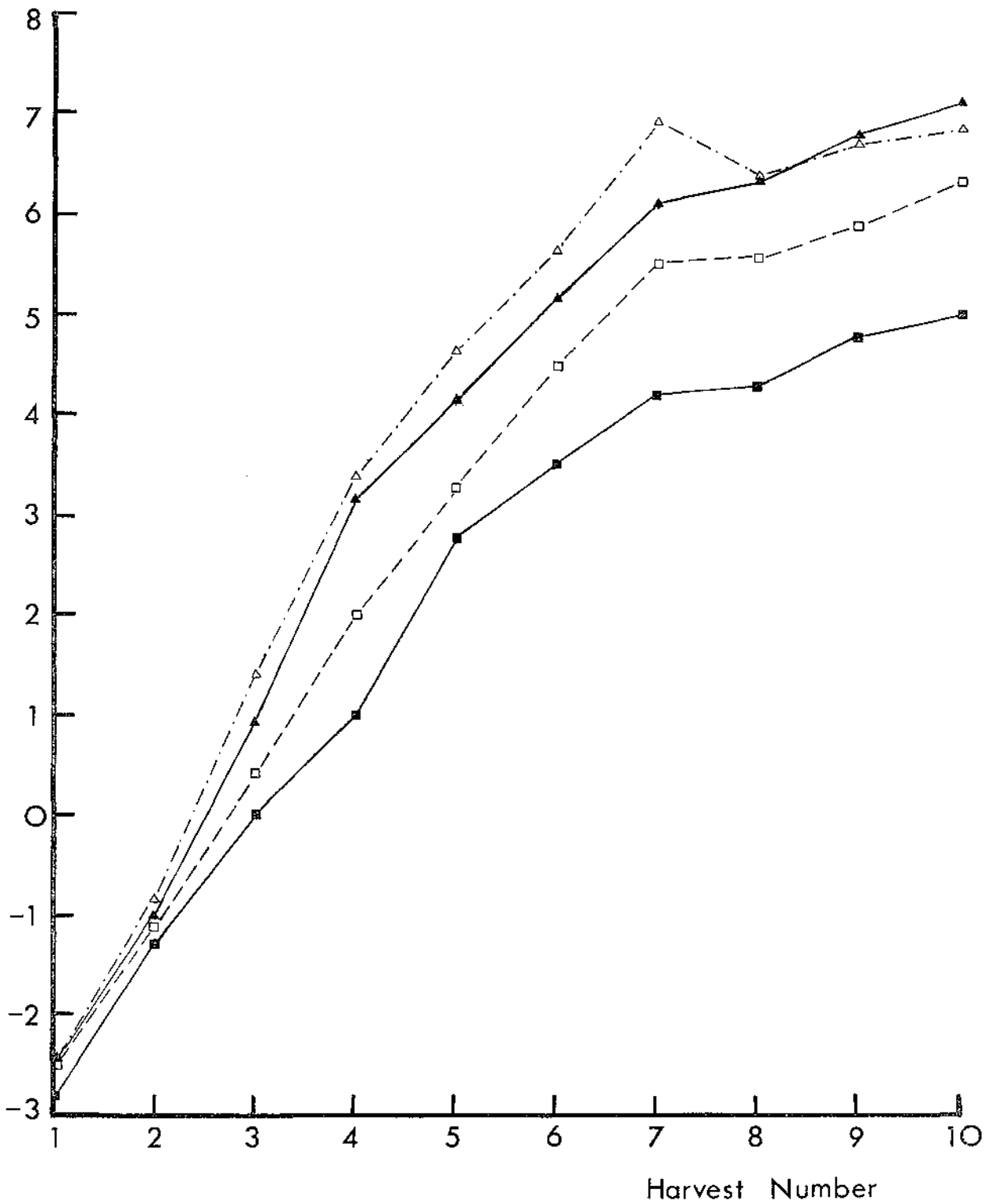


Fig. 11A. The effect of phosphorus fertilizer on nitrogen uptake by Cobham Green.

■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

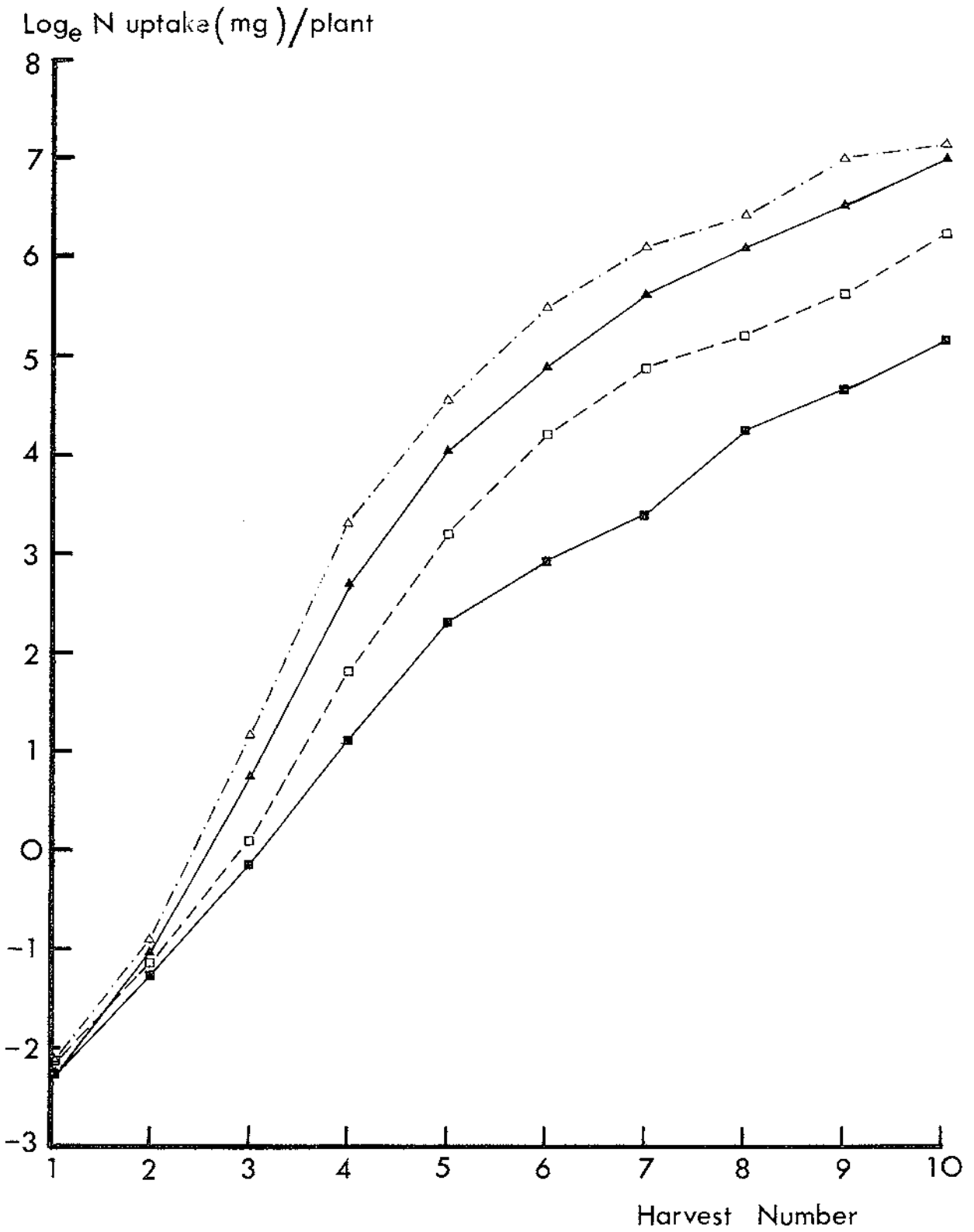


Fig. 11B. The effect of phosphorus fertilizer on nitrogen uptake by Webb's Wonderful.  
 ■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

$\text{Log}_e$  P uptake (mg)/plant

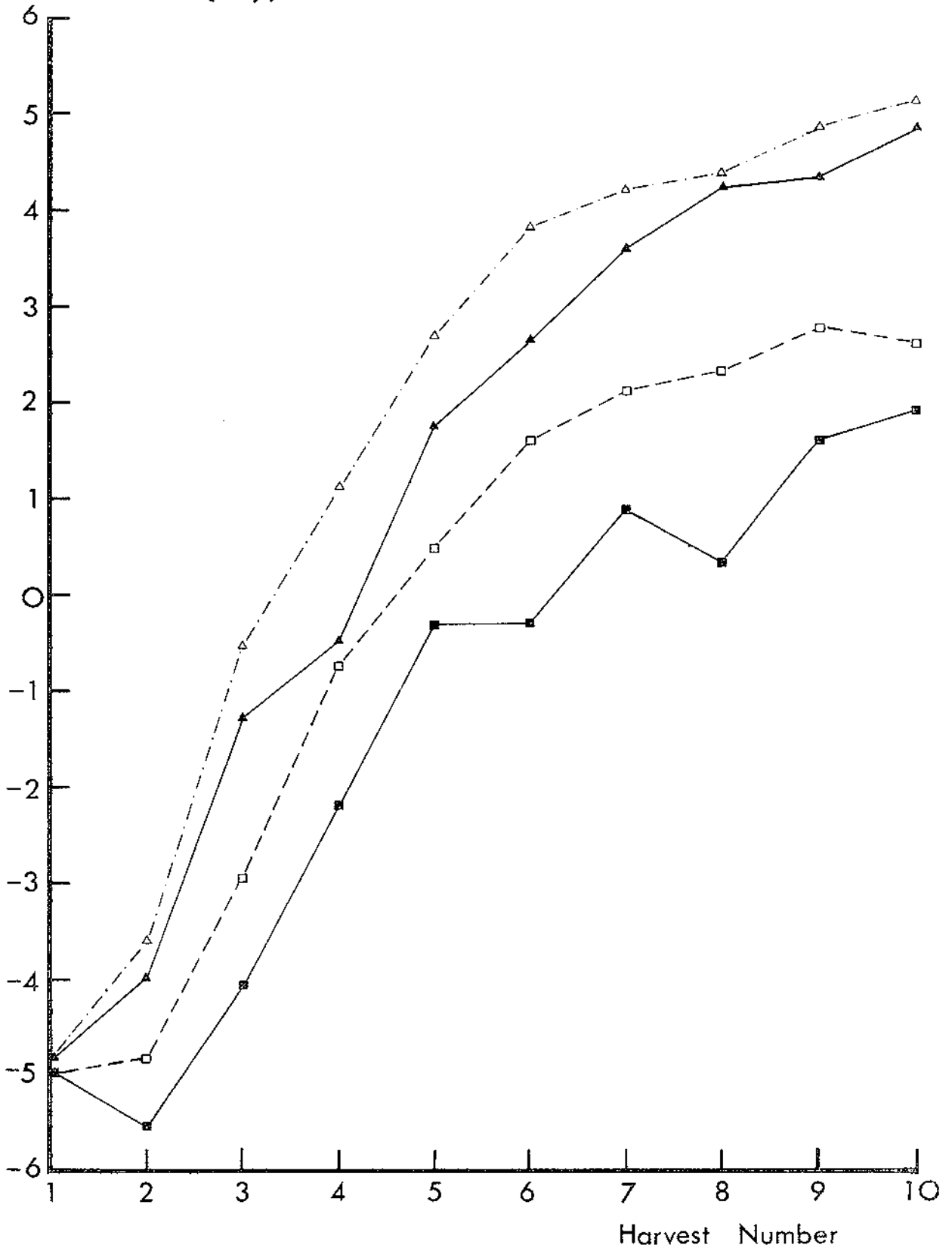


Fig. 12A. The effect of phosphorus fertilizer on phosphorus uptake by Cobham Green.  
■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

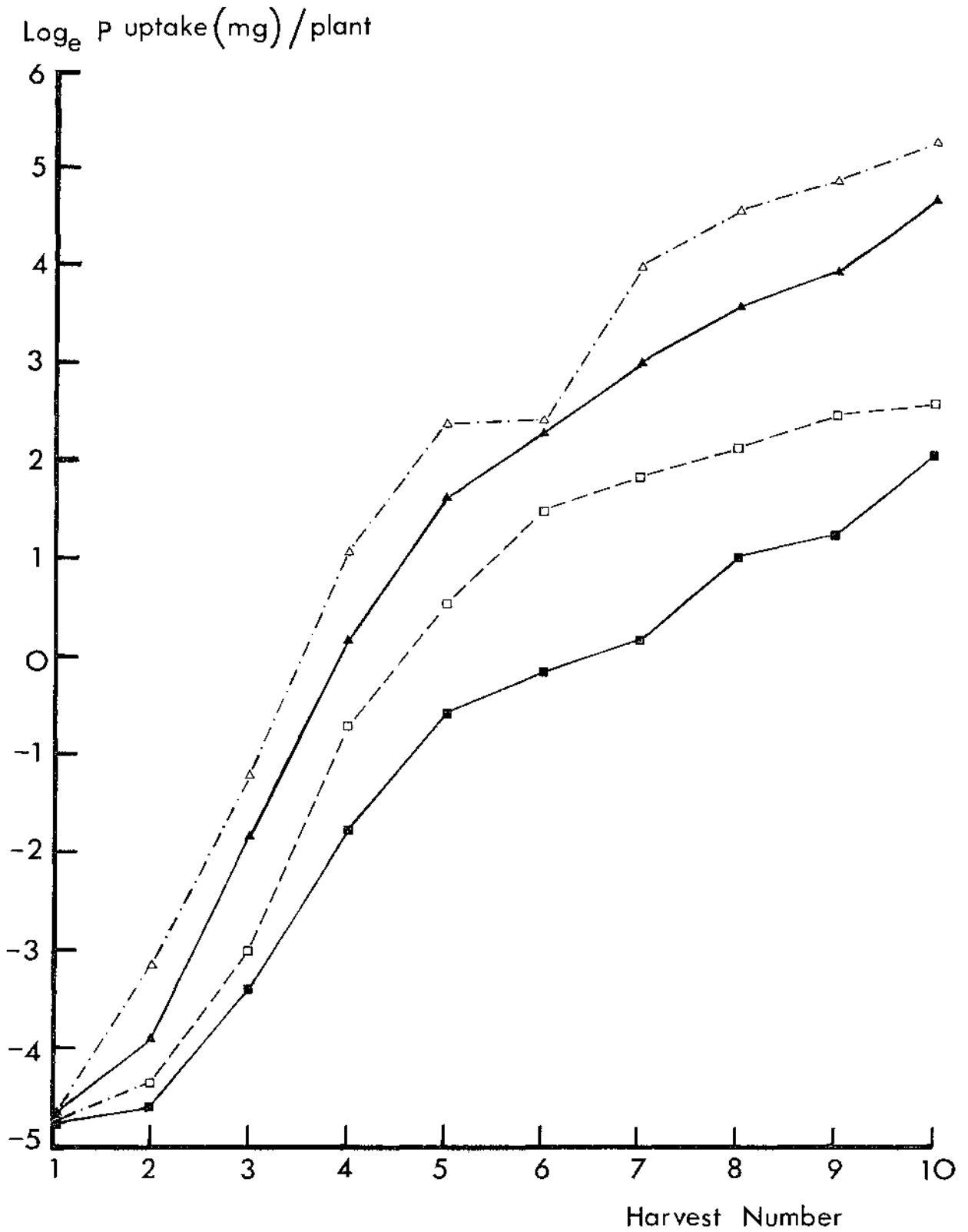


Fig. 12B. The effect of phosphorus fertilizer on phosphorus uptake by Webb's Wonderful.  
 ■ : P<sub>1</sub> level, □ : P<sub>2</sub> level, ▲ : P<sub>3</sub> level, △ : P<sub>4</sub> level.

From 63 days onwards, plants of the P<sub>3</sub> treatment accumulated more than the P<sub>4</sub> and P<sub>5</sub> treated plants. Even then the amount of N taken by the P<sub>5</sub> plants at 70 days was seven times more than that absorbed by the P<sub>1</sub> plants. The P<sub>3</sub> plants at 70 days had absorbed 8 times the amount of Nitrogen than absorbed by the P<sub>1</sub> plants.

In all treatments, the amount of N absorbed during the last three harvests was over 70 per cent of the total amount of N accumulated throughout the growth period.

Similar results were obtained for Webb's except that plants of the higher P supply accumulated higher amounts of N at all stages of growth (Figure 11B). For instance, at 70 days, the N uptake by P<sub>1</sub> plants was one-sixth of that of P<sub>3</sub> plants but only one-ninth of that of P<sub>5</sub> plants but only one-ninth of that of P<sub>5</sub> plants.

Webb's also tended to absorb more N during the last three harvesting periods than Cobham for they accumulated more than 80 per cent of their total N accumulated throughout the growth period.

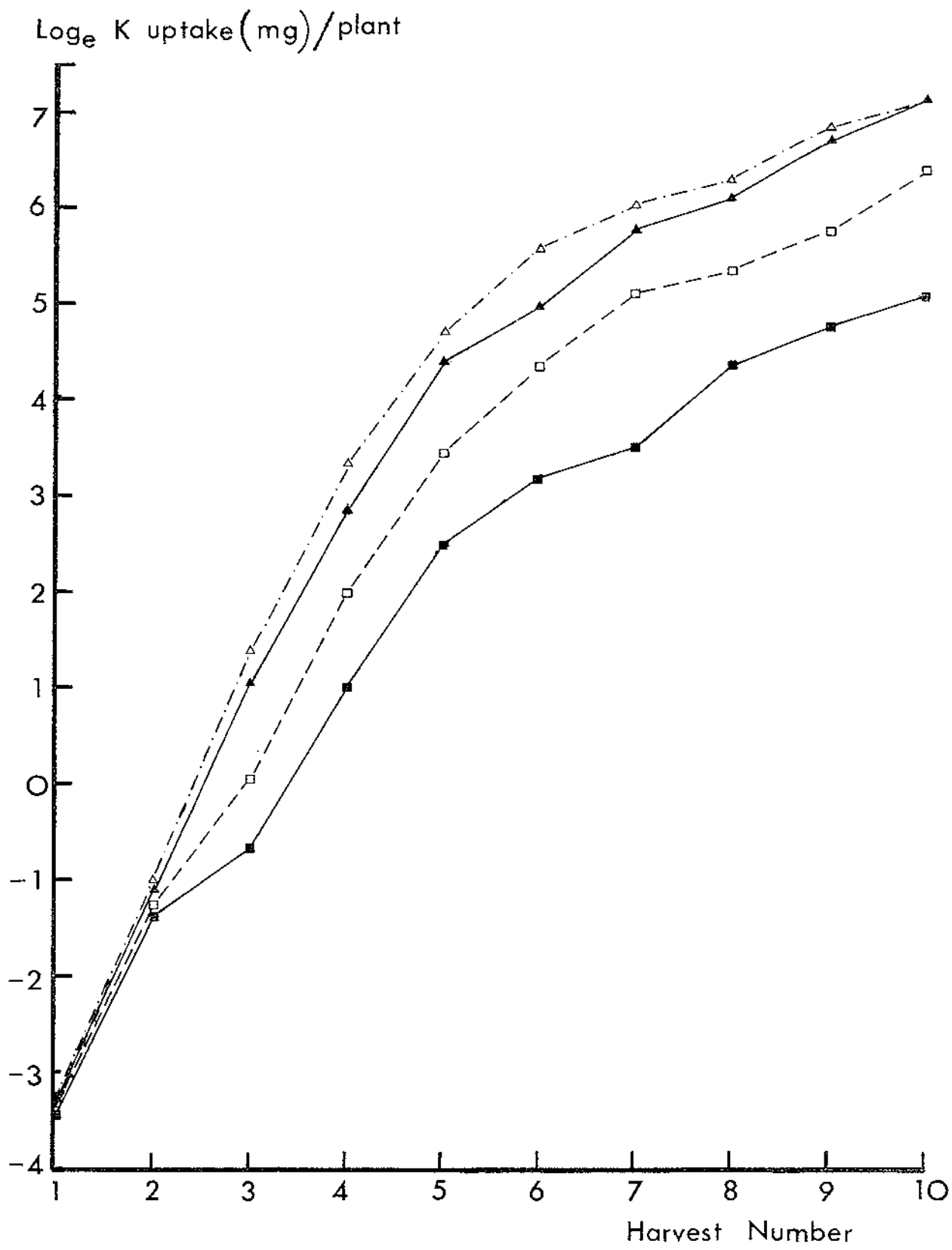


Fig. 13A. The effect of phosphorus fertilizer on potassium uptake by Cobham Green.  
 ■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

(b) Phosphorus uptake

The course of P uptake with five different levels of P supply is shown in Figure 12A. For the first 7 days, P uptake figures in all the treatments were the same, suggesting that plants were using the P in the seeds for their growth. For the next 7 days, the plants receiving low P supply ( $P_1$  and  $P_2$ ) appeared to be dependent on the seed for P, while plants of  $P_3 - P_5$  treatments began to utilize the larger amounts of P available in the medium. Thereafter, all plants absorbed increasingly more P right up to the end of the experiment. Throughout the various stages of growth, the amount of P taken up by the plants increased with increasing P supply.

Similar results were obtained for Webb's (Figure 12B).

From 56-70 days, Cobham absorbed more than 70 per cent of the total P accumulated by plant throughout the growth period. Once again, Webb's had a higher figure of 80 per cent for the same period.

(c) Potassium uptake

The curves for K uptake as affected by different levels of P supply is shown in Figure 13A. The uptake of K was very

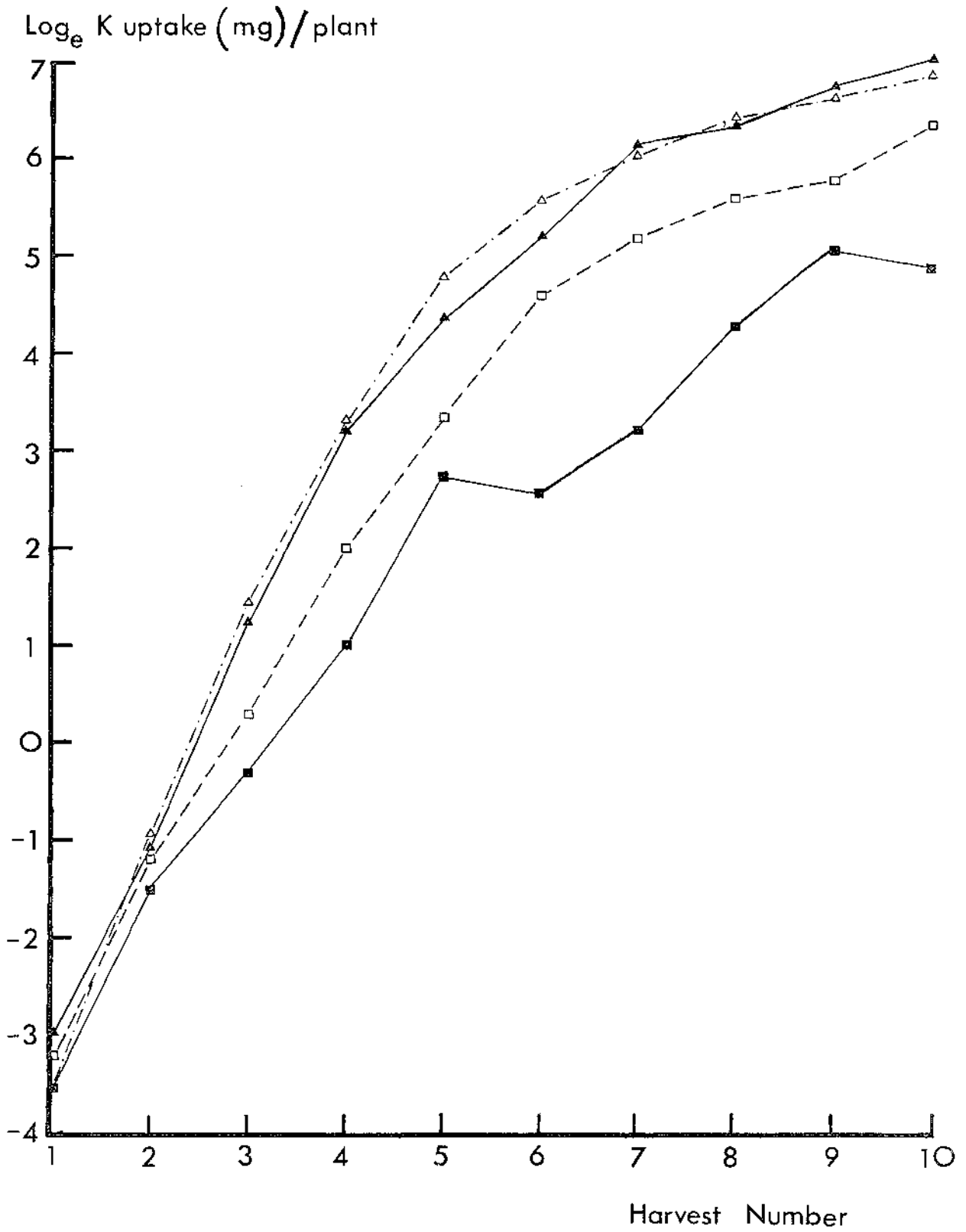


Fig. 13B. The effect of phosphorus fertilizer on potassium uptake by Webb's Wonderful.  
 ■—■ : P<sub>1</sub> level, □—□ : P<sub>2</sub> level, ▲—▲ : P<sub>3</sub> level, △—△ : P<sub>4</sub> level.

slow during the early phase of plant growth, but rapid increase in uptake was soon followed especially in those plants receiving higher P supply.

Similar results were obtained for Webb's (Figure 13B).

During 56-70 days, in excess of 70 per cent of K was absorbed by Cobham, while Webb's had a higher figure of over 80 per cent for the same period.

## CHAPTER V

### DISCUSSION

The accumulation of total plant dry matter by lettuce from the time of emergence until final harvest appeared to be logistic. Initially the increase in dry weight per plant was exponential, but the period of major increase in dry weight was, during the last twenty-one days of the experiment, when in excess of 70 per cent of dry weight was produced, thus confirming the results of Zink and Yamaguchi (1962). Leaf area also followed a logistic pattern. According to Bensink (1971) and Zink and Yamaguchi (1962), lettuce produces leaves at a constant rate. This means that the rapid increase in leaf area was the result of leaf expansion, leading to an increase in ground cover. This increase in ground cover could be important in sustaining the period of exponential growth which occurs in lettuce.

An increase in ground cover means a larger light absorbing leaf area. In this respect, Brouwer and Huyskes (1968) found that the faster growth of one of the two cultivars of lettuce they tested could be ascribed solely to a better exposition of its leaves to light as a result of a larger leaf area.

The growth phases of the two cultivars can be divided into three divisions:

1. During the first three weeks the Webb's were the largest plants due to (a) large initial seedlings, and (b) the thicker leaves being light saturated at higher radiation levels than Cobham.
2. During the next four weeks the Cobham were the largest, due to the higher rate of leaf area production resulting in a larger ground cover.
3. During the final three weeks, Cobham were the largest at the three lowest P levels, but at the higher levels Webb's were the largest.

It is considered that these growth divisions were mainly due to the different rates of leaf area production in the two cultivars. With larger plants, the radiation energy would be completely absorbed by individual plant canopy due to the dense rosette growth form of head lettuce, irrespective of

cultivar, and thicker leaves of Webb's would have no advantage. Hence the larger leaf area and larger ground cover of Cobham would have absorbed more radiation energy than Webb's leading to the production of larger Cobham plants. However, in the P<sub>4</sub> and P<sub>5</sub> Cobham treatments, the extremely large leaf area led to a reduction in photosynthetic efficiency since the older leaves would be receiving light intensities below the compensation point, due to mutual shading. Also it is suggested that by crowding together more and more photosynthesizing leaves per unit area of land might result in a decrease in NAR by lowering the CO<sub>2</sub> concentration of the atmosphere within the crop canopy. Another important factor appeared to be the more severe decaying of the leaves of Cobham leading to a larger Webb's plant in the last three harvests.

The total dry matter production by a crop may vary through change in either the size of the photosynthetic system or in its activity (Cooper, 1966). However, the variation of NAR within and between species is accompanied by a relatively greater variation in leaf area and variation in the yield of a crop is closely correlated with variation in mean leaf area but not with mean NAR (Watson, 1956).

There was no significant difference in RGR between the cultivars even though Cobham had a higher RGR for most harvests. It is thought that this was the result of a higher NAR in Webb's being counterbalanced by a higher LAR in Cobham. Even then it is assumed that the higher growth rate of Cobham was a reflection of higher LAR. However, variation in NAR could contribute to a higher growth rate of Webb's near the end of the experiment. The difference in LAR between these cultivars was due to differences in the specific leaf area (Table XX).

Within each cultivar, however, variation in RGR appeared to be closely related to differences in NAR. LAR did not contribute regularly to the observed variation in RGR.

The relative contribution to RGR of the components can, however, differ with the environmental conditions. Watson (1952) reviewed crop growth studies and concluded that variation in yield caused by the application of manures and seasonal effects were mainly due to their effects on leaf area, rather than to their effects on NAR. MacColl and Cooper (1967) found that the differences in RGR between several forage grasses in the glasshouse in winter were based largely on differences in LAR. Robsin and Jewiss (1968a, b)

TABLE XX

## SPECIFIC LEAF AREA

Treatment	Cobham										Mean
	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	
P <sub>1</sub>	322	291	290	309	426	328	335	254	229	293	308
P <sub>2</sub>	329	370	353	337	402	384	330	347	358	474	368
P <sub>3</sub>	311	327	372	383	520	574	525	646	491	401	455
P <sub>4</sub>	277	390	449	433	572	638	618	739	563	618	530
P <sub>5</sub>	345	359	436	336	565	718	580	864	589	463	526

Treatment	Webb's										Mean
	H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	
P <sub>1</sub>	219	240	200	214	357	227	297	268	223	255	240
P <sub>2</sub>	256	299	258	290	358	349	365	341	339	408	326
P <sub>3</sub>	265	250	332	332	425	463	404	502	397	429	380
P <sub>4</sub>	283	302	370	332	499	470	470	508	339	325	392
P <sub>5</sub>	250	280	335	296	434	525	465	628	352	342	391

reported similar differences in LAR between cultivars of *Festuca* species, but also found that variation in NAR could contribute to RGR differences in certain conditions. On the other hand, Eagles (1967) reported that the differences in RGR between two populations of orchardgrass were associated with differences in NAR. Similarly, Austin (1963) and Nichols (1971) found differences in NAR to account for variation in RGR in vegetables. Eagles (1971) later showed that relative contributions of LAR and NAR to RGR varied with physiological stage of plant development. Loach (1970) found NAR during late, but not early, growth to be correlated with yield of sugar beet varieties.

In this experiment, developmental trends appeared to have been responsible for falling RGR, NAR and LAR even under conditions of improving solar radiation (September to November). Watson, Wilson, Ford and French (1966) found that a decrease in NAR with age was caused mainly by a decrease in the rate of photosynthesis per unit leaf area presumably either by an increase in mutual shading reducing the efficiency of the leaves or by changes in

internal factors. One of these internal factors may increase the proportion of non-photosynthetic tissue relative to the leaf area, which to some extent was indicated by a falling LAR.

Chemical analysis of plant tissue showed that the average content of N and K was close to or above that reported in the literature (e.g. Parups and Goodwin-Wilson, 1958; Zink and Yamaguchi, 1962) indicating a sufficient supply of these elements. As for P, variation in the intensity of P supply had a marked effect on the P concentration of the plant which ranged from 0.06 per cent to 1.18 per cent. For  $P_1$  and  $P_2$  treated plants, P content was lower than normally reported especially during the second and third harvests. It is noted that during these two harvests, P content of Webb's was higher than that of Cobham, which may be why Webb's had bigger seedlings than Cobham. In general, the data of chemical analysis correlated well with the stunted growth of the plants under these two treatments.  $P_3$  plants appeared to have optimal range of P content, but values for  $P_4$  and  $P_5$  plants suggest luxury consumption of P.

In this experiment, P was found to have a marked effect

on the growth and yield of lettuce with the results that only plants with  $P_3$  or higher P supply produced normal plants and formed heads.

The content of P, on a percentage basis, fluctuated throughout the growth of the plant and remained fairly constant except for  $P_4$  and  $P_5$  plants due to luxury uptake (Figure 7), but N and K content fluctuated and decreased towards market maturity (Figures 5 and 9). This is somewhat similar to that found by McGeorge, Wharton and Frazier (1940) in lettuce. Lorenz and Minges (1942) obtained a slightly decrease in N, on the dry weight basis, while P and K remained practically constant throughout growth, while Zink and Yamaguchi (1962) showed a trend for total N and P to decrease as the plant approached market maturity.

Goodall and Gregory (1947) have provided data that shows large differences in plant P concentration soon after the seed reserves are exhausted, under different levels of P supply. These differences gradually give rise to large differences in yield. This was found to be true in this experiment. In harvest two, which presumably corresponded to the period of reserve exhaustion in this experiment, the P concentration of  $P_1$  and  $P_2$  plants ranged from 0.06 per cent

to 0.17 per cent which is similar to the concentration in completely P-starved plant of 0.1 per cent (Grant Lipp and Goodall, 1958).

Seeds of these two cultivars may have low K content as indicated by the low values of K in the first harvest, but the seedlings were able to absorb K rapidly and had sufficient K by the second harvest. Since K has little effect on lettuce growth (Woodman, 1942; Goodall, Grant Lipp and Slater, 1955), this initial low K content would not have much effect on the growth of the plants.

There has been some controversy over which plant parts are to be used in plant analysis (see Review of Literature). However, the tops of lettuce have been used most frequently and Grant Lipp and Goodall (1958) found that the tops of lettuce were useful means in plant analysis. The whole plant was used in this experiment because it was relatively easy to harvest the roots from the containers compared with harvesting roots from the soil out in the field, and in any case the roots are only a small proportion of whole plant dry weight.

### CONCLUSIONS

The effects of applied P on the growth of two cultivars of lettuce given in sand culture were studied in a glasshouse for a period of ten weeks.

There were marked increases in dry matter, as well as leaf area per plant with increases in  $P_1$  and both showed typical logistic growth characteristic. Plants under low P treatments grew slowly, were stunted and did not form heads. Plants supplied with higher phosphate concentrations grew quickly and began to head forty-two days after emergence. However, some of these plants suffered from tipburn disorder.

The applications of phosphate resulted in increases in the net assimilation rates and relative growth rates of the plants but these increases persisted only during the first three harvest intervals. Subsequently, the net assimilation rates and relative growth rates of the plants given higher phosphate regimes were smaller than those of the plants with a lower phosphate supply. Higher phosphate supply always increased leaf area ratios of the plants. Phosphate fertilization was found to have a significant effect on

both net assimilation rate and leaf area ratio.

Both leaf areas and ground cover were higher for Cobham Green than for Webb's Wonderful.

Phosphate fertilization had the positive effect of increasing the tissue concentration of N and P. Chemical analysis of the whole plant showed a trend for total N and K to decrease as the plants approached market maturity. Total P fluctuated and no general trend was observed.

The shape of the N, P and K uptake curves was very similar to that of dry matter production. Most of these elements were absorbed during the last three weeks of the experiment.

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APPENDIX I

MOLAR CONCENTRATIONS OF REAGENTS USED TO OBTAIN FIVE LEVELS OF PHOSPHORUS WITH MINIMAL VARIATION ONLY IN  
SULPHATE ION.

Reagent	Molecular Weight	$\frac{1}{4}$ P		$\frac{1}{2}$ P		1 P		2 P		4 P	
		Molar	Weight (g/L)	Molar	Weight (g/L)	Molar	Weight (g/L)	Molar	Weight (g/L)	Molar	Weight (g/L)
$\text{KH}_2\text{PO}_4$	136.09							.002	.272	.004	.544
$\text{K}_2\text{HPO}_4$	174.18	.00025	.0435	.0005	.087	.001	.174				
$\text{KNO}_3$	101.10	.0035	.3535	.003	.303	.002	.202				
$\text{NH}_4\text{NO}_3$	80.05	.001	.080	.001	.080	.002	.160	.004	.320	.003	.240
$(\text{NH}_4)_2\text{SO}_4$	132.14	.00325	.429	.0035	.462	.003	.396	.002	.264	.003	.396
$\text{K}_2\text{SO}_4$	174.27							.001	.174		
$\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$	246.50	.002	.493	.002	.493	.002	.493	.002	.493	.002	.493
$\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$	236.10	.002	.472	.002	.472	.002	.472	.002	.472	.002	.472

APPENDIX II

MEAN DRY WEIGHTS (g) PER PLANT OF COBHAM AND WEBB'S, WITH FIVE LEVELS OF PHOSPHORUS

<u>Cobham Green</u>										
Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.00154	.00681	.0193	.0498	.239	.664	1.38	1.86	2.77	2.79
P <sub>2</sub>	.00164	.00642	.0230	.132	.497	1.73	3.39	6.36	7.66	11.0
P <sub>3</sub>	.00154	.00782	.0495	.381	1.24	3.25	8.71	10.7	19.8	25.1
P <sub>4</sub>	.00154	.00821	.0621	.485	1.93	5.39	8.37	10.8	16.4	18.7
P <sub>5</sub>	.00162	.00862	.0764	.657	2.20	4.97	9.80	12.2	15.5	22.5

<u>Webb's Wonderful</u>										
Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.00189	.00715	.0199	.0553	.206	.390	.616	1.73	2.61	3.45
P <sub>2</sub>	.00182	.00770	.0233	.122	.475	1.26	2.70	4.14	6.35	10.8
P <sub>3</sub>	.00172	.00837	.0419	.295	1.12	2.51	5.89	9.34	16.3	25.4
P <sub>4</sub>	.00171	.00828	.0577	.485	1.67	4.63	8.45	13.5	25.3	28.8
P <sub>5</sub>	.00183	.00992	.0758	.595	2.13	3.26	8.56	12.3	25.9	33.9

APPENDIX III

RELATIVE GROWTH RATE (g/g/DAY) OF TWO LETTUCE CULTIVARS

<u>Cobham Green</u>									
Treatment	7-14	14-21	21-28	Days from sowing		42-49	49-56	56-63	63-70
				28-35	35-42				
P <sub>1</sub>	.2087	.1419	.1180	.2545	.2052	.1479	.0403	-.0162	-.0551
P <sub>2</sub>	.1944	.1763	.2906	.2449	.1520	.0539	.0705	.0072	.0380
P <sub>3</sub>	.2343	.2507	.2911	.1466	.1150	.1282	-.1201	.0683	.0341
P <sub>4</sub>	.2408	.2976	.2891	.1898	.1365	.0675	.0421	.0687	.0139
P <sub>5</sub>	.2314	.2723	.2686	.1596	.1077	.0960	.0325	.0105	.0468

<u>Webb's Wonderful</u>									
Treatment	7-14	14-21	21-28	Days from sowing		42-49	49-56	56-63	63-70
				28-35	35-42				
P <sub>1</sub>	.1881	.1384	.1353	.2044	.0926	.0549	.1757	.0462	.0471
P <sub>2</sub>	.2077	.1577	.2208	.1675	.1209	.0752	.0555	.0811	.0828
P <sub>3</sub>	.2224	.2386	.3255	.2043	.1202	.1331	.0769	.0733	.0660
P <sub>4</sub>	.2229	.2744	.2991	.1618	.1079	.0914	.0535	.1055	.0437
P <sub>5</sub>	.2521	.2820	.2521	.1555	.0865	.0755	.0618	.1125	.0338

APPENDIX IV

## ANALYSIS OF VARIANCE OF RELATIVE GROWTH RATE

Source of Variation	Degrees of Freedom	Mean Square	F
<u>Main plots:</u>			
Fertilizer	4	.005604	6.32
Blocks	1	.006299	7.10
Main plot error	4	.000887	
<u>Sub-plots:</u>			
Harvests	8	.141202	69.79 **
Cultivars	1	.003402	1.68
Fertilizer x Harvest	32	.006938	3.43 **
Fertilizer x Cultivar	4	.002203	1.09
Harvest x Cultivar	8	.007027	3.47 **
Fertilizer x Harvest x Cultivar	32	.002270	1.12
Sub-plot error	83	.002023	

\*\* Significant at the 1% level

## APPENDIX V

NET ASSIMILATION RATE ( $\text{g}/\text{dm}^2/\text{DAY}$ ) OF TWO LETTUCE CULTIVARS

<u>Cobham Green</u>									
Treatment	Days from sowing								
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63	63-70
P <sub>1</sub>	.1295	.0840	.0555	.0996	.0789	.0787	.0187	-.0095	-.0325
P <sub>2</sub>	.0925	.0869	.1230	.0943	.0516	.0198	.0275	.0031	.0145
P <sub>3</sub>	.1321	.1006	.1079	.0419	.0266	.0281	-.0047	.0171	.0096
P <sub>4</sub>	.1185	.0957	.0851	.0463	.0285	.0132	.0073	.0139	.0030
P <sub>5</sub>	.1106	.0775	.0894	.0430	.0193	.0201	.0048	.0015	.0116
<u>Webb's Wonderful</u>									
Treatment	Days from sowing								
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63	63-70
P <sub>1</sub>	.1345	.1197	.1098	.1015	.0566	.0269	.0946	.0287	.0277
P <sub>2</sub>	.1364	.0947	.1262	.0707	.0440	.0264	.0223	.0371	.0322
P <sub>3</sub>	.1442	.1085	.1146	.0668	.0308	.0418	.0204	.0219	.0208
P <sub>4</sub>	.1252	.1035	.1076	.0491	.0265	.0235	.0118	.0365	.0156
P <sub>5</sub>	.1434	.1208	.0969	.0526	.0210	.0289	.0165	.0277	.0123

APPENDIX VI

## ANALYSIS OF VARIANCE OF NET ASSIMILATION RATE

Source of Variance	Degrees of Freedom	Mean Square	F
<u>Main plot:</u>			
Fertilizers	4	1964.62	25.22 **
Blocks	1	7.90	.10
Main plot error	4	77.89	
<u>Sub-plots:</u>			
Harvests	8	36328.56	101.36 **
Cultivars	1	8476.79	23.65 **
Fertilizer x Harvest	32	777.24	2.17 **
Fertilizer x Cultivar	4	289.83	.81
Harvest x Cultivar	8	691.03	1.93
Fertilizer x Harvest x Cultivar	32	461.27	1.29
Sub-plot error	83	358.40	

\*\* Significant at the 1% level

## APPENDIX VII

LEAF AREA RATIO (dm<sup>2</sup>/g) OF TWO LETTUCE CULTIVARS

<u>Cobham Green</u>									
Treatment	Days from sowing								
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63	63-70
P <sub>1</sub>	1.61	1.69	2.25	2.49	2.57	1.98	2.04	1.67	1.67
P <sub>2</sub>	1.99	2.05	2.34	2.62	3.01	2.69	2.19	2.57	2.61
P <sub>3</sub>	1.84	2.55	2.71	3.61	4.30	4.55	4.59	3.99	3.49
P <sub>4</sub>	2.03	3.13	3.42	4.19	4.80	5.23	5.87	4.88	4.61
P <sub>5</sub>	2.31	3.60	3.01	3.73	5.61	4.75	6.37	5.17	3.99

<u>Webb's Wonderful</u>									
Treatment	Days from sowing								
	7-14	14-21	21-28	28-35	35-42	42-49	49-56	56-63	63-70
P <sub>1</sub>	1.43	1.16	1.27	2.01	1.95	2.01	1.87	1.58	1.65
P <sub>2</sub>	1.52	1.70	1.75	2.37	1.62	2.85	2.39	2.18	2.65
P <sub>3</sub>	1.54	2.20	2.84	3.03	3.89	3.20	3.75	3.38	3.23
P <sub>4</sub>	1.78	2.65	2.78	3.30	4.08	3.90	4.14	3.29	2.69
P <sub>5</sub>	1.77	2.34	2.60	2.99	4.24	3.05	3.73	4.09	2.76

APPENDIX VIII  
ANALYSIS OF VARIANCE OF LEAF AREA RATIO

Source of variation	Degrees of Freedom	Mean Square	F
<u>Main plots:</u>			
Fertilizers	4	253446	51.21 **
Blocks	1	1329	.27
Main plot error	4	4949	
<u>Sub-plots:</u>			
Harvests	8	86653	49.80 **
Cultivars	1	199288	114.53 **
Fertilizer x Harvest	32	7681	4.41 **
Fertilizer x Cultivar	4	18091	10.40 **
Harvest x Cultivar	8	1976	1.14
Fertilizer x Harvest x Cultivar	32	2452	1.41
Sub-plot error	83	1740	

\*\* Significant at the 1% level

APPENDIX IX

LEAF AREA/PLANT (cm<sup>2</sup>) OF TWO LETTUCE CULTIVARS

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.280	1.07	3.25	13.5	68.9	153	319	349	417	505
P <sub>2</sub>	.299	1.28	4.89	31.6	143	491	739	1553	1755	3527
P <sub>3</sub>	.290	1.49	14.0	109	487	1517	3582	5559	7132	7217
P <sub>4</sub>	.250	1.99	22.3	164	907	2766	4255	6862	7078	8460
P <sub>5</sub>	.330	2.10	27.1	181	1041	2872	4695	8165	7018	7661

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.260	.910	2.25	8.37	52.5	69.6	132	303	388	589
P <sub>2</sub>	.290	1.21	3.71	25.8	124	337	748	974	1450	3032
P <sub>3</sub>	.290	1.24	13.2	67.7	403	943	1888	3670	4953	8510
P <sub>4</sub>	.290	1.58	17.1	127	678	1792	3275	5438	7173	7025
P <sub>5</sub>	.300	1.80	20.8	141	764	1910	3289	5990	7415	8844

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APPENDIX X

GROUND COVER/PLANT (cm<sup>2</sup>) OF TWO LETTUCE CULTIVARS

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.280	1.07	3.19	11.8	37.4	84.5	120	111	170	174
P <sub>2</sub>	.299	1.28	4.59	25.5	71.3	184	258	320	349	453
P <sub>3</sub>	.290	1.47	12.3	77.4	220	367	587	575	714	655
P <sub>4</sub>	.250	1.81	19.0	99.0	283	463	555	518	717	592
P <sub>5</sub>	.330	2.07	22.0	110	286	485	679	610	645	535

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.260	.910	2.07	7.88	28.5	38.6	64.9	108	166	152
P <sub>2</sub>	.290	1.22	3.57	22.5	68.1	143	207	244	313	448
P <sub>3</sub>	.290	1.23	12.0	57.0	170	258	515	508	665	812
P <sub>4</sub>	.290	1.56	15.0	87.9	261	354	499	610	871	727
P <sub>5</sub>	.300	1.77	18.5	101	259	383	565	587	775	758

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APPENDIX XI

LEAF AREA/GROUND COVER OF TWO LETTUCE CULTIVARS

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	1.00	1.00	1.02	1.13	2.05	1.84	2.70	2.95	2.54	2.86
P <sub>2</sub>	1.00	1.00	1.07	1.25	2.07	2.66	2.87	4.84	5.05	7.78
P <sub>3</sub>	1.00	1.01	1.12	1.42	2.42	4.20	6.12	9.70	10.13	11.05
P <sub>4</sub>	1.00	1.02	1.17	1.66	2.23	5.98	7.72	13.37	9.85	14.07
P <sub>5</sub>	1.00	1.02	1.23	1.65	3.65	5.95	6.93	13.39	10.78	14.22

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	1.00	1.00	1.01	1.07	1.87	1.77	2.04	3.29	2.36	3.88
P <sub>2</sub>	1.00	1.00	1.04	1.15	1.83	2.36	3.49	3.99	4.64	6.80
P <sub>3</sub>	1.00	1.01	1.10	1.18	2.15	3.66	3.68	7.33	7.46	10.50
P <sub>4</sub>	1.00	1.01	1.14	1.75	2.66	5.05	6.59	9.84	8.41	9.61
P <sub>5</sub>	1.00	1.02	1.13	1.40	3.07	5.01	5.88	10.51	9.62	11.76

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APPENDIX XII

## ANALYSIS OF VARIANCE OF LEAF AREA/GROUND COVER

Source of Variation	Degrees of Freedom	Mean Square	F
<u>Main plots:</u>			
Fertilizers	4	108.53	85.39 **
Blocks	1	2.08	1.64
Main plot error	4	1.27	
<u>Sub-plots:</u>			
Harvests	8	196.69	325.59 **
Cultivars	1	23.54	38.96 **
Fertilizer x Harvest	32	11.46	18.96 **
Fertilizer x Cultivar	4	3.04	5.03 **
Harvest x Cultivar	8	2.27	3.76 **
Fertilizer x Harvest x Cultivar	32	.77	1.27
Sub-plot error	85	.60	

\*\* Significant at the 1% level

APPENDIX XIII

EFFECT OF LEVELS OF PHOSPHORUS ON TOTAL NITROGEN/PLANT (% DRY WEIGHT) AT VARIOUS SAMPLING DATES

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	3.95	4.06	5.27	5.48	6.48	4.97	4.90	4.03	4.29	5.21
P <sub>2</sub>	4.97	5.16	6.61	5.50	5.21	5.07	4.90	4.12	4.04	5.04
P <sub>3</sub>	5.20	4.55	5.07	5.20	5.04	5.28	5.04	4.90	4.47	4.82
P <sub>4</sub>	4.86	5.23	7.11	5.87	5.34	5.16	5.30	5.08	5.00	5.08
P <sub>5</sub>	4.92	5.23	7.09	5.31	5.34	5.24	5.25	4.91	4.99	4.90

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	5.40	3.86	4.33	5.35	5.08	4.73	4.95	4.02	4.07	4.95
P <sub>2</sub>	6.19	4.12	4.76	5.50	5.17	5.34	4.81	4.29	4.31	4.73
P <sub>3</sub>	5.74	4.34	5.11	5.15	5.12	5.38	4.72	4.69	4.16	4.33
P <sub>4</sub>	6.16	4.78	5.65	5.81	5.69	5.21	5.12	4.60	4.38	4.55
P <sub>5</sub>	6.28	4.78	5.64	5.61	5.47	5.56	5.12	4.95	4.38	4.60

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APPENDIX XIV

EFFECT OF LEVELS OF PHOSPHORUS ON TOTAL PHOSPHORUS (% DRY WEIGHT) AT VARIOUS SAMPLING DATES

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.44	.06	.09	.25	.30	.11	.18	.10	.18	.24
P <sub>2</sub>	.47	.13	1.9	.32	.32	.29	.25	.16	.21	.33
P <sub>3</sub>	.51	.23	.57	.38	.46	.43	.41	.62	.39	.49
P <sub>4</sub>	.52	.34	.93	.63	.76	.85	.82	.69	.77	.91
P <sub>5</sub>	.51	.53	1.18	.68	.94	1.07	1.11	1.17	1.08	.97

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.49	.14	.17	.30	.28	.23	.19	.17	.14	.26
P <sub>2</sub>	.62	.17	.23	.40	.37	.35	.24	.21	.20	.35
P <sub>3</sub>	.49	.22	.35	.41	.46	.41	.36	.39	.32	.43
P <sub>4</sub>	.55	.51	.51	.62	.67	.67	.68	.74	.53	.68
P <sub>5</sub>	.60	.64	.50	.70	.76	.96	.85	.85	.72	.79

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APPENDIX XV

EFFECT OF LEVELS OF PHOSPHORUS ON TOTAL POTASSIUM (% DRY WEIGHT) AT VARIOUS SAMPLING DATES

Cobham Green

Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	1.97	3.39	3.78	5.22	6.65	5.20	4.95	3.87	3.83	4.50
P <sub>2</sub>	2.53	4.88	5.58	5.80	5.93	5.78	5.40	4.15	4.38	5.10
P <sub>3</sub>	2.23	4.54	7.02	5.60	6.43	5.78	5.38	5.20	4.40	4.48
P <sub>4</sub>	2.08	4.90	6.92	5.73	6.43	5.05	5.12	5.55	4.64	5.10
P <sub>5</sub>	2.52	5.20	9.01	5.28	5.35	5.45	5.57	4.62	5.05	4.40

Webb's Wonderful

Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	1.67	3.62	2.65	4.93	5.80	6.05	5.33	4.55	4.40	4.54
P <sub>2</sub>	2.17	3.64	4.66	5.98	6.70	6.13	6.15	5.05	5.00	5.63
P <sub>3</sub>	1.90	3.86	7.05	5.78	7.18	5.78	5.43	4.93	5.13	4.90
P <sub>4</sub>	1.59	4.29	6.86	5.73	6.50	5.78	5.00	4.27	3.83	4.37
P <sub>5</sub>	1.33	4.15	6.69	5.40	6.00	5.93	4.74	4.58	3.70	4.05

## APPENDIX XVI

## ANALYSIS OF VARIANCE OF TOTAL NITROGEN/PLANT (% DRY WEIGHT)

Source of Variation	Degrees of Freedom	Mean Square	F
<u>Main plots:</u>			
Fertilizers	4	3.7578	13.30 *
Blocks	1	.0401	.14
Main plot error	4	.2826	
<u>Sub-plots:</u>			
Harvests	9	6.1245	25.18 **
Cultivars	1	1.9385	7.97 **
Fertilizer x Harvest	36	.5847	2.40 **
Fertilizer x Cultivar	4	.0629	.26
Harvest x Cultivar	9	2.7139	11.16 **
Fertilizer x Harvest x Cultivar	36	.2489	1.02
Sub-plot error	91	.2432	

\* Significant at the 5% level

\*\* Significant at the 1% level

APPENDIX XVII

## ANALYSIS OF VARIANCE OF TOTAL PHOSPHORUS/PLANT (% DRY WT)

Source of Variation	Degrees of Freedom	Mean Square	F
<u>Main plots:</u>			
Fertilizers	4	47.9360	773.97 **
Blocks	1	.0246	.40
Main plot error	4	.0619	
<u>Sub-plots:</u>			
Harvests	9	2.4433	16.47 **
Cultivars	1	.7713	5.20 *
Fertilizer x Harvest	36	.8169	5.51 **
Fertilizer x Cultivar	4	1.5175	10.23 **
Harvest x Cultivar	9	.6596	4.45 **
Fertilizer x Harvest x Cultivar	36	.1951	1.32
Sub-plot error	91		

\* Significant at the 5% level

\*\* Significant at the 1% level

APPENDIX XVIII

## ANALYSIS OF VARIANCE OF TOTAL POTASSIUM/PLANT (% DRY WEIGHT)

Source of Variation	Degrees of Freedom	Mean Square	F
<u>Main plots:</u>			
Fertilizers	4	7.2689	15.87 *
Blocks	1	2.5065	5.47
Main plot error	4	.4579	
<u>Sub-plots:</u>			
Harvests	9	68.4296	128.53 **
Cultivars	1	1.5470	2.92
Fertilizer x Harvest	36	2.7671	5.22 **
Fertilizer x Cultivar	4	1.5186	2.87 *
Harvest x Cultivar	9	1.7891	3.38 **
Fertilizer x Harvest x Cultivar	36	.6615	1.25
Sub-plot error	93		

\* Significant at the 5% level

\*\* Significant at the 1% level

APPENDIX XIX

NITROGEN ABSORPTION (mg/PLANT) BY TWO LETTUCE CULTIVARS AT DIFFERENT STAGES OF GROWTH

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.063	.276	1.02	2.68	15.7	33.0	67.0	73.0	119	114
P <sub>2</sub>	.081	.323	1.52	7.22	25.9	87.1	166	262	356	556
P <sub>3</sub>	.080	.356	2.51	23.6	62.7	171	439	542	884	1203
P <sub>4</sub>	.075	.426	4.41	28.6	103	277	441	546	817	951
P <sub>5</sub>	.080	.445	5.41	34.9	117	260	515	598	776	1100

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.102	.276	.861	3.01	10.4	18.4	30.5	69.6	106	170
P <sub>2</sub>	.111	.318	1.11	6.75	24.6	66.8	130	178	274	513
P <sub>3</sub>	.100	.365	2.13	15.3	57.6	135	278	437	677	1097
P <sub>4</sub>	.105	.398	3.27	28.3	95.1	241	431	602	1102	1312
P <sub>5</sub>	.114	.478	4.28	33.4	117	237	437	607	1133	1538

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APPENDIX XX

PHOSPHORUS ABSORPTION (mg/PLANT) BY TWO LETTUCE CULTIVARS AT DIFFERENT STAGES OF GROWTH

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.007	.004	.017	.113	.734	.736	2.50	1.42	4.90	6.69
P <sub>2</sub>	.007	.008	.053	.420	1.60	4.98	8.05	9.88	16.5	36.0
P <sub>3</sub>	.008	.018	.282	1.73	5.67	13.9	35.7	70.0	76.5	122
P <sub>4</sub>	.008	.027	.579	3.06	14.6	45.5	67.7	75.5	125	165
P <sub>5</sub>	.008	.047	.898	4.46	20.1	52.7	108	142	166	215

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.009	.010	.034	.170	.576	.870	1.21	2.85	3.57	7.91
P <sub>2</sub>	.011	.013	.051	.486	1.73	4.48	6.43	8.71	12.3	37.4
P <sub>3</sub>	.008	.020	.162	1.20	5.17	10.3	21.2	35.9	53.0	110
P <sub>4</sub>	.009	.043	.302	3.02	11.2	30.8	53.6	97.3	135	197
P <sub>5</sub>	.011	.064	.385	4.14	16.2	40.6	73.2	103	186	264

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APPENDIX XXI

POTASSIUM ABSORPTION (mg/PLANT) BY TWO LETTUCE CULTIVARS AT DIFFERENT STAGES OF GROWTH

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Cobham Green

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.031	.230	.732	2.73	16.2	34.6	67.2	72.1	160	125
P <sub>2</sub>	.041	.304	1.34	7.61	28.9	99.2	180	264	335	565
P <sub>3</sub>	.055	.355	3.57	25.8	79.8	187	468	576	868	1115
P <sub>4</sub>	.032	.401	4.31	27.8	124	272	424	598	764	936
P <sub>5</sub>	.041	.428	6.88	34.7	117	270	446	562	783	983

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Webb's Wonderful

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Treatment	Harvest number									
	1	2	3	4	5	6	7	8	9	10
P <sub>1</sub>	.032	.259	.517	2.77	11.9	23.5	33.0	79.1	118	157
P <sub>2</sub>	.040	.280	1.07	7.27	31.8	76.7	166	209	318	604
P <sub>3</sub>	.033	.326	2.87	17.1	81.0	145	319	460	832	1252
P <sub>4</sub>	.027	.358	3.97	27.9	109	265	420	552	956	1259
P <sub>5</sub>	.025	.415	5.06	32.1	128	251	415	555	958	1323

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