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PHYSIOLOGICAL AND BREEDING STUDIES USING TOMATO VARIETIES AND THEIR DERIVATIVES

A thesis presented in partial fulfilment of the requirements for the degree of

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SUMMARY.

This thesis describes the genetics and physiological consequences of a "notted 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 F₁ 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 F₃ families derived from the cross Potentate x Yellow seedling.

Yellow seedling was inferior to both Potentate and F₁ 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 F₁ 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 F₃ 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.
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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.

(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\textsubscript{2} - nv) seedling character is derived from a parent line 057VN\textsubscript{2}. The following initial sequence of crossings were made by Mr. Dong Yen, at Otara, Auckland:

\[
\text{C57VN}_2 \times \text{Potentate} \\
\text{F}_1 \times \text{V-548} \\
\text{Potentate }^* \text{F}_1 \times \text{L}_1 \\
\text{Crosses made by Mr. Doug Yen} \\
\text{Selection made by Mr. Giesen} \\
\text{L}_1 \times \text{L}_2
\]

The selection was carried on over some 5 generations by Mr. Giesen until 2 lines (L\textsubscript{1} and L\textsubscript{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\textsubscript{1} hybrid (middle).
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 F₁ generation while the latter used segregating generations.

Using F₁ 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 Current) 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 F₁ 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 F₁ 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 dominance 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 IAR. Therefore variations of RGR can be attributed either to changes in NAR or IAR or both.

The NAR of tomato plants is closely related to the daily radiation (Goodall 1945; Kleiwalla 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 Warding 1967).

Variations in photosynthetic "size" can be expressed, for example, in terms of leaf area ratio (IAR) 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 (Horton 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 Kleiwalla 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; Harada 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\textsubscript{4}-N fed tomato plants is lower than NO\textsubscript{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\textdegree C day and 25\textdegree 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\textsubscript{4}-N promoted vigorous growth in highbush and lowbush blueberries, low level of NO\textsubscript{3}-N could cause extremely poor growth in these plants (Cain 1951; Townsend 1966). Oertl (1963) attributed this difference to the absence of a biochemical system to utilize NO\textsubscript{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 \textit{Lycopersicon} species has been demonstrated by Breda 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 Wearing 1966) beans, dwarf maize and willows (Wearing 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/dm² 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 *Lepideza 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 (Nencakova 1966 cited by Avratovskova 1968; Anderson 1967) and sugar beet (Nevins and Loomis 1970), also decreases chlorophyll concentration, it is unlikely 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 (NH₄⁺ and NO₃⁻-N) forms applied have different effects on photosynthesis of tomato leaves. In comparison with NO₃⁻-N, NH₄⁺-N depresses the photosynthetic rate, reduces chlorophyll concentration and simultaneously causes morphological modifications of tomato leaves. (Puritch and Barker 1967; Marec-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°C 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 CO₂ 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).

<table>
<thead>
<tr>
<th>Surface</th>
<th>Upper epidermis</th>
<th>Lower epidermis</th>
</tr>
</thead>
<tbody>
<tr>
<td>The number minimum, mean and maximum/cm²</td>
<td>0 - 12 - 37</td>
<td>70 - 130 - 202</td>
</tr>
<tr>
<td>size in µm</td>
<td>27 x 20 (guard cell closed)</td>
<td>33 x 23 (guard cell closed)</td>
</tr>
<tr>
<td>length and breadth</td>
<td>10 x 5 (pore open)</td>
<td>13 x 6 (pore open)</td>
</tr>
</tbody>
</table>

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 photorespiration 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 C₄ 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 NO₃-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 NH₄⁺ on the respiratory chain. High NH₄⁺ 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 KNO₃-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 NH₄⁺ 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 NH₄⁺-treated tomato plants contained a higher level of amide, free NH₄⁺-N and free basic amino acids than NO₃⁻-treated plants. The content of malic acid in the NH₄⁺-plants was ten times lower than that in the NO₃⁻-plants (Margolis 1960; Harada et al. 1963). The detoxication of NH₄⁺ by tricarboxylic acid intermediates by assimilating NH₄⁺ into harmless nitrogenous 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 NH₄⁺-treated tomato plants to the toxic effect of high NH₄⁺ concentration, and to the abnormal metabolism of organic acids, Woolhouse and Hardwick (1966) believed that it was caused by the effect of NH₄⁺ 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 (mg/100 g, dry wt) has obtained the following results for tomato plants.

<table>
<thead>
<tr>
<th>N-source</th>
<th>Ca</th>
<th>Mg</th>
<th>K</th>
<th>Na</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO₃⁻</td>
<td>161</td>
<td>30</td>
<td>58</td>
<td>19</td>
<td>268</td>
</tr>
<tr>
<td>NH₄⁺</td>
<td>62</td>
<td>25</td>
<td>29</td>
<td>15</td>
<td>131</td>
</tr>
</tbody>
</table>

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 NH₄⁺. The interaction between NH₄⁺ 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 NH₄⁻ -N as compared with NO₃⁻ -N may be reduced if the NO₃⁻ - reduction is taking place in the root instead of in the leaf. Thus the site (leaf or root) where NO₃⁻ - 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 NH₄⁻ - nutrition (as compared to NO₃⁻ - nutrition) than tomato, Chenopodium album, Buckwheat and Mustard in dry matter leaf yields is probably because of this difference in the site of NO₃⁻ - reduction.

The pH value plays an important role in the utilization of NH₄⁺ -N. At optimum pH bean plant can effectively convert the absorbed NH₄⁺ to organic nitrogen compounds in the roots. Thus the movement of NH₄⁺ to shoot is restricted, and the detrimental effect of high NH₄⁺ concentration in the leaves is prevented or lessened. Sheet and co-workers (1959) reported that NH₄⁺ 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 paralleled 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 NH₄⁺ - 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 $3G : 1Y$ 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).