PHYSIOLOGICAL AND BREEDING STUDIES USING TOMATO VARIETIES AND THEIR DERIVATIVES

A thesis presented in partial fulfilment

of the requirements for the degree of

Master of Horticultural Science

in

Plant Science

at

Massey University

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1971

SUMMARY.

This thesis describes the genetics and physiological consequences of a "netted yellow virescent" seedling characteristic in the tomato. In the first experiment, three tomato lines (Potentate, a commercial variety; Yellow seedling, a closely related line carrying the "yellow" characteristic; and their F_1 hybrid) were grown at three levels of applied nitrogen and sampled sequentially for 7 weeks. A second experiment examined characters such as photosynthesis, respiration and anatomy of the same lines under a range of nitrogen levels and light intensities. A final experiment examined the inheritance of the "yellow" character, and the variation in relative growth rate (RGR), in F_3 families derived from the cross Potentate x Yellow seedling.

Yellow seedling was inferior to both Potentate and F_1 hybrid in most of the characters studied. These differences frequently intensified as the plants advanced in age. The inferior RGR of Yellow seedling was due mainly to a low NAR, in turn due to low photosynthetic and high respiration rates.

It was also observed that Yellow seedling had a low specific leaf weight, low mesophyll cell numbers per unit leaf area and a low chlorophyll content per unit leaf area, and these factors probably accounted for its low photosynthetic rate, and explained the pale green appearance of its leaves. This hypothesis was further supported by the findings that, when photosynthesis, respiration and chlorophyll content were expressed on dry weight basis, the differences between varieties were diminished frequently to non-significance. In addition, Yellow seedling had a low rate of nitrogen utilization. This may have been caused by limited supply of carbohydrates produced by photosynthetic processes.

Unlike Potentate and F_1 hybrid, Yellow seedling was noted for its unresponsive behavior to variations of nitrogen concentration. Little effect of nitrogen level (from 57 to 340 ppm N) was found in experiment one. By extending the range of nitrogen concentration to include stressfully low levels (28 to 280 ppm N) significant effects were noted for characters such as respiration rate, chlorophyll concentration (experiment two) and RGR (experiment three).

In the third experiment it was shown that the F_3 family variation in RGR was entirely associated with the "yellow" trait. From this and the earlier experiments it was concluded that a recessive mutation involving a single gene or a block of tightly linked genes could have caused a general reduction in plant size, with adverse effects on vital physiological processes such as NAR, photosynthesis and nitrogen assimilation.

ACKNOWLEDGEMENTS

I would like to thank Professor Dr. J. A. Veale, Head of Horticultural Department, for introducing me to this thesis topic and for his assistance and advice during the experimental work and preparation of the manuscript.

The author would also like to acknowledge the encouragement and guidance of Dr. R. J. Clements, Lecturer in Plant Breeding of Agronomy Department, who supervised the greater part of this thesis.

A word of appreciation must be conveyed to Massey Librarians and to staff members of various Departments of the University, especially Dr. M. A. Nichols and Dr. B. S. Weir for statistical advice; Mr. K. J. Fisher and Mr. A. G. Robertson for valuable suggestions and those others who have helped me in one way or another.

In addition, I would like to thank Mr. H. J. Giesen, of D.S.I.R., Lincoln, for kindly providing me with the tomato seeds, and Mrs. E. M. Self who typed the manuscript.

Finally, I cannot express fully my appreciation to my parents for their continued encouragement and financial support throughout my study in New Zealand.

TABLE OF CONTENTS.

LIST OF FIGURES

Figures

LIST OF FIGURES

LIST OF TABLES.

LIST OF PLATES.

INTRODUCTION

Tomato plants, because of their economic importance and their wide adaptability, are grown under diverse climatic conditions in both Temperate and Tropical regions. Being highly inbred, tomato plants exhibit extensive variation in, among other characteristics, growth parameters (Table I.7); growth habits (see Barby 1963) and other characters as reviewed by Rick (1956).

The objectives of the three major experiments reported in this thesis were, respectively:

(1) to compare the vegetative growth of two tomato lines, namely Potentate and Yellow seedling, and their F_1 hybrid grown under three nitrogen levels. Quantitative growth analysis using the orthogonal polynomial technique was employed to examine the following growth parameters: dry weight of entire plant and plant parts; shoot/root ratio; specific leaf weight and leaf area; relative growth rate, net assimilation rate and leaf area ratio; relative growth rate and "net assimilation rate" of plant parts. In addition, the chlorophyll concentration, nitrogen percentage, nitrogen yield and rate of nitrogen utilization were also determined to gain a better understanding of the differences in growth between the parents and their F_1 offspring;

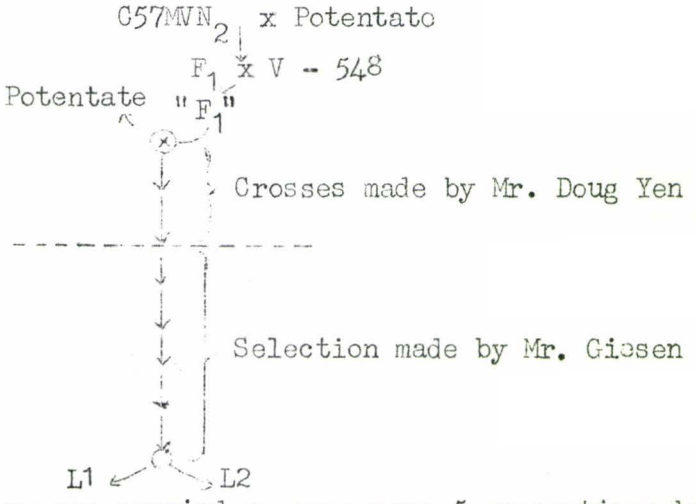
(2) to examine the contribution made by a number of physiological and leaf characteristics to the observed differences in growth of the three tomato lines grown under two nitrogen regimes over various periods of time. These measurements included the photosynthetic rate of leaflets, the respiration rates of roots and leaflets, and various leaf characteristics such as specific leaf weight, leaf thickness index, stomatal length and density, mesophyll cell number and chlorophyll concentration. Furthermore, the rates of cumulative stem elongation and leaf production, and other reproductive characteristics were also determined; and

(3) to examine the effect of the "yellow seedling" phenotypic condition on the genetic variation in relative growth rate of segregating F_3 families grown under two contrasting nitrogen concentrations.

Origin of the parent varieties (1968 D.S.I.R. Lincoln).

(1) Potentate/1 sps as recorded by H. Giesen is a commercial glasshouse tomato variety.

(2) Yellow seedling ex Maia sps 3 ('68). The "yellow" (= "netted virescence" gene Tm_2- nv) seedling character is derived from a parent line C57MVN$_2$. The following initial sequence of crossings were made by Mr. Doug Yen, at Otara, Auckland:



The selection was carried on over some 5 generations by Mr. Giesen until 2 lines (L_1 and L_2) of commercial value were obtained. From these two TMV - tolerant lines,"Hira" and "Maia" were eventually obtained. Both lines produce up to 25% of "yellow" (= "netted virescent") seedlings which are slow-growing and possess comparatively small narrow and pointed pale green cotyledons and true leaves (Giesen 1970).

Plate 1. The general appearance of Potentate (top) Yellow seedling (bottom) and their F_1 hybrid (middle).

CHAPTER 1

Review of Literature.

1.1 Growth Analysis.

The performance of a tomato variety can be evaluated in various ways. One method that has been commonly used is quantitative growth analysis, typically requiring measurement of relative growth rate (RGR) and its components net assimilation rate (NAR) and leaf area ratio (LAR) of the plant parts or whole plant. These growth indices, which vary with time and environmental conditions may also differ with species, varieties and strains in absolute terms and forms of pattern.

Steiner (1967) using water and gravel cultures has obtained growth curves of various parts of tomato plant (Var. Emocross B). He reported that plant height, and number and area of leaves increased in a rectilinear fashion while dry weight of the leaves, stem, roots and fruit increased in a parabolic pattern. This information on the stages and patterns of both vegetative and generative development of the plant is useful for the study on the influence of the mineral elements on the growth of the tomato plant and also for comparing varietal differences.

Genetic analyses of growth in tomato plants has been carried out by Kheiralla and Whittington (1962), and Peat and Whittington (1965). The former workers used the F_1 generation while the latter used segregating generations.

Using F_1 hybrids obtained from all possible crosses between four varieties of Lycopersicon esculentum (var. Potentate, Amateur, Radio and Outdoor Wonder) and one of L. pimpinellifolium (var. Red Currant) Kheiralla and Whittington (1962) found significant differences in growth rates between varieties and between the reciprocal inter-specific hybrids. The growth rates of the hybrids were closer to those of the parents having higher growth rates. The heterotic initial RGR in the inter-specific F_1 hybrids was most marked where L. pimpinellifolium was used as the female parent and appeared to be influenced by the size of the hybrids at emergence. The size of hybrids at emergence in turn was determined by the initial embryo size, the F_1 with smaller seed size having the faster RGR. However, plants with higher RGR also had a higher rate of fall in RGR. The parental varieties responded differently in terms of growth rate to removal or retention of side shoots.

Using the same three varieties of L. esculentum and one of L. pimpinellifolium, Peat and Whittington (1965) confirmed the observation of Kheiralla and Whittington (1962) that the dry weight RGR of the tomato plant was inherited additively with a large dominence component.

The forms of nitrogen can affect the RGR of tomato plants. Woolhouse and Hardwick (1966) showed that nitrate-fed tomato seedlings had a higher RGR than plants grown with ammonium nitrogen.

RGR is the product of NAR and LAR. Therefore variations of RGR can be attributed either to changes in NAR or LAR or both.

The NAR of tomato plants is closely related to the daily radiation (Goodall 1945; Kheiralla and Whittington 1962; Cooper 1966). This linear relationship between NAR and radiation may be disturbed by changes in plant growth and development, since changes in growth may affect the photosynthetic rate and utilization of the photosynthate of the plant (Sweet and Wareing 1967).

Variations in photosynthetic "size" can be expressed, for example, in terms of leaf area ratio (LAR) or leaf area index (LAI). The total leaf area of a plant is a function of leaf number and leaf size. Thus the effect of varieties or mineral nutrition on leaf area may arise from changes in either leaf number or leaf size. Variations in leaf size may in turn arise from effects of treatments on cell number and cell size.

It is generally held that within-species variation in dry matter production is more closely associated with variation in leaf area than with variation in NAR, e.g. increase of nitrogen supply increases dry matter production of sugarbeet mainly by increasing leaf area through increase in both cell number and cell size (Norton and Watson 1948).

Although these growth parameters are widely used to assess and compare the performance of plant species, varieties and genotypes in an endeavour to improve crop production, it is important that reliable growth index is used. For example, in the tomato (which exhibits indeterminate growth), NAR varies widely with the stage of plant development. This index is unlikely to be used in Lycopersicon as a selection index in breeding for better genotypes as pointed out by Kheiralla and Whittington (1962).

1.2 Nutritional and other environmental effects on tomato growth.

Environmental factors which depress the vegetative growth may stimulate reproductive development and vice versa (Salter 1958; Knavel 1969). Based on the results of a number of investigations by other workers, Deinum (1966) stated that the effects of N fertilization on dry weight production vary with:

(a) the rate of N application. Increased rates give increased production with diminishing returns at very high rates of N supply;

(b) the duration of growth;

(c) the time of the year, e.g. better response of tomato plants to a N increment is obtained in summer than in winter (Bunt 1969). This is

obviously related to other environmental factors, particularly light which is closely linked with N assimilation and photosynthesis;

(d) root aeration; and

(e) the water supply. Poor drainage and water shortage both reduce the N response.

The rate of tomato stem extension increases rapidly until fruiting begins. Many factors affect the shoot growth of tomato plant. Shading before the fruiting stage either reduces or has no effect on the mean stem extension rate or plant height depending on time of the year (Cooper 1969). Davis and Lingle (1961) found that increasing the nutrient solution from 1/5 strength to normal level promoted shoot growth in the warm-rooted (27°C) but not in the cool-rooted tomato plants. Increased atmospheric relative humidity also promotes shoot growth. Low night temperatures (e.g. 15.6 and 9.2°C) reduce stem extension and total dry weight of shoots.

The number of leaves and the total leaf area of tomato plants increase in a rectilinear fashion with time (Steiner 1967). A number of factors affect tomato leaf characteristics, and leaf production and growth. Photoperiod affects mature leaf size (the largest being varied from leaf 7 to 18 depending on sowing date) by affecting the duration of leaf growth (Cooper 1961). Both the leaf number and rate of leaf production are affected by light intensity and temperature (Calvert 1959 ; Whatanabe 1959). Consequently, at any given time, the total leaf area and the rate of leaf area production of a plant can be affected by any of these factors and their interactions.

Nutrition, especially N-nutrition, has a marked effect on leaf characteristics, affecting (for example), cell size and number (Abbott 1968), chlorophyll content (McCants and Waltz 1967) and general leaf appearance and structure. In addition the form of N applied can be important; NO_3-N is superior to NH_4-N as a nitrogen source especially at high N levels where NH_4-N is detrimental to tomato leaf and root growth (Woolhouse and Hardwick 1966; Kirkby 1968; Harade et al 1968).

Unlike sweet pepper the shoot/root ratios of tomato plants fluctuate with time, reaching a high value during the period of fruit growth (Van Der Post 1968). Nitrogen levels may affect the distribution of dry weight of different parts of tomato plant, and thus influence shoot/root ratios. While such information appears to be lacking; information derived from the experimental data of Woolhouse and Hardwick (1966) indicates that NO_3- fed tomato plants had higher shoot/root ratios than NH_4- fed plants. Although NH_4-N reduced the dry weight of both shoot and root, it reduced shoot more than root, resulting in lower shoot/root ratios.

N-nutrition is one of the factors which affects the dry weight and

fresh weight of tomato plants. Increased N levels increases fresh weight of tomato plants (Bierhuizen 1959; Howlett et al 1966). In addition the sources of N or the relative amounts of forms of N also affect the plant fresh weight and dry weight. The fresh weight or moisture content of NH_4-N fed tomato plants is lower than NO_3-N or urea-N fed plants. (Harada et al 1968; White 1969). This could be due to the inhibition of water uptake by ammonium ions as observed in sugarbeet roots (Stuart and Haddock 1968).

Environmental factors which affect vegetative growth also influence reproductive development. In particular ; light, temperature and photoperiod (Calvert 1959; Verkerk 1964; Howlett and Kretchman 1966; Abdella and Verkerk 1970) are involved.

It is generally held that too high or too low N supply has a detrimental effect on reproductive growth and fruit quality (Howlett and Kretchman 1966). High N supply usually promotes vegetative growth while retarding reproductive growth and development (Friis-Nielsen 1969). However, Abdella and Verkerk (1970) had shown that under certain environmental conditions, particularly at high temperature (35°C day and 25°C night) high N tended to enhance good fruiting.

Finally, it is interesting to note that big differences exist between plant species, with regard to their reaction to different forms of N, while NH_4-N promoted vigorous growth in highbush and lowbush blueberries, low level of NO_3-N could cause extremely poor growth in these plants (Cain 1951; Townsend 1966). Oerti (1963) attributed this difference to the absence of a biochemical system to utilize NO_3-N. This explanation was supported by the absence of nitrate reducing system in leaves and root of the lowbush blueberry (Townsend and Blatt 1966).

1.3 The effects of nitrogen nutrition on photosynthesis and respiration.

Photosynthesis and respiration are two of the most important physiological processes influencing plant growth. Studies of these two processes, briefly reviewed here in turn, are potentially valuable to an understanding of between - and within - variety differences in response to applied nitrogen.

1.3.1 Photosynthesis.

Genetic variability in both photosynthetic intensity and patterns of fluctuations within Lycopersicon species has been demonstrated by Brezhnet and co-workers (1969). While the photosynthetic potential of a plant is limited by genetic factors, many environmental and plant physiological factors interact to determine the level of photosynthesis at any given time. Since such effects and interactions are well documented (e.g. Heath 1969), only

those most relevant to the experiments in this thesis will be summarised here.

Photosynthetic rates of individual tomato leaves decline with age and vary with leaf position (Jakuskina 1962; Peat 1970). They also vary with temperature and light intensity. According to Ferry and Ward (1959) the photosynthetic rate of tomato leaves has a compensation point at 150 ft.-C and a light saturation point at 2500 ft.-c. While partial defoliation resulting in increased photosynthetic rate of the remaining leaves has been reported in many plants, e.g. Pinus radiata (Sweet and Wareing 1966) beans, dwarf maize and willows (Wareing et al 1968), no such work has been reported for tomato plants.

The chlorophyll concentration exerts a surprisingly weak quantitative influence on the photosynthetic rate of a leaf is well known. Gabrielsen (1948) suggested that only at extremely low chlorophyll concentration below 1 mg/dm^2 will there be a direct correlation between photosynthetic rate and chlorophyll concentration. In addition a number of chlorophyll-deficient plants or mutants, e.g. tobacco aurea mutants Su/su (Schmid 1967) and the chlorophyll-deficient Lespedeza procumbens (Clewell and Schmid 1969) are known to exhibit higher photosynthetic rate/mg chlorophylls under high light intensities than their corresponding green counterparts.

The nutritional effects on photosynthesis may be immediate by affecting the photosynthetic processes or delayed by enhancing senescence of leaves. Although nitrogen deficiency depresses photosynthetic rates of tobacco leaves (Moncakova 1966 cited by Avratovscukova 1968; Anderson 1967) and sugar beet (Nevins and Loomis 1970), also decreases chlorophyll concentration, it is unlikoly that reduced chlorophyll concentration caused by N deficiency has a major effect on photosynthetic rate. Nitrogen supply is more likely to affect photosynthesis by its effects on sink size, leaf longevity, leaf area ratio and metabolic "balance" (e.g. the balance between carbohydrate and N metabolism) whereas reduced nutrient level reduces maximum rate of photosynthesis in tomato leaves has been reported (Peat 1970) no published information concerning the different N levels on photosynthetic rate of tomato leaves is available.

However, the N (NH_4- and NO_3-N) forms applied have different effects on photosynthesis of tomato leaves. In comparison with NO_3-N, NH_4-N depresses the photosynthetic rate, reduces chlorophyll concentration and simultaneously causes morphological modifications of tomato leaves. (Puritch and Barker 1967 ; Maret-Vesk et al 1966).

1.3.1.1. The effects of N-nutrition on some morphological and microscopic features of tomatoes.

The studies of some selected effects of the level of nitrogen nutrition on the morphological and microscopic features of the tomato plant form part of these investigations. Such effects of N on cell division and general leaf morphology could be intimately related to variation in growth rates and photosynthesis. Relevant data on the tomato plant appear to be lacking in the literature but some results are available from studies on other species.

We have seen that varietal differences in growth may be due to efficiency of photosynthetic processes or size of photosynthetic area. Differences in leaf size between and within varieties could be due to variations in either cell size or cell number. Cooper and co-workers (1963) found that in both Lolium and Phalaris an increase in temperature from 10° to 25°C increases cell size but decreases cell division. An increase in light intensity has an opposite effect. Deficiencies of both P and N in strawberry plants decrease leaf area by reducing cell number and to a lesser extent by reducing cell size (Abbott 1968).

N-nutrition may also affect photosynthesis by affecting the general properties of the leaf, including the stomatal density. Thus the reduced photosynthetic rate of N-deficient leaves may be partly due to increased resistance to CO_2 diffusion as a result of such an influence.

Environmental factors such as water supply, light intensity, temperature and nutrition are known to affect stomatal differentiation in a number of plants (Zucher 1963). Although information concerning the effect of N supply on the density and length of tomato stomata appears to be lacking, the number and size of tomato stomata had been reported as follows: (Eckerson 1908).

Surface	Upper epidermis	Lower epidermis
The number minimum, mean and maximum/cm^2	0 - 12 - 87	79 - 130 - 202
size in /u length and breadth.	27 x 20 (guard cell closed) 10 x 5 (pore open)	33 x 23 (guard cell closed) 13 x 6 (pore open)

1.3.2 Respiration

The rate of respiration varies with the external and internal conditions of the living cells, and differ between plant species, between the organs of the plant, between the tissues of the same organ and by the age of

the organ. As different parts of the plant respire at different rates and vary with time, the respiration rate of the whole plant is essentially the resultant rates of the respiration of all the plant parts.

Respiration as a determinant of dry weight production is an important physiological process. It provides energy for the biochemical and physiological processes of the whole plant, e.g. translocation and absorption of water and nutrient. There are two types of respiration, namely the photo-respiration and the dark respiration. The processes of photorespiration and the dark respiration are different and is shown by the fact that the former has a higher optimum temperature than the latter (Hofstra and Hesketh 1969). The presence of photorespiration in the Calvin type plants and the absence of it in the C_4 type plants may partly account for the differences in photosynthetic capacity and efficiency between the two groups of plants (Downes and Hesketh (1968). The efficiency of using the photosynthates and its derivatives by respiratory processes in generating energy for metabolic processes may also partly explain the varietal differences in performance.

Nutrition is one of the many environmental factors which affect respiration. Deficiency or excess of different nutrient elements is known to have different effects on the respiration rates of plants, but here we will consider only the role of nitrogen. It needs to be noted in passing that respiration, especially root respiration, is involved in water and nutrient uptake by roots (Cannon 1932; Kelly 1947; Van Overbeek 1942; Jennings 1963). Thus nitrogen nutrition may influence the plant water economy by affecting water uptake through the effect of nitrogen on root respiration. Shimshi (1970) found that the transpiration rates of nitrogen-supplied bean plants were higher than those of N-deficient plants and that transpiration rates were varied by plant hydration rather than by the stomatal movement. In tomato plants increased nitrogen results in increased plant water content but higher NO_3-N does not affect transpiration rate (Bierhuizen et al 1959). The effect of N on respiration is complicated by the possible combined effect of the concentration of N and the relative amounts of ammonium and nitrate. While it is commonly accepted that low nitrogen levels lead to low respiration rates, a reduced respiration rate could be caused by the inhibitory action of NH_4^+ on the respiratory chain. High NH_4^+ accumulation in tomato plants resulting in root injury, reduced vegetative growth and early yield has been reported (Uljee 1964). In addition it has been shown that water uptake by sugar beet roots can be inhibited by ammonia (Stuart and Haddock 1968).

1.4 Aspects of the uptake and concentration of nitrogen by plants.

Species and varieties differ in their efficiencies of nutrient

absorption and utilization, and susceptibility to salt toxicity (e.g. Vose 1963 and Gerloff 1963). The efficiency of N utilization may be related to the enzyme system responsible for N assimilation. Hageman et al (1961) and Croy (1970) found that the nitrate reductase activity of maize and wheat was positively correlated with water soluble leaf protein and negatively with nitrate content. Thus the differential growth response of tomato varieties to different N levels might be due to differences in the capacity of the nitrate reducing systems. Ward's (1969) suggestion that a KNO_3- absorption regulating system existed in tomato plants seems to support such a possibility. However the situation is complicated by the relative amount of nitrate and ammonium in the growth medium and by the differential sensitivity of different plant varieties or species to NH_4- concentration.

The source of nitrogen not only affects nitrate reductase activity and therefore the nitrate reducing capacity but also alters the N metabolism of the plant (Mulder et al 1959). It has been shown that NH_4-treated tomato plants contained a higher level of amide, free NH_4-N and free basic amino acids than NO_3-treated plants. The content of malic acid in the NH_4-plants was ten times lower than that in the NO_3-plants (Margolis 1960; Harada et al 1968). The detoxication of NH_4^+ by tricarboxylic acid intermediates by assimilating NH_4^+ into harmless nitrogenons constituents lead to lower content of organic acids (Bonner 1950), a general depletion of carbohydrates and reduced uptake of cations Ca, Mg, K and Na (Woolhouse and Hardwick 1966; Montoya and Williams 1967 and Kirkby 1968). While Harada et al (1968) attributed the reduced growth of NH_4-treated tomato plants to the toxic effect of high NH_4 concentration, and to the abnormal metabolism of organic acids, Woolhouse and Hardwick (1966) believed that it was caused by the effect of NH_4 on the potassium and phosphorus metabolism. Kirkby (1968) in a study of the influence of the form of N-nutrition on the inorganic cations in the leaves of various plant species (me./100 g. dry wt) has obtained the following results for tomato plants.

N-source	Ca	Mg	K	Na	Total
NO_3	161	30	58	19	268
NH_4	62	25	29	15	131

In addition Montoya and Williams (1967) have shown that the growth of celery and the plant concentration of the major cations (Ca, K and Mg) were both reduced by NH_4^+. The interaction between NH_4^+ and Mg prevented an adequate uptake of Mg by the celery plants and resulted in leaf chlorosis.

Differences in the cation contents of leaves supplied with NH_4-N as compared with NO_3-N may be reduced if the NO_3- reduction is taking place in the root instead of in the leaf. Thus the site (leaf or root) where NO_3- reduction occurs may be to some extent accounts for the different response of different plant species to variations in the form of N-nutrition. The monocots (rye and oats) were comparatively much less sensitive to NH_4- nutrition (as compared to NO_3- nutrition) than tomato, chenopodium album, Buckwheat and Mustard in dry matter leaf yields is probably because of this difference in the site of NO_3- reduction.

The pH value plays an important role in the utilization of NH_4-N. At optimum pH bean plant can effectively convert the absorbed NH_4^+ to organic nitrogen compounds in the roots. Thus the movement of NH_4^+ to shoot is restricted, and the detrimental effect of high NH_4^+ concentration in the leaves is prevented or lessened. Sheat and co-workers (1959) reported that NH_4^+ could be used effectively for growth of exised tomato roots only when pH was maintained between 6.8 to 7.4. Incidentally this pH range is paralled to the optimum pH of 7.5 for the activity of the tomato enzyme nitrate reductase.

The important role of potassium on ammonium utilization in tomatoes has been shown by Maynard (1967). He found that the appearance of distinctive lesions on tomato stem and the poor growth of tomato plants grown under high ammonium salt conditions were related to high NH_4- K ratios in the plant material. These stem lesions were prevented and normal plant growth restored by the addition of potassium.

1.4.1 Variation of N content of the tomato plants with age and environmental conditions.

The N-content of the tomato plant varies with plant parts and time, and can be easily altered by environmental conditions. According to Ward (1964) the total percentage nitrogen in laminar tissue increases gradually from the bottom to the top of the plant while the reverse occurs with the percentage nitrogen in the petioles.

The N-content of tomato plants decreases with the age of the plant (Ward 1967; Anon 1969). Cadahia and Hernands (1965) reported that the nitrate content of tomato plants began to decline at the time when the flower buds were formed. Two periods of massive uptake of nutrients (N, Ca, Mg, P and K) were observed following the appearance of macroscopic floral buds, and during anthesis. Apart from the long term influence of the plant growth on the total percentage nitrogen the short-term response of the total percentage nitrogen in tomato plants to the environmental conditions is sensitive, result-

ing in considerable fluctuations. Thus conditions such as the withdrawal of N supply, aeration or water supply for a short duration which curtailed nitrate uptake will result in stimulated rate of nitrate absorption when normal conditions had been restored (Gates 1857; Alberda et al 1964; Ward 1969).

The form of nitrogen also affects the N-content of tomato plants. Although both the NH_4 and nitrate nutrition had little effect on the contents of protein-N, the soluble N-content was higher in NH_4-treated than NO_3-fed plants (Harada et al 1968).

The effects of source, concentration and pH on percentage nitrogen in the tomato leaves had been studied by White (1969). When nitrogen was provided as NO_3 or urea increased levels of N-nutrition caused an increase in leaf nitrogen reaching 5% to 6.1% respectively at 1000 p.p.m. The pH had little effect on percentage nitrogen. However when nitrogen was supplied as NH_4-N the pH had a marked effect on percentage nitrogen in the leaves; at pH5 a curve similar to those for urea and nitrate was obtained, at pH7 the leaf nitrogen was increased to 7.5% at 1000 p.p.m., and at pH3 an increase in NH_4-N concentration caused leaf nitrogen to decrease to about 2%.

1.5 Genetics of growth and nitrogen metabolism in the tomato.

The aim of the plant breeder is to produce better genotypes. To accomplish this, he must know the magnitude and nature of the genetic variation that exists in the breeding population. In addition a knowledge of the magnitude of the genotype-environmental interaction variance and genetic correlations among plant characters is also essential in devising and increasing the efficiency of the breeding program.

Hanson (1963) and Robinson (1963) have discussed the concept of heritability and its uses. While heritability of quantitative characters varies markedly between characters and populations, its determination (particularly if determined over a wide range of environmental conditions) is a powerful genetic tool for the plant breeder.

Tomato plants are known to exhibit great genetic variability and genotype-environmental interactions (Rick 1956). Whereas inheritance of various quantitative characters concerning fruit yield and quality has been extensively studied, few experiments have examined the inheritance of growth indices of tomato plants. To date there appears to be no published work on the heritability of RGR of parents and crosses of tomato plants grown under different levels of nitrogen.

1.6 Inheritance of chlorophyll.

The segregation of green and yellow plants in a Mendelian ratio of 3 G = 1 Y in F_2 and F_3 heterozygotes obtained by crossing green and chlorophyll deficient plants had been observed in bengal gram (Sandha and Chandra 1969) and soya beans (Wilcox and Probst 1969).

CHAPTER 2.

2. Materials and Methods.

2.1 Experiment One.

2.1.1 Introduction.

This experiment was designed to study:

(a) differences in RGR between two tomato varieties and their F_1 hybrid grown under three levels of Nitrogen;

(b) whether any differences were due to variation in NAR, LAR, or both;

(c) the time period over which any RGR differences occurred;

(d) the effect of three N levels on growth at specific developmental stages occurring during the entire 7-week growth period, and the differences in efficiency of N-utilization among parents and hybrid as measured by dry matter production per unit of N uptake;

(e) any changes in chlorophyll concentration of a specific leaf of the two parent varieties and their F_1 hybrid as influenced by time and N supply.

2.1.2 Experimental materials and layout.

Seeds of each of the two parent varieties potentate/1 sps and yellow seedling ex Maia sps 3 ('68) and their F_1 hybrid were germinated on 3/6/69 in a medium consisting of 50% peat and 50% river sand at temperatures of 65-70°C. Nine days from sowing, the seedlings were transplanted into 6-inch square plastic pots containing local fine-medium river sand. The seedlings were grouped into 4 complete randomised blocks, arranged on two 8 by 4 ft. wooden benches on one side of a 20 by 26 ft. glasshouse. The combination of 3 tomato lines, 3 nitrogen treatments and 7 harvest times within each replication gave a total of 252 plants. The temperature of the glasshouse was not allowed to drop below 60°F. The experiment extended over a 7-week period commencing on 12/6/69.

Equal amounts of Hewitt's (1966) nutrient solution containing one of three N levels (57, 170 and 340 ppm) were supplied to the tomato plants every alternative day throughout the experiment. The exact composition of the solution is given in Appendix I.

The amount of nutrient solution added to the tomato plants was increased with the growth of the plants to ensure that adequate nutrients (other than N) were available. Accumulation of salts in the pots resulting from transpiration and evaporation of water was prevented by flushing each pot every week with water prior to application of nutrient solution.

Lateral shoots were removed as soon as they appeared.

2.1.3 Sampling technique.

A total of 36 plants, (one plant from each treatment/line combination from each replicate) was harvested every week and the plants were separated into leaves, stems and roots. After each harvest, the position of the remaining plants within each replicate were re-randomised.

The separated stem, leaves and roots were oven-dried at 80°C to constant weight and before weighing were allowed to cool in a desicator containing anhydrous $Cacl_2$. The dry weights of the leaflets from harvest 5 to harvest 7 that were used in determination of chlorophyll concentrations were estimated separately, using leaf-area weight relationships determined at each harvest.

Leaf areas were determined initially by the blue-print method, and later by an airflow planimeter. The choice of these methods was based on their accuracy and practicability.

2.1.4 Nitrogen determination.

The total N content of the oven-dried tomato plants was determined by the Kjeldahl method using selenium as a catalyst. At the first harvest, all the 4 replicates of each variety/treatment combination had to be pooled to give enough dry weight for N determinations. For the same reason, in the second and third harvests the first and second, and the third and fourth replicates were pooled respectively. From harvest 3 onwards, the stems, leaves and roots of a plant were ground together in a mortar and pestle. Results are expressed as % N on a dry-weight basis.

2.1.5 Chlorophyll determination.

The determination of chlorophyll concentration of tomato leaflets was carried out on 5-, 6- and 7- week-old plants. Each week, terminal leaflets from the 7th. leaf of each tomato plant were removed. As each leaflet was sampled, its outline was traced on to a standard paper (for subsequent determination of the leaflet area), after which it was temporarily stored in a refrigerator until all plants had been sampled. Each sample was then treated in the following sequence:

(a) The leaflet was immersed in boiling water for a few minutes to kill the enzymes that might cause the chlorophylls to break down and also to facilitate chlorophyll extraction.

(b) The leaflet was ground in a mortar and the chlorophyll was extracted with absolute accetone.

(c) The extract was then centrifuged using a Bench Centrifuge B.T.L. (Type M202) at 3000 rpm for 3-5 minutes to remove the leaflet debris.

(d) The supernatant was transferred to a volumetric flask and made up with absolute acetone to 25 ml.

(e) The extract was shaken, an aliquot transferred to an absorption cell, and its absorbance determined at wavelengths 649 and 665 with an Hitachi spectrophotometer (model 101 uv-vis).

The components of the chlorophylls were determined by equations of Vernon (1960).

$$\text{Chlorophyll a (mg/litre)} = 11.63\ (A665) - 2.39\ (A649)$$
$$\text{Chlorophyll b (mg/litre)} = 20.11\ (A649) - 5.18\ (A665)$$
$$\text{Total Chlorophylls (mg/litre)} = 6.45\ (A665) + 17.72\ (A649)$$

The chlorophyll concentration was expressed on leaf area and dry weight basis. The dry weight of the leaflets was estimated from the leaflet area : weight relationship.

2.1.6 Calculation of various growth correlations and indices.

The percentage of stems, leaves and roots, shoot/root ratio, specific leaf weight, specific lear area were all calculated on dry weight basis, using the experimental figures. Estimated figures of $\log_e$ dry weight of entire plant and plant parts, and leaf area were obtained from derived quadratic equations, in the following forms:

$$\log_e W = a + bt = ct^2$$
$$\log_e A = a + ft + gt^2$$

where W = dry weight (mg) of entire plant or plant parts.
A = leaf area (cm^2) and
t = time in weeks.

These estimated figures were used in calculating the various growth parameters following the method used by Hughes and Freeman (1967).

Instantaneous relative growth rates of the entire plant and plant parts of each plant were obtained by differentiation of the respective quadratic equations to give

$$RGR = \frac{d\ (\log_e W)}{dt} = \frac{1}{W}\ \frac{dW}{dt} = b + 2ct$$

The leaf area ratio of each plant was obtained using the formula, $\text{antilog}_e\ (\log_e A - \log_e W)$, while the instantaneous net assimilation rates for the entire plant and plant parts were derived as follows:

$$NAR = \frac{RGR}{LAR} = \frac{d\,(\log_e W)}{dt} \cdot \text{antilog}_e\,(\log_e A - \log_e W)$$

$$NAR_s = \frac{d\,(\log_e W)}{dt} \cdot \text{antilog}_e\,(\log_e A - \log_e W_s)$$

$$NAR_l = \frac{d\,(\log_e W)}{dt} \cdot \text{antilog}_e\,(\log_e A - \log_e W_l)$$

$$NAR_r = \frac{d\,(\log_e W_r)}{dt} \cdot \text{antilog}_e\,(\log_e A - \log_e W_r)$$

where W = dry weight (mg) of organs specified by the subscripts.

In addition, correlations between various growth parameters were calculated. Electronic calculators were used for all calculations.

2.2 Experiment two.

2.2.1 Introduction.

The second experiment was set up to study:-

(a) The effects of 2 N levels (28 and 280 ppm) on various plant characters such as cumulative increments of fresh weight, stem, leaf production and side shoot production of the 2 parent varieties and their F_1 hybrid.

(b) The effects of N levels, leaf age and leaf position on the rates of apparent leaflet photosynthesis and respiration of the varieties.

(c) The varietal differences in root respiration rates and the effect of N levels.

(d) The varietal differences in certain leaf characteristics (specific leaf weight, leaf thickness index, stomatal density and length, and mesophyll cell number) which might be related to the efficiency of photosynthesis; and the response of these leaf characters to two N levels.

(e) The effect of N levels on the reproductive habits of the varieties.

(f) The effect of N levels on chlorophyll concentration of the varieties.

2.2.2 Experimental materials and layout.

For this experiment, plants of each parent variety and of their F_1 hybrid were grown individually in 75 ml test-tubes in solution culture. There were thus two nutrient solutions (see Appendix II) containing 28 and 280 ppm nitrogen, respectively and 3 varieties, these with 4 replicates, provided a total of 24 plants. The experimental design is shown diagrammatically in Fig. II.1

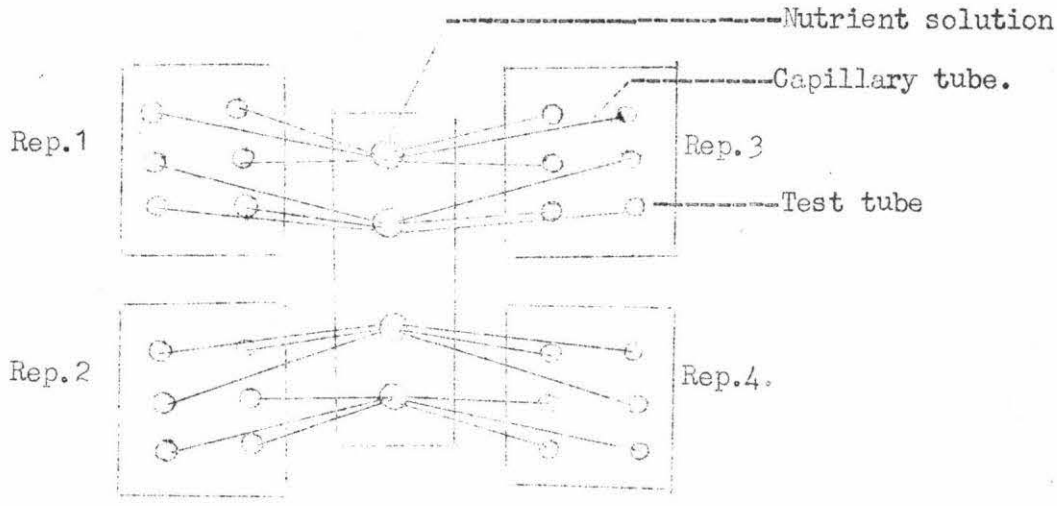


Fig.II.1. Aerial View of the Experimental Layout.

Each tube was supplied continuously with nutrient solution siphoned from a reagent bottle (containing either high or low N nutrient solution) by means of plastic capillary tubes. The nutrient solution was topped every morning and the nutrient solution was completely renewed every week. The bottles containing the nutrient solution were covered with tin foil to minimise evaporation and algal growth.

The plants were grown in nutrient culture over a period of 3 weeks, during which several measurements (see 2.2.3) were made before they were transplanted to 6-inch pots containing river sand. After this, the plants were allowed to adjust to their new growth medium for 14 days before further observations and measurements of various plant characters were made.

2.2.3 Sampling technique.

Cumulative fresh weight increments of whole plants were measured at weekly intervals for 3 weeks, while the cumulative increments of leaf production and side shoot production were measured throughout the experiment, which lasted for 15 weeks.

When measuring fresh weight, the plant was superficially dried with blotting paper before weighing to the nearest mg. The length of stem was measured to the nearest cm. The plants and the capillary tubes were randomised after each weekly measurements, care being exercised to avoid damaging the plants.

2.2.4 General observations and measurements.

2.2.4.1 Measurement of net photosynthesis.

Suitable leaflets from young fully expanded leaves of the 2 tomato varieties and their F_1 hybrid, were removed at a specific time (8.30 am.) and their net photosynthetic rates, as indicated by their apparent rates of oxygen evolution, were determined using a Gilson differential respirometer according to the method of Wilson et al (1969).

2 ml of a buffer solution, consisting of 0.2 M Na_2CO_3 and 0.2 M $NaHCO_3$ (1/9 v/v at 0.2 M) (Wilson et al 1969), and 0.5 ml of distilled water was placed in the reaction vessel and central well of the Gilson flask respectively. The tomato leaflet was carefully placed into the central well in such a position that the blade of the leaflet lay horizontally with the lower epidermis facing the light source while the stalk of leaflet was immersed in the distilled water. The gas evolved during photosynthesis was measured at 10-minute intervals over a period of 6 hours at 3 light intensities (590, 970 and 1300 lumens/ft.^{2}) as measured by a light meter (Model: 705S). Different light intensities were obtained by interchanging screens of sarlon netting with different mesh sizes. The Gilson flasks containing the photosynthesing systems were immersed and shaken in a water bath at 25°C and illumination from below was provided by 14 30W incandescent lamps. During changes of light intensity, the whole system was allowed to equilibrate for half an hour before the readings were recorded.

The apparent photosynthetic rates of a total of 24 leaflets of similar size and physiological age were determined in 2 successive days. This procedure was repeated weekly, using leaflets from different positions with comparable physiological age, so that during the 3-week experimental period the effect of increasing physiological age and leaf position could be examined.

The apparent photosynthetic rates of the tomato leaflets were expressed as $\mu l O_2/min/cm^2$, $\mu l O_2/min/mg$ fresh weight, and $\mu l O_2/min/mg$ dry weight. In leaflet five, the photosynthetic rates were also expressed as $\mu l O_2/min/mg$ of chlorophylls. The leaflet area was determined using a planimeter.

2.2.4.2 Measurements of respiration rates of leaflets and roots.

Leaflet respiration.

The respiration rates of leaflets and roots were determined using a Gilson respirometer.

2 ml 20% KOH (W/V) and 0.2 ml of distilled water was introduced into the reaction vessel and central well respectively. As before, leaflets were removed in the morning at 8.30 a.m., and each was placed in the central well of a separate Gilson flask with the stalk in close contact with the distilled water, while the blade of the leaflet was exposed to the atmosphere inside the flask. The same procedure, used in the determination of photosynthetic rates, was followed except that respiration was measured in very dim light. The O_2 consumed during respiration was measured at 10-minute intervals over 3-hour period at a temperature of 25°C.

The respiration rates of 6-week old tomato leaflets from the fifth leaf, and of 3-week old leaflets from leaves 9 to 14 were determined on 15-16/4/70 and 22-23/4/70 respectively.

Root respiration.

In order to obtain roots at a similar physiological age, a 6-inch plastic pot containing perlite was placed underneath each of the 24 pots housing the experimental plants. After enough roots had grown into the perlite (approximately one week) they were removed and their respiration rates were determined. Jensen (1962) has stated that the determination of tomato root respiration by measuring O_2 consumption is more reliable than measuring CO_2 evolution. The same procedure used in determining leaflet respiration was therefore used to determine root respiration, except that measurements were made in complete darkness, achieved by covering each of the Gilson flasks with tin foil.

2.2.4.3 Chlorophyll determination.

The procedure used in experiment one (2.1.5) to measure chlorophyll concentration of leaflets from leaves 4 and 5 was followed, except that 80% acetone was used as the extractant instead of absolute acetone. In order to increase the precision of leaf area measurements used in expressing chlorophyll concentrations, 3 random leaf discs from each leaflet (sampled by means of a cork borer of known diameter) were used for the determinations. An additional 3 leaf discs from each leaflet were used to establish a leaf weight : area relationship, in order to express the chlorophyll concentrations in terms of dry weight.

2.2.4.4 Measurements of stomatal length and density.

2 or 3 fully-matured leaflets from leaf 9 from each of the 24 plants were removed and kept moistened in separate containers. Pieces of the lower epidermis of the leaflets were removed using a razor blade, placed in a drop of water on a slide, and covered with a cover slip. The length and density of stomata were measured using a microscope fitted with an ocular micrometer (objective X40 and eyepiece X10; one division of ocular micrometer = 0.00318 mm).

In determinations of stomatal density, whole and more than half stomata falling within half the field of vision were counted. For each plant, a total of 5 randomly sampled fields were examined, and the mean of these 5 samples was used for subsequent statistical analysis. The cellulose acetate technique (North 1956) was attempted, but was abandoned because of

the difficulty in removing the film from the epidermis.

2.2.4.5 Measurement of mesophyll cell number.

A method somewhat similar to that used by Brown and Rickless (1950) was employed.

From each plant, 3 leaf discs from fully-matured tomato leaflets from leaf 9 were macerated in 2 ml of 0.5% chromic acid in a 50 ml test tube. The tubes were left for 24 hours to allow the chromic acid to dismember the tissue before the leaf discs were further disintegrated by sucking the cell suspension vigorously in and out of a pipette until no aggregate of cells was visible. Then, by means of a 0.2 ml pipette, a sample of the cell suspension was transferred to a haemacytometer (Mod-Fuch area = 1/16 mm^2; depth = 0.2 mm; and total squares = 144). A cover slip was applied and the mesophyll cells were counted under a microscope. Two measurements were made for each replicate. The cell suspension was shaken before each sampling, and the pipette containing the cell suspension was held horizontally while moving from the test tubes to the haemacytometer.

The cell numbers were expressed in terms of leaf area, and leaf dry weight.

2.2.4.6 Measurements of other plant characteristics.

Vegetative characters.

The following measurements were taken:

Leaf: Specific leaf weight = leaf dry weight (mg)/leaf area (cm^2).
Leaf thickness index = (fresh weight - dry weight)/leaf area, assuming the water content to be a function of volume (Hurd 1968).
Number of leaflets in the seventh leaf; number of leaves before first inflorescence; number of leaves between the first and second inflorescences, and between the second and third inflorescences; and cumulative weekly leaf production (number/week).

Shoot: Cumulative weekly stem extension; and side-shoot production before the first inflorescence.

Reproductive characters.

Number of days to anthesis; the position or height of the first truss; number of flowers and primordia in the first, second and third trusses.

Determinations of fruit quality (pH and sugar content) were abandoned because of the appearance of mineral-induced foliar symptoms, leaf mould and botrytis diseases during fruit ripening.

2.3 Experiment Three

2.3.1. Introduction

The aim of this experiment was to examine the heritability of whole-plant relative growth rate among F_3 families derived from the cross Potentate X Yellow seedling. In particular, the contribution of the "yellow" characteristic to the total genetic variation in relative growth rate was investigated. The parents, F_1, F_2, and both backcrosses (using the original parents as females) were included in the experiment for comparison, but not in the genetic analysis; these are subsequently referred to as ancillary groups, and families refers to F_3 families.

2.3.2. Materials and methods

Seeds of the various families and ancillary groups were obtained as indicated in Fig. III.1. The yellow seedling characteristic segregated in a 1 : 3 ratio in the F_2 (e.g. 7 yellow plants : 26 green plants; χ^2 = P= 0.252 N.S.) Because of poor flowering and fruiting in F_2's carrying the yellow character, relatively small numbers of F_3 seeds were obtained (by acid extraction) from these plants.

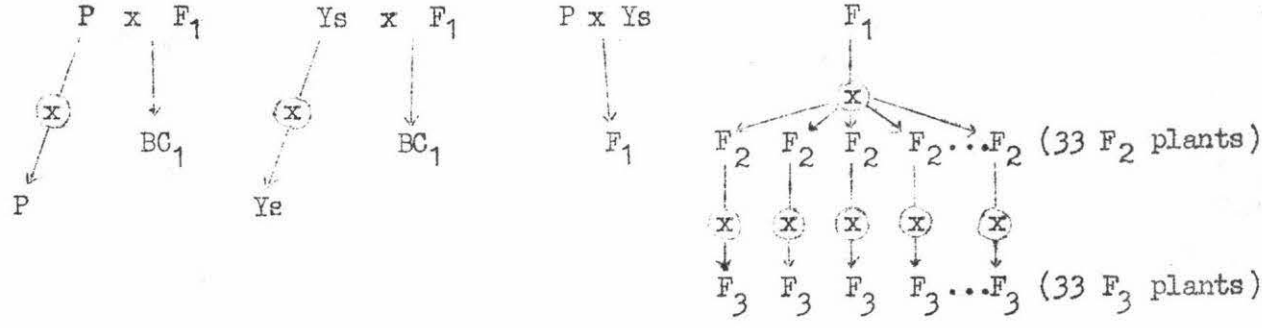


Fig. III. 1. Methods of producing seeds of F_3 families and ancillary groups used in experiment 3.

Of the 33 F_3 families initially produced, 2 were rejected because of insufficient seeds, and a further 14 were rejected because of poor (non-uniform) germination. The final analysis was therefore based on 17 families, and of these, 5 were found to be homozygous for the yellow character, 6 were heterozygous and 6 were homozygous green.

Seeds of the 31 families and 6 ancillary groups were germinated in sand covered with perlite in 6-inch pots in the glasshouse on two occasions (8/9/70 and 18/9/70), and transplanted to 4-inch pots (also containing sand) on 19/9/70 and 3/10/70 respectively. Because of the number of seedlings involved, it was necessary to use a separate glasshouse (controlled to allow maximum and minimum temperatures of 75°C and 65°C respectively) for each

planting date. On each occasion, sufficient seedlings of each family, and ancillary group were sown to allow for 2 replicates, 2 harvest dates and 2 nitrogen treatments (28 p.p.m. and 280 p.p.m. N in nutrient solutions applied daily; see appendix II. for details). The exact number of seedlings in each family varied due to unequal germination, occasional deaths etc., but as far as possible the unit of measurement for each family/harvest/ N treatment/replicate combination was 6 seedlings. For convenience of application of nutrient solution, seedlings of a measurement unit were grouped together, and the units were randomised within replicates. Although initially there were thus 4 replicates (1 and 2 in one glasshouse, 3 and 4 in the other), it was subsequently decided to pool replicates (1 and 4, 2 and 3) in order to increase the size of the measurement unit; this was necessary to avoid extreme variation in the ratio of yellow : green seedlings in families and ancillary groups exhibiting segregation for the "yellow" character. (It was not always possible at transplanting to distinguish between yellow and green seedlings).

Harvests were made 3 and 5 weeks after transplanting. At each harvest, the 6 plants of a unit were washed free of sand, bulked together, dried at 80°C for 48 hours and weighed as a unit; where the number of plants was less than 6, this also was recorded. In the case of families and groups segregating for the yellow character, the seedlings in each category in each unit were weighed separately, the number also being recorded. From the resulting whole-plant dry weight data, relative growth rates between the 3rd and 5th weeks were calculated as described below.

2.3.3. Statistical Analysis of Data.

Calculation of Relative Growth Rates.

Prior to calculating relative growth rates, the dry weights of the measurement units of families and groups segregating for the yellow character were adjusted to avoid errors due to unequal ratios of yellow : green seedlings. In making this adjustment, the mean weights of the yellow and green seedlings in each unit were obtained (after pooling the original replicates as described), and natural logarithms of these means were taken. For each unit the $\log_e$ mean weight of green seedlings was then multiplied by 3, the $\log_e$ mean weight of yellow seedlings was added, and the total was divided by 4. In this way a mean $\log_e$ dry weight of individual plants in these families (or groups) was obtained for each family (group) /N treatment combination at each harvest. For families and groups not segregating for the yellow character, mean $\log_e$ weights were obtained by simply taking $\log_e$s. of the mean weights. Relative growth rates of all families and groups

between the 3rd and 5th weeks were then calculated using the conventional formula :

$$\text{RGR (mg/mg/week)} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

Where W_1 and W_2 are mean dry weights of single plants (mg) at times t_1 (3 weeks) and t_2 (5 weeks) respectively.

These derived data were then analysed in two ways. First an analysis of variance of RGR of all 23 families and groups was carried out to compare the performance of the parents, F_1 - F_3 hybrids and backcrosses. Second, an analysis of variance of RGR of F_3 families alone was performed, and the broad-sense heritability (H) of RGR was derived from the expected mean squares as shown in Table III.1.

TABLE III. 1.

GENETIC ANALYSIS OF RELATIVE GROWTH RATE AMONG F_3 FAMILIES DERIVED FROM THE CROSS POTENTATE X YELLOW SEEDLING.

Source	d.f.	Expected Mean Square
Replicates	R - 1	
N levels (N)	N - 1	
Families (F)	F - 1	$\sigma^2_E + R\sigma^2_{FN} + RN\sigma^2_F$
F X N	(F-1)(N-1)	$\sigma^2_E + R\sigma^2_{FN}$
Error	(R-1)(FN-1)	σ^2_E
Total :	RNF - 1	

$$\text{Heritability (H)} = \frac{\sigma^2_F}{\sigma^2_F + \frac{\sigma^2_{FN}}{N} + \frac{\sigma^2_E}{RN}}$$

† H is the heritability of a family mean RGR, based on a unit of average size 8.5 individuals, (using formula $\eta_0 = \frac{1}{(a-1)}\left(N - \frac{\sum n^2}{N}\right)$ from Snedecor and Cochran (1968) p.290).

In order to examine the genetic variation in RGR after eliminating individuals homozygous for the "yellow" character, a third analysis was undertaken. For this purpose, all yellow seedlings were excluded from the analysis, and means were based on weights of green seedlings only. After calculating relative growth rates, a genetic analysis was again carried out using the 12 families containing green seedlings. This allowed a crude comparison of the genetic (family) variance in RGR before and after eliminating the effects of the "yellow seedling" phenotypic condition.

CHAPTER 3

3. Experimental results.

The details of the environmental conditions in the glasshouse during the first experiment are given in Appendix III. The mean temperature and relative humidity were obtained with a thermohydrograph. Mean light intensities outside the glasshouse, and bright sunshine hours were obtained from Plant Physiology Division, and Grassland Division, D.S.I.R., Palmerston North respectively. Details of the analyses of variance are given in the appendix.

3.1 Dry weight of entire plant.

As shown in Table I.1, there were significant differences between the two parent varieties and their F_1 hybrid in $\log_e$ weight per plant averaged over all harvests, with F_1 hybrid exceeding both parents. However, $\log_e$ dry weight per plant increased very significantly with time in a curvilinear fashion as demonstrated in Fig. I.1. Thus, though there was no significant difference between F_1 hybrid and Yellow seedling, and between the two parents at the first harvest, the difference in $\log_e$ dry weight became increasingly significant with time until at the final harvest the $\log_e$ dry weight per plant of Yellow seedling was 69% of that of Potentate and F_1 hybrid. As shown in Fig. I.1 the $\log_e$ dry weight per plant of F_1 hybrid had an initial heterotic increase over the two parent varieties up to the fifth harvest; after which there was no significant difference between Potentate and F_1 hybrid.

The influence of nitrogen concentration on $\log_e$ dry weight per plant is shown in Table I.2. While no significant effects between the low (N_1) and high (N_3) nitrogen concentrations, and between the low and medium (N_2) nitrogen levels on $\log_e$ dry weight per plant over a 7-week period were detected, there was a significant difference between N_3 and N_2, with N_2 being the apparently optimal concentration.

3.2 Dry weight of plant parts, and leaf area.

Table I.1 shows the varietal differences in mean $\log_e$ dry weight of plant parts. In agreement with $\log_e$ dry weight per plant, the average $\log_e$ dry weight of all plant parts of F_1 hybrid outyielded that of Potentate and Yellow seedling.

The influence of nitrogen levels on mean $\log_e$ dry weight of plant parts is shown in Table I.2. While weight of the roots did not react significantly to the nitrogen concentration there were effects of nitrogen concentration on the $\log_e$ dry weight of stems and leaves. In both cases, N_2 exerted a more favourable influence on the dry matter production of stems and roots than did N_1 and N_3. Thus the effect of nitrogen concentration on $\log_e$

dry weight per plant (3.1) was due to the influence of nitrogen concentration on dry weight yield of stems and leaves.

The interactions of variety x nitrogen on $\log_e$ dry weight of plant parts (Table I.3) were significant for $\log_e$ dry weight of stems and leaves. Although N_2 produced the highest $\log_e$ dry weight of leaves (except Yellow seedling) and stems of all varieties, Yellow seedling did not respond significantly to the applied nitrogen concentrations.

The changes of $\log_e$ dry weight of plant parts with time are shown in Fig. I.2. In all cases, the differences in $\log_e$ dry weight of stems, leaves and roots between Potentate and F_1 hybrid tended to diminish with time, while the differences between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid became increasingly significant as the plants advanced in age.

Other interactions of factors on $\log_e$ dry weight of plant parts were not significant except for $\log_e$ leaf dry weight, where significant time x nitrogen, and time x variety x nitrogen interactions were detected (Appendix IV).

The influence of nitrogen concentration over time became significant from fifth week onwards where the differencos between N_2 and N_1, and between N_2 and N_3 became increasingly significant as the plants advanced in age.

Fig. I.3 shows changes in $\log_e$ leaf dry weight with time of Potentate, Yellow seedling and F_1 hybrid as influenced by nitrogen concentrations. It is apparent that within Potentate and Yellow seedling there was no significant response of $\log_e$ leaf dry weight to variations of nitrogen concentrations over a 7-week growth period. But within F_1 hybrid significant differences between N_2 and N_3, and between N_2 and N_1 on $\log_e$ leaf dry weight became apparent at harvest four, and five respectively and continued to increase with time. In the case of N_1 and N_3, a significant difference between them was detected only during the final harvest for the hybrid.

Under high nitrogen concentration, the $\log_e$ leaf dry weight of Potentate and F_1 hybrid did not differ significantly from each other but that of Yellow seedling became steadily lower in comparison with the other two lines. Under medium and low nitrogen regimes, similar results were obtained, but at medium N there were also increasing significant differences between Potentate and F_1 hybrid from fourth week onwards.

Leaf area.

The mean $\log_e$ leaf area (cm^2) of Potentate, Yellow seedling and F_1 hybrid differed significantly from each other (Table I.1). However, the significant time x variety interaction (Appendix VI; Fig. I.4) indicates that this overall superiority of the hybrid was due only to its larger leaf

area during the first 4 weeks of growth.

The influence of nitrogen concentrations on $\log_e$ leaf area is shown in Table I.2. Although the N_2- and N_3- treated plants had higher $\log_e$ leaf area than that of N_1- plants, the differences were not significant as indicated by the analysis of variance (Appendix VI).

3.3 Shoot/root ratio and percentage dry weight of plant parts.

Yellow seedling differed significantly from Potentate and F_1 hybrid in mean $\log_e$ shoot/root ratios, with F_1 hybrid being intermediate between the two parents (Table I.1). Thus, by proportion, Yellow seedling had a comparatively smaller root system than that of Potentate and F_1 hybrid to give it a higher $\log_e$ shoot/root ratio.

The shoot/root ratio of the tomato plant has been reported (Van Der Post, 1968) to fluctuate with time. In this experiment the changes of shoot/root ratios of each variety with time are shown in Fig. I.5. As shown in the figure, a big increase in shoot/root ratios occurrod in Yellow seedling after the third harvest but this petered out with time to give just significant differences between Yellow seedling and the other lines in 4-week old plants, and between Yellow seedling and F_1 hybrid in 5-week old plants.

It has been known that the shoot/root ratio is influenced by reciprocal correlative influences between the aerial parts of a plant and its roots. Table I.2 shows the effect of three nitrogen levels on the shoot/root ratios. While N_1 and N_2 did not differ significantly in their influence on shoot/root ratios, N_3 exerted a significant depressive effect on shoot/root ratios by decreasing the dry weight of stem and leaves (see 3.2).

Percentage dry weight of plant parts.

Tables I.1, I.2 and I.3 show the effects of variety, nitrogen concentration, and variety x nitrogen interaction on percentage dry weight of various plant parts respectively. Overall varietal differences in $\log_e$ percentages of stems, leaves and roots were significant between the two parents, and between the Yellow seedling and F_1 hybrid (except $\log_e$ percentage of leaf), but there was no significant difference between Potentate and F_1 hybrid.

Regarding the influence of nitrogen concentration, N_3 tended to depress $\log_e$ percentage of stems and leaves but to increase $\log_e$ percentage of roots. Hence high nitrogen concentration appeared to inhibit the dry weight distribution to the aerial parts of the plants.

The interaction of variety x nitrogen was significant only on $\log_e$ percentage of leaf which occurred only in the case of Yellow seedling between N_1- and N_2- plants (Table I.3).

The changes in dry weight distribution with time were very significant (Fig. I.6). Similar time trends of $\log_e$ percentage dry weight of plant parts were found for Potentate and the F_1 hybrid, which did not differ in percentage composition. Initially Yellow seedling was proportionately higher in stem and lower in leaf than the other lines, but after approximately 4 weeks these differences disappeared. After the 3rd week, the proportion of root was lower in Yellow seedling.

Other interactions of factors on $\log_e$ percentage of plant parts were not significant except for a minor interaction of time x nitrogen on $\log_e$ percentage of stem.

3.4 Growth parameters: relative growth rate (RGR), leaf area ratio (LAR) and net assimilation rate (NAR).

RGR and NAR of all varieties increased with time (Fig.I.7), while LAR reached a maximum before declining. Similar time trends in these parameters have been reported in tomato plants (Goodall 1945; Cooper 1965; Newton 1966) and other plant species, examples wheat (Watson 1947) and Callistephus chinensis (Hughes and Freeman 1967). A complex time x nitrogen level x variety interaction for NAR occurred (Fig. I.8), but this did not seriously affect a basic pattern of varietal differences.

Yellow seedling had a consistently lower RGR than the other varieties (Fig. I.7), due to its low NAR. On the other hand, the LAR of Yellow seedling was ultimately higher than that of the other varieties, which did not differ in LAR. The F_1 hybrid initially had a higher RGR and NAR than Potentate, but this heterotic advantage did not persist.

The effect of nitrogen concentration depended on the variety (Table I.6) and varied with time (Fig. I.8). Initially, NAR of Yellow seedling and F_1 hybrid increased with nitrogen level, while that of Potentate decreased. RGR of Potentate and Yellow seedling reached a maximum at the intermediate nitrogen level, while that of F_1 was greatest at the highest level. LAR showed no nitrogen effects. With time, there was a tendency for the nitrogen level at maximum NAR took place to fall (Fig. I.8).

3.4.1 Relative growth rate, leaf area ratio and net assimilation rate as a function of total plant dry weight.

From the changes of growth parameters against time it was not possible to draw direct conclusions concerning the changes of growth parameters with plant size. For this reason the changes of RGR, LAR and NAR were plotted against $\log_e$ dry weight.

As shown in Fig. I.9 the relationship between RGR and $\log_e$ W was

not linear. Since the F_1 hybrid with a higher initial RGR (determined by coefficient b) increased at a slower rate (determined by coefficient c) than that of Potentate, the RGR of Potentate eventually overtook and surpassed that of F_1 hybrid after reaching the total plant dry weight of 3.5 (mg, $\log_e$ scale).

When LAR was plotted against total plant dry weight (Fig. I.10), it was evident that LARs increased and then declined with increasing plant size. At the beginning of the experiment, LAR of Yellow seedling was lower than those of Potentate and F_1 hybrid but increased at a faster rate and subsequently exceeded those of Potentate and F_1 hybrid at a total plant dry weight of 3 (mg, $\log_e$ scale). The maximum LAR of Yellow seedling was reached at a total plant dry weight of 3.8, that of Potentate at 4.1 and that of F_1 hybrid at 3.5.

Similar trends of NAR to the time trends of NAR for the two parents and their F_1 hybrid (Fig. I.7) were observed when NAR was plotted against the total plant dry weight (Fig. I.11). Comparable increases in NAR with plant size have been observed in potatoes and cauliflower by a number of workers (see Hughes and Corkshull 1969).

Finally, the relationship between RGR and NAR and between RGR and LAR for the two parents and their F_1 hybrid are shown in Fig. I.12. In general, the relations were positive between RGR and NAR, and negligible between RGR and LAR.

3.5 Instantaneous relative growth rates and net assimilation rates of plant parts.

In general, relative growth rates of individual plant parts (Figs. I.13, I.14, I.15) and "assimilation rates" of plant parts (Figs. I.16, I.17) showed the same trends as those of whole plants (Fig. I.7). Thus, Yellow seedling had consistently low growth and "assimilation rates", while the F_1 hybrid showed an initial heterotic advantage which was not maintained. The nitrogen regime usually had relatively small effects on RGR and "assimilation" rates (Tables I.5, I.6) and, where differences were significant, the intermediate nitrogen level gave the fastest growth rates. These nitrogen effects were primarily due to the response of the F_1 hybrid; the parents showed little evidence of nitrogen effects. Thus, significant variety x nitrogen interaction terms were frequently observed in the analyses of variance (Appendices VIII, IX). The only remaining significant interaction, a time x nitrogen effect on "assimilation" rates of stems, was of negligible importance (see Appendix Fig.1).

Yellow seedling had, overall, a relatively low specific leaf weight (Table I.4), but this effect took several weeks to appear (Fig. I.19; see also

the significant time x variety interaction in Appendix VI). Yellow seedling also had the lowest rate of leaf area expansion (RLAGR; Table I.4). The other varieties did not differ in either of these characters, nor was there any effect of nitrogen level on specific leaf weight. However, there was an interesting time x nitrogen interaction for RLAGR (Appendix VI; Fig. I.18); the intermediate nitrogen level was consistently better than the lowest level, but the high level seemed initially to inhibit RLAGR and later to promote it.

3.6 Chlorophyll concentration.

Yellow seedling had a chlorophyll concentration less than half those of the other varieties (which did not differ significantly), irrespective of whether concentration was expressed on a leaf area or leaf weight basis (Appendix XI; Table I.4). The effect was consistent over all harvests.

The nitrogen level had no effect on chlorophyll concentration per unit leaf area, but each increase in the nitrogen level caused a significant increase in chlorophyll per unit leaf weight (Table I.6; Appendix XI) in the varieties Potentate and F_1 hybrid. However, chlorophyll concentration of Yellow seedling did not increase with nitrogen level.

3.7 Per cent nitrogen content.

As shown in Appendix X analysis of variance of per cent nitrogen content indicated that all main effects and interaction terms were very significant for this character. The data is graphed in Fig. I.20. The figure indicates the complex interrelationships between varieties, nitrogen levels and time for % N. Overall, nitrogen regime had a surprisingly low effect on % N, suggesting (as is borne out by earlier results, e.g. dry weight accumulation and RGR) that the lowest regime in fact provided sufficient nitrogen for plant needs during the early weeks of growth. Later, the low nitrogen regime was clearly inadequate for Potentate and F_1 hybrid, but not for Yellow seedling. In fact, the ability of Yellow seedling to maintain % N levels (especially in low N regime) at a time when % N of the other varieties (notably F_1 hybrid) was falling gave it an overall superiority which accounts for the significant variety effect in the analysis of variance table (Appendix X). A logical interpretation of these results is that either the total amount or availability of nitrogen in the root environment became limiting in the low N regime as plants reached a certain size (or RGR) --- a size or growth rate that, during the seven weeks of this experiment, was attained first by F_1 hybrid, then by Potentate, and not at all by Yellow seedling. If this explanation is excepted then it can be stated that, where nitrogen was nonlimiting (e.g. the high N regime until week 6) varietal differences in % N were unstable and probably negligible.

3.8 Nitrogen yield.

Log_e N yield of each plant was obtained by taking the natural logarithm of the product of total dry weight and per cent N content. In general, the analysis of variance of nitrogen yield (Appendix X) showed the same trends as that of plant dry weight, indicating that plant weight was a more important cause of N yield variation than was % N.

Thus, significant differences between varieties and nitrogen regimes for log_e N yield (Tables I.4, I.5) followed the same order as those for log_e total dry weight per plant (same tables).

Similarly, the significant time x variety (Fig. I.21) and time x nitrogen regime (Fig. I.22) interactions for nitrogen yield are similar to those previously described for dry weight (Figs. I.1 and I.3 respectively), and simply indicate that the main effects of varieties and nitrogen levels took some time to reach significance.

Ignoring time trends, therefore, the data indicates that Yellow seedling had a relatively low nitrogen yield, due to its low growth rate, and that the intermediate nitrogen regime was optimal for N yield of all varieties.

3.9 Rate of nitrogen utilization.

The rate of nitrogen utilization was obtained by a formula similar to that used by Clements (1970):

$$An = \frac{\log_e N_2 - \log_e N_1}{t_2 - t_1} \times \frac{W_2 - W_1}{N_2 - N_1}$$

where An = rate of N-utilization = average rate of dry weight increase per week per mg nitrogen absorbed between times t_1 and t_2.

N_1, N_2 = N yield at times t_1 and t_2.

W_1, W_2 = dry weight in mg of whole plant at times t_1 and t_2.

Analysis of variance (Appendix X) indicated highly significant effects due to varieties, nitrogen concentrations, time, and interactions of time x variety and of time x nitrogen concentration on rate of nitrogen utilization.

The medium nitrogen regime produced the highest rate of nitrogen utilization (Table I.5 and Fig. I.24) with significant differences between nitrogen concentrations at the end of the experimental period.

Yellow seedling had a lower rate than the other varieties (Table I.4 and Fig. I.23), the rates of which increased with time very much faster than that of Yellow seedling. Initially, F_1 hybrid had a rate superior to

(but later only equal to) that of Potentate.

3.10 Summary of results, experiment one.

Essentially, the results of this experiment were as follows:

(1) Yellow seedling had a low RGR, which was in turn due mainly to a low NAR. For this reason, at any given nitrogen level plants of other varieties became progressively superior in dry weight to Yellow seedling with time. All plant parts showed essentially the same trend.

(2) Yellow seedling had a low chlorophyll concentration and a low specific leaf weight, but its nitrogen concentration was similar to those of the other varieties. It had a high shoot/root ratio, due primarily to a high % stem; thus, its LAR was only marginally higher than those of the other varieties.

(3) F_1 hybrid closely resembled Potentate although it did show some initial heterosis (in the first 6 weeks) for dry weight, leaf area (6 weeks), RGR (4 weeks), NAR (6 weeks), nitrogen yield (7 weeks) and rate of nitrogen utilization (7 weeks). Generally, F_1 hybrid showed a greater ability to respond to the highest level of solution nitrogen, although this was significant only for a few characters (RGR, NAR).

(4) The nitrogen regime had a surprisingly small effect on many characters. The characters which were more sensitive to changes of nitrogen concentration, include dry weight of entire plant, of stem and of root; shoot/root ratio; relative growth rates of shoot; "net assimilation rates" of shoot, of stem and of leaf; chlorophyll concentration (mg/gm); per cent nitrogen content; nitrogen yield and rate of nitrogen utilization. In addition, there were indications that high nitrogen level was detrimental to a number of characters, namely shoot/root ratio, and "net assimilation rates" of stem and leaf.

TABLE I. 1.

Mean varietal differences in several plant characters measured in experiment one.

Characters	Potentate	Yellow seedling	F_1 hybrid	LSD 5%	LSD 1%
Log_e dry wt(mg)entire plant	4.290	3.316	4.524	0.080	1.208
" stem	2.464	1.700	2.705	0.087	0.116
" leaf	3.812	2.818	4.030	0.082	0.108
" root	2.726	1.589	3.009	0.094	0.124
Log_e leaf area (cm^2)	3.059	2.166	3.167	0.104	0.137
" % stem	2.743	2.942	2.760	0.071	0.093
" % leaf	4.107	4.050	4.078	0.053	0.070
" % root	3.039	2.873	3.079	0.120	0.159
" shoot/root ratio	1.322	1.488	1.252	0.138	0.182

TABLE I. 2.

The mean effect of nitrogen levels on several plant characters measured in experiment one.

Characters	57ppm N	170ppm N	340ppm N	LSD 5%	LSD 1%
Log_e dry wt(mg)entire plant	4.025	4.101	4.003	0.080	0.105
" stem	2.269	2.400	2.201	0.087	0.116
" leaf	3.541	3.634	3.485	0.082	0.108
" root	2.421	2.437	2.466	N.S.	
Log_e leaf area (cm^2)	2.784	2.820	2.788	N.S.	
" % stem	2.822	2.846	2.777	N.S.	
" % leaf	4.033	4.071	3.866	N.S.	
" % root	3.025	2.923	3.043	0.120	0.159
" shoot/root ratio	1.349	1.433	1.279	0.138	0.182

TABLE I. 3.

The mean variety x nitrogen concentration interactions on $\log_e$ dry weight (mg) of entire plant and plant parts, $\log_e$ leaf area (cm^2), $\log_e$ percentage of dry weight of plant parts and $\log_e$ shoot/root ratio.

Characters	Potentate			Yellow seedling			F_1 hybrid			LSD	
	57ppm N	170ppm N	340ppm N	57ppm N	170ppm N	340ppm N	57ppm N	170ppm N	340ppm N	5%	1%
Entire plant	4.267	4.356	4.246	3.295	3.319	3.334	4.514	4.629	4.430	N.S.	
Stem	2.462	2.581	2.351	1.692	1.720	1.689	2.654	2.899	2.564	0.152	0.200
Leaf	3.795	3.831	3.811	2.835	2.817	2.802	3.994	4.255	3.841	0.142	0.188
Root	2.719	2.709	2.748	1.519	1.619	1.630	3.023	2.984	3.020	N.S.	
Leaf area	3.002	3.116	3.059	2.183	2.129	2.185	3.167	3.216	3.119	N.S.	
% stem	2.771	2.785	2.672	2.951	2.916	2.960	2.744	2.838	2.698	N.S.	
% leaf	4.099	4.107	4.116	4.090	3.993	4.066	4.060	4.114	4.059	0.092	0.122
% root	3.065	3.008	3.045	2.884	2.812	2.924	3.127	2.950	3.162	N.S.	
Shoot/root ratio	1.336	1.369	1.261	1.505	1.497	1.463	1.208	1.433	1.114	N.S.	

TABLE I. 4.

Mean varietal differences in various growth characteristics (over a 7-week period).

Characters	Potentate	Yellow seedling	F_1 hybrid	LSD 5%	LSD 1%
RGR(mg/mg/week)	0.935	0.556	0.961	0.066	0.087
LAR(cm^2/mg)	0.307	0.327	0.282	0.031	0.041
NAR(mg/cm^2/week)	3.389	1.792	3.747	0.347	0.459
RSGR(mg/mg/week)	0.969	0.540	0.944	0.051	0.068
RShGR(mg/mg/week)	0.940	0.571	0.920	0.034	0.044
RLGR (")	0.961	0.597	0.905	0.083	0.030
RLAGR(cm^2/cm^2/week)	0.859	0.617	0.816	0.053	0.070
RRGR(mg/mg/week)	0.913	0.467	0.870	0.077	0.102
NAR_s(mg/cm^2/week)	0.695	0.335	0.768	0.130	0.172
NAR_{sh}(")	2.734	1.488	2.815	0.301	0.398
NAR_l (")	2.116	1.190	2.421	0.413	0.545
NAR_r (")	0.685	0.243	0.780	0.103	0.136
SLW (mg/cm^2)	2.165	1.946	2.261	0.172	0.227
ch-content(mg/dm^2)	2.641	1.023	2.619	0.523	0.654
ch-content(mg/gm)	8.536	3.772	8.278	1.074	1.419
% N content	3.930	4.001	3.749	0.169	0.223
Log_e N yield	5.652	4.717	5.860	0.132	0.174
Rate of N-utilization	3.269	0.502	3.516	0.687	0.907

TABLE I. 5.

The mean effect of N levels on various growth parameters of two tomato varieties and their F_1 hybrid grown over a 7-week period.

Characters	57ppm N	170ppm N	340ppm N	ISD 5%	ISD 1%
RGR(mg/mg/week)	0.790	0.834	0.829	N.S.	
LAR(cm^2/mg)	0.300	0.308	0.306	N.S.	
NAR(mg/cm^2/week)	3.038	2.928	2.963	N.S.	
RSGR(mg/mg/week)	0.803	0.838	0.811	N.S.	
RLGR(")	0.831	0.851	0.781	N.S.	
RLAGR(cm^2/cm^2/week)	0.730	0.797	0.765	0.053	0.070
RRGR(mg/mg/week)	0.715	0.791	0.744	N.S.	
NAR_s(mg/cm^2/week)	0.578	0.705	0.515	0.130	0.172
NAR_l(")	1.873	2.195	1.658	0.413	0.545
NAR_r(")	0.560	0.585	0.564	N.S.	
SLW (mg/cm^2)	2.179	2.095	2.100	N.S.	
ch-content(mg/dm^2)	2.035	2.078	2.169	N.S.	
ch-content(mg/gm)	5.647	6.789	8.150	1.074	1.419
% N content	3.472	3.921	4.286	0.169	0.223
Log_e N yield	5.268	5.484	5.477	0.132	0.174
Rate of N-utilization	2.027	2.878	2.382	0.687	0.907

TABLE I. 6.

The mean variety x nitrogen level interactions on various growth parameters of two tomato varieties and their F_1 hybrid grown over a 7-week period.

Characters	Potentate			Yellow seedling			F_1 hybrid			LSD	
	57ppm N	170ppm N	340ppm N	57ppm N	170ppm N	340ppm N	57ppm N	170ppm N	340ppm N	5%	1%
RGR	0.938	0.969	0.900	0.545	0.564	0.559	0.887	0.969	1.027	0.113	0.150
LAR	0.299	0.315	0.305	0.335	0.313	0.333	0.268	0.296	0.280	N.S.	
NAR	3.860	3.212	3.095	1.673	1.829	1.874	3.580	3.744	3.918	0.602	0.796
RSGR	0.955	0.995	0.957	0.529	0.527	0.563	0.925	0.993	0.914	N.S.	
RLGR	1.024	0.939	0.921	0.570	0.619	0.603	0.900	0.996	0.819	0.144	0.190
RLAGR	0.834	0.903	0.840	0.583	0.618	0.650	0.773	0.870	0.805	N.S.	
RRGR	0.890	0.954	0.895	0.415	0.470	0.517	0.840	0.949	0.821	N.S.	
NAR_s	0.729	0.775	0.581	0.307	0.330	0.368	0.699	1.009	0.595	0.226	0.298
NAR_l	2.339	2.009	2.001	1.173	1.256	1.140	2.107	3.321	1.834	0.718	0.949
NAR_r	0.714	0.685	0.655	0.201	0.253	0.276	0.765	0.816	0.759	N.S.	
SLW(mg/cm^2)	2.300	2.073	2.123	1.920	1.961	1.958	2.316	2.249	2.219	N.S.	
ch-content(mg/dm^2)	2.778	2.501	2.643	0.993	1.021	1.055	2.335	2.711	2.810	N.S.	
ch-content(mg/gm)	7.017	8.175	10.417	3.858	3.333	4.125	6.067	8.858	9.908	1.518	2.006
% N	3.364	4.034	4.391	3.889	4.386	4.293	3.324	3.840	4.082	0.293	0.387
Log_e N yield	5.461	5.743	5.751	4.650	4.704	4.798	5.693	6.004	5.884	N.S.	
Rate of N-utilization	2.736	3.857	3.213	0.469	0.551	0.485	2.875	4.225	3.448	N.S.	

TABLE I. 7.

Growth parameters of tomato plants obtained by various workers (All the data originally reported were adjusted to give standardised units for comparison)

Treatments	RGR (mg/mg/week)	LAR (cm^2/mg)	NAR (mg/cm^2/week)	References
Winter	-----	-----	§ 0.819	
Summer	-----	-----	§ 0.813	Goodall(1945)
Shortest day	-----	-----	1.077	
Longest day	-----	-----	9.695	Cooper(1965)
CO_2 300 ppm	1.561	0.300	4.970	
1000 ppm	1.792	0.270	6.370	Witter(1965)
Sowing date 31 Oct.	-----	-----	1.127	
19 Feb.	-----	-----	3.598	Newton(1966)
CO_2 1000 ppm, low light intensity From sowing date				
32-39 days: 1.4.66	1.134	0.555	2.048	
23.1.67	1.260	0.565	2.233	Hurd(1968)
Mid-winter Potentate	0.935	0.307	3.389	
Yellow seedling	0.556	0.327	1.792	Experiment one, present work (1969)
F_1 hybrid	0.961	0.282	3.747	
Early summer, 280 ppm N				
Potentate	1.314	-----	-----	
Yellow seedling	0.528	-----	-----	
F_1 hybrid	1.297	-----	-----	
28 ppm N				
Potentate	1.124	-----	-----	
Yellow seedling	0.663	-----	-----	Experiment three, present work (1970)
F_1 hybrid	1.089	-----	-----	

§ This character was computed in term of dry weight (mg/mg/week)

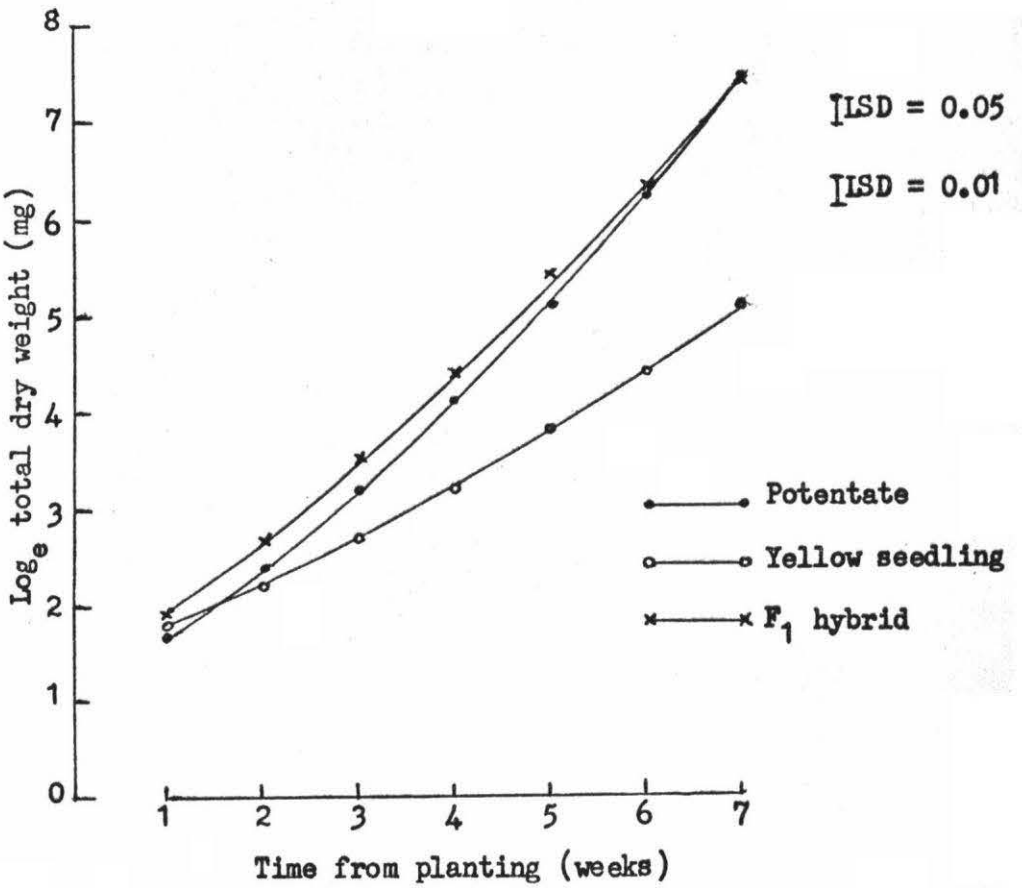


Fig.1.1 Curves derived from quadratic equations for log$_e$ total dry weight as a function of time for tomato varieties (Potentate and Yellow seedling) and their F_1 hybrid.

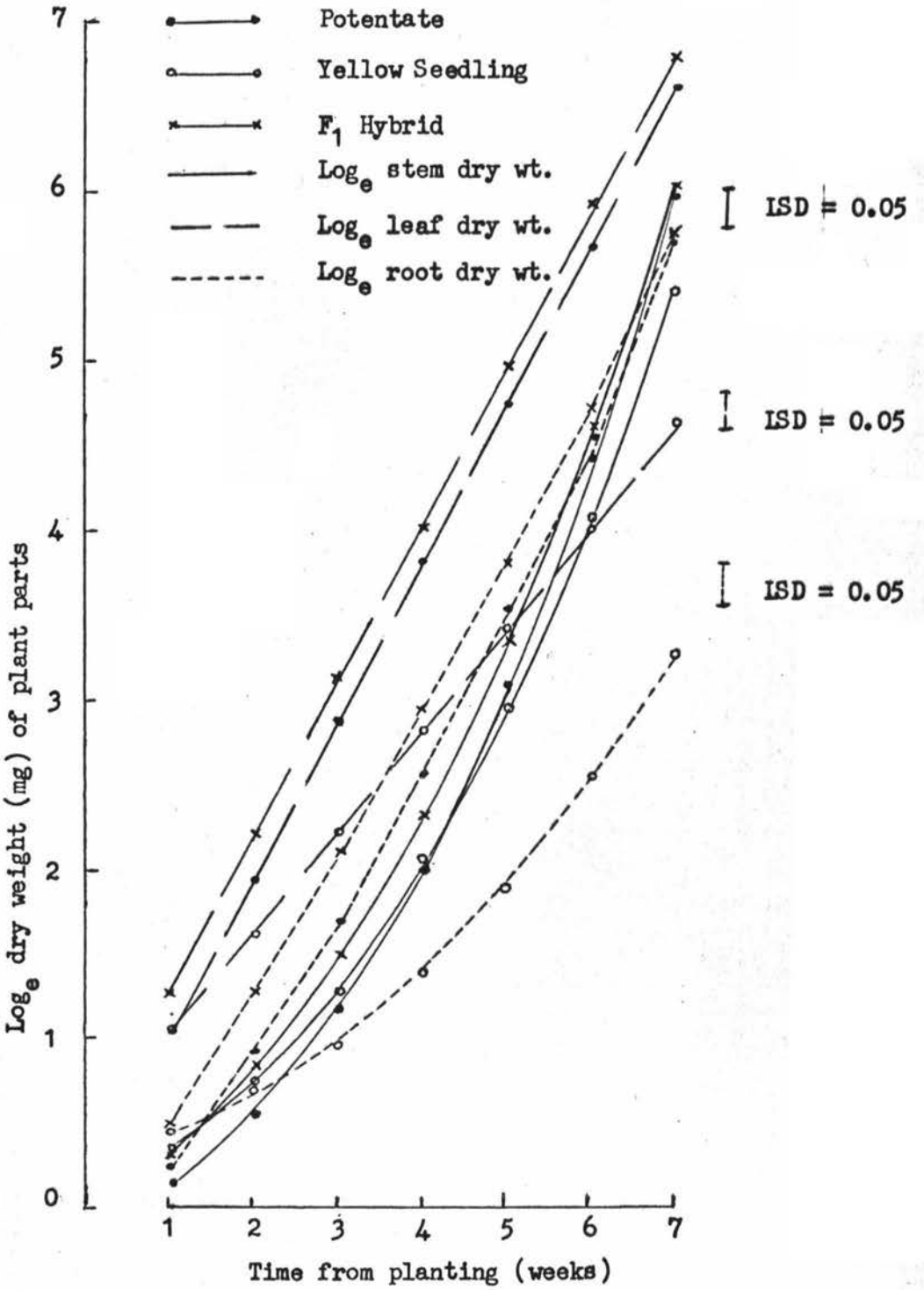


Fig. 1.2. Changes in dry weight of various plant parts of two tomato varieties and their F_1 hybrid during the experimental period. The lines are the quadritic curves fitted to all individual plants.

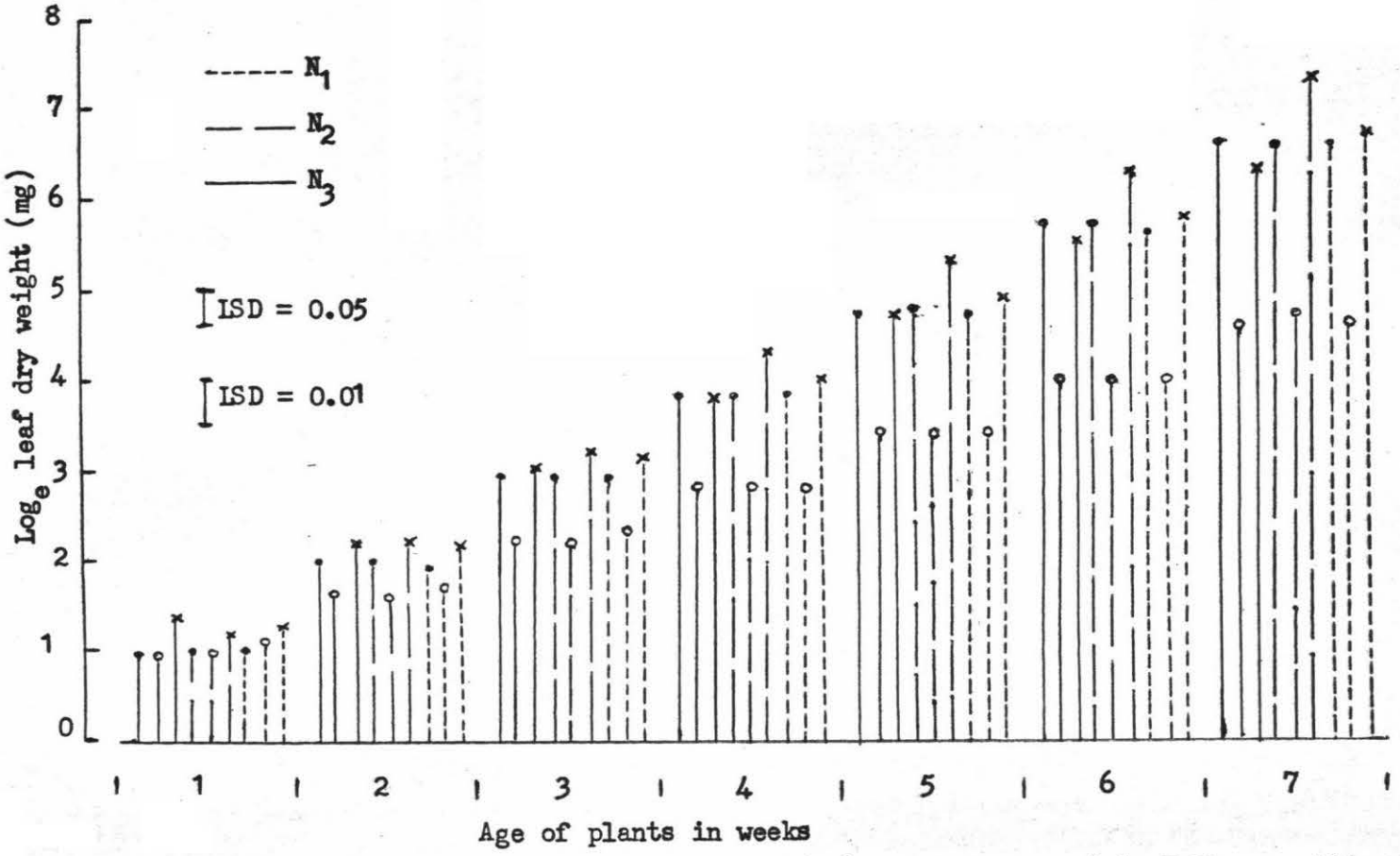


Fig. I.3 Changes in log_e leaf dry weight with time of Potentate (•), Yellow seedling (∘) and F_1 hybrid (×) as influenced by nitrogen concentrations. The figures are estimated from quadratic equations fitted to log_e leaf dry weight.

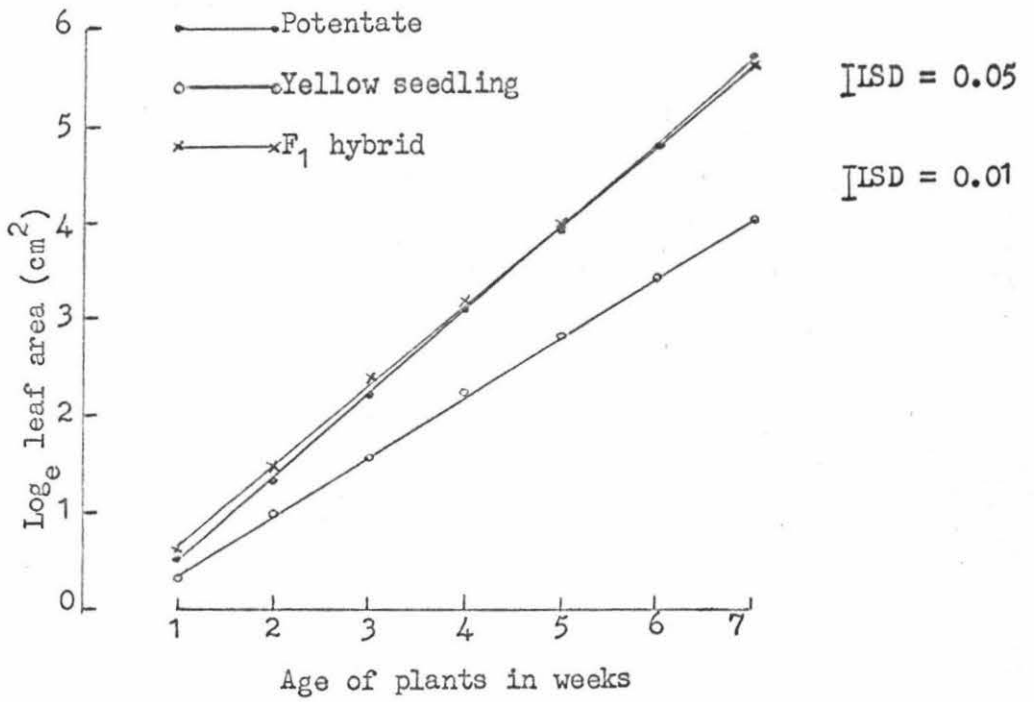


Fig.I.4 The increases of log_e leaf area with time.

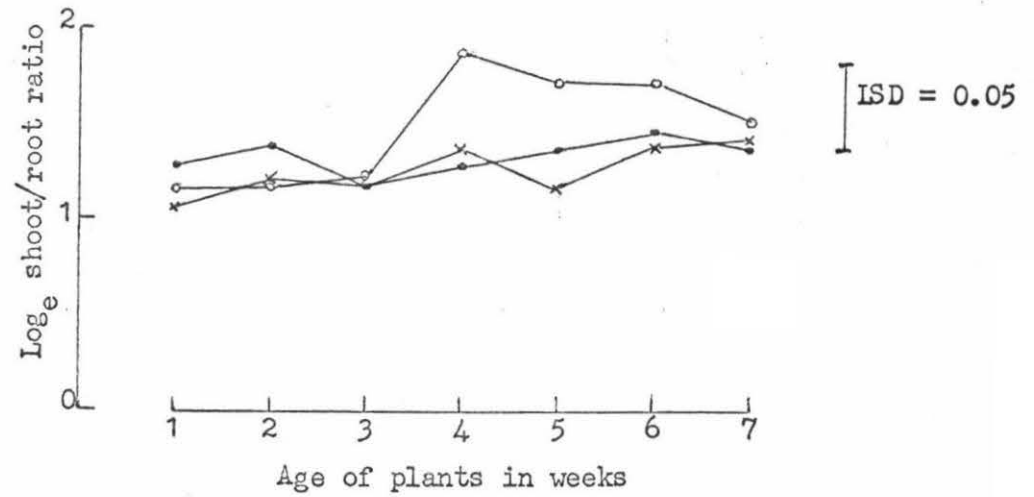


Fig.I.5 Changes in shoot/root ratios with time.
Symbols as the above figure.

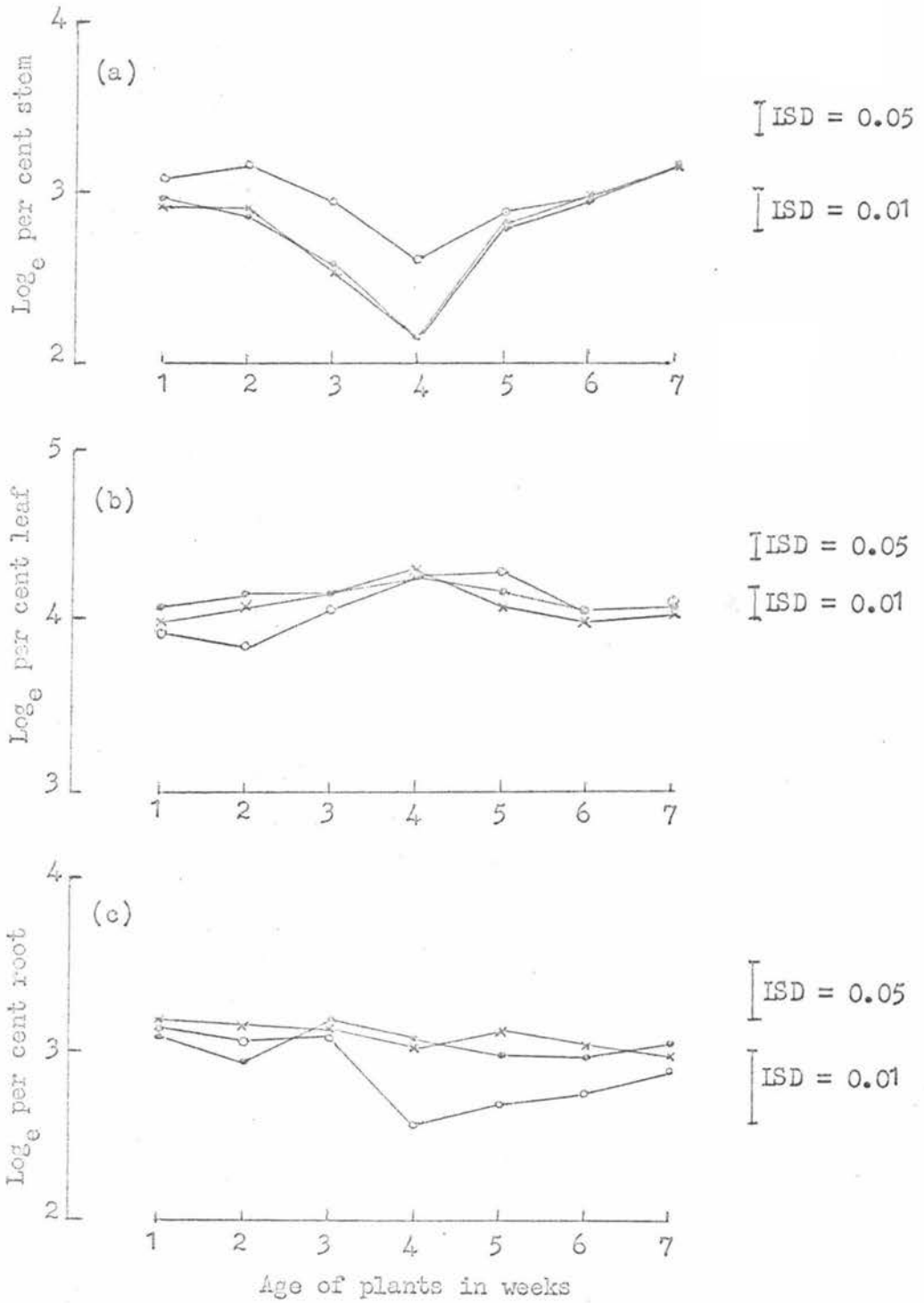


Fig.I.6 Changes in $\log_e$ percentage of dry weight of (a) stems, (b) leaves and (c) roots of Potentate (∘), Yellow seedling (○) and their F_1 hybrid (×) with time.

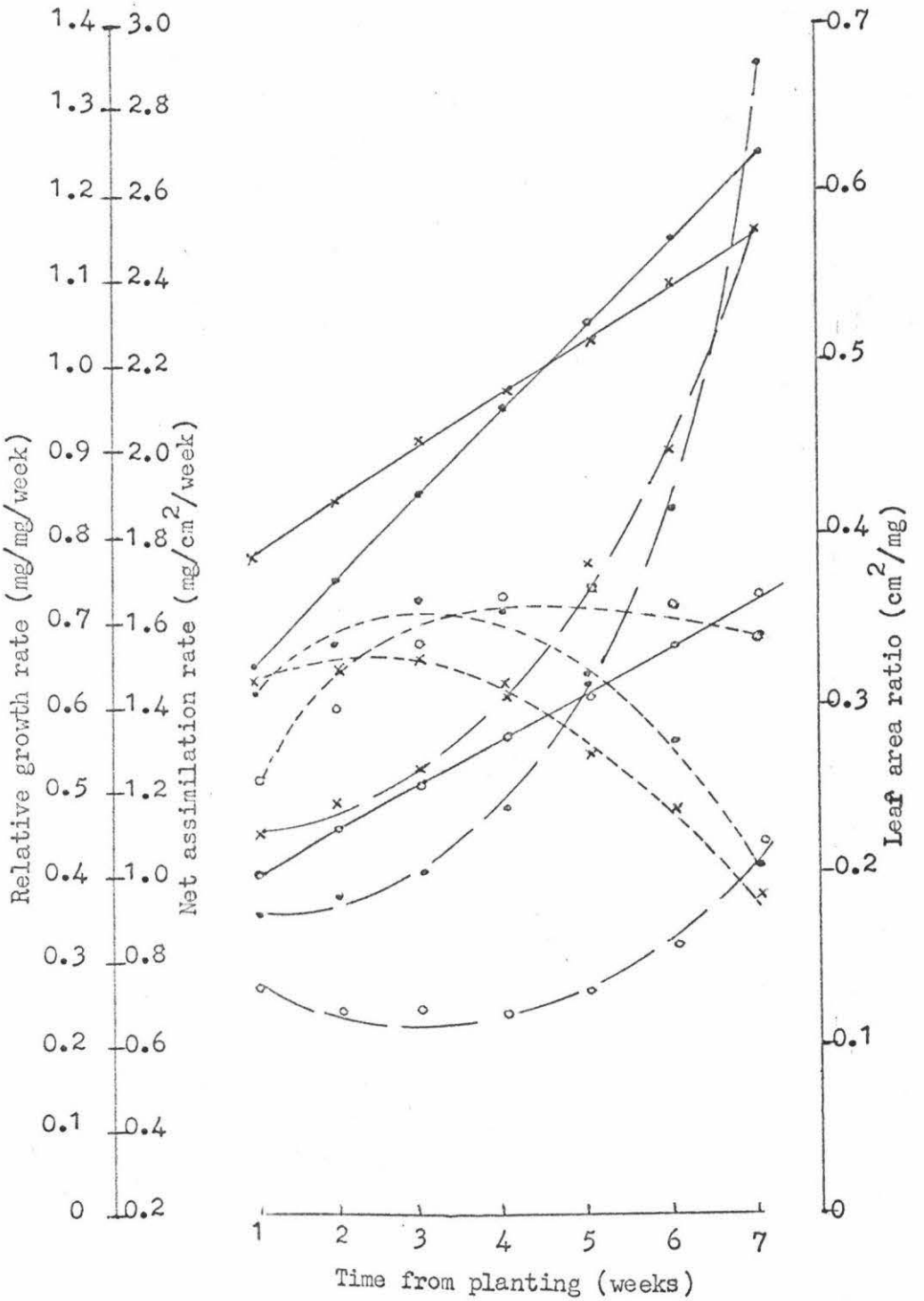


Fig.1.7 Relationships between instantaneous RGR, NAR and LAR, and harvest time for Potentate (•), Yellow seedling (∘) and their F_1 hybrid (×).——RGR,— —NAR,----LAR. LSD at 5% and 1% levels: for RGR = N.S.; for NAR = 0.920, 1.216; for LAR = 0.081, 0.107.

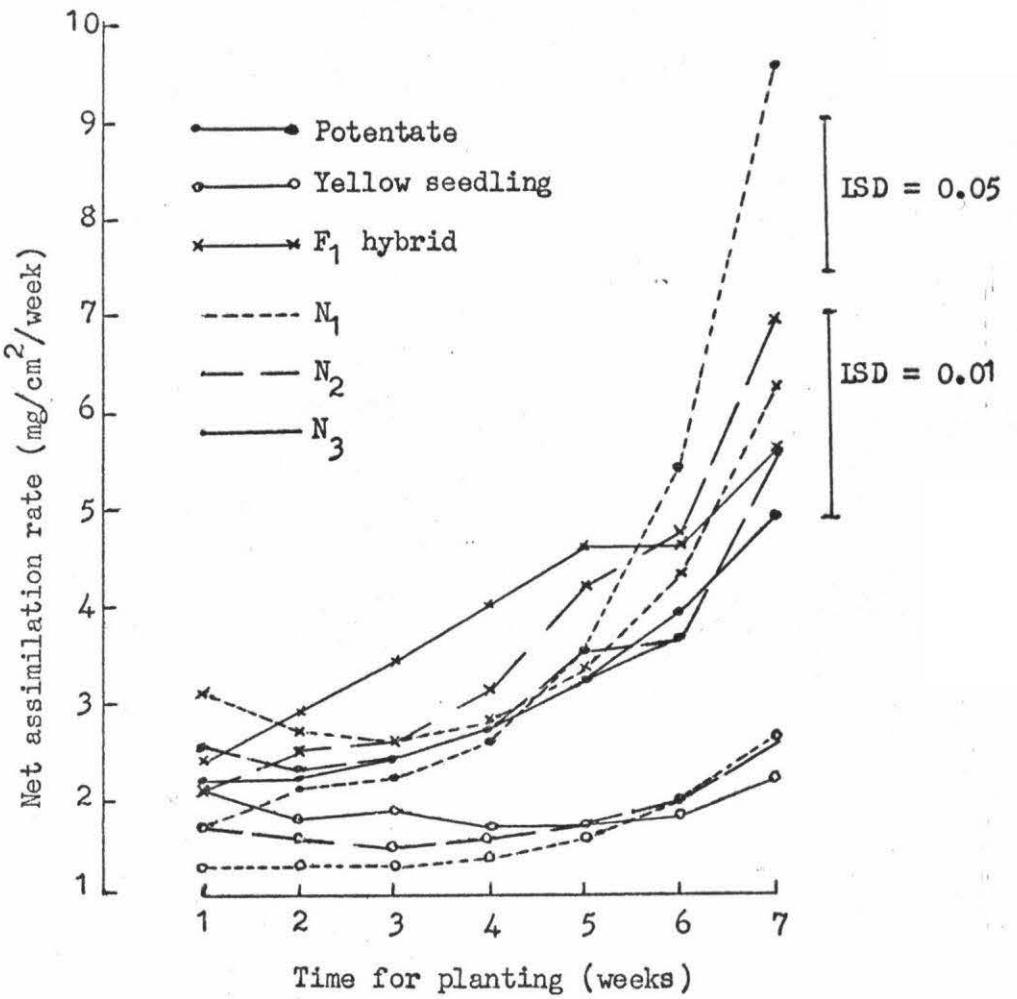


Fig.I. 8 The time trends of net assimilation rates of Potentate, Yellow seedling and F_1 hybrid as influenced by nitrogen concentrations.

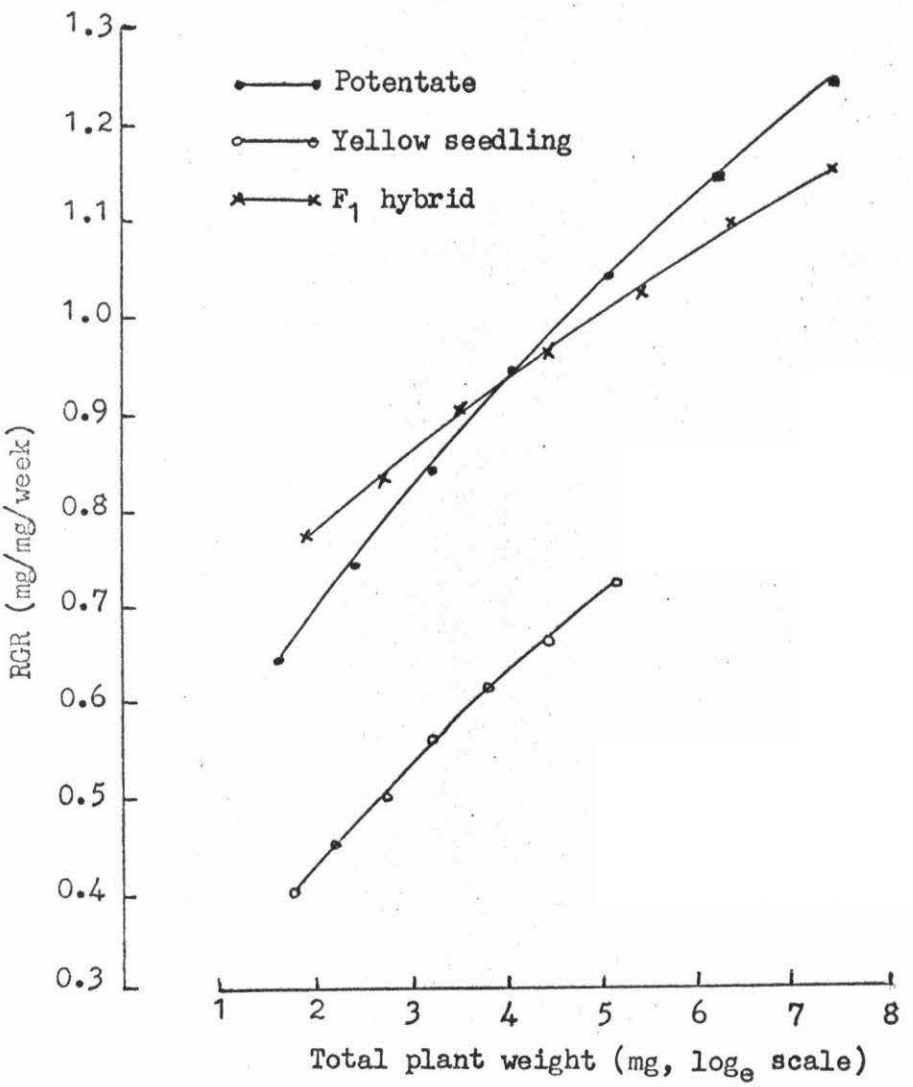


Fig.I. 9 Relationship between RGR derived from quadratic curves fitted to $\log_e$ total dry weight and $\log_e$ total dry weight for Potentate, Yellow seedling and their F_1 hybrid.

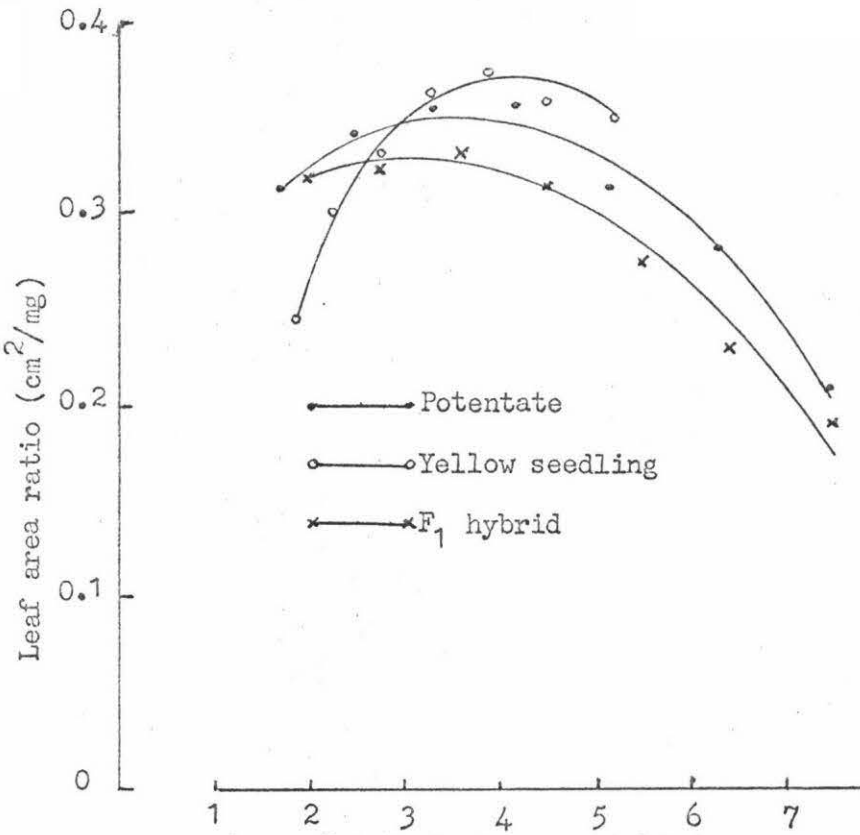


Fig. I. 10 Leaf-area ratio (cm^2/mg) as a function of total plant dry weight (mg, $\log_e$ scale)

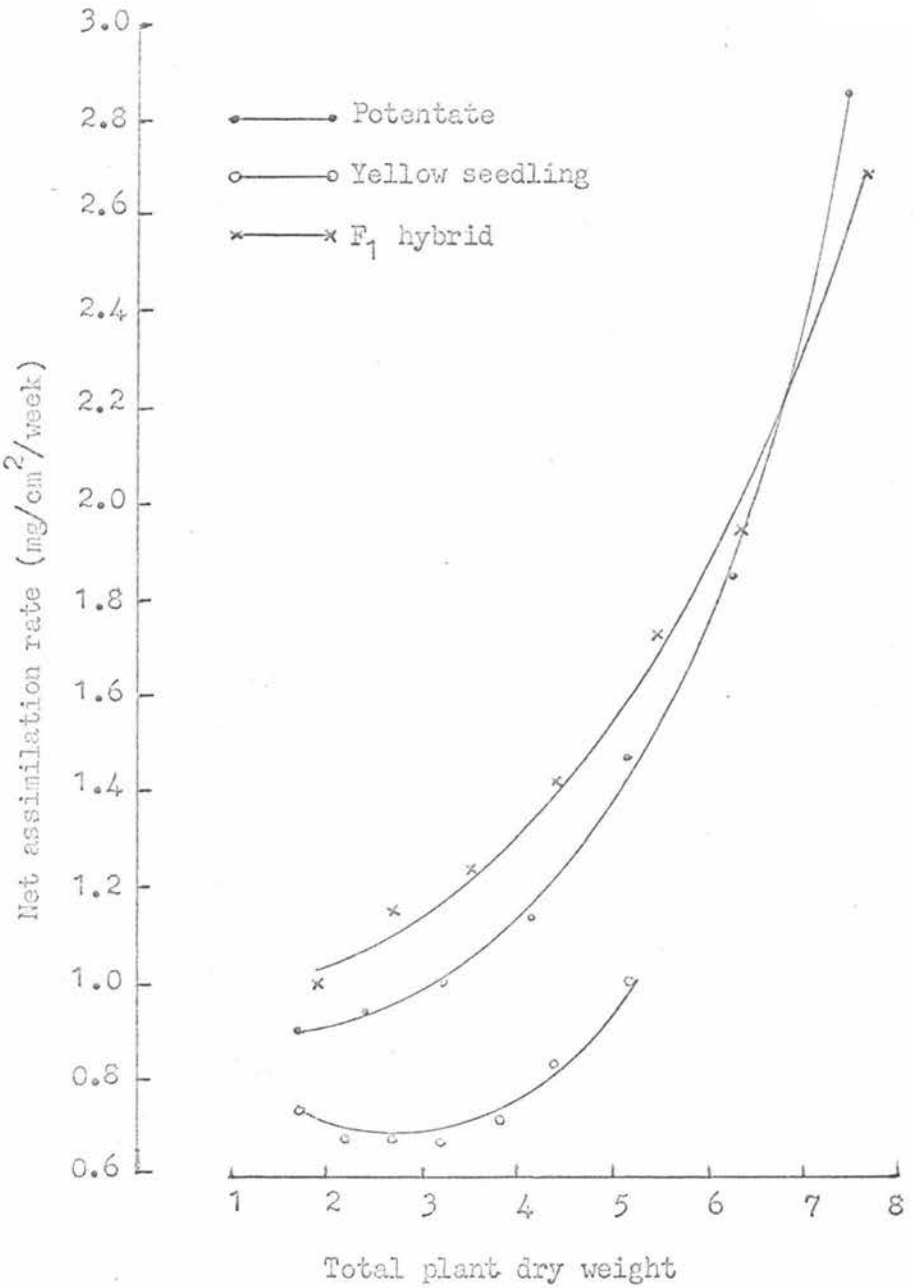


Fig. I. 11 Net assimilation rate ($mg/cm^2/week$) as a function of total plant dry weight (mg, $\log_e$ scale)

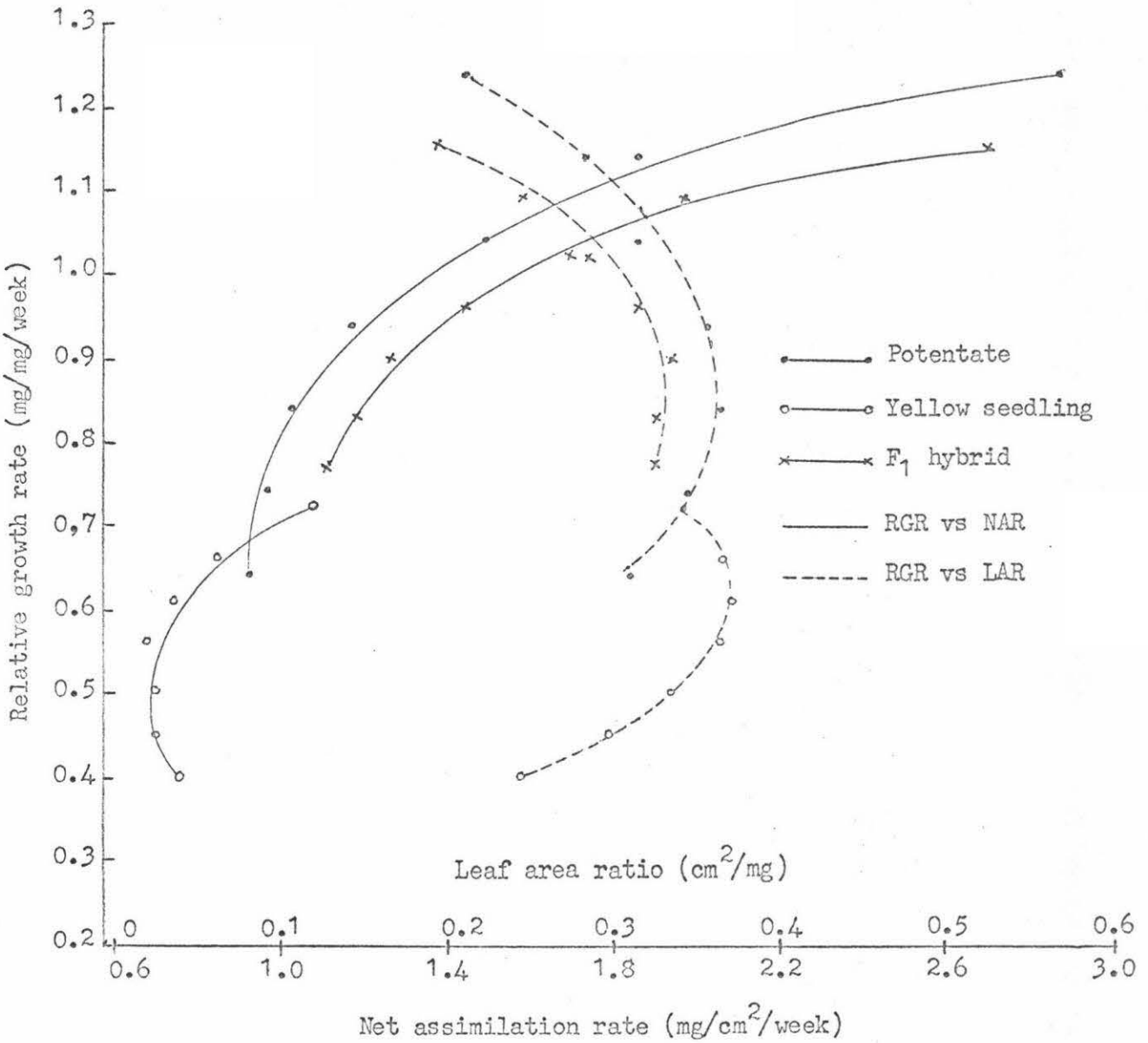


Fig. I. 12 Relationships between relative growth rates and net assimilation rates, and leaf area ratios of Potentate, Yellow seedling and F_1 hybrid.

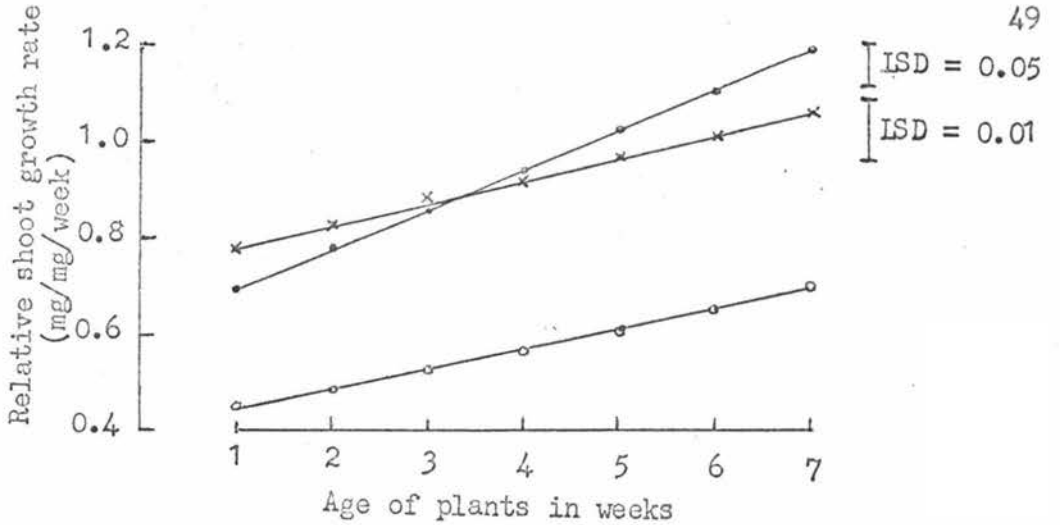


Fig. I.13 The time trends of relative shoot growth rates of Potentate (•), Yellow seedling (○) and their F_1 hybrid (×).

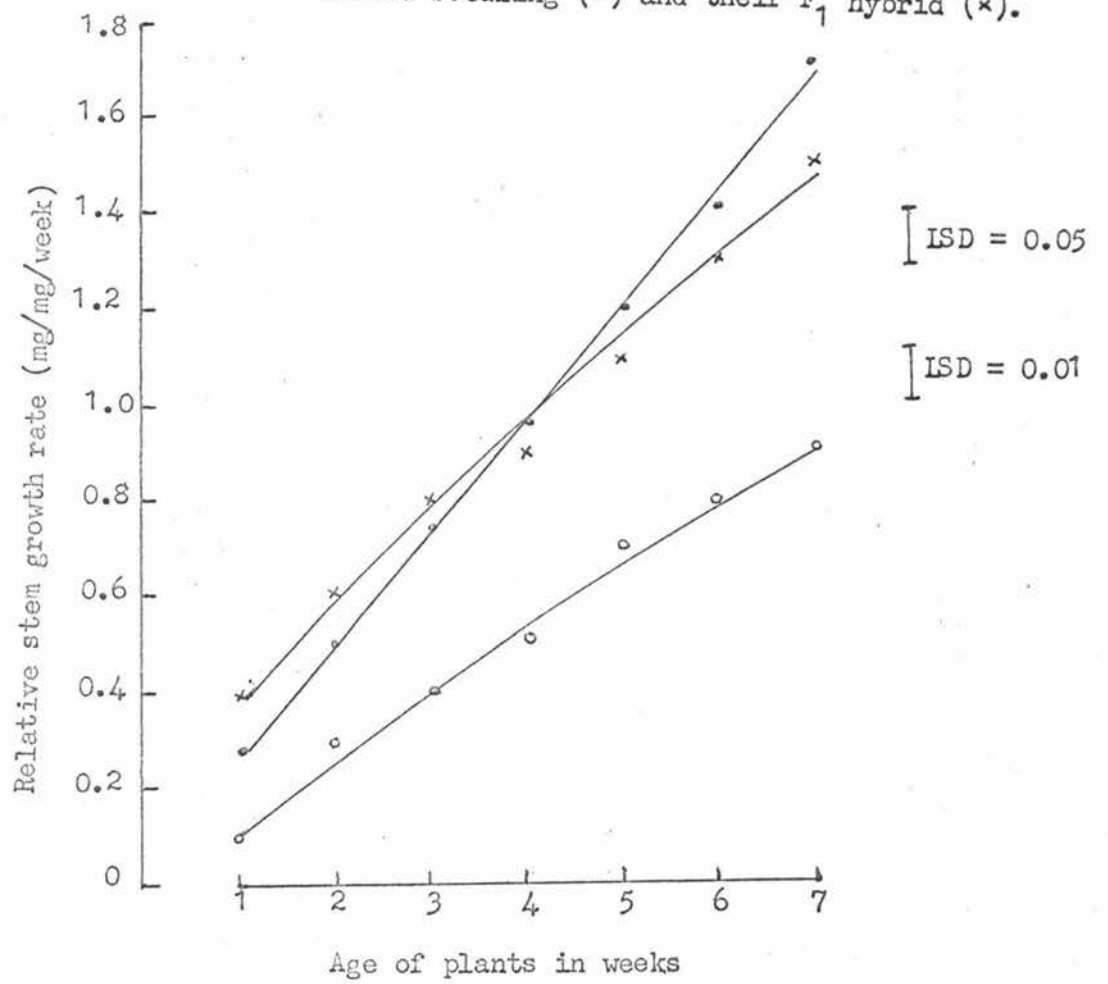


Fig. I.14 Progressive lines of relative stem growth rates of Potentate (•), Yellow seedling (○) and their F_1 hybrid (×), derived from quadratic equation by differentiation as a function of time.

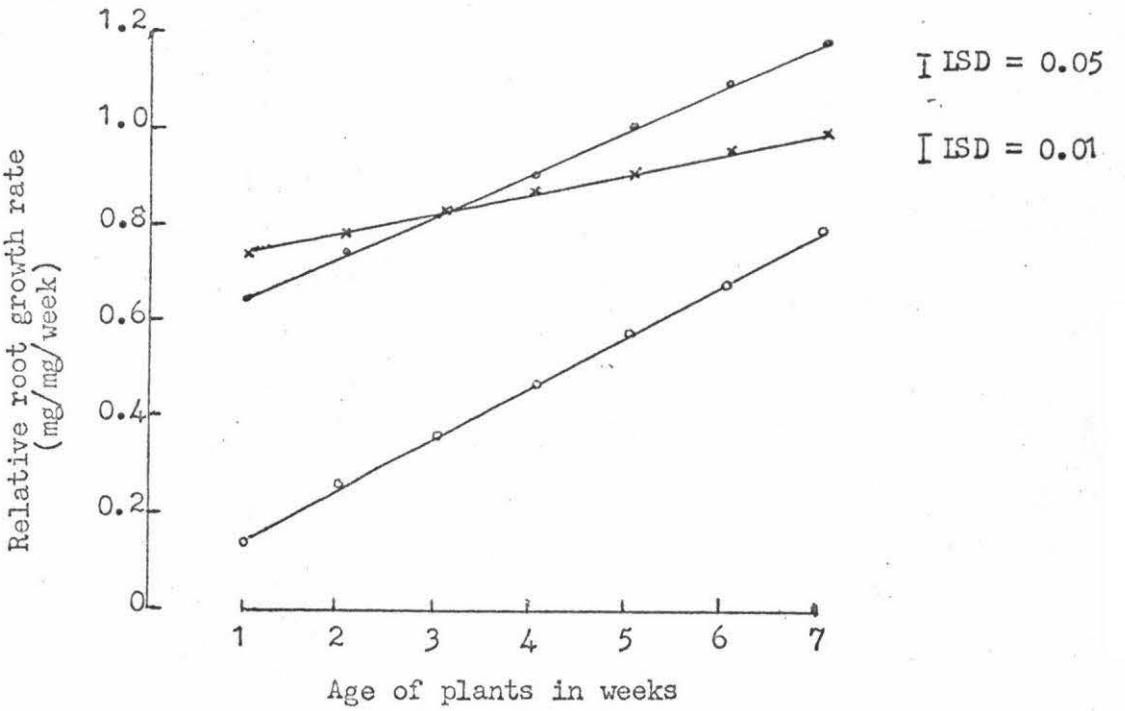


Fig.I. 15 Progressive lines of relative root growth rates for Potentate (•), Yellow seedling (∘) and their F_1 hybrid (×), derived from quadratic equation by differentiation as a function of time.

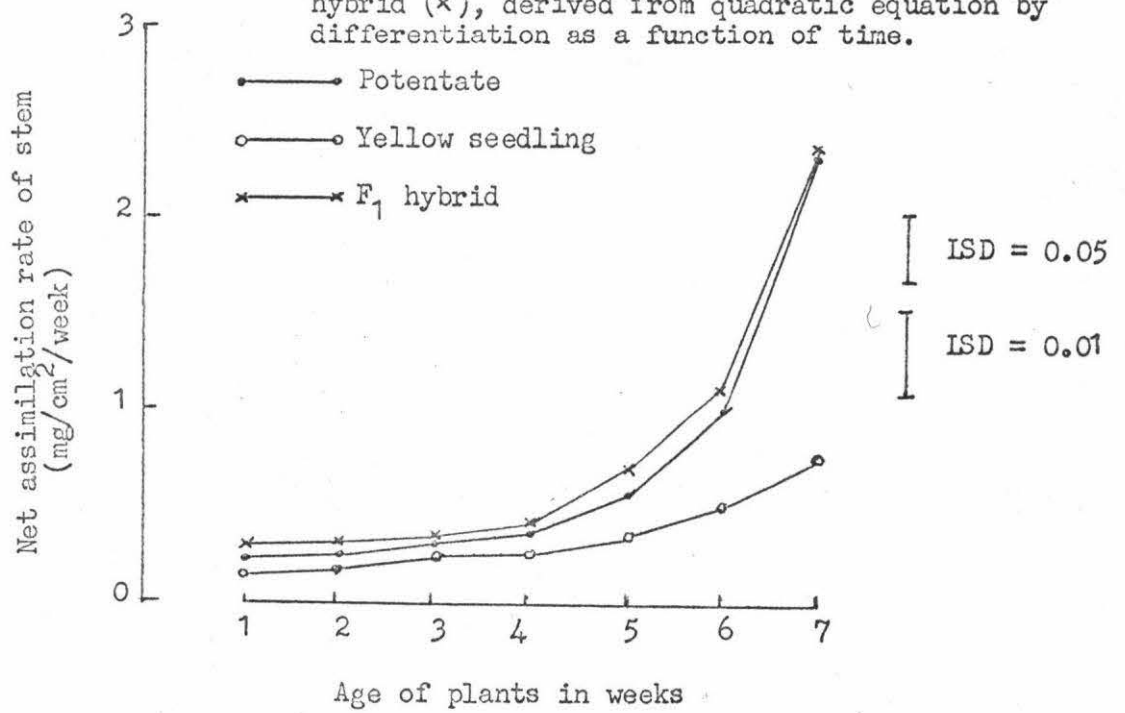


Fig.I. 16 Progressive curves of NAR_s for Potentate, Yellow seedling and their F_1 hybrid, derived fromfitted quadratics of $\log_e$ stem dry weight and $\log_e$ leaf area by differentiation and division.

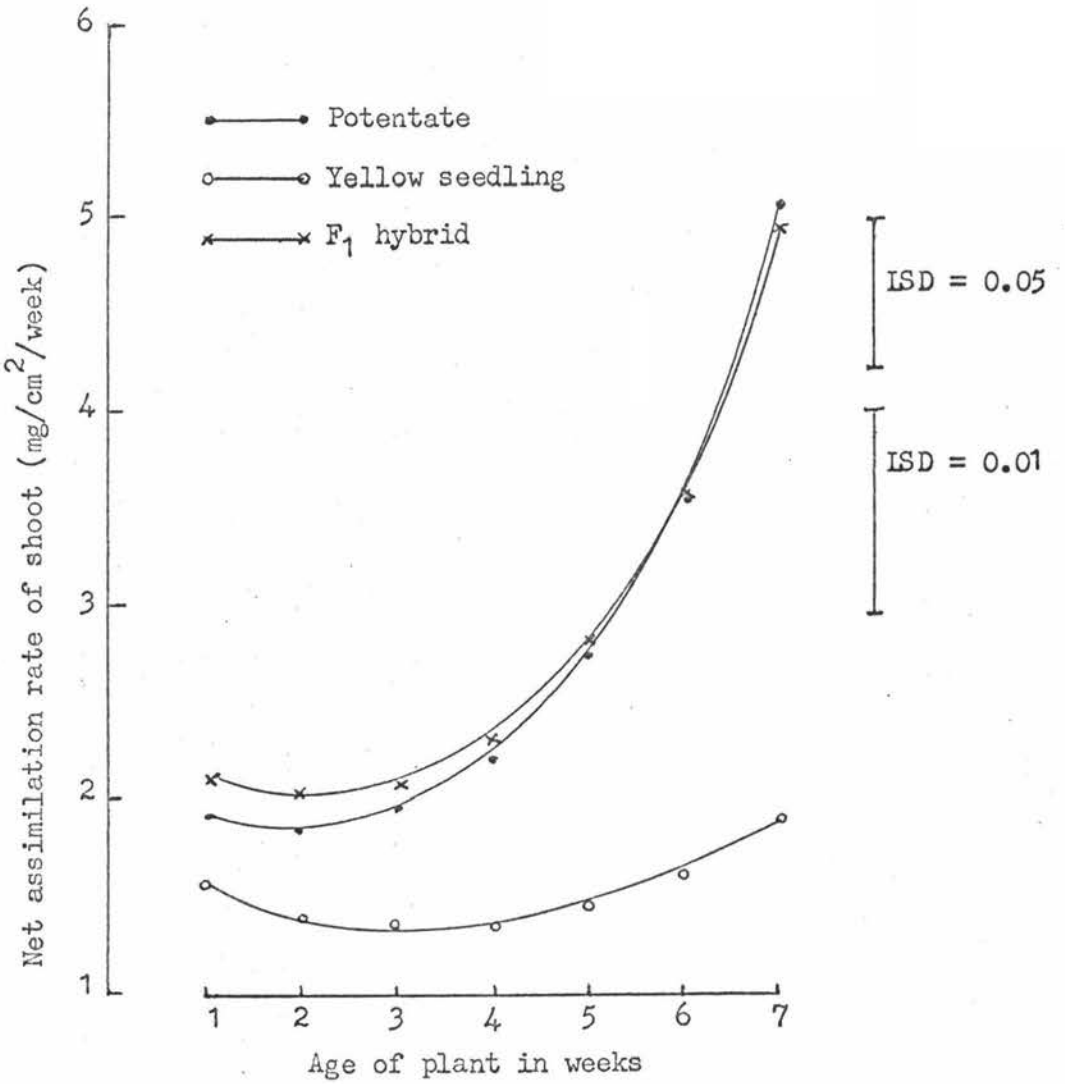


Fig.I.17 Progressive curves of NAR_{sh}, derived from fitted quadratics of $\log_e$ shoot dry weight and $\log_e$ leaf area by differentiation and division.

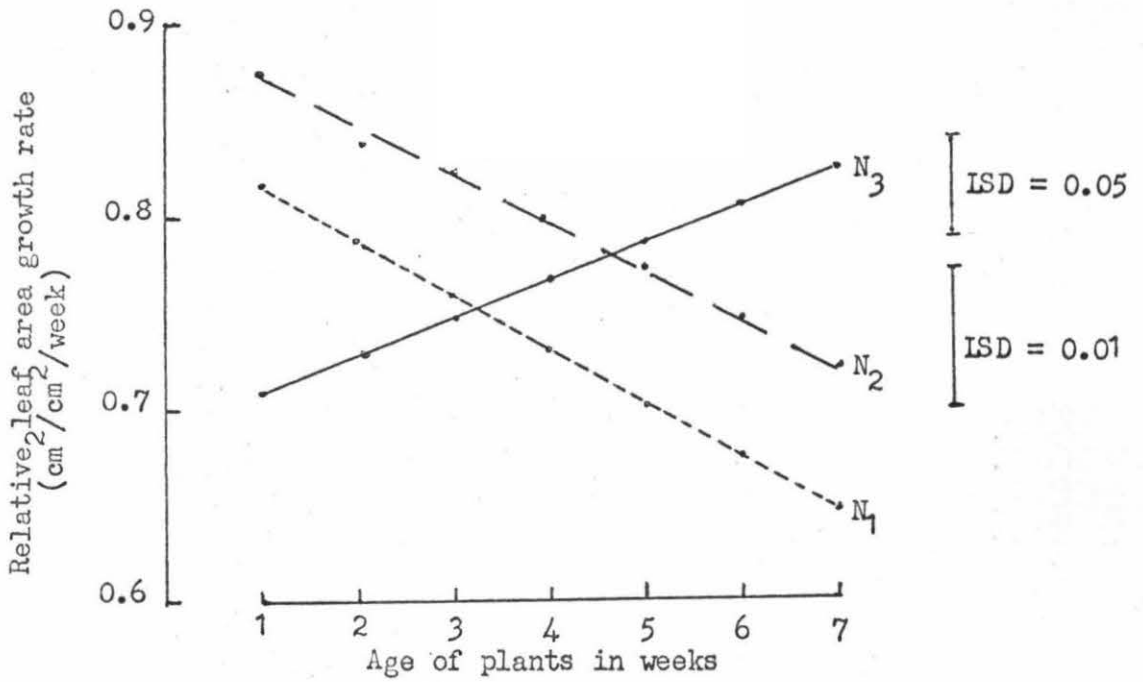


Fig.I.18 The time trends of relative leaf area growth rate derived from fitted quadratics of $\log_e$ leaf area by differentiation as influenced by nitrogen concentrations.

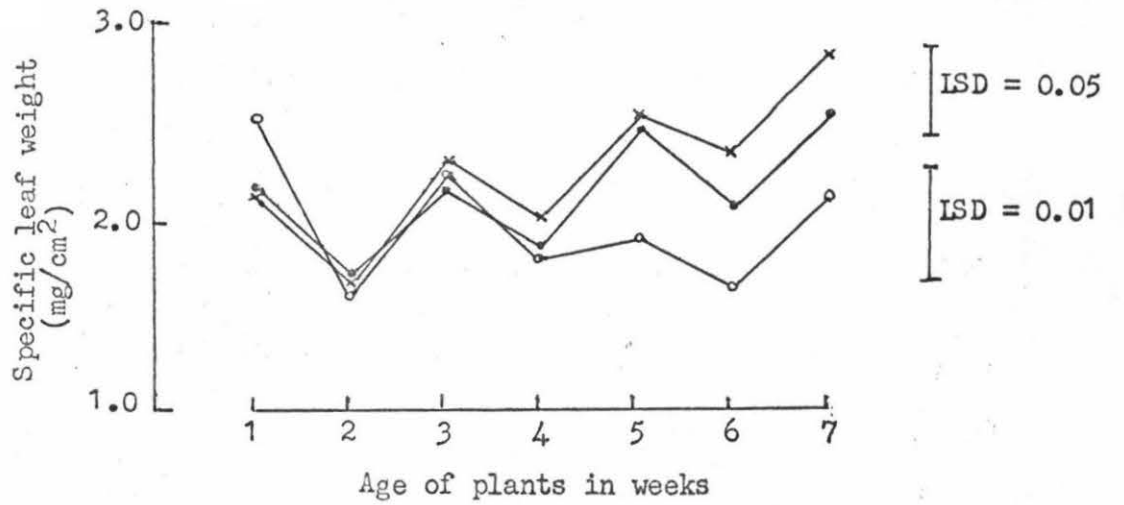


Fig.I.19 Specific leaf weight of Potentate (•), Yellow seedling (○) and their F_1 hybrid (×) as a function of time.

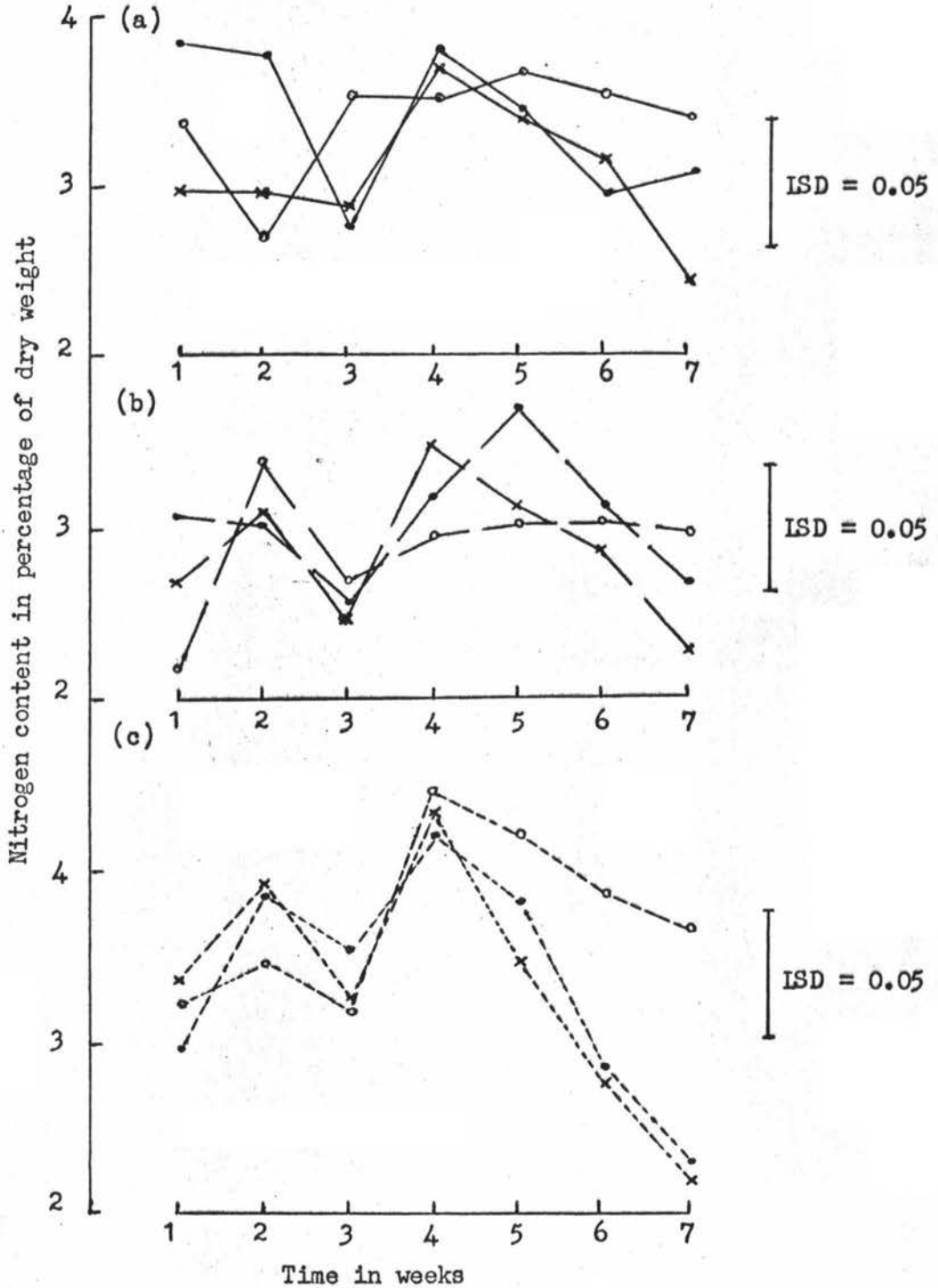


Fig.I.20 Changes in per cent nitrogen content (on dry weight basis) of Potentate (•), Yellow seedling (○) and F_1 hybrid (×) grown under three nitrogen levels (a) 340 ppm N, (b) 170 ppm N, and (c) 57 ppm N.

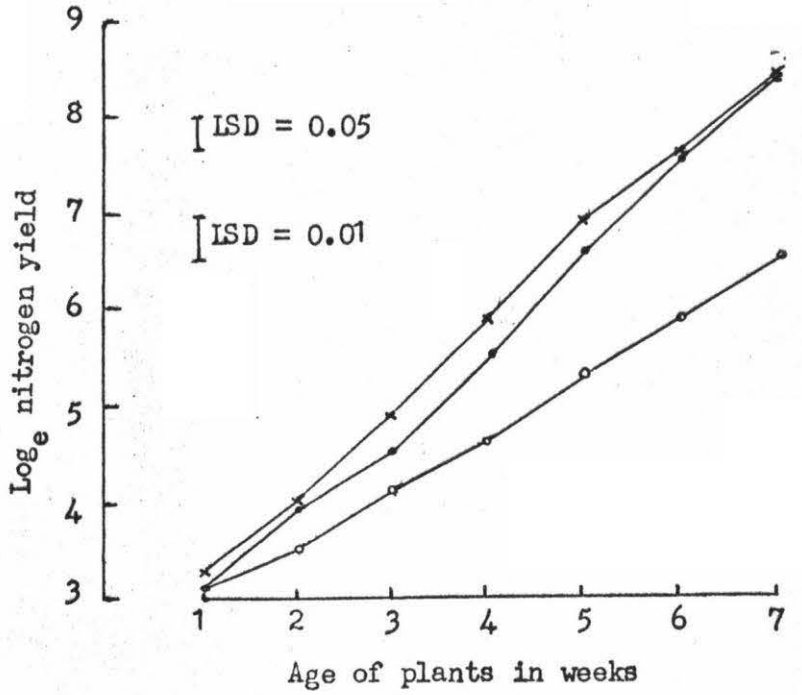


Fig.I.21 Changes in log$_e$ nitrogen yield of Potentate (•), Yellow seedling (○) and their F_1 hybrid (×) with time.

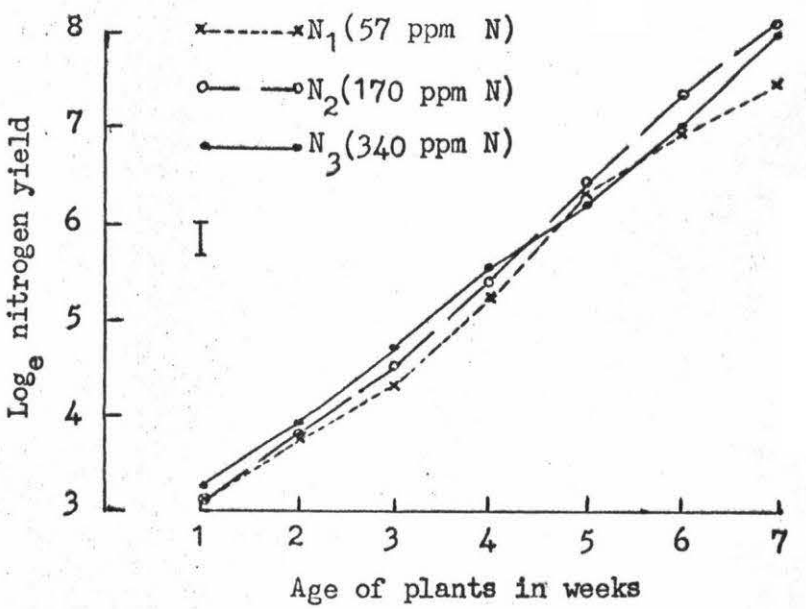


Fig.I.22 The time trends of log$_e$ N yield as influenced by nitrogen concentrations.

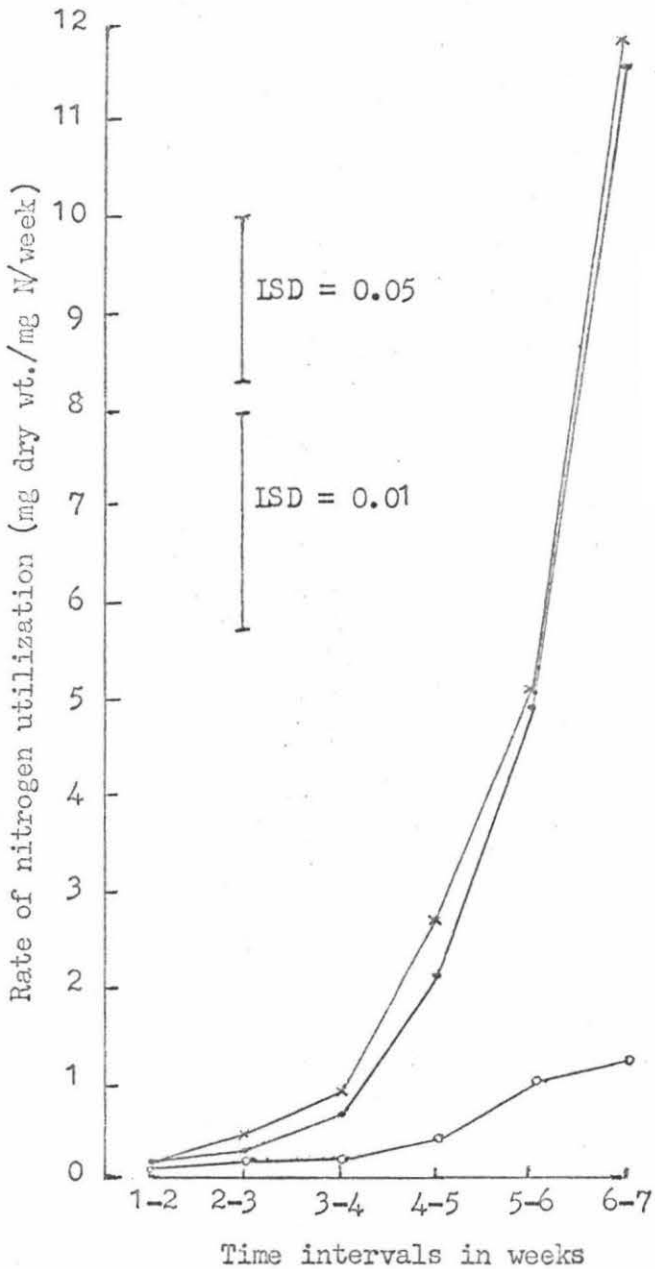


Fig.I.23 The time trends of rate of nitrogen utilization of Potentate (•), Yellow seedling (○) and their F_1 hybrid (×).

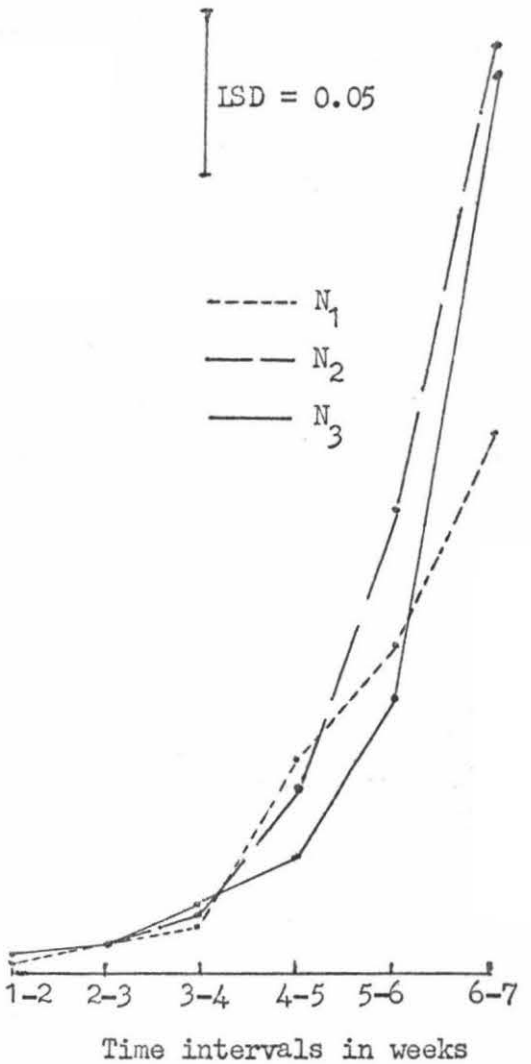


Fig.I.24 The time trends of rate of nitrogen utilization as influenced by nitrogen concentrations.

3.11 Discussion.

The results of experiment one showed that Yellow seedling was inferior to both Potentate and F_1 hybrid in most of the characters investigated except mean percentage of stem, shoot/root ratio, LAR and per cent nitrogen content. The low growth rate of Yellow seedling was associated mainly with its low NAR (Fig.I.12). This, in turn, may have partly resulted from its low SLW. The obvious differences between varieties in chlorophyll concentrations will be discussed in experiment two.

It is interesting to note that, though Yellow seedling had a similar nitrogen content (per cent of dry weight), it had a low nitrogen yield and low rate of nitrogen utilization compared with the other varieties. The latter may be one of the reasons for the slow growth rate of Yellow seedling. This low rate of nitrogen utilization could be caused by low activity or concentration of nitrogen assimilating enzymes, and/or short supply of carbohydrates required for assimilating nitrogen compounds into amino acids and proteins (see Louwerse 1967; Minotti and Jackson 1970).

Assuming that SLW is proportional to leaf thicknesses, the lack of change in SLW with time in Yellow seedling suggests that there was little increase in leaf thickness with time in this variety. On the other hand, the gradually increasing SLW of Potentate and F_1 hybrid (Fig. I.19) indicated that their leaves were probably increasing in leaf thickness up to the end of the experimental period.

Other contrasting time trends between Yellow seedling and the other varieties were found for percentage nitrogen content. In general, and irrespective of nitrogen concentration, the percentage nitrogen of Yellow seedling remained fairly constant while that of Potentate and F_1 hybrid tended to decline with time after reaching a maximum of about 4.5%. The latter result is in agreement with the findings by Wards (1967) and Anon (1969) that nitrogen content of tomato plants declined with the age of the plant.

The small effect of nitrogen concentration on many characters reported in this experiment could be the result of a complex interaction of factors. The low light intensity of the winter months could have influenced nitrogen assimilation directly by affecting the activity of the nitrate reductase or indirectly by affecting photosynthesis which provides the nitrogen assimilation process with energy and carbon skeleton (Hageman et al 1960; Sanderson and Cocking 1964). The concentration and form of nitrogen could be another important factor. It appears that the lowest nitrogen regime (57 ppm N) was, in fact, high enough to support the growth of the plants without any obvious sign of nitrogen shortage. This is supported by the fact that the per cent nitrogen content in the entire plant lay between the mean

minimum (1.35%) and maximum (3.5%) values suggested by Friis-Nielsen (1969) for tomato plants. Harada and his associates (1968) grew tomato plants in nutrient solutions containing 3, 15 and 50 ppm of nitrate nitrogen for 28 days, producing $\log_e$ dry weight of entire plants of 5.99 (400 mg), 6.82 (920 mg) and 7.09 (1200 mg) respectively. From their experimental results it seems that the critically low nitrogen level for tomato plants may be less than 15 ppm. Of course, this figure may depend on other factors, such as growth period, variety and light.

The fact that plants cultured under a high nitrogen concentration (340 ppm N) did not grow better and in some cases showed inferior performance indicated that the 85 ppm ammonium nitrogen (which was not present in the other solutions) may have been responsible. This would agree with many reports of adverse effects of ammonium nitrogen on tomato plants, for example a reduced nitrate-reducing capacity (Mulder et al 1959); root injury and reduced vegetative growth (Uljee 1964); morphological modifications of chloroplasts, loss of chlorophyll content and decrease in net photosynthesis (Puritch and Barker 1967); reduced dry matter leaf yield, and altered ion uptake and ionic balance (Kirkby 1968). In addition, Harada et al (1968) have shown that 50 ppm of ammonium nitrogen alone (i.e., no nitrate) reduced the growth and total dry matter yield, and altered the chemical composition of tomato plants. White (1969) reported that tomato plants were killed by a concentration of ammonium nitrogen above 500 ppm, a level far in excess of that used here. Thus, it seems likely that any beneficial effect of increased nitrogen concentration in the high nitrogen regime may have been offset by the inclusion of ammonium nitrogen. However, the possibility that the difference between nitrogen levels was not wide enough to produce a significant difference cannot be ruled out.

CHAPTER 4.

4.1 Photosynthesis.

Photosynthetic rates of tomato leaflets of various ages (3, 6 and 7 weeks old) which corresponded to various leaf positions (9-14, 5 and 1) were determined on the plants when they were 8, 9 and 10 weeks old respectively.

4.1.1 The influence of some factors on photosynthetic rates per unit leaf area of tomato leaflets.

The net photosynthetic rate of F_1 hybrid was intermediate between those of Potentate and Yellow seedling (Table II.1) with both Potentate and F_1 hybrid significantly higher than that of Yellow seedling.

Table II.2 presents the influence of nitrogen concentrations on net photosynthetic rates. There was no significant difference between the nitrogen concentrations though high nitrogen gave a non-significantly higher photosynthetic rate.

The effect of variety x nitrogen interactions on net photosynthetic rate is shown in Table II.3. While the net photosynthetic rate of Potentate was not affected by the applied nitrogen levels it is interesting to note that F_1 hybrid and Yellow seedling responded in opposite way to high nitrogen concentration. Whereas high nitrogen concentration depressed the net photosynthetic rate of Yellow seedling by 9.7% it increased that of F_1 hybrid by about 15.5%. In other words, the varietal differences in net photosynthetic rates were significant only at high nitrogen concentration.

The photosynthetic activities of leaflets declined with age from 3- to 6-to 7-week old leaflets, although the difference in net photosynthetic rates between 6-and 7-week old leaflets was not significant. In this experiment, because leaflets were taken from different positions on the plants, the effects of age were confounded with any possible effects of leaf positions. Peat (1970) has also shown that the maximal photosynthetic rate of tomato leaf varied with leaf position. There were highly significant differences between the light intensities.

The effects of time x light intensity and time x variety interactions on net photosynthetic rate were highly significant (Appendix XII). Fig. II.2 shows that there were highly significant differences between light intensities on net photosynthetic rates of leaflets within each age group. However within each light intensity significant differences between 3-week and 6-week, and between 3-and 7-week old leaflets were found only for light intensities of 970 and 1300 ft.-c.

Concerning the time x variety interactions on net photosynthetic rates, Fig. II.2 shows that within 6-week old leaflets there were significant

differences between those of Potentate and Yellow seedling. Within 3-week old leaflets the net photosynthetic rates of Potentate and F_1 hybrid were significantly ($P < 0.01$) higher than that of Yellow seedling. Within each variety the net photosynthetic rates of Potentate, Yellow seedling and F_1 hybrid were highly significantly different between the age groups except those between 6-and 7-week old leaflets of Yellow seedling and F_1 hybrid. The 3-week old leaflet of F_1 hybrid had a heterotic rate of net photosynthesis over the two parents ranging from 0.681 through 0.726 to 0.941 with Yellow seedling having the lowest rate. However F_1 hybrid also had a faster rate of fall in net photosynthetic rate with age. As a result, the net photosynthetic rate of F_1 hybrid became intermediate between those of the two parents when the leaflets were 6-week old and continued to 7-week old leaflets.

Regarding the effect of time x nitrogen interactions on net photosynthetic rate, though there were highly significant differences between ages of leaflets within each nitrogen level except those between 6-and 7-week old leaflets, the net photosynthetic rates of leaflets of plants growing under low nitrogen regime declined at a faster rate than those of high nitrogen plants as the plants advanced in age.

Fig. II.3 presents the effect of time x variety x nitrogen interactions on net photosynthetic rate. It is obvious that within high nitrogen concentration, F_1 hybrid leaflets maintained a higher photosynthetic rate (though declined at a faster rate with time) than those of the parents. Significant differences in photosynthetic rate of 3-week old leaflets were found between the parents and their F_1 hybrid, and also between 6-week old leaflets of F_1 hybrid and Yellow seedling. However at low nitrogen concentration F_1 hybrid had the lowest photosynthetic rate than those of the parents with the exception of 6-week old leaflets where it was slightly higher than that of Yellow seedling. During this time the net photosynthetic rate of Potentate was significantly higher than those of F_1 hybrid and Yellow seedling.

Within each variety and at high nitrogen concentration the fall in photosynthetic rates of Potentate and F_1 hybrid from 3-to 7-week old leaflets was highly significant. The rate of decline in photosynthetic rate of F_1 hybrid were also significant from 3-to 6-week old leaflets. On the contrary no significant changes in photosynthetic rate with age were detected for Yellow seedling. The net photosynthetic rate of Yellow seedling was very much depressed by high nitrogen supply during early stage of leaf growth.

Within each variety the rates of fall in photosynthetic rate with age were increased by reduced nitrogen supply. From 3-to 6-week old leaflets the rates of fall were comparatively higher than those of their counterparts grown under high nitrogen concentration. However the changes in net photo-

synthetic rate from 6- to 7-week old leaflets were not significant irrespective of nitrogen concentrations and varietal differences.

Fig. II.4 shows the effect of time x variety x light intensity on net photosynthesis of tomato leaflets. Within light intensity L_1 and within each variety the effect of age on net photosynthetic rate was not significant. At the intermediate light intensity L_2 significant effects of age on net photosynthetic rate were found between 3- and 7-week old leaflets for Potentate, and between 3- and 6-, and between 3- and 7-week old leaflets for F_1 hybrid. In Yellow seedling the changes of net photosynthetic rate of leaflets between 3- to 7-week old were not significant. At the highest light intensity L_3 net photosynthetic rate varied very markedly with age. Thus highly significant differences between 3- and 6-, and between 3- and 7-week old leaflets were found for the two parents and their F_1 hybrid. At all light intensities, the differences in net photosynthetic rate between 6- and 7-week old leaflets of Potentate, Yellow seedling and F_1 hybrid were not significant.

Within 3-week old leaflets of each line significant differences in photosynthetic rate were found between all light intensities. The effect of light intensities declined as the leaflets advanced in age. Thus when the leaflets were 7-week old significant differences in net photosynthetic rate as affected by light intensity were found only between light intensities L_3 and L_2, and between L_3 and L_1 for the parents and their F_1 hybrid.

4.1.2 The influence of some factors on photosynthetic rate per mg dry weight of tomato leaflets.

No significant difference between varieties, nitrogen concentrations, and variety x nitrogen interactions on net photosynthetic rate of tomato leaflets was detected when photosynthetic rate was expressed in term of leaf dry weight (Appendix VII). However, the significant levels of other factors or factor-factor interactions on net photosynthetic rate were exactly the same as those in analysis of variance of photosynthetic rate computed in term of leaf area. The net photosynthetic rate of tomato leaflets varied significantly with the age of the leaflets and light intensity; the interactions of time x light intensity, of time x variety, and of time x nitrogen on photosynthetic rate were all highly significant.

The interactions of time x variety x nitrogen on photosynthetic rate (Fig. II.5) were significant, complex and exhibited no definite pattern. It is apparent that 6-and 7-week old leaflets from low nitrogen plants of Potentate and F_1 hybrid had lower photosynthetic rate than those of high nitrogen-leaflets. This could be due partly to the effect of nitrogen concentrations on ageing processes of the leaflets. In Yellow seedling the same

variations of nitrogen levels had no effect on the photosynthetic rate of 6- and 7-week old leaflets. The fact that the influence of nitrogen concentrations on photosynthetic rates of 3-week old leaflets of the parents and their F_1 hybrid produced just the opposite results as compared to those of older leaflets is difficult to explain.

The changes of photosynthetic rate with age of the leaflets as affected by light intensity were also complex (Fig. II.6). Within 3-week old leaflets of each variety there were significant effects between light intensities on net photosynthetic rate. Within 6-week old leaflets the response of each variety to variations of light intensity was erratic in significant levels. Within 7-week old leaflets highly significant differences between light intensities L_3 and L_1, and between L_3 and L_2 were found for all varieties. In all cases, the net photosynthetic rates were increased by increased light intensity.

Within light intensities L_1 and L_2, highest photosynthetic rate was found for 6-week old leaflets of Potentate and F_1 hybrid. Within light intensity L_3 the photosynthetic rate of 3-week old leaflets was highest for Potentate and F_1 hybrid. But in Yellow seedling the 6-week old leaflets retained the highest photosynthetic rate within each light intensity.

There were no significant differences in photosynthetic rates between the parents and their F_1 hybrid of all ages within light intensity L_1, and within L_2 for 6-and 7-week old leaflets. Within 3-week old leaflets, differences between Potentate and Yellow seedling, and between F_1 hybrid and Yellow seedling in photosynthetic rate were highly significant. Within light intensity L_3, significant differences were found between Yellow seedling and F_1 hybrid for the 6-and 7-week old leaflets.

A differential response of each variety to increased light intensity was noted. For Yellow seedling the response increased with age. On the contrary the responsiveness of Potentate and F_1 hybrid to increased light intensity decreased as the leaflets advanced in age.

4.1.3 The influence of some factors on photosynthetic rate of tomato leaflets expressed in term of unit chlorophyll concentration.

If the efficiency of photosynthetic processes were judged by the amount of gaseous exchanges per mg. chlorophyll, then Yellow seedling was significantly ($P < 0.01$) more efficient than those of Potentate and F_1 hybrid (Table II.1). Similar results have been reported in a number of chlorophyll deficient plants or mutants as described in section 1.3.1.

As presented in Table II.2 the effect of nitrogen concentrations on photosynthetic rates computed in term of chlorophyll concentration was highly significant. Leaflets grown under low nitrogen concentration had higher

photosynthetic rates than those of leaflets supplied with high nitrogen concentration.

Similar responses of photosynthetic rates to variations of nitrogen concentrations were observed in each variety irrespective of nitrogen levels, with photosynthetic rates of Yellow seedling higher than those of green normal plants.

The difference between light intensities on photosynthetic rates per mg chlorophyll was highly significant. The photosynthetic rates increased with increasing light intensity.

4.2 Respiration.

The respiration rates of 6-and 3-week old tomato leaflets which corresponded to leaf position 5 and 9 to 14 respectively were determined and expressed in term of leaf dry weight. In the latter suitable leaflets as judged by the date of their appearance which corresponded to leaf position 9 and 14 of low and high nitrogen treated plants respectively were selected. The respiration rates of tomato root were measured on 12-week old plants.

4.2.1 The influence of some factors on the respiration rate of tomato leaflets.

Mean varietal differences in leaf respiration rate are shown in Table II.1. The mean leaf respiration rate of F_1 was intermediate between those of the parents with Yellow seedling having the highest rate. The differences between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were highly significant.

The increase of nitrogen concentration from 28 to 280 ppm N produced a significant increase in leaf respiration rate (Table II.2). There was no significant variety x nitrogen interaction on leaf respiration rate.

The difference in respiration rate between 3-and 6-week old leaflets was highly significant. The respiration rate of the 3-week old leaflets was about 1.8 times higher than that of 6 week old leaflets. Like photosynthetic rate the effect of age on respiration rate could be confounded by the possible effect of leaf position.

Fig.II.7 shows the varietal differences in changes of respiration rates of leaflets with age. It is obvious that the rate of fall in the respiration rate of Potentate and F_1 was higher than that of Yellow seedling. As a result, while there was no significant difference in respiration rates between 3-week old leaflets of the two parents and their F_1 hybrid, the difference between those of Yellow seedling and Potentate, and between those of Yellow seedling and F_1 hybrid became increasingly significant as the leaflets advanced in age. When the leaflets were 6-week old the respiration

rates of Potentate and F_1 hybrid were about two-thirds that of Yellow seedling.

The time trends in leaf respiration rates are presented in Fig. II.8. The differences in respiration rates between 3- and 6-week old leaflets of the parents and their F_1 hybrid irrespective of nitrogen treatments were highly significant. At the high nitrogen concentration the F_1 hybrid followed Potentate, having a high rate of fall in respiration while that of Yellow seedling declined comparatively slowly.

Within 3-week old leaflets, reduced nitrogen supply depressed respiration rate of Potentate and F_1 hybrid but had no significant effect on the respiration rate of Yellow seedling. There was no significant difference in respiration rate between the parents and their F_1 hybrid at high nitrogen level, but at low nitrogen concentration the differences between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were significant.

Within 6-week old leaflets while the effect of nitrogen concentrations on respiration rate of Yellow seedling had increased, the effect on those of Potentate and F_1 hybrid had diminished to be non-significant when compared to that of 3-week old leaflets. As a result the variations of nitrogen supply did not produce significant differences in respiration rate within each parent and their F_1 hybrid. Furthermore whereas the respiration rates of Potentate and F_1 hybrid, irrespective of nitrogen treatments, were not significantly different from each other, they were significantly lower than those of Yellow seedling.

4.2.2 The influence of some factors on the respiration rate of tomato roots.

Analysis of variance (Appendix XIV) indicates that only nitrogen concentration had a significant effect on the respiration rate of tomato roots. Table II.2 shows that increased nitrogen concentration increased the respiration rate of roots by 17%.

4.3 Chlorophyll concentration.

Chlorophyll concentration determinations were made on fifth leaf on two occasions namely when the leaflets were 5- and 9-week old. Analyses of variance on chlorophyll concentration are shown in Appendix XIII and XV. In addition the chlorophylls a/b ratios of the 9-week old leaflets were also calculated.

4.3.1 The influence of some factors on the chlorophyll concentration over time.

The effects of varietal differences, nitrogen concentrations, and interactions of variety x nitrogen on chlorophyll concentrations (mg/dm^2) as shown respectively in Tables II.1, II.2 and II.3 were highly significant.

Although the mean chlorophyll concentration of F_1 hybrid was slightly higher than that of Potentate, there was no significant difference between them. But differences in mean chlorophyll concentration between Yellow seedling and the other two varieties were highly significant, with Yellow seedling having the lowest value.

Regarding the variety x nitrogen interactions, within Potentate and F_1 hybrid the decrease of chlorophyll concentration by reduced nitrogen supply (from 280 to 28 ppm N) was highly significant as compared to that of Yellow seedling which was just significant at 5% level. As a result, the differences between the Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid tended to decrease as the nitrogen supply was reduced.

Fig. II.9 presents the changes with time in chlorophyll concentrations of the parents and their F_1 hybrid. The changes in chlorophyll concentrations over a 4-week period were highly significant for Potentate but not significant for Yellow seedling. The chlorophyll concentrations of F_1 hybrid, being intermediate between the two parents declined over the same period at a 5% significant level. Within the 5- and 9-week old leaflets, there was no significant differences in chlorophyll concentrations between Potentate and F_1 hybrid. However highly significant differences in chlorophyll concentrations between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were found within 5- and 9-week old leaflets, though the significant level tended to decrease as the leaflets advanced in age.

The effect of nitrogen concentration on the chlorophyll concentration of 5- and 9-week old leaflets from leaf 5 was highly significant within and between the two ages of leaflets. This is graphically illustrated in Fig. II.10.

4.3.2 The influence of some factors on the chlorophyll concentration and the chlorophyll a/b ratio of 9-week old leaflets.

Analyses of variance on chlorophyll concentration and chlorophyll a/b ratio (Appendix XV) indicate that there were significant differences between varieties, nitrogen concentrations and interactions of variety x nitrogen on chlorophyll concentration when it was expressed in term of leaf area. However when chlorophyll concentration was computed in term of dry weight only the effect of nitrogen concentrations on chlorophyll concentration was significant. The only significant factor on chlorophyll a/b ratio was nitrogen concentration.

Varietal differences in chlorophyll concentration and chlorophyll a/b ratio are shown in Table II.1. When chlorophyll concentration was expressed in term of leaf area the chlorophyll concentration of Yellow seedling

was highly significantly lower than those of Potentate and F_1 hybrid.

Table II.2 shows the effect of nitrogen levels on chlorophyll concentration and chlorophyll a/b ratio. Irrespective of unit expression reduced nitrogen supply reduced the chlorophyll concentration expressed in terms of leaf area and dry weight by 44% and 54% respectively. In the case of chlorophyll a/b ratio, low nitrogen treated-plants had a significant higher chlorophyll a/b ratio than that of high nitrogen-plants.

Table II.3 shows that variety-nitrogen interaction on chlorophyll concentrations and chlorophyll a/b ratio was significant only for chlorophyll concentration expressed in term of leaf area. It is clear that while reduced nitrogen supply reduced chlorophyll concentration of Potentate and F_1 hybrid very significantly, it had no significant effect on that of Yellow seedling. In other words while the chlorophyll concentration differed very significantly between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid at high nitrogen concentration, the differences between the parents and their F_1 hybrid grown under low nitrogen regime were not significant.

4.4 Specific leaf weight.

Specific leaf weight was determined on leaflets used in measuring photosynthetic rates. Analysis of variance (Appendix XIV) shows that there were significant differences between varieties, times, time x variety interactions and time x nitrogen interactions.

4.4.1 The influence of some factors on the SLW of tomato leaflets.

Table II.1 shows that F_1 hybrid had a higher mean SLW than its two parents. There was no significant difference between the two parents but the mean SLW of F_1 was significantly higher than that of Yellow seedling.

Fig. II.12 presents the changes with age in SLW of each tomato line. Here again the effect of age was confounded with the possible effect of leaf position. Within the 6-and 7-week old leaflets, highly significant difference between Yellow seedling and F_1 hybrid was found. However the differences between Potentate and Yellow seedling, and between Potentate and F_1 hybrid were not significant. The differences in SLW of 3-week old leaflets between the parents and their F_1 hybrid were also not significant.

The SLW of the parents and their F_1 hybrid exhibited the same patterns of changes with age but differed in magnitude. Thus within Potentate and F_1 hybrid significant differences in SLW were found between 3-and 6-, and between 6-and 7-week old leaflets. In Yellow seedling the SLW changed significantly between ages of the sampled leaflets.

The effect of time x nitrogen interactions on SLW is graphically illustrated in Fig.II.13. It is obvious within high nitrogen concentration

highly significant differences in SLW occurred between the three measured ages of the leaflets. At low nitrogen level the effect of age was lessened so that only differences between 3-and 6-, and between 6-and 7-week old leaflets were still highly significant.

Within each time there was no significant difference between nitrogen levels on SLW. However the effect of nitrogen concentration decreased as the leaflets aged.

4.5 Leaf thickness index.

Using the formula (leaf fresh weight-dry weight/area, (mg/cm^2) used by Hurd (1968) determinations of the leaf thickness indices were made on 3-and 6-week old leaflets which were used in measuring photosynthetic rates.

The effects of varietal differences, nitrogen concentrations and their interactions on leaf thickness index are shown in Tables II.1, II.2 and II.3 respectively. All of these were very significant (Appendix XIII).

The leaf thickness index of Yellow seedling was significantly higher than those of Potentate and F_1 hybrid. Increased nitrogen concentration from 28 to 280 ppm N increased leaf thickness index very significantly.

Varietal response to nitrogen concentrations varied very significantly (Table II.3). Whereas variations of nitrogen concentration had no significant effect on the thickness index of Yellow seedling, reduced nitrogen concentration decreased the thickness indexes of Potentate and F_1 hybrid very significantly. As a result there was no significant difference between the leaf thickness indexes of Potentate and F_1 hybrid at both high and low nitrogen concentrations. In addition there were no significant differences between parents and their F_1 hybrid at high nitrogen concentration but, at low nitrogen regime differences between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were significant.

The effect of time x variety interactions on leaf thickness index was not significant but that of time x nitrogen interaction was highly significant (Appendix XIII). As shown in Fig.II.14 within each nitrogen concentration there was no significant difference between 3-and 6-week old leaflets but within each age there were significant differences in nitrogen concentrations on leaf thickness index.

The changes with time of leaf thickness index of Potentate, Yellow seedling and F_1 hybrid as influenced by nitrogen concentrations were highly significant. As presented in Fig.II.15 within 3-week old leaflets there were no significant differences in leaf thickness indexes between the parents and their F_1 hybrid grown under high nitrogen regime. However at reduced nitrogen supply the leaf thickness indexes of Potentate and F_1 hybrid were

reduced very significantly than that of Yellow seedling. Within 6-week old leaflets grown under high nitrogen concentration the leaf-thickness index of Yellow seedling was significantly higher than those of Potentate and F_1 hybrid. Similar differences between varieties were observed in leaflets raised at reduced nitrogen concentration but the differences were more marked. Thus it appeared that the leaf-thickness index of Yellow seedling was comparatively less sensitive to changes of nitrogen concentrations.

Within each variety significant changes in leaf-thickness index with age were observed in Yellow seedling grown at high nitrogen concentration, and F_1 hybrid grown at low nitrogen level. Finally in contrast to Yellow seedling the leaf-thickness indexes of Potentate and F_1 hybrid grown at high nitrogen regime increased as the leaflets advanced in age. However, at low nitrogen level all the leaflets irrespective of variety decreased with age.

4.6 Mesophyll cell number.

In complementary to measurements of SLW and thickness index mesophyll cell counts computed in terms of both dry weight and leaf area were made to discover how far differences in leaf area and thickness between varieties and treatments could be attributed to differences in cell number.

4.6.1 The influence of some factors on mesophyll cell number.

Varietal differences in mesophyll cell number expressed on leaf area and dry weight bases are shown in Table II.1. There were highly significant differences between varieties with F_1 hybrid having the highest cell number and Yellow seedling the lowest when the cell number was expressed on leaf area basis. However, when mesophyll cell number was computed in term of dry weight the differences between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were highly significant but there was no significant difference between Potentate and F_1 hybrid.

Table II.2 shows the effect of nitrogen concentration on mesophyll cell number. No significant influence of nitrogen concentrations on cell number was found when the cell number was expressed on dry weight basis. But, when it was computed in term of leaf area, leaflets from low nitrogen-plants had a significant higher cell number than those of high nitrogen-plants. This marked difference could not be due to differences in leaf thickness as similar nitrogen concentration had no significant effect on SLW. Therefore leaflets grown under low nitrogen regime must have smaller cell size than those leaflets grown at high nitrogen supply.

Significant interaction of variety x nitrogen on mesophyll cell number is shown in Table II.3. When mesophyll cell number were computed in

term of dry weight no significant difference in mesophyll cell number was found between varieties grown under high nitrogen level, and within varieties raised under both nitrogen concentrations. However under low nitrogen supply the differences in mesophyll cell numbers between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were highly significant. But the difference between Potentate and F_1 hybrid was not significant. Hence the significant variety x nitrogen interaction on mesophyll cell numbers was attributed to the good response of Potentate and F_1 hybrid on one hand and the unresponsive nature of Yellow seedling on the other to changes of external nitrogen concentrations.

Highly significant effects of nitrogen concentrations on mesophyll cell number expressed on leaf area basis were found for Potentate and F_1 hybrid but not Yellow seedling. Within high nitrogen concentration the differences in cell number between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were highly significant. But there was no significant difference between Potentate and F_1 hybrid. Whereas highly significant differences in mesophyll cell number were found between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid grown under low nitrogen regime, the difference between Potentate and F_1 hybrid was only just reached 5% significant level. Here the differential response of Yellow seedling to variations of nitrogen concentrations as compared to those of Potentate and F_1 hybrid was even more marked. Reduced nitrogen supply increased the cell number per cm^2 of Potentate and F_1 hybrid significantly ($P<0.01$) probably by restricting cell enlargement but not cell division. Such a range of nitrogen concentrations had no significant effect on these two processes in Yellow seedling.

4.7 Stomatal length and density.

Measurements of stomatal length and density were made on fully-matured leaflets of leaf position 9 on 12/5/70. Stomatal size and density as factors controlling gaseous exchange of photosynthesis can be important factors in controlling photosynthetic rate.

4.7.1 The influence of some factors on stomatal length and density.

Analyses of variance (Appendix XVI) indicate that among all the treatments on stomatal length and density only the nitrogen concentrations had significant effect on stomatal length. Perhaps low nitrogen supply resulted significantly in smaller stomatal length by restricting the enlargement of stomatal cells.

TABLE II.1.

Varietal differences in a number of physiological and leaf characteristics.

Characteristics	Potentate	Yellow seedling	F_1 hybrid	L.S.D. 5%	L.S.D. 1%
Photosynthesis($\mu l O_2$/min/cm^2)	0.792	0.698	0.783	0.082	0.114
Photosynthesis($\mu l O_2$/hr/mg dry wt)	16.821	16.311	16.344	N.S.	
Photosynthesis($\mu l O_2$/min/mg chlorophyll)	3.035	3.415	2.910	0.271	0.375
Respiration (leaflets) ($\mu l O_2$/hr/mg dry wt.)	2.990	3.687	3.042	0.529	0.733
Respiration (roots) ($\mu l O_2$/hr/mg dry wt.)	8.474	9.336	8.422	N.S.	
Chlorophyll concentration with time (mg/dm^2)	3.341	1.984	3.429	0.375	0.519
Chlorophyll concentration(mg/dm^2)	2.855	1.873	3.159	0.557	0.772
Chlorophyll concentration (mg/gm dry weight)	10.120	8.243	11.478	N.S.	
Chlorophylls a/b ratio	1.185	1.194	1.197	N.S.	
Specific leaf weight(mg/cm^2)	2.736	2.539	2.923	0.355	0.492
Leaf thickness index(mg/cm^2)	14.89	17.70	14.41	1.593	2.205
(Mesophyll cell number/mg dry weight) x 10^7	3.896	3.116	4.072	0.452	0.626
(Mesophyll cell number/cm^2 leaf area) x 10^7	9.979	6.128	11.219	0.828	1.147
Stomatal length (μ) x 10	3.236	3.093	3.093	N.S.	
Stomatel density(number/mm^2) x 10	22.352	23.991	22.090	N.S.	

TABLE II.2.

The influence of nitrogen concentrations on a number of physiological and leaf characteristics.

Characteristics	28ppm N	280ppm N	F test
Photosynthesis ($\mu l O_2/min/cm^2$)	0.751	0.765	N.S.
Photosynthesis ($\mu l O_2/hr/mg$ dry weight)	16.622	16.362	N.S.
Photosynthesis ($\mu l O_2/min/mg$ chlorophyll)	3.309	2.932	***
Respiration(Leaflets)($\mu l O_2/hr/mg$ dry wt)	2.997	3.482	*
Respiration(roots)($\mu l O_2/hr/mg$ dry wt.)	3.955	4.788	*
Chlorophyll concentration(mg/dm^2) with time	2.132	3.704	***
Chlorophyll concentration(mg/dm^2)	1.876	3.382	***
Chlorophyll concentration(mg/gm dry wt)	6.273	13.620	***
Chlorophylls a/b ratio	1.265	1.167	*
Specific leaf weight (mg/cm^2)	2.682	2.783	N.S.
Leaf thickness index (mg/cm^2)	14.200	17.122	***
(Mesophyll cell number/mg dry wt)x 10^7	3.765	3.624	N.S.
(Mesophyll cell number/cm^2 Leaf area) x 10^7	10.048	8.170	***
Stomatal length (μ) x 10	3.000	3.281	*
Stomatal density(number/mm^2) x 10	22.592	23.029	N.S.

*** = $P < 0.001$ ** = $P < 0.01$ * = $P < 0.05$ N.S. = not significant.

TABLE II.3.

The influence of variety x nitrogen interactions on various physiological and leaf characteristics of tomato plants.

Characteristics	Potentate		Yellow seedling		F_1 hybrid		LSD	
	28ppm N	280ppm N	28ppm N	280ppm N	28ppm N	280ppm N	5%	1%
Photosynthesis($\mu l O_2$/min/cm^2)	0.792	0.792	0.734	0.663	0.726	0.839	0.112	0.162
Photosynthesis($\mu l O_2$/hr/mg dry wt.)	17.632	16.010	16.692	15.931	15.542	17.146	N.S.	
Photosynthesis($\mu l O_2$/min/mg chlorophyll)	3.332	2.738	3.573	3.258	3.022	2.799	N.S.	
Respiration(leaflets)($\mu l O_2$/hr/mg dry wt.)	2.661	3.319	3.547	3.828	2.784	3.299	N.S.	
Respiration(roots)($\mu l O_2$/hr/mg dry wt.)	3.853	4.621	4.702	4.635	3.311	5.112	N.S.	
Chlorophyll concentration(mg/dm^2) with time	2.258	4.424	1.700	2.269	2.439	4.420	0.530	0.734
Chlorophyll concentration(mg/dm^2)	1.829	3.882	1.646	2.099	2.154	4.164	0.788	1.091
Chlorophyll concentration(mg/gm dry wt.)	6.030	14.210	6.485	10.000	16.305	16.650	N.S.	
Chlorophyll a/b ratio	1.312	1.056	1.262	1.274	1.221	1.172	N.S.	
Specific leaf weight(mg/cm^2)	2.589	2.883	2.635	2.442	2.823	3.023	N.S.	
Leaf-thickness index(mg/cm^2)	12.82	16.96	17.61	17.78	12.18	16.63	2.253	3.121
(Mesophyll cell number/mg dry wt.)x 10^7	3.964	3.828	2.942	3.290	4.390	3.755	0.639	0.885
(Mesophyll cell number/cm^2 leaf area) x 10^7	11.390	8.569	6.043	6.213	12.709	9.728	1.172	1.622
Stomatal length (μ) x 10	3.101	3.371	2.989	3.196	2.910	3.276	N.S.	
Stomatal density(number/mm^2) x 10	23.073	21.631	23.598	24.384	21.107	23.073	N.S.	

4.8 Vegetative growth.

The influence of nitrogen concentration on various vegetative characteristics of Potentate, Yellow seedling and their F_1 hybrid is shown in Tables II.4, II.5 and II.6. F_1 hybrid had a higher cumulative fresh weight per plant than the two parents irrespective of nitrogen supply. Under low nitrogen supply its superiority became apparent after 2-weeks. At high nitrogen concentration, Yellow seedling became increasingly inferior with time. After 3-weeks, while the fresh weight per plant of Potentate and F_1 hybrid were reduced by low nitrogen supply by 83% and 70% respectively, that of Yellow seedling was reduced by only 27%, compared with the high N treatment.

TABLE II.4.

The influence of nitrogen concentrations on cumulative fresh weight per plant (mg/week) of Potentate, Yellow seedling and their F_1 hybrid.

N-levels	Varieties	Time in weeks			
		0	1	2	3
28 ppm N	Potentate	115.0	225.0	302.5	1022.5
	Yellow seedling	87.5	200.0	290.0	827.5
	F_1 hybrid	90.0	227.5	472.5	2150.0
280ppm N	Potentate	87.5	480.0	1945.0	6200.0
	Yellow seedling	82.5	250.0	355.0	1135.0
	F_1 hybrid	90.0	500.0	2227.5	7025.0

The results for cumulated stem extension rate were similar to those for cumulated fresh weight per plant with respect to varietal differences and effects of nitrogen concentration. As shown in Table II.5 the effect of varietal differences and nitrogen concentration on stem extension rate intensified with the passage of time.

The effects of variety x nitrogen interactions on cumulated leaf emergence as influenced by nitrogen concentration are shown in Table II.5. With respect to varietal differences, again the differences between Yellow seedling and Potentate, and between Yellow seedling and F_1 hybrid were most obvious especially when the plants were grown under low nitrogen supply. Like most of the characteristics measured the cumulated leaf emergence of Yellow seedling which was higher than those of Potentate and F_1 hybrid, irrespective of nitrogen concentration was comparatively less sensitive to changes of nitrogen concentrations.

TABLE II.5.

The effect of nitrogen levels (N_1 = 28 ppm, N_2 = 280 ppm N) on cumulative (1) weekly stem elongation (cm/week) and (2) weekly leaf emergence of Potentate, Yellow seedling and F_1 hybrid over a 12-week period.

(1)

N-levels	Varieties	1	2	3	4	*	7	8	9	10	11	12 (weeks)
N_1	Potentate	3.13	3.28	4.90	6.00		11.75	26.00	40.75	47.38	60.50	67.50
	Yellow seedling	3.35	3.63	5.13	6.63		7.75	13.50	20.38	25.13	31.75	38.50
	F_1 hybrid	3.43	3.95	5.80	8.08		13.75	27.00	36.00	46.25	59.00	66.00
N_2	Potentate	2.68	4.18	7.33	12.30		29.50	51.38	69.13	83.25	96.75	105.25
	Yellow seedling	3.60	4.30	5.70	6.98		11.38	16.50	26.38	32.25	40.50	46.00
	F_1 hybrid	3.45	4.55	8.43	13.10		27.25	47.38	64.50	78.00	87.75	93.75

(2)

N_1	Potentate	0	1.0	2.8	4.8	7.3	9.8	11.5	13.0	14.0	14.8
	Yellow seedling	0	1.0	3.5	6.0	8.0	12.5	14.5	15.5	17.5	19.0
	F_1 hybrid	0	1.0	3.0	5.5	7.0	9.5	11.3	12.8	13.8	14.8
N_2	Potentate	0	2.0	4.5	7.3	10.5	14.0	16.5	18.3	19.5	21.8
	Yellow seedling	0	2.0	4.5	6.5	10.8	14.8	16.8	18.5	19.8	22.8
	F_1 hybrid	0	2.0	5.0	7.3	10.3	13.8	16.0	17.8	18.8	19.8

Each figure is a mean of four replicates.

* The plants were transplanted to 6-inch pots containing sand medium after growing in nutrient solution in urea test tubes for 4-weeks.

The effects of nitrogen concentration on other vegetative characteristics are presented in Table II.6. Here again

Table II.6. The effect of nitrogen levels (N_1 = 28 ppm N, N_2 = 280 ppm N) on

(1) the number of laterals to the first truss (8-week old);

(2) the number of leaves to the first truss (10-week old);

(3) the number of leaves between the first and second truss (8-week old);

(4) the number of leaves between the second and third truss (15 week old); and

(5) the number of leaflets of seventh leaf of Potentate, Yellow seedling and their F_1 hybrid. Each figure is a mean of four measurements.

N-levels	Varieties	(1)	(2)	(3)	(4)	(5)
N_1	Potentate	nil	8.0	4.5	___	14.3
	Yellow seedling	7.4	6.7	6.0	___	10.5
	F_1 hybrid	nil	7.0	4.3	___	16.8
N_2	Potentate	3.0	7.8	3.3	3.0	19.3
	Yellow seedling	7.5	7.5	5.0	3.0	10.3
	F_1 hybrid	3.5	7.0	2.8	2.8	18.8

___ The Third inflorescence of the low nitrogen-plants had not appeared when the measurements were made.

the unresponsive nature of Yellow seedling to variations of nitrogen concentrations was noted.

4.9 Reproductive characteristics.

Table II.7. The effect of N-concentrations (N_1 = 28 ppm N, N_2 = 280 ppm N) on a number of reproductive characteristics of Potentate, Yellow seedling and their F_1 hybrid:

(1) the number of weeks from sowing to anthesis;
(2) the number of flowers and primordia in the first truss;
(3) the number of flowers and primordia in the second truss;
(4) the number of flowers and primordia in the third truss, and
(5) the height of the first truss from the growth medium in cm.

N-levels	Varieties	(1)	(2)	(3)	(4)	(5)
N_1	Potentate	10.0	5.5	4.3	___	50.5
	Yellow seedling	10.0	7.5	6.3	___	18.3
	F_1 hybrid	9.5	5.5	6.0	___	44.6
N_2	Potentate	7.0	8.0	12.0	7.3	36.8
	Yellow seedling	9.0	7.5	7.3	8.0	19.8
	F_1 hybrid	7.5	9.8	10.3	7.0	36.7

___ Same as Table II.6.

Like vegetative characteristics the variations of nitrogen concentrations exerted a comparatively very minor influence on the reproductive characteristics of Yellow seedling. As shown in Table II.7 the reproductive characteristics of Potentate and F_1 hybrid in sharp contrast to those of Yellow seedling varied markedly with nitrogen concentration. All the measured reproductive characteristics of F_1 hybrid followed those of the green parent (Potentate) very closely.

4.10 Summary of experiment two.

Essentially, the results of experiment two were as follows:

(1) Yellow seedling had a low mean photosynthetic rate per unit leaf area probably due to its low mesophyll cell number per unit leaf area, and low SLW. But on a dry weight basis its mean photosynthetic rate was not inferior to those of Potentate and F_1 hybrid. On a chlorophyll weight basis, the mean photosynthetic rate of Yellow seedling was significantly higher than those of Potentate and F_1 hybrid.

(2) Yellow seedling had a low chlorophyll concentration but its chlorophyll a/b ratio was not different from those of Potentate and F_1 hybrid.

(3) Yellow seedling had a high leaflet respiration rate but its root respiration rate was not different from those of Potentate and F_1 hybrid. In general, all the characters of Yellow seedling so far mentioned varied little with leaf age or position.

(4) There were no varietal differences in stomatal length and density.

(5) Effects of nitrogen concentration was noted for a number of characters, for example photosynthetic rate per mg chlorophyll; chlorophyll concentration; respiration rate; chlorophyll a/b ratio; mesophyll cell number/mg dry weight; stomatal length and several other vegetative and reproductive characters. However, nitrogen effects were not observed for photosynthetic rate per unit dry weight, or per unit leaf area.

(6) In contrast to Potentate and F_1 hybrid, Yellow seedling was very unresponsive to increasing nitrogen concentration. This was true for virtually all the characters studied. Though F_1 hybrid resembled Potentate very closely, its photosynthetic rate on a leaf area basis responded positively to increasing nitrogen concentration in contrast to the two parents.

(7) Increased light intensity within the range of 590 to 1300 ft-c. gave higher photosynthetic rates of all varieties, irrespective of ages of leaflets. However, on a leaf area basis, photosynthetic rates of 3-week old leaflets responded more to increased light intensity than those of older leaflets.

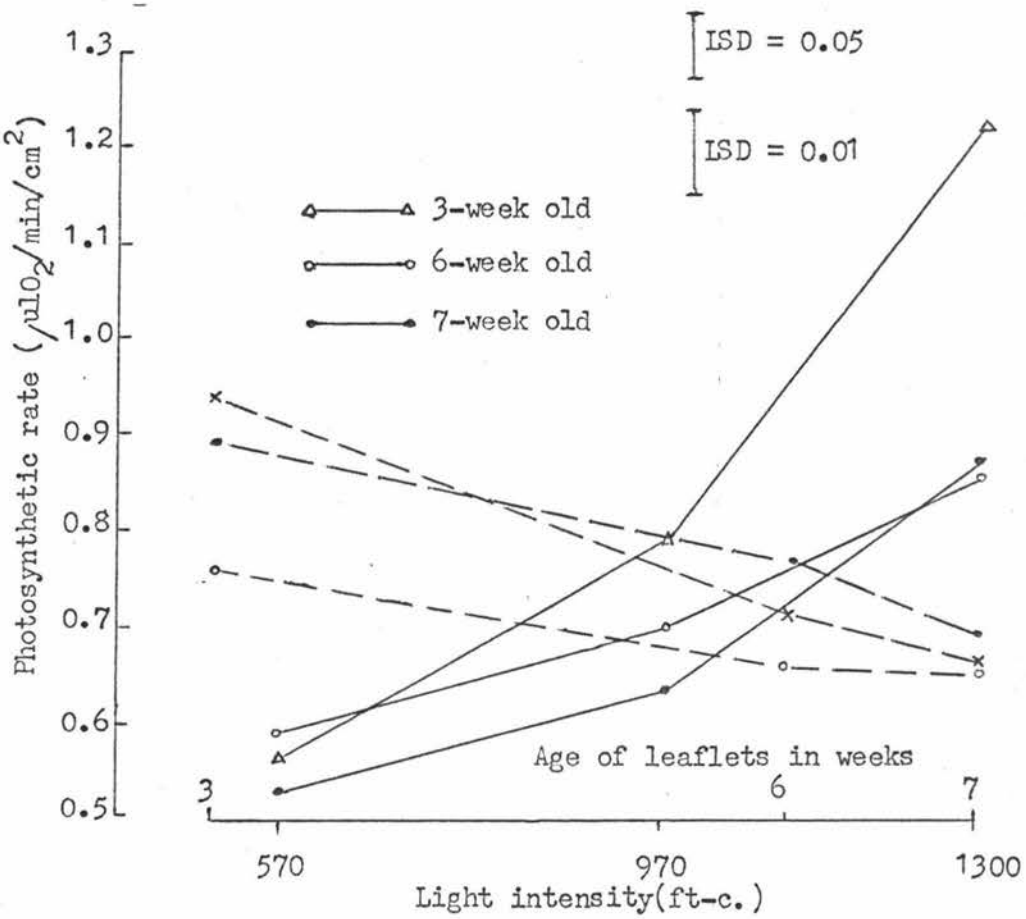


Fig.II. 2. The effects of (a) time x light intensity (solid lines) and (b) time x variety (broken lines) interactions on photosynthetic rates of tomato leaflets. Potentate (•), Yellow seedling (o) and F_1 hybrid (×).

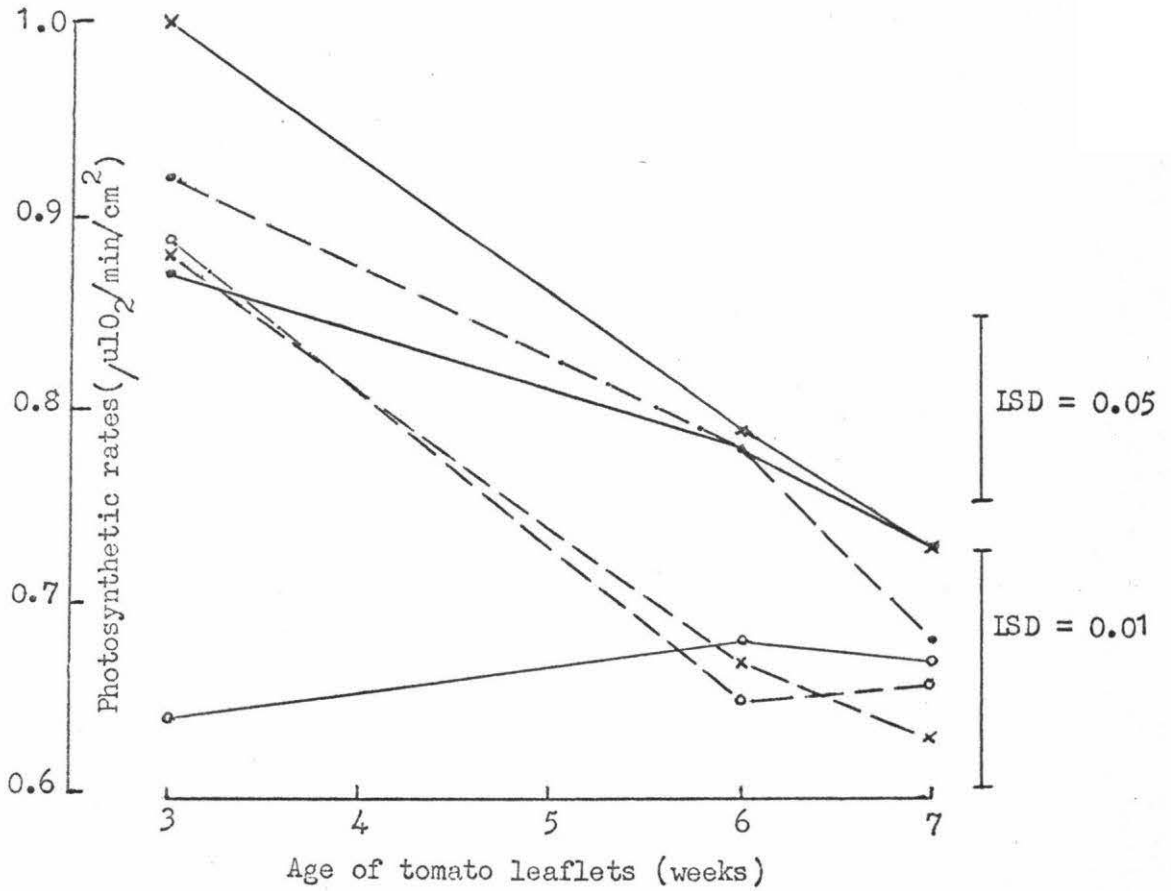


Fig.II. 3. The effects of interactions of time x variety x nitrogen on photosynthetic rates of tomato leaflets. Potentate (•), Yellow seedling (∘) and their F_1 hybrid (×) — — 28 ppm N _____ 280 ppm N.

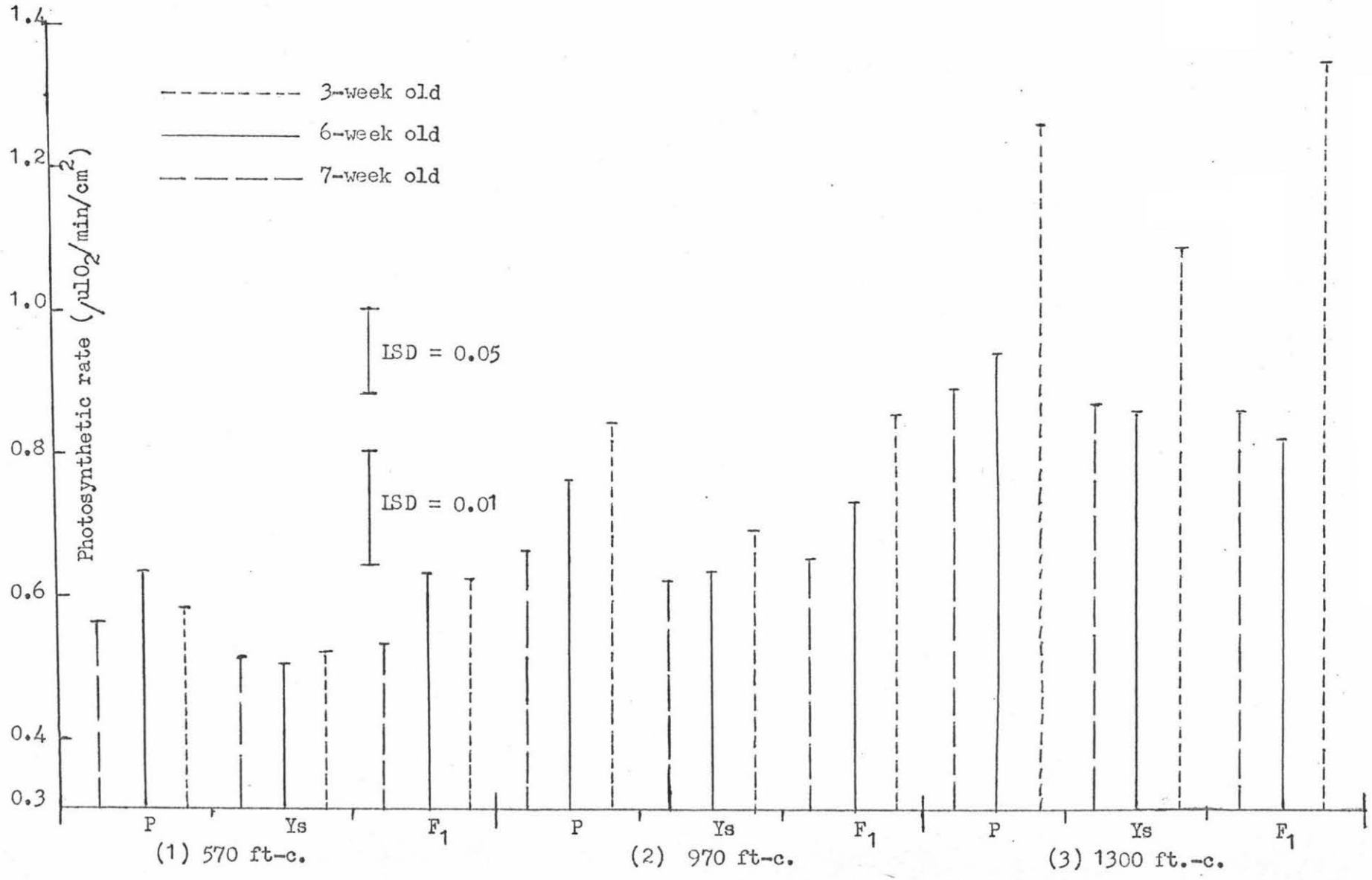


Fig. II. 4. The effects of interactions of time x light intensity x variety on the photosynthetic rates ($\mu lO_2/min/cm^2$) of tomato leaflets.

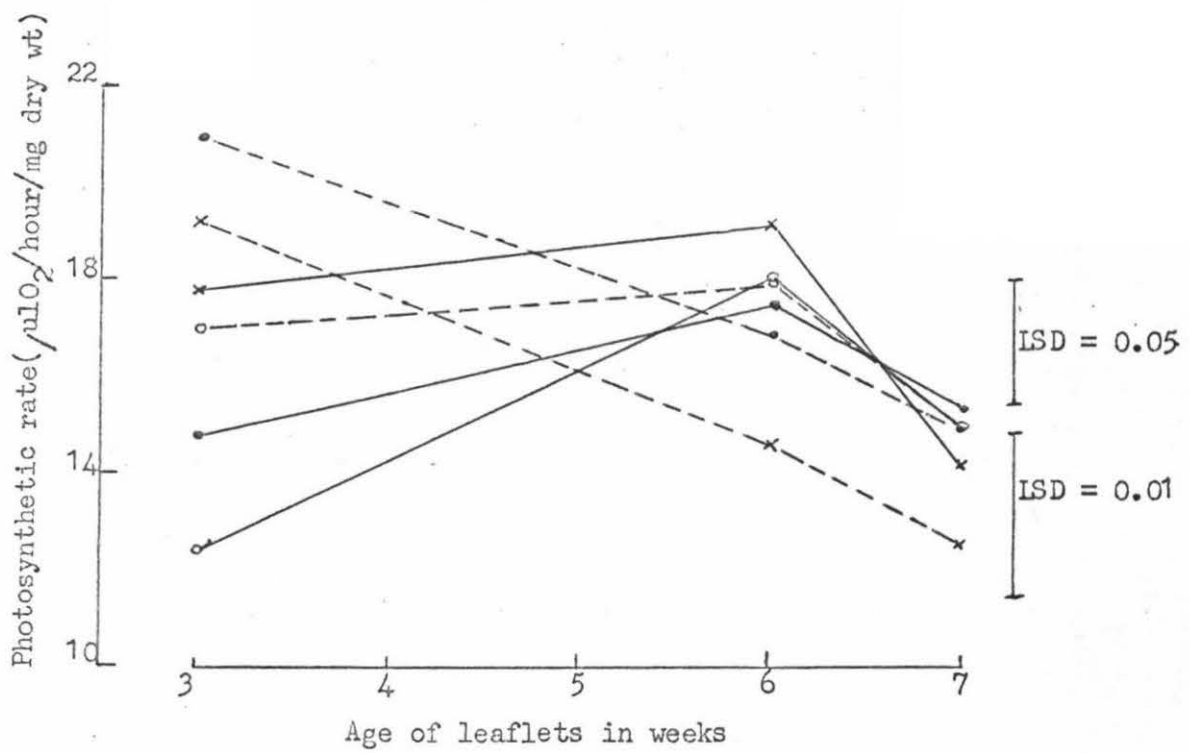


Fig.II. 5. The effects of interactions of T x V x N on photosynthetic rate of Tomato leaflets.
Potentate (•), Yellow seedling (°), F_1 hybrid (×)
-- -- N_1 ——— N_2

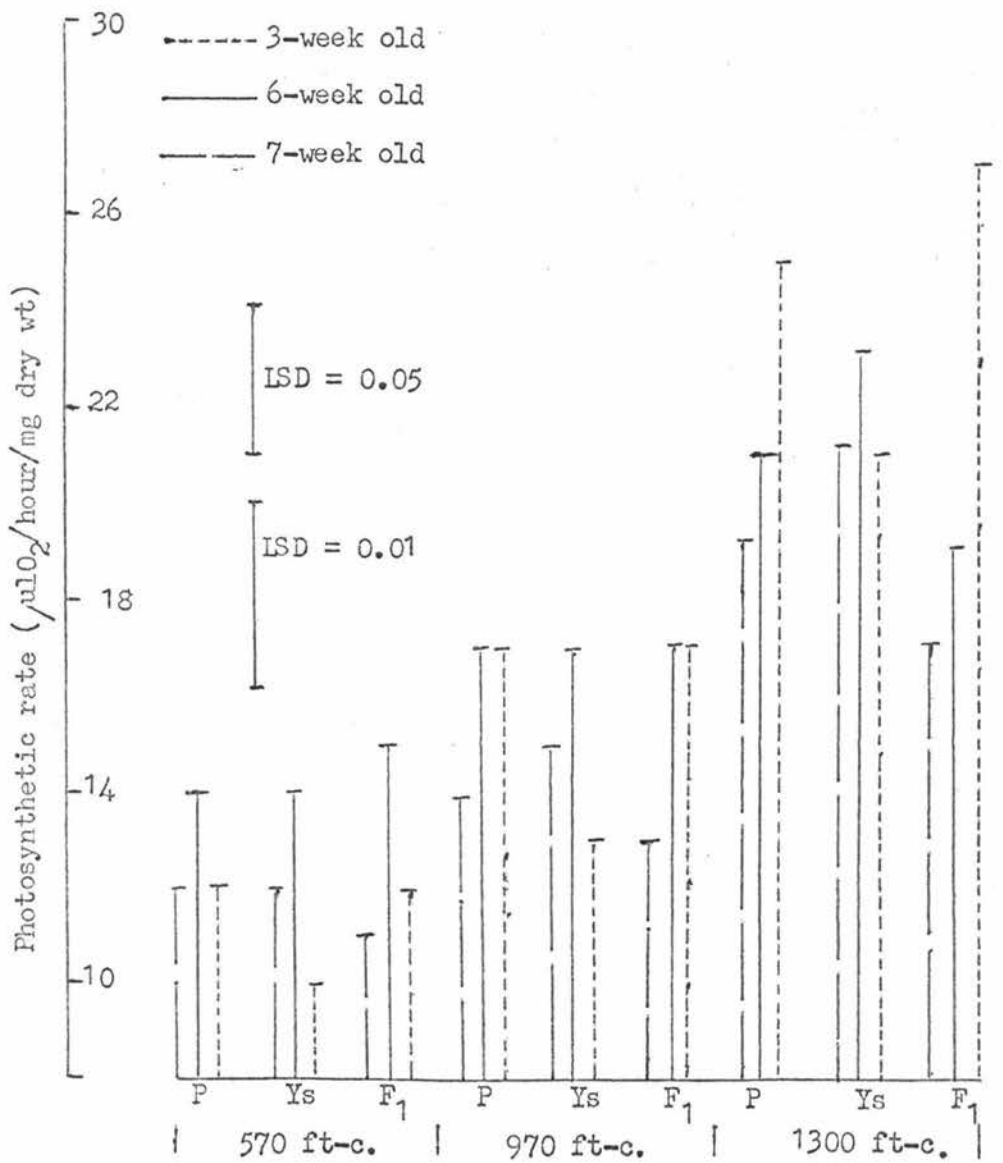


Fig. II. 6. The effects of time x variety x light intensity interactions on the photosynthetic rates (/ulO_2/hour/mg dry wt) of the tomato leaflets.

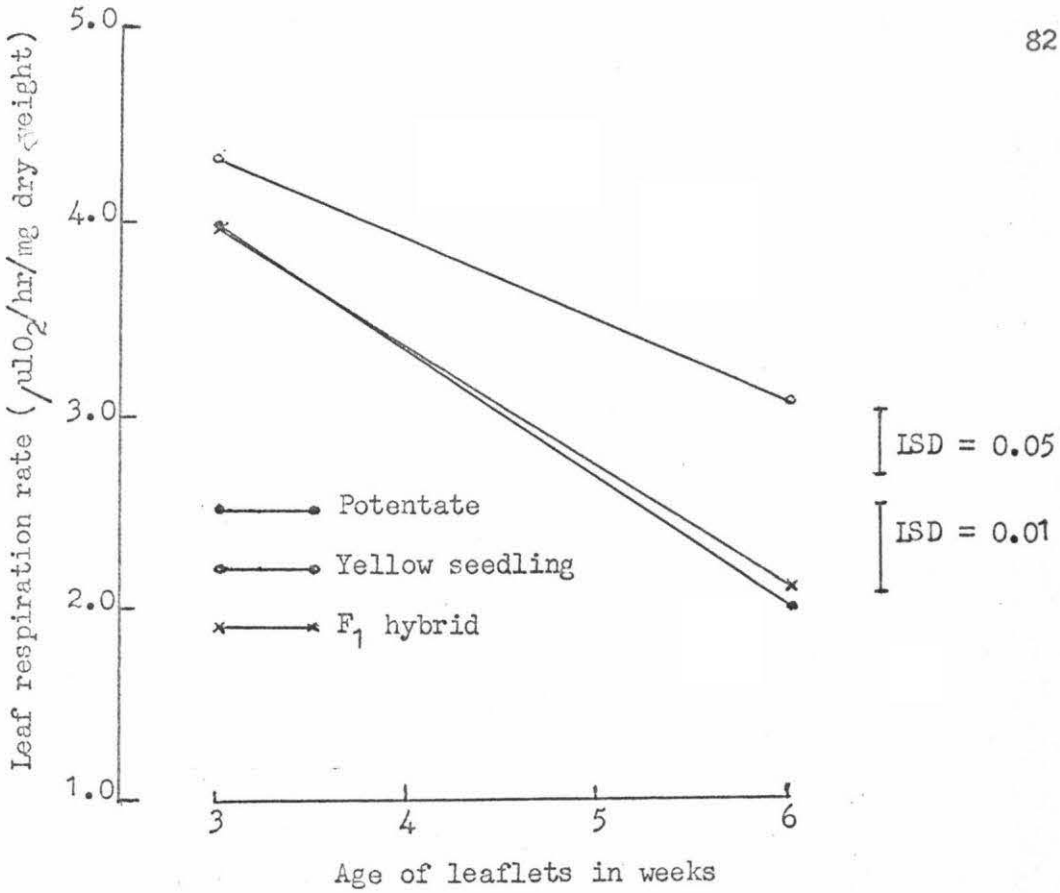


Fig.II.7. Varietal differences in changes of respiration rates of leaflets with age.

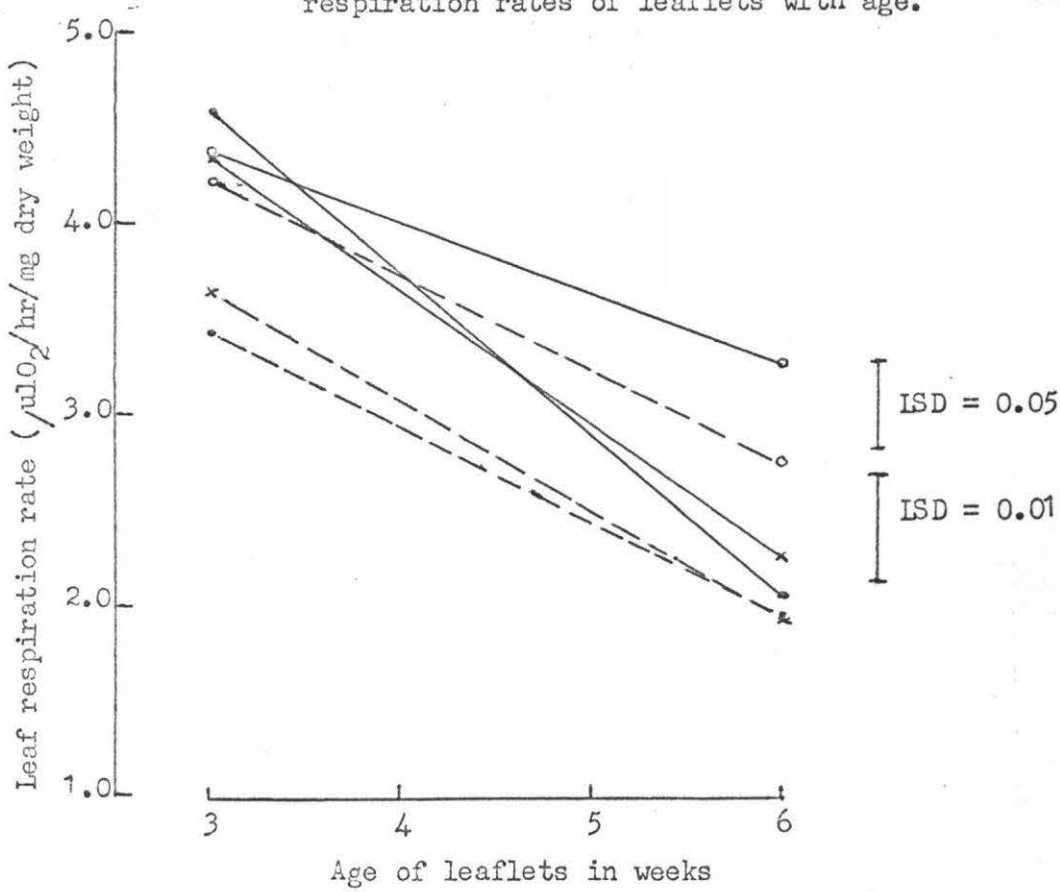


Fig.II.8. Time course of leaf respiration rate of Potentate, Yellow seedling and their F_1 hybrid as affected by N concentrations. Potentate (•), Yellow seedling (○) and F_1 hybrid (×). — — N_1 ——— N_2

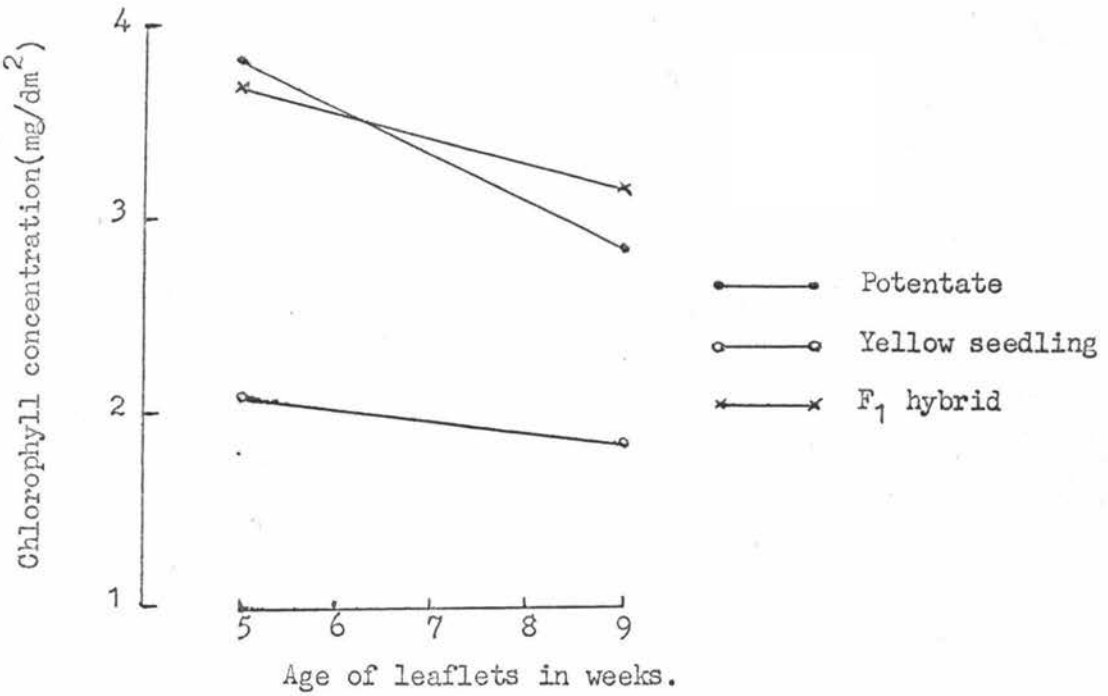


Fig.II. 9. A comparison of chlorophyll concentrations between leaflets of Potentate, Yellow seedling and their F_1 hybrid showing the changes that occurred as the leaflets aged.

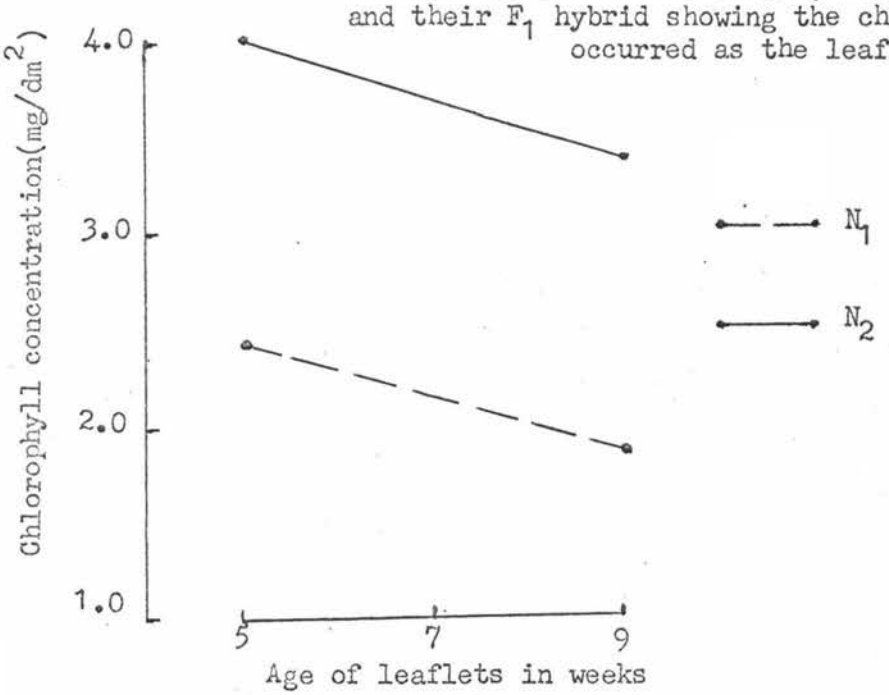


Fig.II.10. The effect of time x nitrogen interactions on chlorophyll concentration of leaflets from leaf 5.

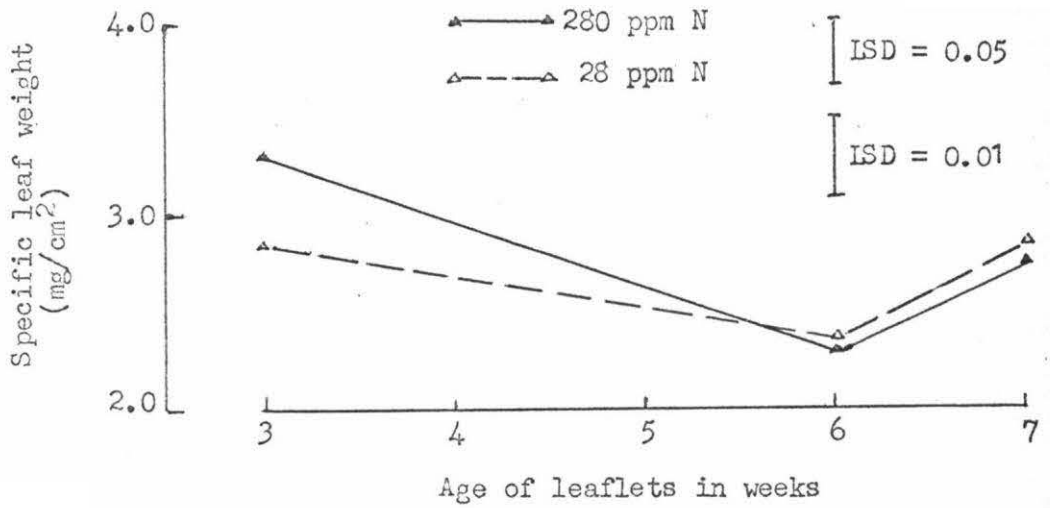


Fig.II.11 The time trends of specific leaf weight of tomato leaflets as affected by N levels.

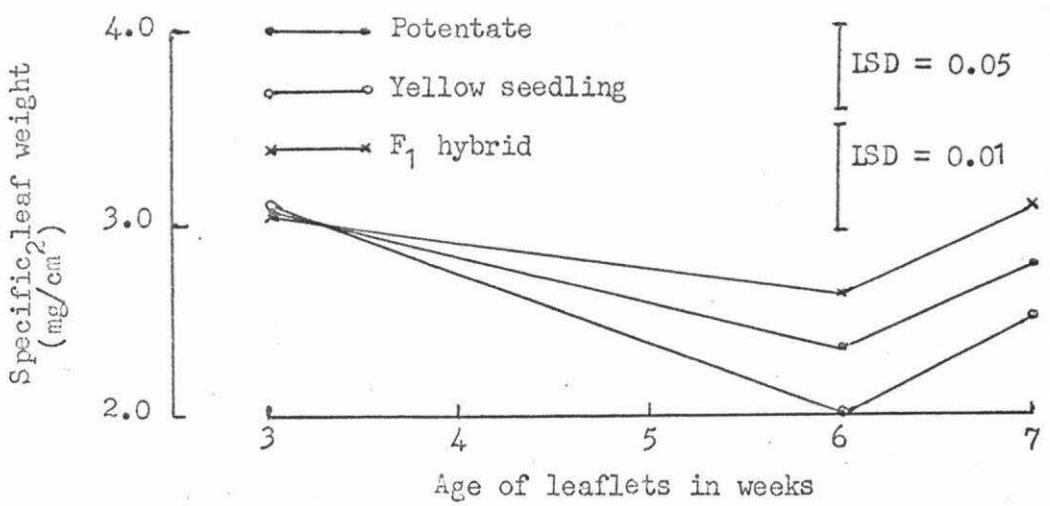


Fig.II.12 Changes with age in specific leaf weight of Potentate, Yellow seedling and their F_1 hybrid.

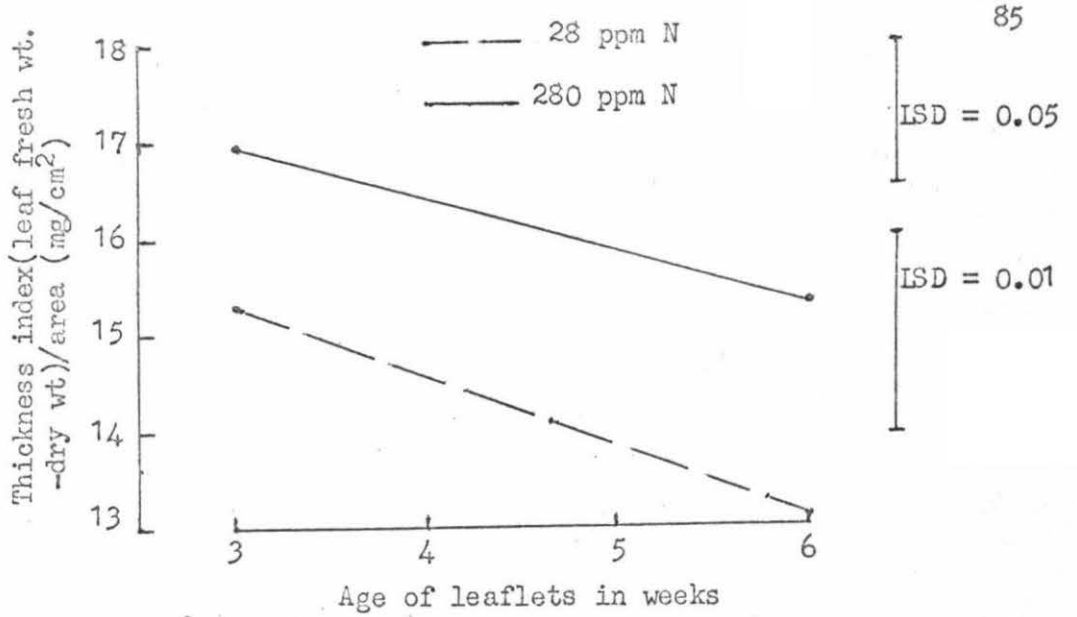


Fig.II.13. The effect of time x nitrogen interactions on leaf thickness index.

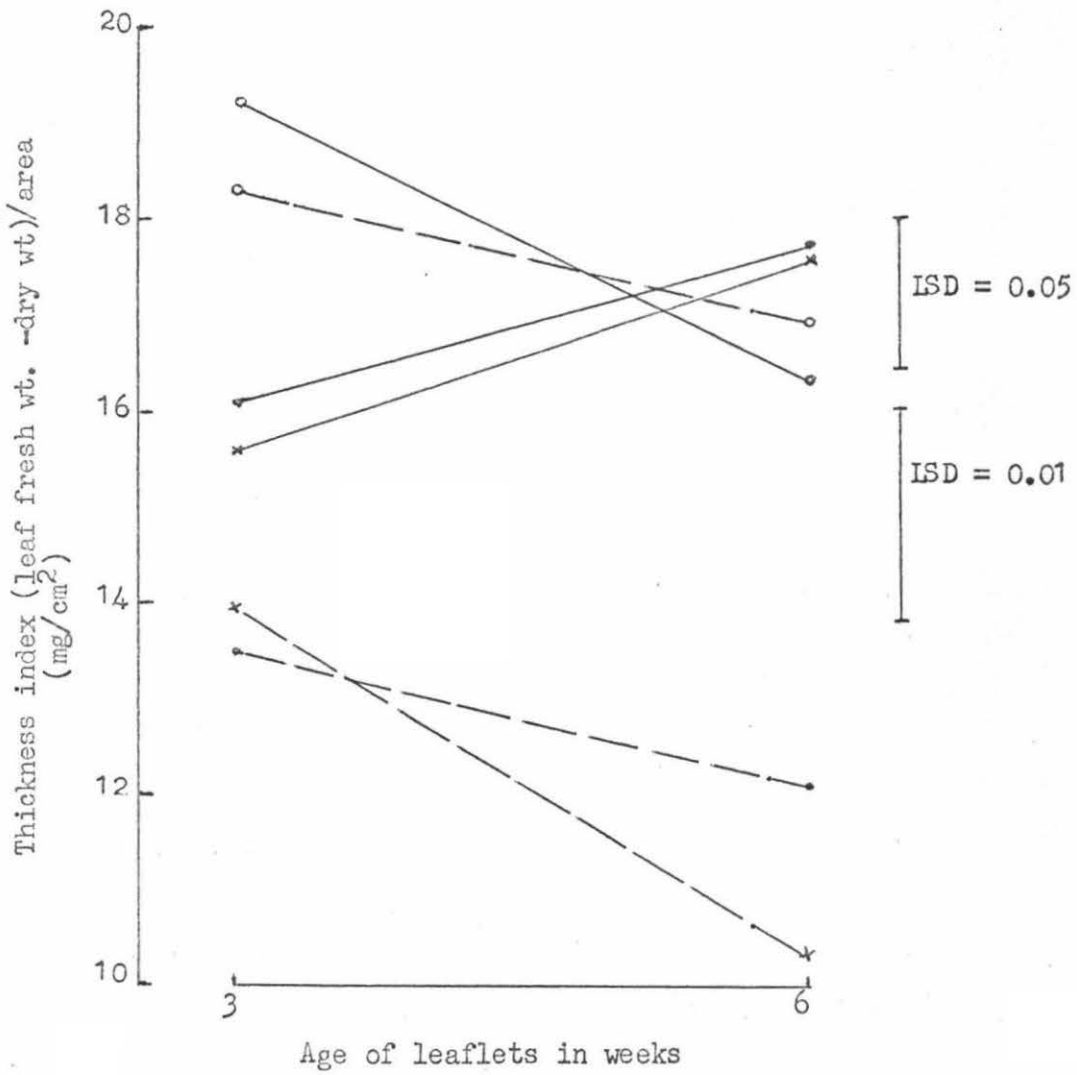


Fig.II.14. Influence of nitrogen concentrations on time trends of leaf thickness index of Potentate (•), Yellow seedling (o) and their F_1 hybrid (×) over a 3-week period. — — 28 ppm N ——— 280 ppm N.

4.11 Discussion.

The above studies showed that in all the physiological and leaf characters studied, there were no significant differences between Potentate and F_1 hybrid. However, marked differences between Yellow seedling and the other two varieties were found in more than half of these characters. Apart from leaf thickness index which in fact was an index of leaf moisture content, only for two characters (i.e. photosynthetic rate per unit chlorophyll and leaflet respirate rate) was Yellow seedling significantly superior to Potentate and F_1 hybrid.

Inspection of Tables II.1 and II.4 indicates complete agreement between the results of this experiment and the previously observed differences in plant growth between the normal green plants (Potentate and F_1 hybrid) and the chlorophyll deficient Yellow seedling (experiment one). The slow growing habit of Yellow seedling together with its low mesophyll cell number could be the result of its low photosynthetic and high respiration rates.

Photosynthesis as a primary process ultimately delimiting plant growth is influenced by many factors, both internal and external either directly or indirectly. These are well documented (see Heath 1969). In the present studies, selected internal factors which could contribute to the varietal differences in photosynthetic rates were studied. The results indicate that Yellow seedling had relatively thin leaves. This effect probably contributed to the significant variations in photosynthetic rates and chlorophyll concentrations computed in term of leaf area. This is supported by the fact that when these characters were expressed on leaf dry weight bases, the mean differences between the parents and their F_1 hybrid became non-significance, though Yellow seedling still had the lowest values. Thus, it is suggested that the relatively low photosynthetic rate of Yellow seedling on an area basis was due to a low photosynthetic cell number, and not necessarily to malformation or malfunctioning of the photosynthetic systems itself, as has been postulated for similar mutants in various plants (see Granick 1955; Von Wettstein and Eriksson 1963). The lack of significant differences in stomatal size and density and chlorophyll composition further supports such an explanation. Thus, if photosynthetic rate per unit leaf weight is taken as a criterion, it seems that the varietal differences in plant growth could well be the result of differences in respiration rates in at least one of the plant organs — the leaves.

The higher photosynthetic rate per mg. chlorophyll of Yellow seedling indicated that its chlorophyll was more efficiently used. This efficiency increased as the light intensity was increased. Similar results have

been obtained from a number of chlorophyll deficient mutants, such as the tobacco aurea mutant Su/su (Schmid 1967), Lespedeza procumbens (Clewell and Schmid 1970) and a virescent cotton mutant (Benedict and Kohel 1970). In addition, the tobacco mutant Su/su also had a low SLW.

Many factors are known to affect the colour of a leaf (Starnes and Hadley 1965). The leaves of Yellow seedling were yellow-green in colour because (i) they contained a low total chlorophyll content, (ii) they were thin, and (iii) their tissues were less compact. Other factors such as the amounts of carotemoid and xanthophylls may have also been involved.

The influence of nitrogen concentration on various characters showed that high nitrogen concentration was more favourable to plant growth. However, it should be pointed out that during the experimental period all the high nitrogen-treated plants (except Yellow seedling) developed brown stem lesions, and gradually slowed down in growth. This was followed by a darkening of leaf colour, and later by the appearance of presumably mineral-induced leaf symptoms which appeared first on young unfolded leaves. It seems probable that barring from the unlikely possibility of pathogenic disease, ammonium nitrogen which competes and interacts with other ions was involved (Kirkby 1968). High ammonium concentrations are known to induce toxicity symptoms and adversely affect the growth of tomato plants (Barker et al 1967; Maynard 1967; Ajayi et al 1970) and barley plants (Suzuki and MacLeod 1970) when associated with a low potassium supply. Other adverse effects of high ammonium concentration have been discussed in section (3.11). In the above mentioned leaf symptoms were caused by high ammonium ions either directly or indirectly, then this is an interesting example of varietal differences in tolerance of ammonium nitrogen, since Yellow seedling (in contrast to Potentate and F_1 hybrid) invariably showed little response to changes of the applied nitrogen concentrations.

Other interactions of factors were of minor importance and do not warrant further discussion.

CHAPTER 5

5. Breeding studies.

5.1 Growth analysis.

Analyses of variance (Table III. 2) indicated very significant differences in RGR among all entries and among F_3 families but not among green F_3 families alone. As indicated in Tables III. 2 and III. 3, this variation in RGR was due to the presence of plants exhibiting the yellow leaf character. Such plants had RGR values only about half those of green plants.

Table III. 2. Analyses of variance of relative growth rate of
(1) all entries,
(2) all F_3 families, and
(3) green F_3 families.

Source	d.f.	M.S. (1)	M.S. (2)	M.S.(3)
Replicates	R - 1	0.017 N.S.	0.003 N.S.	0.013 N.S.
§ Families (F)	F - 1	0.274 ***	0.284 ***	0.011 N.S.
N-levels (N)	N - 1	0.520 ***	0.389 ***	0.478 ***
F x N	(F-1)(N-1)	0.015 N.S.	0.014 N.S.	0.012 N.S.
Error	(R-1)(FN-1)	0.011	0.012	0.010
h^2		------	0.950	-0.111

§ in the case of M.S.(1), "families" includes the ancillary groups.
*** $p < 0.001$
N.S. = not significant.

The effect of nitrogen concentration on RGR was highly significant for the F_3 families and ancillary groups (Table III.2 and III.3; plates 2 and 3).

The complete absence of any indication of entry x nitrogen level interactions (Table III.2) suggests that the effect of Yellow seedling syndrome on RGR is independent of the nigrogen regime, a result completely in agreement with those of experiment one.

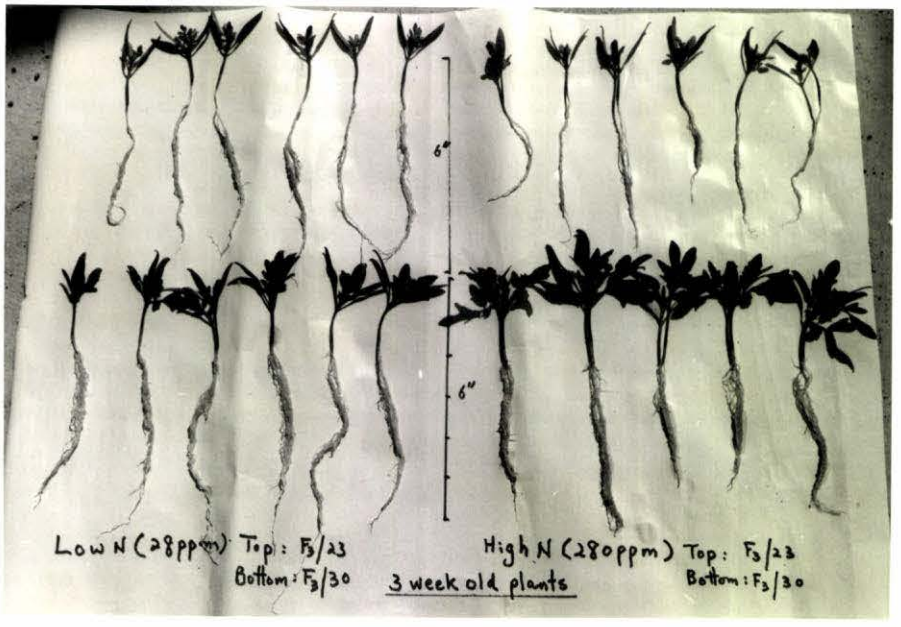


Plate 2: Representatives of normal (F_3/30) and chlorophyll deficient (F_3/23) F_3 plants grown under two contrasting nitrogen regimes for a period of 3 weeks.

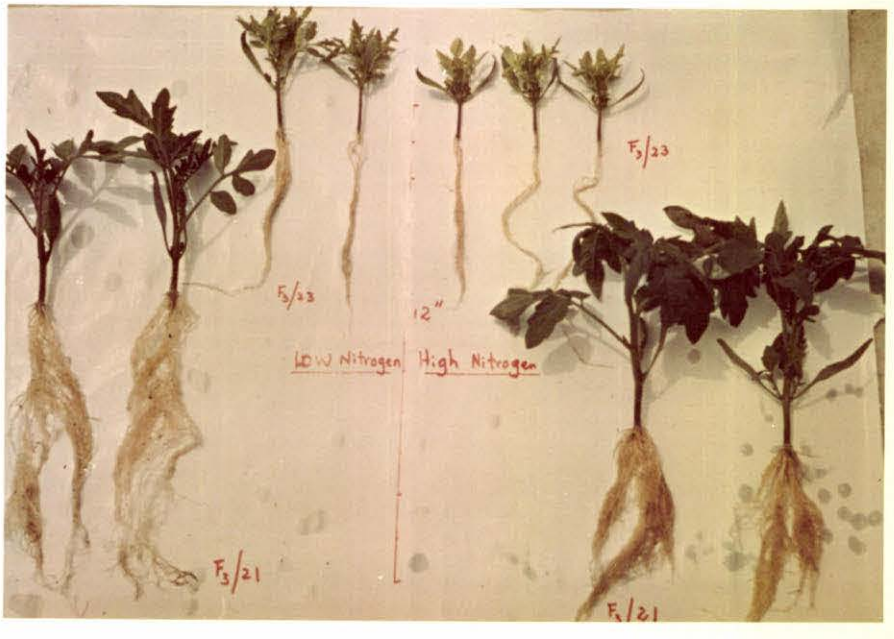


Plate 3: Representatives of normal (F_3/21) and chlorophyll deficient (F_3/23) F_3 plants grown under two contrasting nitrogen regimes for a period of 5 weeks.

TABLE III. 3.

Comparison of relative growth rates among F_3 families and ancillary groups grown under two contrasting nitrogen regimes.

Group	RGR(mg/mg/week) ± S.E. High N	Low N
Potentate (P)	1.314 ± 0.056	1.124 ± 0.216
Yellow seedling (Ys)	0.528 ± 0.011	0.663 ± 0.134
F_1	1.297 ± 0.074	1.089 ± 0.080
F_2	1.313 ± 0.037	1.163 ± 0.017
BC to P	1.367 ± 0.105	1.167 ± 0.017
BC to Ys	1.400 ± 0.124	1.128 ± 0.003
Green F_3	1.329 ± 0.006	1.103 ± 0.048
Segregating F_3	1.303 ± 0.021	1.134 ± 0.019
Yellow F_3	0.675 ± 0.088	0.635 ± 0.100
Mean	1.170 ± 0.058	1.023 ± 0.070

5.2 Genetic analysis

Genetic analyses were made on F_3 families and broad sense heritability estimates for RGR were calculated (Table III.2). When families containing yellow plants were included in the analysis the heritability of RGR was 95%, but when they were excluded, the heritability estimate was negative, i.e. essentially zero. This indicates that the genetic variance of RGR among F_3 families was entirely associated with the yellow character.

The results of this experiment, particularly the facts that the yellow segregants were similar to the yellow parent in all observed characters and growth rates, and that the F_2 heterozygotes segregated green and yellow plants in a 3 : 1 ratio (see 2.3.2) show that a recessive gene or block of genes associated with the yellow character markedly affected RGR. It is unlikely that cytoplasmic factors were involved.

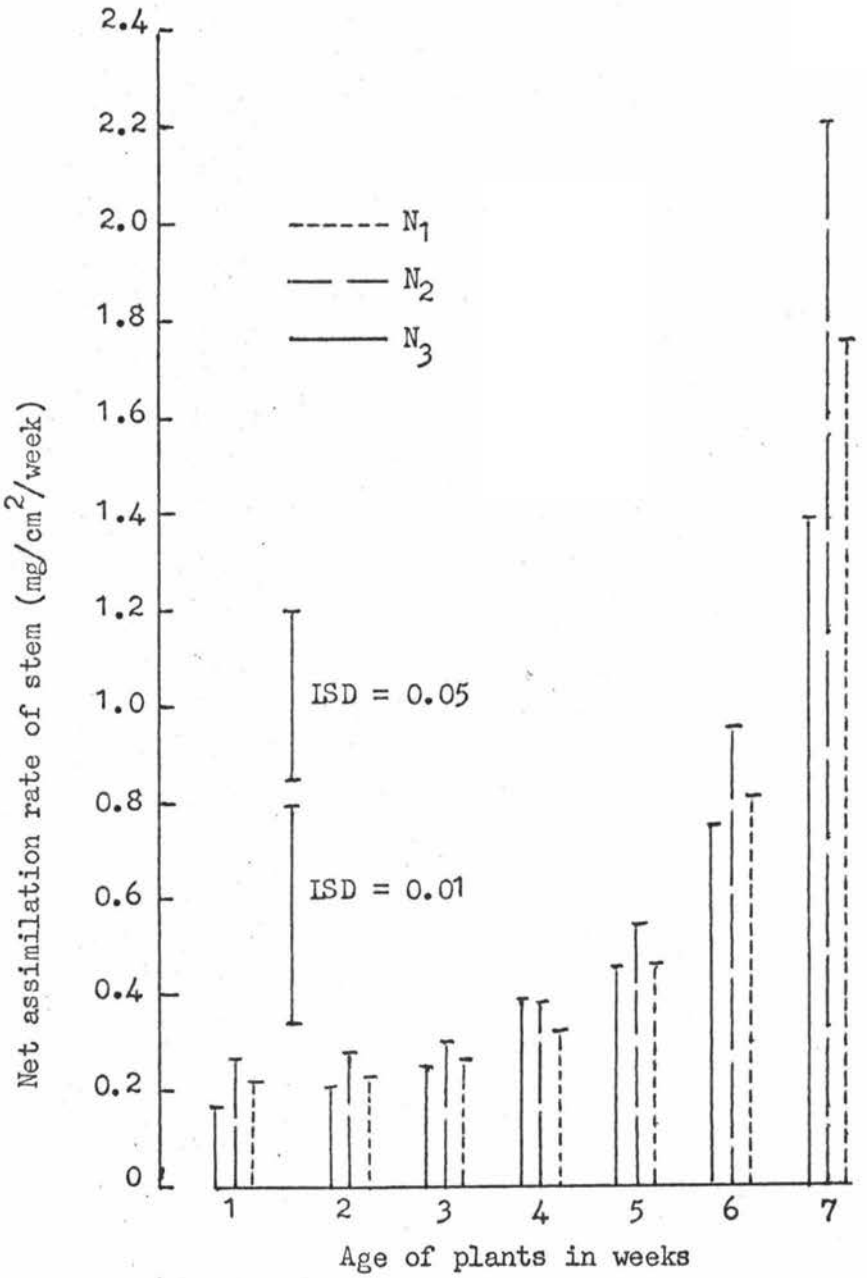
CHAPTER 6.

General Discussion

Since the effects of nitrogen level have been discussed in sections 3.11 and 4.11, these concluding comments will be restricted to a discussion of inferior performance of Yellow seedling.

Yellow seedling was inferior to Potentate and F_1 hybrid in almost all the characters studied. These included the growth parameters (e.g. RGR, NAR and LAR); physiological processes (e.g. photosynthetic and respiration rates, and rate of nitrogen utilization); and other plant characters such as chlorophyll concentration, mesophyll cell number and specific leaf weight. The low RGR of Yellow seedling was due to its low NAR, reflecting a low photosynthetic rate and a high respiration rate. In addition, inefficient nitrogen metabolism may also have contributed, as indicated by its low rate of nitrogen utilization. It is possible that mutation of one or a number of genes, leading to a general reduction of plant size, could have caused all these effects, particularly the low photosynthetic rate. This hypothesis is based on the theory that the rate of plant growth (or sink size) regulates photosynthetic rates (Moss 1962; Sweet and Wareing 1966; King et al (1967).

Attention is drawn to the finding by Scholz and Rudolph (1968) of a ninhydrin-positive substance which occurs widely in higher plants and which, when applied to the tomato mutant "chloronerva", could restore its normal development. This chlorophyll deficient mutant was slow growing, flowerless and unable to produce this substance. Thus, it is felt that the low chlorophyll concentration of Yellow seedling, i.e. the yellow condition itself, is merely part of all overall effect associated with the recessive mutation, and is not responsible for the syndrome. These experiments have provided a very complete description of the syndrome, but have not indicated its underlying cause. It is felt that any further investigation of Yellow seedling should be directed at its chromosome structure, the ultrastructure of its chloroplasts, and activity of the key enzymes controlling its photosynthetic rate and nitrogen metabolism.



Appendix Fig. I. 1 The influence of nitrogen concentrations on the time trends of net assimilation rate of stem.

APPENDIX I

The Composition of the nutrient solution used in experiment one.

Macro-nutrient(gm/100 litre)

Salt	Weight	mg equivalent/litre		p p m		stock solution (mg/2l)
KNO_3	40.4	K^+ 4	NO_3^- 4	K156	N57	202.2
$Ca(NO_3)_24H_2O$	94.4	Ca 8	NO_3^- 8	Ca160	N113	472
$MgSO_4 \cdot 7H_2O$	36.8	Mg 3	SO_4^- 3	Mg36	S48	184
$NaH_2PO_4 \cdot 2H_2O$	20.8	Na^+ 1.33	PO_4^{-3} 4	Na31	P41	104

N levels	KNO_3	$Ca(NO_3)_2 \cdot 4H_2O$	$(NH_4)NO_3$	$CaCl_2$
57 ppm	57	———	———	+
170 ppm	57	113	———	———
340 ppm	57	113	170	———

Micro-nutrient (gm/100 litre)

Salt	Weight(gm)	ppm	Stock solution(gm/l)
Fe Citrate$\cdot 5H_2O$	3.35	5.6 Fe	33.5
§ $MnSO_4 \cdot 4H_2O$	0.223	0.55Mn	2.23
H_3BO_3	0.186	0.33	1.86
$CuSO_4 \cdot 5H_2O$	0.025	0.016-0.032	0.25
$ZnSO_4 \cdot 7H_2O$	0.029	0.13	0.29
$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	0.0088	0.048Mo	0.088

(§ The last 5 minerals were made up with water to 1 litre of solution)

APPENDIX II

The Composition of the nutrient solution used in experiments two and three.

Macro-nutrient

Salt	gm/litre	molar	stock solution(gm/l)	Nutrient Solution (ml/l)
$CaCl_2$	0.167	0.0015	110.99	1.5
KH_2PO4	0.214	0.0015	136.08	1.5
$MgSO_4 7H_2O$	0.514	0.0022	246.50	2.2
$NaNO_3$	0.34	0.004	85.00	2.0
NH_4NO_3			80.00	9.0(high N only)

Micro-nutrient

Salt	stock solution(gm/l)	Nutrient solution
Fe Chelate	16.42	1.0 ml
H_3BO_3	2.86	Trace elements 1.0 ml
$MnCl_2 \cdot 4H_2O$	1.81	
$ZnSO_4 \cdot 7H_2O$	0.22 in one litre	
$CuSO_4 \cdot 4H_2O$	0.08	
$H_2MoO_4 \cdot 4H_2O$	0.02	

N levels	$NaNO_3$	NH_4NO_3
28 ppm	2.0 ml	———
280 ppm	2.0 ml	9.0 ml

APPENDIX III

Mean meteorological readings on weekly basis

Weeks	Solar radiation (Langleys/week)	Bright sunshine (hour)	Temp.C°	% R.H.
1	155.7	3.67	60	68
2	132.3	3.34	57	76
3	109.0	1.97	58	74
4	148.0	3.19	60	70
5	138.6	3.09	61	70
6	158.1	2.44	60	67
7	131.7	1.26	65	70

APPENDIX IV

Analyses of variance of $\log_e$ dry weight(mg) of

(1) entire plant,

(2) stem,

(3) leaf and

(4) root.

Source	d.f.	M.S.(1)	M.S.(2)	M.S.(3)	M.S.(4)
Blocks	3	0.526 ***	0.282 ***	1.115 ***	0.215 **
Var. (V)	2	34.485 ***	23.141 ***	35.089 ***	47.426 ***
N-levels(N)	2	0.221 **	0.859 ***	0.481 ***	0.045 N.S.
V x N	4	0.082 N.S.	0.182 **	0.382 ***	0.042 N.S.
Time(T)	6	109.881 ***	115.925 ***	111.043 ***	95.073 ***
T x V	12	2.633 ***	3.445 ***	1.935 ***	3.418 ***
T x N	12	0.056 N.S.	0.027 N.S.	0.107 **	0.069 N.S.
T x V x N	24	0.022 N.S.	0.020 N.S.	0.065 *	0.062 N.S.
Error	186	0.034	0.041	0.036	0.047

* = $P < 0.05$ ** = $P < 0.01$ *** = $P < 0.001$ N.S. = not significant.

APPENDIX V.

Analyses of variance of

(1) $\log_e$ shoot/root ratio,

and $\log_e$ per cent dry weight of

(2) stem,

(3) leaf and

(4) root.

Source	d.f.	M.S.(1)	M.S.(2)	M.S.(3)	M.S.(4)
Blocks	3	0.156 N.S.	0.157 ***	0.460 ***	0.023 N.S.
Var. (V)	2	1.242 ***	1.022 ***	0.070 **	1.003 ***
N-levels(N)	2	0.497 ***	0.105 *	0.030 N.S.	0.353 *
V x N	4	0.178 N.S.	0.079 N.S.	0.049 *	0.061 N.S.
Time (T)	6	0.836 ***	2.924 ***	0.343 ***	0.411 ***
T x V	12	0.290 ***	0.154 ***	0.066 ***	0.185 **
T x N	12	0.092 N.S.	0.050 *	0.014 N.S.	0.043 N.S.
T x V x N	24	0.109 N.S.	0.036 N.S.	0.017 N.S.	0.068 N.S.
Error	186	0.101	0.027	0.015	0.079

APPENDIX VI

Analyses of variance of

(1) $\log_e$ leaf area (cm^2)

(2) relative leaf area growth rate ($cm^2/cm^2/week$), and

(3) specific leaf weight (mg/cm^2).

Source	d.f.	M.S.(1)	M.S.(2)	M.S.(3)
Blocks	3	0.117 N.S.	0.040 *	1.676 ***
Var. (V)	2	25.384 ***	1.401 ***	2.190 ***
N-levels (N)	2	0.034 N.S.	0.093 N.S.	0.185 N.S.
V x N	4	0.077 N.S.	0.024 N.S.	0.148 N.S.
Time (T)	6	98.334 ***	0.022 N.S.	2.777 ***
T x V	12	1.059 ***	0.010 N.S.	0.728 ***
T x N	12	0.072 N.S.	0.038 **	0.188 N.S.
T x V x N	24	0.016 N.S.	0.009 N.S.	0.137 N.S.
Error	186	0.058	0.015	0.158

APPENDIX VII

Analyses of variance of

(1) relative growth rate ($mg/mg/week$),

(2) net assimilation rate ($mg/cm^2/week$), and

(3) leaf-area ratio (cm^2/mg).

Source	d.f.	M.S. (1)	M.S.(2)	M.S.(3)
Blocks	3	0.151 ***	2.202 *	0.025 **
Var. (V)	2	4.316 ***	91.028 ***	0.043 ***
N-levels (N)	2	0.048 N.S.	0.264 N.S.	0.001 N.S.
V x N	4	0.063 *	2.798 **	0.006 N.S.
Time (T)	6	0.880 ***	42.526 ***	0.043 ***
T x V	12	0.033 N.S.	5.849 ***	0.024 ***
T x N	12	0.022 N.S.	2.182 ***	0.009 N.S.
T x V x N	24	0.018 N.S.	1.536 **	0.003 N.S.
Error	186	0.023	0.647	0.005

APPENDIX VIII

Analyses of variance of instantaneous relative growth rates of

(1) shoot,
(2) stem,
(3) leaf and
(4) root.

Source	d.f.	M.S.(1)	M.S.(2)	M.S.(3)	M.S.(4)
Blocks	3	0.171 ***	0.134 ***	0.343 **	0.013 N.S.
Var. (V)	2	3.627 ***	4.874 ***	3.220 ***	5.077 ***
N-levels (N)	2	0.052 ***	0.029 N.S.	0.111 N.S.	0.124 *
V x N	4	0.017 *	0.024 N.S.	0.107 *	0.060 N.S.
Time(T)	6	0.532 ***	5.743 ***	0.048 N.S.	1.052 ***
T x V	12	0.025 ***	0.124 ***	0.020 N.S.	0.061 *
T x N	12	0.001 N.S.	0.009 N.S.	0.012 N.S.	0.001 N.S.
T x V x N	24	0.008 N.S.	0.011 N.S.	0.013 N.S.	0.021 N.S.
Error	186	0.006	0.014	0.037	0.032

APPENDIX IX

Analyses of variance of instantaneous net assimilation rates of

(1) shoot,
(2) stem,
(3) leaf and
(4) root.

Source	d.f.	M.S.(1)	M.S.(2)	M.S.(3)	M.S.(4)
Blocks	3	2.746 **	0.224 *	1.220 N.S.	0.099 N.S.
Var. (V)	2	46.486 ***	4.512 ***	34.532 ***	6.885 ***
N-levels(N)	2	7.011 ***	0.785 ***	6.136 **	0.015 N.S.
V x N	4	2.693 ***	0.416 **	6.274 ***	0.039 N.S.
Time (T)	6	23.828 ***	11.347 ***	6.056 ***	1.453 ***
T x V	12	3.751 ***	1.278 ***	1.639 N.S.	0.102 N.S.
T x N	12	0.694 N.S.	0.246 **	1.281 N.S.	0.034 N.S.
T x V x N	24	0.321 N.S.	0.083 N.S.	0.970 N.S.	0.044 N.S.
Error	186	0.486	0.091	0.912	0.057

APPENDIX X

Analyses of variance of

(1) per cent nitrogen content in total dry weight,

(2) $\log_e$ nitrogen yield, and

(3) rate of nitrogen utilization.

Source	d.f.	M.S.(1)	M.S.(2)	d.f.	M.S.(3)
Blocks	3	0.047 N.S.	0.456 **	3	2.273 N.S.
Var. (V)	2	1.424 ***	31.122 ***	2	201.649 ***
N-levels(N)	2	13.978 ***	1.265 ***	2	13.145 **
V x N	4	0.566 **	0.171 N.S.	4	2.752 N.S.
Time (T)	6	4.027 ***	103.967 ***	5	340.868 ***
T x V	12	0.740 ***	1.923 ***	10	63.878 ***
T x N	12	0.659 ***	0.269 **	10	11.617 ***
T x V x N	24	0.387 ***	0.072 N.S.	20	3.528 N.S.
Error	141	0.153	0.093	159	2.165

APPENDIX XI

Analyses of variance of chlorophyll concentration

(1) on leaf area basis (mg/dm^2), and

(2) on leaf dry weight basis (mg/gm).

Source	d.f.	M.S.(1)	M.S.(2)
Blocks	3	1.059 N.S.	21.161 ***
Var. (V)	2	30.976 ***	258.369 ***
N-levels(N)	2	0.170 N.S.	56.520 ***
V x N	4	0.413 N.S.	14.295 **
Time (T)	2	0.496 N.S.	6.879 N.S.
T x V	4	0.356 N.S.	2.978 N.S.
T x N	4	0.467 N.S.	1.285 N.S.
T x V x N	8	0.392 N.S.	0.528 N.S.
Error	78	0.627	2.646

APPENDIX XII

Analyses of variance for photosynthetic rates expressed in terms of (1) leaf dry weight ($\mu l O_2$/hr/mg dry weight) and (2) leaf area ($\mu l O_2$/min/cm^2).

Source	d.f.	M.S.(1)	M.S.(2)
Blocks	3	12.903 N.S.	0.103 *
Var. (V)	2	5.864 N.S.	0.192 **
N-levels (N)	1	3.647 N.S.	0.011 N.S.
V x N	2	50.206 N.S.	0.153 *
Error (a)	15	34.707	0.027
Time (T)	2	128.488 ***	0.663 ***
Light intensities (L)	2	1573.216 ***	3.400 ***
T x L	4	64.857 ***	0.257 ***
T x V	4	72.867 ***	0.046 ***
T x N	2	198.734 ***	0.070 ***
T x V x N	4	12.391 ***	0.042 ***
L x V	4	5.870 N.S.	0.003 N.S.
L x N	2	2.536 N.S.	0.014 N.S.
L x V x N	4	1.421 N.S.	0.003 N.S.
T x L x V	8	11.061 *	0.016 *
T x L x N	4	3.678 N.S.	0.007 N.S.
T x L x V x N	8	2.591 N.S.	0.004 N.S.
Error (b)	144	5.094	0.007

APPENDIX XIII

Analyses of variance on (1) photosynthetic rate per mg chlorophyll ($\mu l O_2$/min/mg chlorophyll); (2) chlorophyll concentration(mg/dm^2) and (3) leaf-thickness index (mg/cm^2).

Source	d.f.	M.S.(1)	Source	d.f.	M.S.(2)	M.S.(3)
Block	3	0.401 *	Block	3	0.249 N.S.	5.367 N.S.
Var. (V)	2	1.661 ***	Var (V)	2	10.492 ***	50.527 ***
N-levels(N)	1	2.561 ***	N-levels(N)	1	29.646 ***	102.463 ***
V x N	2	0.224 N.S.	V x N	2	3.056 ***	22.694 ***
Error (a)	15	0.097	Error (a)	15	0.124	2.241
Light intensities (L)	2	1.315 ***	Time (T)	1	4.008 ***	10.407 *
L x V	4	0.024 N.S.	T x V	2	0.564 *	5.161 N.S.
L x N	2	0.078 N.S.	T x N	1	1.977 ***	17.292 **
L x V x N	4	0.058 N.S.	T x V x N	2	0.054 N.S.	12.590 **
Error (b)	36	0.027	Error	18	0.100	1.647

APPENDIX XIV

Analyses of variance of :

(1) specific leaf weight;

(2) respiration rate of leaflets ($\mu l O_2$/hr/mg dry weight) and

(3) respiration rate of roots ($\mu l O_2$/hr/mg dry weight).

Source	d.f.	M.S.(1)	d.f.	M.S.(2)	M.S.(3)
Blocks	3	0.421 N.S.	3	1.370 N.S.	1.531 N.S.
Var. (V)	2	0.886 *	2	2.417 *	0.528 N.S.
N-levels (N)	1	0.181 N.S.	1	2.815 *	4.171 *
V x N	2	0.402 N.S.	2	0.145 N.S.	1.751 N.S.
Error (a)	15	0.167	15	0.495	0.679
Time (T)	2	3.539 ***	1	35.521 ***	
T x V	4	0.280 *	2	0.630 **	
T x N	2	0.623 **	1	0.470 *	
T x V x N	4	0.081 N.S.	2	0.651 **	
Error (b)	36	0.083	18	0.104	

APPENDIX XV

Analyses of variance of :

(1) chlorophyll concentration (mg/dm^2)

(2) chlorophyll concentration (mg/gm dry weight) and

(3) chlorophylls a/b ratio (on leaf area basis).

Source	d.f.	M.S.(1)	M.S.(2)	M.S.(3)
Blocks	3	0.184 N.S.	4.522 N.S.	0.033 N.S.
Var. (V)	2	3.617 ***	21.111 N.S.	0.017 N.S.
N-levels (N)	1	13.600 ***	323.841 ***	0.057 *
V x N	2	1.662 **	24.366 N.S.	0.040 N.S.
Error	15	0.137	11.042	0.012

APPENDIX XVI

Analyses of variance of :

(1) mesophyll cell number/mg dry weight x 10^7;

(2) mesophyll cell number/cm^2 of leaf area x 10^7;

(3) stomatal length (μ) x 10 and

(4) stomatal density (number/mm^2 leaf area) x 10

Source	d.f.	M.S.(1)	M.S.(2)	M.S.(3)	M.S.(4)
Blocks	3	0.167 N.S.	0.036 N.S.	0.025 N.S.	3.513 N.S.
Var. (V)	2	56.370 ***	2.072 ***	0.055 N.S.	8.492 N.S.
N-levels (N)	1	21.152 ***	0.119 N.S.	0.474 *	1.145 N.S.
V x N	2	6.302 ***	0.482 *	0.013 N.S.	5.993 N.S.
Error	15	0.303	0.090	0.055	4.733

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