GROWTH STUDIES
WITH
LETTUCE

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ABSTRACT

Growth studies were made in the field using two cultivars of head lettuce, Webbs Wonderful (a crisphead type) and Cobham Green (a butterhead type).

In a fertilizer and density experiment using a systematic spacing design superimposed on a rotatable fertilizer design evidence is presented to suggest that the 'normal' reciprocal yield-density model

$$W^{-1} = A\rho + B$$

(when W is the mean plant weight at density ρ, and A and B are constants) is only applicable when there is competition at all densities. A 'modified' model is proposed which includes an additional parameter C, the density at which competition begins. The modified model is:

$$W^{-1} = A\rho + B \text{ if } \rho > C$$

$$W^{-1} = AC + B \text{ if } \rho \leqslant C$$

The plant weights in a non-competitive situation were fitted to a logistic model using a 'heat unit' environmental time scale, and an analysis of the logistic parameters showed a response only to serpentine superphosphate. This quadratic response was due to an increased relative growth rate (due mainly to an increased net assimilation rate) from the use of serpentine superphosphate up to 40 cwt./acre.

At low plant densities Webbs Wonderful has a higher relative growth rate compared with Cobham Green due to a slower rate of leaf production, and a higher net assimilation rate. This net assimilation

rate difference is attributed to the heavier leaves of Webbs Wonderful being light saturated at a higher radiation level than the leaves of Cobham Green. This theory is supported by the similarity in the yields from the two varieties at high densities.

The optimum marketable yield spacing for Cobham Green was found to be 1.4 plants/sq.ft. and for Webbs Wonderful 1.1 plants/sq.ft. In spite of a lower plant density the marketable yield from Webbs Wonderful was approximately double that from Cobham Green (at their respective optimum densities) due mainly to the later maturity of Webbs Wonderful, but also due to its higher growth rate.

In an experiment carried out in England, and later in New Zealand, successive sowings (over a total period of 22 months) were sampled at regular intervals from emergence until past maturity. The dry weight per plant data were then fitted to a logistic model, with a single set of parameters for each variety over all the sowings, using chronological time, and a number of environmental time scales. All the environmental time scales tested provided a better fit than chronological time, with solar radiation being superior to 'heat units'. A further improvement with the solar radiation time scale was obtained by valueing all radiation above a certain daily integral at only 50%.

In spite of the marked improvement when using environmental time scales, the results have little commercial application at present as a predictive tool because substantial differences were found in the logistic parameter estimates for the two sites, and also in the estimates of the asymptotes for the different sowings.

It is essential that the asymptotes be the same over all sowings, or that the reason for any variation be known, because being based on a log. scale even a small variation would result in a large difference in absolute weight.

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INTRODUCTION

A detailed knowledge of the relationship between crop yield and the physical and chemical factors affecting plant development is essential if we are to exploit the resources of the biosphere efficiently.

To understand these complex relationships, and the equally important genotype-environment interaction, will demand the harnessing of scientific skills from all disciplines. The rewards, however, provided that dynamic long-term weather forecasting lives up to its early promise, will be increased crop yields, and for perishable horticultural crops, more predictable production and less wastage.

The problem of relating crop yield to the environment is being attacked in a number of ways, namely:

1) The seeking of correlation between growth (or yield) and the environment in the natural environment, using statistical techniques.
2) Studies in a controlled (or partially-controlled) environment in which the level of one or more of the environmental factors is changed, and the plants response noted.
3) Micro-meteorological studies within and above the crop canopy, leading to the development of plant growth models (e.g. Duncan et al. (1967), Idso (1968)).
4) Biochemical studies in the laboratory, leading to a further understanding of the mechanism of specific reactions.

Monteith (1966a) considers that statistics is the wrong tool for exploring crop-weather relationships because it tries to bypass the search for fundamental mechanisms and causes. Nevertheless, the field correlation technique, combined with the judicial use of controlled climate facilities appears to offer the possibility of results of practical value far more rapidly than the potentially more useful (but more long term) crop modelling, micro-meteorological approach. It could be argued that controlled climate experiments will provide all the necessary answers, but it must be remembered that no phytotron has yet been able to simulate the natural environment, and in the final analysis, it is in the natural environment that the majority of crops are to be grown, at least in the foreseeable future.

For this reason the work described in this thesis was carried out in the field. It had been intended to test some of the results in a controlled environment, but this was not possible due to delay in the development of suitable facilities. It must be realised that the testing of field results in controlled climate facilities must be considered an essential part of any crop-weather study, for only in this way is it possible to isolate the independent effects of the different factors which comprise climate.

The Plant Environment

The principal physical and chemical factors affecting plant development can be grouped as follows (de Vries, 1963):

Climatic factors

1) Radiation, including light
2) Cloudiness
3) Precipitation
4) Wind
5) Air temperature
6) Humidity of the air
7) Carbon dioxide content of the air
8) Air pollution

Edaphic factors

1) Composition of soil solid material, including organic matter
2) Soil texture and structure
3) Soil temperature
4) Soil moisture
5) Composition of soil solution
6) Composition of soil air, expecially its carbon dioxide and oxygen contents

A more comprehensive list, which includes three additional groupings (Geographic, Pyric, and Biotic) has been proposed by Billings (1952), but apart from the Biotic effects, which de Vries did not consider, the Geographic and Pyric effects appear to work through the Climatic and

Edaphic factors.

The principal biotic factors affecting plant development are:

Biotic factors (after Billings)

1) Competition
2) Pathogens
3) Man

Climatic factors

1) Radiation, including light

In a recent account on radiation and crops, Monteith (1965) cites three features of radiation which are of biological importance. These are:-

a) Intensity i.e. the amount of energy received by a unit surface in a unit time.
b) The distribution of this energy within the electro magnetic spectrum.
c) The distribution of the energy in time.

1.a) Radiation intensity

The intensity of radiation at the earths surface will depend upon the intensity of radiation just above the earths atmosphere perpendicular to the solar beam, the solar angle, and the losses due to absorption and scattering in the atmosphere. Because the earth moves round the sun in an ellipse, the intensity of the solar beam varies slightly, with a mean value of 2.0 cal./cm^2/min - called the solar constant. Solar radiation at the earths surface is normally measured by means of an Eppley, or a

Kipp pyrheliometer but a reasonable estimate can be obtained by measuring the number of bright sunshine hours by means of a Campbell-Stokes recorder, and then using an empirical formula (e.g. Penman, 1953) to estimate the solar radiation at the earths surface.

$$R_c = R_a \left(.18 + .55 \frac{n}{N}\right)$$

when R_c = radiation at the earths surface

R_a = radiation above the atmosphere

n = bright sunshine hours

N = possible bright sunshine hours

The radiation above the atmosphere (parallel to the earths surface) can be obtained from the Smithsonian Tables, or calculated from the following formula:

$$R_a = H \left(\sin\phi \sin\delta + \cos\phi \cos\delta \cos 2\pi \left(\frac{t-t_o}{24}\right) \right)$$

when R_a = radiation above the atmosphere

H = solar constant

ϕ = latitude

t = time (24 hour clock)

t_o = 12.00

δ = declination

1.b) <u>Spectral composition</u>

Over 99% of the solar radiation reaching the earths surface is between the wavelengths 0.3μ and 4.0μ. The visible spectrum (from 0.4μ to 0.7μ) is of particular importance, mainly because of photosynthesis, but wavelengths outside the visible spectrum can also play a major role in plant growth and development. Short waves such as cosmic, gamma, and X-rays can modify (sometimes drastically) the genetic constitution of a plant, while beyond the visible spectrum is the heating effect of the infrared. Of particular importance in plant development are the red (660 μ) and far red (.730 μ). Van der Veen and Meijer (1959) proposed that from a plant point of view the spectrum be divided into 8 wave bands, based on their physiological effect on plants.

1.c) Distribution of energy with time

The phenomena known as photoperiodism controls the development of a large number of crop plants, e.g. Chrysanthemum. Photoperiodism appears to work through the protein phytochrome, which comprises two interconvertible forms P_{660}, with absorption maximum at .660 μ and P_{730} with absorption maximum at .730 μ . The conversion in the dark of P_{730} to P_{660} appears to be the basis of photoperiodism (Hendricks and Borthwick, 1963).

2) Cloudiness

Cloudiness affect the physical environment in a number of ways:

a) The intensity of solar radiation is decreased, due to the reflection of a fraction of the solar beam away from the earth.

b) The proportion of indirect/direct radiation is increased.

c) Long-wave radiation losses from the earth are reduced.

3) Precipitation

Precipitation is important mainly in relation to its effect on soil moisture. Under certain circumstances, however, precipitation in the form of snow, hail, or even large drops of rain may physically damage plants. Rain can also play an important part by leaching essential minerals from leaves (Tukey and Morgan, 1962).

4) Wind

There appears to be considerable doubt as to the value of low wind speeds over the crop as a means of improving photosynthesis (e.g. Tanner (1963), Gaastra (1963)), but there is no doubt that wind can have a serious effect on plant growth well before physical damage occurs. This effect appears to be due to the increased transpiration which occurs as wind speeds increase, and this leads to increased water stress in the leaves, resulting in reduced leaf expansion (Monteith, 1966a). At higher wind speeds, the stomata may close, leading to a virtual cessation of photosynthesis (Winter, 1965).

5) Air temperature

The growth of higher plants is mainly restricted to temperatures between $0^{\circ}C$ and $60^{\circ}C$, and for crop production the range is further reduced to $10^{\circ}C$ - $40^{\circ}C$. Temperature plays a major role in plant growth, because the rate at which the majority of reactions occur is temperature dependent.

Species differ in their temperature requirements, for example Maize and Sorghum requires warmer temperatures than oats and peas in order to produce heavy yields. This may be due to the differences in photosynthetic pathways (i.e. the Hatch cycle), but Van Dobben (1962) has postulated that peas and oats will yield less at temperatures above optimum conditions, due to the rate of development exceeding the rate of carbohydrate production. Overall the concept of cardinal temperature (maximum, optimum, and minimum) appears to be outdated because the optimum temperature may alter according to the condition of the plant.

Thermoperiodicity has been extensively investigated (Went, 1953) and affords an explanation of the failure of certain temperate crop plants in the tropics. Agronomically 'temperature' can be transformed into 'heat units', and this concept is considered in more detail later in this thesis.

6) Humidity of the air

Humidity of the air can affect plants in a number of direct and indirect ways. The main effect is on transpiration where the greater the vapour pressure deficit in the air the higher the transpiration rate -- all other things being equal. If the internal water status of the plant is such that it cannot support a higher rate of water loss -- due perhaps to soil moisture limitations, then the stomata will close and photosynthesis will be reduced. The humidity of the air can also affect plant development (Heydecker and Pareek, 1969), and can be an important factor in relation to pathogens, especially certain fungous diseases.

7) Carbon dioxide content of the air

This is considered in the section on photosynthesis.

8) Air pollution

The major air pollution chemicals are sulphur dioxide, fluorides, and photochemical smog (ozone and Pan) (Middleton, 1969). These materials, even at low concentrations can cause severe damage to plants and provide a major threat to agriculture in industrial nations (e.g. U.S.A.). In New Zealand this is unlikely to prove important, except in special localised areas, because of the relative isolation, strong winds, and lack of heavy industry. Close to busy highways it is possible for plants to contain excessive amounts of lead, and this is a potential health hazard.

Edaphic factors

Edaphic factors can play a major part in influencing plant development. Compared with climatic factors, the edaphic factors tend to fluctuate less rapidly, mainly because the soil acts as a substantial buffer.

Choice of site will play a major role in determining the composition, texture, and structure of the soil, although man can ameliorate or degrade these characteristics by different husbandry techniques.

Soil temperature can be explained in terms of heat transfer, which can be looked upon as a periodic phenomena, with important agronomic implications, especially in terms of seed germination.

Too much, or too little soil moisture can reduce plant growth. Soil type will determine the soil moisture characteristics, while climatic factors determine water loss or gain.

The composition of the soil solution, i.e. the nutrient status, will depend on soil type, and the rate at which nutrients are added to the soil. Nutrients will also be removed by leaching, fixing, and by plant uptake.

Plant development will depend not only upon the presence of essential minerals, but their relative proportions, and their overall total. If the composition of the soil solution is too concentrated, then osmotic effects can reduce the soil water available to plants.

Actively growing plant roots require oxygen for respiration. The oxygen content of the soil atmosphere is less with increasing depth, while the carbon dioxide content increases. Soil type and structure play an important role in determining the rate at which oxygen moves down the soil profile. This determines to a large extent the effective rooting depth of a crop, and therefore the volume of soil that the crop can exploit for water and nutrients.

At germination Heydecker (1962) has found that seeds were more susceptible to low oxygen rather than high carbon dioxide concentration. Later growth, however was reduced by high carbon dioxide concentration in the soil atmosphere.

Biotic Factors

The effect of competition is considered later in this thesis, while Man and Pathogens can be major influences on plant development.

Crop yield and the natural environment

The factors which comprise the natural environment are in many cases interrelated, many of them being highly correlated. For example the level of solar radiation can greatly influence air temperature, while precipitation and soil moisture can be highly correlated. At this point it is pertinent to draw a distinction between climate and weather. Climate comprises the interaction of the climatic factors listed previously, with normally a seasonal pattern of change which is similar each year. Any deviation from this seasonal pattern is called weather. In modern terminology climate is the wave, and weather is the noise. Climate is a function of latitude, modified by position (altitude etc.), and weather is any short term deviation from normal. The relative importance of climate and weather vary, for example in some countries (e.g. Egypt) climate is the dominant factor, and variations from the mean are small, while in New Zealand or the British Isles climatic averages are a very poor guide, and variations from the mean have greater importance. As a generalisation it can be stated that 'climate determines the crops which can be grown, and weather determines the yield.'

The relationship between crop yield and the weather is one which has intrigued agronomists for at least 100 years. A number of major efforts have been made to relate yield to the weather with what can only be described as a marked lack of success. For example Watson (1963) has described the work by Lawes and Gilbert (1880), Fisher (1924), and Buck (1961) on the winter wheat at Rothamsted in which "after 80 years of intermittent but intensive study of a set of data that appears uniquely suited for the purpose, all that has been established with statistical certainty about the dependence of the wheat yield of Broadbalk is that it decreases with increase in annual rainfall above average." Watson continues "Past experience, therefore does not encourage us to expect that knowledge of how yield depends on weather can come from measurements of yields in naturally varying environments."

Though perhaps somewhat overstating the case, there is little doubt that there has been a marked lack of success in obtaining satisfactory correlations between yield and the weather. This is not to say that some suitable correlations have not been found - for example Cornish (1950) has obtained a satisfactory relationship between rainfall and wheat yield in South Australia. In fact it would be surprising to find that in an arid climate such a relationship did not exist, as the availability of water is one of the major factors limiting production, and would tend to override any of the other environmental factors. The complexity of the problem becomes apparent when with a crop of irrigated cotton in the Sudan Gezira, Jackson (1969) found that a major cause of variation in yield from year to year was due to variations in insect pest damage, and it has been suggested by plant pathologists that a possible cause of the reduced yield of wheat with increased rainfall at Rothamsted is partially due to a more severe infection of disease in the wetter conditions.

No doubt, however, a major difficulty in relating crop yield and the weather has been the complex nature of the relationship between plants and the environment, and the difficulty of knowing what parameters to measure, and how accurately. The difficulty also lies in the fact that the physics of the environment, and the physiological basis of plant growth are still far from clearly understood (Smith, 1967).

This is not to say that it is impossible to determine useful yield/environment relationships in the field, but is to emphasise that for an empirical relationship to be of real value we need to know a lot more about the crop and the environment.

In fact Brougham (1959) has shown that by developing a suitable model (Glenday, 1959) it is possible to determine the effects of seasonal climate and of weekly weather variations on crop growth rate in the field. A study involving replication in time (29) and space, with each 'time' replicate supplying 14 weekly harvest samples. This approach (of replications in time) permits a consideration of the interaction between ontogeny and climate. A most important effect as far as crop production is concerned, and one which most physiologists have avoided in their studies of growth and climate (e.g. Blackman et al., 1955; Warren Wilson, 1967) by using young widely spaced plants at a standard development stage.

Penman (1962) has proposed that crop-weather relationships involve at least 5 divisions, namely:

1) The zero order relationship

The problem of photosynthesis, respiration, and photosynthetic efficiency.

2) The 1st order relationships

The seasonal and secular changes in yield caused by weather changes.

3) The 2nd order relationships

Those arising from pests and diseases, the intensity of their development and spread being frequently associated with the weather.

4) The 3rd order relationships

Those relationships associated with mans stewardship of the earth - i.e. mainly edaphic factors.

5) The 4th order relationships

The effects of meteorological abnormality (e.g. hail, gale etc.), and the effect of certain biological threshhold values being surpassed.

Penman emphasises the need to understand the zero order relationship. He considers that until we find out why the green plant is so inefficient as an energy converter, crop weather relationships must be empirical, and the criterion of a successful analysis may be no more than the ability to express growth as a linear function of some weather parameter. Nevertheless he concludes that valuable 1st order relationships can be determined, provided that the effects of 2nd, 3rd, and 4th order relationships are absent, avoided, or neutralised.

Using this approach, Penman has obtained a satisfactory correlation between the growth (as measured by dry matter accumulation) of grass and accumulated potential transpiration. Gloyne (1965) considers that the correlation between dry matter increases and water usage would seem capable of application to a wide range of food crops, but Milthorpe (1961) has emphasised that transpiration and growth are not causally related, while Monteith (1966b) has shown that potential photosynthesis is governed by the income of solar radiation and potential transpiration by net radiation, and that the constancy of the transpiration/photosynthesis ratio depends on solar and net radiation relationship.

This means that, with increased solar radiation, photosynthesis may be limited due to light saturation, but transpiration will not be limited in this way. This effect is likely to be of most importance for young plants (with a low leaf area index).

Even if a satisfactory ratio between photosynthesis and water usage can be determined, the value of such a correlation will depend upon a near constant ratio between photosynthesis and respiration over the growth of the crop.

Wang (1967) has proposed a system of crop prediction without weather forecasting. He suggests that the current weather is revealed in later crop performance, and that this is more important than future weather conditions. Such a system may be of value where climate is the dominant factor, but appears to offer little of value for countries where climatic variations are of great importance.

Finally reference must be made to the work of Runge(1969) who, using statistical techniques, has shown that in Illinois it is possible to predict corn yields from a knowledge of the temperature and rainfall during the growing season.

Factors affecting Photosynthesis in Crops

The rate of photosynthesis of a leaf is determined by three main external factors:

1) Light intensity (of the right wavelength)
2) Carbon dioxide concentration of the air
3) Temperature

In simplified form, photosynthesis can be divided into

a) A photochemical process
b) A CO_2 transport process
c) A biochemical process

All these processes are interrelated, and the speed of the whole is the speed of the slowest part.

Gaastra (1963) has shown that at low light intensities photosynthesis is limited by the photochemical reaction, while at higher light intensities the diffusion process of CO_2 from the atmosphere to the chloroplasts will be limiting. With normal atmospheric concentrations of CO_2 (300 ppm) temperature mas virtually no effect (at least over the range 10-30°C) but with higher concentration of CO_2, the temperature controlled biochemical processes are limiting. This effect is exploited by growers who combine 'CO_2 fertilisation' with higher temperatures in their glasshouses.

In a crop, efficient light utilisation occurs when the leaf area below the compensation point or above light saturation is minimum. This will occur with a crop with erect rather than horizontal leaves, and in this respect the rosette shape of lettuce is particularly inefficient. In most field crops the CO_2 diffusion process is in fact limiting, because many of the leaves are exposed to saturating light intensities.

The rate at which plants produce dry matter is not solely dependent upon photosynthesis, but also depends upon the rate of respiration.

The HEAT UNIT Concept

A historical account of the development of heat units has been written by Wang (1960). The heat unit concept was introduced over 200 years ago, and was worked out in some detail by Boussingault and De Candolle over 100 years ago. In its simplest form the theory proposes that for each plant a threshold temperature exists below which it does not develop. The amount of "effective heat" accumulating during the day is obtained by subtracting from the daily mean temperature the base (threshold) temperature. The "effective heat" called heat units, degree days, day degrees, or growing degree days, is considered to be a measure of plant development. Initially this concept was used by geographers and ecologists to help characterise climate (Livingston and Livingston, 1913), and it was not until the mid-1930's that degree days were used commercially to schedule plantings and to predict maturity of process vegetable crops (Seaton, 1955). This development followed work by a number of workers (e.g. Boswell, 1924, 1929) in the 1920's who found that the 'heat sum' (the sum of heat units) above a specified base temperature was closely correlated with development of peas and (above a different base temperature) sweet corn. It was found that for any one variety, the figure resulting from summing the number of degree days from sowing date to maturity was nearly the same for each season for a particular location. This figure is known as the 'summation constant' or the remainder index.

The heat unit theory assumes that:

1) The plant response to temperature is linear over the whole temperature range.

2) Day and night temperatures are of equal importance.
3) There is only a single base temperature over the life of the plant.
4) Temperature is the major environmental factor influencing plant development.

Both Went (1950, 1953) and Wang (1960) have strongly criticised the heat unit system on (apparently) sound physiological grounds, but, nevertheless heat units have been of considerable practical value to agriculture, as a predictive tool, and for scheduling plantings. Ample evidence exists in the literature of the application of heat units for ensuring a steady flow of raw products of optimal maturity to the factory (e.g. Seaton), but in addition, heat units have been used for example to determine the maturity of table grapes (Winkler, 1948), and for forecasting the incidence of pest (Lienk, 1963) and disease (Boewe, 1953) occurrence.

There is nevertheless, no doubt that the heat unit system is far from perfect as it tends (Arnold, 1959) to overestimate the rate of plant development in:

1) warm compared with cold parts of the season.
2) warm compared with cool years.
3) low compared with high latitudes.
4) low compared with high altitudes.

These errors may be due to the failure of the linear system to adequately describe a curvilinear temperature response and/or because of the increasing importance of other environmental factors.

Katz (1952) attempted to use an exponential index and found for peas that the difference obtained by direct summation and by the exponential system was small. Large errors can occur with the exponential index method when a high value is given to a high temperature which may in fact be deleterious to plant development. Gilmore and Rogers (1958) modified the heat unit calculation by correcting for the partial effect of temperatures above and below an optimum range. This consisted of:

1) If the daily minimum was less than the base temperature it was given a value equal to the base temperature.
2) If the daily maximum exceeded a selected upper limit
   a) the daily maximum was equated to the upper limit
   b) the excess temperature above the selected upper limit was subtracted from the daily mean temperature.

Arnold (1960) has shown that from a graphic standpoint the 'heat sum' is the area beneath the temperature curve and above the base temperature. This is the same as the mean temperature minus base temperature (as stated previously, except that some modification is necessary when the base temperature lies between the minimum and maximum temperature).

A number of modifications have been proposed to take account of this possible error.

1) Gilmore and Rogers - see earlier.
2) Lindsey and Newman (1956) determined the area under the curve by using the formula:

$$\text{Heat units} = \tfrac{1}{2}\ \frac{(\text{max. temp.} - \text{base temp.})^{2}}{\text{max. temp.} - \text{min. temp.}}$$

3) Anon. (1954) determined the area under the curve by using one of two formulae, depending on the position of the base temperature in relation to the mean temperature.

1) Base temperature greater than mean temperature

$$\text{Heat units} = \frac{\text{max. temp.} - \text{base temp.}}{4}$$

2) Base temperature less than mean temperature

$$\text{Heat units} = \frac{\text{max. temp.} - \text{base temp.}}{2} - \frac{\text{base temp.} - \text{min. temp.}}{4}$$

4) Arnold (1960) showed that a normal temperature curve (although skewed) is very similar to a sine curve, and the areas under the curves show close agreement. Arnold proposed that the area under the temperature curve be based on sine curve calculations.

The choice of method used to calculate the heat sum when the base temperature is between the minimum and maximum could be of some importance. In Table I is shown the effect of using these different methods of calculation on the heat sum.

Base Temp. Method		30°	32°	34°	36°	38°	40°	42°	44°	46°	48°	50°
$\frac{\text{max + min}}{2}$ - base	(1)	10.00	8.00	6.00	4.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00
Gilmore and Rogers	(2)	10.00	9.00	8.00	7.00	6.00	5.00	4.00	3.00	2.00	1.00	0.00
Lindsay and Newman	(3)	10.00	8.10	6.40	4.90	3.60	2.50	1.60	0.90	0.40	0.10	0.00
Anon.	(4)	10.00	8.50	7.00	5.50	4.00	2.50	2.00	1.50	1.00	0.50	0.00
Arnold (sine)	(5)	10.00	8.27	6.77	5.44	4.24	3.18	2.24	1.44	0.77	0.27	0.00

Table I. The effect of calculating heat units by five methods from a temperature curve with maximum 50°, minimum 30°, and a range of base temperatures.

Clearly there are differences in the heat sum calculated by the different methods, and these differences would increase with increasing amplitude of the temperature curve. If we consider the sine curve to provide the best fit, then methods 1) and 3) consistently under-estimate the heat sum, method 2) consistently over-estimates the heat sum - though not excessively, and method 4) gives an under-estimate when the base temperature is near the mean temperature, and an over-estimate when the base temperature is near maximum or minimum temperatures. Errors in 4) could thus tend to cancel out. In any case, as we are normally using heat units to calculate remainder index's for crops between 1,000 and 2,000 units, small errors are unlikely to be important.

The choice of a satisfactory base temperature is critical for the successful application of heat units to plant development. Arnold (1959) has emphasised the empirical nature of heat sums, and has strongly criticised the rejection of satisfactory (statistically) base temperatures on the basis of physiological feasibility.

Heat units are usually based on air temperatures measured in a Stevenson screen by means of maximum and minimum thermometers. Arnold (1960) has shown that there may be locational and seasonal errors in calculating the daily mean from daily maximum and minimum temperatures, compared with a mean temperature, derived from a thermograph. These errors may account for some of the differences in the 'summation constant' for particular crops in different locations, and/or different times of the year. Nuttonson (1955) has suggested that photo-thermal units (obtained by multiplying the day-length by the degree days) could be a more valuable developmental unit, and has used this method extensively in several climate studies carried out at a number of latitudes.

Measuring the temperature of the air (some 4-6ft above the ground) and attempting to relate this to plant temperature at ground level is open to serious criticism, and this is fair comment on the heat unit concept in general, with the proviso that it seems to work reasonably well - in spite of all its obvious faults.

Plant spacing

A knowledge of plant spacing is essential if we are to exploit our resources efficiently. Plant spacing relationships have potential not only as yield predictive models, but also offer scope as a means of analysing and interpreting experimental results more precisely (e.g. Dowker and Mead, 1969). In vegetable production plant spacing is important not only because of the influence it exerts on yield, but also for the effect it can exert on quality.

Spacing comprises a consideration of two distinct factors.

1. Plant Density: the number of plants per unit area, and
2. Plant Arrangement: the spatial distribution of these plants.

PLANT DENSITY

As plant density increases so the yield per plant (total, or marketable) decreases, although the yield per unit area may in fact increase.

The reduction in yield per plant with increased plant density is due to competition. Donald (1963) has stated that "competition begins when the immediate supply of a single necessary factor falls below the combined demands of the plants". The main competition factors are: - light, soil moisture, soil nutrients, and on occasions carbon dioxide in the aerial environment, and oxygen in the soil atmosphere.

Holliday (1960a) in an attempt to characterise yield-density relationships, proposed that there were in fact two relationships

a) An asymptotic one in which with increasing density, yield rises to a maximum and then remains constant at higher densities.

b) A parabolic one in which with increasing density, yield rises to a maximum, and then declines at higher densities.

The suggestion by Holliday (1960b) that total crop dry matter always follows an asymptotic relationship has been shown to be incorrect by (among others) Bleasdale (1966a) and Farazdaghi (1968) who found that in certain situations a falling off in total crop dry matter may occur at high densities. Nevertheless the asymptotic relationship appears to provide a reasonable relationship, not only for total crop dry matter, but also in certain cases for the yield of a vegetative part of the crop e.g. Potato tubers.

Holliday's (1960b) suggestion that reproductive forms of yield conform to a parabolic relationship appears to be supported by experimental results over the past decade. Certain forms of vegetative yield also appear to show this relationship, for example, the root yield of Red-Beet, and the sprout yield from Brussel Sprouts. Harper(1961) has suggested that although the total plant dry matter - density relationship is asymptotic the partitioning of assimilates to the various organs of the plant may change with change in density. Bleasdale and Thompson (1966) have demonstrated that a parabolic relationship also exists when some form of size grading is practised. This provides a good example of the need to consider 'biological' yield initially rather than 'agronomic' yield which may depend entirely on arbitrary grading standards.

PLANT ARRANGEMENT

For row crops, plant arrangement comprises: -

a) the relationship between the in-the-row, and the between-the-row spacing. This is termed rectangularity, and is obtained numerically by dividing the largest distance by the smallest.

b) The orientation of the rows.

c) The regularity of spacing in the rows.

In broadcast crops, plant arrangement can be defined by the unevenness of distribution. Mead (1966) has proposed that each plant is in its own polygon of area, and eccircularity the deviation of the polygon from circular is a measure of rectangularity. An uneven plant distribution, although it may effect crop yield is primarily of importance in vegetable production because it results in uneven competition which leads to a wider variation in the size of the individual plants. The effect of spatial arrangement on crop yield appears to vary with the plasticity of the species, for example Bleasdale (1963) has demonstrated marked increases in yield per unit area for Carrots by keeping the plant density constant, and reducing the between-the-row spacing, while Frappell (1968) suggests that for Red-Beet there may be little advantage in reducing the between-the-row spacing to less than 14".

In general however, one might expect that increased rectangularity will lead to decreased yield per acre, and may also result in a decrease in the optimum density.

On theoretical grounds Loomis and Williams (1969) have demonstrated the advantages (irrespective of latitude and season) of orientating plant rows N - S rather than E - W, in order to get increased photosynthesis. Unfortunately this increase may be more than nullified by localised conditions, for example if the prevailing wind is in the wrong direction for the rows.

The regularity of spacing in the rows is of far more importance at high rather than low rectangularities. Nevertheless the accurate spacing of seed (and hence we hope, plants) in the rows even at low rectangularities is highly desirable as a means of obtaining even-sized plants. The development of precision drills has done much to make this possible.

Competition

a) Light

Competition for light may be caused whenever a plant shades itself or another plant. It is present therefore, in most crops except in the case of newly emerged seedlings. The effect of early shading is not clear, but Bleasdale (1966a) has postulated that no yield advantage will occur provided that the initial plant density is in excess of that where a constant final yield condition exists. This appears to challenge Watson's (1956) concept of an optimal leaf area index.

b) Soil Nutrients

Lang et al.(1956) have demonstrated for grain yield of Maize, which shows a parabolic yield-density relationship, that by increased Nitrogen application, not only was the yield at all densities increased, but the higher the density the greater the increase, and the greater the Nitrogen application, the greater the density at which the maximum yield was achieved.

c) Soil Moisture

Salter's (1961) work with Cauliflower provides a classical example of the interaction between plant density and soil moisture. In this work, Cauliflowers were grown at four densities, and no irrigation was compared with regular irrigation. The results demonstrate: -

1) Increase in total yield with increased density, irrespective of irrigation treatment.

2) Heavier total yield at higher densities with irrigation compared with no irrigation.

3) A substantially higher marketable yield from the irrigated higher densities, compared with the marketable yield with no irrigation at these densities. This is due primarily to the effect of quality grading on the already low non-irrigated yield.

The Effect of Density On The Plant

So far I have considered only the effect of plant density on the population. In vegetable production we are frequently interested in crops which produce only one marketable unit per plant, e.g. Lettuce, Cabbage, Onion. Under these circumstances we are interested not only in the mean weight per plant, but also in the distribution about that mean.

Information on this subject is very limited.

Koyama and Kira (1956) suggest that in a population of initially near uniform plants, the distribution will tend to + ve skewness with time, i.e. the population will comprise an increasing proportion of small plants, and a decreasing proportion of large plants. They suggest that such a tendency occurs independent of competition, but that increased competition would tend to accelerate the move towards what may well be a log. normal distribution. Mead (1966), however, doubts whether the distribution approximates to a log. normal one.

Effect Of Density On Maturity

Changes in density can affect maturity in two ways.

1) It may alter the time of maturity.

2) It may change the spread of maturity

The effects will vary with the crop, for example, widely spaced Cabbages heart earlier than closely spaced ones, whereas widely spaced Onions mature later than closely spaced ones. It is however, the effect of density on spread of maturity which is one of the more valuable attributes of high density production. Snap Beans (Jones, 1967) provide a good example of this effect as at high densities virtually all the lateral growth fails to develop and a concentrated maturity crop suitable for a single destructive harvest is produced. Other examples of high density concentrating maturity are found with Sweet Corn, Brussel Sprouts and Tomatoes. This poses the question of whether the efforts expended by plant breeders to obtain concentrated maturity is really justified?

Density/Arrangement Interactions

Frequently in plant spacing experiments the independent effects of density and arrangement are irrevocably lost, for example in experiments with a constant between-the-row spacing, with varied in the row spacings to give different densities (e.g. Webster, 1969). In order to examine spacing effects efficiently, Nelder (1962a) has developed a series of systematic spacing designs in which the effect of density or rectangularity can be independently determined. These designs offer a means of examining the effect of a wide range of spacings in a small area of land.

Plant Density and Competition Models

The analysis and interpretation of plant density experiments has been facilitated by the development of equations (models) aimed at characterising plant density relationships.

Kira et al (1953) proposed an empirical law, the Competition-Density Effect, which attempted to describe the effect of plant density on the average yield of a plant population, by the equation:

$$W \rho^{a} = K$$

when W is the average weight per plant at plant density ρ , and a and K are constants (with plant density the only variable). Similar models have been proposed by Warne (1951) and by Duncan (1958), who also proposed a semi-log. model.

The effect of harvest date on Kira's model has been described by Shinozaki and Kira (1956), who show that the model is only applicable when there is competition. This means (see figure 1) that the $\log w \sim \log \rho$ relationship approximates to two straight lines, one horizontal covering the lower densities (with no competition), and the other inclined, and covering the higher densities. With increasing time the slope of the inclined line gets steeper, and the range of densities it covers becomes greater, and the horizontal line becomes more restricted. Kira's model only describes the inclined line. With increasing time, the slope of the inclined line tends to 45° -- thus substantiating at any one time the law of constant final yield per unit area, regardless of plant population. Once the slope reaches 45° only the intercept (K) changes (increases) with

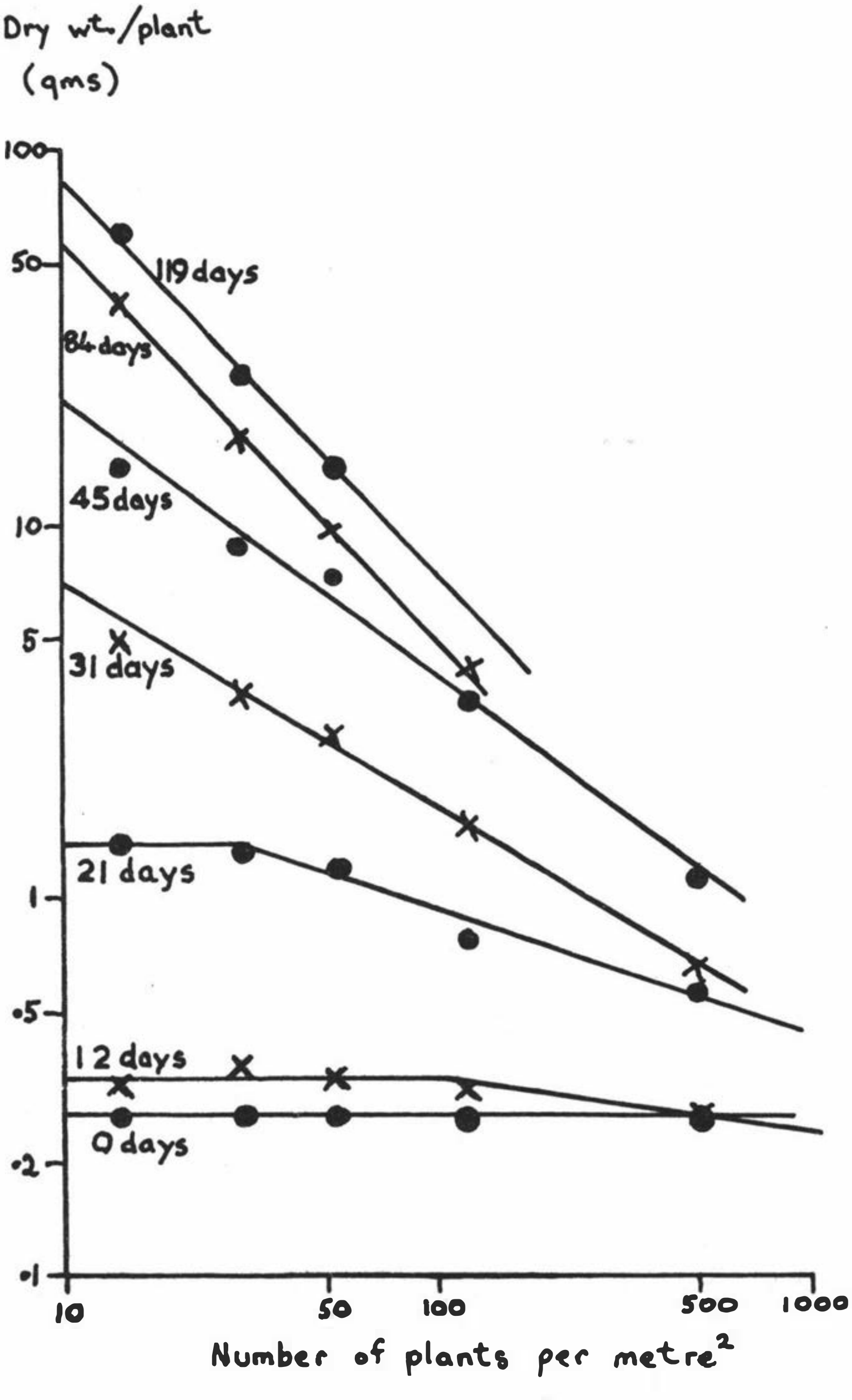

Fig. 1. Competition-density effect in soybean (after Kira et al., 1953)

successive harvests. This model also appears to work for weight per plant part (e.g. root, seed), although the final slope may not, under these circumstances be 45^0.

This power model can present a number of anomalies, for example extrapolation of Kira's soybean regression lines suggest that a higher yield could be obtained from a high density sowing harvested at day 45, compared with one harvested at day 84.

This type of anomaly, and the difficulty of deciding at what density competition begins led to the development by Shinozaki and Kira (1956) of the reciprocal equation (based on the logistic model of plant growth) in which to quote the authors 'both the horizontal and inclined part of the $\log w \sim \log \rho$ line are represented by a smooth curve, covering the whole range of density'. The model proposed was:

$$\frac{1}{W} = A\rho + B$$

when W is the mean weight per plant at density ρ, and A and B are constants, and plant density is the only variable. Inherent in this model is an asymptotic relationship between yield per unit area, and plant density, i.e.

The yield per unit area = $W\rho$, which when $\rho \to \infty$ then $W \to \frac{1}{A}$. Thus A can be considered to be a measure of the yield potential of the environment. By the same process when $\rho \to 0$, $B \to \frac{1}{W}$, and thus B can be considered to be a measure of the genetic potential of a single plant growing without competition.

Although this model adequately describes the yield-density relationship, for the whole plant, the yield of a plant part frequently results in a parabolic rather than asymptotic relationship. Bleasdale and Nelder (1960) therefore proposed a modification to Shinozaki and Kira's equation by adding two further constants:

$$W^{-\theta} = A\rho^{\phi} + B$$

However further experience suggested that the ratio of θ and ϕ were more important than the absolute values, so setting ϕ as unity results in an equation:

$$W^{-\theta} = A\rho + B$$

Bleasdale (1967) has proposed a simple method (based on allometry) of calculating θ for any plant part if the total weight per plant, and the weight of the biologically significant plant part are known at two plant densities,

$$\log_{10} W = \log_{10} K + \theta \log_{10} W_1$$

when W is the total weight per plant, and W_1 is the weight of the plant part. K is a constant, as is θ.

The law of constant total plant final yield per unit area, on which the reciprocal model is based, has been queried by Farazdaghi and Harris (1968), who propose a model

$$\frac{1}{W} = A\rho^{\alpha} + B$$

for the whole of plant relationship, and

$$W^{-\theta} = A\rho + B$$

for examining the yield density relationship for the weight of a plant part. This equation is similar to that proposed by Bleasdale and Nelder (1960).

In addition to plant density effects on yield, plant arrangement is also important. This has led to the extension of the simplified Bleasdale and Nelder model by Berry (1967) to include the effect of varying the between row, and the in the row spacing. The model

$$W^{-\theta} = A\rho + B + C\left(\frac{1}{a} + \frac{1}{b}\right)$$

incorporates an additional constant C, when a in the in the row spacing, and b is the between the row spacing.

THE EFFECT OF SPACING AND FERTILIZERS ON THE GROWTH OF LETTUCE

Materials and Methods

The experimental area (of approximately ½ acre) was sited on Manawatu silt loam soil. The area was fumigated with a mixture of Methyl Bromide (2 parts) and Chloropicrin (1 part) applied by a contractor at the rate of 400 lb/acre in early October 1966. The purpose of this fumigation was to kill weeds, and weed seeds, with any control of soil-borne pathogens regarded as a bonus. Prior to fumigation the area was rotary hoed to a depth of 10 - 12" in order to produce a fine deep tilth, and after fumigation, the polythene film was removed, and the area rotary hoed to a depth of 4 - 6" to ensure the rapid dispersal of the fumigants into the atmosphere.

The experimental design used was the 2nd order rotatable design of Cox and Hunter (1957) and for this, the area was divided into 20 plots, each being 25' x 40'. This experimental design enables linear and quadratic responses of 3 factors at 5 levels to be determined. The levels used for each factor are shown in Table II.

	Level					
Factor	$-\alpha$	-1	0	1	$+\alpha$	
Nitrolime (21% N)	0	4	10	16	20	cwt/
Serpentine superphosphate (7% P)	0	16	40	64	80	acre
Sulphate of Potash (40% K)	0	2	5	8	10	

Table II. Levels of N-P-K used in the experiment.

Superimposed on each plot was a systematic spacing design (Type Ia) of Nelder (1962a), with a rectangularity of 1.0 (a square spacing), comprising plant densities ranging from 0.4 - 4.0 plants per square foot. This spacing design is frequently called the fan design. The two varieties used in the experiment were:-

Cobham Green - a butterhead lettuce - hereafter called 'Cobham'.
Webbs Wonderful - a crisphead lettuce - hereafter called 'Webbs'.

The position of the close spaced portion of the fan was randomized to either the North or South end of each plot. The position in each plot of the two varieties was randomized to be either on the East or West side of each plot. The fertilizer for each plot was spread by hand on 16-17 November 1966 and cultivated in approximately 6" deep with a rotary hoe. The whole area was then rolled with a Cambridge Ring Roller. On 18 November 17 rows (the spokes of the fan design) were sown with each variety per plot using pelleted seeds, and a hand operated Stanhay precision drill calibrated to sow 1 pellet every 1½". The pellets were manufactured by Nelson Lime and Marble Ltd., Port Mapua, Nelson, and consisted of a single lettuce seed surrounded by an inert clay pellet.

Immediately after emergence, poisoned wheat was distributed in the experimental area to reduce bird damage, the lettuces were sprayed with Metasystox to control aphis and the plants thinned to their correct spacings. A total of ten harvests were taken at weekly intervals, commencing on 29th November 1966. The first two harvests were taken from the ends of each plot, and harvests 3 - 10 inclusive were taken from a single random spoke from each variety and plot. Each sample spoke has a single guard spoke on each side. The following data were recorded for each plot and variety.

a) for the first two harvests:-
    1) fresh weight of top.
    2) dry weight of leaves, stem and roots.
    3) leaf area (measured by the 'blueprint' method).
    4) number of leaves over ½" in length.

b) for the last eight harvests:-
    1) fresh weight of top of each plant in the spoke.
    2) stage of maturity of plant.
    3) dry weight of leaves, stem and roots of a close, medium and wide spaced sample plant for each plot and variety.
    4) dry leaf weight/unit leaf area of a medium spaced plant by the 'punch' method.
    5) missing plants.

Rainfall was fairly evenly distributed over the period of the experiment, and only one irrigation was required when the estimated soil moisture deficit was 1 inch.

RESULTS AND DISCUSSION

Data Reduction

It was considered essential to reduce the data to a more manageable amount. Initially the 'fresh weight of top' data was converted to 'total plant dry weight' using the 'fresh weight of top'/'total plant dry weight' relationship for each harvest, variety, plot and spacing. The total plant dry weight data were fitted to the reciprocal yield-density model:

$$W^{-1} = A\rho + B \text{ (Shinozaki and Kira, 1956)}$$

when W is the mean weight per plant at density ρ , and A and B are constants for each plot, variety and harvest. This model was preferred to the more complex models of Bleasdale and Nelder (1960) because:

1) the comparatively low plant densities used in the experiment could make the accurate estimate of θ or $\emptyset$ difficult, if in fact they do differ from 1.0
2) the apparent tendency (Donald, 1963) for total plant weight per unit area to be asymptotically related to plant density.

In fact the yield-density model

$$W^{-\theta} = A\rho + B$$

was fitted for each variety and harvest, resulting in the best estimates of C being $\overset{\frown}{=}$ .6 for Cobham Green and $\overset{\frown}{=}$ .8 for Webbs Wonderful.

These estimates ~~results~~ however appeared to be due to the constancy of the yield per plant at low plant densities, where competition is absent, i.e.

the reciprocal model is only valid when there is competition. Farazdaghi and Harris (1968) have previously questioned the validity of the reciprocal model at low densities, although they offer no experimental evidence to support their concern.

Inherent in the Shinozaki and Kira (1956) reciprocal model is an asymptotic relationship between yield per unit area and plant density, i.e.

Yield per unit area = $W\rho$. When $\rho \rightarrow \propto$, then $W \rightarrow \frac{1}{A}$.

Similarly when $\rho \rightarrow 0$, then $W \rightarrow \frac{1}{B}$.

Nichols (1967) has presented data which supports Bleasdale's (1966) contention that B is independent of soil fertility, and is a measure of genetic potential.

These concepts become incompatible for the early harvests of any yield-density experiment which includes different soil fertilities, unless the reciprocal model is valid only where there is competition. Three possible relationships are shown in figure 2 which includes 3 harvest dates and 3 soil fertilities, with

a) A and B independent
 at all densities
b) A independent, B constant
c) A independent, B constant only where there is competition.

At the first harvest date, there is no competition over the range of densities being studied, at the second harvest competition begins at half the maximum density studied, and at the third harvest there is competition at all densities.

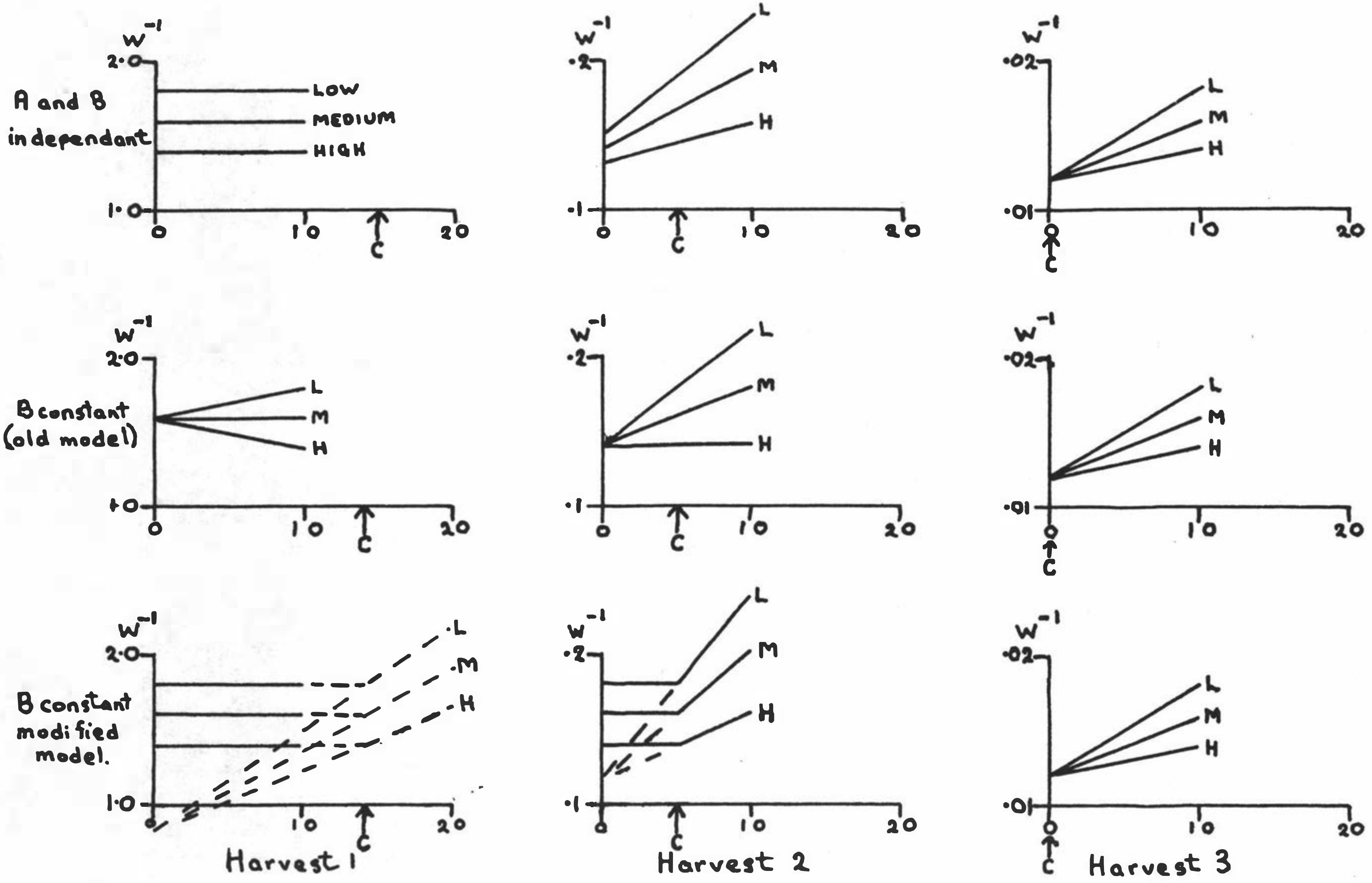

Figure 2. Hypothetical relationship showing the effect of plant density on the reciprocal of total yield per plant at 3 levels of fertility (High, Medium, and Low), on 3 harvest dates, with A and B parameters independent, B constant (old model) and B constant (modified model). C is the density at which competition commences.

When yield-density data are fitted to the reciprocal model over a number of harvest dates, it is possible for the estimates of A in the early harvests to be smaller than the estimates of A for later harvests, in fact if we can assume that B is constant for any one harvest (and genotype) it is possible in soil fertility experiments for A to be negative. These anomalies were noted when analysing the lettuce data, and similar anomalies can be noted in Shinozaki and Kiras (1956) soybean analysis.

This suggests that the reciprocal yield-density model is only valid where there is competition, and this theory was tested by fitting the total plant dry weight data from the lettuce experiment to the model:

$$W^{-1} = A\rho + B$$

assuming that:

1) the model fits at all densities
2) the model fits only where there is competition (the modified model).

A weighted least squares criterion (Nelder, 1963) was used, and in order to determine the density at which competition began (C), the R.S.S. (Residual sum of squares) was minimised over a range of C's for any one harvest, All plants at a smaller density than C being considered to have a density of C.

The results (for the variety Webbs) shown in Table III demonstrates that:

1) there was a marked reduction in the density at which competition begins (C) with successive harvests.
2) Using the modified model, the R.S.S. is reduced, the anomaly in the estimate of A at harvest 4 was eliminated, and the estimates of A in the earlier harvests were increased.

Similar results were obtained from analysing the data from the variety Cobham in the same manner. A comparison between the two models is shown in Figure 3.

There does not appear to be any reason when the parameters A and B calculated by the 'modified method' should not have the same biological meaning as those derived from the normal model (i.e. yield and genetic-potential respectively). In fact it could be argued that the parameters obtained using the 'modified model' are better estimates than those obtained by the 'normal model'. It could also be argued that the more sophisticated reciprocal yield-density models are also only valid when there is competition. An account of these findings has already been published (Nichols, 1970).

Having demonstrated the validity of the reciprocal yield-density model only where there is competition, the total dry weight per plant data for the whole of the experiment were fitted to the modified model, with 'B' constant for each harvest and variety, 'A' independent and 'C' constant for each variety and harvest.

The yield per plant when there is no competition was calculated for each variety, harvest date, and fertilizer plot using the formula:

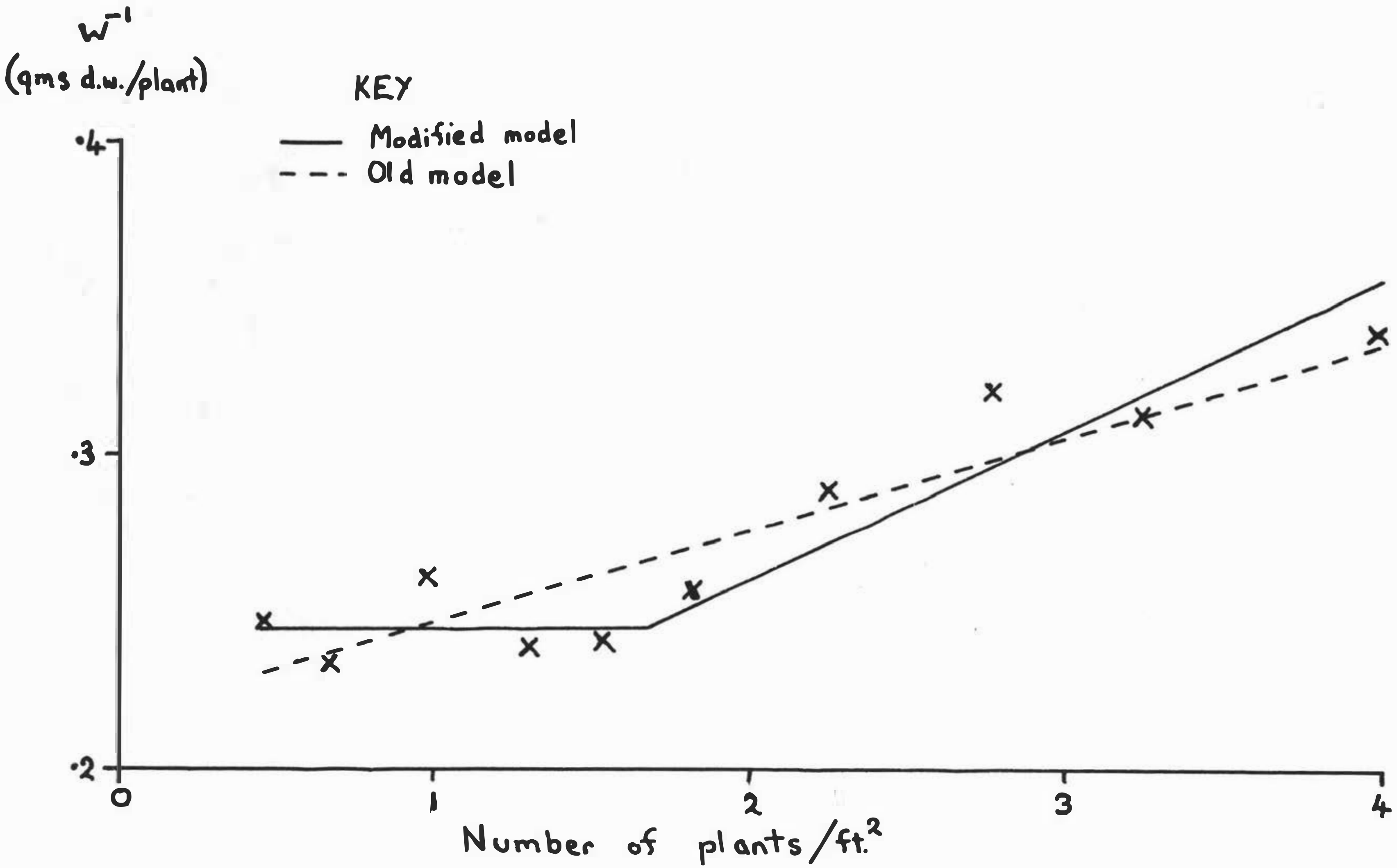

Figure 3. Webbs Wonderful Harvest 5. Showing a comparison of the old and modified reciprocal yield density models.

$$\text{Weight per plant} = \frac{1}{B + A \times C}$$

The results of this calculation, and the total plant dry weights from the first two harvests were now fitted to the four parameter logistic model (Nelder et al., 1960; Nelder, 1961a ; Nelder, 1962b)

$$W = \frac{A}{(1 + e^{-(\lambda + Kt)/\theta)})^{\theta}} ,$$

'harvest'	'normal model'		'modified model'		
No.	R.S.S.	A	R.S.S.	A	C
3	39.02	.226	34.70	3.751	3.6
4	40.48	.018	38.91	.063	3.0
5	28.99	.029	27.90	.047	1.7
6	30.77	.020	29.94	.023	1.0
7	21.79	.014	21.70	.15	.7
8	21.08	.012	20.99	.013	.6
9	20.47	.009	20.23	.009	.6
10	17.68	.010	17.68	.010	< .4

Table III. Residual sums of squares, A parameters calculated for Webbs Wonderful, using normal, and modified reciprocal yield density models.

when W is the weight per plant at time t, A is the asymptote, K is the initial relative growth rate, C defines the point of inflection, and λ is the constant of integration. t can be chronological time, or some environmental time scale, and the first essential was to determine a suitable time scale, by fitting the model to chronological, and a number of environmental time scales. The weather records were obtained from D.S.I.R. Plant Physiology Division Meteorological site - some 200 yards from the lettuce experimental area. The time scales considered were:

1) chronological time.
2) solar radiation (measured by an Eppley solarimeter).
3) Heat Units above a range of base temperatures. Calculated from daily maximum and minimum screen air temperature using the 'Air Ministry Method' (Anon, 1954).

The results (Table IV) show a clear improvement in the goodness of fit (as measured by the reduction in the error sums of squares of $\log_e W$) with any of the environmental time scales, compared with chronological time. Heat Units above a 42°F base temperature provided the most satisfactory fit. This result is in agreement with Salters (1960) findings for cauliflowers, but Nichols (1968) has shown that over a 9 month period, solar radiation is a better time scale for lettuce, than either Heat Units or chronological time. This aspect will be considered elsewhere in this thesis. The choice of a suitable time scale in this particular experiment is probably not critical, provided that the error term is reduced to a reasonable level. For this reason the time scale used for the remaining analyses was the 'heat sum' above a 42°F temperature.

Analysis of Plant Dry Weight Data

The logistic model was fitted to the yield per plant when there is no competition (calculated previously) for each plot and variety. The parameters α $(= \log_e A)$, K and θ for each variety were then fitted to the response surface, and the coefficients (linear, quadratic, and linear interaction) were tested for statistical significance. The results are shown in the appendix.

In all cases the response model showed that the quadratic phosphate coefficient was of major importance, even though significance $(P < .05)$ only occurs in one analysis - the Webbs θ analysis in which in addition to the quadratic phosphate coefficient, the linear nitrogen, and linear phosphate coefficients are also significant.

The lack of significance in the other analyses is somewhat surprising particularly with respect to Cobham θ which has a quadratic phosphate coefficient approximately double the equivalent Webbs coefficient (which is significant). Examination of the Cobham data shows that the absence of significance for θ is due to plot 13, one of the central (0-0-0) plots from which the error variance is calculated. It was decided to reject this value, and substitute a value estimated as follows:-

$$\theta \text{ est. Plot 13 Cobham} = \frac{\Sigma\theta \text{. Cobham}}{\Sigma\theta \text{ Webbs}} \times \theta \text{ Webbs plot 13} = .475$$

This was done because of the size of the disparity between the different 0-0-0 plot θ's for Cobham.

Fitting the response curve to these data with a new estimate of θ plot 13 shows that the quadratic phosphate coefficient is now significant ($P < .05$).

It is pertinent at this stage to consider why the linear nitrogen coefficient is significant for Webbs, and not for Cobham. The parameters θ, K, α and λ are all correlated to some extent, and a high value of θ is usually associated with a low K. This means that the increased value of θ with increased nitrogen is associated with a lower initial relative growth rate with increased nitrogen. There appear to be two possible explanations of the phenomena:

1) The increased nitrogen application has resulted in larger plants at the first harvest, and hence a reduced R.G.R. when fitted to the logistic model. (see appendix)
2) Because θ is the least precisely determined of the parameters, and small changes in K can greatly modify θ.

In fact fitting the logistic model with θ constant (for Webb $\theta = .226$, for Cobham $\theta = .362$) only emphasised the importance of the quadratic phosphate term, although only K for Webbs was significant ($P < .05$). Similarly an analysis of the joint θ's for the two varieties (e.g. for plot 1, θ joint $= (.623 + .423) / 2 = .523$) results in only the quadratic phosphate coefficient being significant.

For these reasons no further attention was given to the linear nitrogen coefficient for θ Webbs, and it was concluded that phosphate exerts the major effect on θ.

Time scale	Cobham	Webbs	Total
Time (chronological)	.1630	.1828	.3458
Solar radiation	.0889	.1305	.2194
H.U. 30	.0966	.1169	.2135
H.U. 40	.0676	.0910	.1587
H.U. 50	.0728	.1125	.1853
H.U. 39	.0702	.0928	.1630
H.U. 41	.0661	.0897	.1558
H.U. 42	.0641	.0882	.1523
H.U. 43	.0661	.0935	.1597

Table IV . Mean error sums squares for Cobham and Webbs.

With θ now fixed for each variety and phosphate level, new α's and K's were estimated for each plot and variety using the logistic model. These θ's were not estimated from the response surface model, but were obtained from the mean of the logistic model estimates.

e.g. θ for $P = -1 = (.514 + .304 + .278 + .638) / 4 = .344$

When the response model was fitted to the α 's and K's calculated with θ fixed according to variety and phosphate level the analysis (see appendix) again demonstrated the significance of the phosphate coefficients, $P < .05$ for Cobham quadratic and Webbs linear, and $P < .001$ for Webb quadratic.

K's were now fixed for each variety (as for θ previously) according to the phosphate level, and new α 's were calculated for each variety and plot. None of the coefficients of the surface response model for α were significant ($P < .05$), although both the quadratic phosphate and linear N x P coefficients were close to significance for both varieties.

In view of the similarity in the results for the two varieties, the weight per plant data were now combined (by adding the logarithms), in the hope of reducing some of the experimental error. The logistic model was used to determine α , K and θ for each plot, and these parameters were fitted to the response surface. This analysis in no case produced any significant coefficients (see appendix), but once again emphasised the importance of the quadratic phosphate term. In fact the quadratic phosphate coefficient was significant at $P < .1$, and the lack of a higher level of significance appears to be due once again to Plot 13.

The data were then fitted to the logistic model, with θ fixed according to the phosphate level, and the response model was fitted to the α 's and K's. Only the quadratic phosphate coefficient for K was significant ($P < .001$) θ and K were now fixed according to the plots phosphate level, and the logistic model again fitted to each plot, and the α 's then fitted to the surface response model. Only the quadratic phosphate coefficient is significant ($P < .05$), but the magnitude of the N x P term should be noted.

The results are in the appendix and are shown graphically in Figure 4. The logistic growth curves for 3 levels of superphosphate are shown in Figure 5.

Of the fertilizers under consideration clearly phosphate exerted the major effect on plant dry weight, irrespective of variety.

There does however appear to be a difference between the two varieties in their response to fertilizer. The peak of the phosphate response curve is much sharper for Cobham than for Webbs. In fact Cobham tends towards a quadratic response, while Webb tends towards a quadratic plus linear response. (see Appendix). Apart from this, the two varieties differ fundamentally in their growth curves (see Figure 6). Webbs having a larger α and K, and a smaller θ (see Table VI) than Cobham, with the result that, in the later harvests Webbs is the larger lettuce, although, at the early harvests Cobham, at least in this experiment, is larger because of more initial capital. It is postulated that this cross-over is partially due to the differences between the two varieties in the rate of leaf production. Cobham, having a greater rate of leaf production, results in shading between leaves on the same plant at an earlier stage than Webbs, and hence a less efficient (see Table V) photosynthetic apparatus.

Harvest	Cobham	Webbs	S.E. (5.D.F.)
1	0.8	0.6	± 0.11
2	4.0	2.9	+ 0.12
3	9.3	6.7	± 0.17
4	16.6	12.1	± 0.39
5	26.3	20.1	± 1.17

Table V . Number of leaves exceeding $\frac{1}{2}$" length.
Analysis of 6, 0-0-0 plots.

Parameter	Cobham	Webbs	S.E. (5.D.F.)
α	3.79	4.64	± .05
K	.0189	.0201	± .0011
θ	.286	.227	± .056

Table VI . Analysis based on the 6,0-0-0 plots.

Finally the near significance of the N x P coefficient for the joint analysis of α suggests that given a more sensitive experimental design, some response to nitrogen application might be anticipated.

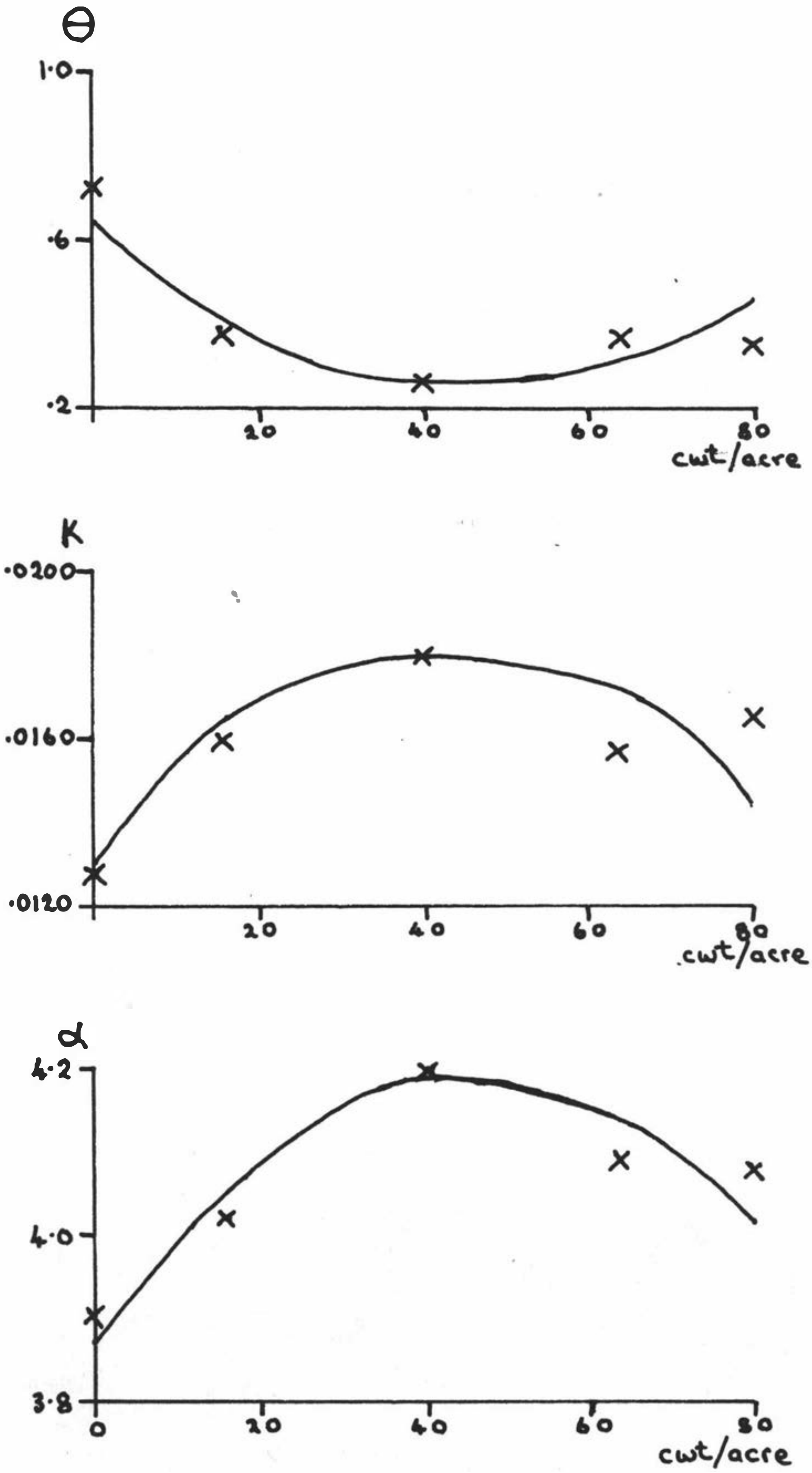

Figure 4. α , k, and θ parameters for the combined Cobham/Webbs dry weight per plant data fitted to serpentine superphosphate application rates.

An interpretation of the results in terms of Growth Analysis

The classical methods of growth analysis as exemplified by Watson (1952) involves the calculation of the Relative Growth Rate (R.G.R), and its components, the Net Assimilation Rate (N.A.R.) and Leaf Area Ratio (L.A.R.). Radford (1967) has defined these growth analysis formulae at an instant of time (t) when

1) W is a measure of plant material present, and
2) A is a measure of the magnitude of the assimilatory system as follows:

The relative growth rate is the increase of plant material per unit area of material per unit of time.

$$\text{i.e.} \quad \text{R.G.R.} = \frac{1}{W} \cdot \frac{dW}{dt}$$

The net assimilation rate is the increase of plant material per unit of assimilatory material per unit of time

$$\text{i.e.} \quad \text{N.A.R.} = \frac{1}{A} \cdot \frac{dW}{dt}$$

The leaf area ratio is the ratio of assimilatory material per unit of plant material present.

$$\text{i.e.} \quad \text{L.A.R.} = \frac{A}{W}$$

The traditional use of these formulae involves the calculation of mean R.G.R's., N.A.R's., and L.A.R's. over the time periods using the formulae:

$$\text{R.G.R.} = \frac{(\text{Log}_e W_2 - \text{Log}_e W_1)}{(T_2 - T_1)}$$

$$\text{N.A.R.} = \frac{(W_2 - W_1)}{(T_2 - T_1)} \times \frac{(\text{Log}_e A_2 - \text{Log}_e A_1)}{(A_2 - A_1)}$$

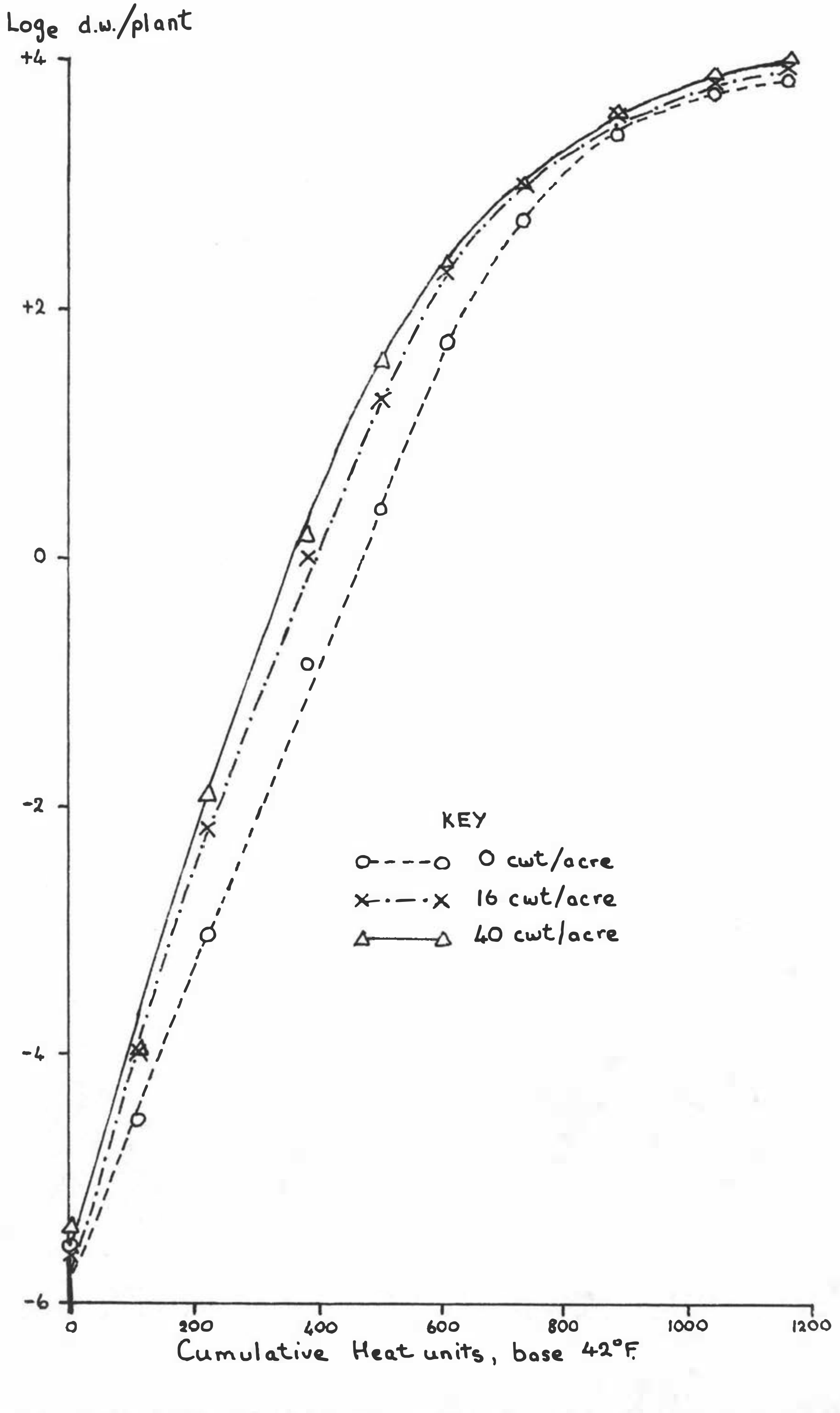

Figure 5. Combined Cobham/Webbs dry weights per plant fitted to the 4 parameter logistic model for 3 levels of serpentine superphosphate application.

$$\text{L.A.R.} = \frac{(A_2 - A_1)}{(W_2 - W_1)} \times \frac{(\text{Log}_e W_2 - \text{Log}_e W_1)}{(\text{Log}_e A_2 - \text{Log}_e A_1)}$$

W_1, W_2 is usually the plant dry weight, and A_1, A_2 the leaf area at times T_1, T_2. Radford (1967) has emphasised that it is the relationships between time and A, and time and W, which should be our primary consideration, with a view to discovering the form of these growth curves.

Both Vernon and Allison (1963), and Hughes and Freeman (1967) have used a polynomial function to examine these growth curves.

Vernon and Allison fitted their data to:

$$W = a + bt + ct^2$$

$$A = a^1 + b^1t + c^1t^2$$

so that at any instant of time:

$$\text{R.G.R.} = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{b + 2\,ct}{a + bt + ct^2}$$

$$\text{N.A.R.} = \frac{1}{A} \cdot \frac{dW}{dt} = \frac{b + 2\,ct}{a^1 + b^1t + c^1t^2}$$

$$\text{L.A.R.} = \frac{A}{W} = \frac{a^1 + b^1t + c^1t^2}{a + bt + ct^2}$$

This was for *Zea mays* post-tasselling data, and the variances for the different harvests were not excessively different.

Hughes and Freeman fitted their data to $\log_e$ functions.

$$\log_e W = a + bt + ct^2 + dt^3$$

$$\log_e A = a^1 + b^1t + c^1t^2 + d^1t^3$$

so that:

$$\text{R.G.R.} = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{d\,(\log_e W)}{dt}$$

$$\text{L.A.R.} = \frac{A}{W} = \text{antilog.}_e\,(\log_e A - \text{Log}_e W)$$

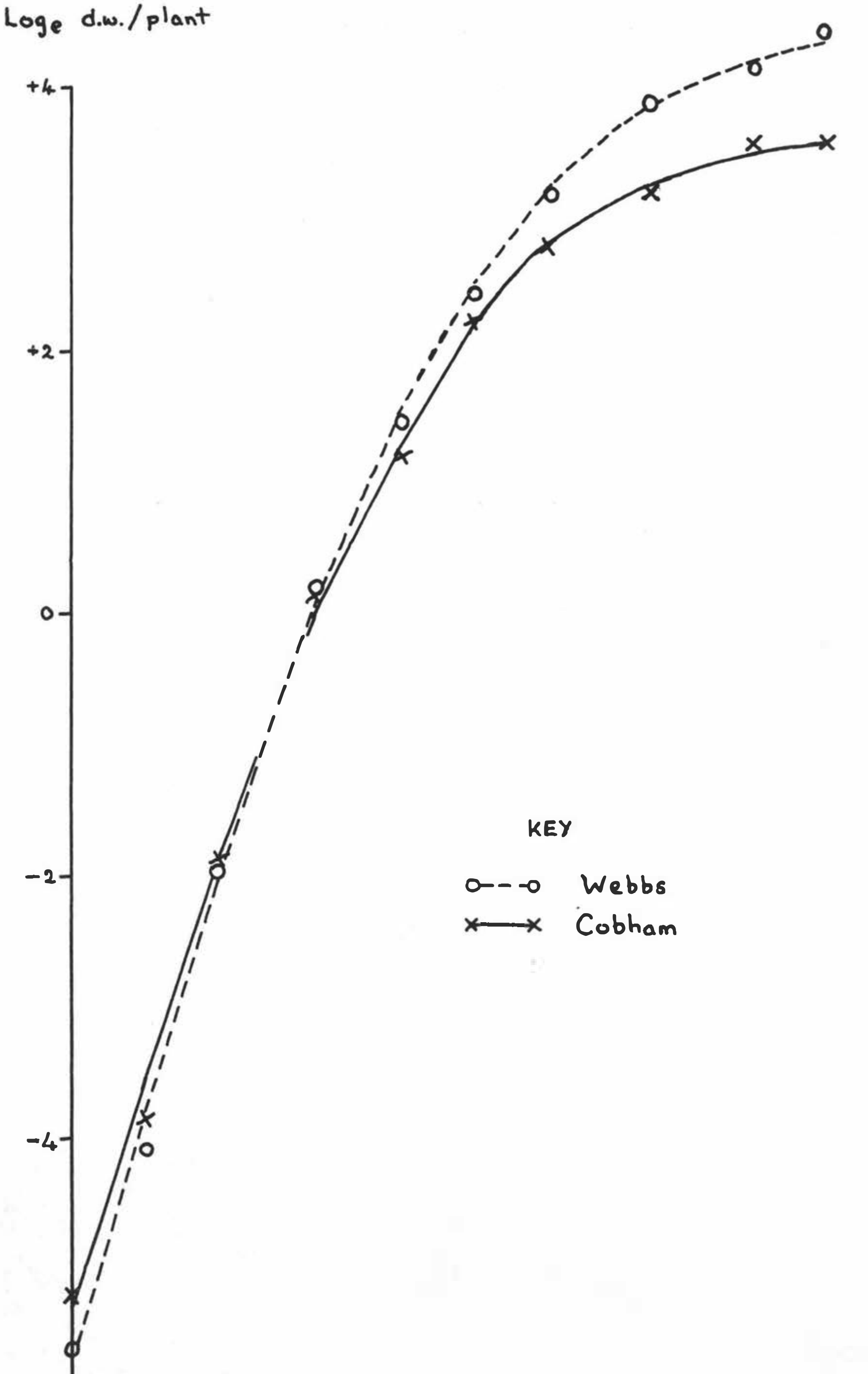

Figure 6. Dry weights/plant for Cobham and Webbs fitted to the 4 parameter logistic model. Based on 0--0--0 plots.

$$\text{N.A.R.} = \text{R.G.R.} \div \text{L.A.R.}$$

Radford (1967) has used an exponential function to describe the growth of tall fescue,

$$W = \alpha + \beta e^{\gamma t}$$

$$A = \alpha' + \beta' e^{\gamma' t}$$

weighting each point according to the inverse of its variance, so that:

$$\text{R.G.R.} = \frac{\beta\gamma e^{\gamma t}}{\alpha + \beta e^{\gamma t}}$$

$$* \ \text{N.A.R.} = \frac{\beta\gamma e^{\gamma t}}{\alpha' + \beta' e^{\gamma' t}}$$

$$\text{L.A.R.} = \frac{\alpha' + \beta' e^{\gamma' t}}{\alpha + \beta e^{\gamma t}}$$

* There is an error in Radford's formula for N.A.R. as the prime for in the denominator has been omitted in his paper.

Having used the logistic model to examine dry weight ~ time trends, it is logical to use the same model to examine the leaf area ~ time relationships. For the first two harvests, leaf areas were measured directly, using an air flow planimeter, but it was necessary to determine the leaf areas for the other 8 harvests indirectly.

This was done by calculating the allometric relationship between leaf dry weight (WL) and total plant dry weight (WT) for each variety, harvest, and plot, using as data the sample plant parts yields of the wide, medium and close spaced plants. The formula used was:

$$\text{Log}_e \text{WT} = \text{Log}_e \text{WL} \times \theta + \text{Log}_e K$$

The leaf dry weight of the hypothetical plant in a non-competitive situation was determined using the allometric relationship for that particular variety, plot and harvest date. As the leaf dry weight/leaf area relationship had previously been determined for each variety, plot, and harvest by the 'punch' method (albeit for a medium spaced plant), the determination of the leaf area of the hypothetical plant was then straightforward.

The leaf areas for each variety (and the mean leaf areas for the two varieties, obtained by combining the logs.), for all 20 plots, were now fitted to the logistic model, using the heat units above a base of 42°F. time scale. From the logistic growth curves for total plant dry weight (obtained earlier) and for leaf area, it is now possible to calculate plant leaf areas, or dry weights at the various harvest dates. Having determined W for any particular time, it is a simple matter to calculate $\frac{dW}{dt}$ from the differential equation on which the logistic model is based:

$$\frac{dW}{dt} = kW \left[1 - \left(\frac{W}{A}\right)^{\frac{1}{6}} \right]$$

$$\text{Then R.G.R.} = \frac{1}{W} \cdot \frac{dW}{dt}$$

$$\text{N.A.R.} = \frac{1}{A} \cdot \frac{dW}{dt}$$

$$\text{L.A.R.} = \frac{A}{W}$$

These results clearly demonstrate a higher overall relative growth rate for Webbs compared with Cobham. This appears to be due to a higher net assimilation rate for Webbs, in spite of Cobham having a larger leaf area ratio. The higher net assimilation rate of Webbs may be due to its smaller leaf area/gm. dry weight of leaf. (see Table VII)

Var./Harvest	1	2	3	4	5	6	7	8	9	10	Mean
Cobham	351	484	351	354	351	552	586	470	534	485	452
Webbs	218	430	352	299	317	413	423	386	408	362	360

Table VII. leaf area/ dry weight leaf. (cm^2/gm.)

The mechanism for the increased net assimilation rate could be either a greater rate of photosynthesis, or a slower rate of respiration or both. One possibility could be that the thicker leaf is able to absorb more radiation. This would be important while plants are small, and not competing for light, but at high densities all the radiation would be absorbed by the crop canopy. This appears to be borne out by the similarity of the yield potential for the two varieties. The differences in leaf area ratio between the two varieties appear to be due solely to differences in leaf area/gm. leaf dry weight, and not due to differences in the partitioning of photosynthate (see Table VIII). The differences at the last two harvests is due to the increasing proportion of stem in the variety Cobham.

Var./Harvest	1	2	3	4	5	6	7	8	9	10
Cobham	69	81	88	91	89	92	89	87	84	81
Webbs	70	82	89	91	89	90	89	86	87	84

Table VIII. Percentage of leaf dry weight/total plant dry weight

An examination of the relative growth rate for the different phosphate levels shows an increasing rate with increased phosphate application up to 40 cwt. This is due predominantly to differences in net assimilation rate. See Figure 9.

There was no apparent difference between the leaf area/gm. leaf dry weight for the different phosphate treatments, and the leaf area ratios were similar. There was, however, a difference in the distribution of photosynthate when the Ocwt/acre phosphate level was compared with the other levels.

	- α phosphate			Mean -1 and 0 phosphate		
Harvest	% Lvs.	%Stm.	%Rts.	% Lvs.	%Stm.	%Rts.
1	60.0	8.1	33.9	69.0	6.1	24.9
2	76.1	7.1	16.8	80.7	6.2	13.1
3	86.0	3.4	10.6	88.3	3.5	8.2
4	90.8	3.5	5.7	90.2	4.2	5.6
5	88.3	4.4	7.3	88.8	5.7	5.5

Table IX. Dry matter distribution, phosphate treatments.

This effect could not be checked as in the experimental design there is only a single no phosphate plot. The prolonged period of exponential growth which occurs in spite of a falling net assimilation rate for the first 5 or 6 weeks appears to be due to changes in the distribution of dry matter, i.e. an increase in the shoot/root ratio with time. Some of this effect is probably due to the failure to obtain more than a nominal amount of roots from the soil in the later harvests, but nevertheless the trend appears to be real.

The near linear manner in which the net assimilation rate falls (see Figure 10) for the - α , -1, θ phosphate treatment may be due to the use of the logistic model to fit the data, and smooth the curve, but could be a real effect. The reason for the effect of phosphate fertilizer on net assimilation rate appears to have no simple explanation.

Relative growth rate, and leaf area ratio time trends for the two varieties, and for 3 phosphate levels are shown in Figures 7 and 8 (Relative Growth Rates) and in Figures 11 and 12 (Leaf Area Ratios).

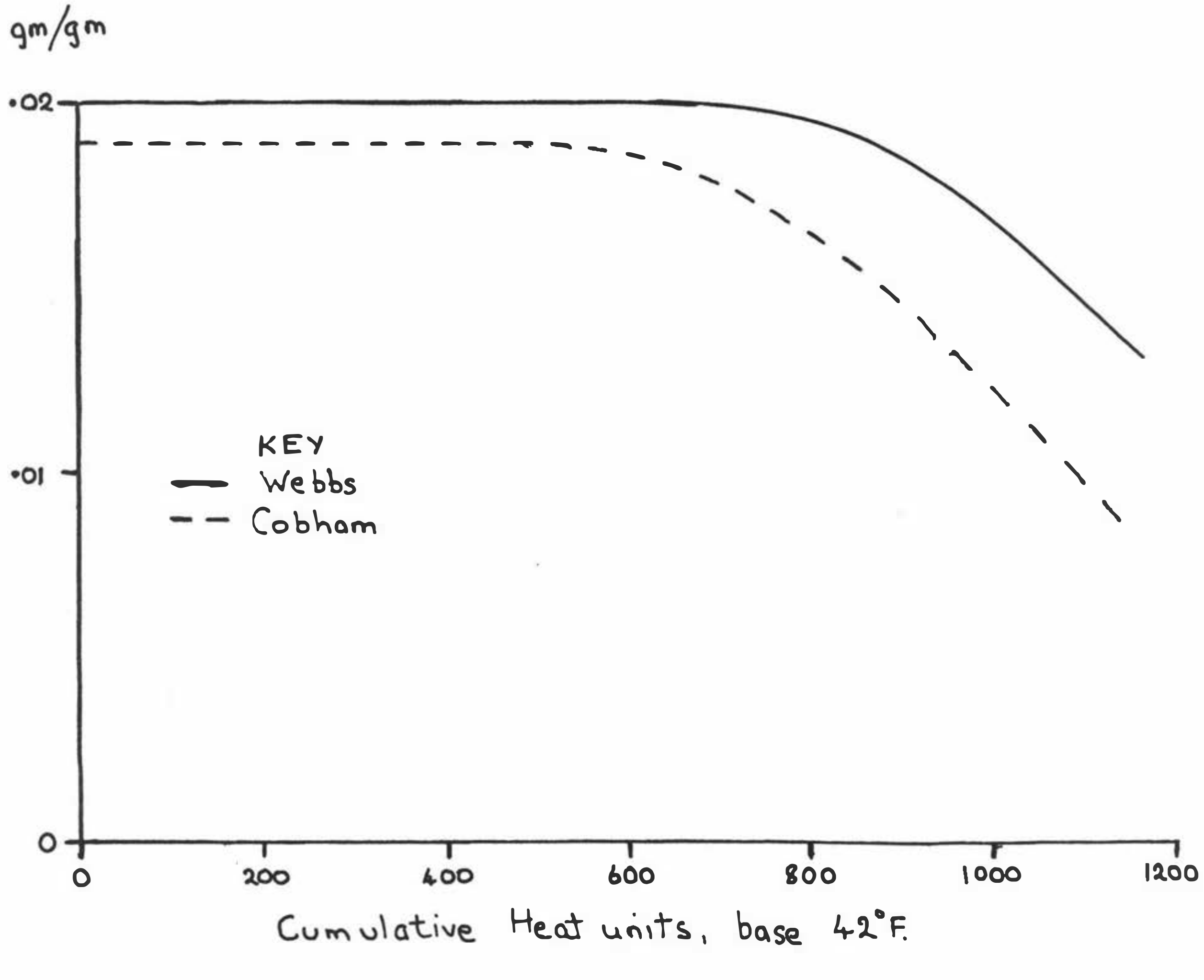

Figure 7. Relative growth rate time trends for Cobham and Webbs.

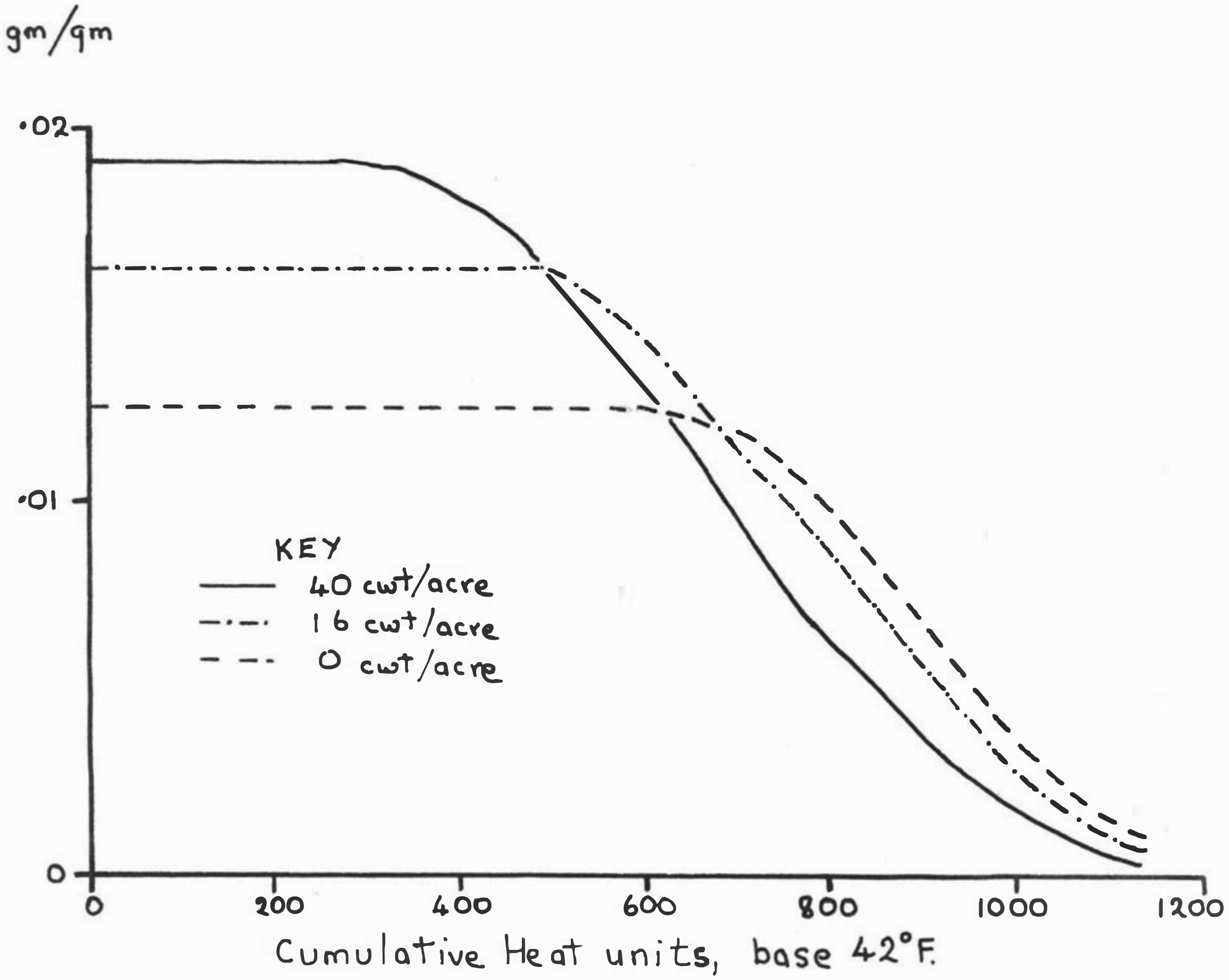

Figure 8. Relative growth rate time trends for joint Cobham/Webbs data at 3 levels of serpentine superphosphate.

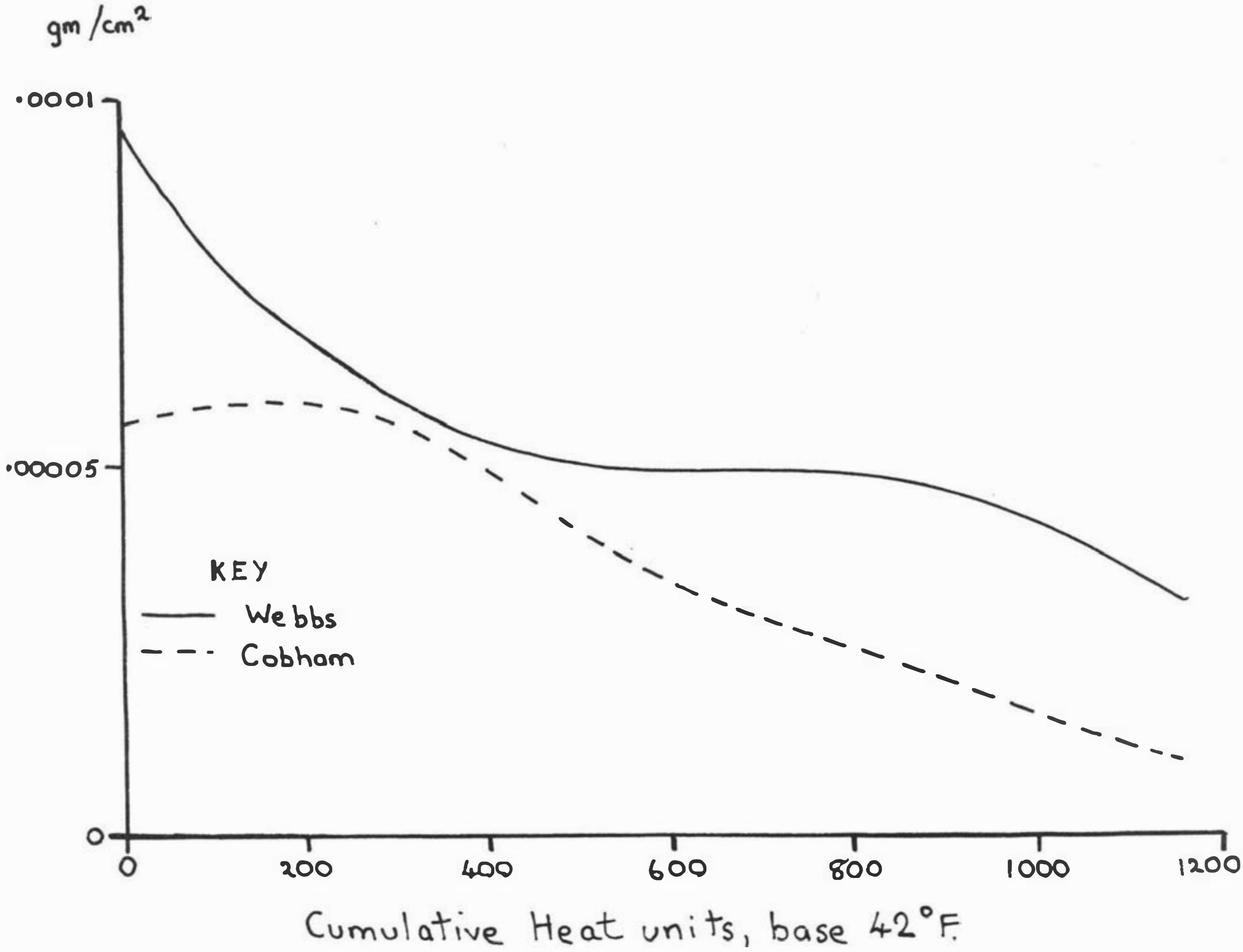

Figure 9. Net assimilation rate time trends for Cobham and Webbs.

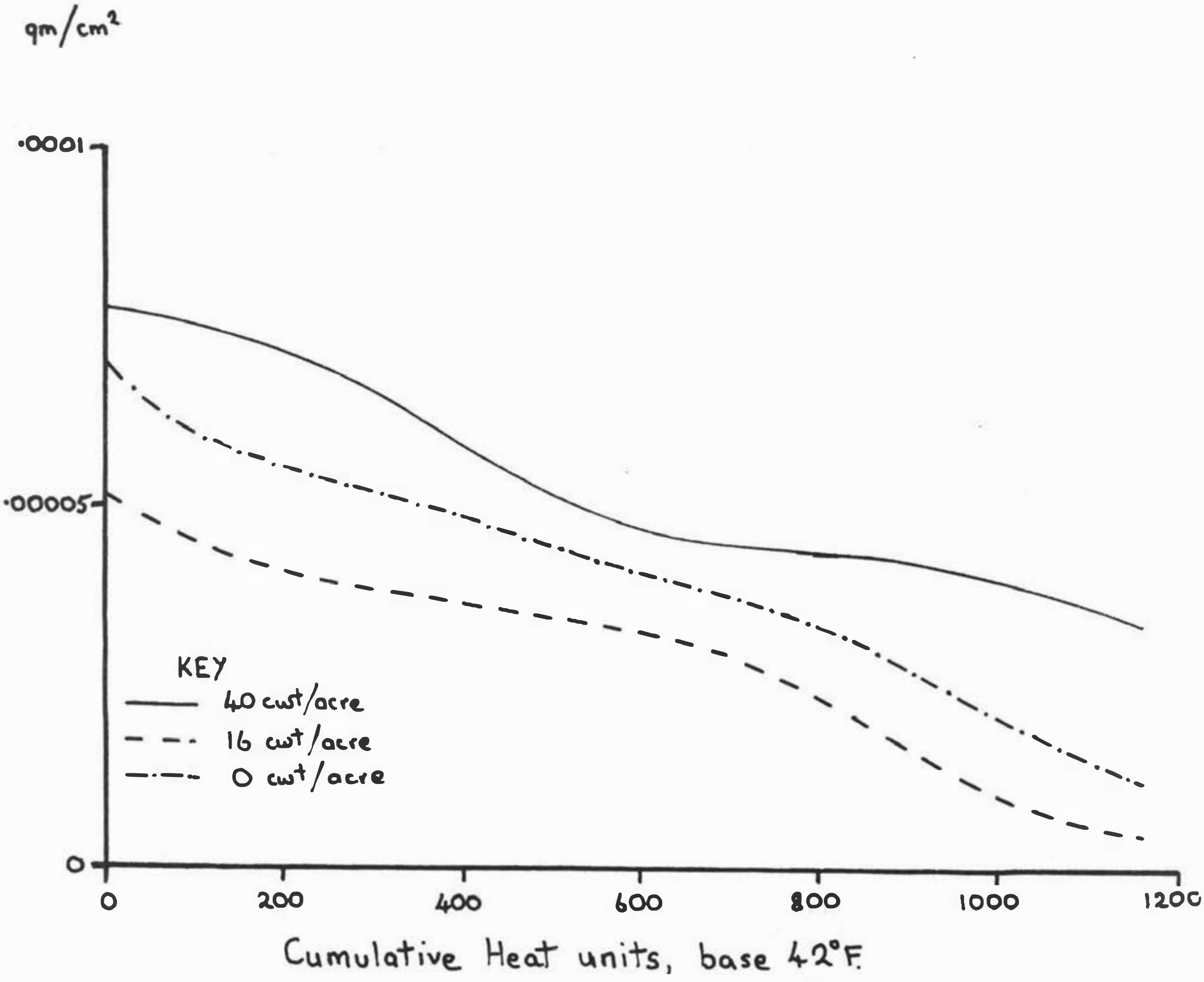

Figure 10. Net assimilation rate time trends for joint Cobham/Webbs data at 3 levels of serpentine superphosphate.

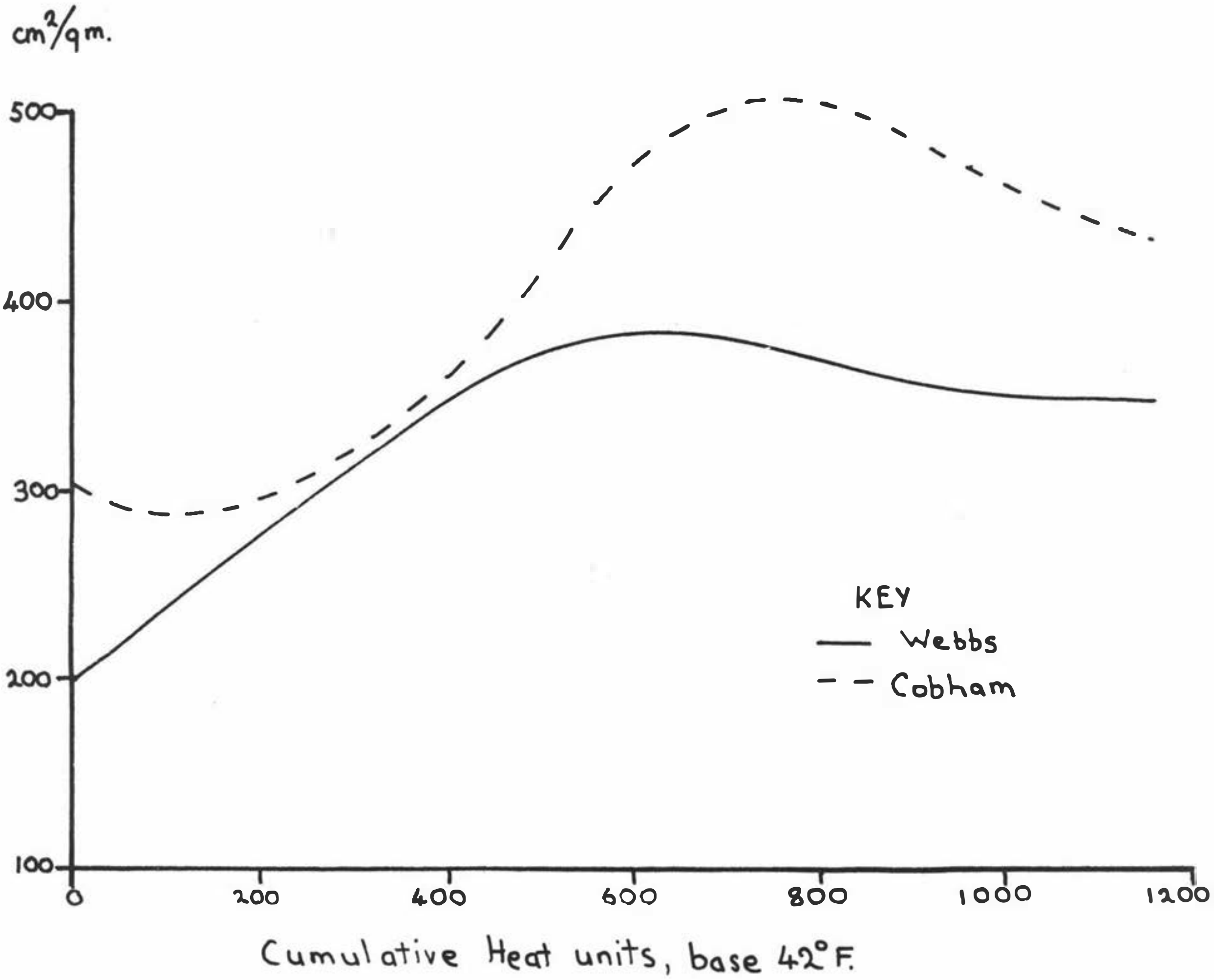

Figure 11. Leaf area ratio time trends for Cobham and Webbs.

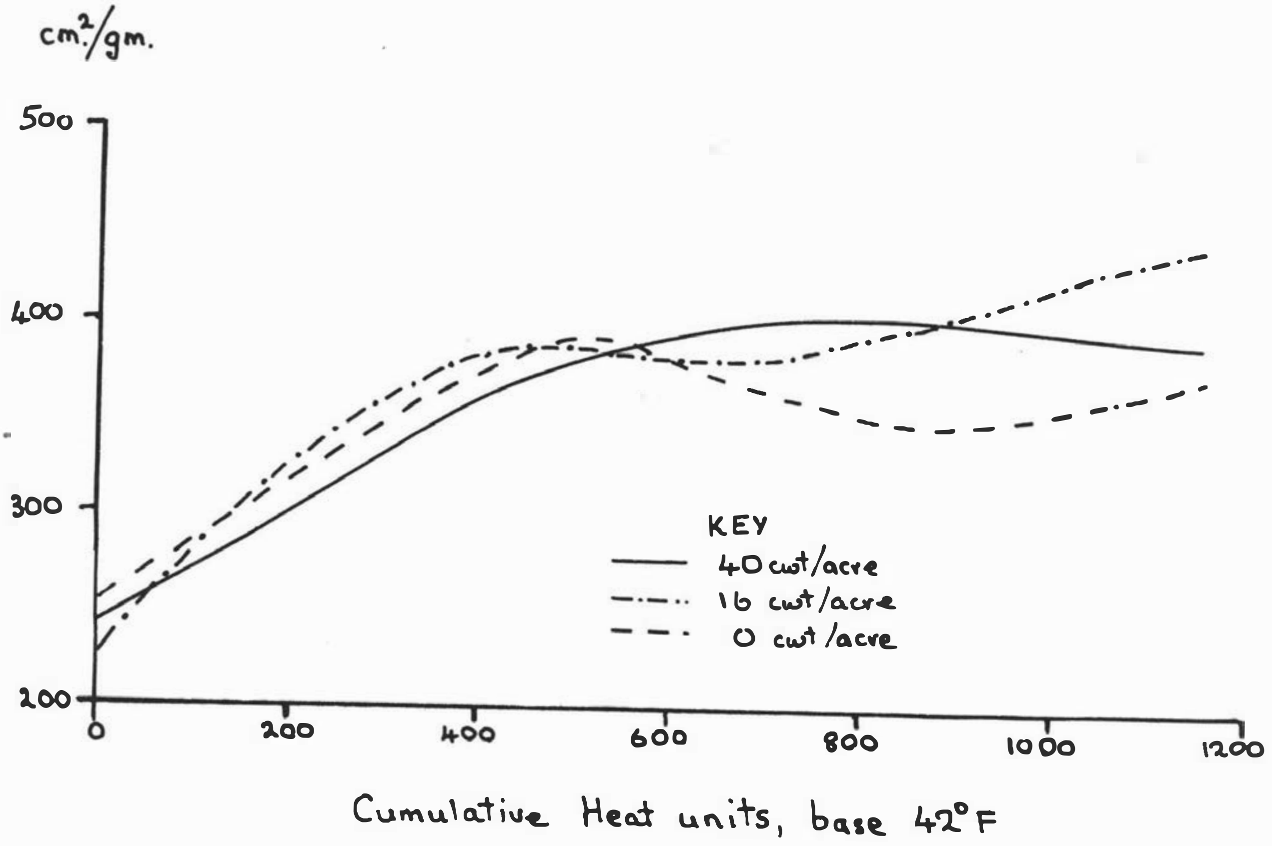

Figure 12. Leaf area ratio time trends for joint Cobham/Webbs data at 3 levels of serpentine superphosphate.

Analysis of A and B parameters

The A and B parameters calculated by the reciprocal yield-density model

$$W^{-1} = A\rho + B$$

with B constant for each variety and harvest, are shown in the appendix.

Because these parameters have been determined from small samples the inaccuracies of such a technique do not permit meaningful analysis of the A's for each plot variety, and harvest. However as both the A and B parameters demonstrate a marked asymptotic relationship with time, it was hoped that fitting a suitable model to the secondary data would eliminate some of the inaccuracies, and further simplify the analysis.

The Exponential model

$$Y = a + b\,e^{-kt}$$

when a, b, and k are constants, t is time, and e is 2.718 - appeared to fit the data while attempts to fit the logistic function to the reciprocal of A (or B) were not successful due to the absence of accurate estimates of A and B for the early harvests.

For this reason the exponential model was used, and initially the B's for each variety were fitted using a weighted multiple regression technique, the weights used being the inverse of the variance of the A parameter of the 6 0-0-0 plots for the variety and harvest.
The results obtained were:

Webbs $B = .005929 + 1.3126\,e^{-1.033t}$

Cobham $B = .020538 + 1.5599\,e^{-1.051t}$

Due to the similarities in the k parameter, and their proximity to 1.0, the data were fitted to a simpler model

$$Y = a + be^{-t} \qquad \text{(i.e. k, fixed at 1.0)}$$

with the following results:

$$\text{Webbs} \quad B = .005213 + 1.2394\ e^{-t}$$

$$\text{Cobham} \quad B = .09843 + 1.3806\ e^{-t}$$

These results are shown graphically in Figure 13, with the dependent variable transformed to a log scale in order to show the relationship more clearly. It is pertinent to note that at all times, the genetic potential (for weight) of Webbs is greater than that of Cobham - somewhat different from the actual results obtained, when Cobham is larger initially, and becomes smaller than Webbs between the 3rd and 4th harvest. This could be due to the inaccuracy with which B is determined in the early harvests. An examination of the A parameters for the two varieties suggests that the A's are independent of genotype. This hypothesis was tested by carrying out an analysis on the 6 central point plots (0 - 0 - 0 plots) of the two varieties by fitting the weighted exponential model

$$Y = a + be^{-t}$$

to each plot and variety, and then testing the significance of the a and b parameters for each variety using an analysis of variance. There was no significant difference found between these parameters for the two varieties, and it is postulated therefore that (in this experiment) the A parameters for the two varieties can be considered to be the same for each plot and harvest. This evidence supports a similar hypothesis of Bleasdale (1966b) for onions.

The weighted exponential model was now fitted to the joint A's for each plot, but the resulting a's and b's still showed too much variation

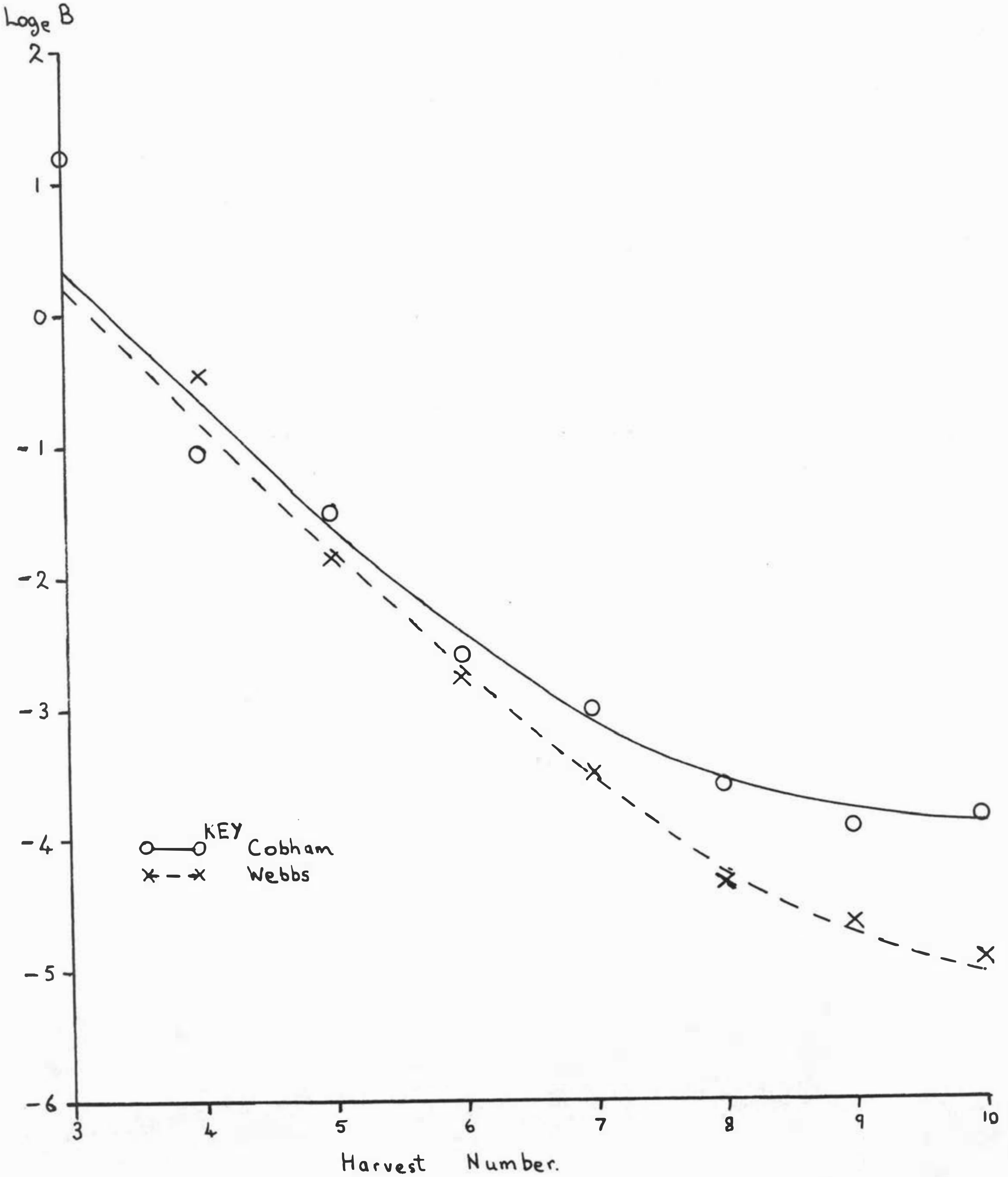

Figure 13. Log$_e$ B (from reciprocal yield–density model) for Webbs and Cobham fitted to an exponential model.

to show a meaningful relationship. Making a, or b constant also proved unsatisfactory because the relationship between a and b appeared to be a proportional one, i.e. the larger a, the larger b. For this reason the model was modified to:

$$Y = a + n a e^{-t}$$

when n is constant for all plots. n was found to be equal to 131, and the resulting 'a' parameters were now fitted to the response surface, and the coefficients tested for significance.

The results (see appendix) show a significant response to phosphate (quadratic), and the N x P interaction.

This interaction is virtually unexplainable, as it shows a high yield potential from

- 1N - 1P and + 1N + 1P

and low yield potentials from

+ 1N - 1P and - 1N + 1P

N P	- 1	+ 1
- 1	.00926	.01232
+ 1	.01091	.00831

0-0-0 plots = .00943

a parameter means

No explan ation is offered for this interaction, and attention is only directed at the significant phosphate response. Although the linear phosphate coefficient is not significant, it must be included in the fitted model (see fig. 14). In fact from the data the fitting of a quadratic model only appears to be a reasonable assumption up to the 0 level. For this reason (and also the difficulty of showing that +1 and + α curves on the same graph as the others) only the - α, -1 and 0

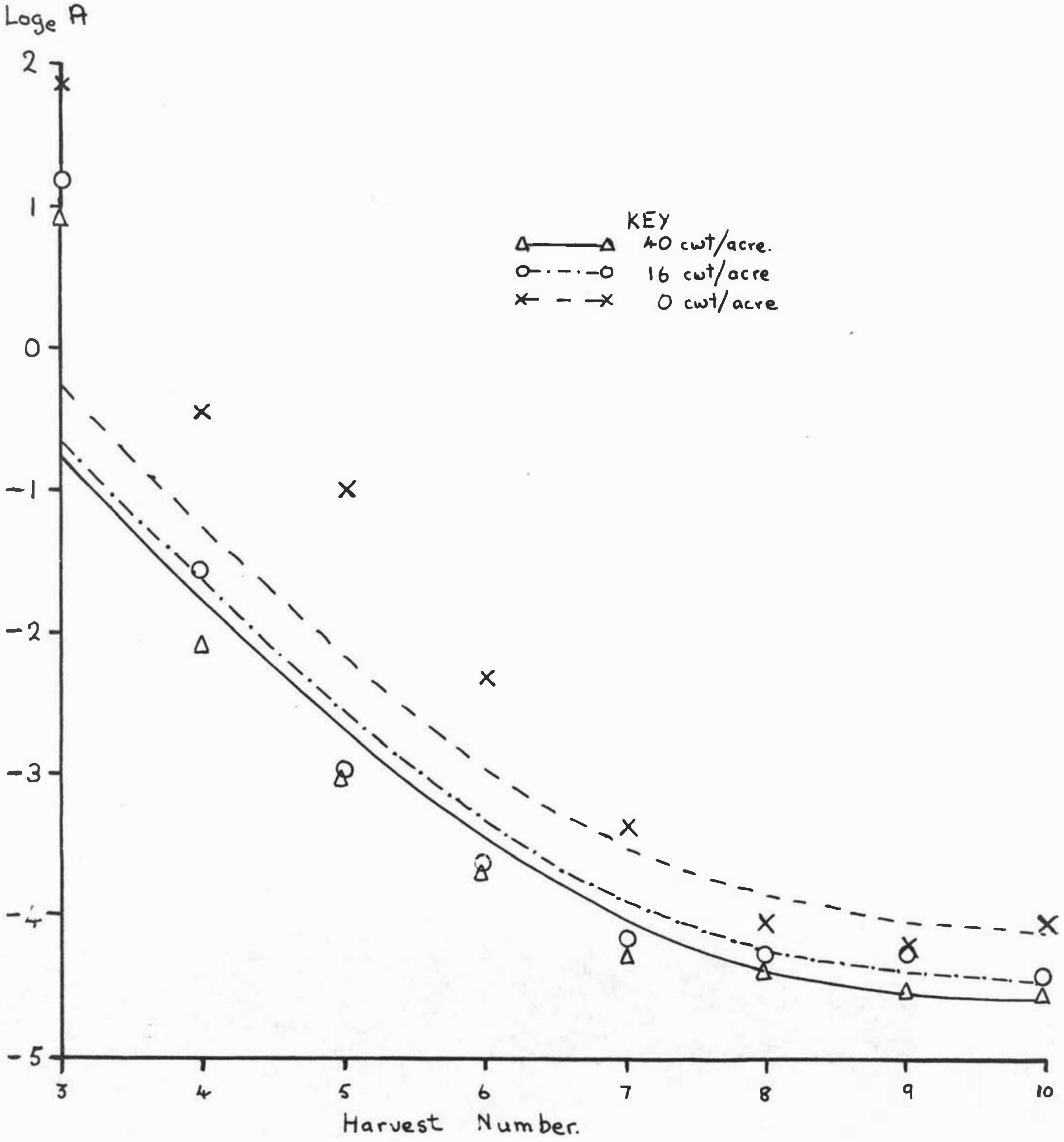

Figure 14. Log$_e$ A (from the reciprocal yield-density model) for 3 levels of serpentine superphosphate, fitted to an exponential model.

phosphate levels are shown of $\log_e$ 'a' against time. Log_e 'a' is used merely to show the results more clearly graphically.

Plant Losses

An unreasonable number of plants were lost towards the end of the experiment due to Sclerotinia, particularly in the variety Cobham. In New Zealand, lettuce is particularly susceptible to Sclerotinia during the summer, but the number lost was far more than one might expect, and the severity of the attack could have been caused by changes in the soil ecological balance following sterilization. In any future experiment with lettuce the systemic fungicide 'Benlate' could reduce the severity of such an attack.

An examination of the pattern of plant losses due to Sclerotinia showed that fertilizer treatment had little effect, and the main differences appeared to be between the varieties, and the effect of time. There was no apparent effect of plant density on the pattern of plant loss with the exception of the final harvest of Cobham - when losses were significantly greater at densities in excess of 2 plants per sq. ft. As Cobham was 'going to seed' at this harvest in terms of marketable yield this is of no commercial importance.

An analysis of variance of the plants missing due to Sclerotinia for the last 4 harvests shows a significant ($P < .001$) variety effect, and a significant ($P < .001$) effect of harvest, but the variety x harvest interaction was not significant. The linear component for harvests was highly significant, and the results are shown in Figure 15.

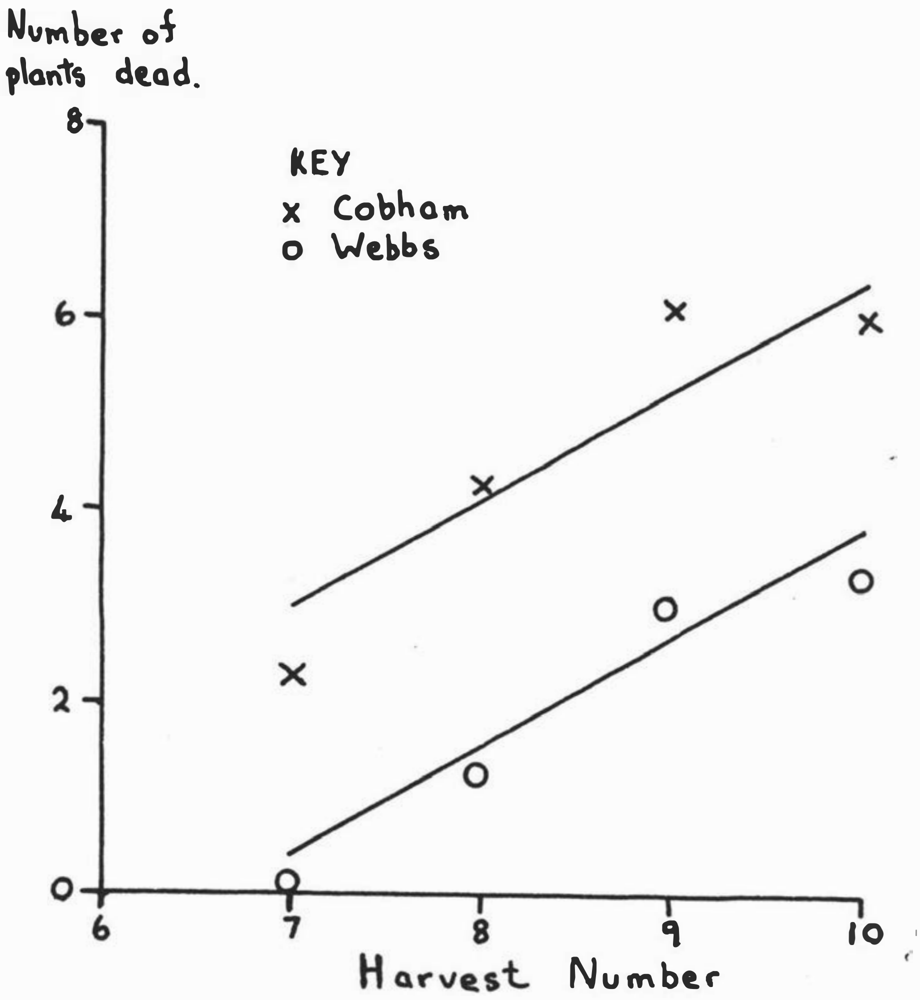

Figure 15. Plant losses due to Sclerotinia, showing the number of dead plants (out of 13) with reference to harvest date and variety.

Marketable Yield

Although dry weight per plant (or per unit area) can be a useful measure for the physiologist, it is of little value to the horticulturist unless it can be related to marketable yield. Marketable yield for lettuce is itself a very nebulous attribute, as it depends entirely upon the market requirements, and the harvesters subjective assessment of maturity. What constitutes a marketable lettuce will vary with the market, the time of the year, and the demand.

In this experiment, a marketable lettuce was one which was considered to be acceptable on a British market in the summer. The reason for basing this on Britain is because Butterhead lettuce is not grown commercially in New Zealand, while both types are grown in Britain in the summer months.

Because of small samples, a reliable assessment of marketable yield proved difficult.

The method used was as follows:

The percentage of marketable lettuce for each spacing, variety and harvest was obtained. The ratio of fresh weight of top/total plant dry weight was determined for each variety and harvest. This fresh weight of top constitutes the potential marketable yield, which becomes the marketable yield when multiplied by the percentage marketable. Total plant dry weight for the different treatments, spacings, harvests, and varieties were derived from the reciprocal yield-density model results. Even so, cetain anomalies had to be 'smoothed out'.

As marketable lettuce were only harvested from harvest 7 - 10, linear regressions were calculated on the reciprocal yield-density parameters A, and B, i.e. The 'genetic potential' $(\frac{1}{B})$ for Cobham, and Webbs was plotted against time. The 'yield potential' $(\frac{1}{A})$ for the $-\alpha$, - 1, and 0 , phosphate levels was plotted against time. This 'yield potential' is a joint one between Cobham and Webbs because of the lack of significance between the varieties in this respect. These 5 regression lines were used to calculate A, and B parameters for the final four harvests, and from these parameters were calculated the total plant dry weight per square foot → total fresh weight of top per square foot, → marketable yield/square foot.

Plotting these estimated marketable yields/sq. ft. against plant density can be shown as a simple quadratic curve, of the form

$$Y = ax + bx^2$$

which can be fitted by plotting

$$\frac{y}{x} \text{ against } x$$

i.e. $y = a\,x + b\,x^2 \qquad y = x\,(a + bx) \qquad \frac{y}{x} = a + bx$

The plant population which has maximum marketable yield is obtained by differentiating

$$\text{i.e.} \quad \frac{dy}{dx} = a + 2\,bx$$

but $\frac{dy}{dx} = 0$ for maximum marketable yield, $x = -\frac{a}{2b}$

The results are shown in Table X, and graphically for each variety in Figures 16, and 17.

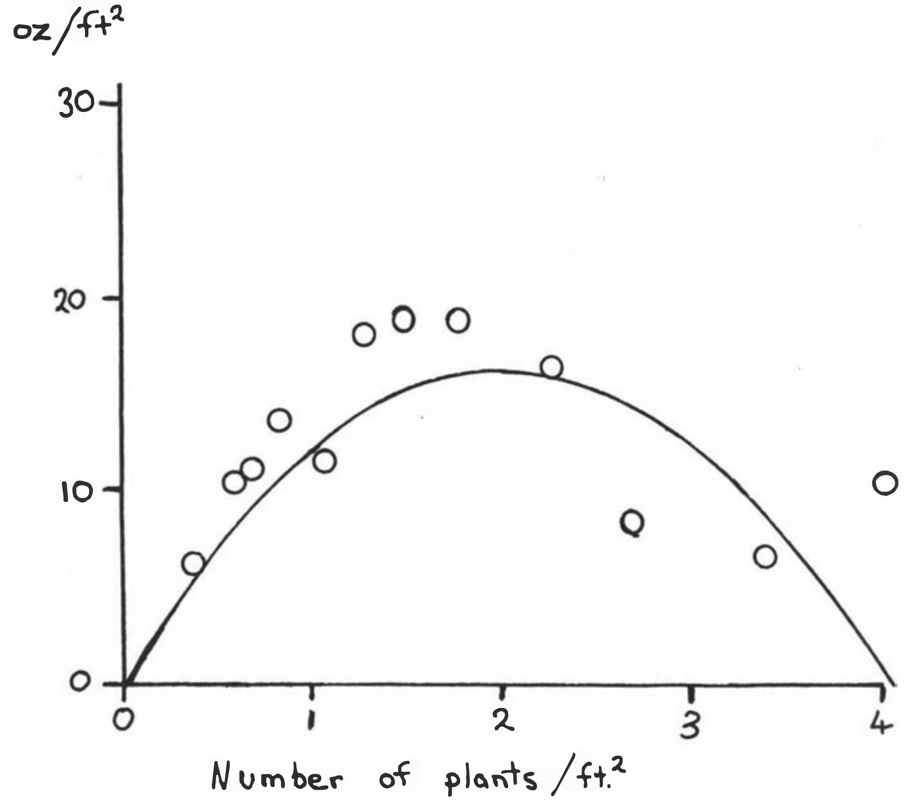

Figure 16. Marketable yield of lettuce/sq.ft. Cobham, harvest 8, with quadratic function fitted.

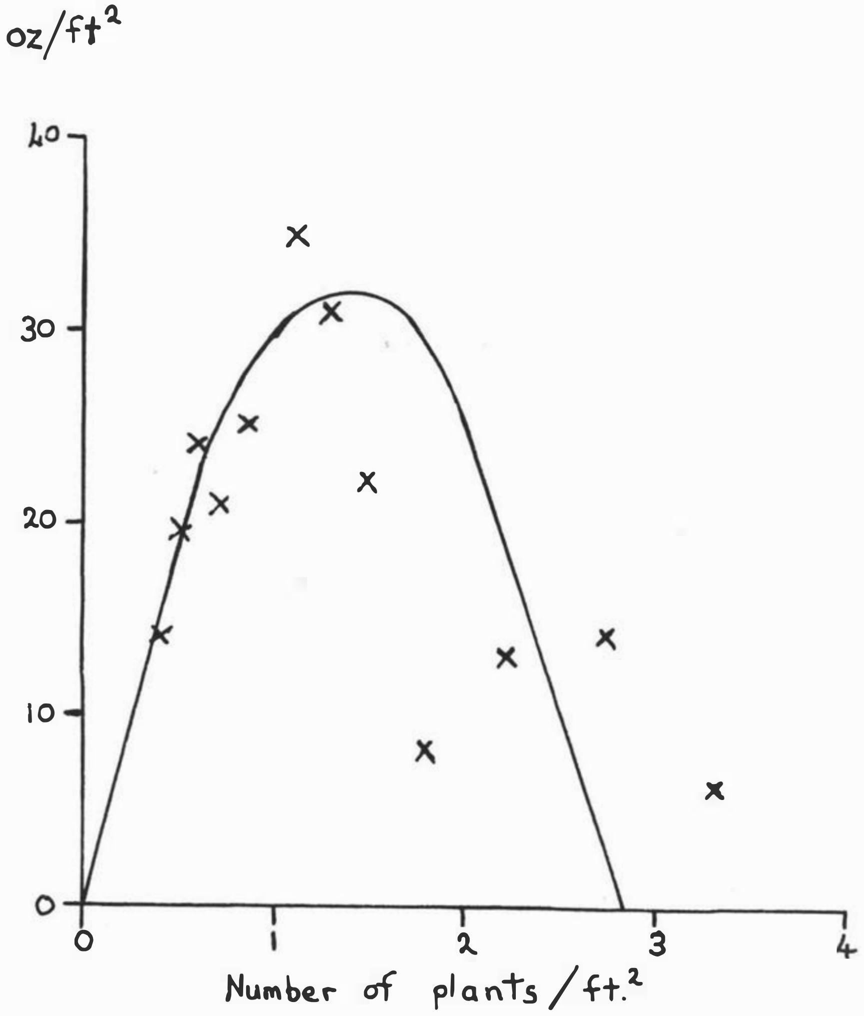

Figure 17. Marketable yield of lettuce/sq.ft. Webbs, harvest 9, with quadratic function fitted.

Variety	Harvest	Phosphate Level	a	b	X max	Yield at X max
Cobham	7	0	10.44	-2.61	2.00	10.4
Cobham	8	- α	13.75	-3.53	1.95	13.4
Cobham	8	- 1	15.58	-3.88	2.00	15.6
Cobham	8	0	16.07	-3.97	2.02	16.2
Cobham	9	0	20.75	-5.57	1.87	19.4
Webbs	9	- α	37.71	-13.90	1.36	25.6
Webbs	9	- 1	44.63	-16.30	1.37	30.6
Webbs	9	0	46.70	-16.99	1.37	32.0
Webbs	10	0	62.05	-22.51	1.38	42.8

Table X. Calculated polynomial parameters, with derived maximum marketable yield and related density.

Although the results for Cobham (harvest 9) and Webbs, (harvest 10) are included as marketable lettuce, it must be stated that although they had not 'gone to seed' they were tending towards overmaturity with the exception of the - α phosphate plot, and the optimum harvest date for quality and yield was harvest 8 for Cobham and harvest 9 for Webbs. As there was only a single - α phosphate plot in the experiment it is impossible to draw any conclusions in this respect. For the same reason although it is probably that the percentage of marketable lettuce from the - α phosphate plot was less than the other plots, the absence of replicates prevented this from being examined.

From these results, for maximum marketable yield, Cobham should be grown at 2.0 plants per square foot, and Webbs at 1.4 plants/square foot, but this takes no account of missing plants something that it is hoped would not normally occur.

As about 25% of the Cobham plants were missing at harvest 8, some modification in the density for maximum marketable yield is necessary. The simplest approach appears to be to increase the area per plant by 25%

i.e. 2.0 plants/sq.ft. = 72 sq.ins. per plant
which + 25% = 90 sq.ins. per plant i.e. about $9\frac{1}{2}$" x $9\frac{1}{2}$"
1.4 plants/sq.ft.

For Webbs at harvest 9, about 20% of the plants were missing, and carrying out a similar calculation as that for Cobham, results in a decrease in the optimum plant density from 1.38 to 1.15 plants per sq.ft. (approx. 11" x 11")

Nelder (1961b) has suggested that optimum density for maximum marketable yield of lettuce is greater for high yielding compared with low yielding crops. This appears to disregard the fact that a marketable lettuce must not only be of 'acceptable' size, and hearted, but should have a fairly flat base, for ease of packing. At high plant densities lettuce tend to develop pointed bases (peaky lettuce), and this has been noted by Sale (1966) who found that maximum marketable yields were achieved for the butterhead variety Borough Wonder at 9" - 10" square under wet or irrigated conditions, and at 12" square under dry conditions. Sales marketable yields - ranging from 10 - 14 oz/sq.ft. at the optimum spacing for a butterhead lettuce, are similar to those obtained in this experiment.

The reason why we can expect a heavier marketable yield from Webbs compared with Cobham - assuming optimum harvest date and plant density, is due mainly to the delay in maturity of Webbs, resulting in additional yield. Nichols (1965) has noted this previously with two butterhead varieties of different maturity times. In the case of Webbs and Cobham, this effect would be supplemented by the difference in carbohydrate assimilation efficiency.

Discussion

It is easy, in retrospect to say that the decision to use a rotatable design in this experiment was wrong, and that some form of randomised block design would have been a more efficient use of resouces. There can be little doubt that the inherent lack of robustness in the rotatable design reduced the value of the results, and substantially increased the number of computing man hours required to obtain meaningful results. Probably the relative lack of success stems from the extremely small sample taken at each harvest, but sample size had to be limited because no technical assistance was available. Webster (1969) has had some success with this design with vegetable fetilizer studies, and Dillon (1968) has advocated this type of design in agronomic fertilizer experiments.

Faced with the same problem today, my first strategy would be to increase the range of plant densities under examination, particularly at the high density end, where a population of (say) 144 plants/square foot should enable a more accurate determination of the yield-density relationship to be obtained, especially at the very early harvests. With plant populations of this density, the systematic designs are no longer feasible, and an alternative could be to sow beds (by means of a Stanhay tandem precision drill), of the different plant populations.

Then, providing that adequate resources in terms of labour and facilities were available, randomised block design would be substituted for the rotatable design. The need for the 'optimum response' to occur near the central points, and the lack of replication at the $-\alpha$ and $+\alpha$ levels would be important reasons for such a decision. Nevertheless it is conceded that starting with very little idea of the type of response one might expect on this soil type, the rotatable design has proved an efficient method to enable a single person to grow and record the effect of variety, spacing, and five levels of N, P, and K. Analysis and interpretation of the results would not necessarily be different although initially it would be necessary with the more precise data to test my assumption that the genetic potential in the reciprocal yield-density model is constant for any one harvest and variety. More precise data could also allow my modified yield-density model to be more stringently tested, particularly at the early harvests.

More precise data would perhaps permit a different type of analysis of the A and B parameters from the yield-density model. It would be especially valuable to determine how the yield potential is affected by time and nutrition, and this should be possible by using higher plant densities, particularly at the early harvests.

Larger samples might permit the analysis of growth at the different densities to be examined solely in terms of a logistic function, although efforts to do this with my data were not successful.

The plants response to soil fertilizer application is very much a function of soil type, and in this particular case the soil type was known to have a big response to phosphate for vegetables, as previous work (Nichols, 1967) with vegetables had shown.

The use of the logistic model to help in interpreting fertilizer responses is not new, having been used with mixed success by Austin et al (1964) at Wellesbourne. Although one reason for their lack of success was the overriding effect of soil moisture stress, it appears likely that another reason could be the difficulty of separating the effect of nutrition and plant density, which become confounded in a very complex manner.

Conclusions

The growth of two varieties of lettuce (Cobham Green, and Webbs Wonderful) was examined in relation to plant density and Nitrogen, Phosphate and Potash fertilizer application, using a systematic spacing design, and a rotatable fertilizer design. The results were analysed by modifying the reciprocal yield-density model to include the case where there is no competition, and then fitting total plant dry weights, and leaf areas estimated for plants in a non-competitive situation, to a logistic model with a suitable environmental time scale.

The logistic model parameters of total plant dry weight showed a significant response to serpentine superphosphate, when fitted to the rotatable design model, but no other fertilizer was significant. The effect of serpentine superphosphate (up to 40 cwt/acre) was to increase the relative growth rate by increasing the net assimilation rate.

Evidence is presented to suggest that the yield-potential at very high density is the same for both varieties, but the genetic potential is lower for Cobham Green due to a lower net assimilation rate, and a more rapid rate of leaf production.

Marketable yields of Webbs Wonderful were found to be higher than for Cobham Green at the optimum plant density for marketable yield (Cobham Green 1.4 plants/sq.ft., Webbs Wonderful 1.1 plants/sq.ft.) mainly due to the additional week required for Webbs Wonderful to reach optimum maturity, but also due to the greater genetic potential.

GROWTH AND DEVELOPMENT OF TWO LETTUCE VARIETIES IN THE NATURAL ENVIRONMENT

Materials and Methods

The varieties used were:

1. Cobham Green -- a butterhead type (hereafter called 'Cobham')
2. Webbs Wonderful -- a crisphead type (hereafter called 'Webbs')

Virus tested seed of the two varieties was obtained from Harrisons Seeds, Leicester, England.

The experiments were sited at two places:

a) At the University of Nottingham, School of Agriculture, Sutton Bonington, Loughborough, England. (Latitude 52° 49' N.) on a sandy loam, overlying Keuper marl.

b) At Massey University, Palmerston North, New Zealand. (Latitude 40° 20' S.) on a Manawatu silt-loam.

The University of Nottingham Experiment (March - December 1963)

The site had been used to grow a Sweet Corn crop in 1962, using simazine for weed control. Because of the danger of simazine residues affecting the growth of the lettuce precautions were taken to dilute the simazine residues with a large volume of soil. After the Sweet Corn crop residues had been removed from the area the soil was rotary hoed to a depth of 6 inches. Following the rotary hoeing, the site was then ploughed (early in November 1962) and sub-soiled, and 12 concrete posts (8ft. tall) were erected in a 4 x 3 pattern at 25ft intervals for bird control (see later). A soil test, analysed by the National Agriculture Advisory Service, provided the following information.

pH	6.3	
Phosphate	100	(High)
Potash	29	(Medium)
Nitrogen	.181 %	

In order to improve the moisture holding capacity of the soil, as well as the nutritional status, spent mushroom compost at the rate of approximately 25 tons per acre was evenly spread over the experimental area early in January 1963. This was followed on 21 March (just prior to the first sowing) with a base dressing over all the area of Hydrated Lime (10 cwt/acre), and Triple Superphosphate (2 cwt/acre).

It had been intended to make the first sowing early in January, but a particularly cold winter resulted in the ground being frozen to a depth of 12 inches until late February, with the result that the ground was unworkable until Mid-March. The mushroom compost, lime and superphosphate was cultivated into the soil by means of a rotary hoe on 22 March, and the first sowing was made on 26 March 1963.

Birds are a major problem at Sutton Bonington, particularly early in the spring, and so to prevent the small lettuce seedlings being damaged, wires were stretched between the concrete posts, which had been erected the previous autumn, and black nylon thread was stretched between the wires at approximately 12 inch intervals, over and around the whole experimental area.

Seed of the two varieties of lettuce was sown at 3 weekly intervals, commencing on 26 March 1963, and ending on 10 October 1963, a total of 10 sowings. The seed was sown by means of a planet junior drill, set to deposit the seed at a depth of $\frac{3}{4}$ inch as recommended by Heydecker (1956). The seed was dusted with Thiram fungicide prior to drilling. Weed control was by push hoeing between the rows, and hand hoeing in the rows. Each sowing was made into a soil close to Field capacity and no other supplementary irrigation was applied.

The experimental design was a fully randomized split plot one, with three blocks, 8 main treatments (the sowing dates), and two sub-treatments (the two varieties). Sowings numbers 9 and 10 were sown where sowings 1 and 2 had been grown. Each main plot consisted of 6 rows of lettuce, 12 inches apart, with the outside row of each main treatment plot being separated from the outside row of the adjoining main treatment plot by 18 inches. There were 3 rows of each variety, and the outside rows of the main plots were treated as guard rows. Harvesting was carried out at 7 day intervals from emergence until the sowing had 'gone to seed' with the exception of the last sowings, when harvesting ceased early in December 1963 following a damaging frost.

The positions of the plants taken as samples at each harvest were randomized, and to further reduce positional effects, each replicate was divided into half, and a sample taken from each half at each harvest, and then bulked. Soon after emergence the two outside rows of each main plot (the guard rows) were thinned to 12 inches apart, while the four centre rows were thinned to 3 inches. Each main plot was sub-divided into 20 plots 3 ft. long, and the first 3 harvest samples were obtained from plants growing at the 3 inch and 9 inch positions in the plots selected. Following these harvests the plants were then all thinned to 6 inches apart, and the 4th harvest was obtained from plants growing at the 6 inch position in the plots selected. The plants were then thinned to a 12 inch spacing. Twenty plants per sample (10 from each half of the replicate) were usually taken for each variety and replicate at each of these early harvests. For the later harvests only 8 plants were usually taken per variety and replicate, 4 plants from each half of the replicate. These plants were guarded on all sides by at least one row of lettuce, but there were no guard rows between the two varieties, and so the randomization for harvest date was the same for the two varieties. This sampling technique was suggested by Mr. R. Mead, who was at that time a Biometrician at the National Vegetable Research Station, Wellesbourne, England. It was necessary because of the restrictions placed upon the design because of space.

The following data were obtained from each sample:

1) Fresh weight of top.
2) Number of leaves (in excess of $\frac{1}{2}$" long).
3) Length of stem.
4) Stage of maturity of plants (i.e. immature, marketable, overmature).
5) Dry weight of leaves.
6) Dry weight of stem.
7) Dry weight of roots.*

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* No effort was made to obtain all the roots except in the early harvests the main aim being to obtain the swollen part of the tap root, and the nearby fibrous roots.

Leaf areas were measured by the 'blue print' method for the early harvests only.

The data for the two sample rows of each variety (i.e. (1) the row guarded on both sides by the same variety, and (2) the row guarded by different varieties) were kept separate.

Weather data were obtained for the duration of the experiment from the standard meteorological station (50 yards away). Solar radiation data were obtained by means of a 'Kipp' solarimeter, some 200 yards from the experimental area. Weather data were also obtained by a number of resistance thermometers placed within the experimental area, and recording on to paper charts by means of a multi-channel recorder. These data were later discarded because of the physical impossibility of handling such masses of data without some form of automatic recording which would facilitate immediate computer analysis.

The Massey University Experiment (April 1967 - March 1968)

The site of the experiment (of approximate $\frac{1}{2}$ acre) adjoined the the site of the lettuce spacing, fertilizer, and variety experiment reported earlier. The area was fumigated with a mixture of Methyl Bromide (2 parts) and Chloropicrin (1 part) applied by a contractor at the rate of 400 lb/acre in early March 1967. As in the earlier experiment, the purpose of the fumigation was predominantly for weed control. Prior to fumigation, the area was rotary hoed to a depth of 10-12 inches, in order to produce a fine tilth. Following fumigation the polythene film was removed, and the area was cultivated to a depth of 4-6 inches to facilitate the rapid dispersal of the fumigants from the soil into the atmosphere.

The experimental design was the same as in the Nottingham experiment, i.e. 3 blocks, 8 main treatments (the sowing dates), and 2 subtreatments (the 2 varieties). There were 10 sowings, sowings numbers 9 and 10 were sited where sowings numbers 1 and 2 had been grown. Because a larger experimental area was available, each sowing comprised 8 rows of lettuce, 4 rows of each variety, with only the two centre rows of each variety being used as sample plants. The sampling technique was similar to that used at Nottingham except that because the sample plants were now guarded on all sides by the same variety, it was no longer necessary to take samples for the two varieties from the same position.

Sowings of the two varieties were made at approximately monthly intervals in rows 12 inches apart using a Stanhay precision drill and pelleted seed. The drill was calibrated to sow one pellet every $1\frac{1}{2}$". Sowings were made at approximately monthly intervals, on:

2 April 1967, 4 May 1967, 7 June 1967, 2 July 1967,
28 July 1967, 6 September 1967, 29 September 1967,
1 November 1967, 2 December 1967, and 5 January 1968.

Plant samples were obtained at 14 day intervals between April and September inclusive, and at 7 day intervals for the rest of the experiment. In spite of the soil fumigation some weed control was required. This was by push hoeing between the rows, and hand hoeing in the rows. Prior to drilling the seed, a base dressing of fertilizer was spread on the soil and cultivated in. The fertilizer comprised:

Serpentine superphosphate	40 cwt/acre
Nitro-lime	10 cwt/acre
Sulphate of Potash	5 cwt/acre

The rate applied was based on the results obtained from the lettuce spacing/fertilizer experiment reported earlier in this thesis. The application of Nitrogen and Potash was not justified by the results, but was applied as an insurance. In sowings numbers 9 and 10 the application of serpentine superphosphate was reduced to 20 cwt/acre.

The following data were obtained from each plant sample:

1) Fresh weight of top.
2) Number of leaves in excess of ½" in length.
3) Dry weight of leaves.
4) Dry weight of stem.
5) Dry weight of roots.
6) Stage of maturity of plant, i.e. immature, mature, overmature.
7) Leaf area, either by air-flow planimeter (when small) or by the punch method.

Once again no real effort was made to obtain all the roots except in the early harvests.

Weather data were obtained from the nearby D.S.I.R. Plant Physiology Division Meteorological Station. Regular sprays were applied of Metasystox (16 fl. oz./acre) in order to control Aphis, and of Difolotan (2 lb/acre) in order to control the various fungus diseases which can afflict lettuce in the Manawatu.

Irrigation (1") was applied whenever the soil moisture deficit exceeded 1". The soil moisture deficit was estimated from a soil moisture budget, with the potential evapo-transpiration being derived from mean monthly weather records using Thornthwaites formula.

Results and Discussion

In an effort to smooth out the effect of year to year variation in crop yield, Nelder et al. (1960) proposed the use of the four parameter logistic equation:

$$\frac{dW}{dt} = K W \left(1 - \left(\frac{W}{A}\right)^{1/\theta}\right)$$

This differential equation comprises a family of curves, of which the Gompertz (when $\theta = 0$) is a special case. When θ is positive, a solution is:

$$W = \frac{A}{\left(1 + e^{-(\lambda + Kt)/\theta}\right)^{\theta}}$$

when W is the weight of a plant or plant part at time t.

K is the relative growth rate at $t = 0$

A is the asymptote

θ is related to the point of inflexion

and λ is the constant of integration.

t may be chronological time, or some environmental time scale, such as solar radiation, or degree days above a specified base temperature. Nelder (1961a) has described a method of determining the least squares fit of data to this model, using an iterative technique because no explicit solution exists, and this technique was used in an attempt to determine a suitable time scale to describe the growth of lettuce in two different climates, and varying weather conditions.

The data used in this analysis were the total plant dry weight per plant obtained from the Nottingham and Massey University experiments described earlier, plus that from the spacing/fertilizer experiment carried out at Massey in 1966-67. The latter data were only for the 40 cwt/acre serpentine superphosphate plots, with the total plant dry weights converted via the modified yield density model (Nichols, 1970) to a plant density of 1.0 per sq.ft. A number of major problems had to be solved before a satisfactory solution could be obtained. The Massey University I.B.M. 1620 computer in addition to being a slow machine (at least by modern standards) has only 40 K rapid access storage. These problems were overcome by using a series of linked programmes, and by storing these programmes, and the data on disk.

Nelders' method of fitting the model is only applicable for a single set of data, and a modification was necessary in order to fit 21 sets of data simultaneously to produce a single set of parameters. This involves some manipulation of the time scales in order to 'superimpose' the growth curves. In a previous report on this work, Nichols (1968) did this by assuming that t_o for each curve occurred at a constant calculated plant weight (actually $\exp_e$ - 10). Using this method (Method 1) the model was fitted to a number of environmental time scales, and the results are shown in table XI .

There is little value in reducing the Error mean square of the fit to the logistic model below that of the E.M.S. of the experiment. The experiments E.M.S. was determined by doing an analysis of variance (Blocks, Varieties, Harvests) on the whole plant dry weight data ($\log_e$ transformed) for each sowing separately. The Degrees of Freedom for Error, and the Sums of Squares for Error were summed (Σ D.F. error, and Σ S.S. error), and Σ S.S. error was then divided by Σ D.F. error, to obtain the error mean square for the whole experiment. The Error

Degrees of Freedom, and Error Sums of Squares and Error Means squares for each sowing, for each site, and for the experiment as a whole are shown in the Appendix. The E.M.S. for the whole experiment was .03514.

Time scale	$\alpha = \text{Log}_e A$	λ	K	θ	Error Mean Square
COBHAM					
H.U. 30	2.9752	-12.9415	.00659535	.6903	.3773596
H.U. 40	3.0396	-13.2052	.0117417	.5736	.2479726
H.U. 50	2.9575	-11.8138	.0303209	.6428	.4331032
H.U. 45	3.0394	-13.0292	.0179354	.5418	.2408410
H.U. 41	3.0437	-13.2107	.0126777	.5628	.2393253
H.U. 42	3.0463	-13.2019	.0137418	.5536	.233513
WEBBS					
H.U. 30	3.6114	-13.8631	.00709491	.4436	.4042178
H.U. 40	3.7705	-14.3901	.0131974	.3342	.2423707
H.U. 50	3.5767	-12.5367	.0322674	.4271	.4213000
H.U. 45	3.7415	-14.1136	.0200430	.3285	.2218607
H.U. 41	3.7765	-14.4017	.0142885	.3276	.2302097
H.U. 42	317772	-14.3874	.0155056	.3232	.2211421
H.U. 43	3.7717	-14.3380	.0168647	.3216	.2160509

Table XI . Logistic growth curve parameters and Error Mean Square

* Method 1.

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* H.U. 40 etc. = Heat Units (Degree F x days) above a base temperature of 40°F.

These results demonstrate that as far as a Heat Units time scale is concerned, that to improve the fit of the model (as measured by reducing the error sums of squares) requires a 'heat sum' with a base temperature between 40 and 45°F.

In an effort to further improve the fit, a weighted linear regression of:

$$\log_e \frac{W^{\theta}}{A^{\theta} - W^{\theta}} \quad \text{against time (chronological or environmental)}$$

was calculated for each sowing. Then using the mean slope for all the sowings used in the calculation, the time scales were adjusted until all the regression lines had the same intercept. This method (Method 2) was found to give a better fit of the data to the model than the previous method (Method 1). The results are shown in Table XII . Because of this improvement, Method 2 was used in all future calculations.

In Table XII , Time is chronological time in days, H.U. 40 is Heat units in degree F.x days calculated from daily maximum and minimum screen air temperatures above a designated base temperature (e.g. 40, 41, 42 etc.) by the method advocated by the Air Ministry (Anon. 1954). Solar radiation is the number of calories/cm^2/day measured by a Kipp solarimeter at Nottingham, and by an Eppley solarimeter at Massey.

These results clearly demonstrate the improved fit to the model which results from using any of the environmental time scales compared with chronological time. With regard to the heat units analysis the best fit occurs for Cobham with a base temperature at 42°F, and for Webbs at a base temperature of 43°F. It could be argued from this, that Cobham will grow at a slightly lower temperature than Webbs, but the substantial improvement in the fit by using a solar-radiation time scale suggests that radiation rather than temperature offers a better time scale.

Time Scale	$\alpha = \text{Log}_e A$	λ	K	θ	Error Mean Square
COBHAM					
Time	2.7993	-116280	.141583	1.4462	.6859785
H.U. 40	3.0329	-12.6490	.0111420	.6726	.2038196
H.U. 41	3.0371	-12.6593	.0120370	.6579	.1985831
H.U. 42	3.0397	-12.6529	.0130501	.6463	.1959627
H.U. 43	3.0401	-12.6231	.0142055	.6384	.1967073
H.U. 44	3.0380	-12.5635	.0155132	.6354	.2014350
H.U. 45	3.0328	-12.4688	.0170005	.6391	.2115363
Solar radiation	3.1146	-12.7479	.000529362	.5371	.1403739
WEBBS					
Time	3.3077	-11.7630	.138655	1.1857	.7610687
H.U. 40	3.7398	-13.6552	.0120200	.4123	.1929416
H.U. 41	3.7459	-13.6814	.0130374	.4015	.1835874
H.U. 42	3.7478	-13.6840	.0141808	.3933	.1769881
H.U. 43	3.7445	-13.6532	.0154670	.3884	.1739216
H.U. 44	3.7357	-13.5816	.0168961	.3875	.1752500
H.U. 45	3.7209	-13.4630	.0184888	.3915	.1822985
Solar radiation	3.7723	-13.6137	.000566331	.3636	.1005017

Table XII. Logistic Growth curve parameters and Error Mean square.

* Method 2.

* H.U. 40 etc. = Heat Units (Degree Fx days) above a base temperature of 40°F.

In an effort to improve the fit to a heat unit time scale, a new time scale, heat units above a base temperature of 42^{o}F minus heat units above a base temperature of 70^{o}F was used, on the assumption that time above a certain temperature, if not deleterious, did not result in more rapid dry matter accumulation. The choice of a temperature of 70^{o}F was purely arbitrary, but the fact that this gave a worse fit to the model than H.U. 42 alone suggests that there was little to be gained by further adjustments using a heat unit scale. H.U. 42 x solar radiation time scale proved to be only slightly superior to chronological time. Finally the mean solar radiation figure per day for the experiment was determined (337 cal./cm^2/day) and a substantial improvement in the fit to the model was obtained if it was assumed that any calories in excess of 337cal/cm^2/day were only 50% as efficient as radiation below 337 cal./cm^2/day. This is shown in Table XIII as Ra (imp.).

Clearly from these results, some form of solar radiation time scale is the most satisfactory. It is axiomatic that the parameters calculated for the logistic model should be the same for the Nottingham data, as for the Massey data, provided that a suitable time scale has been chosen. That this is not so, is clearly an indictment of the failure of the time scales chosen to adequately describe the environment. See Table XIV .

Because a solar radiation time scale reduced the error mean square for the logistic model lower than any other time scale considered, it was decided to consider if some further improvement could be obtained by making certain assumptions regarding the effectiveness of radiation at different intensities.

Time Scale	$\alpha = \mathrm{Log}_e A$	λ	K	θ	Error Mean Square
COBHAM					
H.U.42-H.U.70	3.0407	-12.6712	.0131676	.6453	.1967615
H.U.42 x Ra	2.9003	-10.0166	3.6795x15	.9493	.6000883
Ra (imp)	3.1256	-13.0001	.0587286	.5325	.1121773
WEBBS					
H.U.42-H.U.70	3.7514	-13.7055	.0143103	.3923	.1788897
H.U.42 x Ra	3.4678	-10.5003	3.78535	.6070	.5447312
Ra (imp)	3.7939	-13.8801	.0626602	.3629	.08477033

Table XIII. Parameters and E.M.S. for various complex time scales. H.U. 42 = Heat units (degree F x days) above a base temperature of 42°F (H.U. 70 = same above a base temperature of 70°F). Ra = solar radiation, and Ra (imp) = solar radiation with any radiation in excess of 337 cal./cm^2/day being valued at 50%.

Time Scale	α = Log_e A	λ	K	θ	E.M.S.
COBHAM Nottingham					
Ra	3.0965	-12.9959	.0618466	.4608	.1101767
Ra (imp)	3.1009	-13.0726	.0662232	.4725	.08704389
H.U. 42	2.9723	-12.7702	.0130885	.5670	.2237472
COBHAM Massey					
Ra	3.1393	-13.0143	.0461118	.6237	.1166282
Ra (imp)	3.1481	-13.2364	.0524242	.6099	.1065092
H.U. 42	3.0903	-12.9999	.0130955	.7354	.1555072
WEBBS Nottingham					
Ra	3.9496	-14.2284	.0684903	.2786	.07770041
Ra (imp)	3.9786	-14.2768	.0725278	.2876	.05952406
H.U. 42	3.8484	-13.6315	.0134996	.3667	.2347610
WEBBS Massey					
Ra	3.7523	-13.9661	.0529092	.3596	.07690591
Ra (imp)	3.7396	-14.1105	.0592911	.3710	.08644751
H.U. 42	3.6746	-13.9480	.0148247	.4217	.09404228

Table XIV. Logistic parameters fitted to better fitting environmental time scales for the two sites.

Four assumptions were considered

1) That any solar radiation exceeding a certain daily integral was ineffective.

2) That any solar radiation exceeding a certain daily integral was only 50% as efficient as radiation below that figure.

3) That any solar radiation exceeding a certain hourly integral was ineffective.

4) That any solar radiation exceeding a certain daily integral was was ineffective provided that the plant was below a certain dry weight. The plant dry weight between two harvests was considered to be the mean plant dry weight, calculated by obtaining the mean of the $\log_e$ dry weights at the two harvests.

Some difficulty was obtained in determining hourly integrals of solar radiation for use in assumption 3), as only daily integrals were available.

The method used to determine hourly integrals was as follows:

The solar angle was calculated for the two sites, for the 21st of each month, and for every hour of daylight, using the formula:

Solar angle = $\sin \delta \sin \phi - \cos \delta \cos \phi \cos \left(\frac{N-12}{24} \times 360\right)$ when ϕ is the latitude, δ the declination, and N is the time in hours (continental clock). From these solar angles an estimate can then be made of the radiation occurring per hour as a proportion of the total daily radiation. The method used was to calculate the solar angle at midday, and then at hourly intervals until night (a negative solar angle). From these solar angles an estimate was made of the amount of solar radiation per hour (i.e. $\frac{1}{2}$ an hour on either side of the hour), as a proportion of the daily solar radiation integral. This was done by dividing the solar angle at a specific hour, by the total of the days hourly solar angles,

e.g. for 1.30 p.m. - 2.30 p.m. $= \frac{.623}{5.903} = .106$

This method slightly overestimates the 11.30 a.m. - 12.30 p.m. figure by about 1%. If the daily measured solar radiation integral is multiplied by the proportion of radiation occurring per hour (derived from the solar angle calculation), an estimate of the hourly solar radiation integral can be obtained. This derivation has a number of possible errors, e.g. (1) it assumes that solar radiation at any time is proportional to the daily solar radiation integral, and does not consider the fact that radiation from a clear sky would be about 4x the radiation from a cloudy sky at any one time and place. Nevertheless in the absence of more detailed solar radiation data it does offer a means -- if somewhat crudely, of considering not only the daily solar radiation integral, but also the duration, which as Brouwer and Huyskes (1968) has shown is of importance in determining dry matter accumulation in lettuce.

In the four conditions considered, a number of solar radiation integrals at which radiation becomes ineffective (or 50% ineffective) were considered, in order to find the one at which the logistic model fitting minimised the error mean square. Because of the limitations placed upon the use of the computer, and the slow speed of the machine (each fitting of a single time scale to the 21 sowings of a single variety took about 30 minutes), it was decided to test to the nearest 50calories/cm^2/day in the daily estimates, or to 5 calories/cm^2/ hour in the hourly estimates.

	12 noon	1 pm	2 pm	3 pm	4 pm	5 pm	6 pm	7 pm
1.	.703	.683	.623	.528	.403	.259	.104	-.05
2.	.119	.116	.106	.089	.068	.044	.018	0
3.	47.6	46.4	42.4	35.6	27.2	12.6	7.2	0
4.	30	30	30	30	27.2	12.6	7.2	0

Table XV . Example showing the derivation of hourly radiation integrals.

1. Solar angles calculated for Nottingham in April for afternoon.
2. Proportion of solar radiation occurring over 60 minute period $\left(\frac{\text{solar angle}}{\Sigma \text{ solar angles}} \right)$.
3. Hourly solar radiation integral, assuming daily solar radiation integral is 400 cal./cm^2/day.
4. As for 3, except assuming plants light saturated at 30 cal./cm^2/ hour.

The most satisfactory fit (the least square fit) for each variety, and method was then tested independently for the Massey and Nottingham data.

The results of the various interactions are shown in the appendix, and only the best fitting results for each variety and method, and site are shown in Tables XVI and XVII. There is, in all cases an improvement in the

Time Scale	$\alpha = \text{Log}_e A$	λ	K	θ	E.M.S.
Webbs (both sites)					
Ra 600/day	3.7700	-13.8788	.0581502	.3634	.08993986
Ra 45/hr.	3.8144	-14.0459	.0614856	.3538	.07929785
Ra 50 + X/day	3.8200	-14.0597	.0962069	.3628	.06943987
Ra 400 (-4)	3.8086	-13.9427	.0610549	.3121	.09211650
Webbs (Nottingham)					
Ra 600/day	3.9541	-14.2235	.0689744	.2856	.06968397
Ra 45/hr.	3.9405	-14.1347	.0683456	.3005	.07423527
Ra 50 + X/day	4.0350	-14.6723	.113371	.2751	.04585009
Ra 400 (-4)	3.9739	-14.3949	.0717848	.2556	.07486623
Webbs (Massey)					
Ra 600/day	3.7569	-14.3035	.0545757	.3583	.07067694
Ra 45/hr.	3.7492	-14.2704	.0580791	.3790	.07562589
Ra 50 + X/day	3.7780	-14.3788	.0911359	.3635	.06109875
Ra 400 (-4)	3.8025	-14.3929	.0589122	.2899	.07001027

Table XVI. Logistic parameters calculated for solar radiation time scales for variety and site.

Key: See Appendices IX and X.

Time Scale	$\alpha = \text{Log}_e A$	λ	K	θ	E.M.S.
Cobham (both sites)					
Ra 500/day	3.142	-13.0785	.0568925	.5344	.1180087
Ra 40/hr.	3.1380	-13.1495	.0594338	.5297	.1052571
Ra 100 + X/day	3.1320	-13.0784	.0793031	.5487	.1013797
Ra 400 (-2)	3.1476	-13.2757	.0618478	.4029	.1158129
Cobham (Nottingham)					
Ra 500/day	3.0920	-12.9792	.0637885	.4887	.09779068
Ra 40/hr.	3.0970	-13.0175	.0648538	.4820	.09706146
Ra 100 + X/day	3.1204	-13.3101	.0886214	.4769	.06962685
Ra 400 (-2)	3.1216	-13.3118	.0684119	.3872	.09953221
Cobham (Massey)					
Ra 500/day	3.1509	-13.3917	.0506763	.6040	.1068187
Ra 40/hr.	3.1561	-13.4106	.0541464	.6188	.1022377
Ra 100 + X/day	3.1542	-13.4307	.0710502	.6279	.1027460
Ra 400 (-2)	3.1849	-13.7761	.0551950	.4291	.09718628

Table XVII. Logistic parameters calculated for solar radiation time scales for variety and site.

Key: See Appendices IX and X.

fit to the model, compared with a straight solar radiation time scale. In fact in most cases the improvement is in the region of about 25%.

In all cases, however, there is still a wide divergence between the K parameters (initial relative growth rates) for the two sites, and from this one can only conclude that none of the environmental time scales chosen is entirely satisfactory. In fact the only time scale in which the K parameters for the two sites are similar is Heat Units 42°F, but the error mean square is approximately double that of the better solar radiation time scales.

In a previous analysis of the data from Nottingham, Nichols (1968) showed that a substantial amount of error could be removed by not making the asymptote (α) constant over all sowings, however because all these parameters are correlated it was decided to fit the logistic model to each sowing and variety with only K (the initial relative growth rate) constant for each variety. This was done using the best environmental time scale for each variety, namely:

For Webbs

Ra 50 + X/day, i.e. solar radiation up to 50 cal./cm^2/day plus 50% of any additional radiation.

For Cobham

Ra 100 + X/day, i.e. solar radiation up to 100 cal./cm^2/day plus 50% of any additional radiation.

Because of the similarities in the estimates of the K parameters for the two sites when using a heat unit time scale, the data was also fitted to the logistic model using a heat units above a base temperature of 42°F. (H.U. 42) time scale, with only K constant for each variety over all sowings.

The full results are shown in the appendix, but the consolidated results for the error sums of squares clearly demonstrated that fitting the model with only K constant for each sowing approximately halves the error sums of squares (Table XVIII).

		Error sums of squares	
Time scale	Variety	single set parameters	only K constant
Ra 100 + X	Cobham	24.432	11.163
H.U. 42	Cobham	47.227	21.379
Ra 50 + X	Webbs	16.666	5.868
H.U. 42	Webbs	42.654	20.342

Table XVIII. Total error sums of squares for all sowings determined for for a single set of parameters over all sowings, or with only K constant for all sowings, for 2 varieties, and different environmental time scales.

These results further confirm the earlier findings that solar radiation provides a better environmental time scale than heat units at least in the experiment.

In this respect Emecz (1962) proposed that light would provide a more meaningful time scale than chronological time using the classical technique of growth analysis.

It is pertinent to note that these results are still within the limits set by the experimental error which is .03514, as the error mean square obtained for fitting the model to the best solar radiation time scales, for both varieties, with K constant, is .0483.

The results of fitting the model to the data, with only K constant are shown in figures 18, and 19, and clearly demonstrate a marked falling off in the asymptote (α) in the Nottingham data with successive sowings. No such trend is apparent in the Massey data. This time trend appears to be more marked for Webbs than for Cobham and a linear regression of asymptote against sowing number for Nottingham results in:

Webbs	slope = -.304
Cobham	slope = -.233

In addition the variances of the α parameters for the different sowings of the two varieties shows a larger variance for Webbs (see table XIX).

	Nottingham + Massey	Nottingham	Massey
Webbs	6.079	4.184	1.330
Cobham	4.05	2.343	0.647

Table XIX . α parameter variances

As the major purpose of this experiment was to determine whether a satisfactory time scale exists in order to develop a predictive model

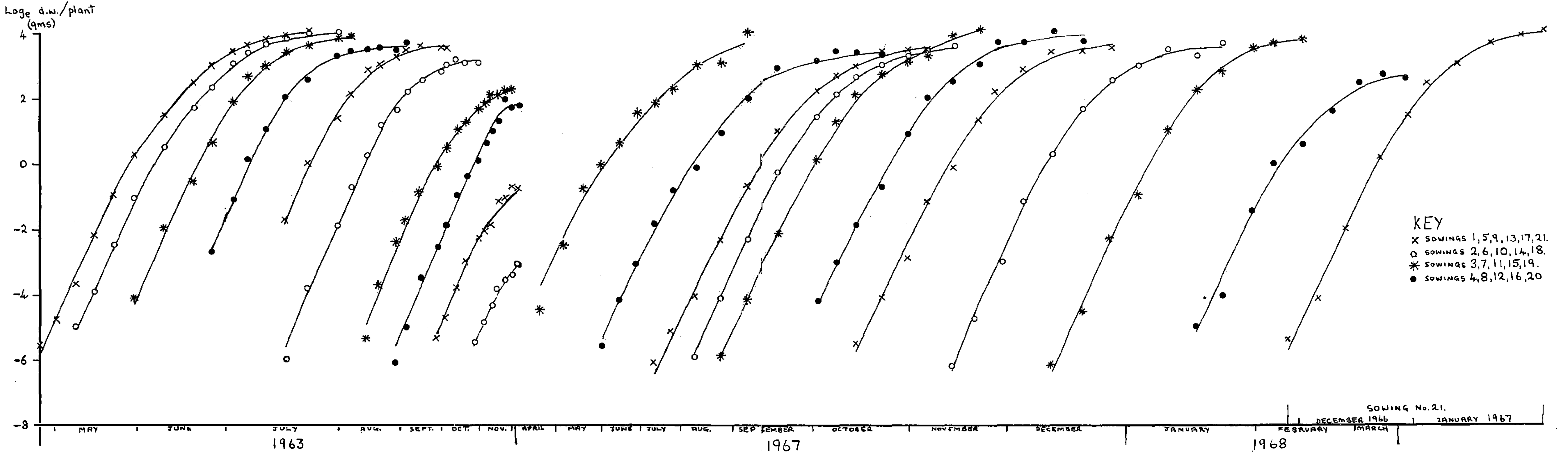

Figure 18. Total dry weight per plant Webbs fitted to the 4 parameter logistic with a solar radiation time scale (Ra 50 + X/day) with K constant for all sowings.

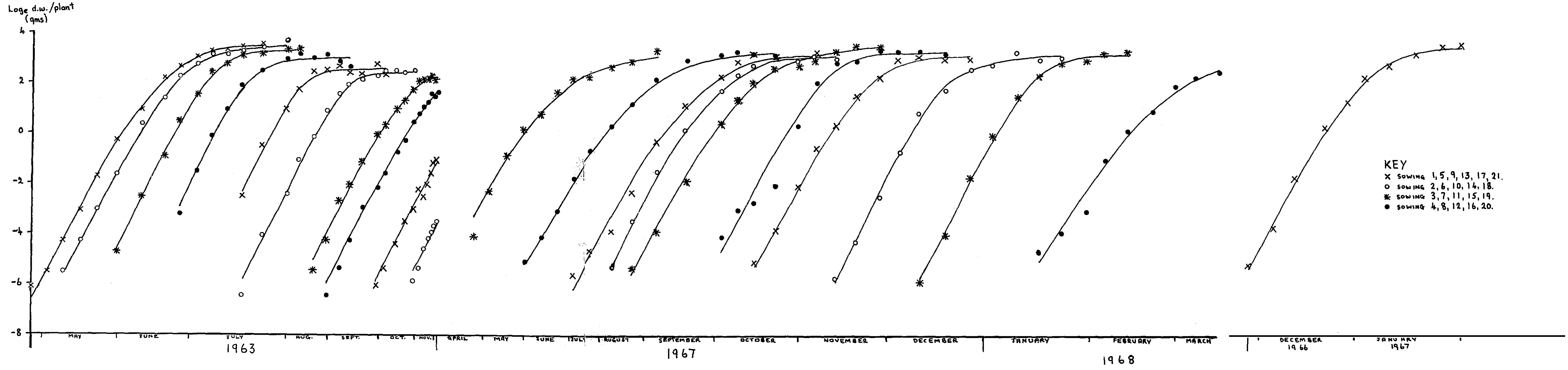

Figure 19. Total dry weight per plant Cobham fitted to the 4 parameter logistic with a solar radiation time scale (Ra 100 + X/day) with K constant for all sowings.

which would enable lettuce production to be regulated more efficiently, the finding that the asymptote is not constant and appears to show a time trend, virtually precludes such an application without further experimental work, because small differences in the asymptote (which is on a $\log_e$ scale) would result in large differences in absolute plant weight.

The variation in the asymptote could be due to:

1) genotype/weather interaction
2) genotype/edaphic interaction
3) some complex combination of the above two.

One possible reason for the falling off of the α parameter with successive plantings at Nottingham, may be that all the fertilizer was applied right at the beginning of the experiment, and not just prior to each sowing, and that this is a nutritional effect.

An effort to explain the falling off in the α parameter at Nottingham in terms of a heat units (or solar radiation) time scale was not successful, and no clear pattern was apparent from carrying out growth analysis on the Massey data.

One possible explanation for the different asymptotes for the different sowings could be that variations in the rate of leaf initiation could affect final size. This appears to be, at least partially, the reason why Cobham produces a smaller lettuce than Webbs, as the higher rate of leaf production by Cobham must lead to earlier, and more severe, shading by leaves on the same plant than for Webbs. Rates of leaf initiation were not available, but the number of leaves exceeding ½" long had been obtained from harvests early on in the life of each sowing, and the rate of leaf production was calculated for some of the Massey sowings over the same time period for each variety, using two time scales;

1) chronological time

2) A solar radiation time scale (actually Ra 100 + X/day.

These leaf production rates, and the ratio of the rates for the two varieties for chronological time are shown in Table XX .

	Leaves/week			**Leaves/Radiation scale**	
Sowing date (1967)	Webbs	Cobham	Webbs / Cobham	Webbs	Cobham
2 April	1.6	2.4	.70	.20	.29
4 May	1.2	1.9	.65	.14	.22
7 June	1.3	1.8	.75	.13	.17
2 July	1.7	2.5	.66	.13	.20
28 July	2.3	3.0	.77	.16	.21
6 September	2.2	3.5	.64	.14	.22
29 September	2.8	4.2	.65	.14	.21
1 November	3.3	4.4	.74	.16	.21
2 December	3.5	5.8	.60	.15	.24

Table XX . Effect of variety and sowing date on the rate of production of leaves in excess of ½" long for early harvests of Cobham and Webbs, Massey data.
Using two time scales, chronological time (weeks) and solar radiation (Ra 100 + X/day).

Clearly the rate at which leaves reach a certain length varied with the time of the year, being slower in the winter than in the summer, but this effect appears to have been smoothed out when using an environmental time scale. This is not to say that the rate of leaf initiation varies with the time of the year, only that the rate of leaf development above a certain size is greatly influenced by the environment.

It is pertinent to note that the ratio of leaf production for Cobham and Webbs remains virtually constant, irrespective of sowing data, so that a simple explanation for the differences between the asymptotes for the two varieties exists, i.e. the greater the rate of leaf production, the less cell building materials are available per leaf, leading to reduced cell division and/or cell expansion, and a smaller leaf. This could be unimportant in some crops, but in a rosette shaped plant like lettuce it could provide a simple explanation of final size differences. It certainly provides at first sight a simple explanation of the final size differences between the two varieties, but attention must also be directed at the different relative growth rates (e.g. Table XIII Ra(imp) Cobham K = .0587, Ra(imp) Webbs K = .0627). This is the relative growth rate at time = zero, and clearly demonstrates a more efficient net assimilation system in Webbs. (In the fertilizer-spacing experiment this was due to a superior net assimilation rate, which was attributed to thicker leaves in Webbs, and it appears reasonable to assume that the same mechanism applies in this experiment, see Table XXI).

The smoothing out of the rate of leaf production for the different sowings when using a solar radiation time scale, precludes consideration of the rate of leaf production from being implicated as a cause of differences in the final plant size. It is clear that this aspect requires closer study with particular reference to the factors which influence leaf size, particularly in view of Brouwer and Huyskes (1968) results which emphasise the importance of the size of the light absorbing surface (as opposed to leaf area) as a major factor in determining the growth of lettuce.

Sowing	Cobham	Webbs
11	510	471
12	443	380
13	526	365
14	401	322
15	383	338
16	445	398
17	371	303
18	378	286
19	384	345
20	445	399
21	407	338
Mean	427	359

Table XXI. Mean leaf area (cm^2) per gm. dry weight of leaves for Cobham and Webbs for first 6 harvests of each sowing.

In my view, at this point, there appears little point in continuing to seek further correlations, or interpretations of these results without obtaining basic information on the interaction between genotype and environment, In particular the effect of light and temperature when the plants are adequately supplied with water and nutrients.

DISCUSSION

Although the dense rosette which develops in head lettuce does not provide a very efficient photosynthetic structure, growth is near exponential until close to hearting, due to an increasing leaf area ratio, in spite of a falling net assimilation rate (see fertilizer/spacing experiment earlier). A further reason for the near exponential growth rate may be because a large part of the increase in leaf area developed at this stage will be due to leaf expansion, leading to an increase in ground cover, rather than an increase in the ratio of leaf area/ground cover, N.B. This is NOT the same as leaf area index, which for a discrete rosette like plant such as lettuce is a virtually meaningless parameter.

There is ample evidence to suggest that temperature is a major factor in influencing leaf expansion, in fact in commercial winter lettuce production under glass, it is common to provide high day and night temperatures in order to get rapid ground cover (and efficient utilization of radiation), and then to lower the temperature in order to produce a firm hearted lettuce.

The fact that in this growth-environment study, solar radiation provided the most satisfactory correlation is not to say that temperature exerted no effect because the two are closely correlated, but it does suggest that particularly over the exponential growth stage, solar radiation was a better time scale than temperature. This could be because temperature does not usually exert a major influence on photosynthesis in the field, whereas solar radiation does. The improvement in the correlation by using solar radiation compared with a temperature time scale may be simply due to the 1-2 month lag in the temperature cycle compared with the radiation cycle.

Potential evapotranspiration was not considered as a time scale because in a previous study (Nichols, 1968) of the Nottingham data the correlation was inferior to both Heat units and Solar Radiation.

The interaction of solar radiation and temperature could perhaps be examined by means of a multiple regression technique on the early harvests (e.g. Warren Wilson, 1966), however of more concern at this stage are:

1) the failure of a single set of parameters to adequately describe the growth of successional sowings of lettuce.
2) The major differences in the parameter estimates for Nottingham and Massey.

It is postulated that the failure of a single set of parameters to adequately fit the data is due primarily to differences in the asymptote, and that these are the result of differences in leaf expansion, caused possibly by temperature (too low), water stress (too high) or some nutritional shortage. Insufficient evidence is available to check this hypothesis, but the potential importance of edaphic factors (and the differences between the Nottingham and Massey results may be due only to soil type and nutrition) points to the need to test such a hypothesis under conditions in which the rooting medium is standardised with respect to availability of water and nutrition. This points to some system of hydroponics being used, but this may have disadvantages in translation to field conditions, particularly under intense evaporative conditions (Warren Wilson, 1967). The need to measure the growth of the individual leaves under conditions where the effect of light and temperature can be independently determined is essential if the results from this study are to have any potential application as a predictive tool. Earlier work on lettuce and the environment is not particularly useful. Dullforce (1965) has pointed out that lettuce are markedly plastic in their response to light and temperature levels, but her work is predominantly directed at the interaction of low light intensity and temperature under winter glasshouse conditions, in relation to hearting.

Bensink (1961) too has been mainly interested in glasshouse lettuce, and has shown that hearting is a morphogenic effect, due to an increase in the breadth/length of leaves ratio. Kimball et al. (1967) have proposed the use of climatographs based on monthly mean maximum and mean minimum temperatures. This technique was proposed in order to delineate potential new production areas in the Western United States. Apart from providing a range of suitable night and day temperatures, this provides no information on growth.

Woodman and Johnson (1947) have assessed the effect of sowing date on the growth of lettuce, but the variety used was May King - a variety suited for cold glasshouse production in the spring and autumn. Growth was measured only in terms of marketable yield, and the work was carried out under glass. The result is that over much of the summer period the plants went to seed, and the results obtained are not informative in relation to my study.

Madariaga and Knott (1951) appear to provide the only study to date in which an effort has been made to predict maturity in relation to the weather. A heat unit technique was used but possibly because it was argued that the base temperature must by physiologically acceptable the results are disappointing. A possible source of error when considering only marketable yield is the harvesters subjective assessment of maturity.

Finally, Brouwer and Huyskes (1968) in a day length/light intensity study with two varieties of lettuce (Rapide and Rapide x Hamadan) found that the more rapid growth of Rapide x Hamadan was due to the formation of a larger light absorbing surface, and that there was no difference between the two varieties with respect to the photosynthetic system.

CONCLUSION

Successive sowings were made of two varieties of lettuce, Cobham Green and Webbs Wonderful in England and New Zealand over a total period of 22 months. Harvests were taken from emergence until past maturity, and the dry weight per plant data was fitted to a logistic model using a number of different time scales.

Chronological time did not fit the data adequately, but the use of certain environmental time scales greatly improved the fit. Solar radiation proved to be a better time scale than heat-units, and the most satisfactory time scales were those in which solar radiation in excess of a certain daily integral was valued at only 50%. The fit to the logistic model was substantially improved by fitting the model with only the initial relative growth rate constant for all sowings, and this suggests, at least in the case of lettuce that a single set of parameters will not adequately describe the growth of lettuce, over a number of sowing dates.

There were major differences in the growth pattern of the two varieties. Webbs Wonderful had a higher initial relative growth rate than Cobham Green. This was attributed to the thicker leaves of Webbs being able to absorb radiation more efficiently when the plants were small. Webbs also produced the largest plants (had the largest asymptote), and this was attributed to the greater rate of leaf production in Cobham leading to increased overlapping of leaves.

There were also major differences in the parameters determined for the different sites, and this could be due to soil, nutrient, or environmental differences, and further interpretation was not possible.

Substantial differences were found in the estimates of the asymptote for the different sowings, and this might be attributed to differences in the rate of leaf expansion, due either to edaphic (nutritional) or environmental causes.

In order to use these results in a predictive manner, it is particularly important that the asymptote be constant over all sowings, or that the reason for any variation be known, because being based on a log. scale even a small variation could result in a big difference in absolute weight. This highlights the need for a more detailed study of the interaction of light and temperature on the growth of lettuce with particular reference to leaf expansion.

Future work

When limited resources are available for research, it is essential that experiments be designed so that the right questions are asked. Although this thesis has answered a number of questions, it has in its turn posed a further set of questions. These have been discussed throughout the thesis, but can be summarised as follows:

1) Plant spacing/fertilizer experiment
   - a) Is the B parameter (genetic potential) constant at all soil fertilities?
   - b) Is the A parameter (environmental potential) constant for any variety?
   - c) Does C (density at which competition begins) vary with soil fertility?
   - d) How do the A and B parameters vary with time?
   - e) Is the higher net assimilation rate of Webbs Wonderful due to a higher rate of photosynthesis, and if so, what is the mechanism?
   - f) What is the mechanism of the phosphate response?
   - g) Why are there differences between the two varieties and Sclerotinia infection?

2) Growth in the natural environment experiment
   - a) Is the difference in the logistic growth curve parameters from Nottingham and Massey data due to edaphic or climatic factors (or some combination of the two)?

b) What are the plant characteristics which determine the final size of a lettuce (asymptote)?

c) How does the environment affect these plant characteristics?

d) How does light and temperature affect the growth of lettuce?

LIST OF APPENDICES

APPENDIX I

Logistic parameters from which response model was fitted.

Plot	Treatment			Cobham			Webbs		
	N	P	K	α	K	θ	α	K	θ
1	1	1	1	3.68	.0138	.623	4.53	.0144	.423
2	0	α	0	3.56	.0159	.432	4.62	.0169	.298
3	1	1	-1	3.65	.0142	.546	4.71	.0176	.270
4	0	0	0	3.88	.0195	.229	4.79	.0254	.144
5	$-\alpha$	0	0	3.70	.0187	.284	4.99	.0318	.100
6	-1	-1	1	3.60	.0141	.514	4.75	.0169	.278
7	0	$-\alpha$	0	3.51	.0119	1.085	4.36	.0135	.516
8	-1	1	1	3.68	.0165	.334	4.80	.0250	.139
9	-1	-1	-1	3.63	.0185	.304	4.53	.0177	.284
10	1	-1	1	3.61	.0183	.278	4.42	.0164	.323
11	-1	1	-1	3.66	.0149	.418	4.40	.0164	.324
12	0	0	0	4.06	.0218	.164	4.67	.0192	.225
13	0	0	0	3.64	.0132	.622	4.54	.0173	.307
14	α	0	0	3.77	.0166	.340	4.61	.0195	.234
15	0	0	α	3.57	.0142	.517	5.03	.0250	.136
16	1	-1	-1	3.50	.0139	.638	4.35	.0145	.491
17	0	0	0	3.76	.0194	.256	4.65	.0211	.203
18	0	0	0	3.81	.0205	.220	4.76	.0191	.226
19	0	0	0	3.59	.0191	.276	4.46	.0186	.259
20	0	0	$-\alpha$	3.59	.0168	.357	4.54	.0177	.278

cont'd..........

Appendix I cont'd.......

Model fitted.

$$Y = b_0 + b_1N + b_2P + b_3K + b_4N^2 + b_5P^2 + b_6K^2 + b_7NP + b_8PK + b_9NK$$

Cobham	b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7	b_8	b_9
θ	.297	.045	-.067	.008	-.006	.152	.038	.040	.018	-.051
K	.0189	-.0005	.0001	-.0002	-.0004	-.0018	-.0012	-.0004	.0001	.0008
α	3.79	0.0	0.03	0.0	-0001	-0009	-0007	0001	0.0	0.02
Webbs										
θ	.226	.052*	-.043*	-.033	-.010	.075*	.004	-.003	.018	.022
K	.0202	-.0025	.0010	.0014	.0012	-.0026	.0003	-.0007	.0005	-.0011
α	4.65	-0.08	0.06	0.10	0.03	-0.08	0.02	0.07	-0.01	-0.09
Cobham (Plot^{13}, θ = .475)										
θ	.272	.045	-.067	.008	.002	.160*	.046	.040	.018	-.051

* significant at 5% level.

APPENDIX II

Logistic parameters from which response model was fitted.

Plot	Treatment			Cobham			Webbs		
	N	P	K	α	K	θ(fixed)	α	K	θ(fixed)
1	1	1	1	3.78	.0146	.480	4.77	.0161	.289
2	0	α	0	3.56	.0159	.432	4.62	.0169	.298
3	1	1	-1	3.70	.0147	.480	4.67	.0173	.289
4	0	0	0	3.78	.0176	.297	4.56	.0204	.226
5	$-\alpha$	0	0	3.68	.0184	.297	4.58	.0204	.226
6	-1	-1	1	3.67	.0148	.434	4.61	.0160	.344
7	0	$-\alpha$	0	3.51	.0119	1.085	4.36	.0135	.516
8	-1	1	1	3.56	.0148	.480	4.44	.0178	.289
9	-1	-1	-1	3.52	.0165	.434	4.44	.0167	.344
10	1	-1	1	3.46	.0157	.434	4.38	.0162	.344
11	-1	1	-1	3.60	.0144	.480	4.46	.0171	.289
12	0	0	0	3.79	.0165	.297	4.67	.0193	.226
13	0	0	0	3.97	.0161	.297	4.72	.0195	.226
14	α	0	0	3.83	.0175	.297	4.63	.0199	.226
15	0	0	α	3.80	.0170	.297	4.74	.0195	.226
16	1	-1	-1	3.64	.0152	.434	4.53	.0159	.344
17	0	0	0	3.71	.0183	.297	4.59	.0202	.226
18	0	0	0	3.70	.0181	.297	4.76	.0193	.226
19	0	0	0	3.57	.0186	.297	4.53	.0198	.226
20	0	0	$-\alpha$	3.67	.0181	.297	4.66	.0193	.226

cont'd.........

Appendix II cont'd.......

Model fitted.

$$Y = b_0 + b_1N + b_2P + b_3K + b_4N^2 + b_5P^2 + b_6K^2 + b_7NP + b_8PK + b_9NK$$

Cobham	b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7	b_8	b_9
K	.0175	-.0001	.0002	-.0002	-.0001	$-.0016^*$	-.0002	.0001	.0002	.0002
α	3.75	.04	.04	.02	-.01	-.09	-.02	.05	.01	-.03
Webbs										
K	.0197	-.0002	$.0007^*$	0	-.0002	$-.0019^*$	-.0004	-.0001	0	-.0001
α	4.65	.04	.06	.02	-.03	-.07	0	.08	.01	-.02

* significant at 5% level.

APPENDIX III

Logistic parameters from which response model was fitted.

Plot	Treatment			Cobham			Webbs		
	N	P	K	α	K(fixed)	θ(fixed)	α	K(fixed)	θ(fixed)
1	1	1	1	3.78	.0146	.480	4.57	.0171	.289
2	0	α	0	3.56	.0159	.432	4.62	.0169	.298
3	1	1	-1	3.71	.0146	.480	4.70	.0171	.289
4	0	0	0	3.78	.0176	.297	4.65	.0198	.226
5	$-\alpha$	0	0	3.78	.0176	.297	4.67	.0198	.226
6	-1	-1	1	3.58	.0155	.434	4.57	.0162	.344
7	0	$-\alpha$	0	3.51	.0119	1.085	4.36	.0135	.516
8	-1	1	1	3.58	.0146	.480	4.54	.0171	.289
9	-1	-1	-1	3.61	.0155	.434	4.51	.0162	.344
10	1	-1	1	3.48	.0155	.434	4.39	.0162	.344
11	-1	1	-1	3.58	.0146	.480	4.47	.0171	.289
12	0	0	0	3.63	.0176	.297	4.59	.0198	.226
13	0	0	0	3.74	.0176	.297	4.67	.0198	.226
14	α	0	0	3.81	.0176	.297	4.64	.0198	.226
15	0	0	α	3.71	.0176	.297	4.70	.0198	.226
16	1	-1	-1	3.60	.0155	.434	4.48	.0162	.344
17	0	0	0	3.80	.0176	.297	4.65	.0198	.226
18	0	0	0	3.76	.0176	.297	4.67	.0198	.226
19	0	0	0	3.69	.0176	.297	4.53	.0198	.226
20	0	0	$-\alpha$	3.72	.0176	.297	4.58	.0198	.226

Model fitted.

$$Y = b_0 + b_1N + b_2P + b_3K + b_4N^2 + b_5P^2 + b_6K^2 + b_7NP + b_8PK + b_9NK$$

	b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7	b_8	b_9
Cobham α	3.74	.02	.01	-.01	0	-.06	-.03	.05	.03	0
Webbs α	4.62	0	.06	.01	0	-.06	-.01	.06	0	-.04

APPENDIX IV

Logistic parameters from which response model was fitted.

Plot	Treatment			Joint analysis							
				(1)			(2)			(3)	
	N	P	K	α	K	θ	α	K	θ (fixed)	α	K (fixed)
1	1	1	1	4.09	.0140	.512	4.24	.0152	.375	4.16	.0157
2	0	α	0	4.08	.0165	.347	4.08	.0165	.347	4.08	.0165
3	1	1	-1	4.14	.0155	.390	4.16	.0158	.375	4.18	.0157
4	0	0	0	4.33	.0223	.180	4.18	.0191	.252	4.22	.0188
5	$-\alpha$	0	0	4.28	.0228	.181	4.13	.0196	.252	4.24	.0188
6	-1	-1	1	4.14	.0153	.378	4.14	.0154	.378	4.07	.0159
7	0	$-\alpha$	0	3.90	.0127	.713	3.90	.0127	.713	3.90	.0127
8	-1	1	1	4.20	.0196	.223	3.98	.0161	.375	4.03	.0157
9	-1	-1	-1	4.09	.0183	.281	3.97	.0166	.378	4.06	.0159
10	1	-1	1	4.01	.0171	.302	3.91	.0160	.378	3.93	.0159
11	-1	1	-1	4.02	.0156	.367	4.02	.0156	.375	4.00	.0157
12	0	0	0	4.36	.0199	.199	4.24	.0180	.252	4.12	.0188
13	0	0	0	4.08	.0151	.423	4.36	.0179	.252	4.22	.0188
14	α	0	0	4.18	.0180	.280	4.24	.0188	.252	4.24	.0188
15	0	0	α	4.22	.0175	.281	4.27	.0184	.252	4.22	.0188
16	1	-1	-1	3.92	.0142	.550	4.09	.0156	.378	4.04	.0159
17	0	0	0	4.20	.0203	.226	4.15	.0194	.252	4.24	.0188
18	0	0	0	4.27	.0197	.225	4.22	.0188	.252	4.22	.0188
19	0	0	0	4.03	.0190	.260	4.05	.0194	.252	4.12	.0188
20	0	0	$-\alpha$	4.06	.0174	.307	4.16	.0188	.252	4.16	.0188

cont'd.......

Appendix IV cont'd..........

Model fitted.

$$Y = b_0 + b_1N + b_2P + b_3K + b_4N^2 + b_5P^2 + b_6K^2 + b_7\ NP + b_8PK + b_9NK$$

	b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7	b_8	b_9
C	.252	.049	-.046	-.016	-.04	$.102^+$	.019	.015	.016	-.010
K	.0194	-.0012	.0005	.0002	.0001	-.0019	-.0009	-.0004	.0003	0
α	4.21	-.03	.04	.04	0	-.09	-.03	.04	0	-.02
K	.0188	-.0002	.0004	-.0001	-.0002	$-.0018^{***}$	-.0004	0	.0001	.0001
α	4.20	.03	.04	.02	-.02	-.09	-.01	.06	.01	-.03
α	4.19	.01	.04	0	0	$-.09^*$	-.02	.06	.01	-.02

+ = significant at 10% level

* = significant at 5% level

*** = significant at .1% level

APPENDIX V

Response model fitting. (Consolidated results).

$$Y = b_0 + b_1N + b_2P + b_3K + b_4N^2 + b_5P^2 + b_6K^2 + b_7NP + b_8PK + b_9NK$$

	b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7	b_8	b_9
Cobham. Analysis (1).										
θ	.297	.045	-.067	.008	-.006	.152	.038	.040	.018	-.051
K	.0189	-.0005	.0001	-.0002	-.0004	-.0018	-.0012	-.0004	.0001	.0008
α	3.79	0	.03	0	-.01	-.09	-.09	.01	0	.02
Webbs. Analysis (1)										
θ	.226	.052*	-.043*	-.033	-.010	.075*	.004	-.003	.018	.022
K	.0202	-.0025	.0010	.0014	.0012	-.0026	.0003	-.0007	.0005	-.0011
α	4.65	-.08	.06	.10	.03	-.08	.02	.07	-.01	-.09
Cobham. (Plot 13 θ = .475)										
θ	.272	.045	-.067	.008	..002	.160*	.046	.040	.018	-.051
Cobham. (θ at best value for phosphate)										
K	.0175	-.0001	.0002	-.0002	-.0001	-.0016*	-.0002	.0001	.0002	.0002
α	3.75	.04	.04	.02	-.01	-.09	-.02	.05	.01	-.03
Webbs. (θ at best value for phosphate)										
K	.0197	-.0002	.0007*	0	-.0002	-.0019*	-.0004	-.0001	0	-.0001
α	4.65	.04	.06	.02	-.03	-.07	0	.08	.01	-.02
Cobham. (θ and K at best value for phosphate)										
α	3.74	.02	.01	-.01	0	-.06	-.03	.05	.03	0

cont'd.......

Appendix V cont'd.........

Webbs (θ and K at best value for phosphate)

α	4.62	0	.06	.01	0	-.06	-.01	.06	0	-.04

Joint analysis

θ	.252	.049	-.046	-.016	-.004	.102^{+}	.019	.015	.016	-.010
K	.0194	-.0012	.0005	.0002	.0001	-.0019	-.0009	-.0004	.0003	0
α	4.21	-.03	.04	.04	0	-.09	-.03	.04	0	-.02

Joint analysis. (0 at best value for phosphate)

K	.0188	-.0002	.0004	-.0001	-.0002	-.0018***	-.0004	0	.0001	.0001
α	4.20	.03	.04	.02	-.02	-.09	-.01	.06	.01	-.03

Joint analysis. (0 and K at best value for phosphate)

α	4.19	.01	.04	0	0	-.09*	-.02	.06	.01	-.02

Joint analysis of a parameter

.00943	.00004	-.00113	-.00001	-.00038	.00108*	.00008	-.00141*	-.00089	.00068

+ = significant at 10% level

* = significant at 5% level

*** = significant at .1% level

APPENDIX VI

Webbs. A parameters, B parameters, and C parameters (C = plant density at which competition commences) for all 20 plots, and final 8 harvests.

	Harvest Number							
Plot	3	4	5	6	7	8	9	10
1	4.696	.2179	.07759	.05073	.01786	.01406	.006688	.013654
2	3.733	.1651	.05543	.02133	.01797	.01050	.009795	.010312
3	4.447	.1338	.06555	.01994	.01882	.01190	.008796	.008244
4	3.476	.0490	.04587	.02226	.01704	.01229	.009694	.011206
5	3.256	.0115	.04836	.01786	.01720	.01300	.009084	.008062
6	4.836	.1650	.09667	.03338	.02052	.01378	.008319	.008552
7	8.666	.6442	.24071	.11110	.04857	.02411	.016119	.014250
8	3.244	.0362	.03449	.02016	.01747	.01428	.011407	.011248
9	3.667	.0854	.04077	.01791	.01222	.00911	.014888	.010212
10	3.973	.2105	.05605	.03876	.02028	.01935	.013907	.014358
11	3.523	.1184	.06105	.02049	.01468	.02059	.013889	.013925
12	3.789	.0571	.04282	.03166	.01869	.01401	.008650	.011648
13	4.761	.0650	.04329	.01909	.02229	.01024	.007824	.012605
14	3.679	.0482	.03073	.02454	.01304	.01337	.012985	.008282
15	3.299	.0289	.05260	.02261	.00868	.01233	.006873	.006994
16	3.811	.4217	.08638	.03061	.01091	.01069	.016567	.012122
17	3.384	.0209	.03193	.01095	.00838	.01471	.012973	.007541
18	3.672	.0459	.04363	.02685	.01508	.01319	.008148	.007609
19	3.183	.1175	.02683	.02229	.01057	.01461	.014528	.013982
20	3.910	.1115	.04565	.02625	.02027	.01059	.009063	.015372
B	-6.2143	.61683	.16059	.06353	.03033	.01291	.00962	.00716
C	3.653	3.042	1.674	.977	.651	.545	.545	.403

APPENDIX VII

Cobham. A parameters, B parameters, and C parameters (C = plant density at which competition commences) for all 20 plots, and final 8 harvests.

	Harvest Number							
Plot	3	4	5	6	7	8	9	10
1	6.0944	.4470	.07562	.05183	.00827	.00915	.00963	.00509
2	1.7067	.1230	.00038	.01379	.01306	.01489	.01312	.01024
3	2.8181	.2544	.04173	.01939	.01273	.00959	.00923	.00747
4	.4637	.2203	.02387	.01863	.01398	.01499	.00708	.00610
5	.7276	.0612	.01282	.01947	.01435	.01357	.01141	.00640
6	3.6739	.2492	.05632	.03573	.01518	.01633	.01299	.01030
7	4.7526	.5758	.48577	.07617	.01765	.01078	.01277	.01930
8	.8867	.1395	.01481	.01677	.01551	.01000	.01381	.01116
9	1.0768	.0331	.01845	.01567	.01030	.01001	.01551	.00888
10	.3743	.2495	.04365	.02050	.01487	.02092	.01455	.02006
11	1.5675	.4196	.06379	.03905	.02400	.01608	.01617	.00875
12	.8803	.1805	.15580	.05355	.02306	.01762	.01063	.00824
13	2.7392	.4827	.13498	.04794	.01222	.01084	.00917	.01304
14	1.2610	.2910	.01997	.02838	.01240	.01199	.01168	.00445
15	1.8702	.2418	.02107	.02221	.00785	.01279	.01766	.00966
16	4.6757	.2476	.06095	.02097	.02113	.01150	.01594	.01371
17	.9167	.0513	.03208	.01440	.01107	.01146	.00963	.00643
18	.5620	.1222	.01974	.02805	.00719	.01044	.01201	.00884
19	.5285	.0636	.05648	.01641	.00364	.01865	.02124	.01076
20	.6787	.1778	.03686	.01503	.01160	.01801	.01561	.01121
B	3.4404	.3414	.2225	.07465	.05129	.02812	.02041	.02182
C	3.042	3.042	1.197	1.197	.784	.784	.545	.545

APPENDIX VIII

Experimental errors derived from Analysis of Variance of $\log_e$ total plant dry weights from each sowing.

Site	Sowing	Error D.F.	Error S.S.	Error Mean Square
Nottingham	1	54	.9947	.01842
	2	50	1.2614	.02523
	3	42	.6054	.01441
	4	46	1.2597	.02738
	5	42	.8587	.02044
	6	54	.8567	.01586
	7	58	1.5442	.02662
	8	58	1.7575	.03030
	9	42	4.7867	.11397
	10	26	.8555	.03291
Total Nottingham		472	14.7806	.03131
Massey	11	42	1.5302	.03643
	12	50	2.7680	.05536
	13	46	1.2464	.02710
	14	42	1.0396	.02475
	15	46	.7202	.01566
	16	46	2.8741	.06248
	17	42	1.3789	.03276
	18	42	1.5122	.03600
	19	38	1.2588	.03313
	20	34	4.2609	.12532
	21	95	1.5975	.01682
Total Massey		523	20.1838	.03859
Total both sites		995	34.9644	.03514

APPENDIX IX

Solar radiation function time scales.

Webbs

Time scale	$\alpha = \text{Log}_e A$	λ	K	θ	E.M.S.
Ra 450/day	3.7745	-13.9590	.0620537	.3787	.09857257
Ra 500/day	3.7798	-13.9545	.0604238	.3696	.09205796
Ra 550/day	3.7799	-13.9195	.0591335	.3657	.09011021
Ra 600/day	3.7799	-13.8788	.0581502	.3634	.08993986
Ra 650/day	3.7787	-13.8295	.0573393	.3637	.09090355
Ra 45/hr	3.8144	-14.0459	.0614856	.3538	.07929785
Ra 40/hr	3.8152	-14.0788	.0636308	.3587	.08138367
Ra 50/hr	3.8100	-13.9985	.0598399	.3525	.08048119
Ra 50+X/day	3.8200	-14.0597	.0962069	.3628	.06943987
Ra 100+X/day	3.8227	-14.0931	.0844595	.3699	.07527520
Ra 150+X/day	3.8140	-14.0460	.0763704	.3764	.08257926
Ra 500(-4)	3.7914	-13.8028	.0588830	.3354	.09532302
Ra 400(-4)	3.8086	-13.9427	.0610549	.3121	.09211650
Ra 300(-4)	3.8309	-14.1112	.0645778	.2816	.09219104
Ra 400(-3)	3.8191	-14.1857	.0653790	.2816	.09231417
Ra 400(-5)	3.7859	-13.7077	.0580259	.3448	.09832105

Key to time scales. for Appendices IX and X.

1) Ra 400/day. Solar radiation time scale with radiation per day above 400 (or figure cited) being considered ineffective.

2) Ra 40/hr. Solar radiation time scale with radiation per hour above 40 (or figure cited) being considered as ineffective.

3) Ra 100+X/day. Solar radiation time scale with radiation per day in excess of 100 (or figure cited) being valued at only 50% radiation below the figure cited.

4) Ra 400 (-4). A solar radiation time scale with radiation per day in excess of 400 (or figure cited) being considered ineffective provided that the $\log_e$ plant dry weight was less than -4 (or figure cited).

APPENDIX X

Solar radiation function time scales.

Cobham Green

Time scale	α = Log_e A	λ	K	θ	E.M.S.
Ra 150/day	2.9358	-12.1818	.107441	.9753	.3670197
Ra 200 "	2.9875	-12.4687	.0870446	.8350	.2786273
Ra 300 "	3.0638	-12.8553	.0686868	.6507	.1694212
Ra 350 "	3.0919	-12.9811	.0643596	.5925	.1391331
Ra 400 "	3.1137	-13.1092	.0611395	.5571	.1235775
Ra 450 "	3.1211	-13.1059	.0587057	.5425	.1185051
Ra 500 "	3.1242	-13.0785	.0568925	.5344	.1180087
Ra 550 "	3.1243	-13.0361	.0555692	.5307	.1204172
Ra 10/hr	3.0430	-12.8028	.138924	.7352	.2102491
Ra 20 "	3.0994	-13.1006	.0837576	.6161	.1376638
Ra 30 "	3.1270	-13.1813	.0668143	.5572	.1108856
Ra 40 "	3.1380	-13.1495	.0594338	.5297	.1052571
Ra 50 "	3.1358	-13.0598	.0556708	.5250	.1126903
Ra 45 "	3.1380	-13.1085	.0552570	.5255	.1078748
Ra 35 "	3.1346	-13.1776	.0624368	.5393	.1058356
Ra 50+X/day	3.1372	-13.1105	.0898366	.5393	.1024852
Ra 100+X/day	3.1320	-13.0784	.0793031	.5487	.1013797
Ra 150+X/day	3.1319	-13.1331	.0719167	.5507	.1054246
Ra 200+X/day	3.1244	-13.0380	.0668613	.5527	.1083824
Ra 400(-4)	3.1336	-12.9768	.0556915	.4765	.1308022

cont'd.........

Appendix X cont'd..........

Time scale	$\alpha = \text{Log}_e A$	λ	K	θ	E.M.S.
Ra 300(-4)	3.1475	-13.1071	.0580072	.4358	.1298640
Ra 200(-4)	3.1710	-13.2967	.0626772	.3732	.1353431
Ra 300(-5)	3.1190	-12.7696	.0537213	.5197	.1445764
Ra 300(-3)	3.1699	-13.3376	.0657169	.3526	.1287176
Ra 200(-3)	3.2064	-13.6451	.0806590	.2543	.1487935
Ra 400(-3)	3.1493	-13.1384	.0596419	.4192	.1228495
Ra 400(-2)	3.1476	-13.2757	.0618478	.4029	.1158129
Ra 300(-2)	3.1633	-13.5664	.0708838	.3268	.1193969
Ra 500(-2)	3.1338	-13.0523	.0570990	.4618	.1234237

Key to time scales: See Appendix IX.

APPENDIX XI

Methods used to measure plant dry weights and leaf areas

Leaf area estimations

During the course of the experiments leaf areas were measured in the following ways:

1) Blueprint method

This method was only used for small plants. The washed and dried leaves were spread on a sheet of glass, followed by a sheet of blue line paper (sensitive side next to the leaves), and a further sheet of glass. The sensitive side of the paper was then exposed to an ultra violet light source, and the image of the leaves then fixed by means of ammonia fumes. The actual leaf areas were then measured by cutting out the leaf images, and either (1) measuring the area on an air flow planimeter; or (2) by drying in a dessicator, and weighing and comparing the weight with the weight of a known area of the same paper.

A further method which is available, but was not used in this work is to measure the area of the leaves by means of a mechanical planimeter.

2) Air flow planimeter

This is a direct method of measuring the area of a leaf (or leaves) once the machine has been calibrated, but our machine is only suitable for small leaves. The leaves were washed and cleaned prior to being measured.

3) Punch method

Using a 'punch' of known area, a sample of leaf cores were taken by random pushing the punch into the leaves. The first ten complete cores were used as a sample, irrespective of what part of the leaf (lamina or mid-rib) the sample came from.

Dry weight estimation

For small plants, all of the plant was dried (as leaves, stem, and roots) in glass bottles, which had been sprayed with a silicone aerosol to prevent the plant material sticking to the glass. The roots were cleaned from soil by means of a jet of water. Leaves and stems were washed free of soil.

For larger plants sub-sampling was necessary, and this was done both at the whole of plant level, and also by sub-sampling the leaves.

Once again all the plant material was washed free of soil, and the samples were dried in zinc gauze trays.

APPENDIX XII

Webbs logistic parameters for each sowing with
K = .0962069 using time scale Ra 50 + X/day.

Sowing	$\alpha = \log_e A$	λ	θ	Error Sums Squares
1	4.3000	-14.8924	.2950	.1684
2	4.2558	-15.0721	.3159	.0763
3	4.0134	-15.2855	.4485	.2201
4	3.6777	-14.6999	.5435	.1423
5	3.6576	-16.3853	.5663	.0977
6	3.2277	-12.8733	.7299	.2648
7	2.4782	-11.7727	.6281	.4112
8	2.2603	-11.5564	1.0731	.5460
9	No Fit			.3980*
10	No Fit			.2836*
11	4.2612	-16.2370	.2439	.5222
12	3.5850	-13.6494	.2929	.3047
13	3.7812	-14.6372	.2860	.2402
14	3.7006	-14.9277	.3267	.0315
15	4.1224	-15.0879	.2963	.1528
16	4.1055	-15.8380	.3000	.3692
17	3.8809	-15.2569	.3108	.4659
18	3.5746	-13.9833	.4018	.1881
19	3.9841	-14.6485	.3590	.1228
20	2.9965	-14.3319	.3591	.5840
21	4.1726	-15.1971	.3484	.2784
			TOTAL	5.868

* Error sums of squares for sowing when all sowings fitted to a single set of parameters.

Total error sums of squares for a single set of parameters = 16.666

APPENDIX XIII

Cobham logistic parameters for each sowing with
K = .0793031 using time scale Ra 100 + X/day.

Sowing	$\alpha = \log_e A$	λ	θ	Error Sums Squares
1	3.5932	-14.1854	.4402	.2930
2	3.5124	-13.5915	.5054	.1819
3	3.2767	-13.3876	.9432	.1040
4	2.9106	-12.5662	1.2145	.4237
5	2.5308	-13.5782	1.8385	.3340
6	2.4487	-11.5255	1.3576	.8180
7	2.3627	-11.4768	.8661	.4535
8	2.0329	-11.0445	1.3456	.4023
9	No Fit			.4257*
10	No Fit			.3370*
11	3.2683	-16.0735	.3531	.2416
12	3.3517	-14.0421	.3337	.1575
13	3.3150	-14.8302	.3494	1.2336
14	3.0810	-14.4307	.4909	.1320
15	3.5041	-14.4845	.3885	.1943
16	3.2689	-15.1180	.6895	3.4769
17	3.1029	-13.8264	.5219	.2188
18	3.0300	-13.3173	.5451	.1963
19	3.0902	-13.0904	.7114	.1746
20	3.8781	-15.1509	.2135	1.1937
21	3.5532	-14.4657	.4450	.1708
			TOTAL	11.1632

* Error sums of squares for sowing when all sowings fitted to a single set of parameters.

Total error sums of squares for a single set of parameters = 24.4325.

APPENDIX XIV

Webbs logistic parameters for each sowing with
K = .0141808 using time scale H.U. 42.

Sowing	$\alpha = \log_e A$	λ	θ	Error Sums Squares
1	3.8482	-11.7065	.8363	2.7220
2	3.8966	-12.1191	.6095	1.5595
3	3.9032	-14.7253	.4850	.3153
4	3.6985	-15.6489	.4480	.1526
5	3.5808	-17.5209	.5142	.0536
6	3.2757	-13.3731	.4226	.3992
7	2.6251	-13.3186	.3178	.1682
8	No Fit			4.9911*
9	No Fit			4.0560*
10	No Fit			.2754*
11	No Fit			.4151*
12	3.4411	-12.2793	.5131	.7219
13	3.5157	-13.7124	.5505	.1109
14	3.5360	-13.4368	.5825	.2614
15	3.9336	-13.6058	.5503	.4304
16	3.8650	-14.4020	.5652	.6383
17	3.4854	-13.0611	.6090	.3371
18	3.5651	-13.9671	.4083	.1185
19	4.0006	-14.6926	.3569	.1519
20	2.8919	-14.4412	.3596	.4614
21	No Fit			2.0027*
				20.3425

* Error sums of squares for sowing when all sowings fitted to a single set of parameters.

Total error sums of squares for a single set of parameters = 42.6541

APPENDIX XV

Cobham logistic parameters for each sowing with
$K = .0130501$ using time scale H.U. 42.

Sowing	$\alpha = \log_e A$	λ	θ	Error Sums Squares
1	3.3326	-11.1286	1.3267	3.9991
2	3.3300	-11.0162	.9825	2.5243
3	3.2599	-13.0828	.8835	.4046
4	2.9162	-13.3492	.9129	.3443
5	2.5256	-14.6496	1.3172	.2509
6	2.4838	-12.1564	.6685	.5723
7	2.5520	-12.8924	.4132	.1709
8	2.6913	-12.5516	.3714	.1462
9	No Fit			3.3704*
10	No Fit			.1502*
11	3.8543	-17.1782	.2928	.2013
12	3.1866	-11.8386	.7763	.8874
13	3.0302	-13.2606	1.0476	.4172
14	2.9889	-12.5561	1.0603	.4078
15	3.3637	-12.7620	.7738	.6015
16	3.1621	-13.7170	2.4988	4.0699
17	2.9835	-11.8460	.9446	.8091
18	3.0028	-13.0205	.6446	.1899
19	3.1215	-13.3727	.6240	.1172
20	3.1030	-14.9366	.2391	1.2080
21	3.4128	-13.1276	.6969	.5362
				21.3787

* Error sums of squares for sowing when all sowings fitted to a single set of parameters.

Total error sums of squares for a single set of parameters = 47.2270

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