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**Some factors affecting the yield and quality of sweet
pepper (*Capsicum annuum* L.) cv. Domino**

A thesis presented in partial fulfilment of the requirements for the degree
of
Doctor of Philosophy in Plant Science (Horticulture)
at
Massey University

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1997

Abstract

A series of studies were undertaken to examine some of the factors which influence yield and quality in sweet pepper. In the first study the influence of soil moisture status (stress and control) and harvesting regime (Green, Green-Red and Red) on growth, yield and Blossom-End Rot (BER) incidence on sweet pepper (*Capsicum annuum* L.) cv. Domino was carried out alongside a second experiment which examined the effect of water stress on fruit growth, and dry matter production and partitioning of destructively harvested sweet pepper plants.

These studies revealed that water stress reduced fruit number, and fresh and dry weights, increased fruit dry matter and hastened fruit maturity, but the stage of harvesting had no effect on both vegetative and reproductive yields. Water stress and harvesting stage had also little effect on the incidence of BER. An analysis showed that water stressed plants had a slightly higher incidence of BER than control plants. Water stress reduced the Ca concentration of fruit and leaves (which had a higher Ca concentration than fruit).

Sweet pepper fruit were the major assimilate sinks 60 days after transplanting and as plants became generative, there was a steady decline in leaf dry weights. RGR and NAR progressively increased while SLA and LAR decreased with plant ontogeny. At the final harvest control plants had accumulated 58% of the dry matter accumulated in their fruit against 49% for the stressed plants.

Fruit Ca, Mg and K increased throughout fruit development although most of the Ca accumulated during the early fruit growth period. The concentration of all these elements declined during the rapid fruit growth period 2-4 weeks after anthesis. A gradient in accumulation of Ca, Mg and K in the fruit was found with the stem-end of the fruit having more nutrients than the blossom-end. Both waxing and KOH treatments had little effect in the accumulation of nutrients in the fruit. Treatment with KOH however, slightly increased the concentration and contents of the mineral nutrients studied.

Sweet pepper plants were grown under Nutrient Film Technique (NFT) system using a nutrient solution of EC 2 mS.cm⁻¹. Higher nutrient conductivity levels of 4, 6, 8 and 10 mS.cm⁻¹ were achieved by adding concentrated KCl solution to the basic nutrient, and a high Ca solution with an EC of 10 mS.cm⁻¹ was developed with a mixture of KCl and CaCl₂ at a ratio of 3:1 (w/w).

Higher nutrient conductivity induced higher BER incidence which was related to the suppression of Ca uptake and accumulation in the fruit. This was accompanied by an increase in the accumulation of Mg and particularly K. Extra Ca at higher EC level promoted the accumulation of Ca by the fruit and reduced the incidence of BER. The reduction in Ca uptake in the fruit at higher EC was more pronounced at the blossom

end of the fruit. Fractionation of Ca compounds revealed that high EC levels reduced the physiologically active acetic acid soluble Ca compound, particularly during the rapid fruit growth stage when BER was likely to appear. Higher solution conductivity further reduced the accumulation of Ca in the roots and leaves while increasing those of Mg and K.

Higher conductivity of the nutrient solution resulted in small sized fruit, reduced fruit dry weights, decreased vegetative yields in terms of lower leaf area, SLA, diversion of more assimilates to shoots than fruit, decreased water consumption, decreased leaf ψ , decreased fruit firmness, increased leaf stomatal resistance, fruit dry matter content, fruit respiration and ethylene production and advancing fruit colour change.

Enclosing sweet pepper fruit with hygroscopic materials such as CaCl_2 and NaCl reduced the RH around the fruit and promoted Ca accumulation by the fruit. Fruit enclosed in polyethylene bags without the hygroscopic materials however, had higher RH and this suppressed Ca accumulation by the fruit. The use of an air flow system to regulate the RH around the fruit had a similar effect.

High RH treatment particularly reduced the Ca concentration in the distal part of the fruit which resulted in more BER. This incidence was related to fruit Ca concentration and content as well as the ratio of Ca to Mg and K. Humidity however, had little effect on sweet pepper fruit growth and the accumulation of Mg and K.

Sweet pepper is considered to be a non climacteric fruit which is independent of ethylene for ripening. Characterization of the changes in $\text{P}^i\text{C}_2\text{H}_4$, P^iCO_2 , P^iO_2 as well as colour change in mature green fruit at 20°C showed that $\text{P}^i\text{C}_2\text{H}_4$ significantly increased in both attached and detached fruit coincident with colour change. Detached fruit showed a steady decline in P^iCO_2 while attached fruit showed an increase in P^iCO_2 during ripening with out the climacteric. It is speculated that the decline in P^iCO_2 and the lower magnitude of $\text{P}^i\text{C}_2\text{H}_4$ in detached fruit was a result of egress of these gases through the pedicel rather than apparent difference in ripening physiology of attached and detached fruit. It was also suggested that the lack of climacteric respiration in attached fruit could be due to the overlapping of a CO_2 dependent photosynthesis by the fruit which declines with fruit age and fruit respiration which obscured the rise in P^iCO_2 . The association between sweet pepper cv. Domino fruit ripening and the significant increase in $\text{P}^i\text{C}_2\text{H}_4$ may indicate that ethylene may be responsible for ripening of sweet pepper fruit.

The maturity of sweet pepper fruit cv Domino was studied to determine objective maturity indices which correlate with physiological maturity. The attributes evaluated were fruit fresh weight, diameter, length, volume, pericarp thickness, firmness. Changes in surface colour change, TSS, P^iCO_2 , $\text{P}^i\text{C}_2\text{H}_4$, fruit respiration as well as ethylene production.

Fruit size and weight increased slowly during the early growth period and increased rapidly towards maturity. From 8 weeks after anthesis (WAA) until the final harvest

there was no a significant change in fruit size although it increased until 9 WAA. Starting from 8 WAA the hue angle values started to decline accompanied by an increase in chroma. Fruit surface colour change also coincided with a significant increase in $P^iC_2H_4$ and a slight increase in P^iCO_2 , respiration and ethylene production. The change in hue angle values was found to be an effective maturity index due to its correlation with most of the attributes evaluated. This coupled with WAA, TSS and fruit firmness appeared to be good indicators of fruit maturity.

On the other hand, treatment of mature green sweet pepper fruit cv. Domino with $1000 \mu l.l^{-1}$ ethylene promoted ripening by advancing colour change, TSS and acidity of treated fruit as compared with control. The treatment also increased fruit respiration and P^iCO_2 . However, treatment of half ripe fruit of the same cv. had less marked effect than mature green fruit. Treating sweet pepper fruit of the cv Evidence with ethylene at different maturity stage however, had no effect on colour change.

Acknowledgements

First and foremost I wish to thank my chief supervisor Dr Mike Nichols for his patient and expert advice, close supervision, unfailing support and encouragement through out the study period. His support was invaluable both academically and financially.

I would like to record my gratitude to Professor Errol Hewett for giving me the chance to study at Massey University through his untiring effort in securing me financial assistance. I would also thank him for his keen interest in the progress of my study and for his valuable advice, encouragement and critical review of the manuscript. His contribution was very valuable to the structure and focus of the study. My heart felt thanks also go to Professor Nigel Banks to whom I am particularly indebted for his generous advice, assistance and enthusiasm in guiding me through the challenges of part of the research. The advice I received from Dr Keith Fisher was most helpful. Thus, I extend my sincere thanks to him.

Thanks also go to the management and staff of Plant Growth Unit who tirelessly helped me in the construction of the study materials and provided the extra materials when needed. I therefore, wish to convey my appreciation to Ray Johnston, Charles Forbes, Giles Russel, Lindsay Sylva, and Lesley Taylor.

I am grateful to Professor Ken Milne for his support and advice and for taking care of my family's welfare. Pamela Howell deserves special thanks for supporting my family and her kindness and cheerfulness is something to be remembered.

I gratefully acknowledge the technical help of Chris Rawlingson, Hugh Neilson, Jonathan Dixon, Sue Nicholson, Lorraine Davis and Matt Alexander in providing facilities and assistance. Thanks are also due to Lance Currie and Bob Toes of the Soil Science Department for their technical assistance in mineral analysis. I wish to

thank Associate Professor Steve Haslett and Dr Bruce Mackay for their valuable advice in statistical analysis and Dr Bruce Christie for his help in graphics. The Department secretaries and staff deserve special thanks for their continued support and encouragement. I also appreciate the friendship of the post graduate students of the Department.

I owe a debt of gratitude to the NZ government for providing me tuition fee scholarship, the Alemaya University of Agriculture for the leave of absence and financial support for my living allowance and Massey University for providing me grant-in-aid to finalize my study. The Department's financial contribution towards my study is gratefully acknowledged.

I am deeply indebted to my parents, brothers and sisters for their love and continued support during my pursuit of education over the years and to my in-laws for their love and support. My wife Geri deserves special credit for her involvement in the experimental phase of this study and for taking good care of our baby Brook. Her resilience, love and support has sustained me through this arduous task of doing a PhD.

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List of Abbreviations

BER	Blossom end rot
DM	Dry matter
AASP	Atomic absorption spectrophotometer
LAR	Leaf area ratio
NAR	Net assimilation rate
RGR	Relative growth rate
SLA	Specific leaf area
LWR	Leaf weight ratio
FWR	Fruit weight ratio
SWR	Stem weight ratio
RWR	Root weight ratio
HI	Harvest index
C	Cytoplasm
V	Vacuole
ER	Endoplasmic reticulum
CS	Casparian strip
ANOVA	Analysis of variance
a.i.	Active ingredient
kg	kilogram
g	gram
P	Probability
SE	Standard error
SEM	Standard error of means
t	time
Ln	natural logarithm
DAA	Days after anthesis
WAA	Weeks after anthesis
C ₂ H ₄	Ethylene
CO ₂	Carbon dioxide
O ₂	Oxygen
STD	Standard
TSS	Total soluble solids
P ⁱ C ₂ H ₄	Internal C ₂ H ₄ concentration
P ⁱ CO ₂	Internal CO ₂ concentration
mm	millimetre
cm	Centimetre
cc ³	Cubic centimetre
Pa	Pascal
kPa	Kilo pascal
Ca	Calcium
Mg	Magnesium
K	Potassium

°C	Degree celsius
EC	Electrical conductivity
pH	Measure of acidity or alkalinity of a solution
ψ	Leaf water potential
NFT	Nutrient film technique
RH	Relative humidity
VPD	Vapour pressure deficit
RCBD	Randomized complete block design
GLM	General linear model
SAS	Statistical analysis system
°	Degree angle
r	Partial correlation
R ²	Coefficient of determination
v/v	volume ratio
w/w	weight ratio
N.D.	no date given

Chapter 1 - General Introduction

Sweet pepper is a popular food crop due to a combination of colour, taste and heat (Howard *et al.*, 1994). In New Zealand it is grown as an annual summer cultivated crop in the field while protected cultivation is practised during the winter and early spring seasons. It is grown as a fresh market, processing and export crop (Burgmans *et al.*, 1986; Anon., 1991). Sweet pepper ranks second to tomato as a product in protected cultivation in New Zealand (Anon., 1992).

Very little research has been undertaken in the past on the growth and physiological responses of sweet pepper to water and osmotic stresses. One undesirable effects of water and osmotic stresses apart from yield reduction is, the incidence of blossom-end rot. Although the factors responsible for it's occurrence have been extensively studied on tomato no information is available on sweet pepper. Moreover, there is a dearth of information on the maturity and ripening behaviour of sweet pepper. Therefore, this thesis reports on the results of series of experiments undertaken on these issues.

Water stress affects a number of developmental processes and also influences the quality of the product. The sensitivity of plants to water stress also depends on the developmental stage of the plant (Wardlaw, 1990), and in sweet pepper was highest at early fruit setting stage (Katerji *et al.*, 1993).

Different aspects of plant growth are affected by water stress. Low leaf water potential is known to affect photosynthesis, regulation of stomata, respiration, cell expansion, cell wall synthesis and translocation (Kramer, 1983a). These changes result in reduction of growth and carbohydrate partitioning (Kramer, 1983a; Schulze, 1986a). When the growth of a major sink is sensitive to water stress, dry matter is preferentially partitioned to other parts which are strong sinks (Wardlaw, 1969) or tolerate a greater level of stress (Westgate and Boyer, 1985). The most common change in the partitioning of assimilate is the increase in root fraction of the total

biomass. According to Forney and Breen, (1985) water stress limited the growth of stem and leaves more than roots while reducing the total dry matter production by the plant (Steinberg *et al.*, 1990). On the other hand, water stress induces Ca deficiency in bulky storage organs such as fruit resulting in blossom-end rot in tomatoes and sweet pepper (O'Sullivan, 1979) as the transport of the mineral is dependent on the rate of transpiration (Mengel and Kirkby, 1987). The work on the effect of water stress on the growth, yield and incidence of Blossom End Rot (BER) is reported in chapter 3.

The dynamics of fruit growth and mineral nutrient accumulation is studied in many fruits and extensive literature is available on this subject. Information on when a particular element is limiting growth is essential in order to design appropriate measures to control physiological disorders such as BER. The majority of the reports refer to accumulation of mineral nutrients during development of different fruit (Halbrooks and Wilcox, 1980; Clark and Smith, 1988; Buwalda and Meekings, 1990). Some reports also are available on specific elements (Ferguson, 1980; Engelker *et al.*, 1990). There is however, very little information available on sweet pepper. The only relevant report is that of Miller *et al.*, (1979) who used field grown plants for their study. However, it is not clear whether results from the study are applicable to greenhouse sweet peppers as field and greenhouse grown plants are subjected to different environmental conditions and different cultivars respond differently (Engelker *et al.*, 1990). Therefore, this problem was assessed and reported in chapter 4.

Osmotic stress has been reported as the factor which reduces the uptake of water and mineral nutrients thereby affecting growth (Ho *et al.*, 1993). A high salt concentration restricts absorption of water by the plant due to an increase in osmotic potential of the growing medium and to toxic effects of high ionic concentration (Hale and Orcutt, 1987; Sanchez and Silvertooth, 1996). It also reduces photosynthesis and

transpiration due to reduced stomatal conductance (Longuenesse and Leonardi, 1994). Moreover, the restriction of calcium uptake under osmotic stress predisposes fruits to Ca deficiency disorders such as BER. This is because salinity affects Ca uptake by the root (Sanchez and Silvertooth, 1996) and its translocation through the xylem conduit. Salinity also affects the development of xylem vessels (Belda and Ho, 1993) which restricts the movement of Ca towards the distal part of the fruit where the incidence is manifested. However, little work has been reported about the effect of osmotic stress on sweet pepper particularly in relation to BER. The influence of this factor on sweet pepper fruit biomass and economic yield as well as quality is reported in chapter 5.

Humidity affects plant growth and nutrient accumulation by the plant particularly calcium (Adams, 1991a). Its effect is in either promoting or suppressing transpiration depending on the levels of humidity. High humidity was reported to reduced the leaf area (Bakker, 1990) and Ca content of leaves (Holder and Cockshull, 1990) and fruit (Baneulos *et al.*, 1985; Cline and Hanson, 1992). On the other hand, other reports indicate that high humidity promotes the accumulation of Ca by tomato fruit (Adams and Holder, 1992; Ho *et al.*, 1993) while Bakker (1990) observed no effects of humidity on tomato fruit Ca accumulation. The use of relative humidity in enhancing the uptake and accumulation of calcium in sweet pepper fruit was investigated in chapter 6.

Precise maturity at harvest is essential in order to ensure optimum eating quality and storage ability of the product. Harvesting fruits without a good knowledge of their maturity can result in harvesting of immature and inferior quality products. This will in turn affect consumer confidence in the product and will also be a financial loss to the producer. Hence, the development of maturity indices which are objective, simple and reliable and which correlate well with eating quality are very important (Knee *et al.*, 1989). Showalter and Shaw (1979) reported that inconsistent quality because

of lack of uniformity of products is one of the factors which limit the sale of sweet pepper. To date, no objective maturity indices have been developed for sweet pepper fruit and very few reports are available on the ripening behaviour of sweet pepper (Saltveit, 1977; Pretel *et al.*, 1995). Chapter 7 and 8 report the maturity and ripening behaviour of sweet pepper fruit cv Domino. Possible maturity indices for determining maturity of the product are also presented.

Finally the implication of the findings from the different experiments are given in the general discussion in chapter 9. This chapter also indicates future research directions.

Chapter 2 - Literature Review

2.1. Introduction

Capsicum is the most widely cultivated species of vegetable crops in the world, both commercially and in home gardens. It is the principal species grown in Hungary, India, Mexico, China, Korea and the East Indies (Dewitt and Bosland, 1993).

The distinction between hot (chilli) pepper and sweet (bell) pepper used to be in their pungency which results from their capsaicinoid content (Iwai *et al.*, 1977; Huffman *et al.*, 1978). Recently however, this attribute is being incorporated into both hot and sweet pepper species through breeding (Dewitt and Bosland, 1993).

Sweet pepper is an increasingly important vegetable crop in terms of production and consumption in the USA (Peirce, 1987). It is the most highly valued winter fresh vegetable after tomato (USDA, 1996).

Both sweet pepper and hot pepper are field grown in the warmer districts of New Zealand as fresh market and process crops (Dept. of Statistics, 1984; Burgmans *et al.*, 1986). In recent years, sweet pepper has become one of the principal crops in protected cultivation second to tomato in New Zealand (Anon., 1992). Green or red ripe sweet peppers are produced both for fresh, processing and export (Anon., 1991).

A consumer survey (Anon., 1993) showed that the popularity of sweet pepper is increasing in New Zealand and currently it ranks 15th out of 30 popular vegetables. Due to the tendency for a change in eating habits of New Zealanders looking for hot and spicy exotic foods, it is expected that the ranking may change in the future. Current world fresh pepper production is shown in Table 2.1.

One of the many factors affecting market quality of fruit and vegetables in general,

and tomatoes and sweet pepper in particular is the presence of cosmetic blemishes. These blemishes may be of pathological or physiological causes. Blossom-end rot is of considerable importance in both tomato and pepper production and thus, it is essential to understand the cause of the problem in order to improve cultural practises to alleviate the problem and improve fruit quality.

In addition, a knowledge of the growth, maturity and ripening behaviour of the fruit assists in making appropriate postharvest handling decisions.

Table 2.1. Capsicum Production in 1993, Source: FAO Year Book, 1993.

	Area under production, 1000 ha	Production, 1000 MT	Yield, Kg.ha ⁻¹
World	1224	10630	8684
North & Central America	111	1118	10054
South America	27	250	9159
Asia	735	5287	7196
Europe	118	2057	17464
Africa	219	1821	8328
Oceania	1	22	15233
New Zealand		1F*	11000

*F = FAO estimate

This review, highlights the nature of the sweet pepper plant and its developmental physiology including fruit growth, maturity and ripening. Blossom-end rot, its causes importance and possible control measures are also discussed.

2.2. Botany, origin, and classification

The pepper plant belongs to the family Solanaceae which also includes tomato, egg plant, potato and tobacco (Tindall, 1983). The genus *Capsicum* was derived from a Greek word 'καρπας' meaning 'to bite' (Dewitt and Bosland, 1993). This genus includes all the peppers which vary widely in size shape flavour and sensory heat (Mathews *et.al.*, 1975). It ranges from the very hot Habanero and cayennes to mild bell pepper (Huffman *et al.*, 1978; Dewitt and Bosland, 1993).

Peppers are perennial sub shrubs native to South America that are grown as annuals in the temperate climates (Heiser, 1976; Tindall, 1983). The plant consists of pinnately vined leaves attached to a major axial system (Morrison *et al.*, 1986). According to Dewitt and Bosland (1993) the number of species identified in the genus *Capsicum* were as many as 28. To date however, only 5 distinct domesticated species have been identified, these are: *C.annuum*; *C.frutescens*; *C.pubescens*; *C.pendulum* (*baccatum*) and *C.chinense*. There are still 22 undomesticated species of pepper in South America (Eshbaugh, 1983). Amongst the domesticated species *Capsicum annum* is the most widely cultivated and includes the varieties, New Mexican, Jalapeno, Wax and Bell pepper (Dewitt and Bosland, 1993).

2.3. The food value and uses of *Capsicum*

The nutritional value of pepper is relatively high (Grubben, 1977) [Table 2.2]. In this respect, peppers are good sources of vitamins mainly (C and A)(Mathews *et al.*, 1975; Andrews, 1984) [Table 2.3]. According to Simpson (1983) sweet pepper is one of the vegetables that has a high content of provitamin A due to the high concentration of β -carotene and β -cryptoxanthin.

Capsicum is used in the food industry as a colouring and flavouring agent in sauces, soups, processed meat, snacks, candies, soft drinks and alcoholic beverages either in

the ground form or as an oleoresin (concentrated extract) (Nagle *et al.*, 1979). It is also used in the preparation of chutneys and salads (Govindarajan *et al.*, 1986). In addition to their use as food or condiments, peppers are also used as medicine and have ornamental values (Heiser, 1976; Grubben, 1977).

Table 2.2. Average nutritive value of sweet and hot pepper, per 100 grams edible product.

	Sweet pepper	Hot pepper
Dry matter (%)	8.0	34.6
Energy (K Cal)	26.0	116.00
Protein (g)	1.3	6.30
Fibre (g)	1.4	15.0
Calcium (g)	12.0	86.0
Iron (mg)	0.9	3.6
Carotene (mg)	1.8	6.6
Thiamine (mg)	0.07	0.37
Riboflavin (mg)	0.08	0.51
Naiacin (mg)	0.80	2.50
Vitamin C (mg)	103.00	96.00
Average nutritive value (ANV)	6.61	27.92
ANV.100g ⁻¹ dry matter	82.60	80.70

After Grubben (1977)

Table 2.3. Comparison of sources of vitamin C and A in mg

	Vitamin A	Vitamin C
Pepper	94.0	310
Orange	37.0	146
Grape fruit	13.5	166
Lemon	39.0	10
Avocado	10.0	216

Source: From Andrews (1984)

2.4. The physiology of pepper plants

2.4.1. The ontogeny of pepper plants

The development of pepper plants may be divided in to two distinct phases: a juvenile vegetative phase and a generative phase where both fruits and shoots are produced (Nielsen and Veierskov, 1988).

Dorland and Went (1947) demonstrated that the pepper plant grows with a single stem until 9-11 leaves have been formed and this main stem terminates with flower. With the development of the first flower bud, the plant branches off at the apex into 2 or 3 shoots and each shoot develops two leaves before it terminates in flower and again branches at the apex (Dorland and Went, 1947; Rylski and Halevy, 1972; Clapham and Marsh, 1987). Accordingly, the growth of the pepper plant assumes a dichotomous branching habit (Dorland and Went, 1947; Rylski and Halevy; 1972; Steer and Pearson, 1976; Nielsen and Veierskov, 1988).

Deli and Tiessen, (1969) indicated that pepper flowers are produced singly in the axil

of the branch. According to Rylski and Halevy, (1972) variation in time of flowering in the plant parts of pepper is because a juvenility factor is associated with the lower buds. Accordingly, lateral buds have to produce more leaves before flowering than terminal ones.

Hall (1977) found that fruits inhibited growth of flower bud, stem and roots. However, when growth rate of developing fruits approached zero, stem, root and flower bud growth resumed and increased sharply (Clapham and Marsh, 1987).

2.4.2. Flowering of sweet pepper

Morrison *et al.*, (1986) reported that the perfect flowers of pepper appear rather early in development and are composed of a short, thick calyx that covers a corolla consisting of 5-7 petals. The perianth enclosed the pistil that is surrounded by 5-7 stamens and the corolla enlarges resulting in a ballooning effect. A cross section of a pepper flower is shown in Fig [2.1].

2.4.2.1. The influence of temperature on the flowering of sweet pepper

Temperature is one of the important environmental factors influencing plant growth, development and yield. Sweet pepper is sensitive to temperature extremes and may be one of the most responsive to temperature management.

The optimum temperature for vegetative growth is reported to be 21-23°C (Bakker and Ufflen, 1988) but the highest rate of photosynthesis is achieved between 24 and 29°C (Nilwick, 1980; Bhatt and Rao, 1989).

Optimum dry matter production (a function of temperature) can be offset by other yield attributes resulting in decreased yields. Thus, the effects of temperature on flowering (Rylski, 1972); fruit set (Rylski and Spigelman, 1982) and fruit shape (Rylski, 1973) account for variation in final yields.

It is generally believed that high temperature promotes production of flowers (Rylski, 1972; Bakker, 1989b). Vander-Werken and Wilcox-Lee, (1988) reported that mulching increased soil temperature and hastened flowering. On the other hand, more flowering implies that there will be a high assimilate demand (Walker and Ho, 1977). Under low light conditions, this may lead to high rates of abortion of newly formed fruits (Schapendonk and Brouwer, 1984).

Bakker (1989b) reported that there was a significant reduction of the total number of flowers with a large day-night temperature amplitude probably because of a high rate of flower abortion at high day/low night temperature conditions (Rylski, 1973). Low mean temperature on the other hand, delays flowering (Deli and Tiessen, 1969; Bakker, 1989b) and can result in the production of abnormal pollen (Polowick and Sawhney, 1985).

2.4.2.2. Flowering versus light intensity and photoperiod

According to Deli and Tiessen, (1969) sweet pepper plants exposed to low night temperature of 12°C and low light intensity (800 f.c.) increased flower number as a result of increased branching compared with plants subjected to high night temperature. However, a combination of high light intensity (1600 f.c.) and a temperature of 18°C advanced flowering. Low light intensity on the other hand, inhibited flowering or led to flower abscission (Wein and Zhang, 1991 ; Kristof and El-Bahadli, 1988). This was in agreement with the reports of Wein et al., (1989) who found that imposing 80% shade for 6 days increased abscission of the reproductive parts by 38% and resulted in an increase in bud ethylene production.

Cochran (1942) and Studencova (1964) investigated the effects of day length on plant development and indicated that pepper plants reach flowering in the shortest time under 12-h photoperiod. Similar results were also reported by Artygina (1967). On the other hand, Kristof and El-Bahadli (1988) indicated that 16 h day length gave the best result than either short (8-12 h) or continuous illumination (24 h). Mathe and El-Bahadli (1990) reported that the sweet pepper variety 'Soroksarihajtato' flowered under varied day light of 8, 12, 16, and 24-h indicating the day neutral nature of the plants.

2.4.2.3. Mineral nutrition and flowering

Flower production and the percentage of fruit set increased in sweet pepper at higher N levels (Cochran, 1932). Ozaki and Hamilton (1956) have shown that yields of pepper increased with added N which was related to increased fruit set. Maynard *et al.*, (1962) also pointed out that the increase in the number of flowers and fruit setting in pepper was associated with increased nitrogen levels from 100 ppm to 400 ppm. Similar results were also reported by Batal and Smittle (1981).

Deficiency of N and P caused a delay of flower initiation in pepper requiring twice as many days after sowing as in the plots supplied with both N and P. In addition, when nutrients were deficient flower buds were differentiated at higher nodes (Eguchi *et al.*, 1958).

2.4.2.4. Flowering versus carbohydrate supply

Sachs and Hackett (1969) formulated the hypothesis that carbohydrate levels are important in the switch from vegetative to reproductive development. According to their nutrient diversion hypothesis the amount of assimilate available to the apex during the sensitive phase has to reach a certain minimum before flower initiation can take place (Sachs, 1987). Davenport (1990) also reported a correlation between carbohydrate in leaves and flower formation in citrus. Girdling stimulated flowering due to accumulation of carbohydrate supporting this view (Iwahori *et al.*, 1990).

Bernier *et al.*, (1981) stated that control of flowering by chemical or environmental factors may be mediated through assimilate supply to the shoot apex or competing sinks.

2.4.3. Fruiting of sweet pepper

2.4.3.1. The effect of temperature on fruit set and development of pepper

Temperature has a large influence on fruit set and development. Rylski and Spigelman (1982) obtained highest fruit set at a night temperature of 15°C while a night temperature of 24°C caused considerable blossom drop. Low temperature however resulted in seedless (parthenocarpic) fruit (Rylski and Aloni, 1990). Unlike fruit set, fruit development, was most rapid at high temperatures (Rylski and Spigelman, 1982; Polowick and Sawhney, 1985; Bakker, 1989b).

Polowick and Sawhney (1985) found that, fruits produced at a low temperature regime of 18°C day/15°C night had the least weight and size compared with high temperature regime of 28°C day/ 23°C night and intermediate temperature regime of 23°C day/ 18°C night. Low temperature grown fruits were parthenocarpic due to abnormal pollen (Ufflen and Bakker, 1989) and deformed (Rylski and Spigelman, 1982; Ufflen and Bakker, 1989). Thus, it is believed that pollination and fruit set could be improved by continuous daily temperatures above 30°C, or temperature extremes of 40-50°C of a very short duration (Gerber *et al.*, 1988).

Available evidences suggest that fruit set requires low night temperature (Rylski and Spigelman, 1982) while fruit growth and development is disturbed by low temperatures because of low seed set due to pollen infertility or deformation of ovary (Rylski and Spigelman, 1982; Polowick and Sawhney, 1985 ; Bakker, 1989b).

2.4.3.2. Light intensity versus fruit set and plant development

Under relatively low light intensity conditions, supplementary lighting increases plant growth and yield of pepper by increasing fruit set (Deli and Tiessen, 1969; Bedding, 1971; Nilwick, 1981). Low light intensity (80% shade) for 6 days increased

abscission of flower buds due to high production of ethylene in the buds (Wein *et al.*, 1989a).

Under light intensities in excess of $600 \text{ cal.cm}^{-2}.\text{day}^{-1}$, shading is of paramount importance in pepper production to reduce sun scald damage of fruits (Rylski and Spigelman, 1986a). Under high light intensity conditions, shading at an early stage of plant development increases cell division, leaf volume and over all plant dry matter by positively affecting fruit growth and yield (Schoch, 1972).

Rylski and Spigelman, (1986a and 1986b) demonstrated that when light intensity was reduced, plant height, number of nodes and leaf size increased. Increase in plant height occurred because both internode elongation and node number increase (Rylski and Spigelman, 1986 a and b). The highest total yield was harvested when using 12% and 26% shading (Rylski and Spigelman, 1986a). Therefore, in tropical regions with high light intensities, partial shading of pepper plants during vegetative growth period may have an advantage.

2.4.4. Assimilate partitioning

Assimilate partitioning may contribute to crop productivity by a) increasing total biomass production and b) favouring assimilate transfer to the harvestable portion of the crop (Patrick, 1988). Physiological analyses have demonstrated that shifts in the pattern of assimilate partitioning in favour of storage organ largely account for increased yield of a range of crop species (Gifford *et al.*, 1984).

Wareing and Patrick (1975) suggested that biomass gain by the harvest organ (sink) is either limited by assimilate supply (source limited) or saturated by assimilate supply (sink limited). Assimilate supply to the floral organs depends on the extent of competition with vegetative (Russel and Morris, 1982) and established fruit sinks (Monselis and GoldSchmidt, 1982). In fleshy fruits, flower initiation is the most critical stage of development, as it is the period of most intense cell division in the

yield tissue (Coombe, 1976). Following anthesis, the potential for cell expansion could limit solute accumulation (Coombe, 1976) in case the excess photosynthates are partitioned to alternate sinks (Chalmers *et al.*, 1975; Starck, 1983).

Warren (1972) and Wareing and Patrick (1975) have indicated that the translocation of dry matter between sources and sinks is governed by the balance between the net assimilation and the gain or loss of material through photosynthesis and respiration.

Nielsen and Veierskov, (1988) reported that increased sink load (greater number of fruits.plant⁻¹) changed the distribution of dry matter between the vegetative parts. Thus, less dry matter were directed to the stem and more to the leaves, but, root dry matter percentage was unaffected by fruit load (Nielsen and Veierskov, 1988). This is contrary to the earlier assumption (Brouwer, 1962; Hall, 1977) that the root system, has a low priority in the partitioning of assimilates.

On the other hand, as plants entered the generative phase a steady decrease in root dry matter percentage was noted and can be overcome by restriction of branching (Nielsen and Veierskov, 1988). These results are in agreement with the findings of Guo *et al.*, (1990).

In a similar study, Bhatt and Rao, (1989) observed that deblossomed plants had more assimilate accumulated in their leaves initially and stem in the later stage of growth, while in fruiting plants the maximum dry matter was accumulated in fruits. Since fruits are the main sink of assimilates, the vegetative growth of the plants will significantly be reduced by the presence of fruits, and in terms of dry matter accumulation of the whole plant, fruits accounted for seventy to eighty percent (Hall, 1977).

2.5. Physiological effects of water stress

Most horticultural crops suffer reduction in vegetative growth and reproductive

development when grown in saline medium or water stress conditions (Bernstein, 1975; Dekoning and Hurd, 1983). Known effects on reproductive development include a reduction in yield of sweet pepper (Lunin *et al.*, 1963; O'Sullivan, 1979; Waterer and Coltman, 1989; Alvino *et al.*, 1990a) reduction in fresh weight to dry weight ratio (Walker *et al.*, 1980) and a decrease in fruit size (Lunin *et al.*, 1963; Fernandez *et al.*, 1977; O'Sullivan, 1979; Walker *et al.*, 1980; Alvino *et al.*, 1990a). Salinity advances ripening of sweet pepper fruits (Walker *et al.*, 1980) as well as intensifying fruit colour (Fernandez *et al.*, 1977; Walker *et al.*, 1980). Most of these studies however, were conducted on field grown sweet pepper plants dealing with yield, while very few reports are available on the physiological responses of water stress on greenhouse grown sweet pepper plants.

Boyer (1976) and Ben-Yehoshua *et al.*, (1983) reported that water stress induces responses in living tissues that are similar to aging. These responses include a decrease in photosynthesis (Boyer, 1976) and respiration (Littman, 1972) an increase in solute leakage (Leopold *et al.*, 1981; Ben-Yehoshua *et al.*, 1983) as well as hastening ripening (Adato and Gazit, 1974; Walker *et al.*, 1980) and senescent yellowing of leaves (Littman, 1972) and an increase in ethylene production in leaves (McMichael *et al.*, 1972) and fruit (Ben-Yehoshua, *et al.*, 1983).

2.5.1. Water deficit and growth processes

Growth is a result of an increase in size resulting from cell division, differentiation and enlargement (Kozlowski *et al.*, 1991). Water is essential to maintain cell turgor which is needed for cell enlargement and thereby growth (Boyer, 1985).

Turgor pressure is crucial in cell expansion, supplying the necessary push or pressure from inside (Lockhart, 1965; Cleland, 1971). Hence, any restriction of growth by water stress must be considered in terms of turgor reduction (Kramer, 1959; Vaadia *et al.*, 1961). A reduction in cell size was correlated with reduction in water potential of the medium in which growing tissue is immersed (Henckel, 1964; Dolley and

Leyton, 1968; Kirkham *et al.*, 1972).

Kramer (1983b) indicated that cell enlargement is more sensitive to water stress than cell division. Kozlowski *et al.*, (1991) stated that the size of a cell affects cell division as cells do not divide prior to attaining a certain size (Hsiao, 1973). Gardner and Nieman (1964) concluded that unlike the situation in primordial initiation where complete suspension occurs, cell division may continue during stress, though at much reduced rate, until quite severe conditions exist. When stress is removed there is an opportunity for rapid resumption of expansion growth (Slatyer, 1969). On the other hand, cell enlargement, the other essential component of growth is affected at very slight stress levels (Slatyer, 1969; Van Volkenburgh and Boyer, 1985). Hence, water stress through its effect on cell turgor may affect cell division and cell enlargement equally.

Pepper plants respond favourably to supplementary irrigation during periods of water stress (O'Sullivan, 1979; Batal and Smittle, 1981). Water stress results in abscission of flowers and small fruits in pepper (Rhee and Park, 1977; Tindall, 1983; Lurie *et al.*, 1986) due to the production of the hormone ethylene (Beaundry and Kays, 1988; Tripp and Wein, 1989).

DeKoning and Hurd (1983) have found that tomato plants exposed to restricted water supply had smaller and fewer leaves on thinner stems than control plants. Similarly, Watts *et al.*, (1981) and Alvino *et al.*, (1990a) demonstrated that water stress delayed reproductive development of pepper as well as reducing bud, flower and fruit number (Watts *et al.*, 1981). Katerji *et al.*, (1993) indicated that pepper plants were more sensitive to water stress applied at early fruit set than at flowering or fruit formation stages.

A progressive reduction in the rate of root elongation as water stress is imposed was reported by Salim *et al.*, (1965) and Newman (1966). However, the response of the stress imposed on root development was not as severe as that of shoot growth. Watts *et al.*, (1981) and Aloni *et al.*, (1991) found that water stress increased the root/shoot

dry weight ratio. This may be due to a reduction in the growth of shoot relative to root (Watts *et al.*, 1981, Munns and Termaat, 1986) or may also result from a stress stimulated increase in the growth of root (Sharp and Davies, 1979).

2.5.2. Water stress, photosynthesis and dry matter partitioning

Net photosynthesis is progressively reduced by water stress and negative values may develop when stress is severe (El-Sharkawy and Hesketh 1964; Alvino *et al.*, 1990a). This response is probably mediated partly by a direct effect of dehydration on the photosynthetic system (Slatyer, 1969).

Reduction in leaf water content results in reduced photosynthetic ability of many plants (Baker, 1993). This may be attributed to lower CO₂ availability due to stomata closure (Kaiser, 1987). Photosynthesis has been shown to be sensitive to changes in osmotic pressure and cell volume (Kaiser *et al.*, 1981; Kaiser, 1982; Schulze, 1986b). The reason for the reduction of photosynthesis by osmotic stress may be due to stomatal acidification (Berkowitz and Gibbs, 1983) or reduction of RUBP content of the cell (Gimenez *et al.*, 1992). This is in agreement with earlier reports of Seeman and Sharkey (1986) who found that salinity reduces RUBP pool size by reducing its regeneration capacity.

Osmoregulation (a net increase in cell's solute) contributes to drought tolerance of crop species (Morgan, 1984) and in part may depend on responses of membrane transport of solutes to alterations in cellular water relations. For instance, increases in sugar concentrations in photosynthetically active leaves subject to water stress may in part result from turgor induced stimulation of membrane transport of sugars into storage compartments of leaf mesophyll cells (Daie and Wyse, 1985). Maintenance of phloem turgor under water stress and solute loading in to the phloem is stimulated at lower cell turgor and hence, sustains assimilate export (Giaquinta, 1983).

Osmotic adjustment is possible by accumulation of organic solutes which could

otherwise have been used for the synthesis of other organic compounds (Munns, 1988; Binzel and Reuveni, 1994). This solute build up is said to be because the supply of photosynthate exceeds utilization (Van Volkenburgh and Boyer, 1985) as cell division and expansion slow down (Shalhevet and Hsiao, 1986).

Soil water deficit reduced dry matter accumulation, leaf area index, crop growth rate, net assimilation rate and relative growth rate of pepper plants (Alvino *et al.*, 1990a and b). These growth parameters were found to be higher under well watered treatments (Alvino *et al.*, 1990b).

Vegetative growth is affected by closure of stomates, leaf rolling and shifts in assimilate partitioning induced by water stress (McGiffen *et al.*, 1992). Accordingly, when soil water is abundant the bulk of the assimilated carbohydrate is partitioned to the shoots, but when water is limiting, roots receive more assimilate (Geddes *et al.*, 1979). This idea was supported by Aloni *et al.*, (1991) as water stress in pepper seedlings inhibited translocation of assimilates to young sink leaves more than translocation to the roots.

2.5.3. Salt stress, plant growth and productivity

The sensitivity of plants to salt stress can be expressed in a variety of ways such as leaf chlorosis, necrosis and abscission, reduced growth rate, and plant death. Physiological and biochemical responses include lowered leaf water potential, increased stomatal resistance, altered ion relations and slower net carbon assimilation rate (Poljakoff-Mayber and Gale, 1975).

Higher salt concentration in the substrate can depress plant growth either by osmotic effects (water stress), (Greenway, and Munns, 1980; Levitt, 1980), specific ion effects (ion imbalance), or toxic effects (excessive accumulation of an ion), (Lessani and Marschner, 1978; Levitt, 1980).

Salinity normally decreases photosynthesis with the exception of halophytes whose rates do not always decrease and may even be enhanced (Gale, 1975). The unavoidable uptake of specific ions by the plant and accumulation of these in the leaves is widely assumed to result in inhibition of photosynthesis (Seeman and Critchley, 1985). In addition, salinity can inhibit photosynthesis due to reduced stomatal conductance (Plaut *et al.*, 1990; Brugnoli and Lauteri, 1991; Bethke and Drew, 1992) or biochemical or photochemical activities within the chloroplast (Seeman and Sharkey, 1986; Piepenbrock and Schmitt, 1991).

Some beneficial effects of salinity have been reported. Salinity reduces the accumulation of water but not dry matter, thus, fresh weight of tomato fruits was reduced while the dry matter percentage increased (Ehert and Ho, 1986b). Increased salinity also improved the percentage dry matter, titratable acidity, sugar and K concentrations in tomato fruit (Cerdea *et al.*, 1979; Adams, 1990) and increased soluble solids concentration and lowered titratable acidity in apple (Ebel *et al.*, 1993). Salinity also improved fruit shape and firmness of tomato fruit (Graves and Hurd, 1983).

Sonneveld, (1979) classified sweet pepper as salt sensitive crop while, Bernstein and Pearson (1954) considered it as semi tolerant. Fernandez *et al.* (1977) showed that the salt tolerance ability of sweet pepper is varietal dependent.

Growth of pepper plants under higher osmotic stress levels resulted in leaf loss and decreased fruit yield (Lunin *et al.*, 1963; Sonneveld, 1979; Walker *et al.*, 1980; Moschrefi, 1990). A relatively low ionic concentrations resulted in increased biomass production and fruit percentage compared with a high ionic concentration (Moschrefi, 1990).

Hoffman *et al.*, (1980) observed that total water potential at dawn for young but not mature leaves of pepper was lower under saline condition than control plants. They reported that this may be the cause of reduced growth under saline conditions.

Salinity also decreases ascorbic acid content of fruits (Walker *et al.*, 1980) reduces fruit size (Lunin *et al.*, 1963; Fernandez *et al.*, 1977) and ultimately yield (Moschrefi, 1990). It also advances fruit ripening (Walker *et al.*, 1980) and intensifies the colour of ripe fruit (Fernandez *et al.*, 1977; Walker *et al.*, 1980).

2.5.4. The role of ABA in relation to water stress

Absciscic acid (ABA) which is synthesized in the root cap (Rivier *et al.*, 1977) is generally involved in plant regulatory processes (Addicott, 1983), particularly in drought stressed plants (Davies *et al.*, 1981; Watts *et al.*, 1981). ABA affects the flux of K⁺ ions in the guard cells which leads to stomata closure (Basiouny *et al.*, 1994).

The influence of drought stress on root and shoot growth may be mediated through endogenous changes of ABA concentration acting as a signal for control of growth processes (Davies *et al.*, 1986). Absciscic acid synthesis induced by water stress has been correlated with a reduction of shoot:root ratio either by reduction of shoot growth (Creelman *et al.*, 1990) or by a large root growth relative to shoot growth (Kramoker and Van Steveninck, 1979). In support of this idea Watts *et al.*, (1981) noted that ABA treatment increased the root/shoot ratio of pepper.

2.5.5. Stress ethylene production

Increased ethylene production is a general response of plant tissues to environmental stresses including water stress (Yang and Pratt, 1978; Naqvi, 1995). However, this surge in ethylene production declines rapidly within 24 hours or less after removal of stress (Tingey, 1980).

The synthesis of amino cyclopropane carboxylic acid (ACC) and consequently

ethylene, markedly increased in response to water stress in detached leaves of wheat (Apelbaum and Yang, 1981; Wright, 1990). However, moderately stressed intact plants of a number of species didn't show increased production of ethylene (Morgan *et al.*, 1990) although, apple fruits from plants subjected to regulated deficit irrigation (RDI) showed increased internal ethylene concentration while attached to the plant (Ebel *et al.*, 1993). Similar results were reported by Lacheene *et al.*, (1986) on tomato and El-Abd *et al.*, (1992) on peas. Salinity stress response in tomato were less severe when ethylene biosynthesis was inhibited, thus giving indirect evidence for the involvement of ethylene in response of plants to stress (Jones and El-Abd (1989).

2.6. Blossom-end Rot: A physiological disorder

Blossom-end rot is a wide spread physiological disorder that affects tomato and sweet pepper. The disorder is reported in virtually every tomato and pepper producing areas of the world and can cause serious lose of marketable fruit. Although the disorder is as important on sweet pepper as the tomato, very little work was done on sweet pepper. Thus, most of the reports on this review deal with tomato. Both crops belong to the same family solanaceae, however, they have different growth and fruiting habits which warrant study on sweet pepper to understand the causes of the incidence in this crop.

The disorder first becomes apparent as a green water soaked area under the fruit wall on the stylar end of the fruit. Initially small brown flecks may develop in the affected area and within a week a brownish coloured lesion attains its full size (Spurr, 1959). At fruit maturity the affected area of the fruit results in a blackened, dry sunken leathery spot (Westerhout, 1962). At the turn of this century the incidence was considered as a pathological disorder (Stout, 1934). This was because of the secondary infection by pathogens which appear due to weak cells following BER.

2.6.1. Causal agents of blossom-end rot

The problem of blossom-end rot on tomato and to some extent on sweet pepper has been recognized by researchers for several years. The major cause of the problem is Ca deficiency and poor Ca distribution between the proximal and distal parts of the fruit. Various factors are implicated in causing Ca deficiency in the fruit such as: unfavourable moisture, type and/or imbalance of nutrients and crop growth rate (Stout, 1934; Robbins, 1937; Raleigh and Chucka, 1944; Geraldson, 1956; Westerhout, 1962; Wilcox *et al.*, 1973; Sonneveld and Voogt, 1981; Adams and El-Gizawy, 1986; Brown and Ho, 1993).

2.6.1.1. Calcium deficiency and blossom-end rot

Blossom-end rot is associated with calcium deficiency (Geraldson, 1956; Spurr, 1959; Brown and Ho, 1993). This is especially true if the calcium deficiency occurs in the fruits (Wiersum, 1966).

Foliar symptom of Ca deficiency appears as yellowing of the young rapidly expanding leaves at the tips and this yellowing spreads around the margin of the leaflet in greenhouse grown tomato (Adams and Ho, 1985).

Calcium deficiency disorders often occur or develop most severely in the most distal regions of the affected organs. Accordingly, the distal placenta and locular tissues had the lowest Ca content in the whole fruit and these sites appear to be the sites of the earliest symptoms of BER (Adams and Ho, 1992). This is attributed to poor calcium distribution to these organs.

The difference in calcium distribution between different parts of the same organ presumably results either from inferior xylem development in susceptible regions (Belda and Ho, 1993) or from ineffective operation of the non-vascular transport pathway of calcium (Battey, 1990). Bangerth (1979) and Adams and Ho (1985) indicated

that the low calcium content in a particular plant organ is generally a result of restricted calcium distribution rather than insufficient Ca uptake by the plant.

Some suggest that Ca deficiency itself retards xylem differentiation. When tomato plants were grown at high salinity levels reduced xylem development was observed (Adams and Ho 1985).

Very little BER will occur if the calcium content of the fruit is in excess of about 0.08% (Wiersum, 1966; Ward, 1973) or even as low as 0.043% (Cerdeira et al., 1979). However, Sonneveld and Vanden-Ende (1975) did not observe calcium concentration in the fruits of tomato less than of 0.11% and yet a high incidence of the disorder was noted. It was suspected that Mg salts could as well be responsible for the incidence for it has resulted in more BER than other salts (Sonneveld and Vanden-Ende, 1975). This implies that in spite of the presence of adequate supply of calcium in the soil or fruit the disorder could still be manifested.

Calcium moves readily from roots to leaves. However, unlike other elements, it is very poorly redistributed from leaves to other plant parts (Guttridge and Bradfield, 1983). Thus, bulky storage tissues or young leaves are likely to be susceptible to localized Ca deficiency induced by poor mobility. Clover (1991) reported that short distance transport of Ca in the fruit is also very important and has indicated that this declines as distance from the pedicle increases making them susceptible to the disorder.

Translocation of calcium is through the xylem and it is not redistributed through the phloem (Barke and Menary, 1971; Mengel and Kirkby, 1987). Owing to the relative immobility of the element in plants (Poovaiah, 1985; Poovaiah and Leopold, 1976) once it reaches the leaves it is not recycled even under Ca stress situations (Hanger, 1979; Poovaiah, 1985). Therefore, a constant supply from the roots to the fruit via the xylem is necessary to avoid Ca deficiency disorders (Wiersum, 1966; Ho, 1989).

The mechanism of transport of calcium within the plant system is believed to be that, during day time it takes place through the transpiration stream (Van de Geijn and Smeulders, 1981; Guttridge and Bradfield, 1983; Ehret and Ho, 1986b) where it will be accumulated mainly in leaves (Clover, 1991) for they have higher transpiration rates than fruits. At night root pressure flow helps to transport Ca to poorly transpiring tissues such as fruit (Guttridge and Bradfield, 1983; Ho, 1989).

It is important to realize that there is little calcium movement out of the mature leaves. So, the Ca supply to new growth depends on water movement (Adams and Ho, 1985). This was further substantiated by the reports of Tachibana (1988). It is generally believed that transport of calcium into fruit mainly takes place at night (Van de Geijn and Smeulders, 1981). Lang and Volz (1993) showed that there is a considerable day-to-day variation in the amount of sap exchange between apple tree and fruit. Out flow of xylem sap generally occurs during day time and inflow at night. The inflow at night is said to be rich in Ca compared to the outflow from the fruit during day time (Lang and Volz, 1993).

Generally, calcium deficiency arises from several causes such as inadequate supply in the nutrient solution or the soil, poor root uptake or failure to transport enough to the fruit distal tissue (Clover, 1991; Ho and Adams, 1989a). Consequently, Ca deficiency results in decreased protoplasmic elasticity and decreased membrane permeability (Vangoor, 1968) which results in collapse of cells and incidence of BER.

2.6.1.2. The effect of unfavourable moisture status on the incidence of blossom-end rot

Unfavourable moisture relationships have been associated with blossom-end rot more often than any other factor (Geraldson, 1956; Shaykewich *et al.*, 1971; Dekock *et al.*, 1979; O'Sullivan, 1979; Pill and Lambeth, 1977; Adams and El-Gizawy, 1986).

Calcium moves mainly through xylem vessels (Clarkson, 1984). It moves apoplastically and appears not to be remobilized once it is fixed in the plant. Thus, Ca accumulates in tissues that transpire rapidly (Marschner, 1974). Low transpiring tissues like enclosed leaves and fruits receive Ca when the transpiration rate is low at night with the aid of root pressure flow (Ho, 1989). Root pressure flow only occurs when the growing medium is favourable for water uptake. Such conditions which inhibit root pressure development are: extended dry periods, excessive fertilization or saline condition (Collier, 1982), and flooding which suppresses O₂ availability for root growth (Tachibana, 1988).

Blossom-end rot can also occur by subjecting plants to water stress in the presence of adequate supplies of Ca (Gerard and Hipp, 1968; Ward, 1973). It is, however, considered that the role of moisture is secondary in that it only helps to facilitate the uptake and translocation of salts including calcium (Geraldson, 1956; Chiu and Bould, 1976).

Insufficient soil moisture or an excessive concentration of salts at the effective root zone can greatly increase the EC levels. Accordingly, water and ⁴⁵Ca uptake and translocation were substantially reduced by high salinity (EC of 17 mS) in tomato (Ehert and Ho, 1986a). Furthermore fruit weight and total Ca contents progressively declined as the salinity of the nutrient solution increased from 2 mS to 10 mS (Adams and Ho, 1985). On the other hand, little or no BER occurred when the EC was reduced to 1.5 mS while it increased with increasing salinity (Uffelen and Bakker, 1989). A still lower rate of EC viz. 0.9 mS was also recommended by Sonneveld and Voogt (1981) to avoid the incidence of BER. The fact that BER is more pronounced in concentrated solution than dilute solution signifies the importance of water in calcium transport.

Guttridge and Bradfield (1983) and Adams and Ho (1985) found humid air and low EC of the nutrient solution helps to maintain a higher root pressure at night. Accordingly, the lowest Ca content and the highest BER was found from plants grown in a too strong nutrient solution and in a dry night atmosphere (Guttridge and

Bradfield, 1983). Like wise, drip irrigation at night reduced the amount of BER compared with non-irrigated plants (Haghuis, 1990).

Since Ca translocation is facilitated by transpiration during day time (Guttridge and Bradfield, 1983), factors which reduce transpirational rate may cause the physiological disorder (Armstrong and Kirkby, 1979). For this reason, high relative humidity of 90% reduces the uptake of water and ^{45}Ca by plants to some extent but mainly affected distribution of ^{45}Ca to the apex (Ehert and Ho, 1986 a and b) possibly due to reduced transpiration rates (Torfs, 1969; Adams and Holder, 1992).

Flooding reduces root development (Sundstrom and Pezeshki, 1988) due to the inhibition of respiration. This problem is manifested in hydroponic culture especially at the later stage of growth due to increased root mass (Tachibana, 1988). Oxygen deficiency inhibits respiration of roots thereby reducing root pressure flow which in turn may reduce calcium transport to the fruits (Zholkevich, 1981; Tachibana, 1988). Thus, the incidence of BER was pronounced by withholding O_2 supply at night (Tachibana, 1988) due to low root pressure flow (Vielemeyer and Weissert, 1991).

Excessive soil moisture on the other hand, favours the accumulation of NH_4 salts and may cause severe Ca deficiency (Geraldson, 1956). BER increased with higher irrigation levels in tomato (Mohamed *et al.*, 1989) possibly due to translocation of more nitrogen to the fruit (Pill and Lambeth, 1977). It was shown that fruit affected with BER had high N contents (Shaykewich *et al.*, 1971; Mohamed *et al.*, 1989).

2.6.1.3. Influence of rate and type of nutrients on occurrence of Blossom-end Rot

Excessive soluble Mg, K, Na, N or NH_4 salts in the growing medium or a deficiency of soluble calcium salts cause a reduced Ca uptake and an increased prevalence and severity of BER (Geraldson, 1956; Miller, 1961; Hamilton and Ogle, 1962; Gerard and Hipp, 1968; Vangoor, 1968; Shaykewich *et al.*, 1971; Murray *et al.*, 1972; Pasture, 1972; Sonneveld and Vanden-Ende, 1975; Pill *et al.*, 1978; Ikeda and Osawa,

1988). This is because of the absorption of NH_4 and K at the partial exclusion of calcium (Guttridge and Bradfield, 1983; Zornoza *et al.*, 1988). However, Barker and Ready (1994) found no relationship between concentration of Ca, K and Mg in tomato fruit with incidence of BER.

High K/Ca and Mg/Ca ratios also appear to be associated with BER (Gerard and Hipp, 1968; Ehert and Ho, 1986b; Pill *et al.*, 1978). However, this relationship was not confirmed by the results of Shaykewich *et al.*, (1971) and Millikan *et al.*, (1972).

Marschner (1974) indicated that restricted mobility of Ca and difference in the proportion of soluble and insoluble forms of Ca in the plant makes Ca concentration an unreliable predictor of nutritional and physiological status.

The levels of soluble and bound Ca in the tissue may provide a more useful index of Ca status in the tissue (Adams and El-Gizawy, 1986). Himelrick and Walker (1982) suggested the ratio of $\text{Mg}+\text{K}/\text{Ca}$ or K/Ca to be a more accurate predictor of physiological disorders than Ca concentration alone.

High levels of N fertilizers induced BER (Raleigh and Chucka, 1944; Barke and Menary, 1971; Shaykewich *et al.*, 1971; O'Sullivan, 1979), and the N sources affected occurrence of the incidence of blossom-end rot. Thus, NH_4 - N increased incidence of BER (Maynard *et al.*, 1957; Barke and Menary, 1971, Wilcox *et al.*, 1973; Pill *et al.*, 1978; Dekock *et al.*, 1979; Pill and Lambeth, 1980; Ikeda and Osawa, 1988) more than NO_3 - N form.

NH_4 - N nutrition resulted in restricted uptake of metallic cations, especially Ca, reduced growth, caused root injury and increased root resistance to water uptake thereby decreasing leaf water potential (Raleigh and Chucka, 1944). It also reduced shoot growth, total and mean fruit weight, fruit number, leaf xylem pressure potential, leaf Ca, Mg and NO_3 concentration and normal fruit Ca, Mg, K, and NO_3 concentrations (Pill *et al.*, 1978). Besides, leaf diffusive resistance and leaf NH_4 and

incidence of BER were increased by NH_4 - N nutrition (Pill *et al.*, 1978). NH_4 nutrition also reduced uptake of K, Ca, and Mg (Zornoza *et al.*, 1988). Similarly, Barker and Ready (1994) also found that NH_4 suppressed Ca accumulation in tomato fruit.

Fruits fed with NH_4 - N contained large amounts of amino acids in their tissues and had relatively small amounts of organic acids (Dekock *et al.*, 1979). Hence, this led to a high K/Ca ratio increasing the incidence of BER (Dekock and Morrison, 1958). High K/Ca reduced Ca uptake more at high compared to low EC (Pill *et al.*, 1978; Ehert and Ho, 1986b; Kreij, 1989).

2.6.1.4. Crop growth rate versus the incidence of Blossom-end rot

Rapid growth of a crop was considered to be an accentuating factor for BER development (Torfs, 1969) because, it tends to increase calcium requirement/unit time (Chamberlain, 1933; Mack and Stout, 1934; Geraldson, 1956).

The disorder appears during dry periods before the plants have established a large root system (Vander-Werken and Wilcox-Lee, 1988). Therefore, early crops are most seriously affected (Bruin and Deiziel, 1989) and the amount of Ca imported during early stages of fruit development was important to avoid the occurrence of BER during the highest growth rate of the fruit (Wolterbeek *et al.*, 1987).

The incidence of BER was associated with vigorous vegetative growth (Evans and Troxler, 1953). Hence, the incidence was increased by application of gibberellic acid but reduced by growth retardants chloromequat chloride and daminozide (Castro and Malvavolta, 1978; Kheshem *et al.*, 1988).

Borkowski (1984) and Adams and Ho (1985) have reported that during rapid growth, Ca accumulation can be lower than the fruit growth. Consequently, the fruit's Ca content decreases making them susceptible to the disorder.

The parts of tissues most sensitive to Ca deficiency are those into which Ca moves least readily such as meristems and fruits (Chiu and Bould, 1976). They further indicated that the deficiency appears when plants are grown rapidly.

It is generally believed that any combination of factors that cause the plant's Ca requirement to exceed the supply be it of temporary nature or of longer duration can cause the disorder. Accordingly, truss pruning to encourage fruit growth favours the incidence of BER as it creates a situation where fruit will grow too quickly (Clover, 1991). This is because the fruit growth rate which needs more Ca for new cell formation doesn't match with that of Ca accumulation. It was also shown that concentration of % Ca in dry matter markedly declined between 11-22 days after flowering in tomato which appears to be the highest fruit growth phase (Adams and Ho, 1985). On the other hand, removal of inflorescence and high N-nutrition or excess water may favour vigorous vegetative growth thereby inducing the incidence of BER (Westerhout, 1962) because of high leaf transpiration and very little Ca going into the fruit.

The incidence of BER was more severe in young fruit (Guttridge and Bradfield, 1983; Tachibana, 1988; Haghuis, 1990). The incidence however decreases as the fruits mature (Westerhout, 1962; El-Gizawy and Adams, 1986). Varieties differ in their susceptibility to the disorder (Donald *et al.*, 1957; Westerhout, 1962; Dekock *et al.*, 1979; O'Sullivan, 1979; Guttridge and Bradfield, 1983; Adams and Ho, 1992). The genetic variation in susceptibility to BER may be attributed to difference in the uptake of Ca and its distribution (Gallaher, 1975) or the growth rate of the fruit or the whole plant (Adams and Ho, 1992).

Generally the most important factors affecting the uptake of calcium and incidence of BER seem to be those which influence long term fruit development and in particular functional xylem tissue development and membrane integrity (Ho *et al.*, 1993).

The availability of calcium plays a crucial role in incidence of physiological disorders

such as blossom-end rot. Hence, understanding the uptake and translocation of the nutrient aids in tackling the problem.

2.6.2. The mineral nutrient calcium

Calcium is known to be involved in many metabolic processes in plants. Because of its involvement in a wide range of cellular functions, Ca regulation has been the subject of several reviews in the recent years. Some of these reviews dealt with Ca and physiological disorders (Bangerth, 1979); Ca movement and transport (Hanson, 1983; Hepler and Wayne, 1985); molecular and cellular aspects of calcium (Poovaiah, 1988) and Ca signalling (Poovaiah and Reddy, 1993; Bush, 1995).

In plants, Ca regulates many cellular functions and physiological processes known to be affected by calcium (Table 2.4) including cell elongation, abscission, senescence and tuberization (Poovaiah and Reddy, 1987); ionic balance (Ward and Schroeder, 1994); gene expression (Broam, 1992; Wegner *et al.*, 1992); carbohydrate metabolism (Brauer *et al.*, 1990). Table [2.4] shows the list of physiological processes known to be affected by calcium.

Apart from the well recognized functions of calcium, new dimensions are being added to its versatility. These features are outlined as:

- 1) maintenance of extremely low concentration of free Ca^{2+} in the cell cytosol (Ferguson and Drobak, 1988; Poovaiah, 1988)
- 2) regulation of cytoplasmic Ca^{2+} concentration by various extra or intra-cellular signals such as light (Roux *et al.*, 1986; Serrano *et al.*, 1988), gravity (Roux and Serlin, 1987; Gehering *et al.*, 1990) and hormones such as auxin (Felle, 1988) GA_3 (Bush, 1992; Gilroy and Jones, 1993), ABA (Gehering *et al.*, 1990) and cytokinin (Saunders and Hepler, 1981)

Table 2.4. Calcium regulated physiological processes in plants

Physiological processes affected by calcium	Ref.
Plant growth hormone action	32, 34, 34a
Auxin-induced elongation	35, 36
Auxin binding	36a
Auxin transport	37
Auxin-mediated H ⁺ secretion	38
Cytokinin-induced bud formation	39
Abscission	40—40b
Senescence and ripening	41, 41a
Cotyledon enlargement	33
Secretory processes	
Cell wall material secretion	42
α -Amylase secretion	43, 44
Polysaccharide secretion	45
Peroxidase secretion	46, 47
Tropism	
Gravitropism	48—50
Spore germination	51
Chloroplast movement	52—55
Cytoplasmic streaming in <i>Nitella</i>	56
Membrane depolarization of <i>Nitella</i> cells	57
Phototactic behavior	58
Cell division	59, 60
Osmoregulation	61—63
<i>Mimosa</i> leaf movement	64, 65
Pollen tip growth	66, 67
Tuberization	68
Membrane structure and function	
Ultrastructural membrane alteration	69
Membrane damage and leakiness	70
Betacyanin synthesis	71, 72
GA-induced hypocotyl growth	73
Cation transport	74
Transmembrane Ca ²⁺ fluxes	75, 76
Wound-induced nuclear migration	77
Circadian leaf movement	78
Guard cell swelling	79, 80
Protoplast fusion	81
Freezing injury	82, 83
Cell polarity	84, 85
Ripening	19
Photosynthesis	86
Physiological disorders	18, 86a, 86b

Source: From Poovaiah and Reddy (1987) and references therein

- 3) the presence of Ca^{2+} binding protein (Calmodulin) and its role in intracellular metabolic responses (Poovaiah, 1988; Ferguson and Drobak, 1988).

Calcium acts as a secondary messenger in the response of plants to external signals (Hepler and Wayne, 1985; Poovaiah and Reddy, 1987) because of Ca binding protein, calmodulin and of Ca/calmodulin stimulated enzyme activities (Ferguson and Drobak, 1988).

2.6.3. Calcium availability, uptake and translocation

2.6.3.1. Calcium availability

Calcium is the 5th most abundant element and constitutes about 3.6% of the earth's crust (McLean, 1975). Adequate Ca availability can be met by concentrations ranging from 5 to 40 ppm at the root surface, unless ionic antagonism caused by unbalanced competition of the soil solution occurs (Loneragan *et al.*, 1968).

Calcium uptake however is more related to its proportionate concentration to that of other ions in the solution than its absolute concentration (Shear, 1975). Likewise, $\text{NH}_4 > \text{K} > \text{Mg} > \text{Na}$ depress uptake of Ca in tomatoes (Geraldson, 1971; Cerda *et al.*, 1979; Barker and Ready, 1994). The cations Rb, and Al also inhibit Ca uptake (Yamada, 1975), whereas anions such as NO_3 , and H_2PO_4 promote its uptake (Kirkby and Knight, 1977; Jakobsen, 1979).

2.6.3.2. Calcium uptake

Calcium uptake is mainly by mass flow as ionic Ca (Barber *et al.*, 1963; Clarkson, 1988) but diffusion also seems to occur to a considerable extent (Smith and Wallace, 1956; Harker *et al.*, 1988; Chamel, 1989). Delivery of ions to the xylem is metabolically controlled, while upward movement in the xylem is passive mass flow

(Broyer and Hoagland, 1943).

The rate of Ca uptake is dependent on external concentration and transpiration (Clarkson, 1988). He indicated that the increased uptake at high transpiration and high external concentration appears partly due to water flow in the plant (Clarkson, 1988). Likewise, in plants of high salt status transpiration may affect salt transport to the shoots (Broyer and Hoagland, 1943; Harker *et al.*, 1988). However, at low external Ca concentration, transpiration has little influence on Ca uptake (Loneragan and Snowball, 1969).

2.6.3.3. Calcium movement

After reaching the root surface Ca moves across the cortex either by diffusion, by displacement exchange in the free space or a combination of these processes (Bangerth, 1979). Movement of Ca from the cortex into stele and xylem vessels is restricted by a suberized Casparian strip of endodermis (Himelrick and McDuffie, 1983). Hence Ca ions must move through the symplast passing through one or more membranes along a cytoplasmic continuum (Himelrick and McDuffie, 1983).

Calcium uptake and transfer to the xylem is generally restricted to the younger parts of the root such as root tips and sites of branch root initiation where suberization lags behind endodermal cell division (Ferguson and Clarkson, 1975). Once in the stele Ca ions may enter the xylem vessels through active secretion by xylem parenchyma cells (Yu and Kramer, 1969) or by passive leakage into the vessels (Bowling, 1971).

Clarkson (1988) stated that solutes can reach the endodermis either by movement through the porous cell wall (the apoplast) or via the plasmodesmata into the cortex-endodermis junction (symplast) [Fig.2.2].

The activity of free Ca in the cytosol (cytoplasm) is kept between 10^{-4} and 10^{-3} mol m^{-3} by a combination of internal sequestration in the endoplasmic reticulum (ER) and

other organelles and efflux pumping across the plasmalemma (Hepler and Wayne, 1985; Giannini *et al.*, 1987). Hence, symplastic transport of Ca^{2+} is small and inadequate to supply the needs for Ca^{2+} in the shoot apoplast (Clarkson, 1988). Thus, the apoplast is the preferred pathway for the movement of Ca^{2+} across the root.

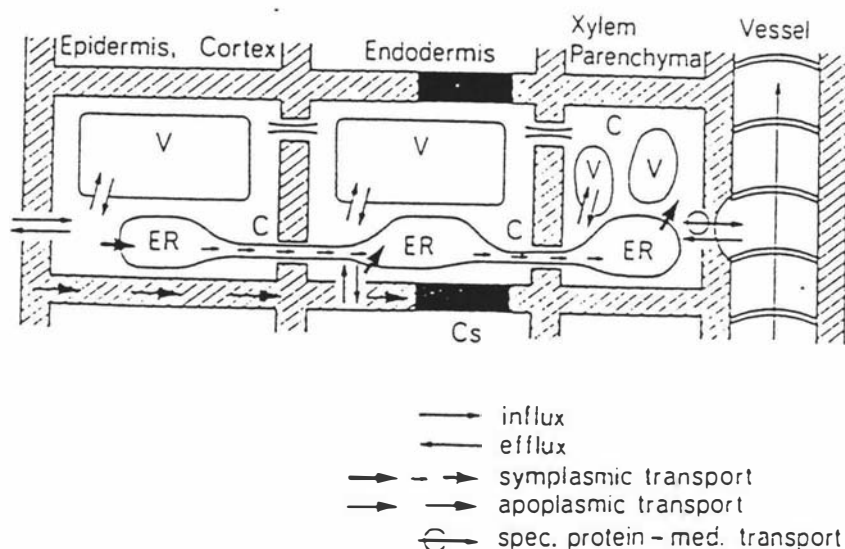


Fig. 2.2. Pathway of calcium transport in plant cells (Adapted from Lauchli, 1976).

2.6.3.4. Calcium translocation

Translocation of calcium from root to other parts of the plant is thought to be through the xylem vessels via the transpiration stream (Stebbins and Dewey, 1972; Clarkson, 1988) or root pressure when transpiration is reduced (Palzkill and Tibbitts, 1977; Guttridge and Bradfield, 1983).

Translocation is slow and typically in two phases: a reversible exchange phase and

an irreversible accumulation phase (Biddulph *et al.*, 1961; Bell and Biddulph, 1963) occurring as ion exchange on the plasma membrane (Bell and Biddulph, 1963; Shear and Faust, 1970). In this instance, the xylem cylinder acts as an exchange column, and chelated Ca is more readily translocated than free Ca (Ferguson and Bollard, 1976; Van de Geijn and Petit, 1979). Hence, Ca nutrition could be affected by other cations due to competition for the negative (exchange) site. Singh and Jacobson (1979) reported that previous absorption of Ca or other cations such as K, resulted in the saturation of the apoplastic electronegative complex, thereby increasing Ca transport (Vang-Petersen, 1980).

Calcium moves mainly in xylem vessels with half as an ion and the other half as complex of malic and citric acids (Bradfield, 1976). There is however, some evidence of phloem transport of Ca to a limited extent (Stebbins and Dewey, 1972; Faust and Klein, 1974).

Calcium is fixed in the cell wall and is then almost immobile for recirculation through the phloem (Mengel and Kirkby, 1987). This is because of the ability of Ca to form inter and intra molecular coordination complexes in the apoplasm (Wuytack and Gillet, 1978) and low Ca concentration in the cytosol and phloem sap. Due to such fixation of Ca, older leaves may have sufficient calcium and young leaves and fruits may have Ca deficiency. Thus, the content of Ca in older leaves doesn't reflect the Ca status in fruits (Shear and Faust, 1970; Chiu and Bould, 1977). On the other hand, because of such fixation, the Ca requirement of enlarging organs may not be met by the xylem transport even when large amount of this ion are supplied to the plant (Kirkby, 1979; Wiersum, 1979a).

Uptake of Ca into the fruit of apple increases until the time fruit growth changes from cell division to expansion (Jones *et al.*, 1983). In the second phase there will be an influx/outflux of Ca from the fruits (Wilkinson, 1968). The input of Ca with xylem sap at night however out weights the outflux of Ca during day time (Lang and Volz, 1993). According to Vang-Peterson, (1980) in the second phase of growth, the 'sink' effects of fruits is less pronounced than that of young leaves and shoot tips

where delivery of assimilates through phloem vessels increases reducing the Ca supply. As a consequence of lack of redistribution of Ca, organs with high metabolism such as fruit and other parts of the plant depend on a continuous Ca uptake from the root (Poovaiah, 1985).

Competition between sinks will be high when the Ca content in xylem sap is low and transpiration is great (Clarkson, 1984). As leaves mature however, the influx of Ca into such leaves declines in spite of constant transpiration (Koontz and Foote, 1966).

2.6.4. Factors affecting calcium uptake and transport

2.6.4.1. Temperature

Calcium uptake is governed by root activity which increases as temperature rises and declines as EC rises (Clover, 1991). High root temperature is associated with increased water uptake and translocation of nutrients (Moorby and Graves, 1980; Graves, 1983).

Moorby and Graves, (1980) observed symptoms of Ca deficiency on mature tomato plants grown in flowing nutrient solution at the lowest root temperature of 13°C. Root temperature of 14°C depressed Ca uptake by tomato plants (Adams, 1988). This is presumably due to reduction in the rate of water uptake and transpiration which is the primary mechanism of translocation of Ca into the leaves (Moorby and Graves, 1980) thereby, depressing the Ca contents of tomato shoots (Ganmore-Neumann and Kafkafi, 1980).

Ganmore-Neumann and Kafkafi (1980) showed that Ca content of the shoots of young tomato plants increased with root temperature over the range of 18-24°C when grown with NO_3^- - N source of fertilizer, whereas, Maher, (1977) indicated that the Ca content of the leaves of fruiting tomato plants was 12% higher when the roots were heated to 25°C than those at ambient root temperature. On the other hand, Ca

content of young leaves increased at the highest root temperature of 26°C initially which was later reduced to 18°C in the later stage of growth of tomatoes (Adams, 1988). He, therefore, indicated that the Ca content of fruits increases with root temperature up to 22°C and declines thereafter. Burrage (1992) suggested that the optimum root temperature for nutrient uptake should be maintained at 20°C.

2.6.4.2. Humidity

High humidity reduces calcium movement since the rate of transportation is mainly determined by the rate of transpiration (Mengel and Kirkby, 1987). Similarly, Ehert and Ho (1986a) noted that the percentage distribution of ^{45}Ca to the apex was reduced by high humidity. Adams and Holder (1992) also reported that high humidity decreased the leaf Ca content but increased that of fruit. This was said to be due to their effect on translocation of Ca from roots to shoots (Drew and Biddulph, 1971; Adams and Holder, 1992).

Barta and Tibbitts (1986) reported that enclosing young developing leaves of lettuce with polyethylene reduced transpiration and leaf Ca concentration thereby advancing the incidence of tip burn. This is due to the high humidity created as a result of the enclosure. On the other hand, Banuelos *et al.*, (1985) and Cline and Hanson (1992) found that exposing fruit to low RH promotes Ca accumulation by tomato and apple fruit by promoting fruit transpiration.

The calcium concentration of low transpiring leaves of cabbage (Palzkill *et al.*, 1980; Weibe *et al.*, 1977) and strawberry (Bradfield and Guttridge, 1979) was increased and necrosis prevented when plants were subjected to higher Relative Humidity (RH) in the dark due to the root pressure created and low RH in the light and soil conditions encouraging rapid water uptake by the roots. Bakker (1988), however, reported that RH had no effect on vegetative growth and Ca content of sweet pepper leaves.

2.6.4.3. Salinity

At high salinity decreased uptake of Ca by the roots and increased resistance to xylem transport inside the fruit have been identified as the main causes of BER (Ehert and Ho, 1986a). Ho and Adams (1989a) demonstrated that the effect of salinity on the accumulation of Ca by tomato fruit is primarily an osmotic effect, reducing the uptake of Ca by the roots and translocation of Ca in the xylem stream. This is because raising the salinity levels by either macro nutrients $\text{Ca}(\text{NO}_3)_2$ and KNO_3 or NaCl have similar effects (Ho and Adams, 1989a).

2.6.4.4. Indole Acetic Acid (IAA)

There is experimental evidence that IAA plays an important role in Ca transport (Banuelos *et al.*, 1987). Accordingly, IAA transport inhibitors led to Ca deficiency related disorders (Bangerth, 1976) and reduced Ca uptake in avocado (Cutting and Bower, 1989). Trees with vigorous vegetative growth, which are likely to produce more IAA (Leopold and Kriedemann, 1975) tend to have fruit with less Ca content than those with less vigorous growth (Witney, *et al.*, 1990). This may be due to poor capacity of flowers and to some extent young fruits to export IAA and being weak sinks for non-transpirational Ca^{2+} as compared to vegetative parts (Cutting and Bower, 1989). It is thus likely that organs which are physiologically active and show more IAA export may accumulate more Ca in their tissues. Marcelle and Lennes (1981) found that injection of IAA into the pedicel of pepper fruit increased their accumulation of Ca while injection of TIBA (an auxin transport inhibitor) reduced it. The presence of seeds in fruit was also reported to stimulate Ca accumulation (Bramlage *et al.*, 1990) which is also linked to auxin transport mechanism.

On the other hand, Brown and Ho, (1993) failed to substantiate this assertion because, in their experiment they found no evidence to suggest that basipetal IAA movement is essential for the concurrent uptake and transport of Ca in tomato fruit through out its development. They found that, although CME (inhibitor of auxin

transport) reduced the transport of ^{45}Ca , IAA efflux increased for only 2 weeks after anthesis while, the uptake of ^{45}Ca increased steadily and maintained at high levels for over 3 weeks after anthesis. Thus, the role of IAA in Ca transport was limited only to a short period of fruit development. This suggests that the initial efflux of IAA may be involved in the regulation of xylem network development through which Ca is transported (Brown and Ho, 1993).

2.6.5. Suggested remedies to control the incidence of Blossom-end rot

There is a dilemma in controlling blossom-end rot in tomato and pepper. This is because, factors favouring photosynthesis such as high temperature, light and excess water and CO_2 supply encourage faster production and transport of assimilates from leaves. However, such rapid growth doesn't favour the uptake and distribution of calcium thus, the fruit's Ca demand may not be met. Therefore, it is advisable to make every effort to ensure that the demand for Ca in the growing fruit is not outstripped by its growth rate.

Different methods have been suggested to combat BER. Adams and Ho, (1985) indicated that BER may be avoided by maintaining a suitable EC, adequate water supply and high humidity at night. This is in agreement with the reports of Sonneveld and Voogt, (1981); Guttridge and Bradfield, (1983); and Uffelen and Bakker, (1989) who indicated that growing of tomatoes and pepper in soils where the EC is not higher than 1.5 mS successfully prevented BER. Tan and Dhanvantari, (1985) and Vander-Werken and Wilcox-Lee, (1988) reported that irrigation and mulching markedly reduced the incidence. Similarly, drip irrigation at night for greenhouse grown crops can overcome the disorder (Haghuys, 1990).

Avoidance of excess application of soluble salts such as K, Mg, and NH_4 as well as total salts which possibly increase the soil EC levels could reduce incidence of the

disorder. At lower EC levels addition of lime (Geraldson, 1956) and at high EC levels addition of superphosphate or poultry manure reduced BER incidence (Prezotti *et al.*, 1991).

Multiple stem pruning to induce plants to produce two vigorous shoots in addition to the main stem reduced the disorder compared to standard single stem pruning in tomatoes (Westerhout, 1962). Application of calcium to the soil or spraying fruits with Ca significantly reduced incidence of BER in tomatoes (Evans and Troxler, 1953; Borkowski and Ostrzycka, 1973; Vander-Werken and Wilcox-Lee, 1988).

2.7. Fruit Growth, maturity and ripening physiology

2.7.1. Fruit growth

Growth of a fruit is followed by measuring one or more of the following attributes such as: diameter, length, volume, fresh weight, dry weight of fruit samples at intervals during their growth period (Bollard, 1970). In some cases diameter growth could also be followed with one fruit without detachment throughout the season. However, fruit diameter growth is generally a poor measure of fruit growth as it is not linearly related to either fruit fresh weight, dry weight or volume (Bollard, 1970; Westwood, 1993). Bollard (1970) suggested that for physiological studies, it is advisable to follow fruit growth by volume, fresh or dry weight measurement. Diameter growth could also be converted to volume growth by developing appropriate formula for conversion. Experimental evidence for non-destructive measurement of fruit growth by manual or automatic measurements of diameter (or circumference) and/or length or even fruit volume is available (Higgs and Jones, 1984; Marcelis, 1992a).

Many fruits show a pattern of growth that follows a single sigmoidal growth curve

(Rhodes, 1980a, Dey and Brinson, 1984), which is characterized by an initial phase of slow growth during cell division, followed by a rapid exponential increase in weight dominated by cell expansion and a final period of a declining growth rate until harvest when ripening is initiated (Bollard, 1970; Coombe, 1976).

There are however, other fruits which show a double (Bollard 1970; Coombe, 1976) or triple (Pratt and Reid, 1974) sigmoidal pattern of growth. Such fruits exhibit two or three rapid growth phases interrupted by one or two periods of little or no growth (Bollard, 1970, Rhodes, 1980a). Rhodes (1980a) indicated that the bulk of the fruit growth is achieved during the second phase of rapid growth for fruits exhibiting a double sigmoidal growth. Fruit growth is a result of cell division and enlargement or both (Weaver, 1972). Cell division predominates in the early stage of growth, whereas cell expansion predominates during the later stages (Weaver, 1972; Dey and Brinson, 1984). An exception to this is avocado fruit where cell division continues right until harvest (Rhodes, 1980a; Dey and Brinson, 1984). A list of fruit grouped according to their growth pattern is given in Table [2.5].

Field grown chilli pepper (Pety and Cotter, 1984) sweet pepper (Miller *et al.*, 1979) and New Mexican type peppers (Biles *et al.*, 1993a) follow a single sigmoidal curve. According to Nitsch (1965) cell division generally takes place during pre-anthesis although the base of the ovary and some parts of the developing fruit remain meristematic at anthesis and a part of post-anthesis (Munting, 1974). This suggests that capsicum fruit growth is mainly due to cell expansion during post-anthesis (Munting, 1974).

2.7.2. Maturation and ripening

Several authors have attempted to define developmental processes in fruits (Lott, 1945; Gortner *et al.*, 1967). Watada *et al.*, (1984) proposed a set of definitions pertaining to developmental processes in order to overcome the deficiencies of the previous terminologies. This is depicted in Fig. [2.3].

Table 2.5. List of fruits showing different patterns of sigmoidal growth (Source, Rhodes, 1980a).

Single	Double	Triple
Apple	Apricot	Chinese Gooseberry
Avocado	Black currant	
Banana	Blueberry	
Date	Fig	
Mango	Grape	
Melon	Olive	
Orange	Peach	
Pear	Raspberry	
Pineapple	Raspberry	
Strawberry	Sour Cherry	
Tomato	Sweet Cherry	

Development ⇔

the series of processes from the initiation of growth to death of a plant part.

Growth ⇔

the irreversible increase in physical attributes (characteristics) of a developing plant or plant part.

Maturation ⇔

the stage of development leading to the attainment of physiological or horticultural maturity.

Physiological Maturity →

the stage of development when a plant or plant part will continue ontogeny even if detached.

Horticultural Maturity →

the stage of development when a plant or plant part possesses the prerequisite for utilization by consumers for particular purpose.

Ripening ⇔

the composite of the process that occurs from the latter stages of growth and development through the early stage of senescence and that results in characteristics aesthetic and/or food quality as evidenced by changes in composition, colour, texture or other sensory attributes.

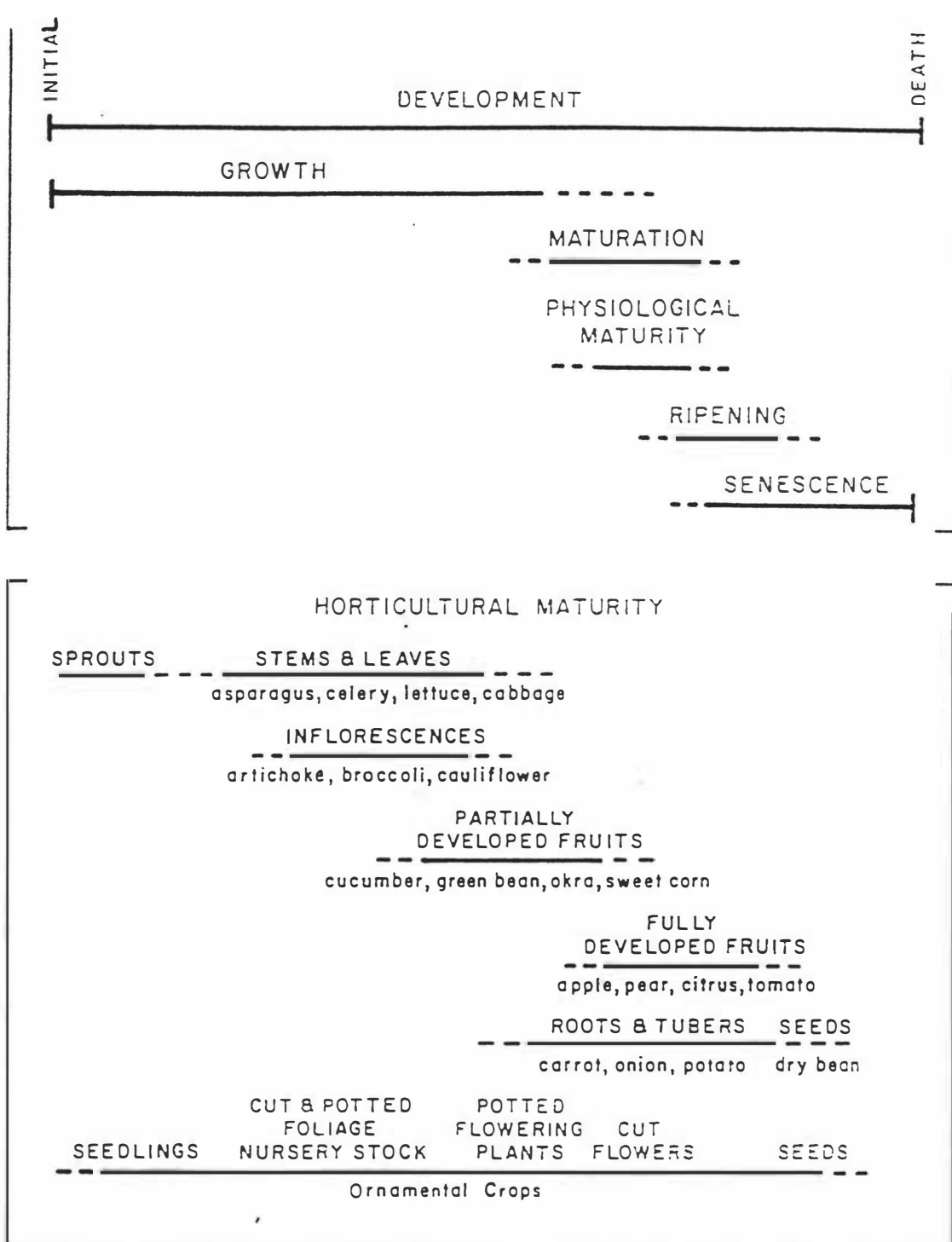


Fig.2.3. Stages of development and senescence based on physiological processes and usage of horticultural crops (Adapted from Watada et. al., 1984).

2.8. Fruit ripening

Ripening is a time of high metabolic activity. A loss of energy occurs as respirable substrate is converted in to simpler molecules, heat and phosphate bond energy (Patterson, 1970). The energy formed is used for various physiological activities and maintenance of the integrity of the cell (Ben-Yehoshua, 1964). Grierson (1983) stated that the timing of ripening is not directly related to chronological age, but, is determined by developmental sequences which are under genetic control. Rhodes (1980b) indicated that the biochemical changes during ripening may be anabolic like the production of flavour volatiles or new pigments or catabolic as in the breakdown of chlorophyll or cell wall constituents during tissue softening.

Ripening involves a series of parallel and sequential metabolic events including changes in juvenility hormones, pigmentation, texture, aroma, carbohydrates, organic acids, respiration, the production of ethylene, and other flavour volatiles (Grierson, *et al.*, 1985; Speirs and Brady, 1991). Patterson (1970) classified these changes as external changes as colour, odour, sweetness, acidity, astringency and texture and internal changes such as respiration, ethylene production and production of volatiles.

Patterson (1970) classified odour, sweetness, acidity and astringency as external changes assuming that they can be detected by human sensory organs. However, for the sake of clarity and considering the actual metabolic changes which bring about the change in these said attributes, they will be treated as internal changes in this review.

I. Internal changes

2.8.1. Fruit respiration

Respiration is a central process in living cells that mediates the release of energy

through the breakdown of carbon compounds and the formation of carbon compounds necessary for maintenance and synthetic reaction after harvest (Kays, 1991).

In terms of their respiratory behaviour and the nature of ethylene production, fruits are divided into climacteric and non-climacteric types.

It was observed by Kidd and Went (1924) that the rate of respiration of detached apple fruits decreased initially and after reaching a minimum suddenly increased rapidly, peaked and then declined. They named this sudden rise in respiration as climacteric. This phenomenon was later found to be present in many fruits (Rhodes, 1970). On the other hand, those fruits which do not show this kind of behaviour are referred to as non-climacteric. These include, citrus (Biale, 1960); strawberry (Knee *et al.*, 1977), and pepper (Saltveit, 1977; Pretel *et al.*, 1995).

Unlike climacteric fruit, non-climacteric fruits show no peak in either ethylene production or respiratory activity (Bruisma, 1983; Mizutani *et al.*, 1988). The respiratory pattern of climacteric and non-climacteric fruit as shown by Biale (1960) is depicted in Fig. [2.4.].

The climacteric rise in respiration has been attributed to the enhancement of protein synthesis (Richmond and Biale, 1966), decrease in organizational resistance of cells (Ben-Yehoshua *et al.*, 1983) and the synthesis of ripening enzymes (Rhodes, 1970). The nature of some of these ripening related enzymes was determined as endopolygalacturonase, NADP, malic enzyme, ACC synthase and ACC oxidase (EFE) (Dilley and Wilson, 1992).

Climacteric fruits are known to endogenously produce and respond to endogenous and exogenous ethylene with an increase in respiration (Biale, 1960; Rhodes, 1970). On the other hand, non-climacteric fruits such as citrus may have an increase in respiration in response to exogenous application of ethylene but do not produce appreciable amount of ethylene during normal development (McMurchie *et al.*, 1972).

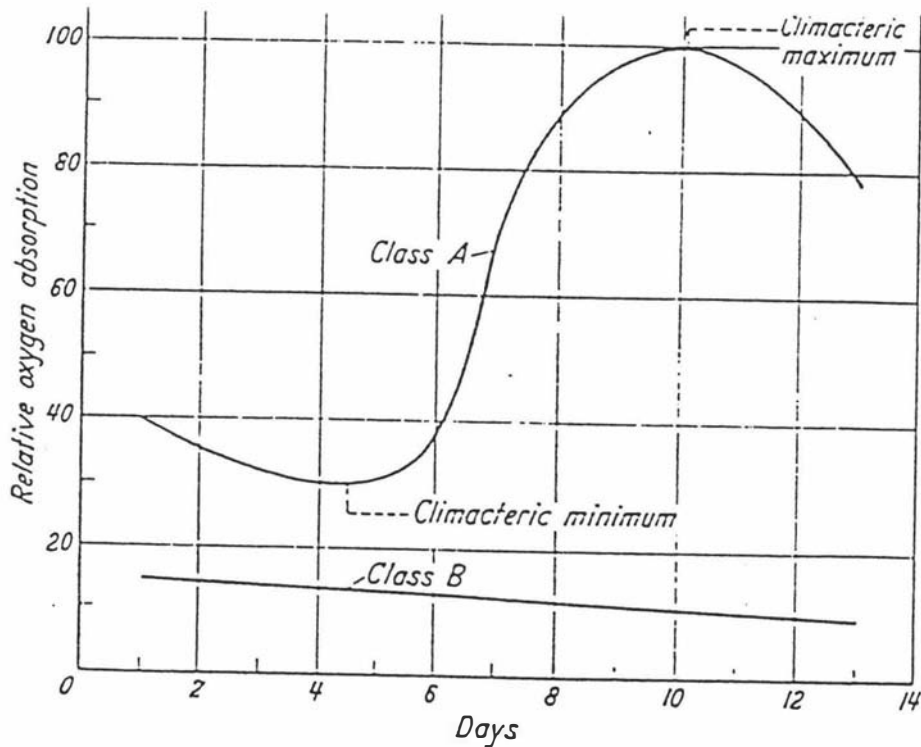


Fig. 2.4. The two classes of respiratory patterns in fruits. Class A = climacteric; Class B = non-climacteric (After Biale, 1960).

Some pepper varieties were classified as non climacteric because of their low respiration during maturity (Saltveit, 1977; Lu *et al.*, 1990). However, some hot pepper and sweet pepper cultivars exhibited a rise in respiration with colour change (Gross *et al.*, 1986; Lurie and Ben-Yehoshua, 1986) indicating an intermediate response as they normally show low rates of respiration. This shows that the respiration behaviour of sweet pepper fruits needs further study.

McGlasson (1985) indicated that treatment of climacteric fruit with ethylene or other ethylene releasing chemicals such as propylene, acetylene, and ethephon may induce a rise in respiration rate prematurely. However, he contends that once autocatalytic

ethylene production has commenced the ripening process is irreversible. On the contrary, a climacteric like respiratory increase can be induced in non-climacteric fruit by treating them with ethylene or its analogues (Biale and Young, 1981). They also indicated that respiration rate declines fairly rapidly once the fruit is removed from the ethylene atmosphere. If ethylene is removed, then the rates of respiration and chlorophyll loss fall back to the original level in non-climacteric fruit (Rhodes, 1970). This shows that the action of exogenous ethylene is reversible in non-climacteric fruit (Biale, 1960). Treatment of sweet pepper fruit cv. California Wonder with propylene did not affect fruit respiration rate suggesting that the fruit are non-climacteric (Pretel *et al.*, 1995).

With climacteric fruit the sequence of events seems to be very condensed and all those related to ripeness are switched at the same time (Phan, 1987). In non-climacteric fruit, this change is much slower and the individual metabolic changes seem to be set in motion at different times or stages (Phan and Hsu, 1973).

2.8.2. Hormonal regulation of ripening

Tropical fruits such as mango and avocado do not ripen while they are attached to the tree probably because of the presence of some hormonal ripening inhibitor derived from the vegetative parts (Burg and Burg, 1965a; Gazit and Blumenfield, 1970; Blanpied, 1993). Mapson and Hulme (1970) suggested that the inhibitor either inhibits ethylene production or raises the threshold value at which ethylene becomes physiologically active in promoting ripening.

The nature of this foliar inhibiting hormone is still unknown but hormonal levels of auxin are known to inhibit fruit ripening (Frenkel and Dyck, 1973; Tingawa and Young, 1975). However, its complex relationship with ethylene in increasing C_2H_4 production (Mousdale and Knee, 1982; Abeles, 1985) and modifying tissue response to ethylene (Yang and Hoffman, 1984) makes it difficult to explain its direct effect with regard to ripening of fruit.

On the other hand, gibberellins are known to exert some influence on ripening by retardation or even reversal of the degreening process (Goldschmidt *et al.*, 1977; Bruisma, 1983).

Cytokinin does not have a direct effect on the ripening process. The hormone however, stimulated C_2H_4 production in conjunction with other treatments which increase ethylene synthesis. Accordingly, C_2H_4 production from IAA-treated or water stressed tissue rises in response to the application of benzyladenine as a result of greater ACC synthase activity and the consequently increased ACC accumulation (Yang and Hoffman, 1984).

Absciscic acid accumulates late in fruit development and during ripening (Kitamura *et al.*, 1983) and some have reported that treating fruits with absciscic acid induces ripening (Mizrahi *et al.*, 1975; Vendrell, 1985). Hence, there is some presumption that ABA may be involved in the ripening process. However, this is not well established. According to Tsay *et al.*, (1984) no consistent relationship was found between ripening and levels of ABA in fruit.

By and large, ethylene is the dominant hormone in fruit ripening and regulation of ripening concerns the control of ethylene synthesis and action (Bangerth, 1978; Bramlage *et al.*, 1980; Williams, 1980). The other hormones may act by either affecting the biosynthesis of C_2H_4 or the sensitivity of the tissue to this hormone.

2.8.2.1. The ripening hormone ethylene

Ethylene elicits biological response at very low concentrations. As a plant hormone it is unique in its structural simplicity and in being gaseous. Unlike other hormones it is not transported directionally but accomplishes its integrative functions by diffusing rapidly through the tissues (Mattoo and Suttle, 1991).

McGlasson *et al.*, (1978) reported that ethylene plays a major role not only in the

initiation of fruit ripening but also in the coordination of various ripening phenomena.

The production of ethylene is regulated by a number of developmental and environmental factors such as pigmentation (Poincelot, 1980), ripening (McGlasson *et al.*, 1978) senescence (Matto and Suttle, 1991), abscission (Sexton *et al.*, 1985), auxin (Yoshii and Imaseki, 1981; Abeles, 1985), wounding (Hoffman and Yang, 1982) and a variety of stresses (Naqvi, 1995).

2.8.2.2. Ethylene biosynthesis

A number of researchers have attempted to identify the pathway of ethylene biosynthesis. Lieberman and Mapson (1964) proposed methionine to be the precursor of ethylene. Subsequently Lieberman *et al.*, (1966) demonstrated the *in vivo* conversion of [^{14}C] methionine to [^{14}C] ethylene in apple tissues.

Adams and Yang (1979) established the pathway of ethylene biosynthesis as follows:

Methionine \Rightarrow S-Adenosyl-L-Methionine (SAM) \Rightarrow 1-Amino Cyclopropane-1-Carboxylic acid (ACC) \Rightarrow C_2H_4 .

Since the ethylene production system is extremely labile and is completely lost by tissue disruption, the 1st characterization has been made at the living tissue level (Yang, 1985) [Fig.2. 5.].

Hoffman and Yang (1980) compared the level of ACC in several climacteric fruits to their C_2H_4 production rates and found that ACC content is very low in pre-climacteric fruit but increased dramatically in conjunction with the surge in C_2H_4 production.

Ethylene production in pre-climacteric fruit is limited by lack of conversion of SAM to ACC, and both ACC synthase and ACC oxidase (formerly known as EFE) must

increase during ripening to account for a large rise in C_2H_4 production (Brecht and Kader, 1984). During the post climacteric phase, ACC may increase while C_2H_4 production declines (Hoffman and Yang, 1980).

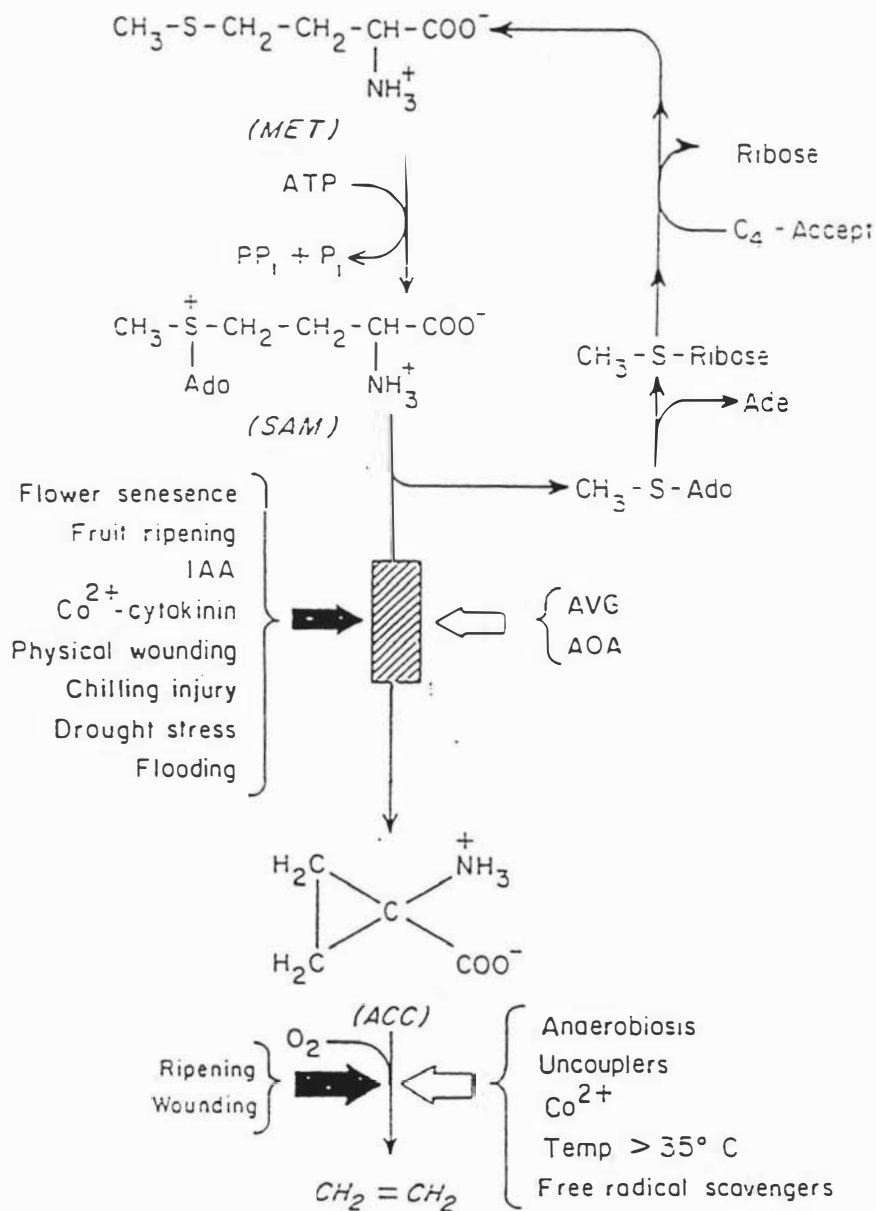


Fig. 2.5. The pathway of ethylene biosynthesis (after Yang, 1981)

Until recently the system converting ACC to C_2H_4 is thought to be quite labile (Apelbaum *et al.*, 1981) and that ACC oxidase activity was lost as the tissue was homogenized (Hoffman and Yang, 1980; Kende, 1989). Ververidis and John (1991) showed that it is possible to solubilize the ACC oxidase from plants and retain full activity. The enzyme requires Fe^{+2} and is stimulated by ascorbate (Ververidis and John, 1991; Fernandez-Maculet and Yang, 1992). This might be the reason for the failure of earlier attempts to solubilize and purify the enzyme.

Formation of ACC is stimulated in ripening fruits (Hoffman and Yang, 1980) as is the conversion of ACC to C_2H_4 (Hoffman and Yang, 1982). Pretel *et al.*, (1995) showed that during ripening of sweet pepper fruit cv. California Wonder, both ACC synthase and ACC oxidase activities fell during maturity and ripening of fruit which was the basis for classifying the fruit as non climacteric. Treatment with C_2H_4 above a threshold concentration triggers a large increase in C_2H_4 production in climacteric fruit (Abeles, 1973). According to Walsh (1977) it may be the length of time that fruit is exposed to above threshold levels of C_2H_4 and temperature during this time rather than the concentration *per se*, that is most important for ripening. There is however, reports that exogenous application of C_2H_4 inhibits endogenous C_2H_4 production (Brecht and Kader, 1982; Riov and Yang, 1982).

It has been shown that ethylene plays an essential role in fruit ripening by stimulating the expression of ripening related genes (Grierson *et al.*, 1985; Abeles *et al.*, 1992).

2.8.3. Carbohydrate changes

Developmental changes in soluble carbohydrate concentration of fruit are often associated with change in activities of sucrose metabolizing enzymes within the fruit (Hubbard and Pharr, 1992). In this regard, changes in Sucrose Phosphate Synthase (SPS) and acid invertase activity have been shown to be important in determining the soluble sugar content in developing fruits of several species.

Increased activity of SPS in muskmelon (Hubbard *et al.*, 1989) banana (Hubbard *et al.*, 1990) and mango (Hubbard *et al.*, 1991) were associated with increased sucrose concentration during ripening. On the other hand, high acid invertase activity was related to the accumulation of hexose sugars in papayas (Chan *et al.*, 1979) tomato (Yelle *et al.*, 1991) and pepper fruit (Nielsen *et al.*, 1991; Hubbard and Pharr, 1992). The hexose sugars in pepper were reported to be composed of glucose and fructose (Hubbard and Pharr, 1992). According to Nielsen and Veierskov (1990) photoassimilate is translocated primarily as sucrose in pepper plants. It is assumed that it is this imported sucrose which will later be converted to hexose sugars in pepper fruit (Nielsen *et al.*, 1991; Hubbard and Pharr, 1992). Wall and Biles, (1993) reported that the total and reducing sugars of chilli pepper fruit increased significantly after the 50% colour change.

2.8.4. Changes in organic acid composition

Generally fruits show a decrease in acidity and an increase in sweetness during ripening (Rhodes, 1980a). The decline in the levels of organic acids is because they are respired or converted to sugars (Wills *et al.*, 1989). This decline however, may not be true for all species. In banana and pineapple for instance, the highest levels are attained at full ripe stage (Wills *et al.*, 1989). Luning and Duk, (1992) reported that the acid contents of sweet pepper fruits increased during ripening.

The absolute levels of sugars and acids as well as their ratio play an important role in the taste of ripe fruit. The two acids which are most frequently found in fruit cells are malic and citric acids (Rhodes, 1980a). The major organic acids in pepper are also citric and malic acids (Penkeva, 1985; Vander Beek and Boulekebech, 1987) with citric acid predominating.

2.8.5. Changes in aroma

In addition to the balance between sugars and acid, an important factor in the flavour of a fruit is their aroma. It arises from the production of volatile compounds.

Of the 17 odour compounds identified in bell pepper volatiles, 92% of the contribution to the total odour is from 2-Methoxy-3-isobutylpyrazine and 7% from Nona-trans, Cis-2-6-dienal (Govindarajan *et al.*, 1986).

The flavouring principle of pepper fruit also appears to be associated with the carotenoid pigments (Andrews, 1984). He indicated that strong colour and strong flavour are linked. When colour of dried peppers fade, they lose their flavour.

II. External changes

2.8.6. Colour change

Colour change is the most obvious sign of ripening in most fruits. These changes are primarily a degradation of chlorophyll and synthesis of carotenoids and anthocyanin (Patterson, 1970).

Sweet pepper is a Solanaceous fruit in which, over the course of ripening, the plastids undergo a dramatic change from chloroplasts to chromoplasts (Spurr and Harris, 1968). The latter contain large deposits of newly synthesized carotenoids, which along with phytosterols are products of the mevalonic acid-isopentenoid biosynthetic pathway (Camara and Moneger, 1978).

Over 27 carotenoid pigments have been identified in red bell pepper (Curl, 1962). Like tomatoes, red peppers have basically two pigment colours, red and yellow which combine to give a total colour (Reeves, 1987). According to Reeves (1987) red

pepper colour is primarily caused by the xanthophylls, capsanthin and capsorubin which make up the largest pigment percentage while beta carotene and violaxanthin contribute to the yellow-orange colour.

The amount of pigment in tissue depends upon factors such as species, variety, maturity and growing conditions (Rahman *et al.*, 1978). There is a wide variation in the total pigment content as well as the ratio of components between varieties (Davies *et al.*, 1970).

Chlorophyll a and b were the major pigments at the immature stage in green cultivars (Rahaman and Buckle, 1980) and the chlorophyll concentrations decreased significantly with maturity and completely disappeared at full ripeness (Camara and Brangeon, 1981). This is accompanied by *de novo* synthesis of the proteins (chromoplast A and chromoplast B) during chromoplast development (Newman *et al.*, 1989).

2.8.7. Firmness and cell wall components

Tissue rigidity is a complex parameter with inputs from cell wall strength, cell to cell adhesion, turgor and tissue anatomy (Simon, 1977; Bartley and Knee, 1982; Holt and Schoorl, 1985). Therefore, it is difficult to be sure what are the principal causes of loss of rigidity during ripening (Heyes, *et al.*, 1994).

A substantial loss of firmness occurs in many fruits during ripening. Some researchers have tried to explain the softening process in relation to structural changes in cell wall components (Bartley and Knee, 1982). Softening due to moisture loss was also reported for lemon and bell pepper (Ben-Yehoshua *et al.*, 1983), while others have implicated the enzymes involved in the degradation of the cell wall components (Huber, 1983).

Polygalacturonase has been strongly implicated in the softening process (Brady *et*

al., 1983). Tomato softening for instance, is accompanied by increased activities of Pectinesterase (PE) (Hobson, 1963) and Polygalacturonase (PG) (Hobson, 1964; Grierson *et al.*, 1981). According to Sawamura *et al.*, (1978) the loss of pectic substances from tomato cell wall during softening was correlated with the action of PG.

Grierson *et al.*, (1981) reported that tomato PG is absent in green tomatoes and appears to be synthesized during ripening with its activity first appearing at the onset of coloration. They further indicated that unlike PG the PE activity was present in green fruit and increased during ripening, reaching a maximum level at the ripe stage and declined thereafter.

Tigchelaar *et al.*, (1978) proposed that PG activity may initiate ripening while the PE activity may be involved in the softening phenomenon by influencing PG activity (Jen and Robinson, 1984).

Unlike tomato very little information is available on the pectolytic enzymes of pepper. This may probably be due to the anticipated low enzyme activities in pepper as the texture degradation process is slow. Unlike tomato little softening of the outer pericarp occurs in pepper during ripening although solubilization of pectin has been shown to occur with ripening (Lurie *et al.*, 1986).

Jen and Robinson (1984) found that PG activity in pepper fruit increased during ripening and was maximal at the turning stage while PE activity declined during ripening and was maximal at the light green stage. They also reported that bell pepper texture measurement were found to decline with increase in PG activity but did not correlate well with PE activity. The recent report of Sethu *et al.*, (1996) also confirms the previous observation that the texture of the fruit declined with an increase in PG activity. Increased PG activity with advancement in ripening stages of tomato was also observed (Sawamura *et al.*, 1978; Tucker *et al.*, 1982). On the other hand, Gross *et al.*, (1986) didn't detect any PG activity in hot peppers.

A histochemical study of cell wall pericarp of pepper fruit revealed that pectins are the main components of fruit cell wall which constitutes 2/3 of the mesocarp cell wall (Jona and Foa, 1979). They indicated that the epicarp cell wall are rich in non-cellulosic polysaccharides and contain some cellulose which is scarce in the mesocarp cell wall. A cross section of *Capsicum* fruit and pericarp tissues of the fruit are shown in Figs. 2.6a and 2.6b.

Calcium is essential to maintain the structural integrity of membranes and cell walls (Hanson, 1983; Paliyath, *et al.*, 1984). The cementing effect is due primarily to Ca-pectate of the middle lamella (Knee and Bartley, 1981; Hanson, 1983; Poovaiah, 1986). Dey and Brinson (1984) reported that calcium appears to serve as intermolecular binding agent that stabilizes pectin-protein complexes of the middle lamella.

Solubilization of Ca is suggested to be the cause of softening in ripening fruits (Poovaiah *et al.*, 1988) by PG (Poovaiah and Nukaya, 1979). This notion was supported by several results whereby softening was inhibited or reversed by pre-harvest Ca sprays or post-harvest Ca infiltration into fruit tissues (Lidster *et al.*, 1979; Buescher and Hobson, 1982; Sams and Conway, 1984; Stow, 1989).

Recent studies indicate that polygalacturonase action is not the sole determinant of texture changes (Speirs and Brady, 1991) because of the failure of PG to promote softening in *rin* (ripening inhibitor) tomatoes (Giovannoni, *et al.*, 1989).

The lack of relationship between the extent of softening in different fruits and their PG levels suggests that other enzymes also play an important role in cell wall modification and softening. There is a growing evidence that β -galactosidase may contribute to fruit softening (De Veau, 1993; Ali *et al.*, 1995). A 70% increase in β -galactosidase activity with ripening of sweet pepper fruit was also observed (Sethu *et al.*, 1993).

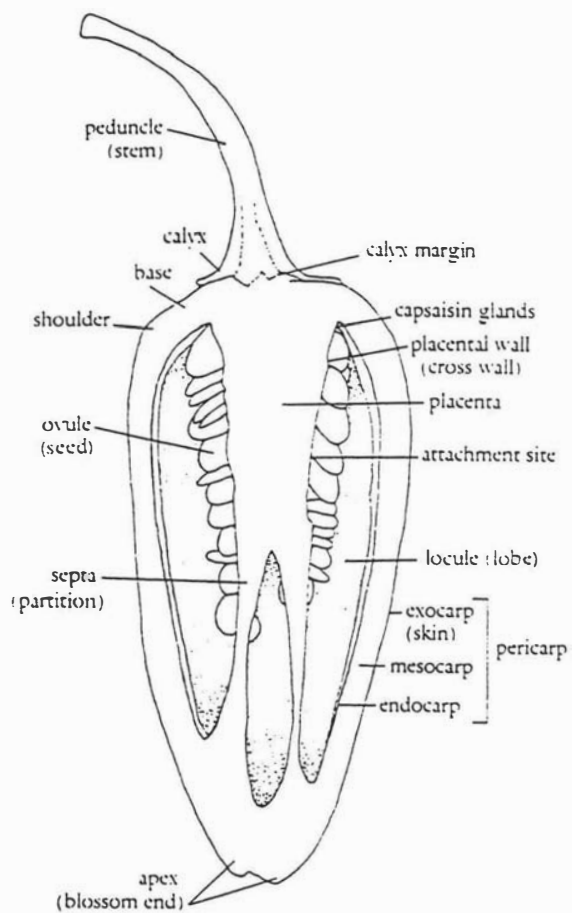


Fig. 2.6a. Cross section of a capsicum fruit (From Andrews, 1984).

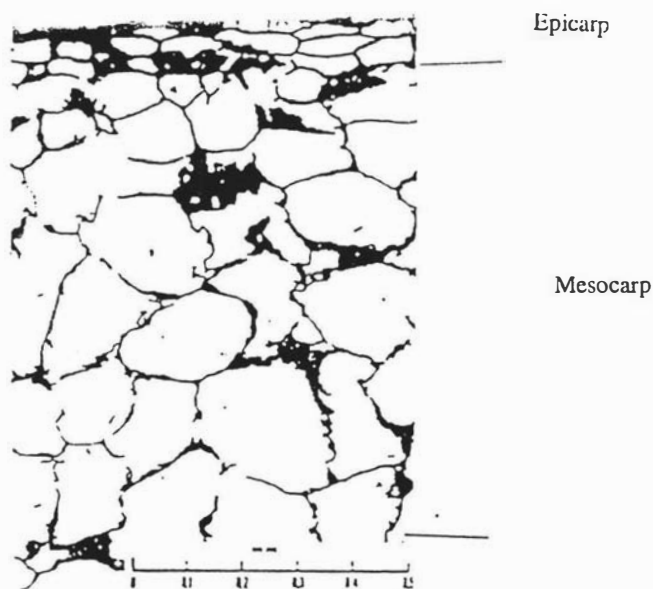


Fig. 2.6b. Periodic Acid Schiff (PAS) stained pericarp tissues of pepper 'Zohar Naharia' (Adapted from Jona and Foa, 1979).

In addition to the solubilization of pectin a net loss of hemicellulose nucleotide sugar residues also occurs during the ripening process of many fruits (Knee *et al.*, 1977; Gross and Wallner, 1979; Ahmed and Labavitch, 1980). According to Gross and Sams, (1984) tomato, sweet pepper and hot pepper lost 39, 42 and 56% respectively of their total cell wall nucleotide sugars during ripening. The net loss of these sugar residues during ripening involved primarily galactose and arabinose containing polymers which are major nucleotide sugar components of pectic polysaccharides (Gross and Sams, 1984). The loss of galactose however, does not appear to be directly related to fruit firmness since in the case of tomatoes, *rin* fruit soften only slightly although a considerable net loss of galactose containing polymers occurs (Gross and Wallner, 1979).

2.9. Determination of fruit maturity

Maturity at harvest is an important factor affecting consumer perception and quality changes during storage (Shewfelt, 1993).

Picking fruit before or after it reaches optimum maturity risks fast deterioration, susceptibility to pathogen attack and poor nutritional, transportability and storage quality (Beaundry *et al.*, 1993; Scott *et al.*, 1993). Therefore, to minimize these risks it is essential to determine the optimum maturity of a product to be harvested.

As maturity approaches, many physical and physiological changes occur in the fruit which enable the fruit to ripen after harvest. Such changes include, changes in fruit firmness, total soluble solids, size and colour as well as respiration and ethylene production at least in case of climacteric fruits.

The rate at which these changes occur can indicate how close to maturity fruits are (Truter and Hurndall, 1988). However, due to poor correlation between different parameters (Knee *et al.*, 1989) and variability between season and individual fruit,

several parameters should be considered to obtain a reliable maturity index in any one cultivar (Shaw and Rowe, 1982; Truter and Hurndall, 1988).

2.9.1. Maturity indices of various fruit

The definition of maturity as the stage of development giving minimum acceptable quality to the consumer implies a measurable point in the commodity development. Hence, the need for techniques to measure maturity (Reid, 1992).

Maturity could be judged subjectively as often is the case for most commodities by visual inspection of attributes such as size, gloss of the fruit surface, external surface. The shortcomings of this however, is that not only it needs experience but there is also a likelihood of misjudging the maturity of a product. Sale of immature products may consequently result in a loss of consumer confidence.

Objective maturity indices on the other hand, enable growers to predict with a good measure of certainty when their product is ready for harvest.

Maturity indices can be determined in several ways such as; measurement of size, weight, or density; estimating the duration of development; considering physical attributes such as colour, firmness moisture and solid content; and chemical attributes like starch, sugar or acid content (Reid, 1992; Shewfelt, 1993).

According to Reid (1992) characteristics of maturity index should be simple and require inexpensive equipment. The index should preferably be an objective rather than a subjective evaluation. He further suggested that the index should be non-destructive and correlate well to the quality and post harvest life of a commodity. Table [2.6] shows the possible methods of maturity determination.

At present there are some maturity indices in use for some fruit crops. However, due to their poor correlation with other quality attribute, the search for maturity indices

Table 2.6. Methods of maturity determination (Reid, 1992)

Index	Methods of determination	Subj.	Obj.	Dest.	Nondest.
Elapsed days from full bloom	Computation		x		x
Mean heat units	Computation from weather data		x		x
Development of abscission layer	Visual or force of separation	x	x		x
Surface structure	Visual	x			x
Size	Various measuring devices, weight		x		x
Specific gravity	Use of density gradient solutions, flotation techniques, vol'wt		x		x
Shape	Dimensions, ratio charts	x	x		x
Solidity	Feel, bulk density, γ -rays, X-rays	x	x		x
Texture: Firmness	Firmness testers, deformation		x	x	
Tenderness	Tenderometer		x	x	
Toughness	Texturometer. fibrometer (also:chemical methods for determination of polysacharides)		x	x	
Colour, external	Light reflectance, visual colour charts	x	x		x
Colour, internal	Light transmittance, delayed light emission		x		x
Internal structure	Light transmittance, delayed light emission		x		x
	Visual examination	x		x	
Compositional factors: Total solids	Dry weight		x	x	
Starch content	KI test, other chemical tests		x	x	
Sugar content	Hand refractometer. chemical tests		x	x	
Acid content	Titration, chemical tests		x	x	
Juice content	Extraction, chemical tests		x	x	
Oil content	Extraction, chemical tests		x	x	
Tannin content	Ferric chloride test, chemical tests		x	x	
Internal ethylene	Gas chromatography		x	x	
Subj.= Subjective, Obj.= Objective	Dest.= Destructive, Nondest.= Non destructive				

continues. For products such as pepper no reliable objective measurement has been developed.

Apple maturity is predicted with the aid of fruit firmness and starch index (Lau, *et al.*, 1986). Other maturity indices for apple include, internal C_2H_4 levels, readiness to synthesise ethylene, soluble solids, seed and skin colour and bloom date, background colour development, and titratable acidity (Lau *et al.*, 1986; Watkins *et al.*, 1989; Beaundry *et al.*, 1993).

The maturity indices used in other fruit include total soluble solid (TSS) content and firmness in kiwifruit (Harman, 1981; Crisosto *et al.*, 1984); colour change, seed age, ratio between TSS and acidity and formation of jelly like material in tomato fruit (Kader *et al.*, 1972; Reid, 1992); starch-iodine reaction in banana (Blankenship *et al.*, 1993); groundspot colour and rind gloss in water melon (Corey and Schlimme, 1988); oil content or dry weight of avocado (Lee, 1982; Lee *et al.*, 1983) specific gravity of pineapple (Smith, 1988) TSS, TSS to Acidity ratio and dry matter content in prunes (Scott *et al.*, 1993), the levels of malic to citric acid ratio and ground colour in peaches (Chapman and Horvat, 1990; Lauchsinger and Walsh, 1993), colour change, firmness, TSS and juice levels in tamarillo and pepino (El-Zeftawi *et al.*, 1988) and days from anthesis and morphological changes such as the ratio between fruit width and length in mango (Wang and Shiesh, 1990).

2.10. Summary

The forgoing review was made to gain insight into the present state of knowledge as regards water management vis-a-vis the development processes in plants. It was also attempted to make a thorough review of the factors affecting the incidence of BER and the maturity and ripening of crops. In the course of this review, it was attempted to point out the existing knowledge gap in the aforementioned areas with particular reference to sweet pepper.

The following study therefore, was aimed to address some of these problems. The study can generally be classified in to two parts. 1) Preharvest management factors affecting the yield performance and quality of sweet pepper with special emphasis on the incidence of BER. 2) Studies on the ripening behaviour of sweet pepper and the influence of nutritional factors on this process.

With regard to Blossom-end rot, this study attempts to assess the influences of season, water management, growing technique, osmotic stress and humidity on the incidence of BER. Meanwhile, the effects of water stress and osmotic stress on the growth and development of sweet pepper were investigated.

In a parallel study, the fruit growth and ripening behaviour of sweet pepper fruit were characterized. Moreover, the effects of preharvest nutritional factors on these characteristics was also examined.

Chapter 3

Plant growth, development and fruit quality of sweet pepper (*Capsicum annuum* L.) cv Domino in relation to moisture supply

3.1. Introduction

Water stress may reduce growth and impair other metabolic processes in plants (Hsiao, 1973; Jones, 1986). It suppresses vegetative growth of crops due to closure of stomates, leaf rolling and shifts in assimilate partitioning (McGiffen *et al.*, 1992).

A high root:shoot ratio is one of the mechanisms of adaptation to water stress, as it permits the stressed plant to maintain higher internal water content (Fitter and Hay, 1987). This in turn helps to maintain cell turgor thereby stimulating the growth of the crop (Turner and Burch, 1983). It is also suggested that regulating the ratio between effective root surface and leaf area is another adaptive mechanism to stress (Lomiss, 1983).

The sweet pepper plant is considered to be very sensitive to water stress (Batal and Smittle, 1981; Bees *et al.*, 1982). The peak moisture requirement of sweet pepper occurs during the blooming and fruiting period (Longbrake, 1983). In tomato, adequate moisture supply during flowering, fruit set and fruit development is crucial (Wudiri and Henderson, 1985).

In fleshy fruits, flower initiation is the most critical stage of development as it is the period of most intense cell division (Coombe, 1976). He indicated that following anthesis, the potential for cell expansion could limit solute accumulation. Moreover, excess photosynthates are partitioned to alternate sinks (Chalmers *et al.*, 1975; Starck,

1983).

Moisture stress not only restricts plant growth and yield (Sanders *et al.* 1989; Aloni *et al.*, 1991), but also affects fruit quality (Adams and Ho, 1985) and dry matter partitioning (Geddes *et al.*, 1979; McGiffen *et al.*, 1992).

When water supply is adequate the bulk of the assimilates is partitioned in favour of shoots while, under stress conditions, roots receive more assimilates (Geddes *et al.*, 1979). This was confirmed by the results of Aloni *et al.*, (1991) in sweet pepper and McGiffen *et al.*, (1992) in tomato.

Recently, withholding water for certain period of time has been used as a management tool to improve quality of tomato fruits. This improvement is achieved by increasing soluble solids concentration and dry matter yields. However, the gains in quality improvement were accompanied with reduced yields (Alvino *et al.*, 1990a; Mitchell *et al.*, 1991) decreased fruit size (Alvino *et al.*, 1990b) and increased susceptibility to blossom-end rot (O'Sullivan, 1979; Ho *et al.*, 1987).

Blossom-end rot is a physiological disorder of tomato and sweet peppers which may arise primarily to calcium deficiency in the fruit (Murray *et al.*, 1972; Cerda *et al.*, 1979). Other factors which are associated with the incidence of this disorder include, fluctuating moisture supply (O'Sullivan, 1979); poor aeration (Tachibana, 1988); heavy application of fertilizers particularly ammonium salts (Dekock *et al.*, 1979; Pill and Lambeth, 1980) and high EC of the nutrient medium (Adams and Ho, 1985; Adams and El-Gizawy, 1986). Varietal differences in the susceptibility of the disorder have been reported (Adams and Ho, 1992).

Studies on the production and distribution of a crop plant's dry matter helps to understand the production potential of the crop and helps to produce maximum harvest (Gifford *et al.*, 1984). Likewise, a balance between the supply and use of assimilates is of considerable importance. This balance in turn is affected by moisture

supply.

In sweet pepper plants the fruit may account for up to 70-80 % of the increase in dry matter (Hall, 1977). However, cultivar and environment markedly affects this distribution.

Very little work has been done to analyze sweet pepper growth and dry matter production and accumulation rate in the field (Bees *et al.*, 1982; Hedge, 1987). Moreover, very few studies have been done with regard to dry matter production and distribution on greenhouse grown sweet pepper plants (Hall, 1977).

The aim of the present investigation was, therefore:

- 1.1. To examine the pattern of dry matter production and distribution during the development stages of the sweet pepper plant and the influence of water stress on such mechanism.
- 1.2. To assess the effects of different watering and harvesting regimes on blossom-end rot incidence and other yield components of sweet pepper.
- 1.3. To measure accumulation of calcium during growth of the crop and define a relationship between calcium content of fruits and blossom-end rot incidence.

3.2. Materials and Methods

Two experiments were conducted in a greenhouse at the PGU, Massey University, in the winter season using sweet pepper (*Capsicum annuum* L.) cv. Domino.

Plants were grown in a 6 m by 6 m greenhouse which was heated when the temperature fell below 15°C and ventilated by fans when the temperature rose above 25°C.

Experiment one The effect of water stress and harvesting regimes on the incidence of blossom-end rot, fruit yield and dry matter partitioning of sweet pepper plants cv. Domino.

3.2.1. Treatments and plots

The treatments comprise three harvesting regimes namely: fruit harvested at the mature Green, Green-Red and Red mature stages; and two irrigation treatments, viz Wet and Dry.

Each plot consisted of four plants and each block comprised 24 plants (3 harvest regimes x two irrigation treatments x 4 plants per treatment). Each plant was fed through a trickle irrigation system from a tank at a rate of 45 ml min⁻¹, and 405- 675 ml pot⁻¹ of nutrient solution was applied daily to the plants.

The solution contained 0.1007 kg.l⁻¹ of nutrient with the composition of nutrient

elements shown in Table 3.1. The EC of the leachate was monitored regularly.

Table 3.1. Mineral analysis (mg l⁻¹) of the nutrient feed, pH and conductivity.

Nutrient	Quantity
Nitrogen	237
Phosphorous	55
Potassium	325
Calcium	192
Magnesium	44
Sulphur	62
Sodium	22
Iron	9.1
Manganese	1.9
Zinc	0.1
Copper	0.08
Boron	0.36
pH	6.7
EC	2.5

3.2.2. Greenhouse procedures

Seeds were sown on 10 April 1992 in polystyrene transplant trays (Speedling type trays) and transferred to 8 cm diameter Ace pots at the cotyledon expansion stage on 30 April. Seedlings were transplanted on 18 June into PB' 18 (18 l) polyethylene bags filled with peat with the following base fertilizer. Dolomite Lime, 1; Calcium Nitrate, 0.127; Serpentine Superphosphate, 0.40; and Micromax, 0.009 kg 100 l⁻¹. (Burge *et al.*, Undated).

Until the plants were put into the PB'18 bags the seedlings were hand watered daily and twice weekly they were fed with half strength Hoagland solution (Lorenz and Maynard, 1988).

Fertigation started on 26 June 1992 when the plants were fed three times a day for 3-5 minutes depending on the weather condition. The liquid feed was allowed to run longer in warm weather to compensate for evapotranspirational loss and conversely, plants were fed for only three minutes in dull weather.

The stress treatment was first imposed on 15 July when the inflorescences of the first node were visible on half of the plants. The plants at this stage had a single shoot, 14 leaves and were about 10 cm in height.

Stressed plants were rewatered before visible symptoms of wilting were noted. The frequency varied from 1-3 days depending on the weather condition. Each pot was brought to container capacity before watering (feeding) ceased.

On three different occasions plants were sprayed with chemicals Lannate L. and Ronilan flow at a concentration of 400 g a.i ha⁻¹ and 2.5 g a.i. 10 l⁻¹ respectively against aphids and *Botrytis cinerea*. Plants were supported with wire and string to keep them upright, and were allowed to grow naturally without restricting the stem number.

Selective harvests based on fruit size and colour were made starting 12 October 1992 and terminating on 2 January 1993 after 11 weeks of harvesting.

3.2.3. Recording, sampling, and analysis

3.2.3.1. Yield and yield components

Non-destructive measurements of fruit diameter and length were made during the growth period on two fruits per treatment and replicate. The data was subsequently fitted to Richards function.

The number, fresh and dry weight, and length and diameter of fruit were recorded for each fruit harvested.

Fresh and dry weights of fruit and plant component parts were recorded using a Mettler balance. The dry weight of plant materials was recorded to the nearest 0.01 g after samples were oven dried at 80°C for 3 days (Ho, 1989). Fruit length and diameter were measured using digital callipers.

Yield components (HI, Leaf area, LAR, SLA, LWR) were evaluated at the final harvest according to the methods described by Hunt, (1978 and 1990).

3.2.3.2. Blossom-end rot score

Observations were made during each harvest for Blossom End Rot (BER) incidence and severity. Incidence of the physiological disorder was calculated as percent fruits showing any size of lesion of BER, while, severity was determined by measuring the average diameter of the lesion(s) and comparing it to the diameter of the fruit (Trinklein and Lambeth, 1976; Pill and Lambeth, 1980).

3.2.3.3. Tissue mineral analysis of Ca, Mg and K

Leaf and fruit samples were collected from plants representing the treatment combinations. Later, samples were dried and ground for mineral analysis.

Potassium, calcium and magnesium were assessed by Atomic Absorption Spectroscopy (AAS) following digestion in nitric acid (Technicon, 1973).

Tissue mineral analyses of Ca, Mg and K were done using 0.1 g of dried, finely ground tissue samples. Samples were put in acid washed (2M HCl) digestion tubes, covered with funnels to stimulate refluxing, and digested with 4 ml of concentrated nitric acid (70% HNO_3) for 8-10 hrs on a heating block maintained at a temperature of 150°C. After the solution had cleared, the funnels were removed and the remaining liquid was boiled off by raising the temperature to 250°C for 2 hrs.

The digested samples were finally diluted to a volume of 50 ml with a stock solution made up of strontium nitrate ($\text{Sr}(\text{NO}_3)_2$), caesium chloride (CSCl), 0.2M hydrochloric acid (HCl) and deionized water.

3.2.3.4. Nitrogen and Phosphorous

Total phosphorous and nitrogen were determined by colorimetric autoanalysis following the Kjeldahl digestion technique (Twine and Williams, 1971). In this procedure, samples were prepared as above. To these samples, 4 ml of Kjeldahl digest solution (25 g K_2SO_4 , 2.5 g selenium powder and 2.5 l of concentrated H_2SO_4) was added. The solution was digested at 350°C for 4-5 hrs. After the solution has cleared the digest was made up to 50 ml using distilled water.

3.2.4. Determination of minerals

The following standard solutions were prepared for determination of minerals with an atomic absorption spectrophotometer (AASP). Calcium (Ca), 2, 4, 6, 8, and 10 ppm; magnesium (Mg), 0.2, 0.4, 0.6, 0.8, and 1 ppm; potassium (K), 3, 6, 9, 12, and 15 ppm. These standards were made from a stock solutions of 1000 ppm Ca, Mg and K each.

The readings from the AAS expressed in ppm were used to determine tissue mineral concentration using the following formula:

$$Y = \frac{a \times b \times [c]'}{d}$$

[3.1]

where:

- Y = Concentration of the mineral in (mg.gdw⁻¹)
 a = volume after digestion (50 ml)
 b = AAS reading (ppm)
 [c] ' = this variable is the dilution rate applicable for determination of Mg and K in fruit and was also applicable if the tissue is leaf.
 d = weight of sample used for digestion

Tissue mineral content was determined by multiplying the mineral concentration (Y) by tissue total dry weight.

Experiment two Studies on dry matter production and partitioning in sweet pepper plants cv. Domino during ontogeny.

3.2.5. Treatments and procedure

Commencing 27 days from transplanting, 2 plants each of stressed and control plants were randomly selected and destructively harvested for dry matter determination on 6 different occasions from the seedling stage up to the fruit maturity (130 days from transplanting).

At each harvest, roots were washed clean and the plants were divided into leaves, stems, flower buds, flowers, and fruits and their fresh and dry weights were recorded. The dry weights of fruits previously harvested from these plants was added to determine the dry matter distribution in the fruits.

Leaf area was measured before drying using Leaf Area Meter Model Li-Cor 3100, and then, Leaf Area Ratio (LAR), Net Assimilation Rate (NAR), Relative Growth Rate (RGR), Specific Leaf Area (SLA), Leaf Weight Ratio (LWR) and harvest Index (HI) were computed according to the methods described by Hunt (1990) and Hedge (1987) by fitting polynomial curves to \log_e transformed primary data as follows:

$$\log_e W = a + b \cdot t + c \cdot t^2$$

[3.2]

$$\log_e A = a' + b' * t + c' * t^2$$

[3.3]

$$\log_e W_L = a'' + b'' * t + c'' * t^2$$

[3.4]

$$RGR = b + 2 * c * t$$

[3.5]

The following were derived from the above equations:

$$LAR = \exp * (\log_e A - \log_e W)$$

[3.6]

$$NAR = \frac{RGR}{LAR}$$

[3.7]

$$SLA = \exp * (\log_e A - \log_e W_L)$$

[3.8]

$$LWR = \exp * (\log_e W_L - \log_e W)$$

[3.9]

$$HI = \frac{W_F}{W_T}$$

[3.10]

where:

W is the plant dry weight at times (t)

A is the leaf area at times (t)

W_L is leaf dry weight at times (t)

$a, b, c, a', b', c', a'', b'',$ and c'' are constants.

W_F Dry weight of fruit

W_T is above ground dry mass

3.2.6. Statistical procedure

The design used for evaluating sweet pepper yield and yield components was a Randomized Complete Block (RCB) with 3 x 2 factorial arrangement with three replications.

The dry matter partitioning was compared for each harvest time and fruit growth studies was replicated and studied in time series as repeated measure analysis (Fernandez, 1991). At the last harvest dry matter distribution in the different organs was evaluated using a t-test.

Blossom-end rot was expressed as the percentage of fruits which showed symptoms. For analysis the data was converted by arcsine transformation and means were then compared with a t-test. The mean values were then transformed back to percentages.

Finally, data were subjected to analysis of variance and when appropriate regression analysis was done following the SAS Proc glm and proc reg procedures (Freund and

Littell, 1991). Furthermore, to validate the assumption of ANOVA residual analysis was also made (Fernandez, 1992).

For curve fitting and graphics the GLE graphics package was used.

3.3. Results

3.3.1. Total fresh fruit yield

Regularly watered plants gave markedly higher total yields in terms of fresh weight than stressed plants (Table 3.2). However, no appreciable yield difference was noted between the three maturity classes evaluated, and no interaction was observed between irrigation and maturity.

Table 3.2. Effects of water stress and harvesting regime on the total fruit yield (kg.plant⁻¹) of sweet pepper plants.

Irrigation	Maturity			Mean ¹	Signf
	Green	Green-Red	Red		
Control	0.488±0.04 ^y	0.467±0.04	0.485±0.04	0.48±0.02a	***
Stressed	0.213±0.04	0.210±0.04	0.230±0.04	0.22±0.02b	
Mean	0.351±0.03	0.338±0.03	0.378±0.03		
Significant ^x	ns	ns	ns		

¹ means followed by different letters are significant according to Duncan's multiple range test at $p \leq 0.001$.

^x *, **, ***, ns= significant at $P \leq 0.05$, 0.01, 0.001 levels or non significant.

^y ± are standard error of mean

3.3.2. Total fruit dry weight

Well watered plants had twice the total fruit dry weight of stressed plants. The maturity classes, however, didn't show a significant yield difference although there was a trend for an increase in dry weight with maturity (Table 3.3a).

On the basis of dry matter percentage stressed plants appeared to have a higher dry weight to fresh weight ratio as compared to regularly watered plants (Table. 3.3b). This appeared to be due to the fact that well watered plants had more water content than stressed plants (data not presented). On the other hand, fruit dry matter content showed an increasing trend with maturity ($P \leq 0.08$) (Table 3.3b).

3.3.3. Fruit number and average fruit size

Irrigation significantly increased the mean number of fruits produced in sweet pepper plants by more than 100% (Table 3.4a). There were no difference in fruit number between the three maturity classes and no irrigation x maturity interaction was noted although, there was a trend for a greater number of fruits in the earlier harvests of control plants.

No difference occurred for average fruit weight of fresh or dry weights (Table 3.4b) or for diameter and length expressed as a ratio between the two attributes (Table 3.4c).

3.3.4. Incidence of blossom-end rot

Although there was little effect of treatment on appearance of blossom-end rot, stressed plants had a slightly higher but non significant percentage affected fruit than well watered plants (Table 3.5a). There was no effect of treatment or maturity on

Table 3.3. Total dry weight (g.plant⁻¹), and percent dry matter content of sweet pepper fruits in relation to irrigation and stage of harvesting.

a) Total fruit dry weight					
Irrigation	Maturity				
	Green	Green-Red	Red	Mean ¹	Significant
Control	44.67±3.42 ^y	47.00±3.42	49.08±3.42	46.92±1.92a	***
Stressed	21.83±3.42	22.17±3.42	25.42±3.42	23.17±1.92b	
Mean	33.25±2.42	34.67±2.42	37.33±3.42		
Significant	ns	ns	ns		
b) Fruit dry matter content (%)					
Control	5.25±0.2 (9.15) ^z	5.85±0.2 (10.20)	5.78±0.2 (10.06)	5.63±0.114 (9.80)b	*
Stressed	5.94±0.2 (10.34)	6.15±0.2 (10.70)	6.33±0.2 (11.12)	6.14±0.114 (10.69)a	
Mean	5.59±0.14 (9.75)b	6.0±0.14 (10.45)ab	6.05±0.14 (10.59)a		
Significant	P≤0.08	P≤0.08	P≤0.08		

¹ means followed by different letters are significant according to Duncan's multiple range test at P≤0.05 and P≤0.001.

^x *, **, *** and ns = significant at P≤0.05, 0.01 or 0.001 levels or non significant respectively.

^y ± standard error of means

^z values in bracket are back transformed arcsine values.

Table 3.4. Fruit number, average fruit size and fruit length:diameter ratio as affected by irrigation and maturity treatments.

a) Fruit number					
Irrigation	Maturity				
	Green	Green-Red	Red	Mean	Significant
Control	81±5.91 ^y	73±5.91	69±5.91	74±3.41a ¹	***x
Stressed	37±5.91	34±5.91	34±5.91	35±3.41b	
Mean	59±4.18	53.5±4.18	51.5±4.18		
Significant	ns	ns	ns		
b) Mean fruit fresh weight (g)					
Control	72.8±9.18	77.1±9.18	84.4±9.18	78.1±5.29	ns
Stressed	76.1±9.18	76.2±9.18	84.3±9.18	78.84±5.29	
Mean	74.4±6.49	76.6±6.49	84.4±6.49		
Significant	ns	ns	ns		
c) Fruit diameter to length ratio					
Control	1.20±0.07	1.26±0.07	1.20±0.07	1.22±0.02	ns
Stressed	1.19±0.07	1.16±0.07	1.18±0.07	1.18±0.02	
Mean	1.20±0.02	1.21±0.02	1.19±0.02		
Significant	ns	ns	ns		

^{K=} Keys as table 3.3.

Table 3.5. The effects of irrigation treatment and fruit harvest maturity on the incidence (%) and severity (mm.cm⁻¹) of BER on sweet pepper fruit.¹

a) Incidence of BER					
Irrigation	Maturity				
	Green	Green-Red	Red	Mean	Significant
Control	1.25 (2.18) ²	3.53 (6.14)	2.40 (4.18)	2.39 (4.17)	ns
Stressed	5.75 (9.93)	2.55 (4.44)	4.21 (7.31)	4.17 (7.23)	ns
Mean	3.50 (6.06)	3.04 (5.29)	3.31 (5.75)		
Significant ^x	ns	ns	ns		
b) Severity of BER					
Control	0.039	0.031	0.057	0.042	ns
Stressed	0.031	0.021	0.054	0.036	ns
Mean	0.035	0.026	0.055		
Significant	ns	ns	ns		

¹ values are average of 3 reps and 4 plants.rep.⁻¹

² values in brackets are back transformed arcsine values.

^x ns nonsignificant

a) SEM-irrigation, maturity and interaction are: 1.76, 2.15, and 3.04 respectively.

b) SEM-irrigation, maturity and interaction are: 0.009, 0.012 and 0.017 respectively.

severity of BER (Table 3.5b). However, blossom-end rot was highest in the earlier harvests and progressively decreased as the season advanced (Table 3.6). When the data was pooled over all harvests, fruits from stressed plants had significantly higher BER incidence ($t \leq 0.05$) than well watered plants (Table 3.6).

Blossom-end rot first appeared on fruits 89 days after transplanting and 42 days after plants were exposed to water stress treatment. Blossom-end rot fruits usually appeared on fruits of lower rather than higher nodes.

3.3.5. Tissue mineral analyses

Fruits generally had a lower Ca concentration than leaves (Table 3.7). Moreover, the Ca concentration in fruits of stressed plants appeared to be lower than in well watered plants ($P \leq 0.05$) (Table 3.7). The concentration of N, P, K and Mg in fruit was not affected by treatment. However, it appears that the stress treatment decreased fruit N and P while increasing K and Mg but non significantly (Table 3.7).

Water stress increased leaf K concentration ($P \leq 0.01$) while slightly decreasing leaf Ca concentration ($P \leq 0.06$) as compared to the control treatment (Table 3.7). The concentrations of N, P and Mg however, were not significantly affected by treatment (Table 3.7).

Fruit Ca concentration decreased during fruit development period while leaf Ca concentration increased (Fig 3.1 a and b). The decline in Ca concentration was more pronounced for stressed plants than well watered plants particularly with advancement in growth and development ($P \leq 0.05$).

Table 3.6. Effect of watering levels on the incidence of BER on early and late harvested fruit and maturity.¹

Treatment	Early harvest ²		Late harvest		Total harvest	
	fruit number	BER ^y %	Fruit number	BER %	Fruit number	BER %
Control	131	4.78±1.56 (8.32) ^z	92	3.01±1.43 (5.23)	223	2.39±0.39 (4.17)
Stressed	87	5.90±1.56 (10.30)	19	0.0	105	4.14±0.39 (7.23)
Significant	ns ^x	ns	*	ns	*	*
SEM (df=2)	19.60	0.009	18.32	0.008	9.90	0.003

¹ values are average of 3 blocks from pooled maturity classes.

² Total for 2 months

^x *, ns are significant at $t \leq 0.05$ level or non significant.

^y percentage of fruit harvested

^z values in bracket are back transformed arcsine values.

Table 3.7. Major nutrient concentration (mg.gdw⁻¹) of sweet pepper fruit and leaves subjected to water stress and regular watering.¹

a) Fruit mineral concentration (mg.gdw ⁻¹)					
Treatment	N	P	K	Ca	Mg
Control	21.03	3.04	26.87	0.91a	1.62
Stressed	19.77	2.87	30.93	0.69b	1.66
SEM (df=4)	1.3	0.3	2.14	0.15	0.06
b) Leaf mineral concentration (mg.gdw ⁻¹)					
Control	30.6	9.6	48.8b	32.8	11.97
Stressed	28.6	10.5	53.2a	26.2	12.20
SEM (df=4)	0.91	0.39	0.67	1.85	0.44

¹ values are average of 3 fruits or 3 plants' leaves per treatment.

^x means with different letters are significant according to Duncan's test.

3.3.6. Fruit growth of sweet pepper

Weekly monitoring of the diameter and length cumulative growth of sweet pepper fruits revealed that they both followed a simple sigmoid growth pattern (Fig 3.2a and 3.3a).

Water stress appeared to have a negative effect on the diameter and length growth of sweet pepper fruit 1 to 3 weeks after anthesis ($P \leq 0.05$). This effect diminished with an advancement in fruit growth. Water stress seems to have little effect on the RGR of fruit diameter and length (Fig. 3.2b and 3.3b).

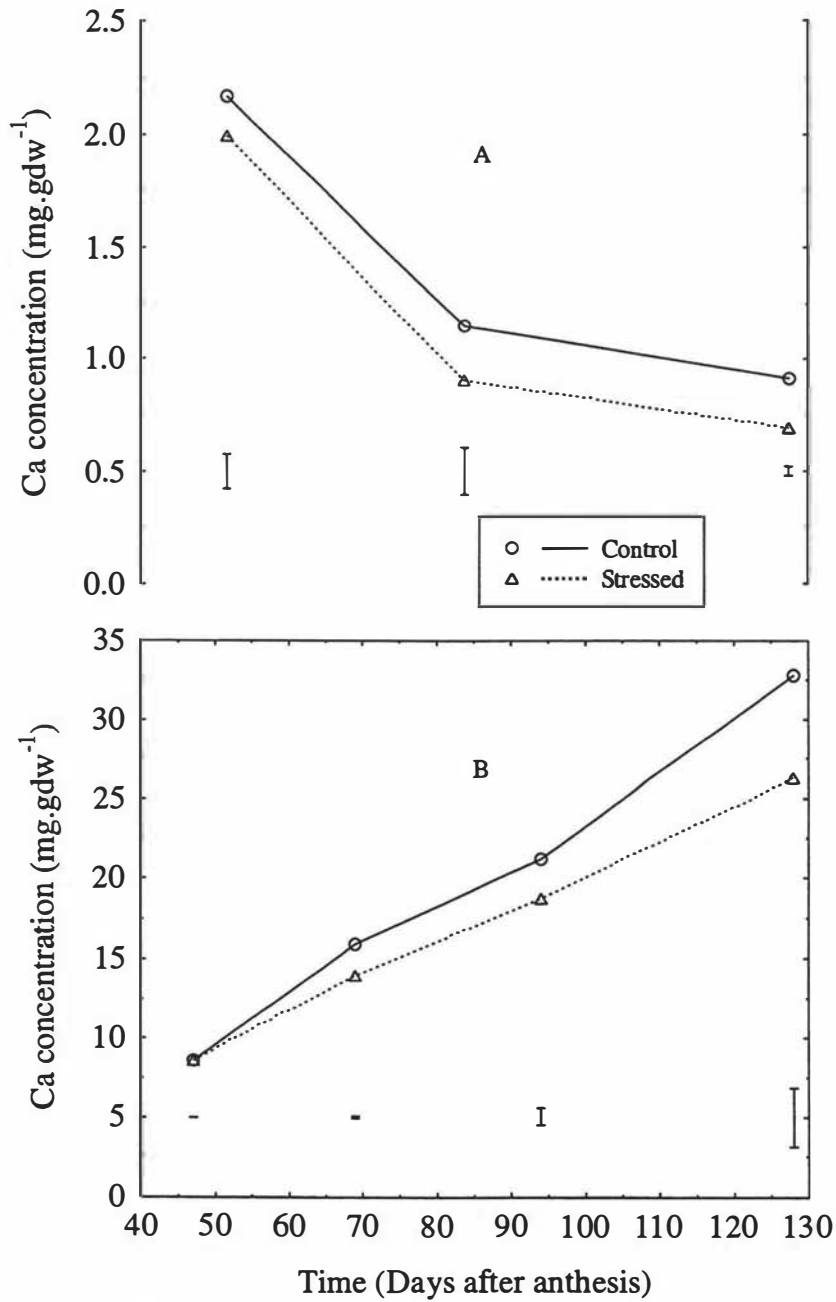


Fig 3.1: Seasonal accumulation of calcium in sweet pepper fruit (A) and leaf (B) as affected by water stress. Each data point is an average of 2 fruit and a composite sample of 2 plants' leaves. Vertical bars indicate standard error of means.

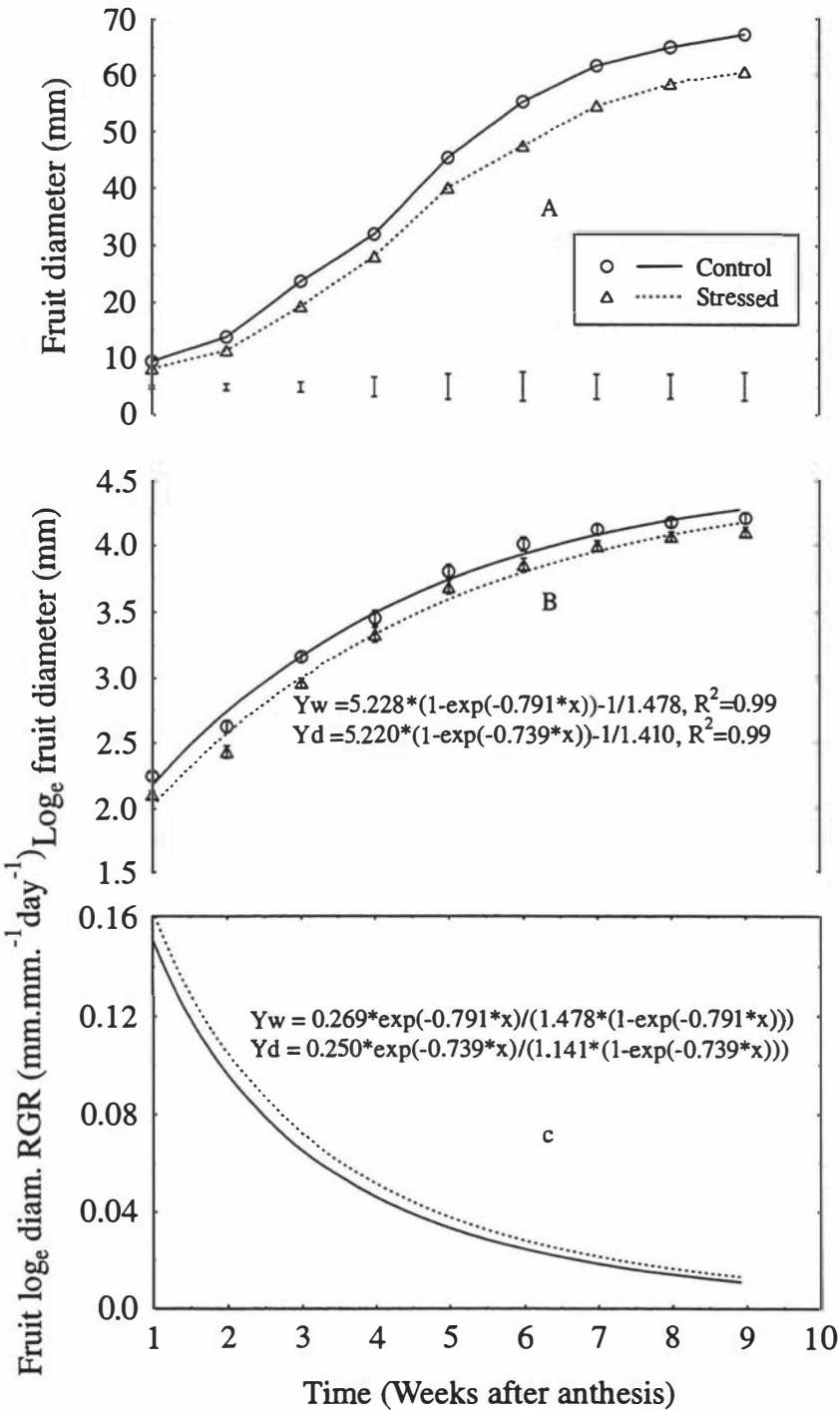


Fig 3.2: Cumulative diameter growth of sweet pepper fruit (A) Log_e length (B) and RGR (C) as affected by water stress. Each data point is an average of 6 fruit. Log_e data fitted to Richards function. Vertical bars indicate standard error of means.

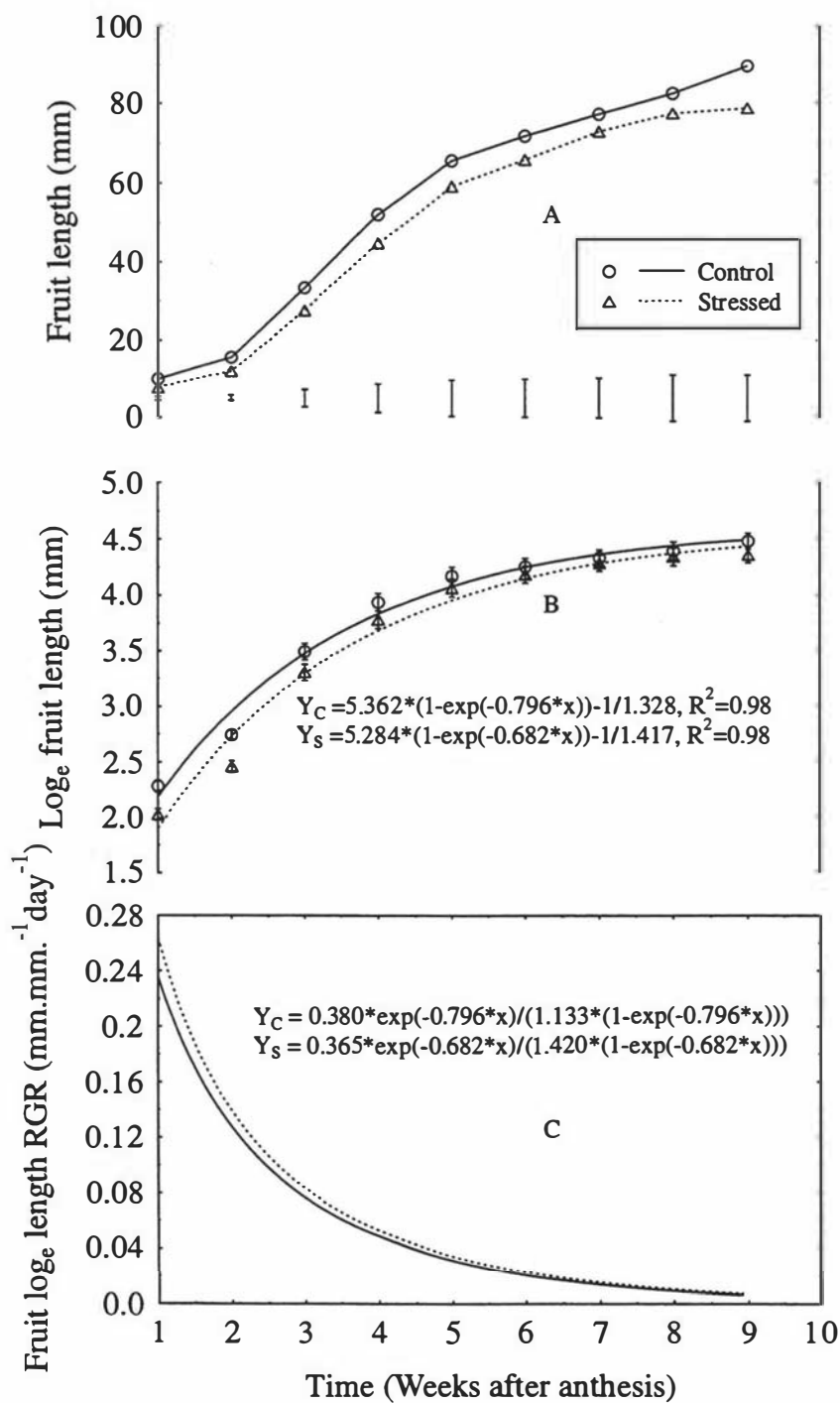


Fig 3.3: Cumulative length growth of sweet pepper fruit (A) Log_e length (B) and RGR (C) as affected by water stress. Each data point is an average of 6 fruit. Log_e data fitted to Richards function. Vertical bars indicate standard error of means.

3.3.7. Dry matter production and distribution

3.3.7.1. Crop growth indices

Total dry weights (\log_e) of plants were fitted to quadratic functions with high coefficients of determination (Fig. 3.4a). Generally a continuous increase in growth was noted. Stressed plants had a slower growth rate than well watered plants from 47 days after transplanting. The RGR of the plant increased for both stressed and well watered plants but, control plants had a significantly higher RGR than stressed plants ($t \leq 0.05$) except 128 days after transplanting (Fig. 3.4b).

During the initial growth of the plant total dry matter accumulation of the plant was slow up to nearly 70 days after transplanting (Fig. 3.4a). The increase continued later for control plants up to the final measurement while stressed plants showed a lag about 100 days after transplanting. From 69 days after transplanting control plants had significantly higher ($t \leq 0.01$) total dry weight than stressed plants.

The leaf area ratio (LAR) showed a steady decline, with the highest value at the seedling stage (Fig. 3.5a). At the early stage of plant growth the LAR was high for well watered plants ($t \leq 0.05$). At about 128 days after transplanting both had more or less similar LAR (Fig. 3.5a) as a result of an increase in LAR of stressed plants due to new flush of leaf growth after fruit harvest.

The net assimilation rate (NAR) showed a progressive increase through out the growth of the plant (Fig. 3.5b). There was a slightly higher NAR for control plants than stressed plants early in the growth period although it was not statistically significant. This was reversed at the later stage of growth until the final harvest when stressed plants showed a slightly higher NAR than control plants. RGR is a function of both NAR and LAR ($RGR = NAR \times LAR$) (Hunt, 1982). In this experiment NAR increased with time with little difference between treatments as did the RGR of both control and stressed plants. Using linear regression, RGR had a close positive

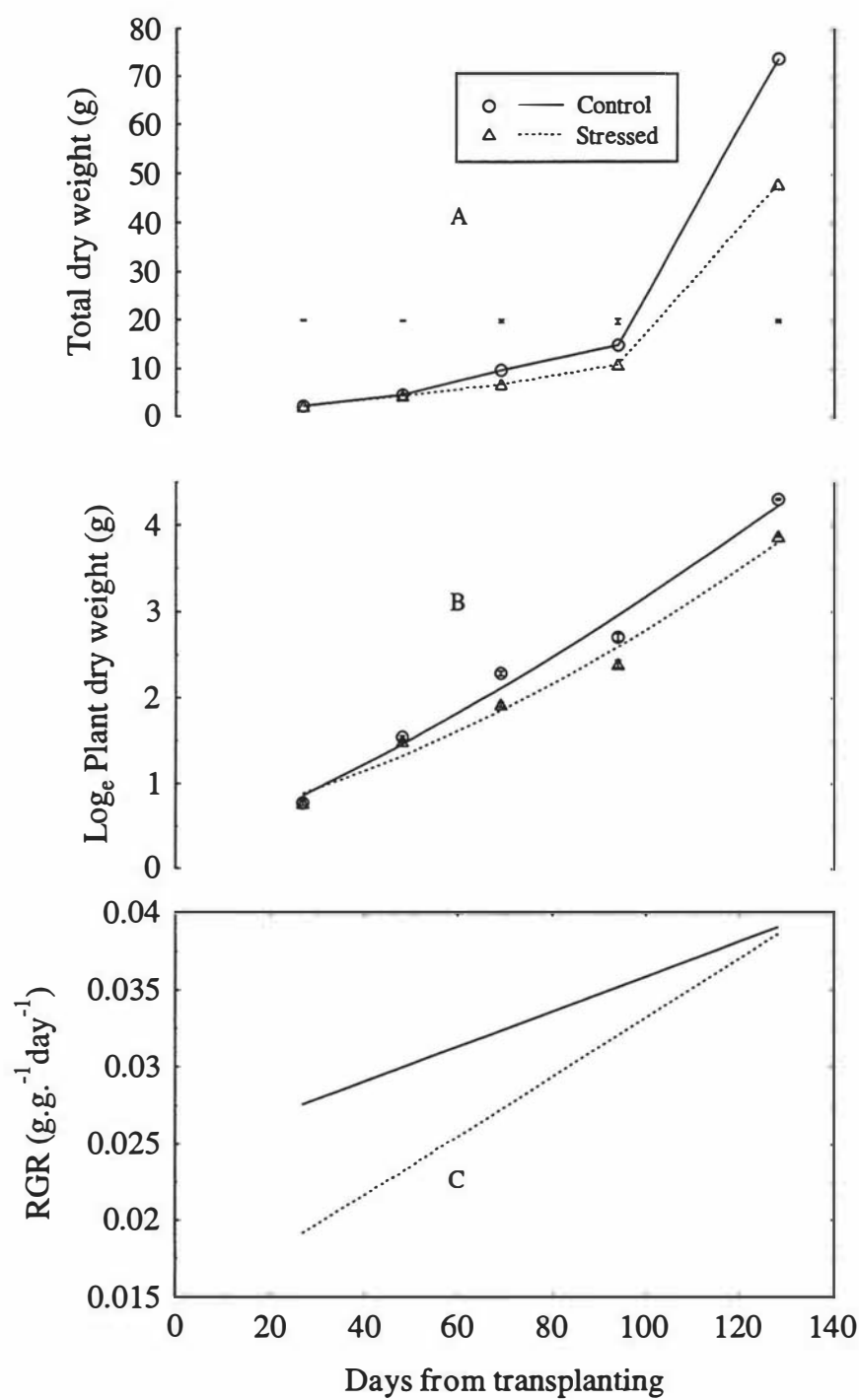


Fig 3.4: Cumulative dry weight growth (A) (\log_e) dry weight (B) and RGR (C) of sweet pepper plant as affected by water stress. Each data point is an average of 2 plants. Vertical bars indicate standard error of means.

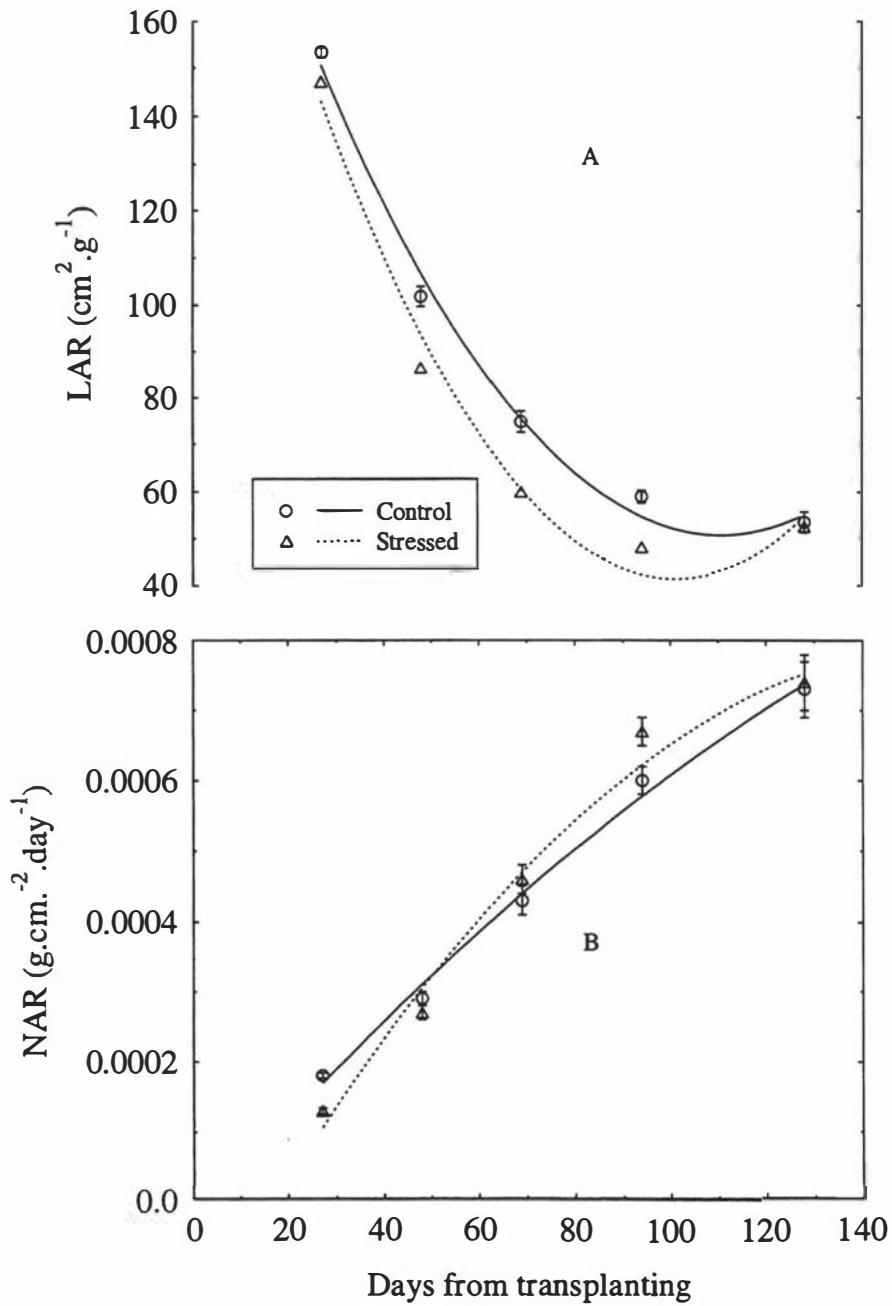


Fig 3.5: LAR (A) and NAR (B) derived from a fitted curve as affected by water stress. Each data point is an average of 2 plants. Data fitted to quadratic functions.

correlation with the NAR of control ($r=0.99$) and stressed ($r=0.98$) plants. On the other hand, LAR showed a negative correlation with both control ($r=-0.90$) and stressed ($r=-0.83$) plants.

Total dry weight accumulation showed a close negative correlation with LAR, ($r=-0.88$ and -0.78), and a positive correlation with leaf area ($r=0.98$ and 0.94) and NAR ($r=0.97$ and 0.92) in both control and stressed plants respectively.

SLA and LWR declined with time in both control and stressed plants (Figs. 3.6a and b). The SLA of control plants slightly increased and remained unchanged until 69 DAT and declined at a fast rate afterwards. The SLA of stressed plants however, declined progressively with time. LWR declined in both cases in a similar fashion although there was a slight increase 128 days after transplanting in both treatments.

3.3.7.2. Dry matter distribution during ontogeny

The major proportion of dry weight in pepper plants accumulated in leaves during the initial growth stage (Fig. 3.7). From 60 days onwards there was a steady decline in the proportion of dry weight in the leaf parts which is approximately the stage at which the plants entered the generative phase. However, there was no significant difference in LWR between control and stressed plants. The buds+flower weight ratio was low at all stages of growth and it was not affected by treatment. The root weight ratio (RWR) declined with time and irrigation favoured the RWR of control plants around 70 DAT while stressed plants appeared to have higher RWR afterwards ($P\leq 0.05$).

The stem weight ratio (SWR) declined during growth until about 100 DAT when it peaked due to stem branching (Fig. 3.7). There was no significant difference between treatments in SWR except at the start of this growth flush when stressed plants had higher proportion ($P\leq 0.05$). There was no difference in BFWR between control and

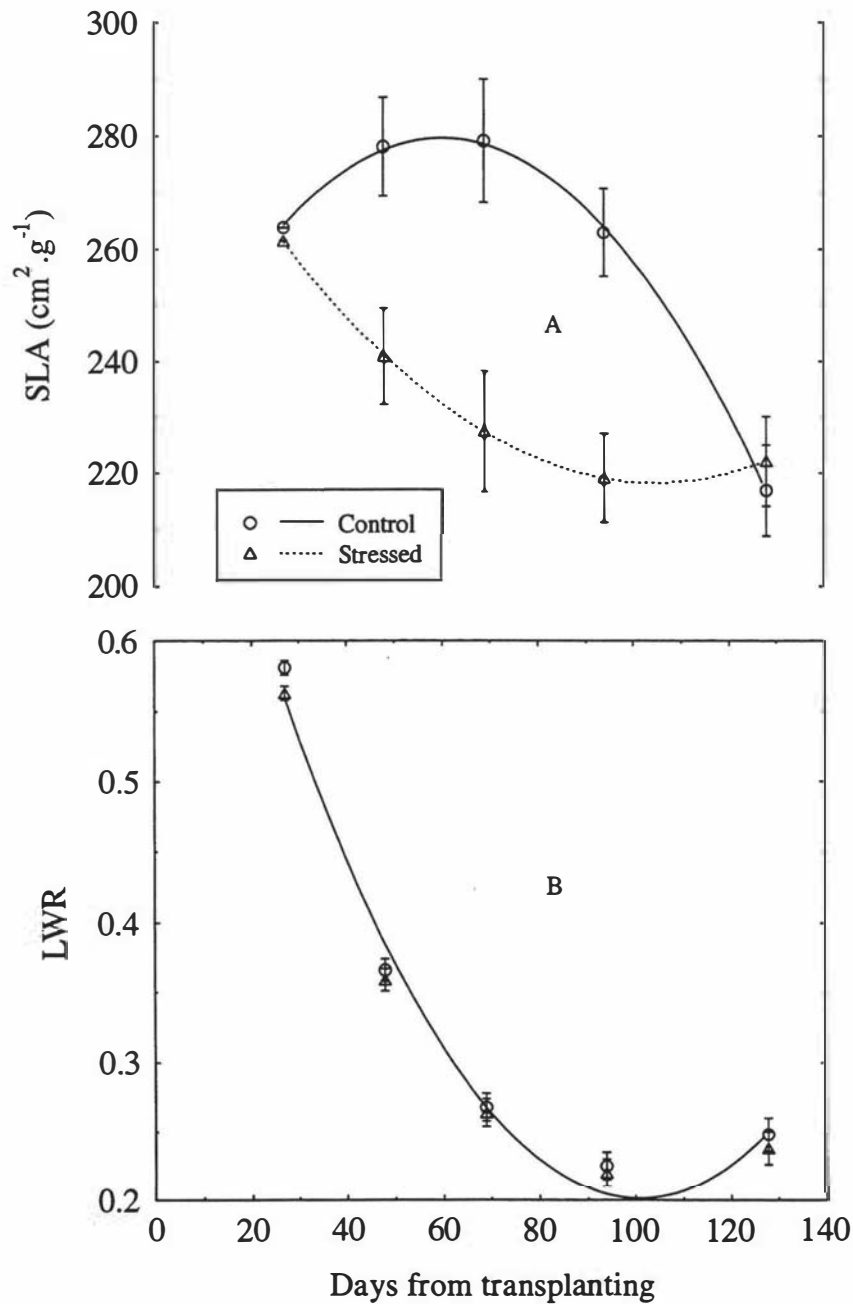


Fig 3.6: SLA (A) and LWR (B) derived from a fitted curve as affected by water stress. Each data point is an average of 2 plants. Data fitted to quadratic functions.

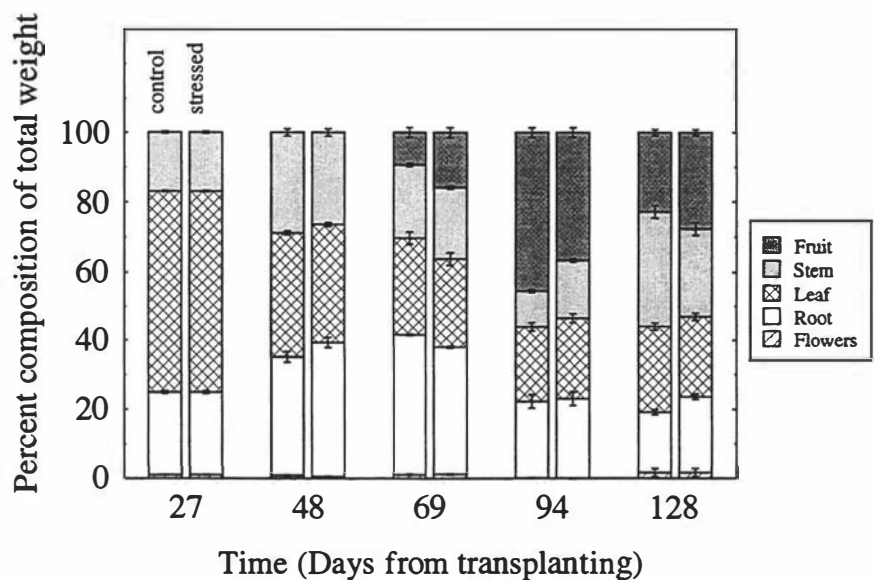


Fig. 3.7. Effect of water stress on dry matter partitioning between the different plant organs of capsicum plants during ontogeny. Each data point represents the mean of 2 plants. Vertical bars indicate standard error of means. Flowers include flower buds.

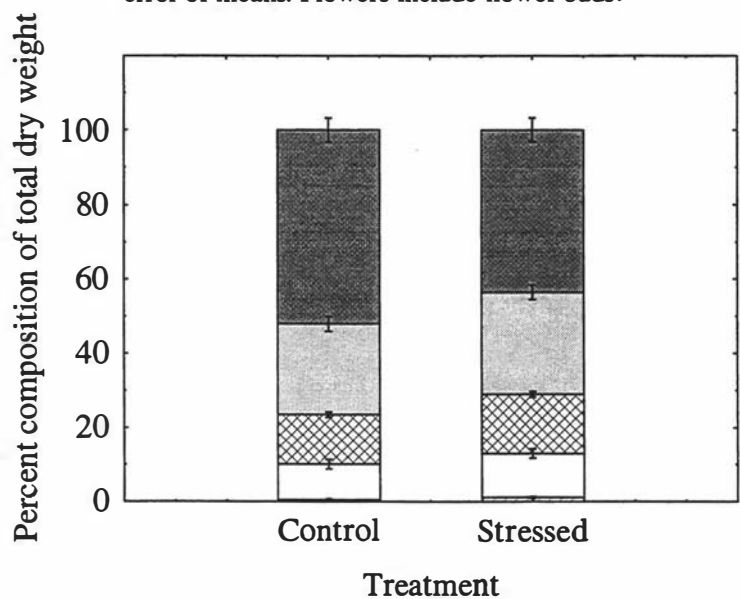


Fig. 3.8. Effect of water stress on dry matter partitioning between different plant organs of sweet pepper plants at the final harvest (187 days after transplanting). Each data point represents the means of 9 plants. Vertical bars indicate standard error of means.

stressed plants (Fig. 3.7). Seventy days after transplanting, a significant proportion of plant dry weight was accounted for by fruits (Fig. 3.7). The fruit weight ratio (FWR) of stressed plants was found to be significantly lower than control plants.

3.3.7.3. Dry matter distribution at the final harvest

Water stress has a profound effect on both the vegetative and reproductive yields of sweet pepper plants (Table 3.8a and b). However, the water stress seems to have little effect on plant height, leaf number produced and SLA (Table 3.8a).

Control plants had a higher leaf area than stressed plants while, the LAR and LWR of stressed plants was higher than control plants (Table 3.8a).

Water stress significantly reduced total fruit fresh weight in sweet pepper plants ($P \leq 0.001$) (Table 3.8b). However, fruit number and average fruit size and root to shoot ratio were not affected by treatment (Table 3.8b). Water stress had a beneficial effect in terms of increasing the dry matter content of fruits as compared to control treatment (Table 3.8b).

The harvest index of sweet pepper was significantly different between irrigation treatments (Table 3.8b). Control plants had 58 % of their dry matter diverted to fruit as compared to water stressed plants which had only 49%. Fruit accounted for the major distribution of assimilates in pepper plants at harvest (Fig. 3.8). It was shown that stressed plants had a lower proportion of assimilates partitioned to their fruits than well watered plants with no difference in the remaining parts (Fig. 3.8).

Table 3.8. The effect of water stress on the vegetative growth and quality of sweet pepper plants¹.

a) Vegetative growth						
Treatment	Plant height (cm)	Leaf number	Leaf area (cm ²)	LAR (cm ² .g ⁻¹)	LWR	SLA (cm ² .g ⁻¹)
Control	82.99	287	6769.11	20.19	0.134	151.14
Stressed	77.40	252.7	5516.29	24.87	0.161	153.32
Significant ^x	ns	ns	0.08	*	*	ns
SEM (df=16)	3.15	25.85	483.87	1.50	0.007	4.71
b) Fruit yield and quality						
	Fruit number	Total Fruit fresh weight (kg)	Average fruit size (g)	Fruit dry matter content (%)	Harvest Index	Root:top
Control	22.9	1.783	79.40	5.67(9.87) ^y	0.58	0.112
Stressed	19.0	0.959	60.50	5.91(10.30)	0.49	0.155
Significant	ns	***	ns	ns	*	ns
SEM (df=16)	2.60	0.133	8.16	0.22	0.033	0.019

¹ values are average of 9 plants treatment⁻¹

^x *, ***, ns indicate significant at $t \leq 0.01$, 0.05 levels and non significant.

^y values in bracket are back transformed arcsine values.

3.4. Discussion

3.4.1. Sweet pepper growth and fruit yield

Restricting water supply to winter grown sweet pepper plants hastens maturity, reduces fruit number and total yield while increasing fruit dry matter content. This is in agreement with the results of Alvino *et al.*, (1990b). Water stress also reduced leaf area but with little effect on plant height and leaf number. DeKoning and Hurd (1983) also reported similar results on tomato. It was the water restriction accompanied presumably with limitation in nutrient supply (Tables 3.3 and 3.8) which brought about such difference in growth and yield of sweet pepper in this experiment. Water stress affects photosynthesis by lowering stomatal conductance (Schulze, 1986a; Wolf and Rudich, 1988). This is due to a reduction in cell water, electron transport and inhibition of phosphorylation (Kozlowski, 1976). As a consequence, total marketable fruit yield of sweet pepper was significantly reduced by 55 % in stressed plants as compared to well watered ones (Table 3.2). This may also be due to a reduction of turgor in the fruit which inhibits its growth and activity, and thus the translocation of assimilates to that organ is consequently reduced (Begg and Turner, 1976).

O'Sullivan (1979) found that yield increment in irrigated sweet pepper plants was a result of a significant increase in the amount of green fruits. In this experiment, no significant difference in either number of fruits or total yield between the three stages of maturity was noted although somewhat higher number of green fruits were harvested than either turning or red mature fruits. Generally, however, water stress significantly reduced fruit number (Table 3.4). This is in conformity with the reports of Doorenbos and Kassam (1979) and Alvino *et al.*, (1990b). According to Doorenbos and Kassam (1979) water shortage just prior to and during early flowering reduces the number of fruits in sweet pepper. In the current experiment, since water stress was imposed at the onset of flowering, it appears to have had similar results.

Average fruit size was not affected by water stress nor was fruit diameter, fruit length and their ratio (Table 3.4). Fruit size in tomato decreased as EC levels increased (Clover, 1991) due to a reduction in turgor pressure in the fruits when at 17 mS tomato fruits accumulated less than 2 g of water a day compared with 3 g at 7 mS. Thus, higher EC has a serious consequence on the size of tomato fruit. In the present experiment EC was only 2.5 mS.cm⁻¹, too low to cause a marked effect on fruit size parameters. Moreover, since the plants were rewatered after being subjected to stress for a few days, this may have prevented any reduction in fruit diameter and length size that would probably have occurred had water stress persisted. Although water stress did not affect fruit size at the final harvest it significantly reduced diameter and length during the early growth period (Figs. 3.2 and 3.3). This reduction in fruit growth at an early stage may be due to competition for assimilate between vegetative parts and the newly developing fruit (Fig. 3.7). As the fruit grows it shows a strong sink activity so as to attract more assimilate in spite of reduced vegetative growth. This is because, photosynthesis is less sensitive to water stress than plant growth (Li *et al.*, 1991).

Limiting water supply always reduces crop leaf area (Table 3.8). Leaf area ratio (LAR) appeared to be higher towards harvest for stressed plants than for well watered ones thus confirming the reports of Hedge (1987) and Alvino *et al.*, (1990b). The expenditure of more energy into the photosynthetic apparatus in turn increased the LWR of stressed plants (Table 3.8). The reduced vegetative growth in sweet pepper in water stressed plants may be due to a reduction in cell expansion in leaf and possibly by lower rate of cell division as observed in tomato (DeKoning and Hurd, 1983).

The higher leaf area ratio for stressed plants particularly towards the final harvest indicates that such plants adapt themselves to stress conditions through reduced dry mass and leaf area production.

Well watered sweet pepper plants diverted a greater proportion of their dry matter in

to fruits than stressed plants as indicated by an increased harvest index. Reduced leaf area with water stress reduces the photosynthetic capacity of the crop (Bethke and Drew, 1992) and lowers the sink strength of the fruit due to a reduction in water content (Adams and Ho, 1989). Therefore, due to availability of more photosynthates and increased sink activity and size of control fruit, more assimilate was accumulated in control fruit than in fruit of water stressed plants. On the other hand, more assimilate was accumulated in vegetative organs than in the reproductive organs in stressed plants. Hedge (1987) reported that plants irrigated at 40 % available soil moisture (ASM) had a higher harvest index than those irrigated at either 20 % or 80 % ASM.

Although stressed plants showed a slightly higher root:top ratio, this was not statistically significant. This presumably is due to the level of water stress which was not quantified under the condition of the experiment. Therefore, it may have failed to have a major impact on the root:top ratio which is generally recognized as stress adaptation mechanism of plants (Fitter and Hay, 1987). Sweet peppers generally prefer moderate moisture. Thus, both frequent irrigation (Sadykov and Mikhael, 1982) and high soil moisture deficit (Sirjacobs and Dada, 1985) adversely affect its productivity.

Fruits from stressed plants were harvested about a week earlier than from well watered plants although the effect of water stress was not significant on the yields of red ripe fruits (Table, 3.6). The early harvest of fruit from stressed plants is believed to be due to an increase in stored carbohydrate (DeKoning and Hurd, 1983). This may be the reason for an increase in dry matter content of individual fruits in stressed plants compared to control fruit (Table, 3.3). Also the decrease in vegetative growth and flower bud initiation due to low turgor might hasten reproductive maturity by decreasing competition for carbohydrate (Sylvertsen, 1985). Moreover, lower Ca concentration in water stressed fruit may also have contributed to the early maturity of the fruit. Calcium is known to delay fruit maturity by reducing tissue softening and ethylene production (Stow, 1993; Gerasopoulos *et al.*, 1996).

3.4.2. Incidence of blossom-end rot

The incidence of BER was not statistically different when irrigation and maturity treatments were compared (Table 3.5). This might be due to inconsistency in the incidence of BER between maturity classes, where the stress treatment induced a high but non significant BER incidence, whereas the pooled analysis of BER incidence over all maturity classes showed that, water stress indeed induced BER in sweet pepper fruit (Table 3.6). Calcium deficiency is the most likely reason for BER incidence, as calcium provides rigidity to the cell wall (Dey and Brinson, 1984) as it regulates cell cohesion by forming Ca bridges between pectic polymers (Fry, 1986). It is also involved in maintaining membrane integrity. The loss or deficiency of Ca leads to weakening of the cell wall and leakage of solutes resulting in collapse of the cell inducing BER.

Water stress induce BER by influencing the uptake and transport of Ca from roots to fruit either by impairing root development or by reduced transpiration. Calcium is known to be transported through xylem vessels in the transpiration stream (Clarkson, 1984). Although the plant water status was not measured in this experiment, it is well established that as water stress is imposed the water relation of the plant will be disturbed leading to the closure of stomata (Kaiser, 1987). This in turn reduces transpiration and consequently Ca uptake and accumulation in the fruit decreases (Table 3.7 a and b). Water stress can also inhibit the development of root pressure at night which is likely to favour the accumulation of Ca in fruits (Collier, 1982).

The low incidence of BER in this experiment may have been a result of the environment as low light and high relative humidity reduce fruit growth rates. Under these conditions, fruit grows slowly due to reduced photosynthesis and translocation of assimilate. The slow growth of the fruit in this experiment (Figs. 3.2 and 3.3) may have reduced the development of the disorder as deficiency symptoms appear only when fruits grow rapidly (Chiu and Bould, 1976). The resulting acceleration in

growth requires extra Ca for the synthesis of new cell walls.

Fruit Ca accumulation may also be enhanced and Ca deficiency disorders such as BER avoided by high night RH as this condition favours the development of root pressure to supply Ca to the fruit (Guttridge and Bradfield, 1983). Since the nights were cool during the current experiment the possibility exists. Another possible reason for the low incidence of BER could be the level of water stress imposed and EC level used. The level of BER is said to be highly influenced by the level of salt concentration in the medium (Sonneveld, 1979; Adams and Ho, 1985). The EC level used in the current experiment was 2.5 mS.cm^{-1} (Table 3.1) although higher than the minimum 0.9 mS.cm^{-1} recommended by Sonneveld and Voogt (1981) for tomato or the 1.5 mS.cm^{-1} for sweet pepper (Uffelen and Bakker, 1989) is standard. As demonstrated by Guttridge and Bradfield (1983) and Adams and Ho (1985) low EC levels of the nutrient medium as compared to higher EC helped maintain higher root pressure at night which promoted Ca uptake and its subsequent translocation to fruits.

Adams and Ho (1985) observed that at EC of 2 mS.cm^{-1} calcium concentration in the solution was 165 mg.l^{-1} , while at 10 mS the Ca concentration was 670 mg.l^{-1} . Despite this, Ca concentration of the fruit was reduced substantially from 3.48 mg at 2 mS^{-1} to 2.44 mg at 10 mS^{-1} . In this experiment the Ca concentration in the solution was 192 mg.l^{-1} (Table 3.1) at 2.5 mS which is within the optimum limit of 150 to 250 mg Ca in a solution suggested by Adams and Ho (1985). Thus, the low incidence of BER in the current experiment could be because of slow growth of the fruit and availability of adequate Ca in the medium.

The difference in the incidence of blossom-end rot between well watered and stressed plants (Tables 3.5 and 3.6) may be explained in terms of difference in Ca concentration of fruit (Table 3.7) where control fruit had significantly higher Ca concentration than fruits from water stressed plants.

BER occurred mainly in the early harvested fruits picked from the lower nodes on

the plant (Table, 3.6), while very little or no BER occurred in later harvested fruits from the upper nodes, which were smaller in size and fewer in number (Table 3.6). It is suggested that the lower fruits exert a limitation on size of fruits on upper nodes of sweet pepper because, the lower fruits are metabolically active sinks (Ali and Kelly, 1992). Thus more assimilate and phloem mobile elements such as N, P, K, and Mg would be delivered to the fruit which would not be matched by xylem mobile Ca to sustain new cell growth. With the decrease in Ca accumulation and increase in dry matter accumulation, the Ca concentration decreases while K:Ca and Mg:Ca ratios would increase leading to the incidence of BER in the larger fruits on the lower nodes while the smaller fruits on the upper nodes escape. BER can also appears during dry periods before the plants have established a large root system (VanderWerken and Wilcox-Lee 1988) thus implying that the root system may not be able to supply enough Ca to the fruit during early plant establishment. This problem is likely to be aggravated by water stress.

Fruits on the lower nodes are likely to have greater competition from leaves for Ca supply than fruits produced on the upper nodes. Fruits on the lower nodes are produced after 9-11 leaves are formed (Dorland and Went, 1947) unlike the upper fruits which are formed after every two leaves are produced (Rylski and Halevy, 1972; Clapham and Marsh, 1987). Thus, the fruits from the upper nodes may have less competition from highly transpiring leaves. Consequently more Ca could be translocated to these fruits thus, reducing the incidence of BER.

3.4.3. Accumulation of nutrients

Sweet pepper fruit accumulated calcium continuously but at a variable rate through out development (Fig. 3.1a). The Ca concentration declined with increased fruit size suggesting that dilution of the nutrient occurred. The fruit Ca concentration declined 50 to 80 days after transplanting which is 2 to 3 weeks after anthesis (Fig. 3.1). During the same period the fruit had the highest growth rate (Figs. 3.2b and 3.3b).

As the fruit grows and expands due to accumulation of photosynthates, new cells are formed which require Ca for wall synthesis increasing the demand for Ca. If Ca accumulation doesn't cope with this demand, the increase in fruit size dilutes the already available Ca, resulting in sharp declines in Ca concentration.

Despite adequate Ca in the nutrient solution, water stress tended to reduce the translocation of Ca into the fruit. This was due to the increased osmotic potential of the nutrient medium which suppressed the absorption and transport of water within the plant. This in turn reduced leaf transpiration (Collier, 1982) possibly due to closure of stomata thereby, reducing Ca transport through transpirational stream.

Transpiration has an effect on the distribution of calcium in the plant at low conductivity (Ehert and Ho, 1986a). With an increase in humidity and a consequent reduction in transpiration, more Ca accumulated in mature leaves as well as stem with relatively less going to the young expanding leaves and fruit (Armstrong and Kirkby, 1979; Ehert and Ho, 1986a). Since the current experiment was conducted during the winter season when transpiration is reduced, this may in part explain why sweet pepper leaves had high Ca concentration compared to fruits (Table 3.7). The high Ca concentration in leaves relative to fruit is also associated with the mode of transport of Ca in the plant. Its movement through xylem vessels in the transpiration stream will give a comparative advantage to leaves because of higher transpiration potential than fruit.

Differences in the accumulation of calcium and of other elements suggests that Ca is imported into the fruit by different mechanism than N, P, K and Mg (Table 3.7). This is because water stress did not have a significant effect on the accumulation of the other elements while fruit and leaf Ca concentration were affected. It shows that the other elements are transported in both xylem and phloem vessels along with leaf assimilate (Ehert and Ho, 1986a), while Ca supply to the fruit is predominantly through xylem vessels with water transport. The high leaf K concentration in water stressed plants may suggest that some kind of leaf osmotic adjustment had occurred

(Behboudian *et al.*, 1994). Leaf osmotic adjustment in pepper leaves has also been observed previously (Wullschleger and Oosterhuis, 1991).

3.4.4. Fruit growth

The sigmoidal pattern of sweet pepper fruit growth was similar to those reported for other cultivars (Miller *et al.*, 1979; Nielsen *et al.*, 1991; Pretel *et al.*, 1995). Initially the diameter and length growth increased slowly while the RGR was high. This indicates that the biosynthesis activity of the fruit was high during early growth and development and then it declined.

The lack of difference in fruit growth rate between control and water stressed fruit may be due to the season and the dull weather. Under such circumstances the fruit may not grow rapidly. Cell expansion takes place in response to the accumulation of carbohydrate and water (Schechter *et al.*, 1993). Carbohydrate production and supply in turn is favoured at moderately high temperature and adequate radiation (Karlsson and Heins, 1992). Although optimum temperature was maintained in the greenhouse throughout the fruit growth period, the reduction in light intensity and duration during the winter may have not favoured a high accumulation of photosynthates in the fruit and therefore resulted in a lower fruit growth rate. Fruit growth is also less sensitive to water stress than other above ground portions of the plant (Forshey and Elfving, 1989). This may be because, photosynthesis is less sensitive to water stress than vegetative growth (Higgs and Jones, 1991) which may make more assimilate available for fruit growth due to reduced vegetative sinks.

Early in the season fruit growth was affected by water stress. The reason for this is not clear but, fruit water relations in apple fruit are influenced by water stress (Mills *et al.*, 1996) and may undergo osmotic adjustment to maintain turgor and fruit growth but at a reduced rate. With advancement in fruit growth however, the fruit accumulates more assimilates which decreases its osmotic potential and maintain its

water content (Beuter, 1989).

Although there was no significant difference in fruit RGR between water stressed and control plants, the former showed a slightly higher rate than the latter. This may be because upon rewatering the stressed fruit may have grown at a faster rate to compensate for a previous reduction in fruit growth. This phenomenon has been noted in deficit irrigated Asian pear and grape fruit (Mitchell *et al.*, 1986; Cohen and Goell, 1988; Caspari *et al.*, 1994). This rapid growth after rewatering is possible due to utilization of dry matter accumulated during the stress period (Cohen and Goell, 1988).

3.4.5. Dry matter production and distribution

3.4.5.1. Dry matter production

The use of regression techniques in plant growth analysis has been widely practised (Hunt, 1978, 1990). The major problem however, is the choice of appropriate growth curves for the data from the array of available models because of 'underfitting' or 'overfitting' the data (Poorter, 1989). Hurd (1977) after reviewing the different models concluded that the use of polynomials particularly quadratic functions against time are preferred for growth analysis of crops in controlled conditions as these provide meaningful results when biological expectations are taken in to account. Hall (1977) used various degrees of polynomials to fit the growth of sweet pepper plant parts to derive standard growth indices. According to Hurd (1977) 'biological expectations' where the constants have biological meaning is more decisive criterion for the choice of the degree of polynomials than statistical tests. The alternative to fitted equations is to fit different curves at short intervals during the growth period, a process which needs multiple harvests. The principle of fitting one curve over the whole growth period was adopted during the current experiment using quadratic functions as it provides useful information with biological value (France and Thornley, 1984). Log

transformation of the data was necessary in order to avoid the confounding effects of size and ontogeny (Evans, 1993).

Cumulative growth of sweet pepper plants was slow until 70 days after transplanting and increased after 100 days after transplanting (Fig. 3.4a). The observed increase in the cumulative growth may be attributed to increase in leaf area and consequently the light interception ability of the leaves. Thus, the lower growth in stressed plants can be explained in terms of a difference in leaf area development between the two treatments.

Relative growth rate increased steadily during the growth period in both control and stressed plants (Fig. 3.4b). The increase in the RGR is a result of an improvement in the growing environment as plants were grown from winter to spring. The limiting factor is most likely light (Canell *et al.*, 1984) as plants were grown without restriction of branching and were planted during the winter when the photosynthetically active radiation was reduced by mutual shading and low light levels. The RGR of sweet pepper plants increased with an increase in light intensity (Bruggink and Heuvelink, 1987). The light absorbed by leaves is known to be the principal factor controlling crop growth rate and plant development (Gardner and Auma, 1989). With an increase in light intensity, leaf photosynthesis and export of assimilate increased (Grange, 1987; Dorais *et al.*, 1996). Both low irradiance and water stress tended to reduced the CER (CO_2 exchange rate) of pepper leaves (Alvino *et al.*, 1991). In this experiment water stress did not reduce the NAR appreciably presumably due to the level of water stress applied. Stressed plants also have the ability to reduce water stress and maintain productivity by changing their leaf angle to lower the incident radiation (Alvino *et al.*, 1991).

Values for the net assimilation rate increased with the advancement in plant growth (Fig. 3.7a) confirming the reports of Virgona and Farquhar (1996) on sunflowers. It is however, in conflict with the reports of Hughes and Freeman (1967); Hedge

(1987); Alvino *et al.*, (1990b). A drop in NAR suggests the functional relationship between assimilate demand and NAR (Hall, 1977). It is also a result of mutual shading of leaves which reduces the light interception ability of the leaves. This is possible if plants are grown under favourable weather conditions. As the plants of the current experiment were planted during the winter and grown from winter/spring towards summer, improvement in weather condition particularly light may have helped in attaining increased NAR. In this experiment, no difference in NAR between water stressed and control plants was noted in contrast to the findings of Vassey and Sharkey (1989). This could be due to difference in cultivars, the level of water stress applied and season of the growing period.

The leaf area ratio declined with time (Fig. 3.5a) indicating the diversion of assimilates initially into stems and root and later to the fruit. The peak of the curves for LAR found early in the growing season is in agreement to those reported by Clawson, *et al.*, (1986) for soybean and Hedge (1987) for sweet pepper. The reduced LWR also demonstrates the effect of competition of other plant organs particularly the fruits with leaves which are dominant sinks for assimilates.

It is clear from the present result that RGR was highly correlated to NAR and LAR. This result agrees well with the findings of Curtis and Lauchli (1986) on kenaf and Cramer *et al.*, (1990) on barley. High coefficient of determination was found for RGR versus LAR and NAR (Cramer *et al.*, 1990). Unlike that of barley, the RGR of sweet pepper is to a greater extent related to the NAR which is an index of the photosynthetic capacity of the plant (a physiological parameter) and equally to the LAR which shows the leafiness of the plant (a morphological parameter). Although both NAR and LAR were associated with the RGR of stressed plants it was the NAR ($P \leq 0.001$) than LAR ($P \leq 0.01$) which was the primary factor controlling growth. This helps the stressed plants to maintain good growth (Ashenden *et al.*, 1975).

Total dry weight was closely related to both leaf area and NAR. Hence, the observed difference in fruit yield as well as RGR between control and stressed plants could be

attributed to their difference in leaf area development than NAR as little difference was observed in this particular case. Although the NAR appeared to be the same between treatments an increase in maintenance respiration in stressed plants may have accounted to yield difference (Schwarz and Gale, 1981).

3.4.5.2. Dry matter distribution

Dry matter partitioning is defined as the distribution of dry matter between the plant organs (Marcelis, 1996). Dry matter distribution showed a higher proportion during the earlier growth period in favour of leaves and a shift towards fruit after fruit set. Stressed plants had a lower proportion of dry matter allocated to fruit than control plants (Fig 3.7a).

Dry matter partitioning is the end result of a set of transport and metabolic processes associated with the flow of assimilates from source organs via a transport path (phloem) to sink organs (Marcelis, 1996) whose activities change with plant development (Patrick, 1988). In this complex process dry matter partitioning may be controlled by the source (source limited), sink (sink limited) and/or the transport path (Wardlaw, 1990).

Dry matter partitioning is affected by fruit development in many fruit vegetables and thus brings about a significant change in sink load. Several researchers have indicated that fruit accounts for the major portion of the dry matter in sweet pepper, tomato and cucumber fruits (Cooper, 1972; Hall, 1977; Marcelis, 1992a). In contrast, the presence of fruit didn't alter the total accumulation of dry matter in some sweet pepper plants (Nielsen and Veierskov, 1988).

In the present experiment a difference in dry matter partitioning between treatments was noted (Fig. 3.7a). Fruit development accounted for 58 % of the dry matter in well watered plants but only 49 % in stressed plants (Table, 3.8). Hall (1977)

reported this as 70-80 %; Nielsen and Veierskov (1988) as 45%; and Hedge (1987) between 50-55%. The unrestricted growth in this experiment may have accounted for the lower proportion of the dry matter in fruits when compared to the values given by Hall (1977). The plants were also grown during the winter months which might limit growth. In spite of this, fruit still remained the major sink of assimilate in sweet pepper.

Stressed plants exhibited a reduced translocation of assimilates to their fruits (Fig. 3.7b). This may be due to reduced rate of photosynthesis; stress induced senescence; or leaf and flower drop. In severely stressed plants stomata remained partially closed even three days after rewatering which may account for reduced photosynthesis (Aloni *et al.*, 1991). Since there was no appreciable difference in the NAR of stressed and control plants in this experiment, it is likely that leaf, flower and fruit drop resulted in a lower fruit weight ratio (FWR) in stressed plants. The reduced leaf area and fruit number in stressed plants supports this assumption (Table 3.8). The higher proportion of assimilates in fruits of control plants as compared to stressed plants was therefore a result of higher fruit production (Fig 3.7b and Table 3.8). A close correlation between the proportional distribution of dry matter to fruits and fruit load on the plant was noted (Marcelis, 1992b).

The development of fruit suppressed the growth of other vegetative organs, particularly that of roots from 94 DAT onwards (Fig. 3.7a). However, the second flush of growth has improved the proportion of assimilate supply to stems and leaves around 128 DAT. Through out the growth period however, flower buds and flowers appeared to be weak sinks as compared to other organs particularly fruit. Fruit growth dominates the growth of vegetative tissues while, flowers in contrast to fruit appear to be poor competitors under source limiting conditions (Hall, 1977; Ho, 1984; Clapham and Marsh, 1987; Wardlaw, 1990).

3.5. Conclusion

Data from this experiment show that sweet pepper fruit set was affected by lack of moisture which results in reduced yields and a possible increase in the incidence of blossom-end rot. Although other factors such as high day/low night temperature, cultivar and nutrition affect fruit set, consideration should also be given to the irrigation requirement of the crop if higher yields are to be realized. However, fruit maturity appeared to have very little effect on the characteristics evaluated.

Because water stress resulted in an increase in dry matter accumulation in the fruits, this would indicate the possibility of improving fruit quality. Nevertheless, in the present investigation the stress level used significantly reduced yields.

Water stress depressed the calcium content of sweet pepper fruits. Low Ca concentration in the fruits of stressed plants may have been a result of reduced Ca uptake by the roots and its subsequent distribution within the fruit rather than from insufficient Ca levels in the nutrient solution.

It was concluded that when the calcium concentration in the solution is not limiting, the fruit Ca content is associated with the water uptake rate of the plant. Moreover, the fact that leaf Ca content is significantly higher than fruit Ca content implies that when Ca is limiting the presence of more leaves will be detrimental to stressed plants. This is because transpiration promotes the movement of Ca into the leaves rather than fruits which results in BER due to inadequate supply of Ca to the young fruits. Hence, this signifies the importance of water for the distribution of Ca in the plant provided that there is sufficient amount of Ca in the medium.

Finally results of this study underlie the importance of watering on dry matter production and partitioning in sweet pepper plants.

Chapter 4

Accumulation and distribution of calcium, magnesium and potassium in sweet pepper fruit during ontogeny as affected by chemical treatment.

4.1. Introduction

Seasonal changes in the mineral composition of the plant can have important implications on the nutritional and physiological disorders and postharvest storage quality of produce (Ludders, 1980). Information to indicate when a particular element is limiting growth is vital to combat the associated physiological and nutritional disorders. This can be achieved by monitoring the dynamics of mineral uptake and accumulation regularly through out the growth period.

A number of researchers have studied nutrient accumulation in various fruits during ontogeny, including tomato (Halbrooks and Wilcox, 1980) apple (Haynes and Goh, 1980) kiwifruit (Clark and Smith, 1988) tamarillo (Clark *et al.*, 1989) Japanese pear (Buwalda and Meekings, 1990) and persimmon (Clark and Smith, 1990). Others have studied specific elements of interest in kiwifruit (Ferguson, 1980) cucumber (Engelker *et al.*, 1990) and apple (Jones *et al.*, 1983). There is however, very little information available on greenhouse grown sweet pepper fruit although some field grown sweet pepper mineral data is available (Miller *et al.*, 1979).

Calcium is one of the essential nutrients for plant growth and fruit quality. Calcium deficiency in fruits is associated with a number of physiological disorders including blossom-end rot of tomato and sweet pepper. In light of this a number of researchers

have attempted to enhance the Ca content of fruits by various techniques such as direct preharvest application to the fruit (Robson *et al.*, 1989) postharvest dipping (Hopkirk *et al.*, 1990) or vacuum infiltration (Rajapakse *et al.*, 1992).

Calcium is mainly transported through xylem vessels in the transpiration stream (Clarkson, 1984). Therefore, factors which promote water loss from the fruit surface are likely to enhance the uptake and accumulation of Ca in the fruit while, transpiration inhibitors will depress its uptake and accumulation.

Potassium salts have widely been used for drying grasses and legumes for hay making (Johnson *et al.*, 1984). Norton and Godipon (1984) found that application of KOH was effective in drying of three tropical grasses leaves. Grncarevic and Lewis, (1976) also reported that grapes could be dried by treatment with K salts or oils and emulsifiers. The main effects of K treatment was considered to be due to the opening of stomata (Hartley, *et al.*, 1982). In addition, the permeability of the cuticle to water as studied by Schonherr and Schmidt (1979) was greater when cations in the buffer solution were K^+ rather than Na^+ . According to Chiang and Park (1994) surface dipping of seeds in 1% KOH greatly reduced the wax of the cuticular surface of the seed coat thereby reducing the internal resistance to water diffusion.

On the other hand, wax coatings have been commercially used to reduce moisture loss from harvested fruit. Coating of fruit resulted in marked reduction in weight loss of oranges (Ben-Yehoshua, 1969) but was minimal for banana and apples (Banks, 1984; Smith and Stow, 1984). Weight loss in sweet pepper fruit was significantly reduced by wax coating (Gonzalez and Tiznado, 1993).

The present investigation was carried out in order to determine the uptake and distribution of Ca, Mg and K by sweet pepper fruit during ontogeny and investigate the effects of treating the fruit with transpiration promoting or reducing chemicals.

4.2. Material and Methods

4.2.1. Greenhouse procedure

Plants of the cultivar Domino were grown during the autumn season of 1994 using a trickle irrigation system. In this system sweet pepper plants were planted into polyethylene bags filled with a bark medium. The bags were placed on a substrate mat in the greenhouse ventilated above 25°C and heated below 15°C.

The plants were placed at a distance of 50 cm in a row with a plant population of 4 plants/m². Each pot was supplied with two 4 l h⁻¹ emitters and plants were irrigated 3-4 time a day using a time clock depending on the weather conditions.

The plants were fertigated through the trickle irrigation system using stock solutions of A and B (chapter 3). The leachate from the pots was regularly checked with a portable CF meter.

4.2.2. Plant growing system and treatment application

Plants were trained to three branches and a single fruit was allowed to grow on each branch. The date of anthesis of each flower was recorded. Plants were arranged in a Randomized Complete Block Design with 5 blocks. Treatments were randomly applied to each fruit every week commencing at anthesis. The treatments consisted of:

- 1) 0.5 M KOH
- 2) Prima fresh wax coating
- 3) uncoated control.

The KOH and wax treatments were applied on the fruit surface every week until harvest using a soft brush.

4.2.3. Data collection and analysis

Fruit harvesting was carried out every 4 days from the date of anthesis for a total of 13 harvests. At each harvest, fresh weight, and dry weight were measured for each harvested fruit from the respective treatment group.

Fruit mineral analysis was undertaken on the dried samples to determine tissue Ca, K and Mg concentration and contents. This was done following the method described in section 3.2.3.3.

4.2.4. Statistical procedure

Data were analyzed using SAS GLM procedure in a repeated measure analysis. Data were checked whether they conform to the assumption of ANOVA. To maintain uniformity of variance over time the primary fruit weight data were transformed to a natural log. Percentage data were also arcsine transformed and back transformed for presentation. The mineral data were checked to determine whether branch position has an effect on the attributes evaluated.

4.3. Results

4.3.1. Fruit growth

On a log scale, sweet pepper fruit growth in terms of fresh weight and dry weight gain showed a rapid growth of fruit 8-16 days after anthesis and thereafter it grew very slowly (Fig. 4.1).

Fruit fresh and dry weight for the various treatments was more or less similar except towards the final harvest ($P \leq 0.05$). An asymptotic function best fitted these data rather than linear function. This indicates that plant dry weight appeared to have reached maximum values towards the end of harvest. The analysis of the coefficients of the Richards function revealed that there was a significant difference in the a, b and c values representing the initial weight, the slope and asymptotic yield respectively (Table 4.1).

4.3.2. Mineral concentration and content of Fruit

The total Ca, Mg and K concentrations in sweet pepper fruit declined with time for the three mineral elements (Figs. 4.2, 4.3 and 4.4).

The Ca concentration of control fruit markedly decreased from an initial value of 7.43 mg.gdw⁻¹ to as low as 1.89 mg.gdw⁻¹ during the rapid fruit growth period (Fig. 4.2a). From 24 to 36 days after anthesis this decline levelled off (Fig. 4.2a). The Mg concentration on the other hand, showed a slow decline as compared to fruit Ca concentration. From 20 days after anthesis until the final harvest it showed very little change in Mg concentration (Fig. 4.3a). The K concentration also showed a similar trend to Mg showing a slow decline with time before it increased towards the final harvest (Fig. 4.4a).

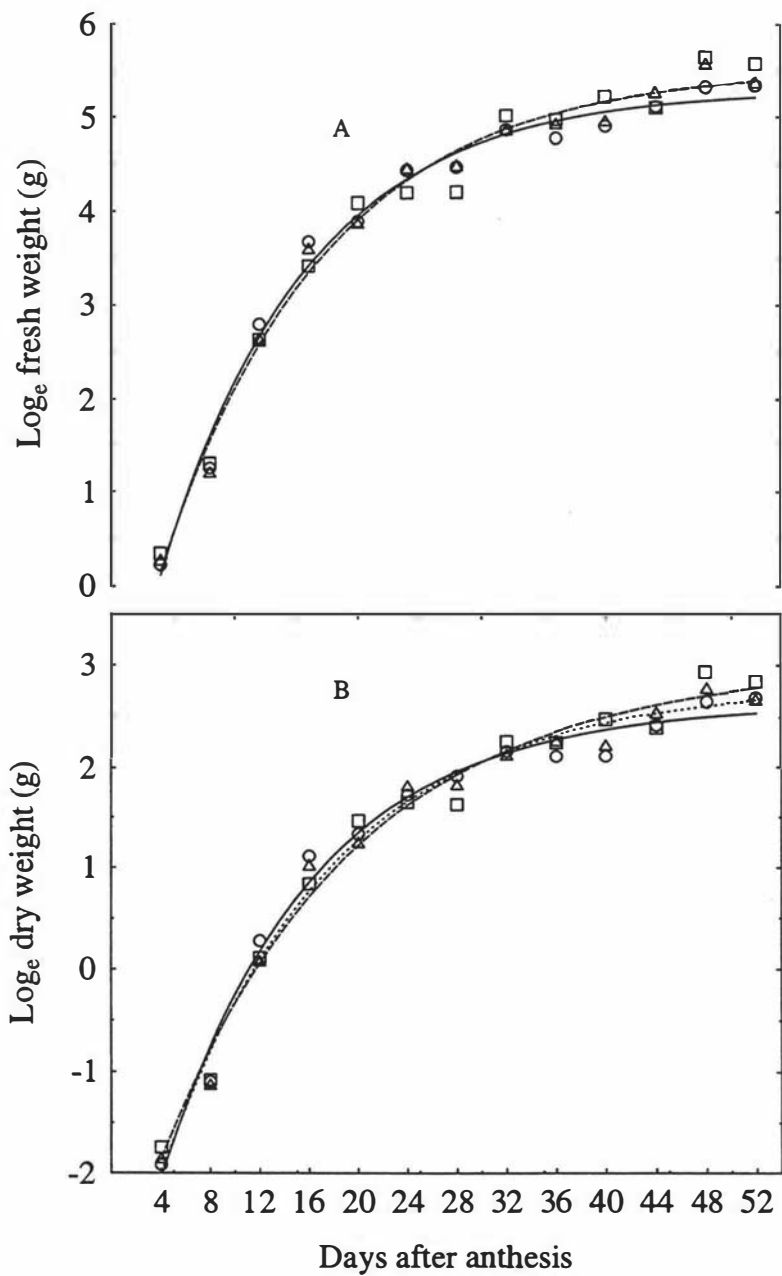


Fig 4.1: Sweet pepper fruit \log_e fresh weight (A) and \log_e dry weight (B) growth over time. Each data point is an average of 5 fruit. KOH (○), Wax (△), Control (□). Data fitted to Richards function.

Table 4.1. Coefficients of the Richards function for sweet pepper fruit fresh and dry weights.

Treatment	Fresh weight			
	Coefficient			
	a	b	c	d
KOH	5.309 c ^y	0.315 a	0.084 a	1.608e ⁺¹⁴
Wax	5.531 b	0.275 ab	0.076 ab	1.411e ⁺¹⁴
Control	5.748 a	0.215 b	0.067 b	1.778e ⁺¹⁴
Significant ^x	**	*	*	ns
SEM (df=8)	0.06	0.02	0.004	
	Dry weight			
	a	b	c	d
KOH	2.642 b	0.893 a	0.080 a	2.114e ⁺¹⁵
Wax	2.844 a	0.813 b	0.071 b	8.906e ⁺¹⁴
Control	3.008 a	0.733 c	0.063 b	2.498e ⁺¹⁴
Significant	**	**	**	ns
SEM (df=8)	0.05	0.02	0.003	

^x *, ** and ns significant at $P \leq 0.05$, $P \leq 0.01$ and non significant

^y means followed by the same letter are not significantly different from each other according to Duncan's multiple range test.

Fruit total Ca, Mg and K contents increased with time with no apparent difference between treatments (Figs. 4.2b, 4.3b and 4.4b). There was an increase in Ca content of control fruit between 28 and 36 days after anthesis after which it increased almost linearly. Similar trends in a linear increase after 36 days after anthesis were observed for wax and KOH treated fruit. This mode of accumulation was also true for Mg and K (Figs. 4.3 and 4.4).

Log_e fruit dry weight against log_e Ca, Mg and K contents showed that the nutrients

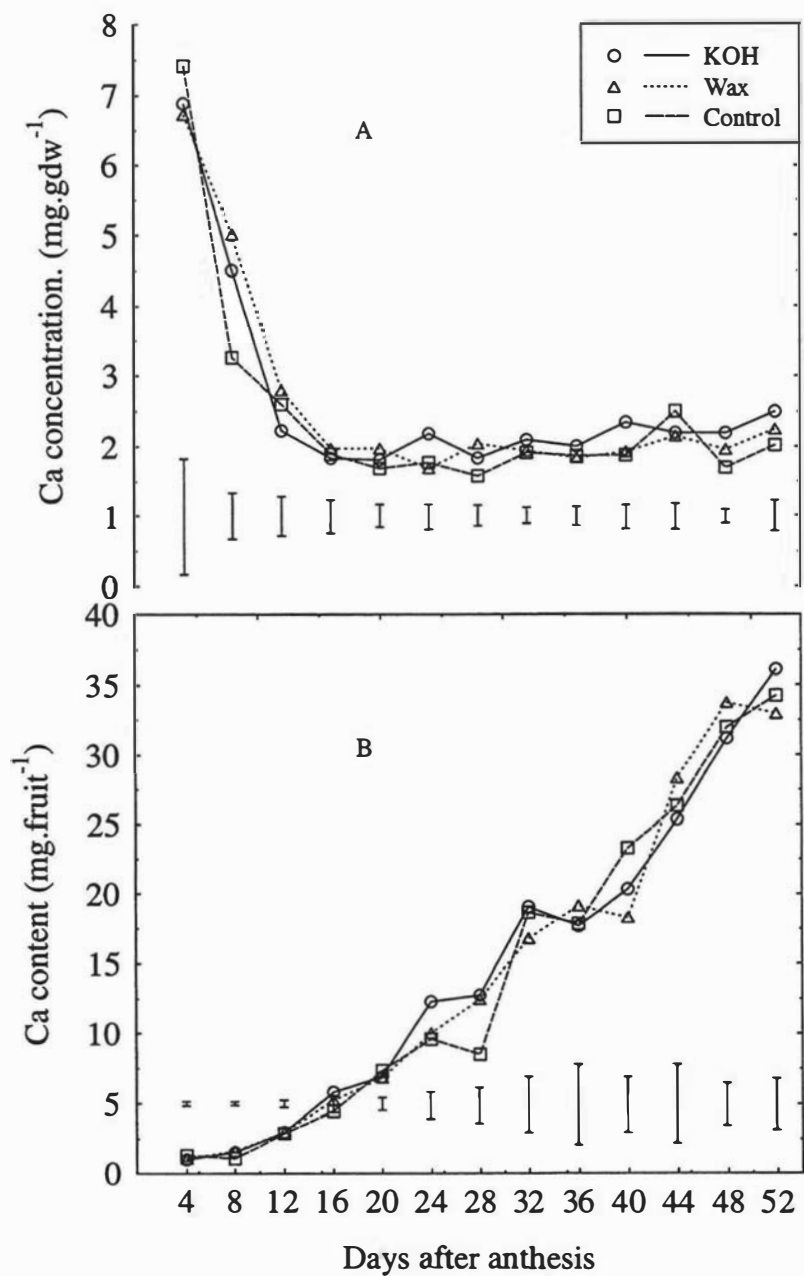


Fig 4.2: Sweet pepper fruit Ca concentration (A) and Ca content (B) over time. Each data point is an average of 5 fruit. Vertical bars indicate standard error of means.

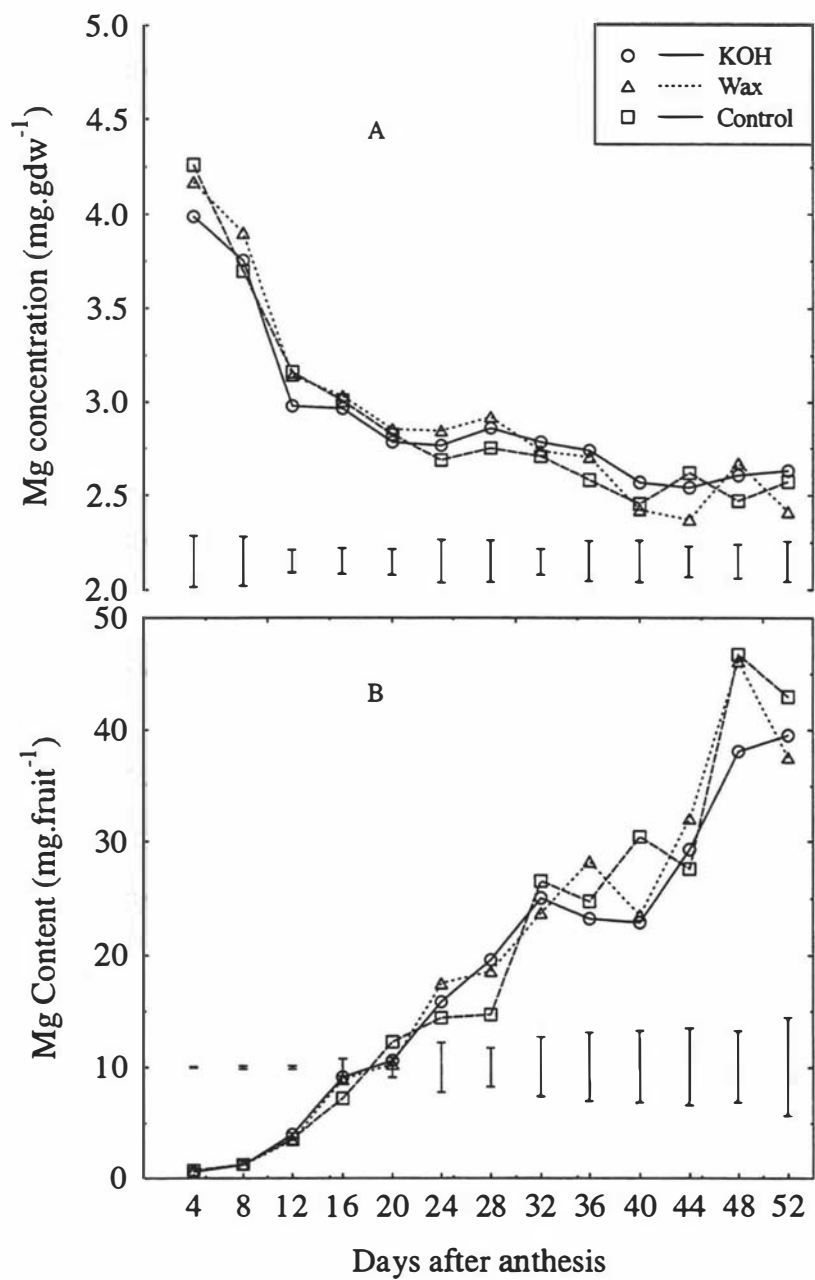


Fig 4.3: Sweet pepper fruit Mg concentration (A) and content (B) of the fruit over time. Each data point is an average of 5 fruit. Vertical bars indicate standard error of means.

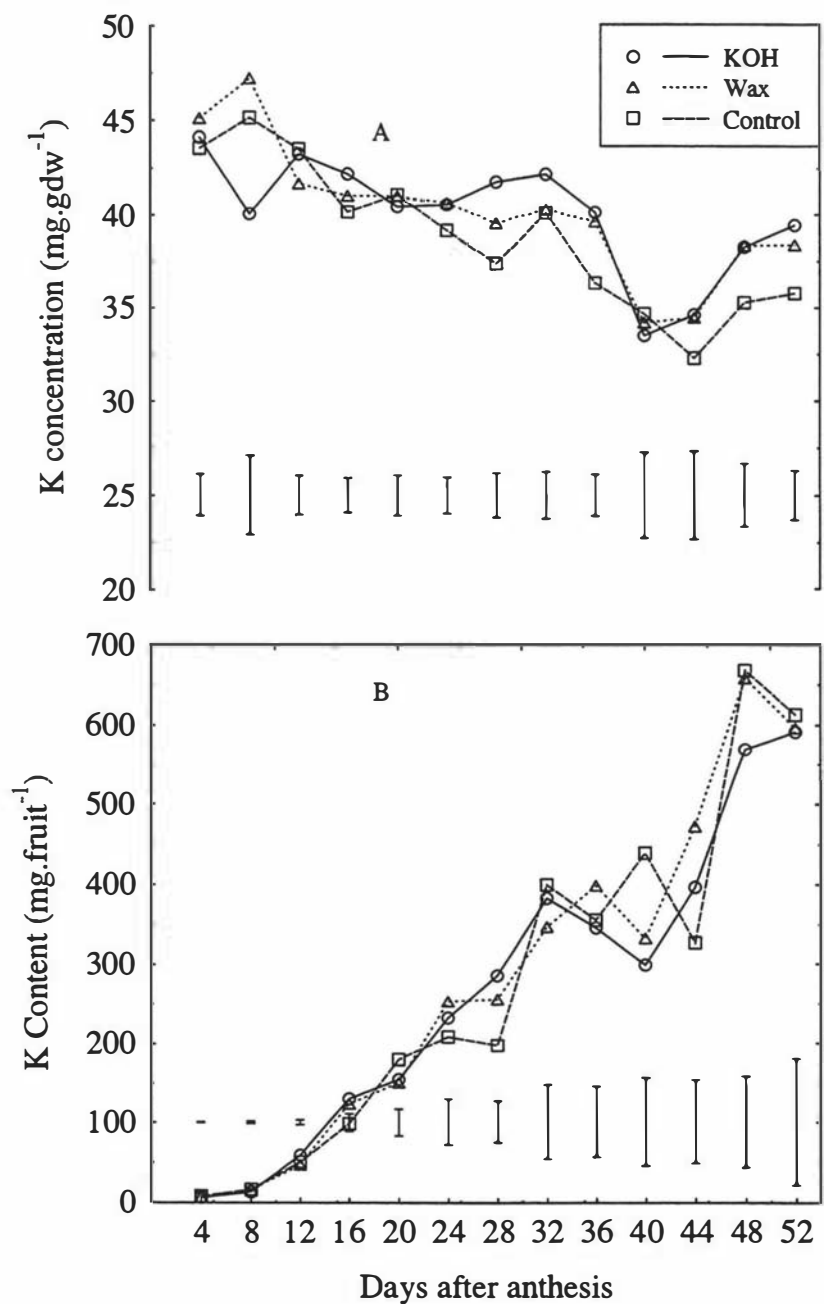


Fig 4.4 Sweet pepper fruit K concentration (A) and content (B) of the fruit over time. Each data point is an average of 5 fruit. Vertical bars indicate standard error of means.

increased almost linearly with an increase in fruit dry weight (Fig. 4.5). These linear increase was noted especially after 12 days after anthesis. However, there was no difference between the treatments.

4.3.3. Mineral distribution within the fruit

The distribution of Ca, Mg and K in the various portions of the fruit is shown in Tables 4.2, 4.3 and 4.4. Most of the Ca nutrient was located in the placenta⁺ (which includes: the pedicel, seed, calyx as well as placenta) of the fruit during the early fruit growth period (12 days after anthesis) ($P \leq 0.0001$). The blossom-end of the fruit had the least amount of Ca during this period particularly KOH treated fruit (Table 4.2). Both the Ca concentration as well as content were higher in placenta⁺ than either the stem-end or blossom-end of the fruit regardless of treatments.

Fifty two days after anthesis, the placenta⁺ still has the highest Ca concentration in all the treatments ($P \leq 0.01$) with little difference between the stem-end and the placenta (Tables, 4.2, 4.3 and 4.4). The blossom-end portion had the least Ca concentration. The Ca content and percentage composition were high in the stem-end and least in the placenta⁺ in KOH treated fruit (Table 4.2). Although similarly high Ca content was observed in the stem-end of control fruit, it was the blossom-end which had the least Ca content (Table 4.3). Similar trends were noted in wax treated fruit with out significant difference (Table 4.3). Magnesium followed a similar pattern to Ca (data not shown).

The potassium concentration in young fruit was high in the placenta⁺ and least in the stem-end in all treatments with little difference between the placenta⁺ and blossom-end in control fruit ($P \leq 0.001$) (Table 4.2, 4.3 and 4.4). The K content was also high in the placenta⁺ in control fruit (Table 4.4) with similar but non significant difference in KOH treated fruit (Table 4.2). Wax treated fruit also had no difference in partition of Ca but blossom-end had the highest content. With maturity (52 days after anthesis)

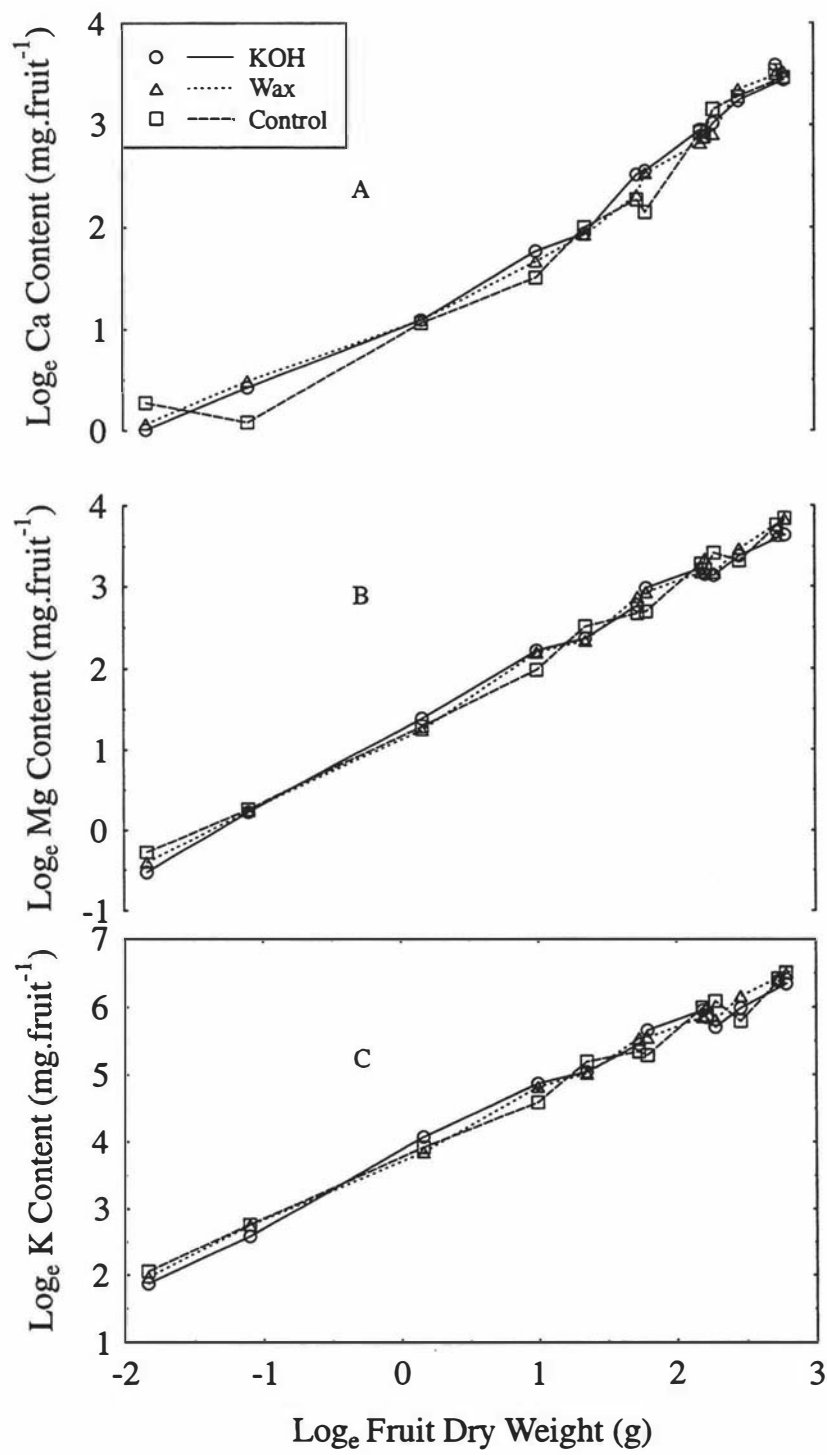


Fig 4.5: Sweet pepper fruit Ca content (A) Mg content (B) and K content (C) plotted against Log_e fruit dry weight for the three treatments. Each data point is an average of 5 fruit.

Table 4.2. Distribution of calcium and potassium in different portions of KOH treated sweet pepper fruit.

Tissue	Calcium Conc. mg/gdw	Calcium content mg/fruit	% of total Calcium content	Potassium conc. mg/gdw	Potassium content mg/fruit	% of total potassium content
12 days after anthesis						
Placenta ⁺	4.03±0.210 ^x a ^y	1.71±0.105 a	35.17±1.78 (57.49) ^z a	48.08±0.615 a	21.00±1.82	20.72±1.77 (36.17)
SE	1.73 b	0.79 b	15.26 (26.27) b	39.438 c	17.98	17.44 (30.47)
BE	1.09 b	0.48 b	9.35 (16.23) c	42.686 b	19.95	19.14 (33.40)
Significant	***	***	***	***	ns	ns
52 days after anthesis						
Placenta ⁺	2.972±0.137 a	9.968±1.195 b	15.99±1.85 (27.49) b	48.29±1.86 a	174.75±11.91 b	16.29±1.31 (28.43)
SE	2.749 a	14.634 a	23.89 (40.49) a	35.40 b	191.69 ab	18.73 (32.68)
BE	2.034 b	11.501 ab	18.72 (32.02) ab	38.75 b	225.31 a	22.28 (38.89)
Significant	**	*	*	**	*	*

^x ± standard error of means^y means followed by the same letter are not significant according to Duncan's multiple range test^z the percentage data are arsine transformed. The back transformed data is presented in brackets.

Table 4.3. Distribution of calcium and potassium in different portions of wax treated sweet pepper fruit.

Tissue	Calcium conc. mg.gdw ⁻¹	Calcium content mg.fruit ⁻¹	% of total calcium content	Potassium conc. mg.gdw ⁻¹	Potassium content mg.fruit ⁻¹	% of total potassium content
12 days after anthesis						
Placenta ⁺	5.65±0.549 ^x a ^y	1.742±0.096 a	35.52±1.48 (58.02) ^z a	47.378±0.88 a	16.468±1.64	19.720±1.72 (34.418)
SE	2.09 b	0.732 b	14.27 (24.62) b	37.344 c	13.354	16.625 (29.016)
BE	1.294 b	0.512 b	10.0 (17.36) b	41.064 b	17.208	20.951 (36.566)
Significant	**	***	***	***	ns	ns
52 days after anthesis						
Placenta ⁺	3.596±0.504 a	10.342±0.852	17.799±1.609 (30.52)	52.828±6.19	179.28±18.67	16.16±2.049 (28.204)
SE	2.316 ab	12.622	22.691 (38.55)	35.588	197.31	20.027 (34.956)
BE	1.778 b	9.982	18.035 (30.93)	36.732	219.91	21.109 (36.842)
Significant	*	ns	ns	ns	ns	ns

^x ± standard error of means^y means followed by the same letter are not significant according to Duncan's multiple range test^z the percentage data are arsine transformed. The back transformed data is presented in brackets.

Table 4.4. Distribution of calcium and potassium in different portions of control sweet pepper fruit.

Tissue	Calcium conc. mg.gdw ⁻¹	Calcium content mg.fruit ⁻¹	% of total calcium content	Potassium conc. mg.gdw ⁻¹	Potassium content mg.fruit ⁻¹	% of total potassium content
12 days after anthesis						
Placenta ⁺	4.640±0.582 ^x a ^y	2.024±0.134 a	43.999±1.51 (69.33) ^z a	46.50±0.742 a	22.90±1.87 a	25.43±1.73 (44.374) a
SE	1.742 b	0.546 b	10.963 (19.01) b	38.13 b	11.95 b	13.99 (24.416) b
BE	0.958 b	0.332 b	6.702 (11.66) b	44.44 a	15.61 b	17.88 (31.210) b
Significant	**	***	***	***	**	**
52 days after anthesis						
Placenta ⁺	2.46±0.121 a	11.50±1.11 ab	20.142±2.3 (34.31) ab	40.78±1.65 a	200.15±18.74	18.294±1.90 (31.932)
SE	2.25 a	13.57 a	23.369 (39.7) a	34.19 b	207.63	19.558 (34.136)
BE	1.47 b	9.15 b	15.13 (26.0) b	33.11 b	205.14	19.443 (33.936)
Significant	**	*	*	*	ns	ns

^x ± standard error of means^y means followed by the same letter are not significant according to Duncan's multiple range test^z the percentage data are arcsine transformed. The back transformed data is presented in brackets.

the trend was maintained in K concentration as in young fruit in all treatments. The K content, however, was highest in blossom-end in both KOH and wax treated fruit with no difference in control fruit.

4.4. Discussion

4.4.1. Fruit growth

Fruit growth was not affected by treatments during most of the growth period which is in agreement with the reports of Bakker (1989b and c). Application of CaCl_2 to apple fruit also did not affect its weight compared to the control treatment (Witney *et al.*, 1991). The effect of humidity in the greenhouse was generally on the vegetative growth of plants by increasing leaf area (Bakker *et al.*, 1987) and photosynthesis (Bunce, 1984) which may contribute to increased yield in greenhouse environment. At the final harvest the KOH treated fruit showed slightly lower fresh and dry matter yield compared to the control treatment. The reason for its reduced yield is not clear. It may presumably be due to reduced fruit water content which may reduce the fresh weight of the fruit. Reduced growth of muskmelon fruit with low RH was reported by Combrink *et al.*, (1995).

4.4.2. Mineral nutrient accumulation by sweet pepper fruit

Sweet pepper fruit tended to accumulate Ca, Mg and K throughout the fruit growth period albeit at a reducing rate. This is unlike kiwifruit or tamarillo whose Ca and Mg contents level off earlier (less than 10 weeks after pollination) in the growing period (Ferguson, 1980; Clark *et al.*, 1989). It is however, similar to apple, Japanese pear, feijoa and tomato fruits whose Ca, Mg and K nutrient contents increased with fruit growth (Haynes and Goh, 1980; Harman, 1987; Buwalda and Meekings, 1990, Ehert and Ho, 1986a). Engelker *et al.*, (1990) showed that the Ca content of pickling cucumber fruit increased with fruit age.

The fruit nutrient concentration on the other hand, declined with time which is characteristic of many fruits (Ferguson, 1980; Harman, 1987; Clark and Smith, 1988

and 1990; Clark *et al.*, 1989; Buwalda and Meekings, 1990). The decline in nutrient concentration is attributed to the rate of accumulation being less than fruit growth which results in dilution of the already accumulated nutrient. Belda and Ho (1993) suggested that the density of vascular bundles falls drastically during fruit enlargement which paralleled a sharp decline in Ca concentration as observed in this experiment.

The difference in the pattern of the decrease in K concentration compared with Ca concentration reflects the path by which these two mineral nutrients are supplied to the fruit. The slow initial decrease followed by maintenance of a more or less constant concentration of K indicates a close relationship between K and the movement of assimilates from leaf to fruit through the phloem. Magnesium is more mobile in the phloem than Ca (Steucek and Koontz, 1970) but less than K. Thus, the relative importance of phloem influx into the fruit with fruit enlargement slightly increased the K and Mg concentration as compared to Ca which is mainly mobile in xylem vessels. As a result the Ca concentration sharply declined during this time.

The increase in nutrient accumulation with time is common in many fruits. It is however, important to realize that a substantial amount of these nutrients are accumulated during the early growth period (Ferguson, 1980; Clark and Smith, 1988; Tromp and Vuure, 1993) as is the case of kiwifruit and the apple cv Cox's Orange Pippin. About 4 weeks after anthesis the sweet pepper fruit had accumulated more than half of its Ca. This reduction in accumulation later in fruit growth is said to be a result of either the cessation of cell division in the fruit (Wilkinson and Perring, 1964) or a change of the route of transport from xylem to phloem (Ferguson, 1980). Since cell division terminates early before anthesis in capsicum (Munting, 1974), then the most likely explanation is a change in the supply route.

The non-uniform accumulation of Ca in fruits of sweet pepper indicates that its movement is influenced by season. This trend was also noted by Clark *et al.*, (1989) in tamarillos. Environmental factors such as air temperature, root temperature, and

air humidity may influence the mode of water supply to fruits (Wiersum, 1979c). Solar radiation and root temperature as well as salinity and humidity affect the uptake and distribution of Ca in fruits (Adams and Ho, 1993).

The most notable result from this experiment is that the three mineral elements studied accumulated continuously in developing sweet pepper fruit until the final harvest. This trend was also reported for feijoa fruits by Harman (1987).

Application of 0.5 M KOH to the sweet pepper fruit increased the Ca concentration in the fruit, particularly at the blossom-end (Fig. 4.5; Table 4.1). This is probably due to the enhancement of hydrolysis of the polymers of cuticle by the alkaline solution (Kolattukudy, 1981). Water uptake of oat seeds was promoted by treating the seeds with 5.3 N KOH (Hou and Simpson, 1994). Treatment of *Chrysanthemum coronarium* L. seeds with 1% KOH also reduced the wax of the cuticular surface of the seed coat (Chiang and Park, 1994). Thus it is possible that by removing a barrier to transpiration the KOH treatment has effectively increased sweet pepper fruit transpiration and that in turn this has increased the amount of Ca delivered into the fruit through xylem vessels (Clarkson, 1984). The lack of a significant difference may be a result of the confounding effect of fruit position.

4.4.3. Gradient of minerals in the fruit

The mineral content of fruit particularly that of Ca declines from the pedicel end towards the blossom-end of the fruit (Tables, 4.2, 4.3 and 4.4). Ehert and Ho, (1986a) showed that the vascular network of the fruit increased in branching from the proximal half to the distal half of the fruit. The number of bundles and their density decreased from the pedicel to the blossom-end of tomato fruit as did the number of functional xylem vessels (Belda and Ho, 1993). Therefore, this anatomical feature may increase the resistance of xylem water movement from the proximal to the distal half resulting in a reduced Ca content (Ehert and Ho, 1986a). The presence of more

Ca in the placenta⁺ (which includes seeds) may suggest that the seeds by virtue of their higher auxin concentration attract more Ca into the fruit. This assumption is based on the fact that unlike Ca, both the Mg and K concentrations and content are not dependent on the availability of seeds, as both the placenta and BE had similar concentrations (Table 4.4). The presence of seeds in the fruit enhanced the translocation of Ca but not Mg and K (Bramlage *et al.*, 1990). This is probably linked to Ca accumulation via auxin synthesis and transport (Baneulos *et al.*, 1987).

4.5. Conclusion

This experiment demonstrated that the accumulation of Ca, Mg and K in sweet pepper fruit closely follows fruit dry weight. In spite of this however, most of the Ca accumulated during early fruit development. The concentration of these nutrients particularly Ca decreased 2-3 weeks after anthesis when fruit enlargement was very rapid. There was a gradient of accumulation of these nutrient which decreases from the pedicel to the blossom-end of the fruit.

Chapter Five

The influence of conductivity of the nutrient solution on fruit growth, incidence of blossom-end rot, dry matter partitioning and gas exchange characteristics of sweet pepper (*Capsicum annuum* L.) cv. Domino.

5.1. Introduction

Crop production is affected by a variety of stresses. One of these constraints is salinity which affects crop productivity in a variety of ways. Salinity affects a number of developmental processes such as seed germination (Francois, 1985; Mohamed *et al.*, 1986) seedling (Chartzoulakis, 1990) vegetative (Jones *et al.*, 1989) and reproductive growth (Sonneveld and Voogt, 1978; Chartzoulakis, 1990). Reduction of plant growth under high salinity is attributed to a reduction in water uptake and that of uptake of essential nutrients (Levitt, 1980).

High salinity markedly affected the total fresh and dry weights of fruit and shoot but, did not affect the proportional distribution of dry matter into the various organs of tomato (Ehert and Ho, 1986b). However, in cucumber plants salinity both affected the yield as well as dry matter partitioning to the respective organs (Ho and Adams, 1994).

Salinity also affects ion relations (Binzel *et al.*, 1987) and ethylene production (Abou-Hadid *et al.*, 1986). In this respect, uptake of ions such as Ca which are mainly transported through the xylem vessels in the transpiration stream (Wiersum, 1979a)

are very much restricted. This in turn leads into the development of physiological disorders such as bitter pit in apples and blossom-end rot (BER) in tomato and pepper (Shear, 1975; Bangerth, 1979).

In some plants elevated concentration of Ca in the nutrient solution mitigated the adverse effects of NaCl by inhibiting Na uptake (Cramer *et al.*, 1985; Banuls *et al.*, 1991) and reducing the leakiness of cells (Leopold and Willing, 1984). The beneficial effects of high Ca concentration in a saline environment may be due to the maintenance of K/Na selectivity and adequate Ca status in the root (Kent and Lauchli, 1985).

The incidence of BER is related to a decrease in the absorption and translocation of calcium due among other things to excessive salinity (Ehert and Ho, 1986a). Although BER incidence increases as the calcium content in the medium decreases (Borkowski, 1984; El-Gizawy and Adams, 1986), BER may still be manifested in conditions of high salinity even if sufficient Ca is present in the medium (Adams and Ho, 1985). These effects may be due to the limited capability of plants to regulate the internal distribution of calcium, in particular to low transpiring organs (Marschner, 1986). High temperature and radiation aggravate the problem of BER by favouring a high fruit growth rate (Ho, 1989). Salinity also depresses the calcium content of fruits (Belda and Ho, 1993) through its effect on the long term development of the xylem vessels (Ehert and Ho, 1986b) through which Ca is mainly transported (Wiersum, 1979a).

The susceptibility of distal pulp tissue to BER is related to low total Ca in the tissues (Adams and Ho, 1992) as well as to a low deposition of Ca pectate and Ca phosphate fractions (Minamide and Ho, 1993) as these two Ca compounds are directly involved with either cell wall or cell membrane structure (Ferguson, 1984; Ho and Adams, 1989) consequently affecting the occurrence of BER.

The following experiment was therefore initiated to;

1. Gain an understanding of the seasonal accumulation and distribution of the three elements Ca, K and Mg in sweet pepper fruit and how osmotic stress affects this process.
2. Assess whether the occurrence of BER is related to the total as well as the different fractions of Ca compounds in the fruit tissue and the ratio of Ca with the other two elements.
3. Determine the effects of osmotic stress on the overall growth of sweet pepper plants and the distribution of assimilates between the different organs.
4. Examine the influence of osmotic stress on the quality and other physiological attributes related to maturity of the fruit.

5.2. Materials and Methods

5.2.1. Plant material and culture

Sweet pepper (*Capsicum annuum* cv. Domino) seeds were sown on September 22, 1994 in Jiffy-7 blocks. Seedlings were pricked into small pots at cotyledon leaves expansion on October 22, 1994. When the seedlings had 9-11 leaves they were further selected for uniformity and placed in the nutrient film technique (NFT) channels on November 11, 1994. The greenhouse was heated below 15°C and ventilated above 25°C during the growing period.

5.2.2. Plant growing system

The nutrient film technique (NFT) was used to grow sweet pepper plants. In this system, the nutrient solution was circulated through the gullies at a flow rate of approximately 3 l min⁻¹ by means of submerged pumps. The recycled nutrient solution in the tanks was managed by topping up the water lost by evaporation and water and nutrient used by the plant every day. This is done to maintain constant electrical conductivity (EC) of the nutrient solution.

The basic nutrient solution was made up of solution A and B (Cooper, 1979) and equal amount of these stock solutions (appendix 1) were added to the tank to adjust the EC of the solution. All tanks were emptied and replaced with new solutions fortnightly to avoid a drift in the concentration of the elements in the solution.

The EC and pH of the nutrient solution in each tank were recorded daily using portable pH and conductivity meters. The pH was adjusted with either 10% solution of phosphoric acid (H₃PO₄) or a 0.05% solution of potassium hydroxide (KOH).

The NFT channels were made of PVC plastic pipes which were laid out horizontally on steel supports. There were a total of 18 pipe rows with drainage slots at the lower end of the pipe. Each pipe was 5-7 m long and held 9 plants in each row. Three randomly assigned pipe rows were supplied from and drained into a separate 100 l tank holding the nutrient solution. Pipes were spaced 0.5 m apart being oriented N-S 1 m from the ground level and with a slope of 1 in 100.

5.2.3. Plants and treatments.

Control treatments were supplied with equal proportion of solution A and B of the stock solution and maintaining at EC of 2 mS cm^{-1} . The other four treatments were obtained by addition of fertilizer grade concentrated KCl solution to the basic nutrient solution. An additional treatment was made by supplying a mixture of concentrated solution of KCl and CaCl_2 in 3:1 (w/w) proportion to the basic nutrient solution. Overall six treatments were evaluated in this experiment. Accordingly, ECs of the following osmotic concentrations were obtained 2, 4, 6, 8, 10 and 10^+ (which is made up of KCl and CaCl_2 solution). The higher conductivity treatments were established a week after the plants were set on the NFT channels. The recirculating nutrient solution was adjusted daily to pH of 6.5 and the appropriate nutrient conductivity level when necessary.

5.2.4. Recording sampling and analysis

5.2.4.1. Assessment of yield

Yield assessment was made by considering the number and weights of all harvested fruit. Fruit dry weight was recorded after samples were dried in an oven at 80°C for at least 48 hours.

5.2.4.2. Incidence and severity of Blossom End Rot (BER)

Both internal and external symptoms of BER were recorded on all harvested fruit. Internal BER was defined as grey, brown or black area of tissue located at the distal end of the placenta of the fruit and the closely associated seeds. This was done by cutting the fruit and inspecting it for the presence of the symptom.

5.2.4.3. Fruit fresh weight

The fruit growth attributes were evaluated periodically on destructively harvested fruit. Fruit fresh weight was determined by transporting the harvested fruit in closed plastic bag to the laboratory. The weight of fruit was measured to the nearest 0.01 g.

5.2.4.4. Fruit dry weight

The dry weight of fruits was determined after samples were oven dried for at least 48 hrs to a constant weight at 80°C. The dry weight was estimated to the nearest 0.001 g.

5.2.4.5. Fruit diameter and length

Fruit diameter and length were determined by measuring the respective attributes with a digital vernier calliper. Unless stated otherwise, the attributes measured were the longest fruit diameter and length.

5.2.5. Fruit growth analysis

Fruit growth was analyzed using some of the above growth attributes by computing their relative growth rate (RGR) (Hunt, 1990) as described in chapter 3.

5.2.6. Plant component evaluation

Leaf Area Ratio (LAR), Leaf Weight Ratio (LWR), Harvest Index (HI) and Specific Leaf Area (SLA) at the final harvest was calculated according to the method described by Hunt (1982).

where:

$$LAR = \frac{LA}{W}$$

[5.1]

$$SLA = \frac{LA}{W_L}$$

[5.2]

$$LWR = \frac{W_L}{W}$$

[5.3]

$$HI = \frac{W_F}{W_T}$$

[5.4]

LA = Leaf area (cm²)

W = total plant dry weight (g)

W_L = Leaf dry weight (g)

W_F = Fruit dry weight (g)

W_T = dry weight of above ground plant parts except fruit (g)

5.2.7. Stomatal resistance (r_s)

Stomatal resistance of the abaxial (lower) surface of the leaves was measured with a diffusion porometer (Delta T Devices, Model MK 3) calibrated with a plastic plate over a range of known resistances for temperatures ranging from 23 to 31°C and RH of 41 to 73%. A plot of the count vs resistance was used to calculate the stomatal resistance corrected for temperature. Measurements were made between 11.00 and 13.00 hrs New Zealand time on 12 occasions.

5.2.8. Leaf water potential (ψ)

This measurement was made only once (towards the final harvest of the crop) using a Scholander pressure bomb. Xylem ψ was measured on a sunlit mature leaf. The leaf was enclosed in a plastic bag just prior to measurement to prevent water loss. Each xylem ψ presented represents the average of 3 leaves block⁻¹ treatment⁻¹.

5.2.9. Tissue mineral analysis and determination.

The date of anthesis was recorded for all flowers on bud three and the fruit developed was used to determine the seasonal accumulation of Ca, K and Mg. For the purpose of fruit mineral analysis only one fruit was allowed to develop on the plant trained to a single stem.

The distribution of the mineral nutrients within the fruit were determined by cutting the fruit into stem-end and blossom-end portions.

The method of sample preparation analysis and determination is described in section 3.2.3.3.

5.2.10. Fractionation of calcium

The concentration of the different Ca compounds in the fruit tissue were determined by a sequential fractionation technique (Ferguson *et al.*, 1980).

A 0.1g dried and ground samples of tissue were prepared from each fruit part treatment¹. To these samples 3.5 ml of 80% acetic acid was added and homogenized by vigorously shaking the samples on a shaker for 30 minutes at 300 rpm at room temperature. The tissue samples were then centrifuged at 3000 ppm for 10 minutes and the supernatant was collected in centrifuge tubes filtered through 9 cm whatman filter paper placed in a funnel. After the remaining pellet samples were mixed up with another 3.5 ml acetic acid for the 2nd time, they were homogenized and centrifuged and the supernatants were added to the previous sample which was stored in a labelled centrifuged tube as fraction I (soluble Ca). The same procedure was repeated to the pellets for extraction of calcium oxalate fraction using 0.25M HCl. This sample was labelled as fraction II (Insoluble Ca). Finally the residue (Non extractable Ca) and the two other fractions were digested by taking 5 ml aliquot each

of Fraction I and II and the residue following the standard procedure for Ca analysis as described in chapter 3.

5.2.11. Dry matter partitioning

The partitioning of dry matter within the plants was estimated at the final harvest. Two plants treatment⁻¹ replicate⁻¹ were harvested and divided into leaves, stem, root, and fruit. Samples were oven dried to determine their dry weights. Leaf area was measured with a leaf area meter.

5.2.12. Measurement of respiration and ethylene production (static system)

Fruit respiration (CO₂ evolution) and ethylene production were determined by sealing individual fruits.

Four fruits were randomly selected from each treatment group which were free from defects and any sign of BER. The fruits were weighed and individually sealed in 1.2-litre plastic jar and incubated for 1 h at 20°C in the dark by covering them with black plastic.

The jars were sealed after being ventilated with air from a fan in order to avoid any build up of gas in the container. The sealing time and time of withdrawal of gas was recorded for each fruit which was used to calculate fruit respiration and ethylene production.

After 1 hr of incubation period, the air in each jar was mixed using an Omnifix syringe. Then two 1 ml gas samples were withdrawn from the head space of the jar with monoject-tuberculin syringes for CO₂/O₂ and C₂H₄ analysis. Finally fruit volume

was determined by water displacement technique proposed by Lownds *et al.*, (1993).

5.2.12.1. Analysis of gases (CO₂ and O₂)

The CO₂ and O₂ samples were analyzed using a Gas chromatograph, model, Shimadzu (GC-8A) fitted with thermal conductivity detector, model 90 mA. Using a 1 ml monoject-tuberculin or gas tight 100 µl syringe gas samples were injected into the GC in a stream of H₂ carrier gas flowing through the system at a flow rate of 25 ml min⁻¹. The response to injected sample was expressed as peak area using Hewlett Packard integrator, model 3390A.

The temperature of the column, injector and detector were maintained at 30°C, 60°C and 60°C respectively. Before any analysis was made a calibration curve was made by injecting gas samples of a known standard.

5.2.12.2. Analysis of ethylene

Concentration of Ethylene in gas samples was determined using a Photovac Model 10A10 gas chromatograph (Thornhill, Ont., Canada) with a photoionization detector and activated alumina column. Measurement was taken in a Laboratory at 20°C.

Samples were injected into the Photovac manually using either 1 ml monoject-tuberculin syringes or a gas tight 100 µl syringe.

5.2.12.3. Determination of gas concentration from chromatographic data

Peak area was used to determine the concentrations of CO₂, and C₂H₄. In the analysis, the peak area was used by the integrator to determine the concentration of

injected samples as follows:

$$CO_2 (\%) = \frac{\text{Sample peak area} * \text{Concn.of STD}[2.02\%]}{\text{Mean STD peak area}} \quad [5.5]$$

$$C_2H_4 (ul^{-1}) = \frac{\text{Sample peak area} * \text{Concn.of STD} [0.101 \text{ ppm}]}{\text{Mean STD peak area}} \quad [5.6]$$

The rate of carbon dioxide and ethylene production were calculated as follows:

$$FCO_2 = \frac{([CO_2]_f - [CO_2]_i)}{100} * (V_{jar} - V_{fxt}) * \frac{1000}{FWT} * \frac{60}{T} \quad [5.7]$$

$$FC_2H_4 = \frac{([C_2H_4]_f - [C_2H_4]_i)}{1000} * (V_{jar} - V_{fxt}) * \frac{1000}{FWT} * \frac{60}{T} \quad [5.8]$$

Where:

FCO_2 = rate of CO_2 production ($ml \text{ kg}^{-1} \text{ h}^{-1}$)

FC_2H_4 = rate of C_2H_4 production ($ul \text{ kg}^{-1} \text{ h}^{-1}$)

$[CO_2]_f$ = final CO_2 concentration (%)

$[CO_2]_i$ = initial CO_2 concentration (%)

$[C_2H_4]_f$ = final C_2H_4 concentration ($ul \text{ l}^{-1}$)

$[C_2H_4]_i$ = initial C_2H_4 concentration ($\mu l\ l^{-1}$)

V_{jar} = jar volume (ml) or (cm^3)

V_{frt} = fruit volume (ml) or (cm^3)

fwt = fruit fresh weight (kg)

T = time of incubation (h)

5.2.13. Measurement of maturity and quality attributes

Maturity was assessed by evaluating the following attributes.

5.2.13.1. Fruit skin colour

Fruit skin colour was measured on three positions on the fruit surface representing the shoulder, equatorial, and base of the external surface of the fruit. Colour was measured using a Minolta Chromameter (Model CR-100 Minolta Camera Limited, Osaka, Japan) with LCH mode calibrated with standard white plate ($C\ Y=87.5$, $x=0.308$, $y=0.315$) (Francis, 1990). Skin colour was expressed as lightness, chroma and hue angle. The three readings from each fruit were averaged prior to data analysis.

5.2.13.2. Fruit firmness

Fruit firmness (the force required to penetrate the tissue in kg) was measured at the locule and carpel wall at the equatorial region (Showalter, 1973)

Firmness was measured using a hand-held Effegi penetrometer fitted with a 11.1 mm diameter probe. The reading (expressed in kgf) was converted to Newton (N) by

multiplying by 9.80665 ms^{-2} (Soule, 1985).

5.2.13.3. Total Soluble Solids (TSS)

Soluble solid concentration (%) of the expressed juice was determined using a hand-held Atago N-10 refractometer (Model N_TMcCormick Fruit tech, brix range 0-10% at 20°C). The juice from whole fruit pericarp squeezed with a garlic press was used for TSS estimation.

The refractometer was initially calibrated using distilled water and the prism surface was wiped with tissue paper and distilled water after each run. The data presented is an average of two readings from each fruit sample.

5.2.13.4. Percent dry matter

Dry matter content of fruit was determined by computing the ratio of fruit dry weight and fresh weight and multiplying it by 100.

5.2.14. Statistical procedure

Data were analyzed using Statistical Analysis system (SAS) program (Littel *et al.*, 1991). This statistical package was used to compute ANOVA, mean and the standard error of means. When necessary \log_e or arcsine transformation of data was made before analysis. Details of the analysis was given in chapter 3.

5.3. Results

5.3.1. Fruit growth

The raw data and \log_e fresh weight of sweet pepper fruit are presented on (Fig. 5.1A and 5.1B). The two figures indicate that the fruit grows rapidly until 4 weeks after anthesis and thereafter it increased at a very slow rate. It was also demonstrated that every increment in the conductivity of the nutrient solution had a detrimental effect on the growth of fruits. Accordingly, all fruits grown at higher than control (EC=2) had reduced growth. \log_e transformed fresh weight data fitted Richards function and the RGR showed a declining trend with the control fruit having the highest RGR the first few weeks after anthesis (data not presented). The parameter values for Richards function are presented in appendix 2. Fruit growth in terms of dry weight, diameter and length also followed a similar pattern as fresh weight (data not shown).

5.3.2. Accumulation of calcium, potassium and magnesium.

5.3.2.1. Concentration in the fruit

Both the Ca content and the weekly rate of accumulation was reduced by higher ECs (Figs. 5.2B). The Ca concentration decreased rapidly during early fruit development and declined progressively with increasing EC. This reduction in Ca concentration was noted right from the 1st week after anthesis and persisted through out the fruit growth period (Fig. 5.2A). On the other hand, there was still reduction in the Ca content (Fig. 5.2B) although this reduction was quite clear from week three onwards. On the average conductivity had reduced the Ca concentration by 44% in the highest EC levels as compared to the control. The corresponding figure for Ca content was 57%. It is however, worth noting that higher Ca availability in the nutrient solution promoted the Ca accumulation in the fruit despite high conductivity of the nutrient

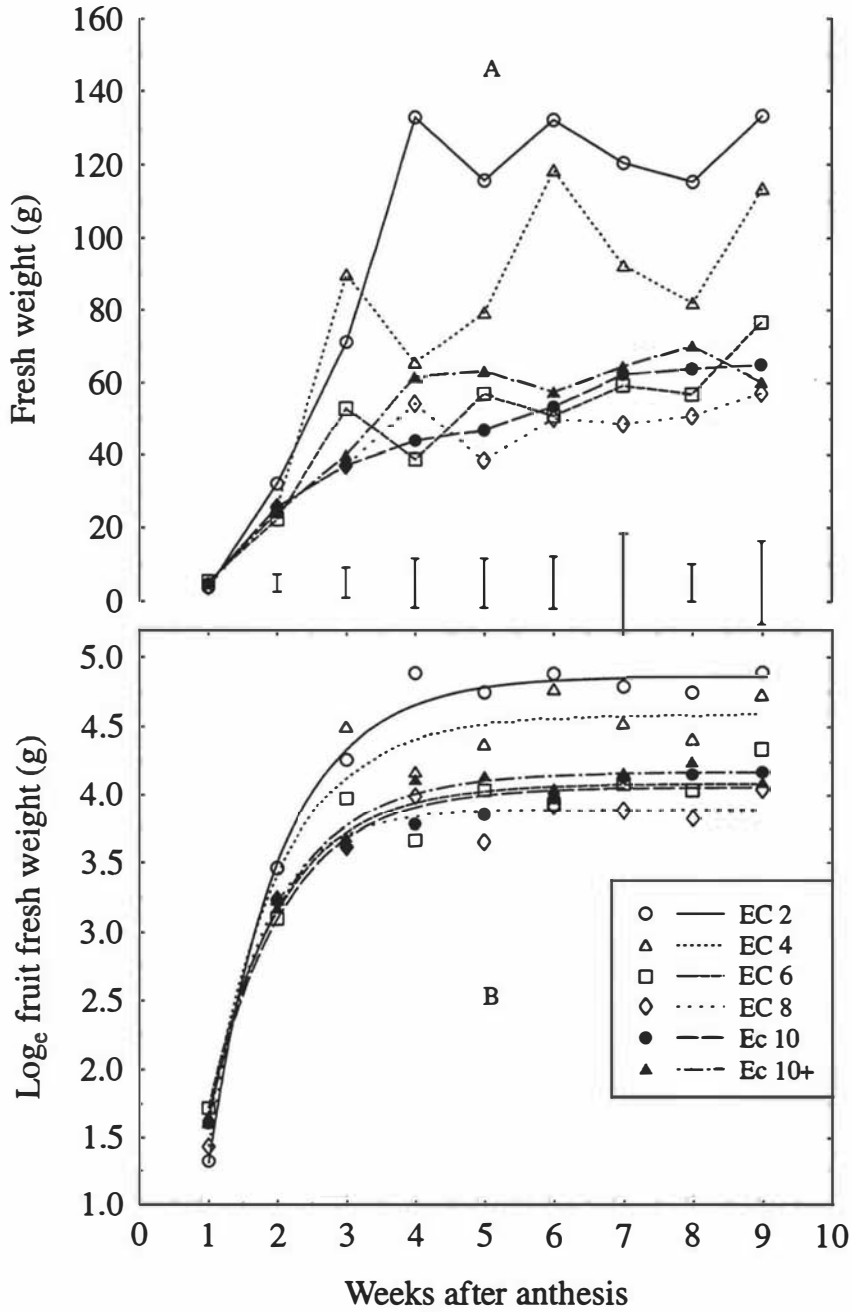


Fig. 5.1: Cumulative fresh weight (A) and Log_e fresh weight (B) of sweet pepper fruit as affected by the ionic strength of the nutrient solution. Each data point is the mean of 3 fruits. Vertical bars indicate standard error of means. Data fitted to Richards function.

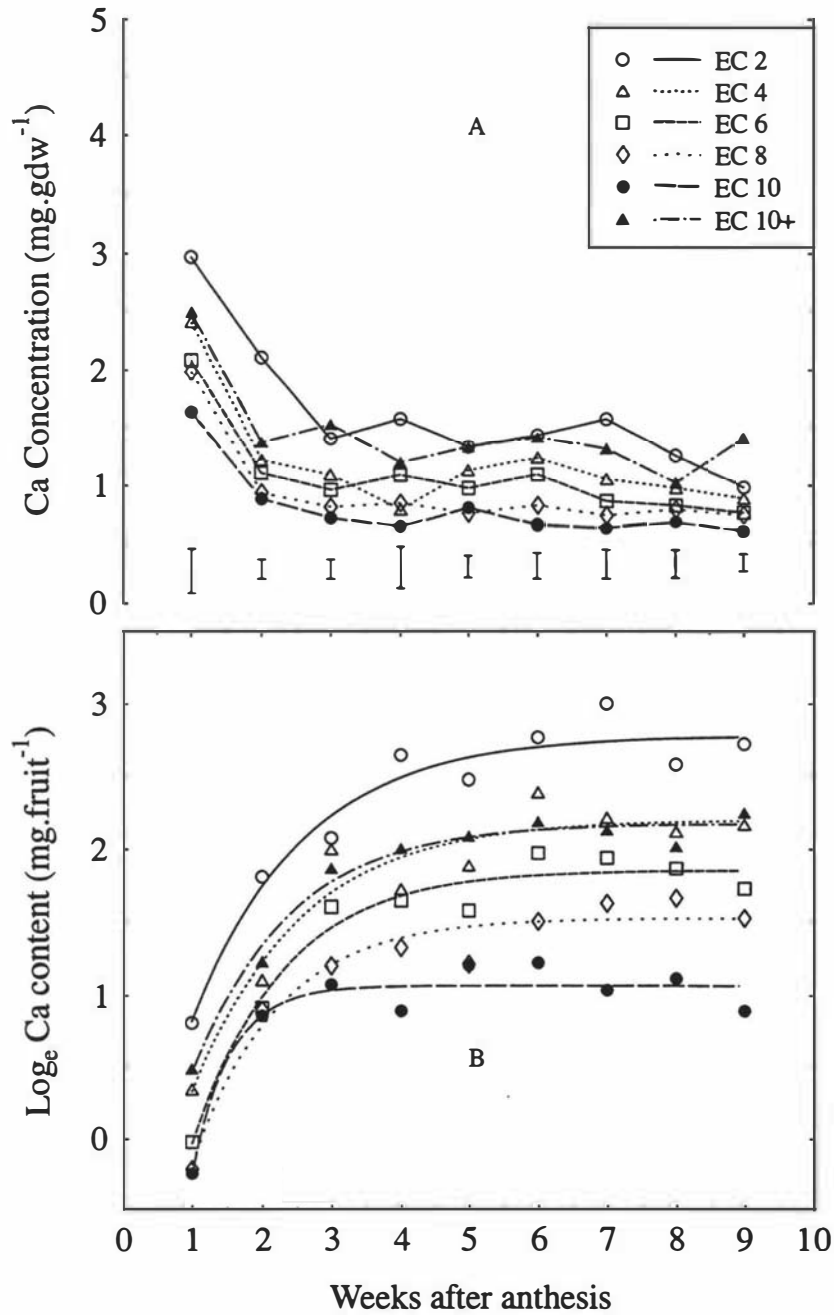


Fig 5.2. Fruit Ca concentration (A) and Ca content (B) as affected by the ionic strength of the nutrient solution. Each data point is an average of 3 fruit. Vertical bars indicate standard error of means. The Ca content data was fitted to Richards function.

solution (Figs. 5.2A and B). The effects of higher conductivity of the nutrient solution on the concentration of fruit Mg was similar as that of Ca (Fig. 5.3A). However, high conductivity significantly increased the concentration of K in the fruit (Fig. 5.3B).

5.3.2.2. Calcium distribution within the fruit

Most of the calcium which was absorbed and transported to the fruit accumulated in the stem-end of control fruit (Fig. 5.4b). Accordingly, the distal tissue always appeared to have less Ca than the proximal portion. It was also noted that although the Ca concentration and content in the fruit showed a declining and increasing trends respectively in both portions, this was more pronounced in the stem-end than blossom-end portion.

Generally higher conductivity of the nutrient solution reduced the Ca concentration and content of the fruit more significantly in the blossom-end than the stem-end of the fruit. (Figs. 5.4a and 5.4b).

5.3.2.3. Calcium fractionation

Calcium concentrations in all fractions significantly differed among the stem-end and blossom-end portions of the fruit grown at different EC levels ($P \leq 0.05$) (Table 5.1 and 5.2). Both tables also show that the acetic acid soluble Ca fraction (FI) progressively increased in both the blossom-end and stem-end of the fruit while the HCl soluble Ca fraction (FII) declined with time in the stem-end, but FII increased in the blossom-end with time until fruit maturity.

In control (EC 2) fruit, whole fruit Ca concentration was the highest in fraction II at the early stage of fruit growth followed by fraction I. With fruit maturity however,

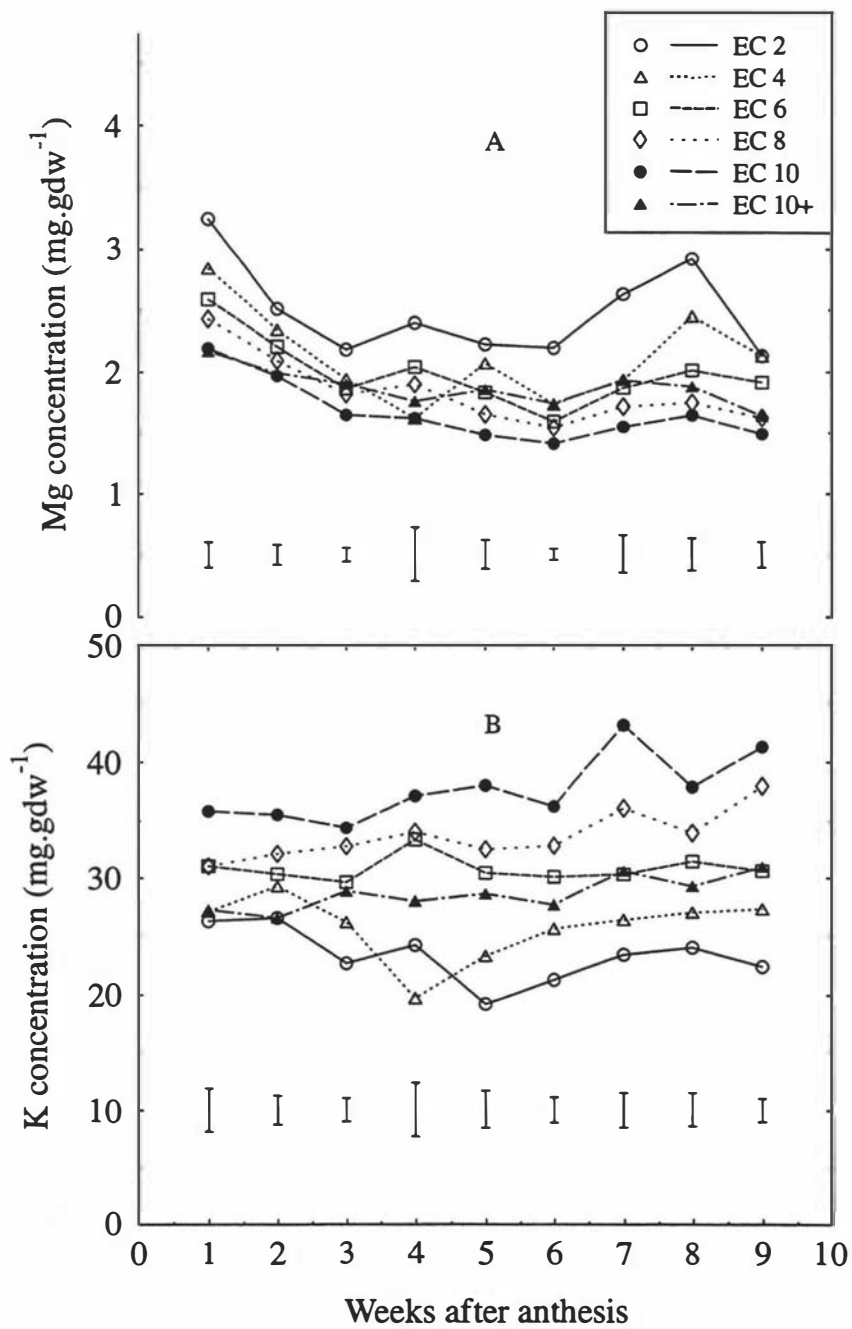


Fig 5.3. Fruit magnesium (A) and potassium (B) concentrations as affected by the ionic strength of the nutrient solution. Each data point is an average of 3 fruit. Vertical bars indicate standard error of means.

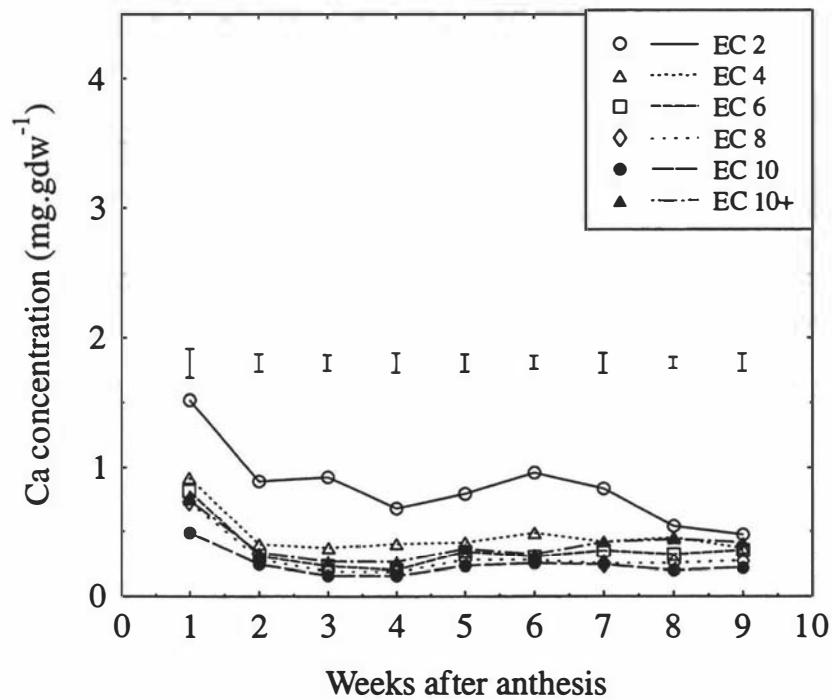


Fig 5.4a. Fruit blossom-end calcium concentration as affected by the ionic strength of the nutrient solution. Each data point is the mean of 3 fruit. Vertical bars represent standard error of means.

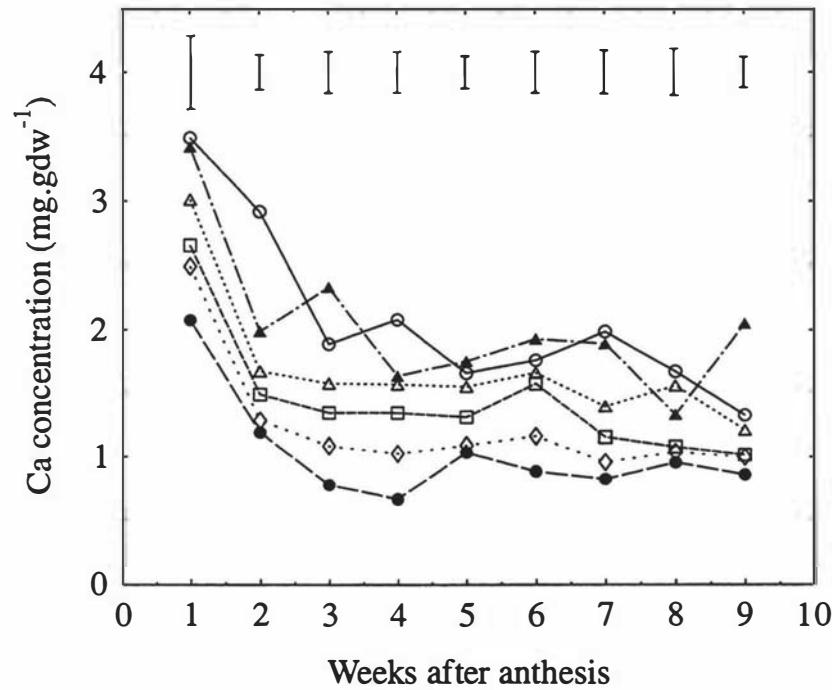


Fig 5.4b. Fruit stem-end calcium concentration as affected by the ionic strength of the nutrient solution. Each data point is an average of 3 fruit. Vertical bars indicate standard error of means.

Table 5.1. Calcium concentration (mg/gdw) of the different Ca fractions in the blossom-end of sweet pepper fruit as affected by the conductivity of the NFT solution.

Fraction I				
Week				
Treatment	2	3	5	8
EC 2	0.307 a ^x	0.316 a	0.291 a	0.454 a
EC 4	0.194 b	0.226 b	0.237 b	0.383 b
EC 8	0.171 b	0.198 b	0.226 b	0.220 b
SEM (df=4)	±0.002	±0.0001	±0.0001	±0.011
Significant	*	***	**	*
Fraction II				
EC 2	0.362	0.388 a	0.453 a	0.444 a
EC 4	0.328	0.221 b	0.256 b	0.305 ab
EC 8	0.222	0.202 b	0.171 b	0.188 b
SEM	±0.011	±0.002	±0.002	±0.009
Significant ¹	ns	*	**	*
Fraction III				
EC 2	0.154 a	0.186	0.207 a	0.202 a
EC 4	0.117 a	0.126	0.125 ab	0.118 b
EC 8	0.099 b	0.116	0.105 b	0.096 b
SEM	±0.001	±0.005	±0.002	±0.001
Significant	*	ns	*	*

^x means followed with the same letter are not statistically significant at $P \leq 0.05$.

¹ *, **, *** and ns indicate $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$ and non significant for this table and succeeding ones.

Table 5.2. Calcium concentration (mg/gdw) of the different Ca fractions in Stem-end of sweet pepper fruit as affected by the conductivity of the nutrient solution.

Fraction I				
Week				
Treatment	2	3	5	8
EC 2	0.402 a ^x	0.348 a	0.592 a	0.536 a
EC 4	0.284 b	0.339 ab	0.560 a	0.421 ab
EC 8	0.265 b	0.292 b	0.402 b	0.275 b
SEM (df=4)	±0.001	±0.001	±0.004	±0.005
Significant	*	*	*	*
Fraction II				
EC 2	0.995 a	0.643	0.669 a	0.507
EC 4	0.724 ab	0.567	0.554 b	0.427
EC 8	0.508 b	0.564	0.437 c	0.373
SEM	±0.018	±0.017	±0.001	±0.017
Significant	*	ns ¹	**	ns
Fraction III				
EC 2	0.427 a	0.565 a	0.416	0.331
EC 4	0.297 ab	0.376 b	0.253	0.245
EC 8	0.220 b	0.323 b	0.211	0.242
SEM	±0.005	±0.004	±0.011	±0.001
Significant	*	*	ns	*

^x means followed by the same letter are not statistically significant at $P \leq 0.05$.

this trend was reversed and the acetic acid soluble fraction increased in concentration while fraction II remained the same or slightly reduced. It was also observed that EC reduced the Ca concentration in all fractions. (Figs. 5.5 and 5.6A and B).

5.3.3. Leaf and root concentrations of Ca, Mg, and K.

Leaf Ca concentration significantly decreased with an increase in the level of conductivity in the nutrient solution (Fig. 5.7a). Similar results were also observed for root Ca concentration (Fig. 5.7b). It was also noted that the availability of more Ca in the nutrient solution could still improve the uptake of Ca into these organs as it did to the fruits (cf. Figs. 5.2A and B). With respect to Mg concentration, the conductivity of the solution has substantially reduced the Mg concentration of the leaf tissue while that of root was slightly increased with increasing EC levels (Figs. 5.8a and b). On the other hand, the K concentrations increased in both leaf and root with increasing levels of conductivity of the growing medium. (Figs. 5.9a and b).

5.3.4. Incidence of blossom-end rot

A higher incidence of BER was related to high EC of the nutrient solution. Plants grown under high EC levels tended to have more fruits affected with BER and they also had a higher percentage BER (Table 5.3). Plants grown under higher levels of Ca tended to have a lower incidence of BER than those with lower Ca. There was no significant difference in fruit number plant⁻¹ under each EC treatment. These data also show that BER is negatively correlated to the fruit Ca content and to some extent to its Ca concentration ($r=-0.85$ and -0.42) respectively, and positively correlated to fruit K concentration ($r=0.78$). Furthermore, a close negative and positive correlation respectively was noted between the incidence of BER and the ratio of Ca:K and $a_k/\sqrt{a_{Ca}+a_{Mg}}$ (Table 5.4). This relationship holds true whether the whole fruit or the blossom-end portion of the fruit are analyzed (Table 5.4) and both

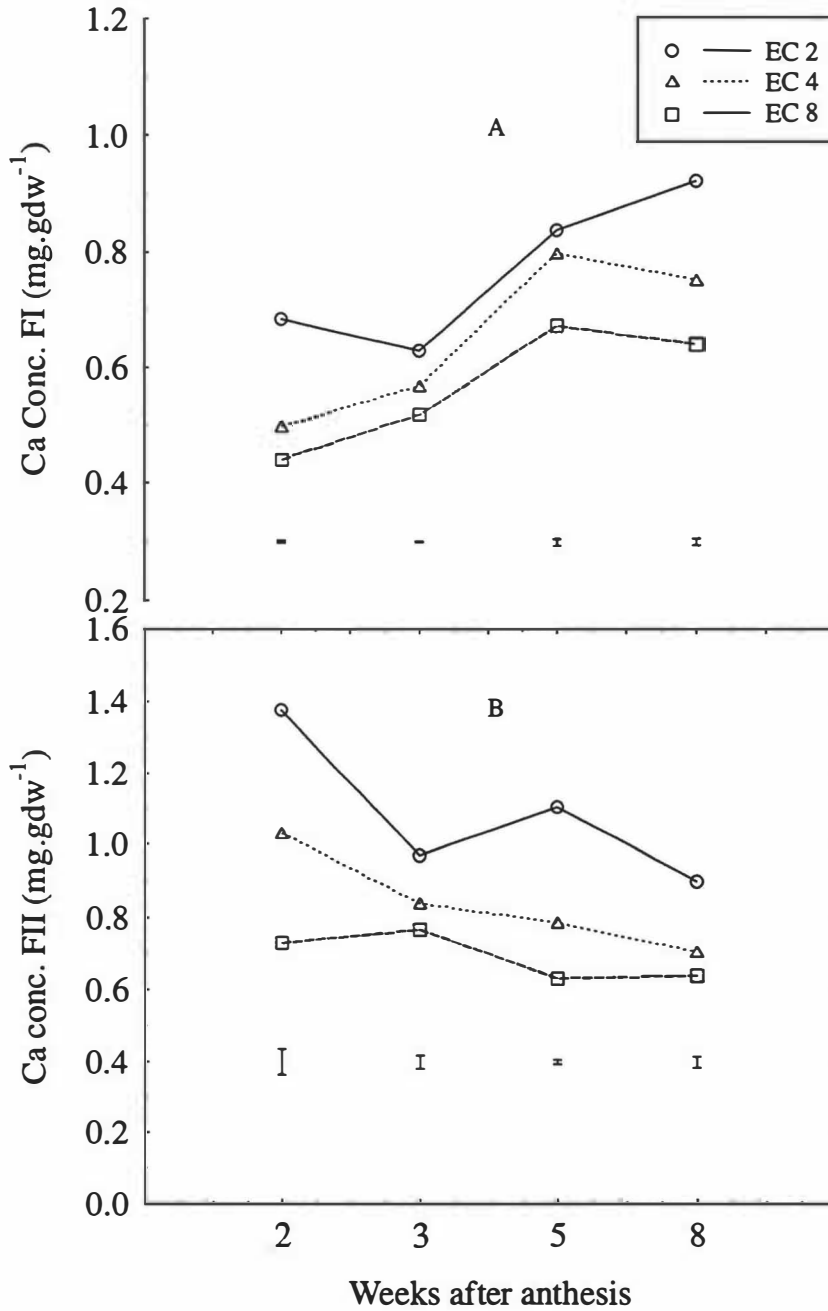


Fig 5.5: Acetic acid soluble (A) and Hydrochloric acid soluble (B) calcium concentration in sweet pepper fruit as affected by the ionic strength of the nutrient solution. Each data point is an average of 3 fruit. Vertical bars indicate standard error of means.

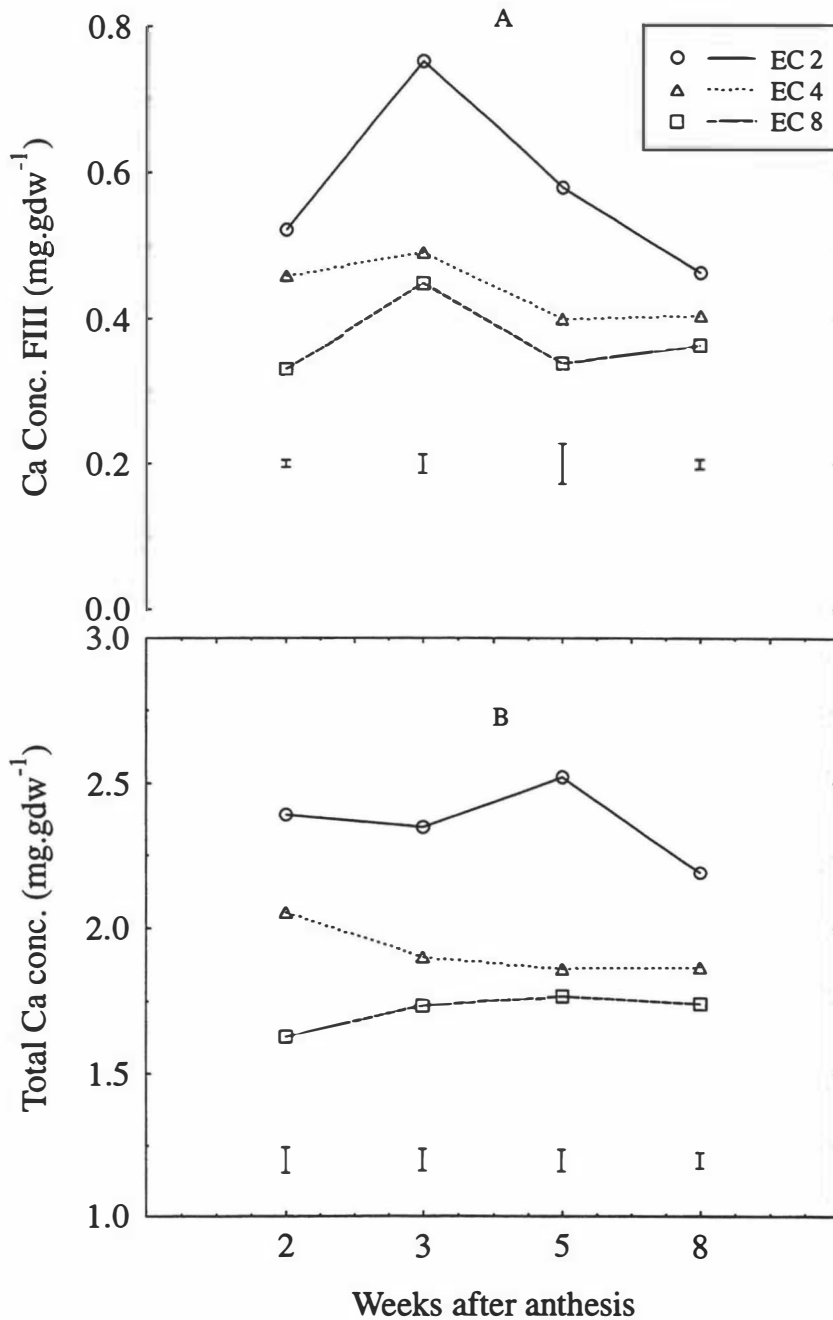


Fig 5.6: Non extractable (A) and total fractionated (B) calcium concentration in sweet pepper fruit as affected by the ionic strength of the nutrient solution. Each data point is an average of 3 fruit. Vertical bars indicate standard error of means.

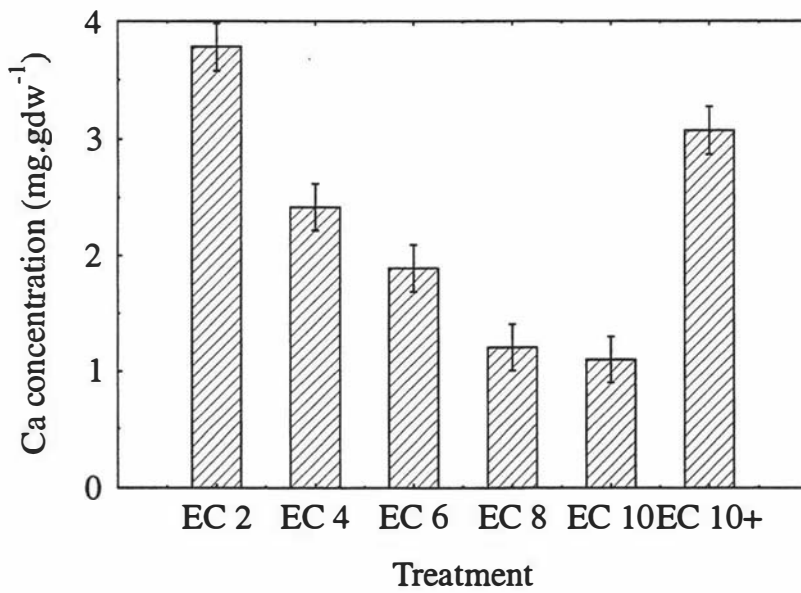


Fig 5.7a: Leaf calcium concentration as affected by the ionic strength of the nutrient solution. Each data point is average of 6 plants' leaves. Vertical bars indicate standard error of means.

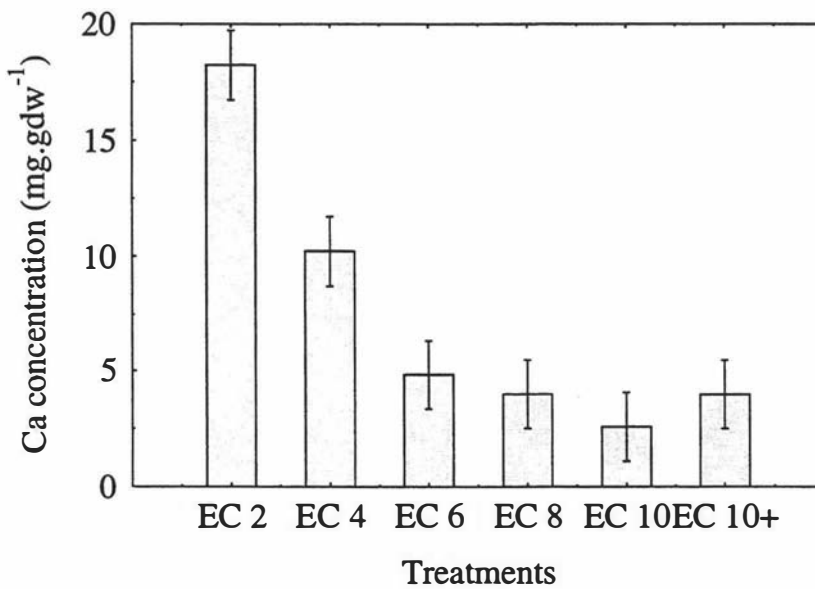


Fig 5.7b: Root calcium concentration as affected by ionic strength of the nutrient solution. Each data point is an average of 6 plants' root. Vertical bars indicate standard error of means.

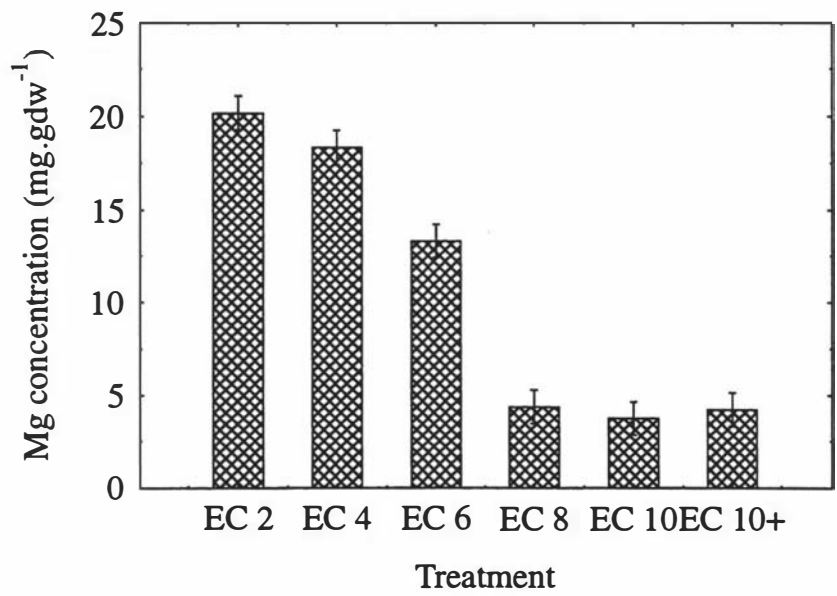


Fig 5.8a: Leaf magnesium concentration as affected by the ionic strength of the nutrient solution. Each data point is average of 6 plants' leaves. Vertical bars indicate standard error of means.

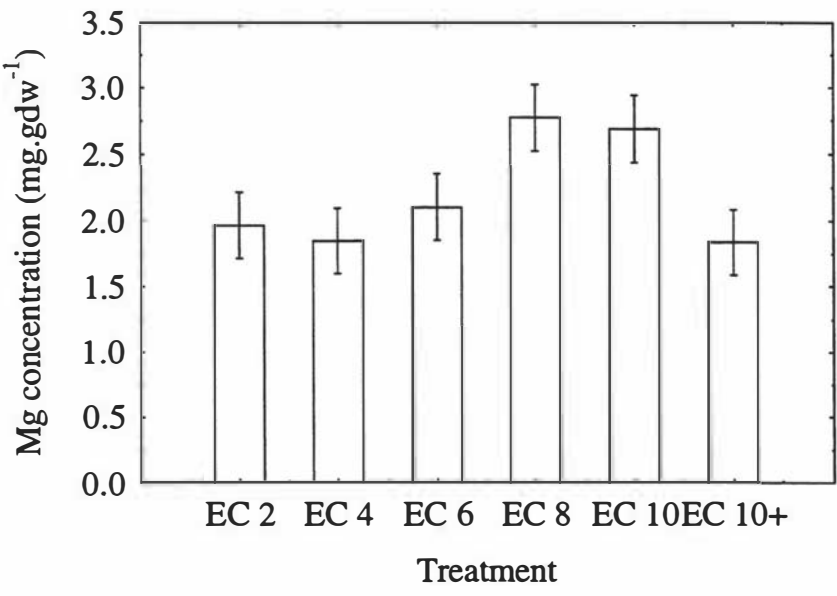


Fig 5.8b: Root magnesium concentration as affected by ionic strength of the nutrient solution. Each data point is an average of 6 plants root. Vertical bars indicate standard error of means.

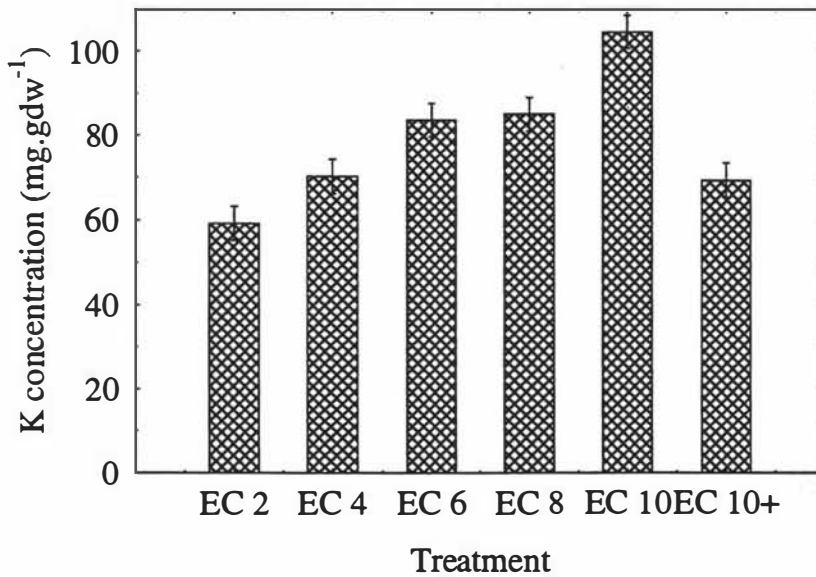


Fig 5.9a: Leaf potassium concentration as affected by the ionic strength of the nutrient solution. Each data point is an average of 6 plants' leaves. Vertical bars indicate standard error of means.

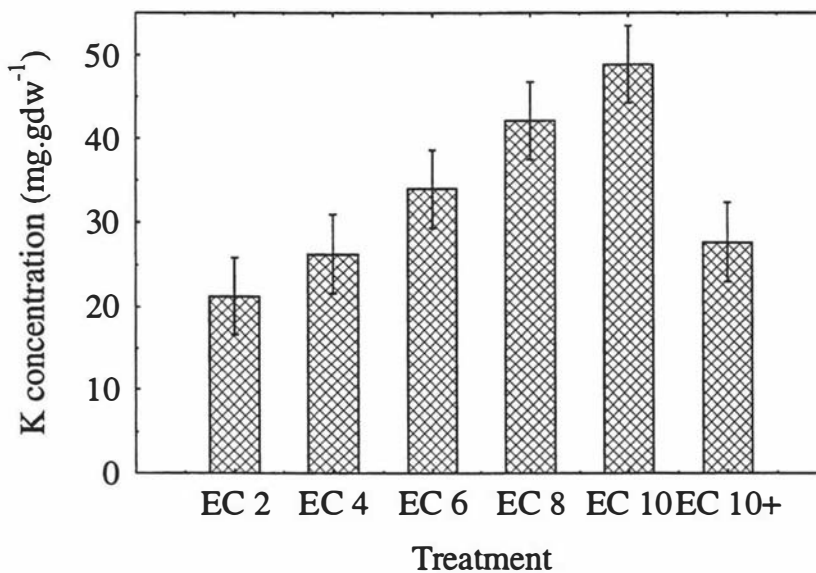


Fig 5.9b: Root potassium concentration as affected by ionic strength of the nutrient solution. Each data point is an average of 6 plants' root. Vertical bars indicate standard error of means.

EC and $a_K/\sqrt{a_{Ca}+a_{Mg}}$ showed a similar relationship to BER.

Table 5.3. The effects of conductivity of the nutrient solution on the number of BER affected fruit and percentage BER of sweet pepper fruit.¹

Treatment mS.cm ⁻¹	Number of fruit harvested	Number of BER affected fruit	BER %
EC 2	75.7	39.67 b ^x	31.4 (52.0) ² d
EC 4	78.3	56.00 ab	45.8 (71.3) bc
EC 6	68.0	52.00 ab	49.5 (75.7) ab
EC 8	79.0	65.00 a	55.4 (82.3) a
EC 10	64.7	52.70 ab	54.9 (81.7) a
EC 10+	65.7	41.70 b	39.8 (64.0) cd
SEM	5.501	5.294	2.68
Significant	ns	*	***

¹ fruits were harvested from a total of 9 plants block⁻¹ and 3 blocks treatment⁻¹.

^x means followed by the same letter are not significantly different using Duncan's multiple range test.

² values in bracket represent back transformed arcsine values.

Table 5.4. Correlation coefficient table showing the relationship between the incidence of BER and fruit Ca, Mg, K and ionic activity ratios.

Variables	BER % versus total fruit	Significance	BER % versus BE	Significance
Ca Conc.	-0.419	*	-0.510	*
Ca content	-0.849	***	-0.727	***
Mg concn.			-0.426	0.1
Mg content	-0.686	**	-0.763	***
K concn.	0.775	***	0.592	**
K content	0.430	0.1	0.733	***
Ca:K	-0.726	***	-0.673	**
$a_K/\sqrt{a_{Ca}+a_{Mg}}$	0.723	***	0.624	**

No significant difference was observed in terms of severity of BER (data not presented), but there was a trend for fruits grown under high levels of conductivity to have a larger lesion than those grown under low conductivity. It was noted that BER appears initially as internal blackening of the placenta tissues and a few seeds at the blossom-end of the fruit starting 2 weeks after anthesis. This earlier manifestation was mainly in fruits grown under high levels of conductivity, but the distinction between internal and external BER disappeared once the symptom was observed on the external blossom-end surface of the fruit 3 weeks after anthesis.

5.3.5. Fruit yield and size

Plants grown under higher conductivity of the nutrient solution produced lower yield as well as smaller sized fruit (Table 5.5). In this respect, fruits produced under the highest EC level had produced only 1/3 of the control treatment while, the lowest yield reduction was at EC 4 where the yield was 2/3 of the control treatment.

Water consumption of sweet pepper plants under different ECs of the nutrient solution is shown on Table 5.6. The data was obtained by measuring the amount of water to be applied each day to maintain a set amount of solution in the each container of the respective treatments. Therefore, it is assumed that it is that amount of water replaced which is lost through transpiration. Accordingly, it was found that control plants consumed more water than the other treatments with increased conductivity levels.

5.3.6. Stomatal resistance (r_s) and leaf ψ

Stomatal resistance of plants from high conductivity treatment was significantly higher than the control treatment over the whole measurement period (Fig. 5.10). This shows that such plants were partially closing their stomata in order to maintain their

turgor potential. Similarly, the leaf ψ measurement confirms this observation that plants from solution of high conductivity maintained a higher negative water potential than those of control plants (Table 5.7).

Table 5.5. Effects of conductivity of the nutrient solution on the total number, average size, water content and yield of sweet pepper fruit.¹

Treatment mS cm ⁻¹	Fruit number	Fruit water content (%)	Total fruit fresh weight (g)	Average fruit size (g)
EC 2	41.0	67.56(92.43) ² a ^x	4308.8 a	104.97 a
EC 4	45.7	65.41(90.93) b	3277.0 a	71.53 b
EC 6	37.3	64.53(90.27) c	1909.5 b	51.80 c
EC 8	48.0	64.59(90.33) bc	1855.8 b	38.70 cd
EC 10	40.0	64.60(90.33) bc	1411.2 b	35.63 d
EC 10+	33.0	64.80(90.48) bc	1353.0 b	41.77 cd
SEM	3.91	0.243	335.06	4.737
Significant	ns	***	***	***
Linear ^y		***	***	***
Quadratic		***	*	**
Cubic		*	ns	ns

¹ fruits were harvested from a total of 6 plants block⁻¹ and 3 blocks treatment⁻¹.

² values in bracket are back transformed arcsine values

^x means followed with the same letter are not significant according to Duncans multiple range test.

^y orthogonal contrast was made excluding treatment EC 10+

Table 5.6. The water consumption (l) of sweet pepper plants under different conductivity levels of the nutrient solution over 64 days.¹

Treatment mS cm ⁻¹	Average water consumption Plant ⁻¹ day ⁻¹
EC 2	0.79
EC 4	0.66
EC 6	0.45
EC 8	0.47
EC 10	0.37
EC 10+	0.36
SEM	0.04

¹ only means and standard error were evaluated for this attribute

Table 5.7. Leaf water potential (MPa) of plants grown under different conductivity of the nutrient solution.

Treatment mS cm ⁻¹	Leaf water potential (ψ)
EC 2	-1.07 c ^x
EC 4	-1.41 b
EC 6	-1.54 ab
EC 8	-1.59 ab
EC 10	-1.87 a
EC 10+	-1.74 ab
SEM(df=10)	0.029
Significant	***

^x Means followed by the same letter are not significantly different from each other according to Duncan's multiple range test.

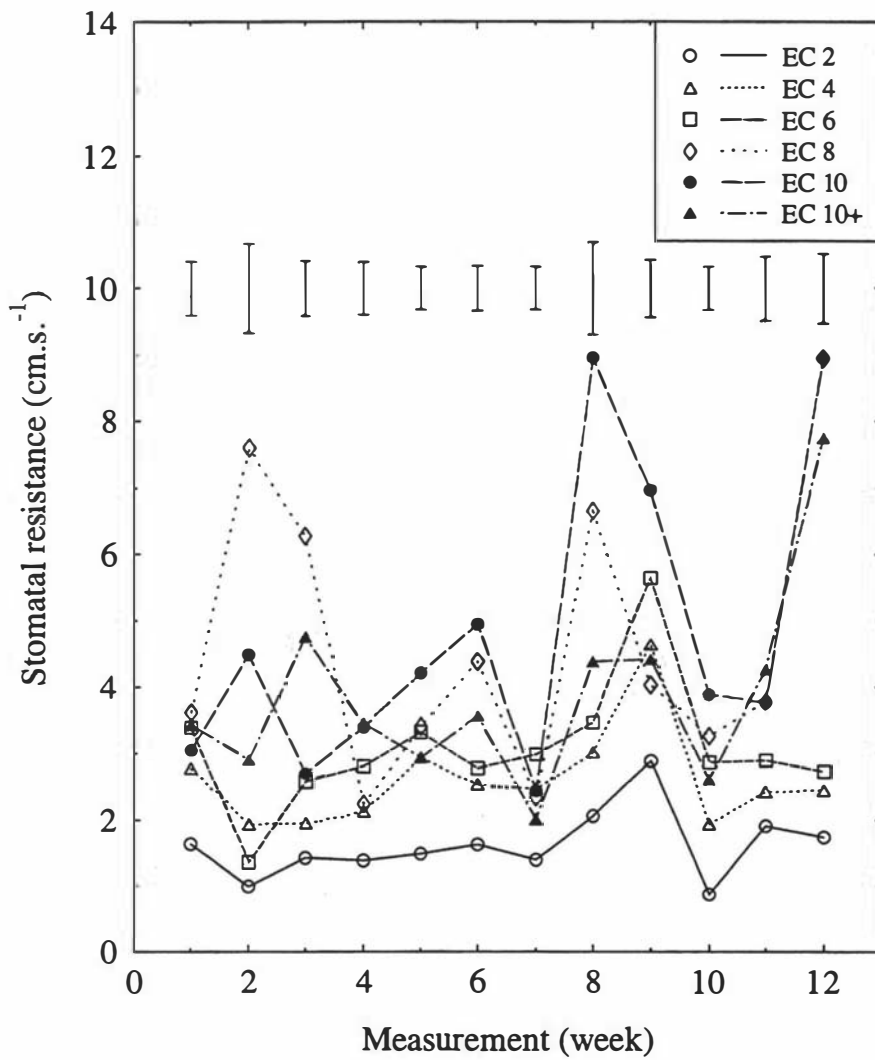


Fig 5.10. Leaf stomatal resistance of sweet pepper plants as affected by the conductivity of the nutrient solution. Each data point is the mean of 10 leaves. Vertical bars indicate standard error of means.

5.3.7. Dry matter partitioning

High conductivity of the nutrient solution decreased the total dry weights of plants. Control (EC 2) plants had significantly higher total dry weight than the other conductivity treatments, and consistently produced higher total dry weights in all plant parts (Table 5.8).

The fresh weight of individual fruit was nearly 3 times greater in control than the highest conductivity treatments (Table 5.8). However, the dry matter content of fruit was lower in the former than the latter case (Table 5.10).

It was found that control plants diverted a higher proportion of their photosynthates towards fruit as expressed in their harvest index (HI). On the other hand, plants grown with high conductivity solution had high leaf weight ratio (LWR) by diverting more photosynthates to their leaves (Table 5.9). Although it was not consistent over all treatment levels, high EC of the nutrient solution appeared to reduce leaf area but not the leaf area ratio (LAR) (Table 5.9). It was also noted that higher EC levels in general favour a higher proportion of biomass allocation to roots as compared to control plants. The partition of dry matter in different organs of sweet pepper plants is given in Fig. 5.11. It was shown that unlike the control plants, plants grown under higher conductivity of the nutrient solution diverted a greater portion of their photosynthate to the vegetative parts to sustain growth. This in turn led to a significant reduction in the harvestable yield of the crop.

5.3.8. Fruit quality

Growing sweet pepper plants under higher than average EC levels helped to improve some quality attributes of the fruit (Table 5.10). This improvement appeared in terms of increment in dry matter percentage. Increasing the conductivity from EC 4 to EC 10 increased the dry matter content of fruit ($P \leq 0.001$). This is in contrast to its effect

Table 5.8. Effect of conductivity of the nutrient solution on the total dry weight (g) and partitioning of dry weight in sweet pepper at harvest.¹

Treatment mS cm ⁻¹	Plant part					
	Whole plant	Shoot ²	Leaf	Stem	Root	Fruit
EC 2	189.67 a ^z	88.99 a	46.57 a	42.42 a	9.18 a	91.83 a
EC 4	144.33 b	78.88 a	39.90 a	38.98 a	8.85 a	56.97 b
EC 6	148.33 b	88.64 a	45.31 a	43.34 a	9.04 a	50.88 b
EC 8	90.33 c	49.13 b	25.69 b	23.44 b	4.04 b	37.49 c
EC 10	81.00 c	49.07 b	27.82 b	21.25 b	4.26 b	28.10 d
EC 10+	79.00 c	48.45 b	25.75 b	22.70 b	3.53 b	27.52 d
SEM (df=10)	8.38	5.34	2.69	2.72	0.84	2.83
Signif ^x .	***	****	***	***	***	***
Linear ^y	***	***	***	***	***	***
Quadratic	ns	ns	ns	ns	ns	**
Cubic	ns	ns	ns	ns	ns	*

¹ average of 3 plants block⁻¹ and 3 blocks treatment⁻¹.

² shoot = leaf plus stem with out fruit.

^x *, **, *** ns= significant at P≤0.05, 0.01, 0.001 and non significant respectively

^y orthogonal contrast was made excluding treatment EC 10+

^z means followed by the same letter are not statistically significant according to Duncan's multiple range test.

Table 5.9. The effect of conductivity of the nutrient solution on the growth components of sweet pepper plants.

Treatment mS cm ⁻¹	HI	Leaf area cm ²	LWR	LAR cm ² .g ⁻¹	SLA cm ² .g ⁻¹	RootTop
EC 2	0.48 a	9904 b	0.245 e	52.49 c	214.36 b	00500 b
EC 4	0.39 bc	12108 a	0.276 d	83.87 a	303.94 a	00652 a
EC 6	0.41 b	9418 b	0.305 bc	63.40 b	207.94 b	00648 a
EC 8	0.34 c	5851 c	0.283 dc	64.56 b	227.68 b	00467 b
EC 10	0.35 c	5843 c	0.342 a	71.86 b	210.34 b	00549 ab
EC 10+	0.36 c	4975 c	0.320 ab	62.91 b	198.01 b	00452 b
SEM (df=10)	0.04	496.8	0.008	3.26	10.423	0.004
Signif.	***	***	***	**	***	**
Linear ^y	***	***	***	ns	*	ns
Quadratic	*	*	ns	*	*	ns
Cubic	**	***	**	**	***	ns

^y orthogonal contrast was made excluding treatment EC 10+

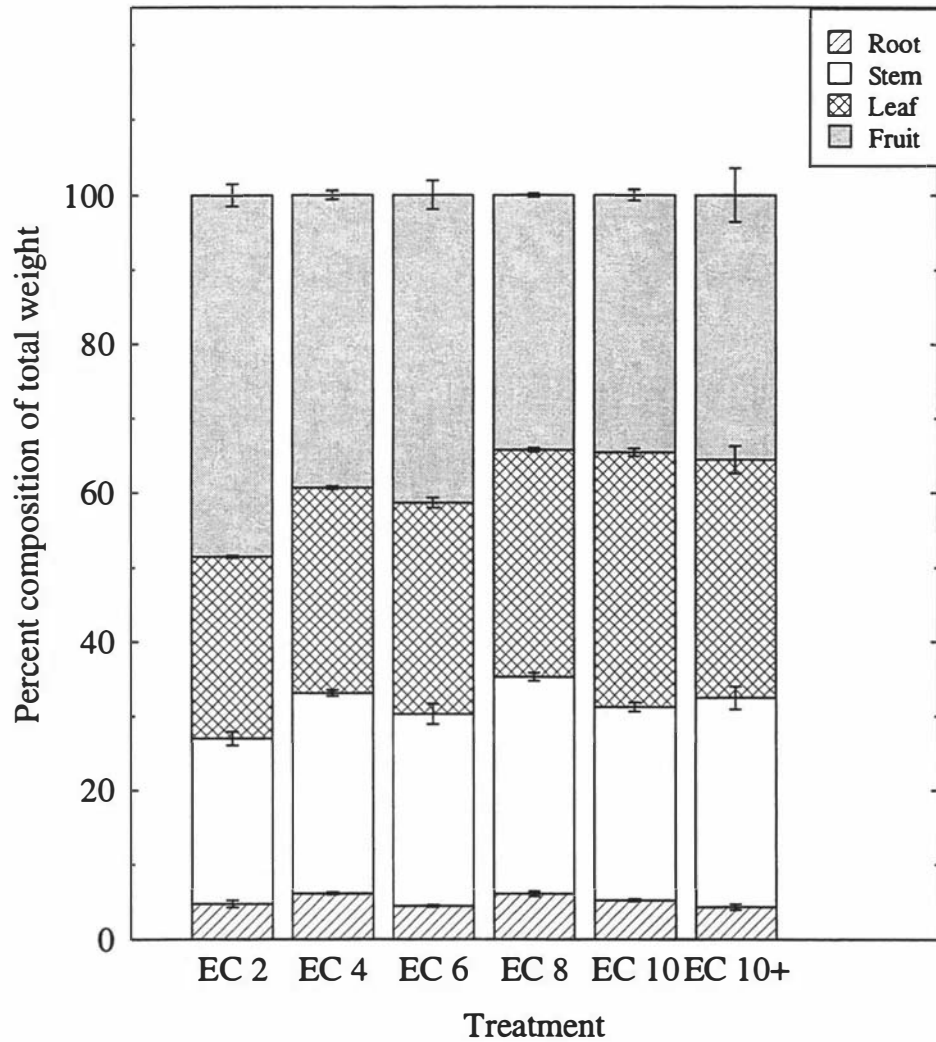


Fig. 5.11. Effect of ionic strength of the nutrient solution on dry matter partitioning between the different plant organs of sweet pepper plants at the final harvest. Each data point is the mean of 3 plants. Vertical bars represent standard error of means. Each bar represents the mean of 3 plants. Vertical lines indicate the standard error of the mean.

Table 5.10. The effect of conductivity of the nutrient solution on some quality attributes of sweet pepper fruit. (n=7).

Treatment mS cm ⁻¹	Fruit dry matter %	TSS °Brix	Fruit firmness Newton
EC 2	7.54 c	7.56	21.61 a
EC 4	9.06 b	7.14	19.26 ab
EC 6	9.73 a	6.83	17.41 bc
EC 8	9.67 a	6.94	15.38 c
EC 10	9.67 a	6.69	15.20 c
EC 10+	9.52 ab	6.61	15.90 c
SEM	0.18	0.478	0.929
Significant	***	ns	***

in reducing the fresh weight of fruit (Table 5.5). High conductivity therefore reduced the water content of fruit.

On the other hand, increasing the EC levels by addition of either potassium alone or in combination with Ca didn't affect the total soluble solid (TSS) content of the fruit, but tended to reduce the firmness of the fruit significantly.

5.3.9. Fruit ripening

5.3.9.1. Colour change

Analysis of colour change over time revealed that the time of ripening was shortened by higher EC treatments as compared to control. Fig. 5.12B shows that colour change in terms of hue angle values declined gradually in control treatment. On the other

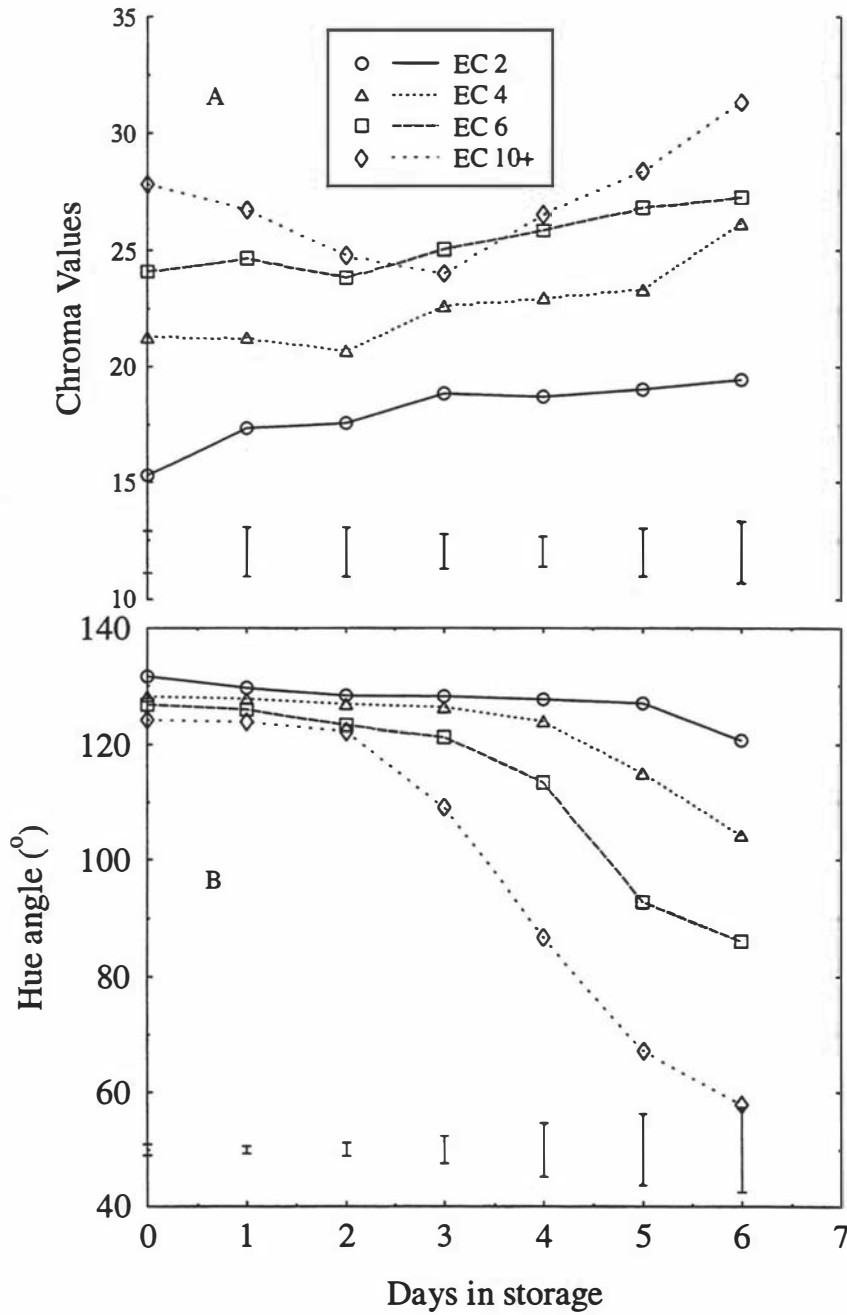


Fig. 5.12: Chroma values (A) and hue angle (B) of sweet pepper fruit with time as affected by the ionic strength of the nutrient solution. Each data point is the mean of 4 fruits. Vertical bars indicate standard error of means.

hand, for fruit from plants grown under increased conductivity of the nutrient solution, this change was quite marked. However, fruit variability was noted in this respect. As the hue angle values declined following fruit ripening, the chroma values showed a progressive increase after colour break (Fig. 5.12 A). Likewise, the chroma values for fruits from plants grown under higher EC was higher than the control treatment.

On the other hand, lightness had no definite pattern with respect to treatments. However, it was generally noted that it appeared to have higher values in immature fruits and gradually declined following harvest. As the fruit ripens, it tends to increase as the colour intensity increased (Fig. 5.13).

5.3.9.2. Fruit respiration and ethylene production

Growing sweet pepper plants under increased conductivity of the nutrient solution tended to increase fruit respiration (Fig. 5.14A). It was also observed that fruits from plants grown under the higher EC levels appeared to have their peak respiration at least a day earlier than those grown at low to moderate EC levels. Similarly, Fig. 5.14 B depicts that higher EC levels significantly increased the ethylene production rate of sweet pepper fruit. It was also noted that higher conductivity of the nutrient solution shifted the peak ethylene production time earlier than the control treatments. This peak in ethylene production followed the rise in respiration.

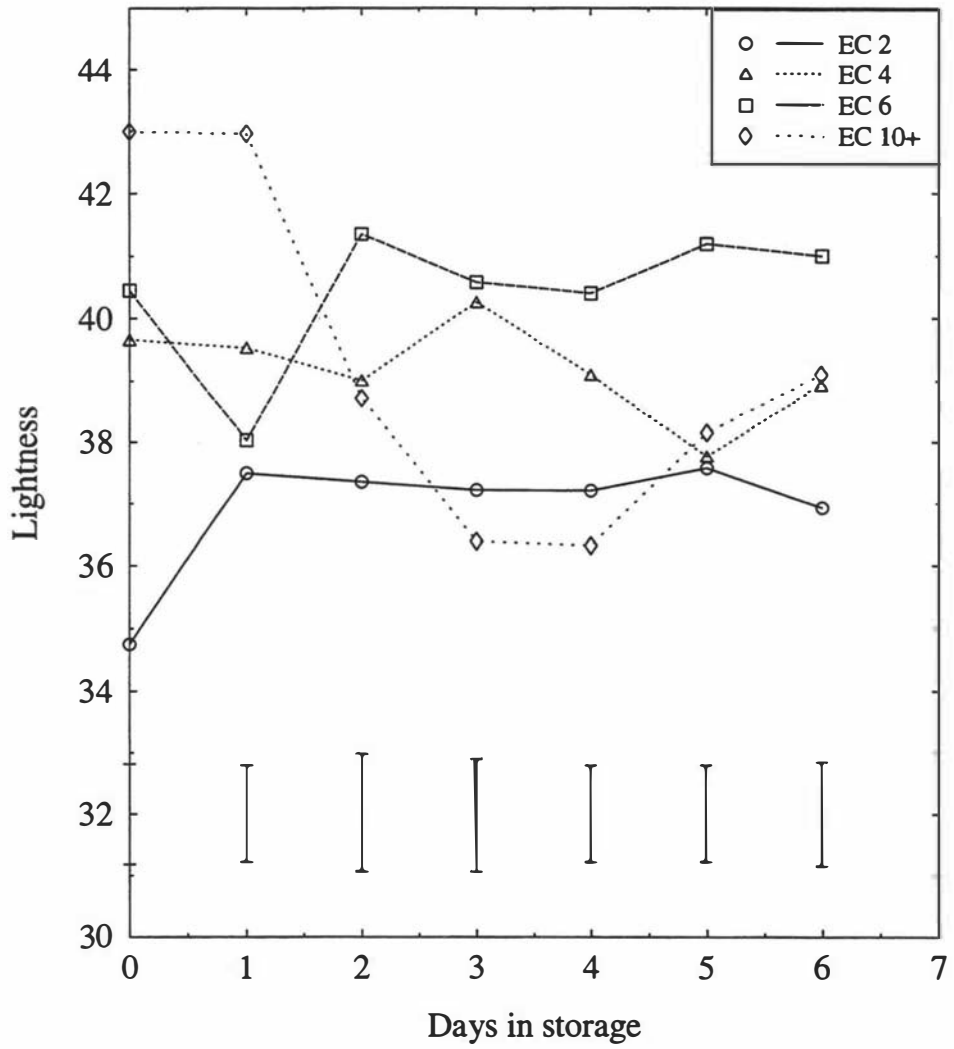


Fig 5.13: Lightness of sweet pepper fruit with time as affected by conductivity of the nutrient solution. Each data point is an average of 4 fruits. Vertical bars indicate standard error of means.

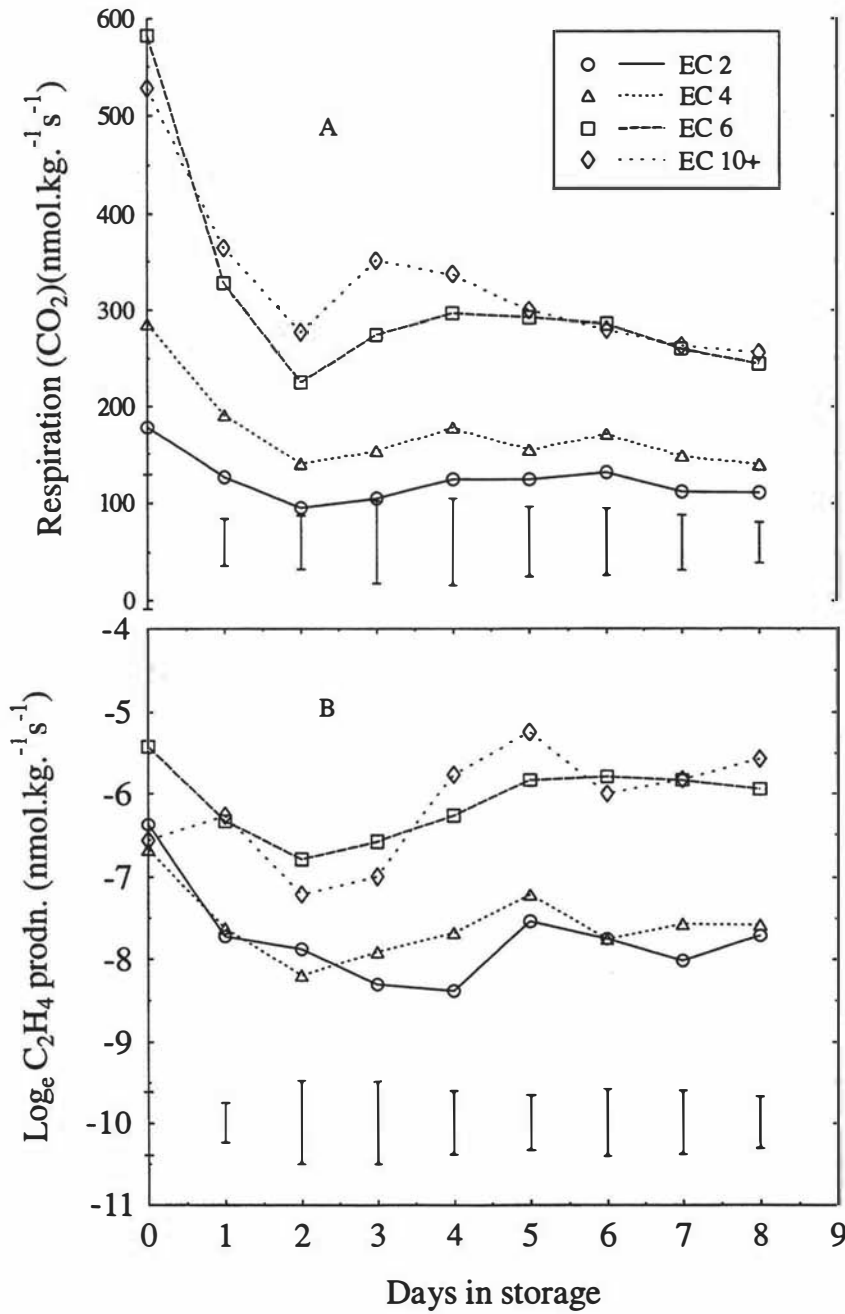


Fig. 5.14: Sweet pepper fruit respiration (A) and ethylene production (B) with time as affected by the ionic strength of the nutrient solution. Each data point is the mean of 4 fruits. Vertical bars indicate standard error of means.

5.4. Discussion

5.4.1. Fruit growth

Water stress is known to reduce cell division and cause cell enlargement to cease. This leads to a slow down of expansion growth rate (Slatyer, 1967), and may be the cause of a reduction in fresh, dry weight, diameter and length growth of the sweet pepper fruits under high conductivity treatments.

Salinity may inhibit growth by either upsetting the water balance thereby reducing of turgor or through depletion of the energy required for metabolism involved in growth (Lacheene *et al.*, 1986). This disturbance in water balance may result from either the interference in water uptake and transport within the plant or from toxic effects caused by excess mineral ions in the tissue (Poljakoff-Mayber, 1982).

High EC levels substantially reduced the fruit water potential of tomato plants (Xu *et al.*, 1994). Johnson *et al.*, (1992) further demonstrated that fruit water potential correlates positively with water potential elsewhere in the tissue. Although fruit water potential was not recorded in this experiment, the leaf ψ readings appear to support the findings of Xu *et al.*, (1994).

It therefore, appears that the reduction in growth in plants grown under higher solution conductivity resulted from reducing the water uptake (Ehert and Ho, 1986b) and a possible reduction in photosynthesis (Xu *et al.*, 1994) which leads to a reduction in the net transport and accumulation of assimilates into the fruit.

5.4.2. Mineral nutrient accumulation

The effects of conductivity of the nutrient solution on the uptake of calcium into

sweet pepper fruit showed that it reduces the uptake as well as concentration of Ca in the fruit. Higher conductivity levels further suppress the Ca content and concentration particularly of the distal portion of the fruit. The findings are consistent with reports on tomato (Ehert and Ho, 1986a; Adams, 1991).

Increasing NaCl or other salts in the nutrient solution reduces the ratio of Ca to other cations which result in less absorption of Ca (Shear, 1975). The reduction in calcium uptake by salinity may be due to direct osmotic effect on the uptake process or on root development (Ho and Adams, 1989a) or the indirect effect of salinity on transpiration due to reduced leaf size which decreases the amount of Ca to be transported to the shoot (Abd-Alla *et al.*, 1993).

Sweet pepper fruit accumulated Ca throughout its development at a variable rate. The uptake of Ca by the whole fruit was in parallel to the increase in dry weight of the fruit, but the highest uptake rate was recorded during early fruit development (Fig. 5.2B). This suggests that at this period fruit had a higher surface area to volume ratio which promoted transpiration. Fruit transpiration is the driving force for the influx of Ca into the fruit (Ferguson and Watkins, 1989). As the fruit grows this ratio changes and this is accompanied by further deposition of wax on the surface. Furthermore, the plant will also have developed more foliage. Hence, competition between leaves and fruit for water could reduce the Ca transport to the fruit particularly when the plant is under stress from low humidity (Adams and Holder, 1992) or high salinity (Ho, 1989). This would lead to a sharp reduction in Ca concentration during the rapid fruit growth period especially in large sized fruit like that of 'Domino' (Fig. 5.2A) where the fruit Ca uptake rate did not keep pace with dry matter accumulation.

The calcium concentration of fruit was further reduced by the high conductivity of the nutrient solution which further reduced the initial Ca content. As a result the total Ca content remained low. This reduced uptake could be due to competition between Ca and K during uptake from the root surface (Kirkby, 1979) and/or the reduced

osmotic potential of the nutrient solution which affects water uptake by the roots. If plants are grown under higher EC levels they tend to produce shorter as well as necrotic root tips (Cramer *et al.*, 1990) consequently reducing the amount of Ca absorbed as Ca uptake takes place at the root tip of the plant (Ferguson and Clarkson, 1975).

Supplemental Ca is known to reduce the adverse effects of salinity (Kent and Lauchli, 1985; Cramer *et al.*, 1986; Banuls *et al.*, 1991). The present results show that KCl at high concentration has reduced both fruit growth as well as Ca accumulation (Figs. 5.1 and 5.5) while, supplemental Ca at high conductivity levels improved the Ca status, possibly by maintaining the selectivity of K/Na (Kent and Lauchli, 1985; Cramer *et al.*, 1986). It is known that the upward movement of Ca ions occur in the xylem vessels via the transpiration stream by mass flow when adequate Ca is present in the medium (Ferguson and Clarkson, 1975 ; Harker *et al.*, 1988) or by an exchange system if Ca is low (Bell and Biddulph, 1963; Harker *et al.*, 1988). The movement of Ca into non vascular tissues has also been proposed by exchange under low extracellular Ca concentration and by diffusion if Ca is abundant (Harker and Ferguson, 1988; Harker *et al.*, 1988). Thus, the presence of more Ca in the nutrient medium at higher EC level may have helped in occupying the exchange sites in the xylem walls (Singh and Jacobson, 1979; Vang-Peterson, 1980) during loading of Ca and promote the transport and unloading of the element into the fruit tissues (Harker *et al.*, 1988). This may be the reason why fruit from plants grown under increased Ca availability at higher EC level accumulated more Ca in the fruit. It is also possible that the accumulation of more Ca and K at the pedicle and stem-end of the fruit helps to lower the osmotic potential of the fruit thereby helping to draw more water and Ca into the fruit. This could be plausible because fruits grown at high conductivity with supplemental Ca had more Ca and K in their fruit.

The presence of more Mg and K in the fruit indicates that these elements are transported in different mechanism as opposed to Ca. Both elements are highly phloem mobile especially during the time when xylem fractional import is minimal

(Wolterbeek *et al.*, 1987), namely at the time of fastest fruit dry weight increase.

When sweet pepper plants were grown with the higher conductivity nutrient solutions, the supply of Ca, Mg and K to the foliage and roots was affected. Accordingly, higher EC levels reduced the Ca and Mg levels in this tissues while increasing that of K. This could be due to the availability of more K in the nutrient solution thus confirming the results of Norrie *et al.*, (1995), who however, noted that salinity had no effect on the Mg content in the foliage. This difference may be because in the current experiment a recirculating system was used which avoids the build up of nutrients in the medium while they used peat medium which could retain the Mg as well as K in the medium. The high concentration of K in the leaves of sweet pepper plants also suggests that this element may have been used as an inorganic constituent for the osmotic adjustment of leaves. The role of K in osmotic adjustment of leaves in response to water stress has been demonstrated by Jensen *et al.*, (1993).

Additional Ca at higher conductivity levels promoted accumulation of higher levels of Ca in the leaves and roots of sweet pepper plants compared to high EC without Ca. Shannon *et al.*, (1987) showed that increasing the salinity levels from 0 to 150 mmol with the addition of NaCl and CaCl₂ increased leaf and root Ca content in tomatoes.

5.4.3. Longitudinal gradient of calcium.

There was more Ca in the stem-end than at the blossom-end of the fruit (Figs. 5.4A and B). Similar results have been reported in other fruits (Chaplin and Scot, 1980; Ehert and Ho, 1986b). This is considered to be due to fewer xylem vessels at distal than the stem end (Belda and Ho, 1993), as the proximal end of the fruit contains more cells and vascular bundles in the pericarp than the distal end (Bohner and Bangerth, 1988), and this could result in lower xylem transport capacity (Brown and Ho, 1993). Higher conductivity nutrient solutions further reduce the content as well

as concentration of Ca in the distal end (Ehert and Ho, 1986b). This is because salinity or osmotic stress interferes with the development of functional xylem vessels which are already few in this portion of the fruit (Ho and Adams, 1989a, Belda and Ho, 1993; Ho *et al.*, 1993). The ion exchange capacity of the xylem vessels may be related to the lignin deposition (Ferguson and Bollard, 1976). The discrepancy in the availability in xylem vessels between proximal and distal ends of the fruit is more pronounced in large sized fruit (Belda and Ho, 1993) which therefore makes them more susceptible to BER because of poor transport of Ca to this region.

5.4.4. Calcium fractionation

Sequential fractionation of calcium in sweet pepper fruit demonstrated that the composition of Ca compounds differ during fruit development (Fig. 5.5A and B and 5.6 A and B). In young fruit about 2 weeks after anthesis most of the Ca is in FII while as the fruit enlarges and matures FI predominates. Higher conductivity reduced the Ca concentration in all fractions and the reduction was more pronounced in the distal than proximal portion of the fruit. Fraction I is assumed to be composed of water soluble Ca such as CaCl_2 , $\text{Ca}(\text{NO}_3)_2$ as well as Ca pectate and Ca phosphate and Ca carbonate (Himelrick, 1981; Clark *et al.*, 1987). On the other hand, fraction II mainly contains Ca oxalate (Ferguson *et al.*, 1980) while fraction III contains mainly Ca silicate (Clark *et al.*, 1987). The concentration of the total Ca was not exactly the same as the non fractionated Ca in the current experiment. Ferguson *et al.*, (1980) indicated that such procedures may not remove precisely the well defined fractions because of the dissolution of the different Ca compounds in the different solvents. However, this could be considered as a rough guide as to the composition and distribution of the various Ca compounds.

The physiological implication of the various Ca compounds in relation to BER could be explained in such a way that the high incidence of BER in young fruit is a result of both low Ca concentration as well as less amount of Ca in Fraction I. Because Ca

phosphate and pectate are involved in cell membrane structure (Ferguson, 1984; Ho and Adams, 1989b) this signifies their importance during rapid fruit development when they are in a greater demand. Consequently, a deficiency of these compounds may lead to the incidence of BER. This is in conformity to the findings of Minamide and Ho (1993) in tomato. The low amount of FI Ca towards maturity in the stem end could be a result of ripeness of the fruit and the corresponding loss of Ca pectate from the middle lamella.

5.4.5. Incidence of blossom-end rot

In the current experiment (in the summer) the incidence of BER was associated with warm weather and high levels of solar radiation in summer. The import of assimilates and rate of fruit enlargement is favoured at high temperature (Walker and Ho, 1977b). This results in accelerated growth of the fruits demanding more Ca for the synthesis of walls of newly developing tissues. If the extra Ca demanded can not be met, it results in leaky membrane and ultimate collapse of cells which cause BER. This condition is aggravated by salinity which hinders the uptake of Ca into the fruit (Ho, 1989).

BER generally occurs 2-4 weeks after anthesis as internal BER; as a blackening of the distal placenta and seeds of the fruit. This is usually when fruit growth rate is at its peak. During the same period the Ca concentration in the tissue rapidly declines. Woterbeek *et al.*, (1987) reported that during rapid fruit growth period there is high delivery of Mg and K (but not Ca) to the fruit through the phloem. This in turn reduces the Ca:K ratio as it was observed in this experiment. This implies that Ca uptake didn't match the rate of accumulation of other dry matter (Ehert and Ho, 1986b).

On the other hand, salinity induces water stress especially when the evapotranspiration demand is high as occurred during this particular experiment (Adams, 1991; Awang *et al.*, 1993a). It is also well documented that Ca moves

through the transpiration stream from root to shoot (Marschner, 1986), and reduction in xylem translocation rate due to high EC (Ehert and Ho, 1986b) can affect the supply of water and mineral nutrients particularly Ca.

Generally, higher transpiration promotes the movement of Ca to rapidly transpiring organs namely fully developed leaves. Less transpiring organs such as fruit will be disadvantaged as Ca is not redistributed from leaves to fruit (Poovaiah, 1985), and under such conditions are likely to suffer from BER. The high incidence of the disorder in this experiment can therefore, be seen as a result of higher fruit growth rate due to high temperature and radiation levels. During this period the fruit accumulates assimilates rapidly. These assimilates are transported through the phloem and contain a substantial amount of Mg and K but little or no Ca (Wolterbeek *et al.*, 1987). Therefore, in spite of low EC levels the incidence is likely to appear in summer. Salinity on the other hand, aggravates the problem since it interferes with the water balance and consequently movement of water and other mineral nutrients mainly Ca to the shoot and subsequently to fruit.

Thus, as Ehert and Ho (1986b) and Belda and Ho (1993) suggest the effect of salinity on Ca accumulation could be a result of short term effects on; the uptake of calcium by the roots; its movement from roots; and its long term effects on xylem tissue development. It is also important that since sweet pepper is very sensitive to Ca deficiency and hence BER, it is imperative that adequate Ca should be available early in the growth period. As is also demonstrated in this experiment, increasing the Ca availability during the rapid fruit growth period could help to make more Ca accumulate in the fruit thereby, avoiding the sharp reduction in Ca concentration during rapid fruit development and thus BER.

Recently, Nonami *et al.*, (1995) claimed that BER may not be caused by calcium deficiency, because when growing tomato plants with high Ca concentration in the nutrient solution they didn't observe any beneficial effects. However, in the current experiment it was observed that BER may be reduced by supplementary high Ca

concentration in the solution. It is because in spite of very high osmotic concentration to the plant roots uptake of Ca may not be hindered since under high external concentration diffusion will be operational (Harker *et al.*, 1988). Nonami *et al.*, (1995) also showed that BER affected fruit had higher Ca concentration than control fruit due to the added Ca-zeolite. Nonami *et al.*, (1995) also argue that both control and BER affected fruits had similar concentration of Ca in the fruit. This may be because they analysed the fruits just after they started to exhibit BER, however, tomato fruits show the symptom during early fruit development ie approximately 2-3 weeks after anthesis, and this time the Ca concentration in the fruit is still high and the difference may not be realized at that stage. Moreover, salinity has both short term and long term effects on both restricting the uptake of nutrients ie osmotic effect (Ehert and Ho, 1986b) and long term effects on xylem tissue development (Belda and Ho, 1993). Thus, if the fruit analysis was carried out later during fruit growth differences might have emerged.

5.4.6. Osmotic stress and plant growth and yield

The vegetative as well as reproductive development of sweet pepper plants in terms of plant height, total leaf area and yield were significantly reduced by higher conductivity of the solution. These growth attributes were negatively correlated with EC levels. The decrease in yield of high conductivity treatments was a result of a reduction in fruit size rather than of fruit number and this is in agreement with the reports of Ho *et al.*, (1995) on tomato. The lack of difference in fruit number could be a result of the promotional effect of potassium on fruit set (Satti *et al.*, 1994). The reduction in yield in this experiment is consistent with results reported by many other authors (Adams, 1991; Adams and Ho, 1989; Ho and Adams, 1989a; Sonneveld and Vander Burg, 1991; Chartzoulakis, 1992).

In this experiment salinity injury symptoms were not apparent in all the treatments, although leaf rolling and slight burning of leaf margins was noted towards the end

of the experiment especially in the very high EC treatments.

Greenway and Munns (1980) indicated that salts such as NaCl increase the osmotic potential of the solution and this may affect the water relations of the plant and may cause nutritional abnormalities and a poorer energy balance (Pasternak, 1987). Low plant water status may cause loss of turgor, and in order to avoid this plants grown under higher EC levels tend to adjust their internal osmotic condition (Lacheene *et al.*, 1986; Awang *et al.*, 1993a). Osmotic adjustment also require more respiration energy expenditure on maintenance energy (McCree, 1986). In addition, there is a substantial reduction in the rate of photosynthesis (Seeman and Critchley, 1985; Bethke and Drew, 1992; Cheesman, 1988; Xu *et al.*, 1994). Thus, since both photosynthesis and respiration products are used for the provision of osmotica for osmoregulation and the maintenance of damaged cells (Lacheene *et al.*, 1986) less will be available for growth which will lead to a reduction in growth and yield of the crop. Thus the reduced growth in sweet pepper could have been a result of the inability of the plants to adjust osmotically to increased conductivity of the solution or from the excessive energy demands required by such system (Lachaye and Epstein, 1971), although leaf osmotic adjustment in capsicum plants in response to water deficit stress has been reported by Wullschleger and Oosterhuis, (1991).

It was also demonstrated in this experiment that high conductivity of the nutrient solution resulted in the uptake of more K and decreased the uptake of Ca and to some extent Mg. This in turn might have led to a reduction in growth and yield due to nutrient deficiency.

The use of K and Ca to ameliorate the effects of NaCl salinity has improved the fruit weight and increased fruit set of tomato (Satti *et al.*, 1994). In this experiment however, no beneficial effects on yield were achieved by using Ca along with K to increase salinity. This may be because NaCl whose main effect is to maintain the K/Na selectivity and promote the uptake of K (Kent and Lauchli, 1985) was not used to increase salinity. It is possible however, that if the supplementary Ca was added

at lower levels of salinity it may have a different effect than observed.

5.4.7. Stomatal resistance and leaf water potential

High conductivity of the nutrient solution induced the partial closure of stomata which increases their stomatal resistance (Fig. 5.10). Stomatal closure occurs when a threshold value of water potential is reached (Garnier and Berger, 1987). Photosynthesis recovers fully on rehydration only if leaf ψ during stress did not fall below -1.3 MPa and it is completely inhibited at -2.0 MPa (Aloni *et al.*, 1991). Therefore, the reduced yield in plants grown under high EC levels may be a result of reduced leaf ψ , leaf area and consequent reduction in photosynthesis. Stomatal response to water potential was also demonstrated for a variety of crops (Castel and Fereres, 1982; Tan and Buttery, 1982; Cohen and Cohen, 1983). Although periodic measurement of leaf ψ was not made in this experiment, the reduced water uptake by plants grown under increased conductivity levels (Table 5.6) and the significant reduction in leaf ψ measured at the final harvest (Table 5.7) supports the previous assumptions that stomatal closure is related to the leaf ψ .

5.4.8. Dry matter partitioning

Increasing the level of conductivity in the nutrient medium had a marked effect on the dry matter partitioning of sweet pepper plants, as well as substantially reduced the total dry matter production and accumulation in the different organs of the crop (Table 5.8). The distribution of assimilates were also affected by higher EC levels, as more assimilates were diverted to shoots and less to fruit when plants were grown under the higher conductivity nutrient solutions (Fig. 5.11). This is in agreement with the findings of Ho and Adams (1994) who observed that salinity reduced both dry weights as well as partitioning in cucumber. Conversely, Ehert and Ho (1986a) however, reported that although salinity reduced the fresh weights of tomato plants

it did not reduce the dry weights or the proportional distribution of dry matter to fruits, vegetative shoots or roots of tomato plants from EC 2 to 6 mS cm⁻¹. Higher salinity levels of 10 mS.cm⁻¹ however, substantially reduced the dry weights of fruits (Ehert and Ho, 1986a). Ieperen (1996) also recently reported that high salinity reduced the distribution of assimilates to fruits in favour of the vegetative parts of tomato.

At higher EC levels, the rate of CO₂ fixation can be reduced (Xu *et al.*, 1994). Hence, the reduction in plant dry weight could be because of lower photosynthetic capacity due to smaller leaf area and lower sink strength especially of shoots.

The harvest index of plants was substantially reduced by higher conductivity of the nutrient solution (Table 5.9). This is because of the reduced photosynthetic capacity of plants grown under higher EC levels (Bethke and Drew, 1992) and also the reduced water uptake by such plants (Ehert and Ho, 1986a) which would affect the synthesis and transport of assimilates to the different organs. A reduced water uptake by plants grown in high conductivity levels was also observed in the present experiment (Table 5.6). It is also possible that since higher solution conductivity has reduced the fruit size, less assimilates will be drawn into the fruit. Patrick, (1988) indicated that the growth of individual plant organ may be restricted by assimilate availability (source limited) or by the ability of the organ to utilize assimilates (sink limited). Accordingly, higher EC levels restrict the photosynthetic capacity of the plant by reducing the leaf area which in turn limits the availability of photosynthate and by reducing the fruit size affect the organ's ability to accumulate assimilates.

SLA which is the ratio of leaf area and leaf dry weight is essentially a measure of leaf thickness (Fernandez and Miller, 1987). In this experiment, higher EC reduced the SLA of plants because of inhibition of the leaf expansion rate. Cosgrove (1986) reported that plant water content as a result of uptake and loss can influence tissue turgor which helps in cell elongation. Plants grown under higher conductivity levels had higher LAR as compared to the control plants (Table 5.7). An increase in LAR

in turn requires additional investment on the photosynthetic apparatus (Konings, 1989) consequently increasing the LWR but reducing the SLA.

5.4.9. Fruit quality

Higher conductivity levels of the nutrient solution tended to reduce the water content of sweet pepper fruit resulting in higher dry matter content. This is in agreement with the findings of Adams (1991) on tomato, Janse (1989) on sweet pepper and Chartzoulakis, (1992) on cucumber. Higher conductivity of the nutrient solution substantially reduced the fresh weight of fruits as compared to their dry weights.

It was shown in this experiment that at higher EC levels, sweet pepper fruits have low firmness possibly due to a lower Ca content. Similar results were reported by Janse (1989) that fruits grown at higher salinity levels tended to have a short shelf life. Higher conductivity levels however, failed to increase the TSS content of sweet pepper fruit. The reason for this is not clear. However, it may be because most of the other researchers used either NaCl or a balanced nutrient solution to increase salinity. Thus, increasing the salinity with only KCl may have hindered the uptake of the other essential elements contributing to the sweetness of the fruit. Gough and Hobson (1990) also observed no difference in reducing sugars of cherry tomatoes grown under salinity treatments ranging from 3-8 mS cm⁻¹. The absolute content of sugars was lower at higher salinity levels in strawberry (Awang *et al.*, 1993b).

It was also shown that sweet pepper fruit from higher conductivity levels had higher K content in their fruit as compared to control treatments. According to Adams *et al.*, (1978) acidity in tomato is positively correlated to K content. Although acidity was not evaluated in this particular experiment it is assumed that since fruits grown under high EC levels had more K in their fruit it may possibly contribute to higher acid levels. Gough and Hobson (1990) also noted higher organic acid content of tomato

fruits grown at higher salinity levels which also contained higher K levels.

5.4.10. Fruit ripening

5.4.10.1. Colour change

Graphs that represent changes in colour traits over time were shown in Figs. 5.12A and B and Fig. 5.13. The increase in chroma values which corresponded with a fall in hue angle suggests the gradual fall in the level of chlorophyll and an increase in carotenoid synthesis due to conversion of chloroplasts to chromoplasts (Leshem *et al.*, 1986). Carotenoid compounds are yellow to red pigments compounds of isoprene units which are normally fat soluble (Bunnell and Bauernfeind, 1962). The major red colour in capsicum comes from capsanthin and capsorubin, while the yellow-orange colour comes from beta carotene and violaxanthin (Bosland, 1993). Both capsanthin and capsorubin increase proportionally with advanced stages of ripeness (Kanner *et al.*, 1977). Reeves (1987) on the other hand, suggested that the amount of carotenoids in fruit tissue depends on factors such as cultivar, maturity stage and growing condition.

As it is demonstrated in this experiment the initial value of hue angle was high for all treatments. As ripeness progressed a decrease in hue angle was observed for all treatments. However, the change was more pronounced for those fruits grown under high conductivity levels. In line with a decline in hue angle there was a gradual increase in chroma values suggesting an increase in colour intensity which chroma describes (Tourjee *et al.*, 1993). It was also shown that the rate of colour change was much faster when the plants were grown under high conductivity treatments as compared to the control.

Application of Potassium nutrition has increased the red colour of tomato fruits (Trudel and Ozbun, 1971). In this experiment it was found that fruits grown under

high conductivity levels had higher K levels in their tissue (Fig. 5.7B). As carotene is the main pigment of capsicum fruit the contribution of K towards increased red pigmentation is a possibility.

On the other hand, lightness which measures the reflection of total visible light from a surface (Tourjee *et al.*, 1993) appeared to have less value in determining the colour change in sweet pepper fruit at least in this particular experiment. This is because this attribute changed very little and inconsistently during the ripening phase of the fruit.

5.4.10.2. Ethylene production

Increased conductivity of the nutrient solution showed an increased production of ethylene in sweet pepper fruit. This is assumed to be in response to stress ethylene production. The average basal rate of ethylene evolution for all age groups was $50.97 \text{ nl kg}^{-1} \text{ h}^{-1}$. The corresponding increase for higher EC 6 treatments was $229.50 \text{ nl kg}^{-1} \text{ h}^{-1}$. This is a 4.5 times increase from the control treatment. Addition of extra Ca in the nutrient solution didn't reduce the stimulation of ethylene production rate at higher EC. Similar results were reported by Lacheene *et al.*, 1986; El-Abd *et al.*, 1992). Feng and Barker (1993) proposed that environmental stresses through net protein hydrolysis result in accumulation of methionine, the precursor of ethylene biosynthesis (Yang and Hoffman, 1984), which in turn stimulates ethylene biosynthesis. This view was also shared by Corey and Barker, (1989). Yang and Hofman (1984) also found that environmental stresses induce *de novo* synthesis of ACC synthase which results in high production of ethylene. It was also suggested by El-Beltagy and Hall (1974) that the increased ethylene evolution under salinity is likely to be due to the lowering of the water potential in the medium as this stimulates ethylene production.

5.4.10.3. Fruit respiration

Fruits grown under high EC of the nutrient solution exhibited significantly higher rates of CO₂ production than those grown under low EC conditions. The increase in respiration of fruits under high EC condition may be a result of the plant in an attempt to reduce further water loss and retain partial turgor tends to opt for osmotic adjustment. This process in turn requires greater expenditure of energy by maintenance respiration (McCree, 1986). It could also be possible that fruits grown under higher conductivity of the nutrient solution tend to accumulate more organic and inorganic solutes in their tissues as expressed by increased dry matter percentage in this experiment and others (Ehert and Ho, 1986a, Cornish, 1992). Thus, this may be used as a substrate for respiration (Azcon-Bieto *et al.*, 1983). The combined effects of increased respiration and ethylene production in turn advanced the ripening of sweet pepper fruit as it is exhibited in this experiment.

5.5. Conclusion

Results of the present investigation revealed that BER in sweet pepper fruit is due to a deficiency of Ca, mainly the physiologically active Ca compounds at the distal-end of the fruit. This deficiency occurs during the rapid growth stage of the fruit ie 2-4 weeks after anthesis. High conductivity of the nutrient solution exacerbates the problem further by reducing the uptake and translocation of Ca into the fruit particularly at the distal-end by favouring that of Mg and K. On the other hand, supplementary Ca in the solution promotes the accumulation of Ca in the fruit and tends to reduce the incidence of BER. It was also demonstrated that apart from the concentration of Ca in the fruit the incidence of BER is also related to the ratio of Ca:K in the fruit. Thus avoiding high conductivity levels as well as provision of supplemental Ca in the solution particularly during the rapid fruit growth period may help to reduce the incidence of BER.

It was also shown that high conductivity levels tend to reduce the vegetative as well as reproductive yields of the crop. This is assumed to be due to reduction in the uptake of water, uptake and translocation of mineral nutrients and a possible reduction in the photosynthetic ability of the crop. It was also shown that high conductivity of the nutrient solution reduces fruit firmness and the water content of the fruit. The beneficial effects of such treatments were however, in terms of increasing the dry matter content of the fruit and advancement of fruit ripening.

Chapter 6

The effect of relative humidity around the fruit or leaves on the accumulation of calcium, magnesium and potassium by leaves and fruits of sweet pepper grown in NFT.

6.1. Introduction

The transport of Ca from roots to low transpiring organs has been considered as a major reason for the low accumulation of the mineral in these organs. Calcium is considered to be mainly transported through the xylem vessels in the transpiration stream (Clarkson, 1984) although phloem transport is not ruled out (Faust and Klein, 1974). Wiersum (1966) suggested that the xylem is the primary conducting tissue supplying Ca early in the season and phloem predominates later. Hence, Ca is supplied to leaves and young fruits early in the season (Wilkinson, 1968) through the transpiration stream where Ca moves freely with water (Mengel and Kirkby, 1987).

Fruits are able to import a considerable amount of Ca early in the season because of a high surface area to volume ratio and easy permeability to water (Blanke and Lenz, 1989). Later in the season however, the reduction in surface area to volume ratio and the deposition of cutin and waxes substantially reduce water permeability thereby Ca import will be reduced (Ferguson and Watkins, 1989). In addition, stomates will be sparse and non functional and the ratio of leaf to fruit number and surface area increases which will further reduce fruit transpiration and subsequently movement of water and Ca into the fruit (Jones *et al.*, 1983; Blanke and Lenz, 1989). Moreover, the net rate of Ca uptake decreases through the season while that of phloem mobile

elements such as K, Mg, P, and N increases along with the translocation of photosynthates (Tromp, 1975). This in turn reduces the Ca ratio with the other elements particularly Mg and K which may result in the physiological disorders such as Blossom-End Rot (BER).

Humidity affects transpiration and thereby the uptake, transport and distribution of Ca (Ho, 1989). Several researchers have attempted to manipulate the relative humidity around the plant or fruit in an effort to modify transpiration, however, the effects on Ca accumulation of fruit is conflicting. Adams and Holder (1992) showed that high humidity decreased the Ca accumulation by the leaves of tomato while promoting its accumulation by the fruit. In tomato fruit Ca deficiency appeared at constant high humidity (Banuelos *et al.*, 1985). Similarly, low RH around the fruit of paprika pepper promoted Ca accumulation by the fruit (Marschner, 1983). The report of Cline and Hanson (1992) didn't give a clear account of the effect of humidity on Ca accumulation. They reported that mainly low RH promoted Ca accumulation into apple fruits although there were times when high RH promoted Ca accumulation in the fruit. On the other hand, Bakker (1990) observed no effect of humidity on Ca accumulation by sweet pepper fruit. These reported differences appear to be due to interaction of humidity effects with other variables.

The objective of the present investigation was to assess the influence of RH on the accumulation of Ca, Mg and K by fruits and leaves of sweet pepper plants.

6.2. Materials and Methods

6.2.1. Glasshouse procedures

Sweet pepper seeds (cv. Domino) were sown in late December, 1994 following the nursery practices as described in section 3.2.2. Seedlings were transferred to gullies of recirculating nutrient solution (NFT) on March, 1995. Plants were grown in the NFT with electric conductivity of 2 mS cm^{-1} and pH of 6.5 through out the experimental period by daily adjustment. Details of the management of the NFT culture have been described in section 5.2.2.

6.2.2. RH treatment application

6.2.2.1. Experiment one

The treatments comprised:

- 1) Low RH
- 2) Medium RH
- 3) High RH and
- 4) Control

The three different RH levels were achieved by enclosing fruit in 1 l low density polyethylene bags to which either 50 g of desiccant grade CaCl_2 for low RH or food grade NaCl for medium RH was added. No salt was added to the bags of high RH fruit and control fruits were left uncovered. All chemicals were dried at 80°C for 48 h and they were heat sealed prior to placement in the bags using spunbonded polyethylene packages (Shirazi and Cameron, 1990). The bags were suspended over the fruit by tying them with strings attached to a horizontal wire laid over the plants. The bags containing a single fruit were secured around the pedicel of the fruit which

were surrounded with cotton for cushioning purpose. Small holes of 1 mm size were provided for aeration purpose and the air inside the bags was monitored periodically to avoid the build up of CO₂. The temperature and relative humidity within the bag were monitored during the experimental period using temperature and humidity probes and the data was logged into Grant squirrel data logger (Grant Instruments (Cambridge) Ltd Barrington Cambridge CB2 5SQ, England).

6.2.2.2. Experiment two

Three RH levels viz,

- 1) Low (30%)
- 2) Medium (60%) and
- 3) High (90%)

were used in this experiment. The ratios were established from the data given by Forney and Brandl (1992). These levels were maintained using glycerol-water solutions as recommended by (Forney and Brandl, 1992). The flow-through system used for this experiment is shown in Fig. 6.1. Compressed dry air was used as a gas source to be humidified which was regulated by a flow meter and passed at a flow rate of 100 ml min⁻¹ through chamber A which contained the desired level of Glycerol-water solution. The humidified air was then passed on to the next chamber (B) which contained sweet pepper fruit and leaf. This gas finally exits through the outlet provided in tube 3.

A 2 l capacity respiration jars were used as chamber A and the fruit and leaves were enclosed in 1 l polyethylene bags. The different humidities were maintained by mixing distilled water with glycerol or only distilled water for the high RH treatment (Fisher, 1986). Due to the fact that dry air removes about 1.6 mg of water minute⁻¹ (Forney and Brandl, 1992) water was added to the solution to maintain the original

volume. Moreover, few drops of saturated CuSO_4 solution was added to the solution to prevent microbial growth. Through out the experimental period the temperature and RH within the bags of the different treatments were monitored as above.

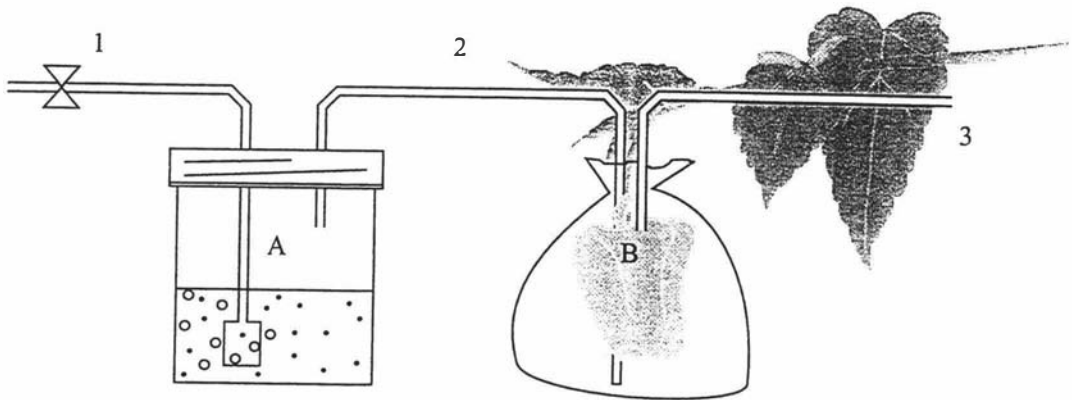


Fig. 6.1. System used to humidify flow-through chambers. Compressed air flows through tube 1 into the glycerol-water solution in jar A. Humidified air then flows through tube 2 into the polyethylene bag (B) containing sweet pepper fruit and exits into the atmosphere through tube 3. (Adapted from Forney and Brandl, 1992).

6.2.3. Sampling and mineral analysis

Fruit were tagged at anthesis and the respective RH treatments were applied. Fruit

or leaf samples were harvested each week for mineral analysis.

At each harvest fruit fresh weight, diameter, length and volume were recorded for the respective treatments. The fruit were then separated into basal and distal portion and the dry weights of the respective sections were recorded, following oven drying at 80°C for at least 48 h.

A single leaf enclosed along the fruit of the respective age in each RH treatment was used for leaf mineral analysis. Analysis of tissue Ca, K and Mg was made following the method described in section 3.2.3.3.

6.2.4. Evaluation of the incidence and severity of blossom-end rot

Harvested fruit were examined for the presence or absence of external symptoms of blossom-end rot. The severity of the incidence was recorded by measuring the diameter of the lesion and comparing it to the fruit diameter. Internal blossom-end rot was also checked after the fruit was cut into blossom-end and stem-end portions.

6.2.5. Statistical procedure

All data were subjected to analysis of variance using General Linear Model (GLM) procedure of SAS (SAS Institute Inc., 1989). When appropriate, arcsine transformation was made for BER incidence and back transformed for presentation. Treatments were analyzed as Randomized Complete Block Design (RCBD) with 10 and 3 blocks respectively for experiment one and two. A separate analysis were carried out for each harvest, and treatment means were compared by Duncan's multiple range test.

6.3. Results

6.3.1. Effect of hygroscopic materials or air-flow system on RH around the fruit

The presence of hygroscopic materials within the fruit enclosure in experiment one reduced the RH around the fruit. On average a day time RH of 27.0% and a night time RH of 28.9% was achieved for the CaCl_2 treatment while NaCl and Polyethylene had 50.2% and 56.9% and 77.6% and 93.0% respectively of day/night humidity. The ambient relative humidity was 60.9% and 65.8% day/night (Figs. 6.2A and 6.2B). These measurements were recorded from 6 May to 22 May, 1995 at intervals of 2 h and scanning interval of 15 minutes. There was no difference in the temperature of the enclosures and that of the ambient temperature which averaged 20°C/13°C day/night temperature (data not presented).

Subsequent recording of RH and temperature for experiment two were made from 22 May to 08 June, 1995. Figs. 6.3A and B show that in the low RH treatment a day/night RH of 17.9% and 22.8% were achieved while the medium and high RH treatments had 46.2% and 47.2% and 79.9% and 84.5% respectively of day/night. The corresponding figure for the ambient RH was 79.6% and 87.1% day/night. As in experiment one the temperatures in the bags appeared to be similar to that of the ambient temperature (data not presented).

6.3.2. Fruit growth

Fruit growth in terms of fresh weight and dry weight increased rapidly during the measurement period for both experiments. However, only the fresh weight data is presented as the others followed a similar trend (Fig. 6.4 and 6.5). On the other hand, RH treatment had a significant effect on the growth of sweet pepper fruit in terms of

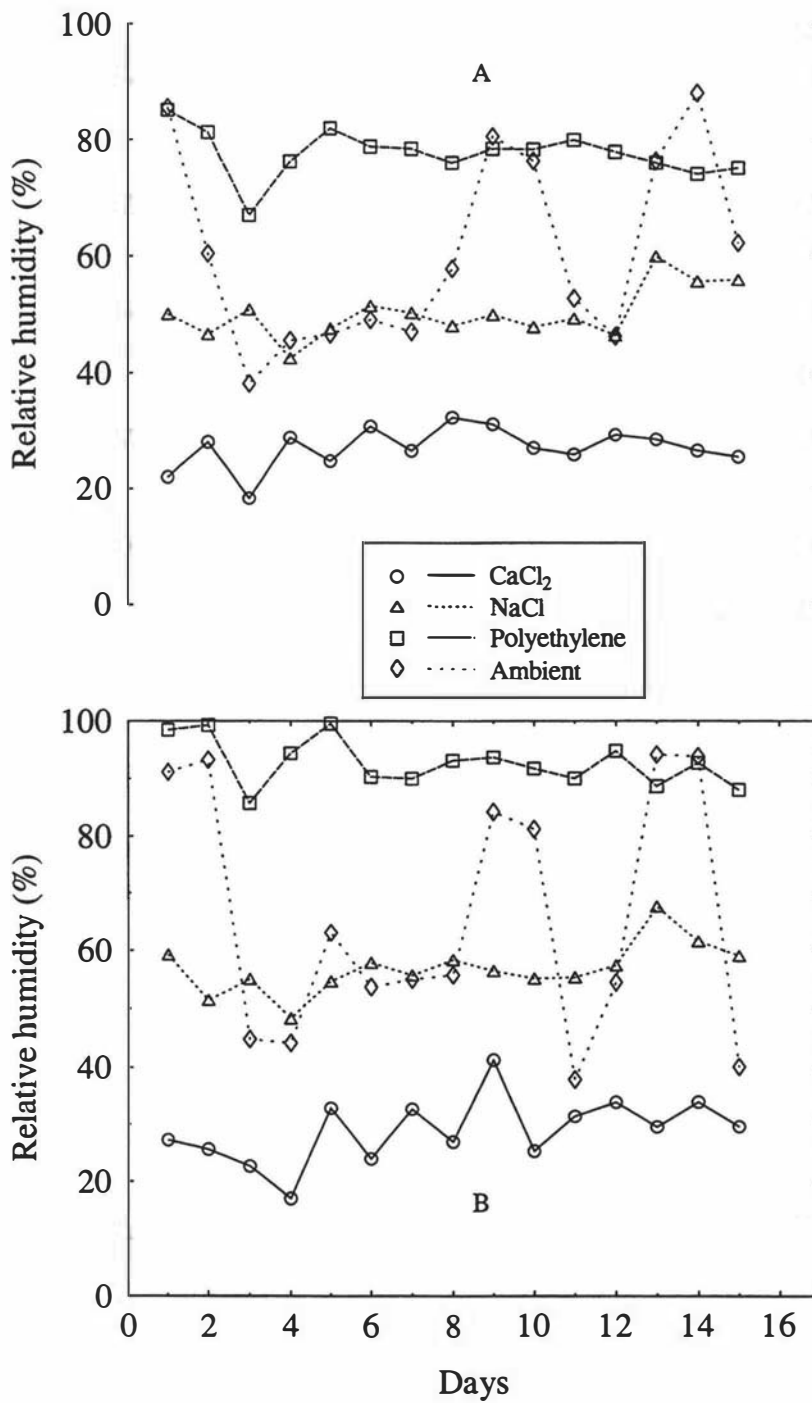


Fig 6.2: Day time (A) and night time (B) relative humidity within the artificial enclosure as affected by the level of RH around the fruit. Each data point is a mean of 6 measurements at 2 h intervals.

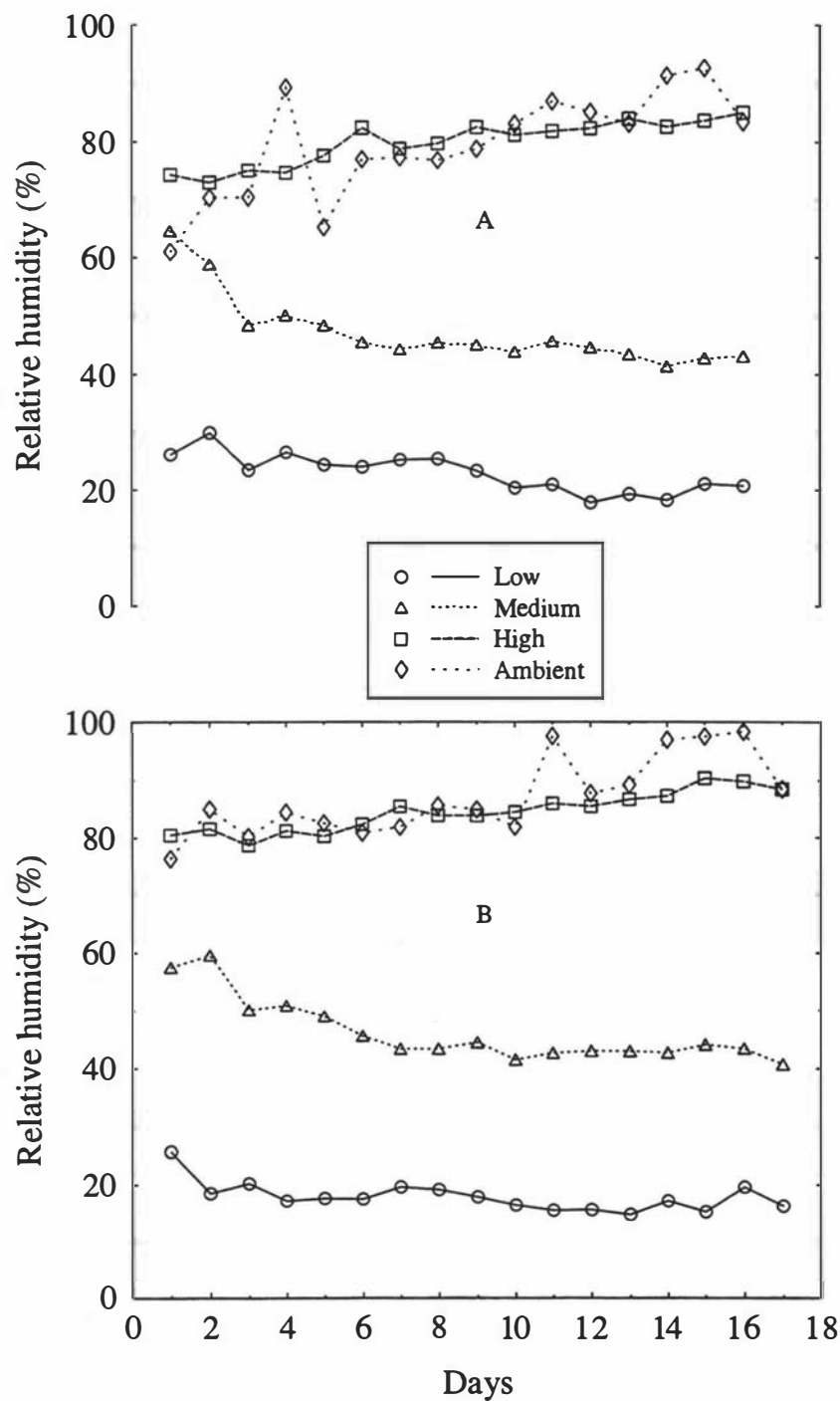


Fig 6.3: Day time (A) and night time (B) relative humidity within the artificial enclosure as affected by the level of RH around the fruit. Each data point is a mean of 6 measurements at 2 h intervals.

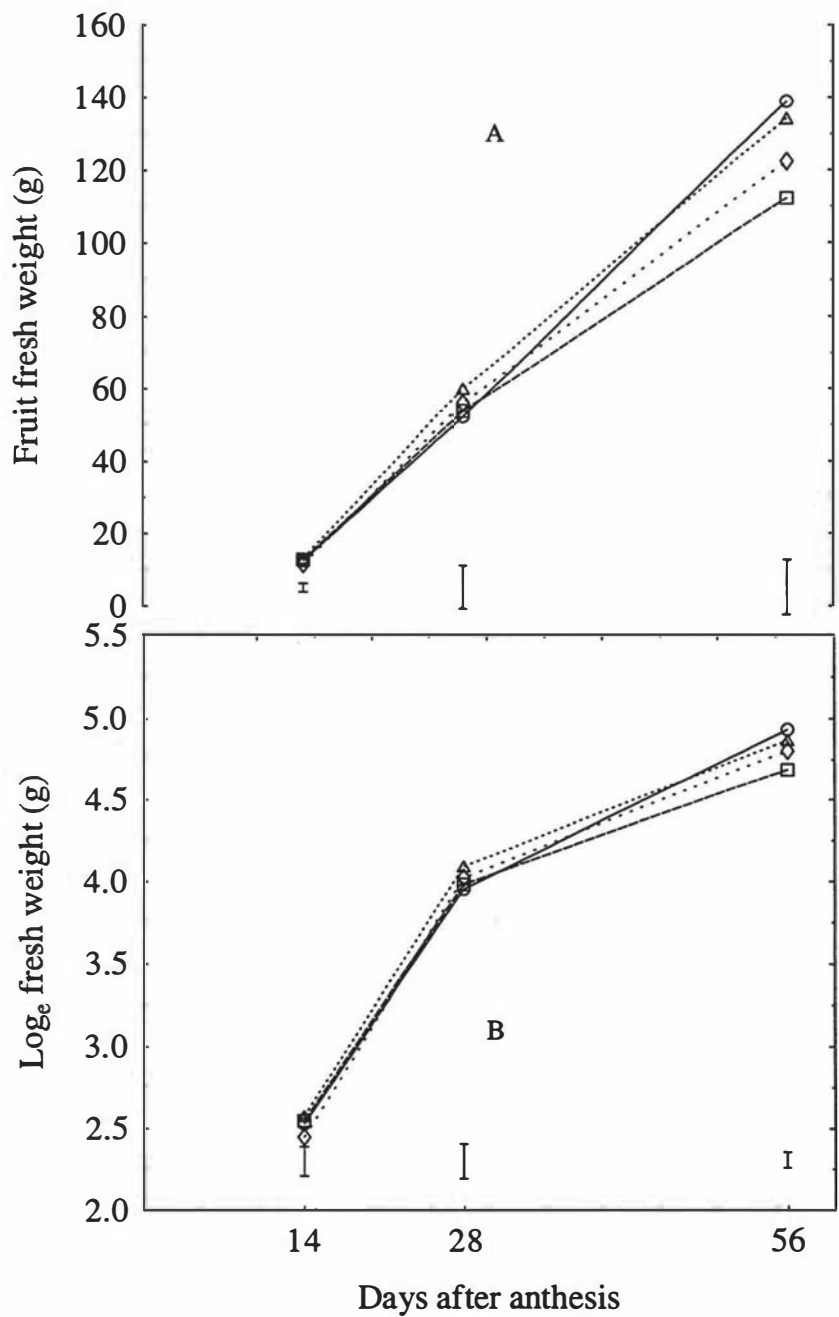


Fig 6.4: Fruit cumulative fresh weight (A) and Log_e fresh weight (B) as affected by the level of RH around the fruit. Each data point is an average of 10 fruit. Vertical bars indicate standard error of means. CaCl₂ (O), NaCl (Δ), Polyethylene (□), Control (◇).

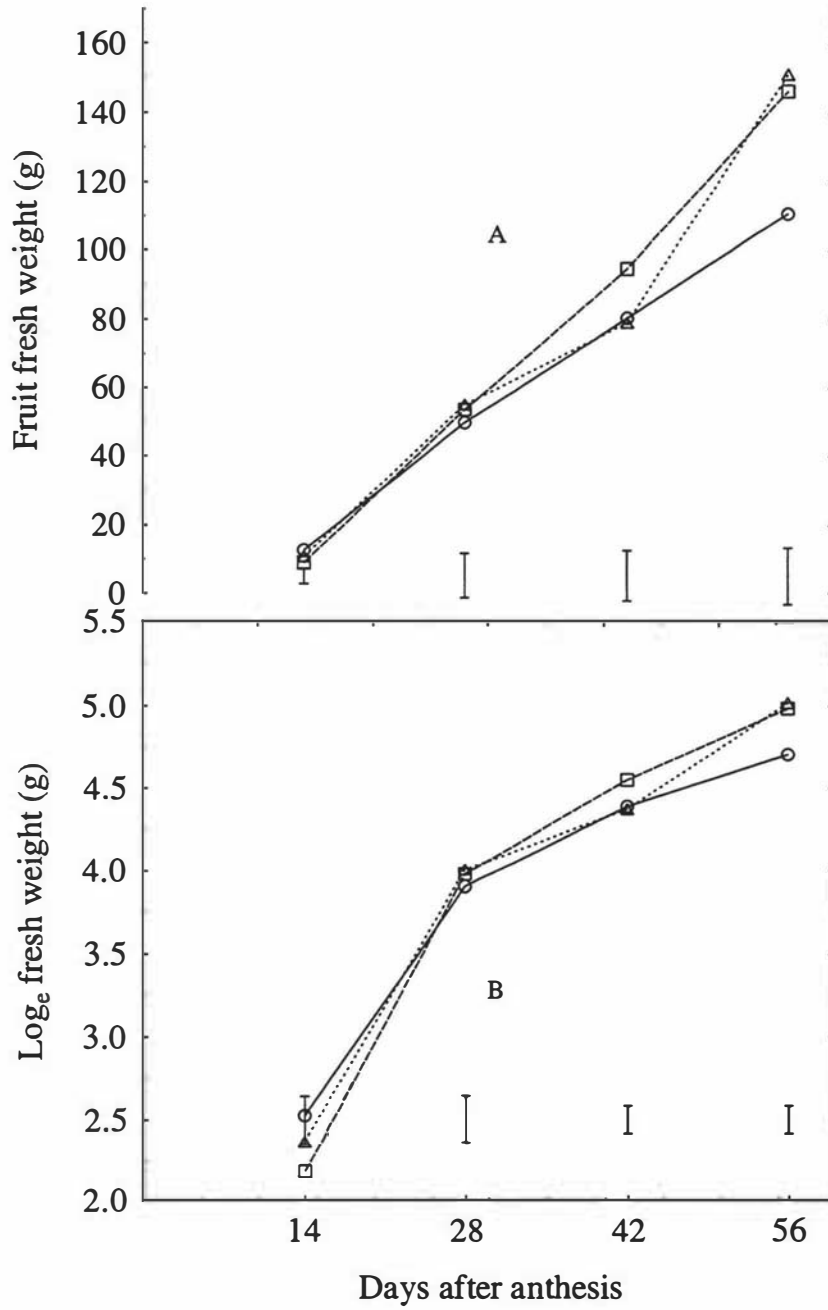


Fig 6.5: Fruit cumulative fresh weight (A) and Log_e fresh weight (B) as affected by the level of RH around the fruit. Each data point is an average of 6 fruit. Vertical bars indicate standard error of means. Low (○), Medium (△), High (□).

fresh weight, dry weight, diameter and length growth only at the final harvest $P \leq 0.05$ (Figs. 6.4 and 6.5).

Treatment effects on growth attributes were inconsistent, with lower yields in the high RH treatment in experiment one, but not in experiment two (Figs. 6.4 and 6.5).

Fruit final weight in experiment one was significantly higher in low RH treatment than the rest of the treatments $P \leq 0.05$ (Table 6.1). This difference however, was not expressed in terms of difference in moisture content although the Ca concentration appeared to be higher for low RH treatment $P \leq 0.001$. However, a clear difference was not observed between the low and high RH treatments in experiment two with respect to final fresh weight (Table 6.2). The fruit Ca concentration was however, significantly improved by the low RH treatment (Table 6.2).

6.3.3. Incidence and severity of blossom-end rot

The high RH treatment induced the incidence of blossom-end rot in sweet pepper fruit (Tables 6.3 and 6.4). The incidence of blossom-end rot was shown to have slight but significant correlation to the Ca concentration, Ca content and Ca:Mg and Ca:K ratios at the blossom-end of the fruit (Table 6.5). Similarly, Ca and Mg concentrations, K content and the ratios of Ca:Mg and Ca:K were significantly correlated to the incidence of BER (Table 6.6). No significant difference was observed in BER severity (Tables 6.3 and 6.4).

Table 6.1. Effect of RH treatment on sweet pepper log_e fruit weight and dry weight, moisture content (arcsine) and levels of fruit calcium at the final harvest (Experiment one).

Treatment	Mean day/night RH (%)	Fresh weight (g)	Dry weight (g)	Moisture content (%)	Fruit Ca conc. (mg.gdw ⁻¹)
CaCl ₂	27/29	4.93 a ^x (138.9) ¹	2.31 a (10.17)	67.98 (92.69)	1.374 a
NaCl	50/53	4.87 ab (134.2)	2.26 ab (9.95)	67.81 (92.58)	1.043 bc
Polyethylene	78/93	4.69 b (112.2)	2.07 b (8.24)	67.96 (92.68)	0.908 c
Control	61/66	4.78 ab (122.3)	2.21 ab (9.39)	67.41 (92.29)	1.106 b
SE		0.069	0.074	0.350	0.063
Signif. ²		*	*	ns	***

^x means followed with the same letter are not statistically significant according to Duncan Multiple Range Test.

¹ values in bracket are back transformed ones.

² *, **, *** and ns indicates level of significance at $P \leq 0.05$, 0.01, 0.001 or non-significant for this and subsequent tables.

Table 6.2. Effect of RH treatment on sweet pepper log_e fruit weight and dry weight, moisture content (arcsine) and levels of fruit calcium at the final harvest (Experiment two).

Treatment	Mean day/night RH (%)	Fresh weight (g)	Dry weight (g)	Moisture content (%)	Fruit Ca conc. (mg.gdw ⁻¹)
Low	18/23	4.679 b ^x (110.82) ¹	2.158 (8.96)	66.80 b (91.87)	1.466 a
Medium	46/47	5.003 a (151.42)	2.295 (10.14)	68.93 a (93.30)	1.148 b
High	80/85	4.964 ab (146.55)	2.302 (10.11)	68.45 ab (92.99)	0.898 c
SE		0.086	0.069	0.628	0.071
Signif. ²		*	ns	*	***

^x means followed with the same letter are not statistically significant according to Duncan Multiple Range Test.

¹ values in bracket are back transformed ones.

² *, **, *** and ns indicates level of significance at $P \leq 0.05$, 0.01, 0.001 or non-significant for this and subsequent tables.

Table 6.3. The incidence and severity of blossom-end rot on sweet pepper fruit as affected by the level of RH around the fruit (Experiment one).

Treatment	Mean day/night RH (%)	BER incidence (%)	BER severity (mm.cm ⁻¹)
CaCl ₂	27/29	5.84 (9.99) ¹ b ^x	0.818
NaCl	50/53	13.62 (23.31) ab	2.297
Polyethylene	78/93	17.51 (29.97) a	3.099
Control	61/66	9.73 (16.65) ab	2.471
SE		2.78	1.228
Significant		*	ns

¹ values in bracket are back transformed percentages from arcsine data.

^x means followed with the same letters are not significantly different according to Duncan's Multiple Range Test.

Table 6.4. The incidence and severity of blossom-end rot on sweet pepper fruit as affected by the level of RH around the fruit (Experiment two).

Treatment	Mean day/night RH (%)	BER incidence (%)	BER severity (mm.cm ⁻¹)
Low	18/23	4.83 (8.33) ¹	0.093
Medium	46/47	12.07 (20.83)	1.785
High	80/85	9.65 (16.67)	1.877
SE		2.99	1.115
Significant		ns	ns

¹ values in bracket are back transformed percentages from arcsine data.

Table 6.5. Correlation coefficient table showing the relationship between BER and mineral nutrient levels in the blossom-end of the fruit (experiment one), n=40.

Tissue mineral	BER incidence	Significant
Ca concentration	-0.601	***
Ca content	-0.606	***
Ca:Mg	-0.537	***
Ca:K	-0.560	***

Table 6.6. Correlation coefficient table showing the relationship between BER and mineral nutrient levels in the blossom-end of the fruit (experiment two), n=18.

Tissue mineral	BER incidence	Significant
Ca concentration	-0.401	*
Mg content	0.449	*
K content	0.506	*
Ca:Mg	-0.473	*
Ca:K	-0.486	*

6.3.4. Accumulation of Ca, K and Mg during fruit and leaf development

6.3.4.1. Fruit mineral accumulation

Accumulation of calcium, magnesium and potassium by fruit was examined at different times during the growth and development of sweet pepper fruit in both experiments until fruit maturity.

Fruit exposed to low RH in experiment one had higher Ca concentrations than control fruit ($P \leq 0.0001$) (Fig. 6.6a). Similarly, the low RH treatment also increased the Ca concentration of the fruit in experiment two ($P \leq 0.001$) (Fig. 6.6b). The Ca concentration in control fruit in experiment two decreased from 2.441 mg/gram dry weight to as low as 1.722 mg/gdw during the rapid fruit growth period (Fig. 6.6b). It finally increased slightly towards maturity. On the other hand, the fruits exposed to lower RH had not experienced this fluctuation in experiment one which remained essentially high (Fig. 6.6a). Although a declining trend in fruit Ca concentration was seen during the rapid fruit growth period in experiment two, the Ca concentration even at this stage was higher than the one recorded for control fruits in experiment one (1.890 mg/gdw versus 1.722 mg/gdw) (cf. Figs. 6.6a and 6.6b).

On the other hand, fruit which were exposed to high RH (covered with polyethylene bags only) consistently gave lower Ca concentration as well as Ca content throughout the fruit growth period (Fig. 6.6a). This trend was also shown in experiment two where fruits subjected to the high humidity condition had lower Ca status (Fig. 6.6b). It was further shown that low humidity favoured the accumulation of Ca in both young and old fruits as its effect persisted throughout the fruit growth period (Fig. 6.6a and b).

Unlike that of calcium, RH had little effect on the accumulation of both Mg and K in sweet pepper fruits in both experiments (Figs. 6.7A & B and 6.8A & B).

6.3.4.2. Longitudinal gradient of Ca, Mg and K in the fruit

Lower RH treatment promoted the uptake and accumulation of Ca into the blossom-

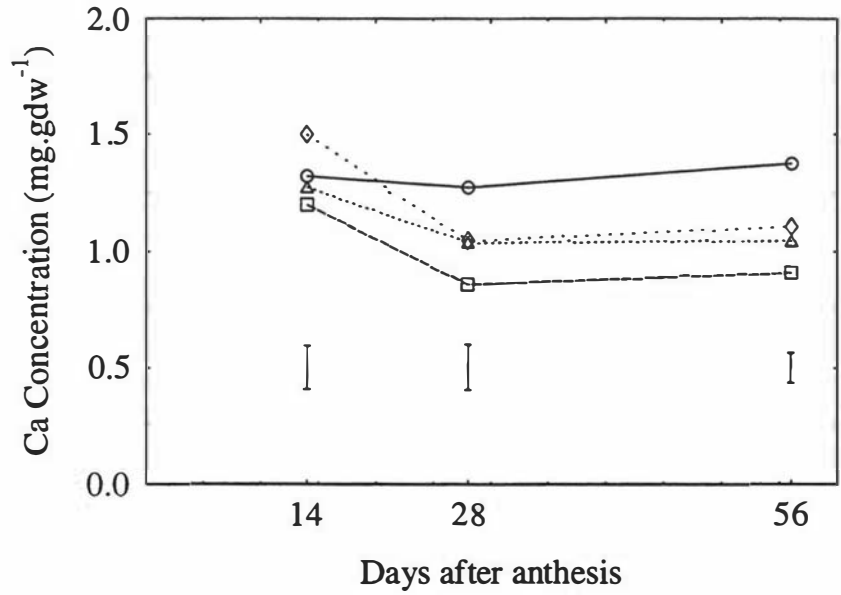


Fig 6.6a. Total fruit calcium concentration as affected by the level of RH around the fruit. Each data point is an average of 10 fruit. Vertical bars indicate standard error of means. CaCl₂ (O), NaCl (Δ), Polyethylene (□), Control (◇),

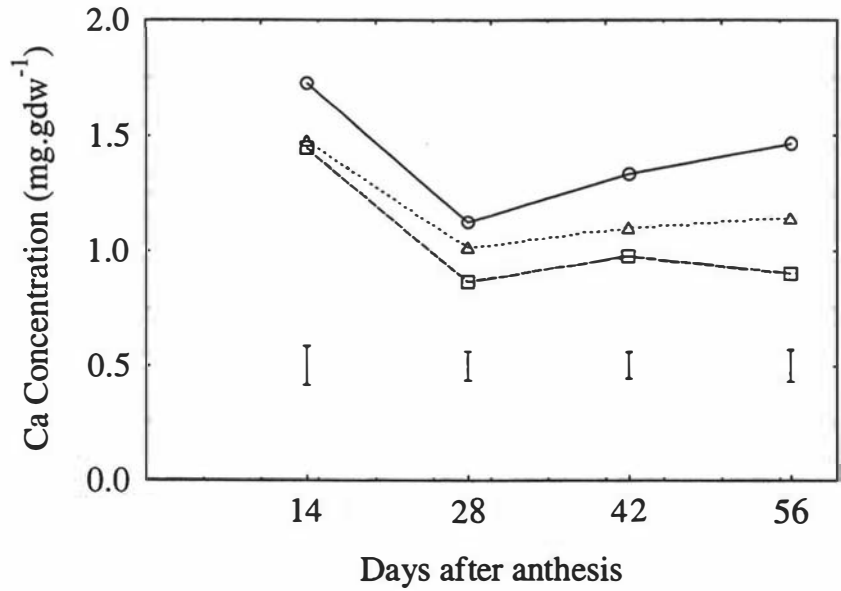


Fig 6.6b: Total Fruit Ca concentration as affected by the presence of leaf and level of RH around the fruit. Each data point is an average of 6 fruit. Vertical bars indicate standard error of means. Low (O), Medium (Δ), High (□),

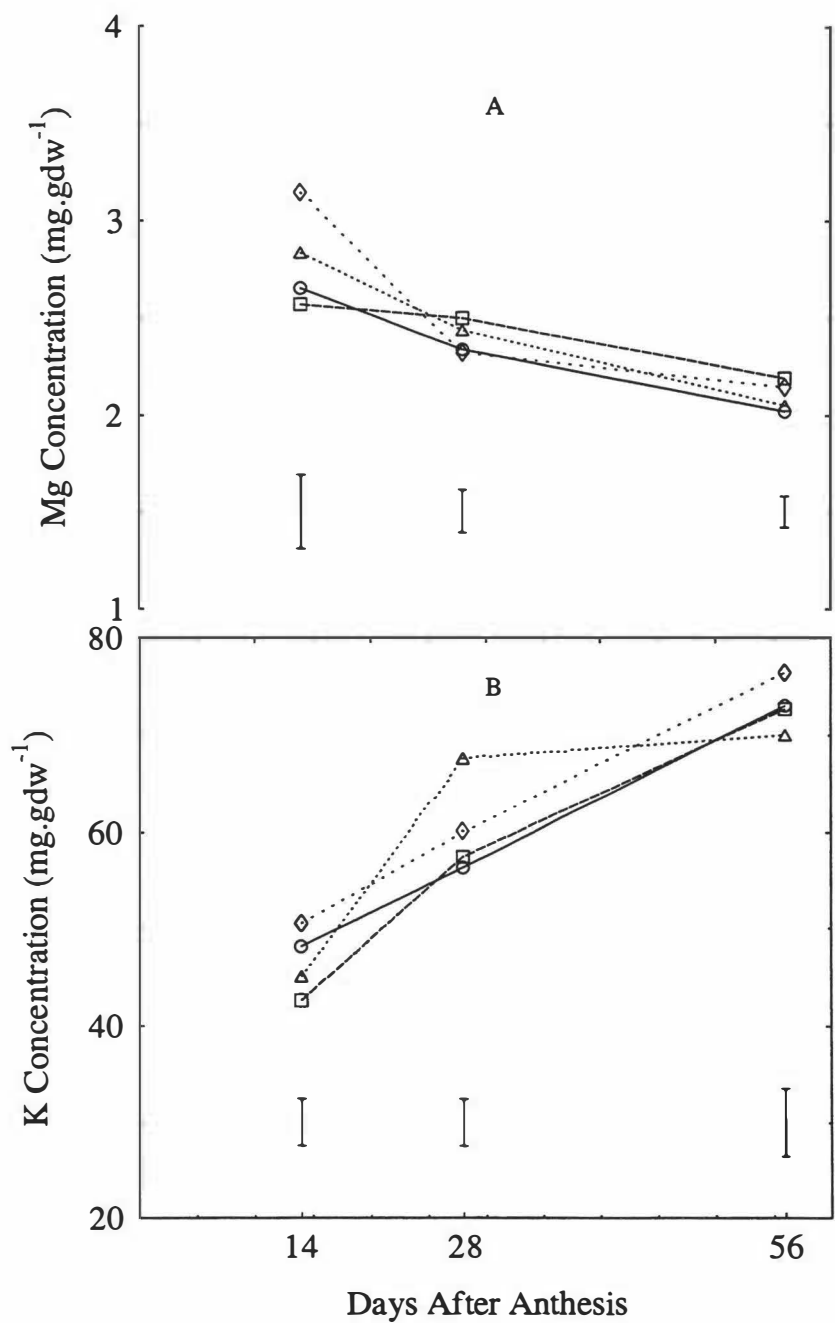


Fig 6.7: Total Fruit Mg (A) and K (B) concentration as affected by RH around the fruit. Each data point is an average of 10 fruit. Vertical bars indicate standard error of means. CaCl₂ (○), NaCl (△), Polyethylene (□), Control (◇).

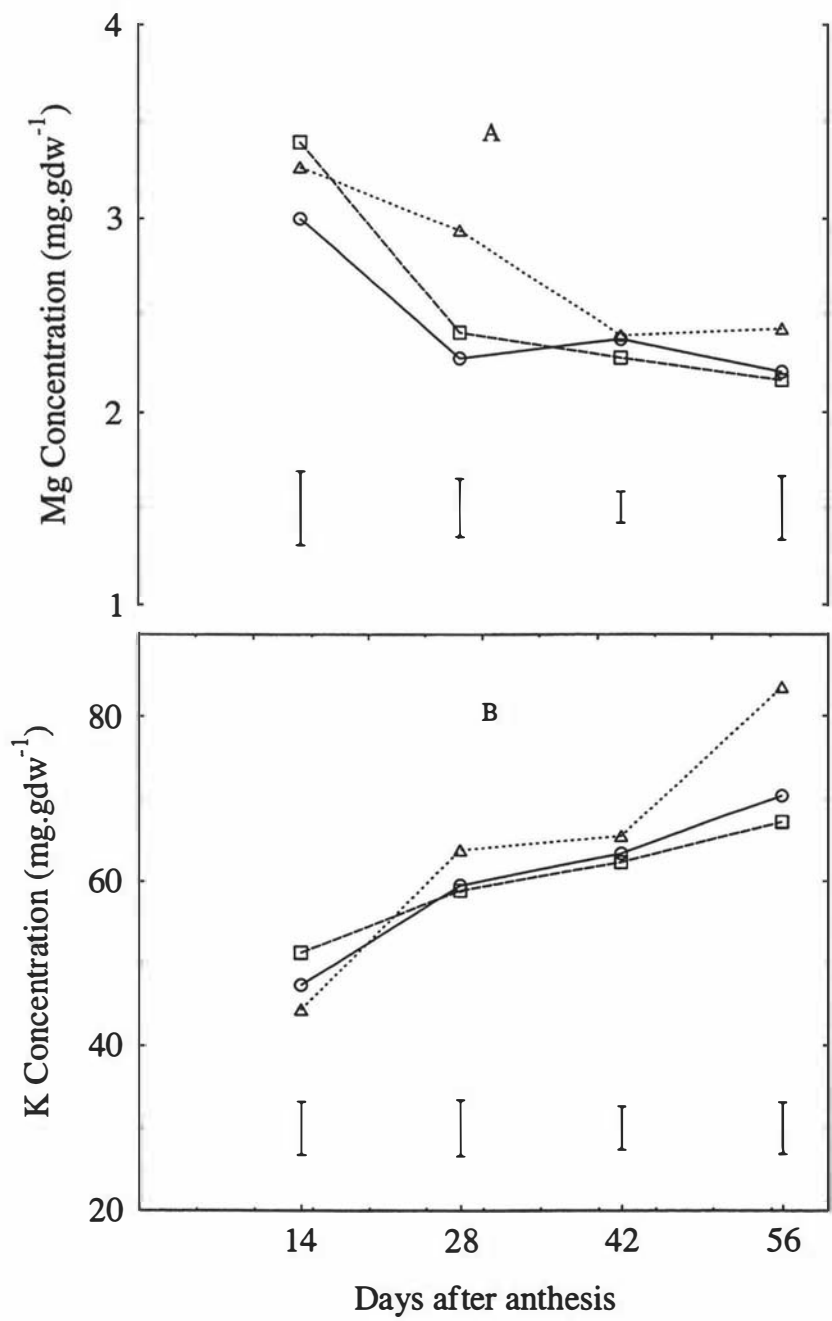


Fig 6.8: Total fruit Mg (A) and K (B) concentration as affected by RH around the fruit. Each data point is an average of 6 fruit. Vertical bars indicate standard error of means. Low (O), Medium (Δ), High (□).

end portion of sweet pepper fruit ($P \leq 0.01$) (Fig. 6.9A). Higher RH on the other hand suppressed the Ca concentration of the blossom-end portion of the fruit. This indicates that exposing fruits to lower RH could aid in the transport of Ca into the distal portion of the fruit which has normally low Ca status. It was also shown that the Ca concentration increased in this portion when the control fruits showed a depression. This in turn could have a significant influence on the incidence of blossom-end rot as discussed later. Similar trends were seen in experiment two (Fig. 6.10A).

In young fruit, low or medium RH reduced the Ca concentration in the stem-end of the fruit as compared to the control treatments without a statistically significant effect (Fig. 6.9B). In older fruits however, lower RH has a beneficial effect in increasing the Ca concentration of the fruit ($P \leq 0.01$) (Fig. 6.9B). In experiment two exposing fruit to lower RH also increased the Ca concentration in the stem-end of the fruit (Fig. 6.10B). Generally, it was observed that the fruit distal end has a lower Ca concentration and content compared with the stem-end portion regardless of RH treatment (Figs. 6.9A and B and Figs. 6.10A and B).

6.3.4.3. Leaf mineral accumulation

Analysis of leaf and fruit tissues of sweet pepper revealed that Ca is found in smaller quantity in the fruit regardless of RH treatment as compared with leaves.

No significant difference was observed in mineral accumulation of leaves with respect to RH treatments (Figs. 6.11A, B and C). It was however, noted that at each time of the sampling period, the Ca and Mg concentration and content were higher in low RH than high RH treatments. Leaf K however, didn't respond to the RH treatment. It was also shown that the concentration of the three mineral nutrients increased with an increase in the age of the leaves.

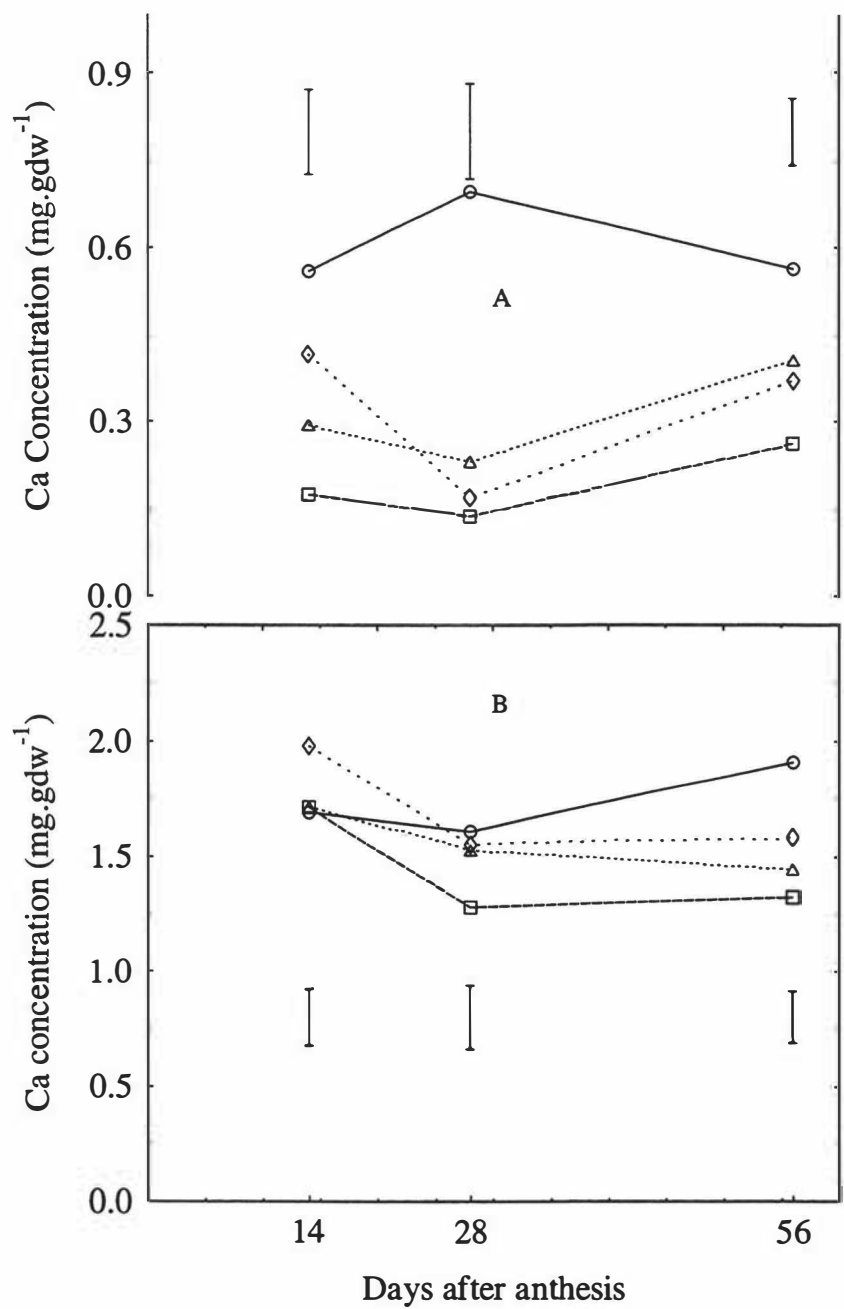


Fig 6.9: Fruit blossom-end (A) and stem-end (B) Ca concentration (B) as affected by the level of RH around the fruit. Each data point is an average of 10 fruit. Vertical bars indicate standard error of means. CaCl₂ (○), NaCl (△), Polyethylene (□), Control (◇).

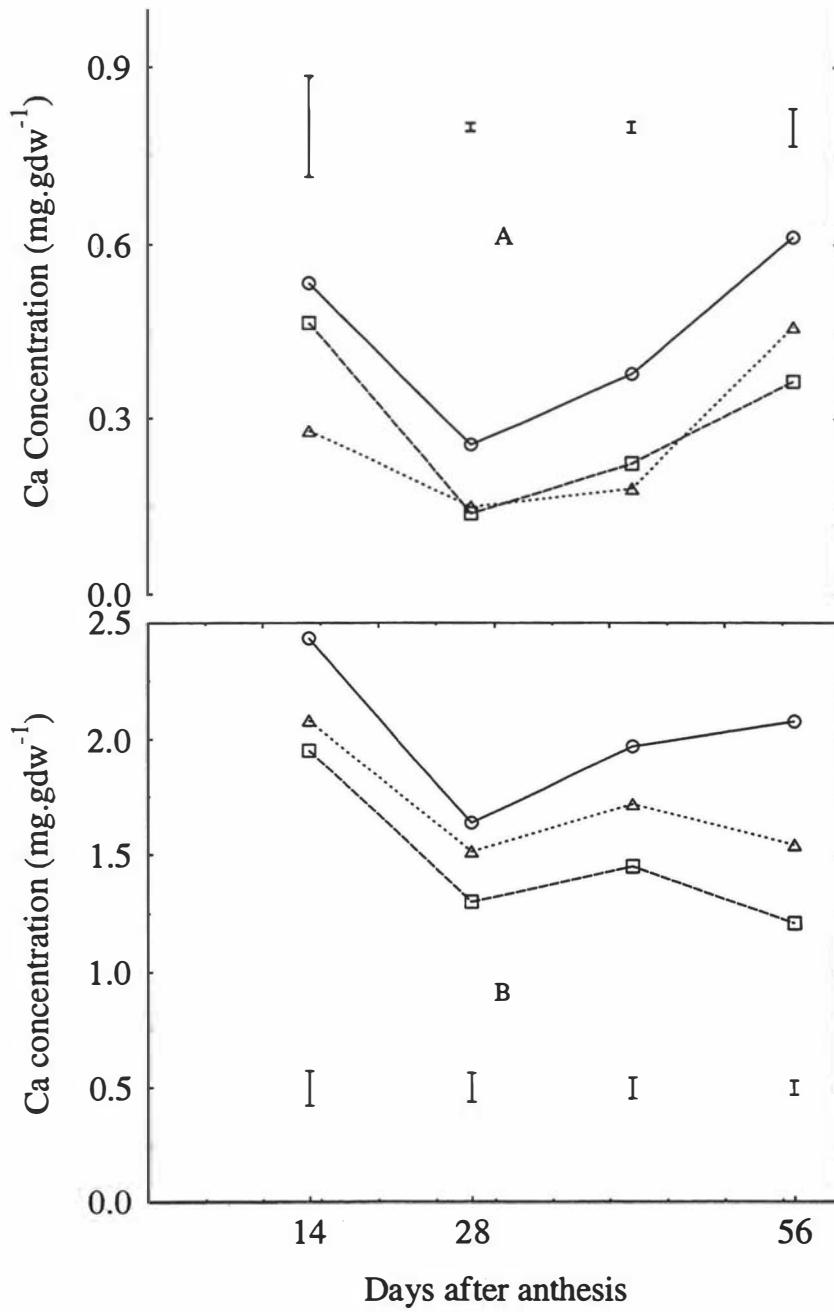


Fig 6.10: Fruit blossom-end (A) and stem-end (B) Ca concentration (B) as affected by the level of RH around the fruit. Each data point is an average of 6 fruit. Vertical bars indicate standard error of means. Low (○), Medium (△), High (□).

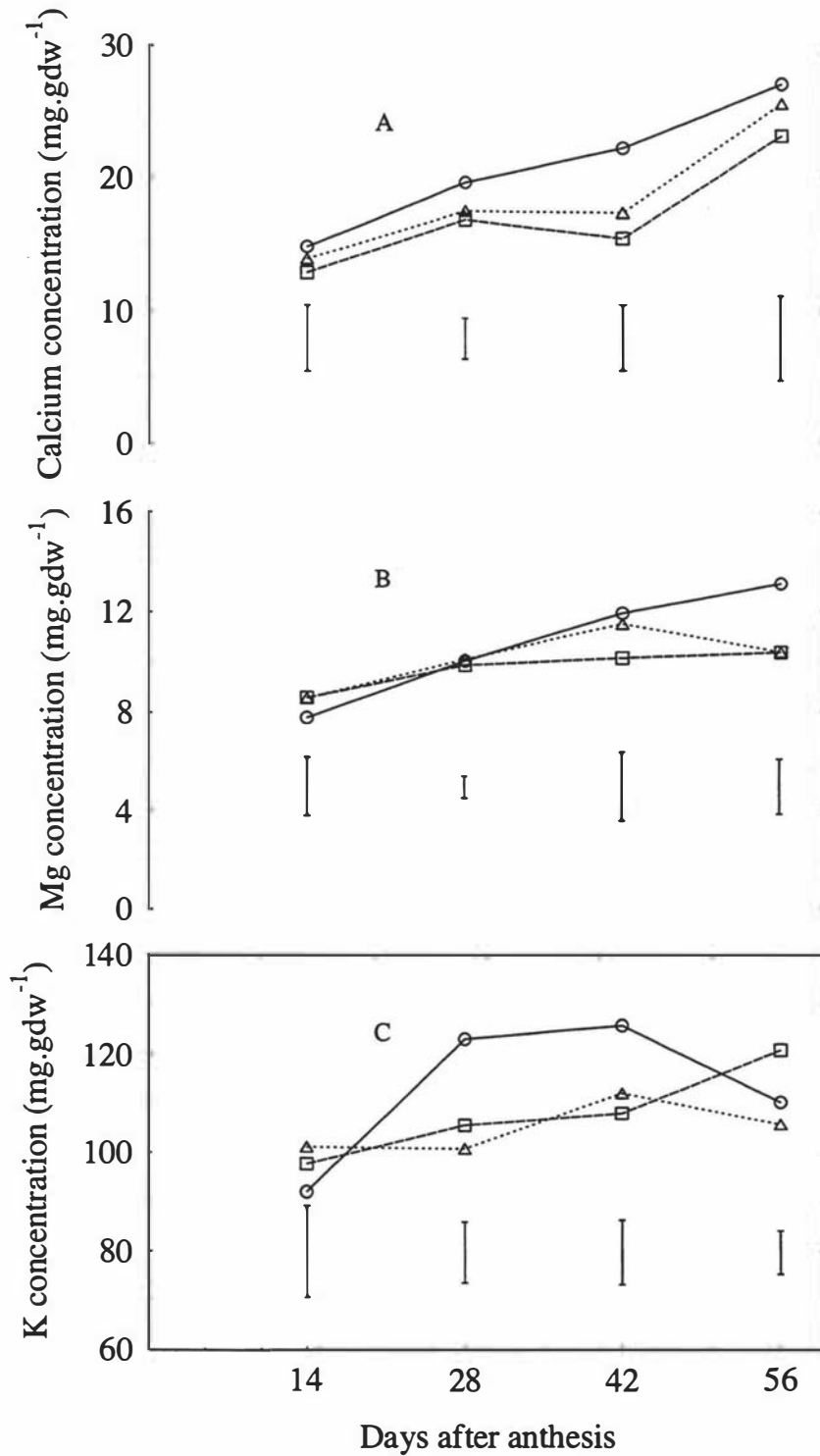


Fig 6.11: Sweet pepper leaf Ca (A) Mg (B) and K (C) concentrations as affected by RH. Each data point is an average of 3 composite leaves. Vertical bars indicate standard error of means. Low (O), Medium (Δ), High (\square).

6.4. Discussion

6.4.1. Fruit dry matter accumulation

The humidity treatments in this study had no appreciable effect on the fresh or dry weights of either young or old fruits. This is in agreement with the results of Bakker *et al.*, (1987) in cucumber, Bakker (1989c) on sweet pepper, Bakker (1990) and Adams and Holder (1992) in tomato and Cline and Hanson (1992) and Tromp *et al.*, (1993) in apple. It is however, in conflict with the reports of Banuelos *et al.*, (1985) who indicated that high RH increased the dry weights of fruit in a short period without a corresponding increase in Ca which resulted in a higher incidence of BER. Tomato fruits grown under low RH conditions at night showed slightly faster growth (Bradfield and Guttridge, 1984). Low RH however had a negative effect on muskmelon fruit growth as it decreased the mean fruit growth rate (Combrink *et al.*, 1995).

6.4.2. Incidence of blossom-end rot

The correlation coefficient between various factors and BER reveal that the Ca concentration or content or Ca:K or Ca:Mg ratios provided the best correlation. This relationship suggests that the ratio of Ca:K has as a similar influence on BER as the Ca concentration in the fruit. Thus, any factor which promotes K accumulation or which suppresses Ca uptake is likely to result in more BER. This relationship however, is revealed only if the blossom-end of the fruit is used for the analysis, as the stem-end portion mineral content showed no significant relationship with the incidence of BER.

With respect to the effects of RH around the fruit on the incidence of BER, it was found that high RH promotes more BER than lower RH. This is due to the effect of

higher RH on the suppression of the Ca concentration and content of the fruit particularly the blossom-end portion (Table 6.1 and 6.2, Figs. 6.9a and 6.10a).

It must be emphasised that RH may have somewhat different effects if plants are grown under conditions favouring high fruit growth rate since under the present experimental conditions fruit growth was not as rapid as it would have been in summer grown sweet pepper. As a result, the fruits were relatively small which reduced their susceptibility to BER. When fruits are grown rapidly they depend more on phloem supply of water and assimilates than xylem (Wolterbeek *et al.*, 1987). Thus, they tend to have a higher K/Ca ratio than slower growing fruits (Marschner, 1983). This in turn results in higher incidence of BER. It is however, worth noting that low relative humidity around the fruit has the potential to increase the Ca concentration and content in the fruit thereby reducing the incidence of BER.

6.4.3. Mineral nutrient accumulation

6.4.3.1. Fruit mineral accumulation

The results shown in Figs. 6.6a and b demonstrate that high relative humidity suppresses Ca accumulation by fruit. This is in agreement with the findings of Mix and Marschner (1977b) and Marschner (1983) on paprika and bean and Ehert and Ho (1986c) on tomato fruit who reported that a high RH of 90% at 20°C reduced the uptake of ^{45}Ca by tomato fruit grown at 2 mS cm⁻¹. Low RH (22%) improved the translocation of Ca into muskmelon fruit peel (Combrink *et al.*, 1995). The present results are also in direct agreement with the results of Ohita *et al.*, (1991) who found that low RH resulted in reduced fruit cracking of tomatoes due to higher transpiration and increased firmness. In faba beans, low RH increased the accumulation of K, Na, Ca, Mg and Cl (Salim, 1987).

The present results however, are in conflict with the results of Adams and Holder

(1992) on tomato fruit who indicated that high rather than low RH promote Ca uptake into the fruit. The discrepancy can be explained because unlike the current experiment they exposed the whole plant (not the fruit alone) to either low or high humidity treatments and grew the plants at EC of 5 mS cm⁻¹. For most minerals the driving force for xylem transport is transpiration but Ca may also move by exchange via negatively charged sites along the walls of xylem vessels to growing tissues where new exchange sites are being synthesized (Van de Geijn *et al.*, 1979). Clarkson (1984) suggested that when root Ca supply is relatively low and transpiration rate is high, Ca concentration in the xylem sap will be low. Therefore, movement by exchange to growing tissues will predominate over the effects of transpiration. This may explain the lack of positive effect of low RH on Ca accumulation of tomato fruits in the results of Adams and Holder (1992) as they grew the plants at higher than normal EC which suppresses Ca availability (or uptake) due to osmotic stress.

Fruits import most of their Ca directly from the roots during their development (Ho, 1989). He indicates that the proportion of xylem sap imported by the fruit is affected by the transpiration of the mature leaves which direct the main stream of xylem flow in the plant, and that during the day leaves accumulate most of the Ca as fruits do not transpire as well as leaves (Ehert and Ho, 1986c). However, as transpiration is reduced at night the proportion of xylem sap flowing into the leaves will be reduced making more xylem sap available for the fruit. On the other hand, as is demonstrated in the present experiment, such factors which increase fruit transpiration such as low RH might help the fruit to redirect the Ca rich xylem sap into this organ.

The fact that high RH reduces the Ca uptake by the fruit implies that high RH has suppressed xylem supply of Ca because high RH did not result in a consistent reduction in fruit weight as photosynthetic products and minerals such as N, P, K and Mg are supplied by phloem transport (Tromp, 1975; Wolterbeek *et al.*, 1987). If RH had affected phloem supply, similar reduction in fruit weight may have been expected at high RH treatments. Although fruit transpiration decreases with fruit age, the RH treatment effect persisted throughout the development of the fruit. Cline and Hanson

(1992) suggested that the decline in Ca content of fruit late in the season could be due to the export of calcium out of the fruit in response to high evaporative demand. Lang and Thorpe (1989) report that water flows out of grape berries into the vine in response to a water potential gradient. Similar observations have been made for apple fruit (Tromp, 1984; Lange, 1990). Mix and Marschner (1977b) also found that at high transpiration rates 20% of the ^{45}Ca injected into the fruit of Paprika pepper left the fruit. However, Lang and Volz (1993) showed that even though xylem sap exchange takes place between the tree and fruits of apple due to difference in water status, little out flux of Ca takes place from the fruit and eventually it is replaced by Ca rich xylem sap at night. In the current experiment, the low RH treatment around the fruit (by lowering the water potential gradient of fruit) may have been able to attract additional water and subsequently Ca from other plant parts with high water potential gradient during day time with additional Ca inflow at night.

High RH often reduced fruit Ca content and concentration indicating the importance of transpiration in Ca transport into sweet pepper fruit confirming the results of (Ehert and Ho, 1986a) in tomato and (Cline and Hanson, 1992) in apple.

Unlike Ca which is mainly xylem mobile ion both K and Mg are transported through both phloem and xylem conduits. Thus, the high accumulation of K is a result of its delivery through the phloem sap together with assimilates (Ho and Adams, 1995). Similarly, the accumulation of Mg which is also a phloem mobile element could be seen in a similar manner as that of K (Steucek and Koontz, 1970; Ho and Adams, 1989a).

6.4.3.2. Leaf mineral accumulation

High RH significantly reduced the Ca, Mg and K content of tomato leaves. They also reported similar effects of RH on other species but without statistically significant differences (Gislerod *et al.*, 1987). The present results also showed that high RH

reduces the Ca concentration and content of sweet pepper leaves but not significantly. The adverse effects of high RH on leaf Ca content (reported by several researchers) (Bakker *et al.*, 1987; Bakker, 1990; Gislerod and Mortensen, 1990; Adams, 1991b; Adams and Holder, 1992) is considered to be due to suppression of the transpiration rate which promotes Ca uptake. On the other hand, low transpiring inner leaves of cabbage and lettuce were reported to benefit from high RH conditions (Palzkill *et al.*, 1976; Barta and Tibbitts, 1986) due to the root pressure created as a result (Bradfield and Guttridge, 1984).

From these results it is clear that increasing or decreasing RH had little effect on the concentration and content of K and Mg in both leaves and fruit. It may appear that phloem mobile elements have more or less similar concentration regardless of treatment effects while Ca which is mainly if not solely transported through xylem vessels is significantly depressed by high RH around the fruit or fruit/leaves.

Transpiration is a function of the amount of radiation absorbed and subsequent diffusion of water in a form of vapour to the unsaturated ambient air (Aikman and Houter, 1990), who also indicated that at low light levels there will be reduced rates of radiative transpiration and hence less Ca flow to the growing region. Holder and Cockshull (1989) reported that leaves developing during periods of low solar intensity and high humidity are likely to be deficient in Ca which may result in yield loss. Thus, under conditions of the present experiment where the solar radiation was low and temperature was cool, the provision of low RH around the fruit or fruit/leaf may have had the beneficial effect in attracting more Ca into the fruit or leaves. This may be because of a higher uptake of Ca during the day which is influenced (among other environmental factors) by humidity (Ho, 1989).

Regardless of treatment, the leaf Ca concentration increased with sampling time (Fig. 6.11A). These result therefore, agrees with the data obtained with other species (Jeschke and Pate, 1991; Bhatti *et al.*, 1993). It is interesting to note that Mg concentration also increased with leaf age (Fig. 6.11B) indicating that xylem import

exceeded phloem export in spite of the fact that Mg is essentially phloem mobile (Steucek and Koontz, 1970) and readily exported from leaves (Jeschke and Pate, 1991). The low Ca concentration in young leaves is due to the limited capability of the xylem sap to supply Ca to low transpiring organs such as young leaves and fruit (Marschner, 1986).

6.5. Conclusion

The present findings demonstrated that the level of RH around the fruit has a profound effect on both the Ca status of the fruit and the incidence of BER in sweet pepper fruit.

Exposure of the fruit to low RH conditions promoted the accumulation of Ca in the fruit. High RH on the other hand, suppressed its accumulation which in turn subjected the fruits to the incidence of BER. The incidence of BER was related to the Ca concentration and content as well as the ratios of this element with Mg and K. It also explains how the relative accumulation of the three elements in the fruit is a result of their mobility in xylem or xylem/phloem vessels. RH on the other hand, had little effect on sweet pepper fruit growth and non significant effect on the accumulation of Ca, Mg and K by the leaves.

Chapter 7

The ripening behaviour of attached and detached sweet pepper (*Capsicum annuum* L.) cv. Domino fruit.

7.1. Introduction

Fruits are classified as climacteric or non-climacteric based upon whether they exhibit a dramatic rise in respiration and ethylene production coincident with ripening (Wills *et al.*, 1989; Abeles *et al.*, 1992). Kays (1991) proposed that the climacteric rise in ethylene production is the triggering mechanism for induction of the rise in respiration. On the other hand, respiration slowly declines in harvested non-climacteric fruit such as citrus, cherry and strawberry (Blanpied, 1972; Hartman, 1989) and ethylene production decreases with ripening (Biale and Young, 1981; Perkins-Veazie *et al.*, 1995). Biale and Young (1981) suggest that although the production of carbon dioxide and ethylene may rise and fall in relation to the ripening of climacteric fruit, there is no correlation between the peak levels of carbon dioxide and ethylene produced.

Ethylene is considered to be the hormone coordinating and initiating ripening events in climacteric fruits (Rhodes, 1980a) while, in non climacteric fruits such as water melon, ripening proceeds without significant increase in ethylene production (Elkashif and Huber, 1989).

Sweet pepper is classified as a non-climacteric fruit based on the nature of its respiration and ethylene production during its ripening process (Saltveit, 1977; Lu *et al.*, 1990). However, Gross *et al.*, (1986) found 'Choorahong' hot peppers to be climacteric in terms of their respiration and Lurie and Ben-Yehoshua (1986) also

noted a rise in respiration with colour change of 'Maor' sweet pepper. This suggests that the classification of sweet pepper as non-climacteric fruit may be inconclusive as different cultivars show different behaviour.

Some reports indicate that the pattern of ripening of fruits (such as melons) after harvest or when still attached to the plant, may differ (Lyons *et al.*, 1962; Miccolis and Saltveit, 1991; Shellie and Saltveit, 1993). This defies the classic definition of climacteric in fruit as such fruit exhibit the climacteric respiratory behaviour only when detached from the plant in spite of showing the expected rise in ethylene production whether on or off the plant.

Internal C_2H_4 partial pressure ($P^iC_2H_4$) has been considered a more appropriate criterion to classify climacteric and non-climacteric fruit (Spencer, 1966) and to accurately estimates the ethylene climacteric date (Blanpied and Prittis, 1987). Moreover, the internal concentration of ethylene is physiologically more relevant to ripening than its rate of synthesis or evolution (Burg and Burg, 1965a).

$P^iC_2H_4$ has commonly been estimated from periodic measurement of freshly harvested fruit (Chu, 1984; Knee *et al.*, 1983; Saltveit, 1982) or attached fruit fitted with a syringe needle inserted into the core cavity (Blanpied, 1980; Blankenship and Sisler, 1993; Saltveit, 1977) or directly taking gas samples from the core cavity (Pratt *et al.*, 1977; Saltveit, 1977) or fruit with artificial cavity fitted with a serum stopper (Saltveit, 1977; Shellie and Saltveit, 1993). External chambers have also been used to measure the internal gas concentration of fruit (Banks and Kays, 1988; Saltveit, 1993), while others have applied vacuum to the tissue prior to the extraction of ethylene (Blanpied, 1971; Kwano and Shimokawa, 1994).

Some of these techniques are destructive, making continuous measurement of the same fruit impossible, while external chambers are only appropriate for tissues having lenticels. Vacuum extraction on the other hand has been criticized for affecting the gas equilibrium or its inclusion of dissolved gases in the cell sap thereby possibly

inflating the result (Solomos, 1987).

The following series of experiments was conducted to:

1. To evaluate and identify an appropriate technique for sampling the internal gas composition of sweet pepper fruit.
2. To characterize changes in the internal C_2H_4 , CO_2 and O_2 concentrations as well as colour change in sweet pepper fruit during ripening after harvest or while attached to the plant.
3. To characterize the relationship between rate of colour change and ethylene and carbon dioxide concentration in the fruit.

7.2. Materials And Methods

Experiment on evaluation of sampling techniques for internal gas extraction from sweet pepper fruit.

7.2.1. Fruit source

Fruit samples for this experiment were purchased from a local greenhouse grower. Sixty five fruit of the cultivar "Evidence" were selected for uniformity of size and maturity. All fruit used for this experiment were mature green weighing on the average 120 g with their pedicel attached. During sorting, some fruit were discarded thus, only 65 fruit were used. Data were collected for a total of 15 days by taking measurement every other day from fruit stored at 20°C.

7.2.2. Treatments

7.2.2.1. Measurement from a cavity through a rubber seal

This is a modification of Saltveit's (1977) method for repeated sampling of internal gas samples. The sweet pepper fruit were surface sterilized with 0.25% (v/v) solution of sodium hypochlorite (1:20 dilution of 5% commercial bleach) (Rahman *et al.*, 1993) and a 1.2 cm diameter hole was cut in the ovary wall using a cork borer. The hole was sealed with a 'Toray' rubber seal which was reinforced with Ados contact adhesive. On top of this, a 1.4 cm (diam.) tube cut out from a syringe was fitted using Ados contact adhesive. The small tube was filled with water to prevent gas leakage and contamination with atmospheric air. The edge of the rubber was further sealed with vaseline to prevent possible gas leakage. No microbial contamination resulted from this technique.

7.2.2.2. Direct measurement in air

Gas samples were extracted in a similar way as that of the above method except no artificial hole was made. The fruit were surface sterilized as above. A 'Toray' rubber seal with a fitted cut syringe was fixed on the surface of the fruit to identify a spot for repeated sampling. This system is assumed to result in periodic wounding of the fruit. In spite of this, no microbial contamination was observed.

7.2.2.3. Direct measurement under water

Direct measurement of gas under water was made as the method described by Saltveit (1982). Before samples were taken the dead air space in the 1 ml syringe and air trapped between the septum and the syringe wall were replaced by flushing the syringe with warm (degassed) water and the syringe was emptied under water before withdrawal of gas samples from the fruit cavity.

Fruit were submerged in water and a 3 ml disposable hypodermic syringe was fitted with a stainless steel canula. The mouth of the canula was covered by a pin head to prevent blockage with tissue during insertion into the fruit. The canula was inserted into the locular cavity through the pericarp walls at the equatorial region of the fruit and it was withdrawn slightly so that the pin head remained in the fruit with the canula mouth open.

After gas samples were withdrawn from the fruit the canula was detached from the syringe and a serum stopper was fitted over the tip of the syringe. The process of gas sampling from each fruit took less than 30 seconds. During the whole operation, the fruit and gas samples were kept under water to avoid contamination of gas samples with atmospheric air.

7.2.3. Data collection

Fruit skin colour was measured using a Minolta Chromameter as described in section 5.2.13.1. Internal gas concentrations of C_2H_4 , CO_2 , and O_2 were collected as mentioned above and analyzed as described in sections 5.2.12.1. and 5.2.12.2.

Experiment on monitoring of changes in $P^iC_2H_4$, P^iCO_2 , P^iO_2 and surface colour change of attached and detached sweet pepper fruit.

7.2.4. Fruit source

Fruit of the cultivar "Domino" were grown in a greenhouse at PGU for this experiment using the nutrient film technique described in section 5.2.2. The greenhouse temperature was maintained by heating below 15°C and ventilated above 25°C and RH of the greenhouse was 75-80%. All the plants were grown in nutrient solution with EC of 2 mS cm^{-1} from seedling stage until harvest. Flowers were tagged at anthesis and fruit growth was monitored weekly. At maturity 40 fruit of similar date of anthesis and size were randomly selected and divided in to two lots. One group was left to ripen on the plant and the other group was removed from the plant and stored at 20°C and RH of 80-85% for storage and further analysis. The pedicel of the fruit was allowed to remain attached to the fruit to mimic gas exchange by attached fruit. In both group of fruits internal gas samples were withdrawn as described in section (7.2.2.1.) above. After gas samples were withdrawn, the tip of the hypodermic needle was capped with a rubber septum and transported to the laboratory and analyzed within 5-10 minutes of sampling. The Laboratory temperature was maintained at 20°C and RH ranges between 70 to 80% during analysis.

7.2.5. Data collection

Internal gas samples of CO₂, O₂ and ethylene were extracted and analyzed as described in sections (7.2.2.1.) and (5.2.12.1. and 5.2.12.2.). Skin colour change was monitored using a Minolta chromameter as mentioned in section (5.2.13.1).

7.2.6. Statistical procedure.

Data from both experiments were analyzed using Statistical Analysis System (Littell *et al.*, 1991a). The package was used to compute ANOVA, mean and standard error of means by a repeated measures analysis. The raw data was checked to conform to the requirements of ANOVA and when necessary log_e transformation of the original data was made.

7.3. Results

7.3.1. Sampling technique on colour development

Lightness (reflectance of light) remained approximately constant and was not affected by treatments (Figs. 7.1A). On the other hand, chroma values increased with time for all treatments ($P \leq 0.05$) with no difference noted between treatments (Fig. 7.1B).

The hue angle decreased as the fruit ripened from green to red stage indicating the destruction of chlorophyll and synthesis of carotenoids ($P \leq 0.001$) (Figs. 7.2A). Although treatment 2 (gas extraction through rubber with out cavity) appeared to show a reduced hue angle values, there was no significant difference between the three treatments. Regardless of treatment the chroma values increased as the hue angle started to decline rapidly (Figs. 7.1 B and 7.2A).

7.3.2. Sampling technique on $P^iC_2H_4$

The $P^iC_2H_4$ of fruit was high at harvest regardless of treatments (Figs. 7.2B) and changed with time ($P \leq 0.001$). Initially there was higher internal C_2H_4 at harvest and this tended to subside with time and remained low for some time until it peaked on the 9th day for treatments 1 (gas extraction through rubber seal and cavity) and 2 and on the 11th day for the control treatment (gas extraction under water). Apart from this, there was no significant difference observed between the treatments. Moreover, although there was the reported increase in internal C_2H_4 in the later stage of fruit ripening it was not associated with colour change as it had already occurred by that time (Fig. 7.3A).

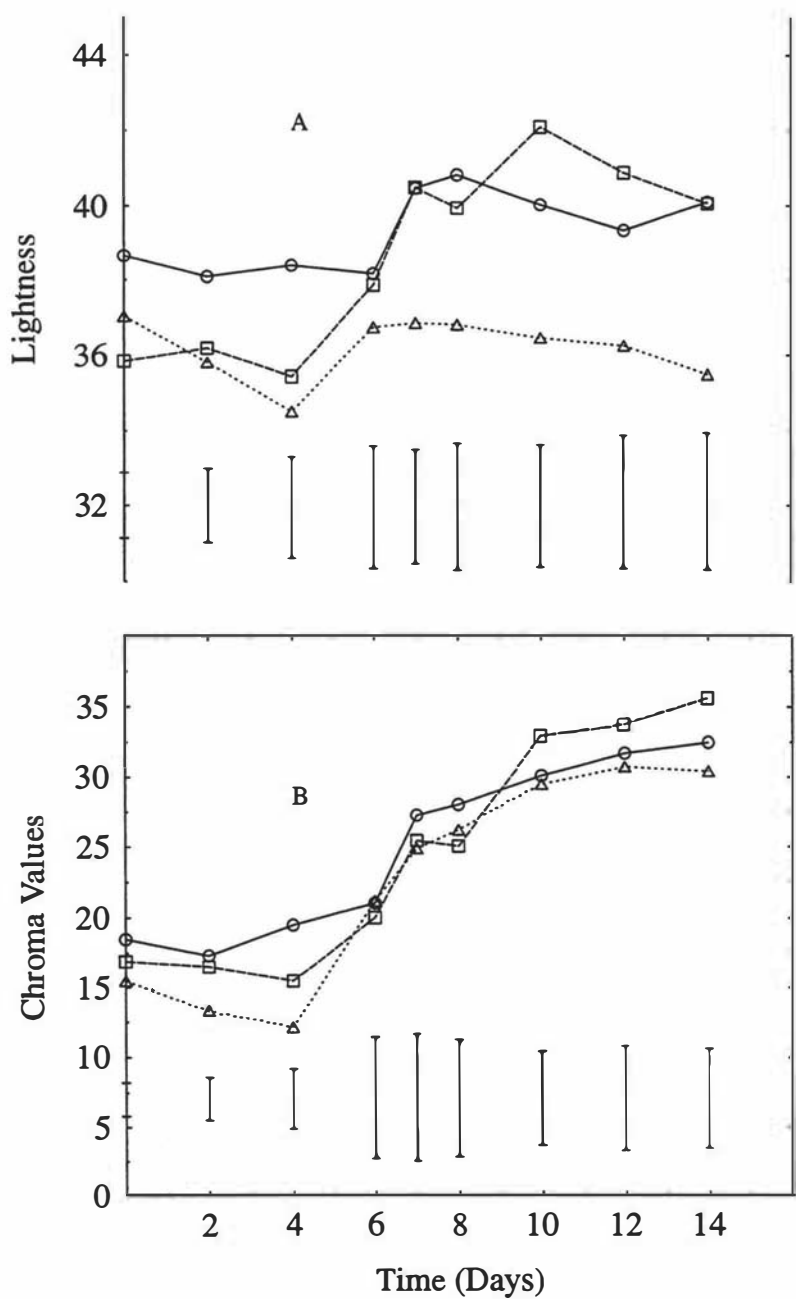


Fig.7.1: Lightness(A) and chroma values (B) of sweet pepper fruit with time as influenced by the method of extraction of the internal atmosphere. Each data point is the means of 5 fruit. Septa + hole (O), Septa - hole (Δ), Control (□). Vertical bars represent standard error of means.

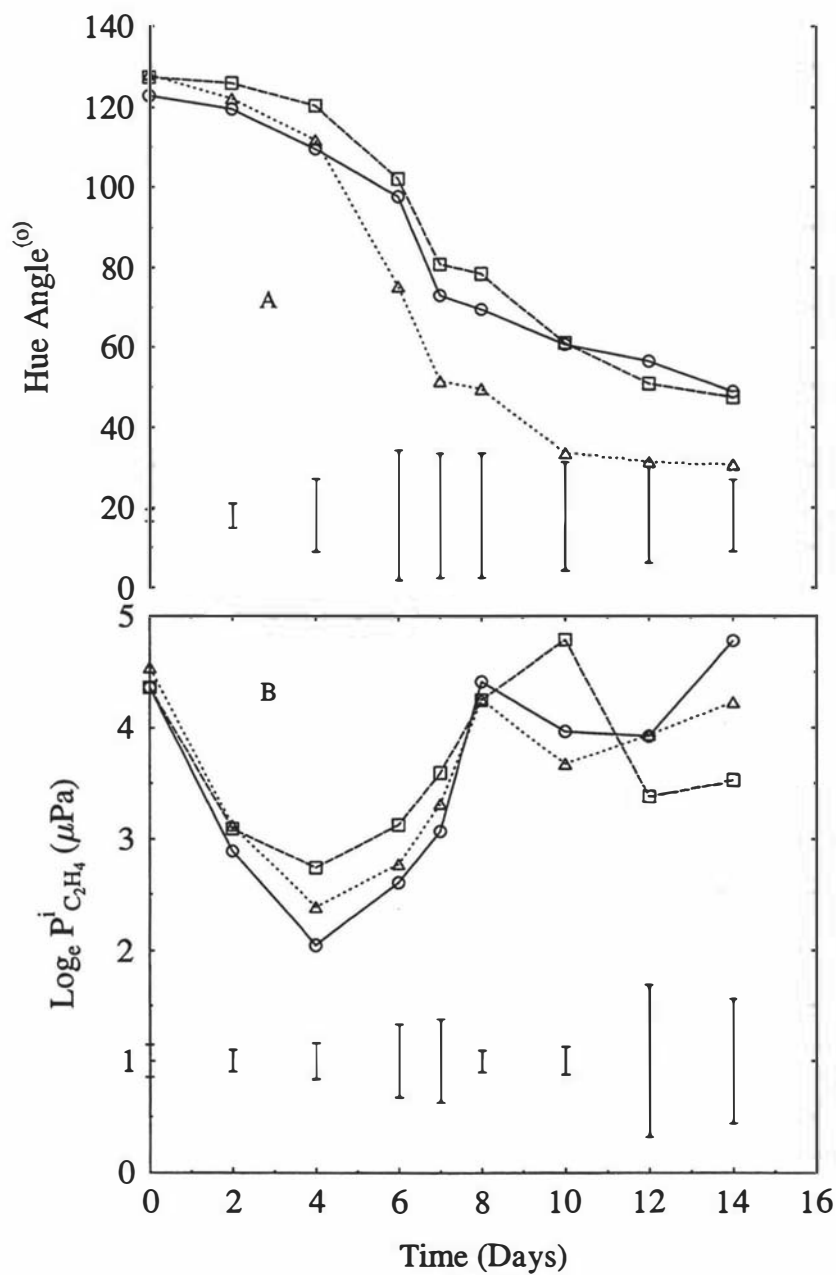


Fig.7.2: Hue angle (A) and $\log_e P^i_{C_2H_4}$ (B) of sweet pepper fruit with time as influenced by the method of extraction of the internal atmosphere. Each data point is the means of 5 fruit. Septa + hole (○), Septa - hole (△), Control (□). Vertical bars represent standard error of means.

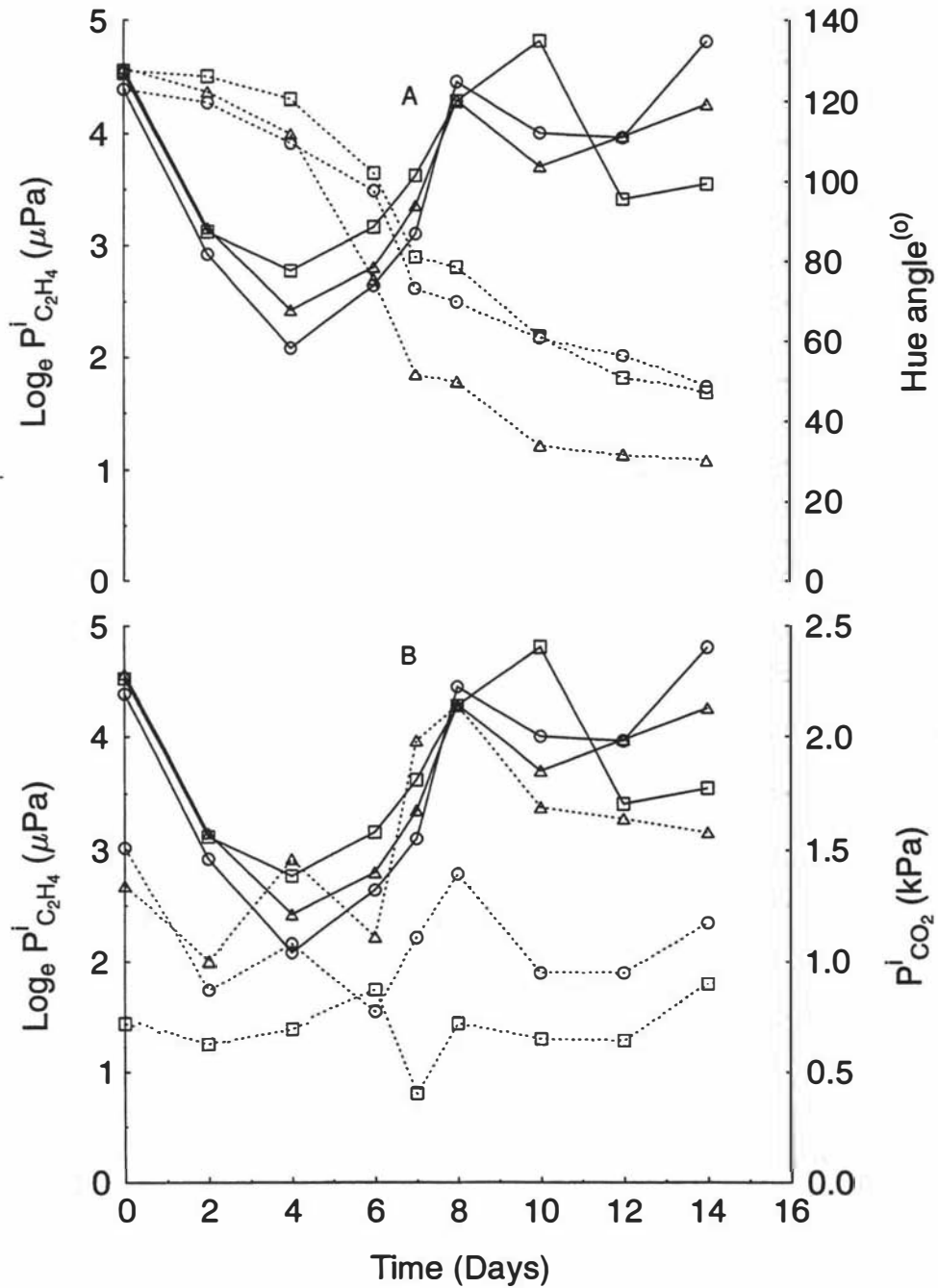


Fig.7.3: $\text{Log}_e P^i_{C_2H_4}$ and hue angle (A) and $\text{log}_e P^i_{C_2H_4}$ and $P^i_{CO_2}$ (B) of sweet pepper fruit whose external gas was extracted by different techniques. Sepata + hole (○), septa - hole (Δ), control (□). Each data point is the means of 5 fruit. Solid lines represent $P^i_{C_2H_4}$ and broken lines represent hue angle (A) and $P^i_{CO_2}$ (B).

7.3.3. Sampling technique on P^iCO_2 and P^iO_2

Fig. 7.4A shows that extracting of internal gas samples through septa without hole resulted in periodic wounding thereby increasing the internal CO_2 concentration of fruit throughout the experimental period ($P \leq 0.01$). Internal oxygen concentration followed the opposite trend of internal CO_2 (Fig. 7.4B). It was further observed that the rise in internal ethylene and CO_2 concentrations were synchronized in case of treatments 1 and 2 (Fig. 7.3B). This was not however, true for the control treatment which respired in an erratic fashion (Fig. 7.3B).

7.3.4. Colour change of attached and detached fruit

Lightness of both attached and detached fruit showed little change during ripening. However, higher values of lightness (lighter colour) were recorded for detached fruit than attached fruit ($P \leq 0.001$) (Fig. 7.5A). Moreover there was a tendency for lightness to decline with ripening ($P \leq 0.05$) in both attached and detached fruit which implies a decrease in reflectance of light by the fruit (darker colour) (Fig. 7.5A). On the other hand, chroma which measures the colour intensity remained low before the onset of ripening but increased after colour break ($P \leq 0.01$) (Fig. 7.5B). There was no appreciable difference in chroma values after the onset of ripening but prior to that detached fruit had higher chroma values than attached fruit ($P \leq 0.05$).

Hue angle was unchanged and remained high for 7 or 8 days after measurement started on attached fruit (Fig. 7.6A). However, detached fruit showed a rapid initial decline in hue angle starting 5 days after the initiation of measurement (Fig. 7.6A). Once ripening was initiated, (8-9 days after measurement began), attached fruit showed a rapid decline in hue angle while detached fruit exhibited a slow but steady decline ($P \leq 0.001$) (Fig. 7.6B). There was however, no significant difference in hue

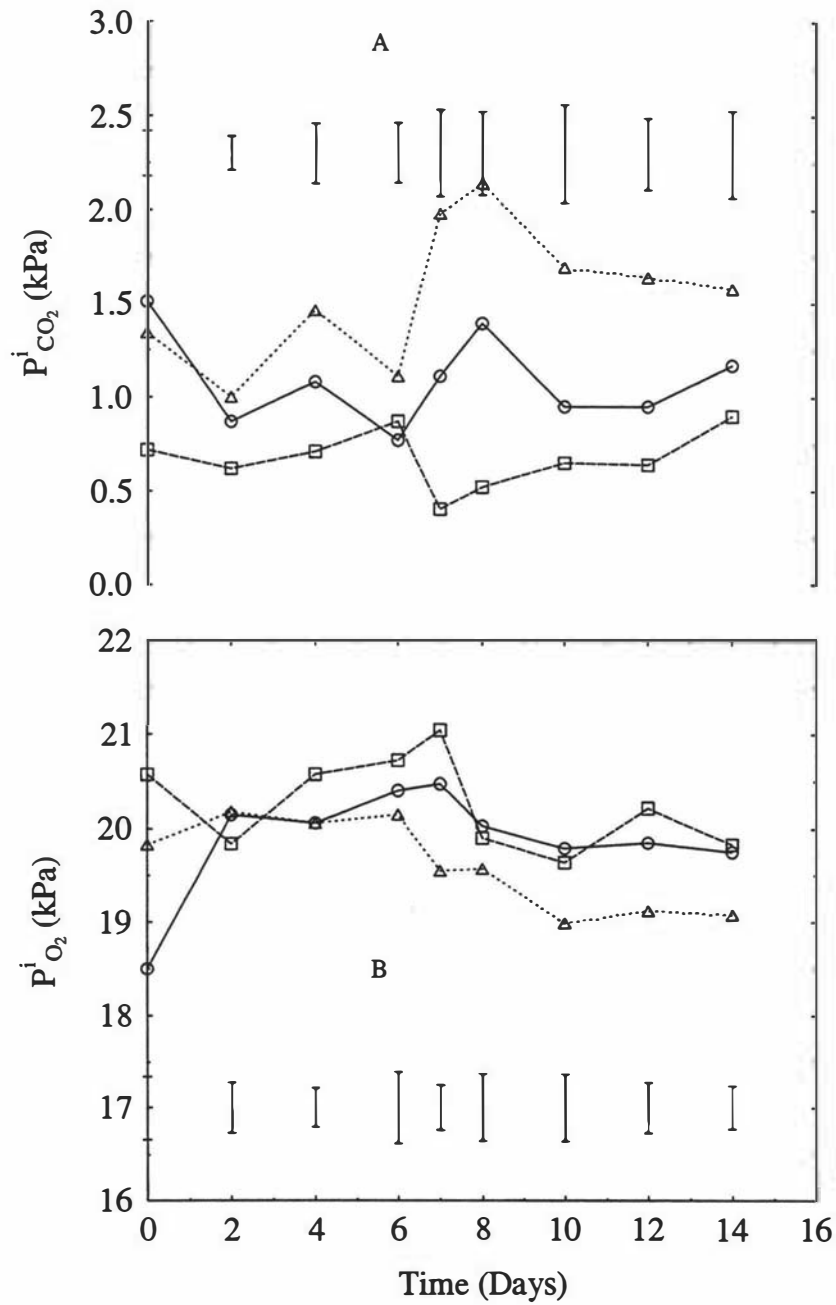


Fig.7.4: $P^i_{CO_2}$ (A) and $P^i_{O_2}$ (B) of sweet pepper fruit with time as influenced by the method of extraction of the internal atmosphere. Each data point is the means of 5 fruit. Septa + hole (○), Septa - hole (△), Control (□). Vertical bars represent standard error of means.

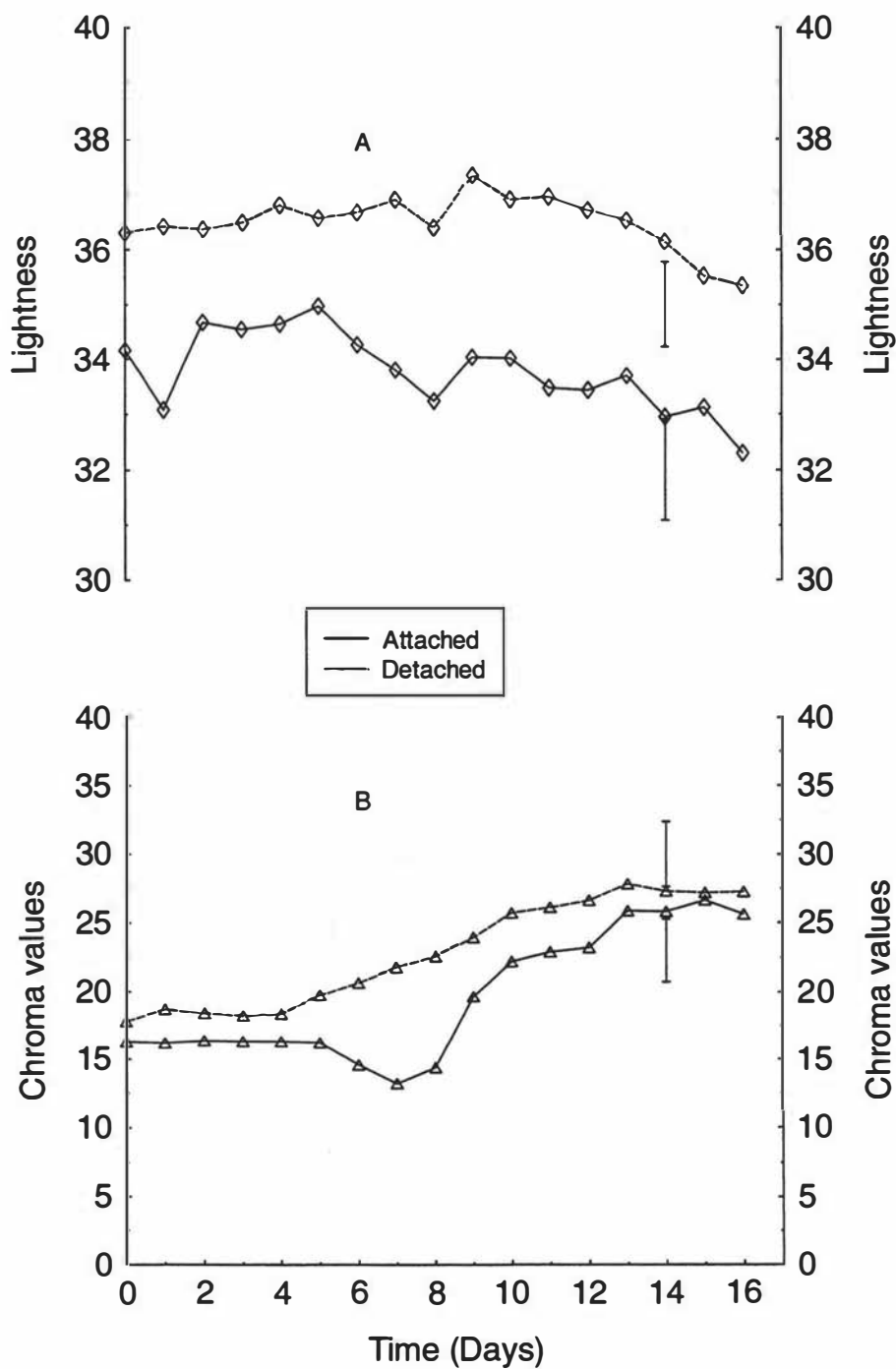


Fig.7.5: Lightness (A) and chroma (B) of attached and detached sweet pepper fruit. Each data point is the mean of 20 fruits. Vertical bars indicate pooled standard error of means.

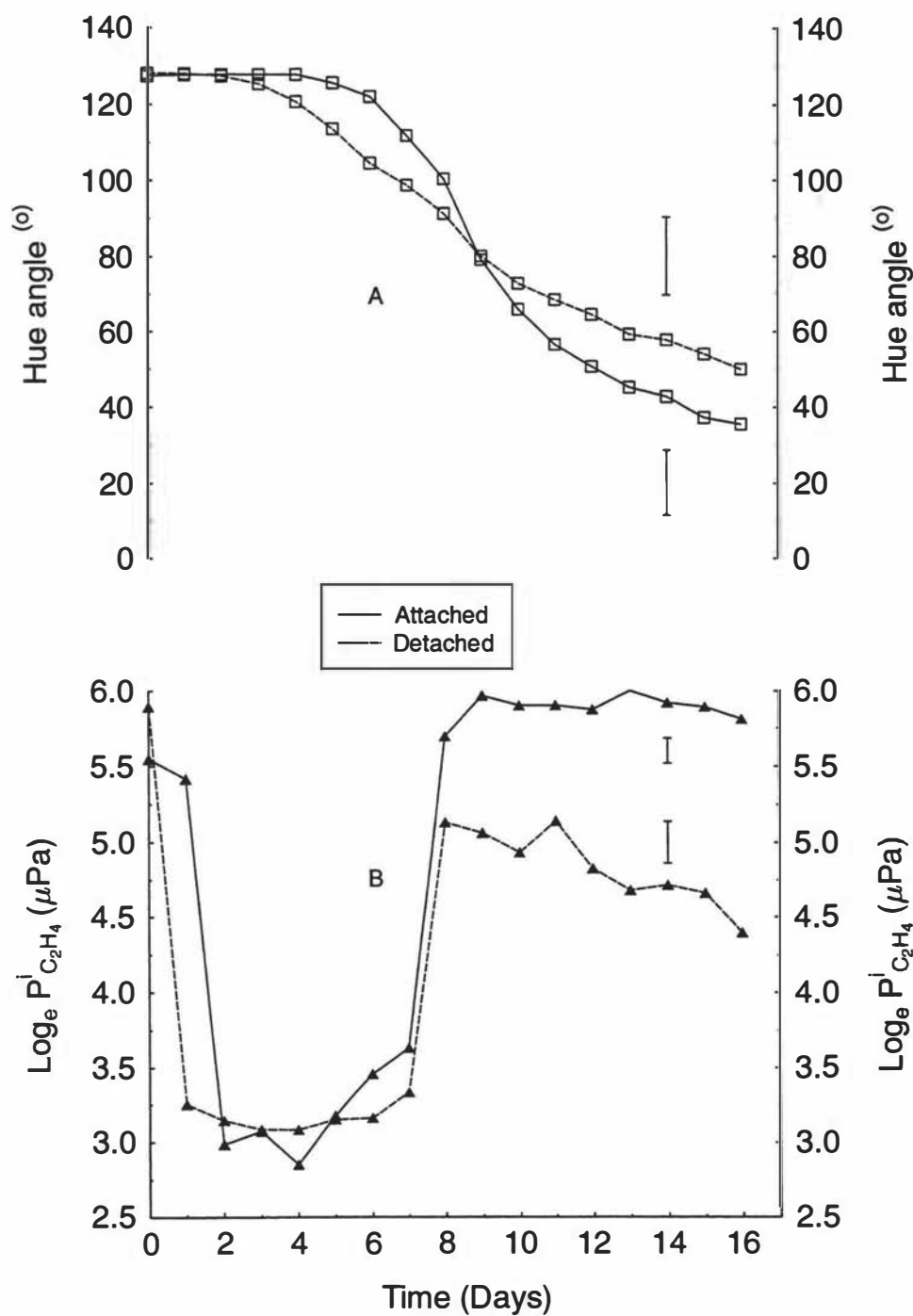


Fig.7.6: Hue angle (A) and $\text{Log}_e P^i_{C_2H_4}$ (B) of attached and detached sweet pepper fruit. Each data point is the mean of 20 fruits. Vertical bars indicate pooled standard error of means.

angle of both attached and detached fruit except 6 days after harvest ($P \leq 0.05$). The rate of colour change however, was similar for both attached and detached fruit with respect to hue angle (Table 7.1). It was also noted that the increase in chroma values corresponds to the decline in hue angle of both attached and detached fruit (Fig. 7.7A and B).

7.3.5. Changes in P^iCO_2 of attached and detached fruit

The internal concentration of CO_2 (P^iCO_2) measured within 1-2 hour after harvest for detached fruit or making the artificial cavity for attached fruit was higher at the beginning of measurement and steadily declined in detached fruit throughout the ripening period ($P \leq 0.001$) (Fig. 7.8A). Contrary to this, attached fruit exhibited higher internal CO_2 levels initially which slightly declined during the next few days. These levels later peaked and remained high during the ripening phase and beyond (Fig. 7.8A). There was a 2 times higher internal CO_2 levels during the ripening phase of attached fruit ($P \leq 0.001$).

On the other hand, the internal O_2 concentrations (P^iO_2) of both attached and detached fruit were low at the beginning but started to increase in detached fruit during ripening ($P \leq 0.001$) (Fig. 7.8B). Detached fruit on the other hand, showed a suppression of their P^iO_2 concentration measurably associated with high respiratory demand ($P \leq 0.001$) (Fig. 7.8B). Generally, the P^iO_2 of both fruit showed the opposite trend of internal CO_2 (Fig. 7.8B).

It should be noted that the rise in P^iCO_2 appeared to coincide with the stage of rapid colour change in attached fruit (Fig. 7.9A) although this was not observed in detached fruit (Fig. 7.9B).

Table 7.1. Effect of treatment on the rate of colour and gas exchange day⁻¹ of sweet pepper fruit cv. Domino, n=40.

Day 0-4						
Treatment	Lightness	Chroma	Hue	PiC ₂ H ₄	PiCO ₂	PiO ₂
Attached	0.161	0.027	-0.020	-69.555	0.168	-0.159
Detached	0.131	-0.111	-2.488	-1.241	-0.206	0.272
Significant ¹	ns	ns	ns	***	***	***
SEM	0.128	0.122	1.13	3.01	0.03	0.06
Day 5-8						
Attached	-1.136	-0.853	-10.127	90.21	0.153	-0.540
Detached	-0.062	0.945	-7.467	54.23	0.083	-0.354
Significant	ns	*	ns	**	***	ns
SEM	0.47	0.63	2.44	7.49	0.037	0.227
Day 9-12						
Attached	-0.201	1.192	-9.486	-14.933	-0.107	0.201
Detached	-0.210	0.883	-5.165	-11.084	-0.041	-0.196
Significant	ns	ns	ns	ns	ns	***
SEM	0.17	0.64	1.9	6.36	0.03	0.05
Day 13-17						
Attached	-0.461	-0.081	-3.118	-23.10	-0.06	-0.035
Detached	-0.395	-0.188	-3.120	-8.207	-0.036	-0.054
Significant	ns	ns	ns	*	ns	ns
SEM	0.126	0.26	1.36	4.54	0.03	0.04

¹ * *** and ns significant at P≤0.05, 0.001 and non significant.

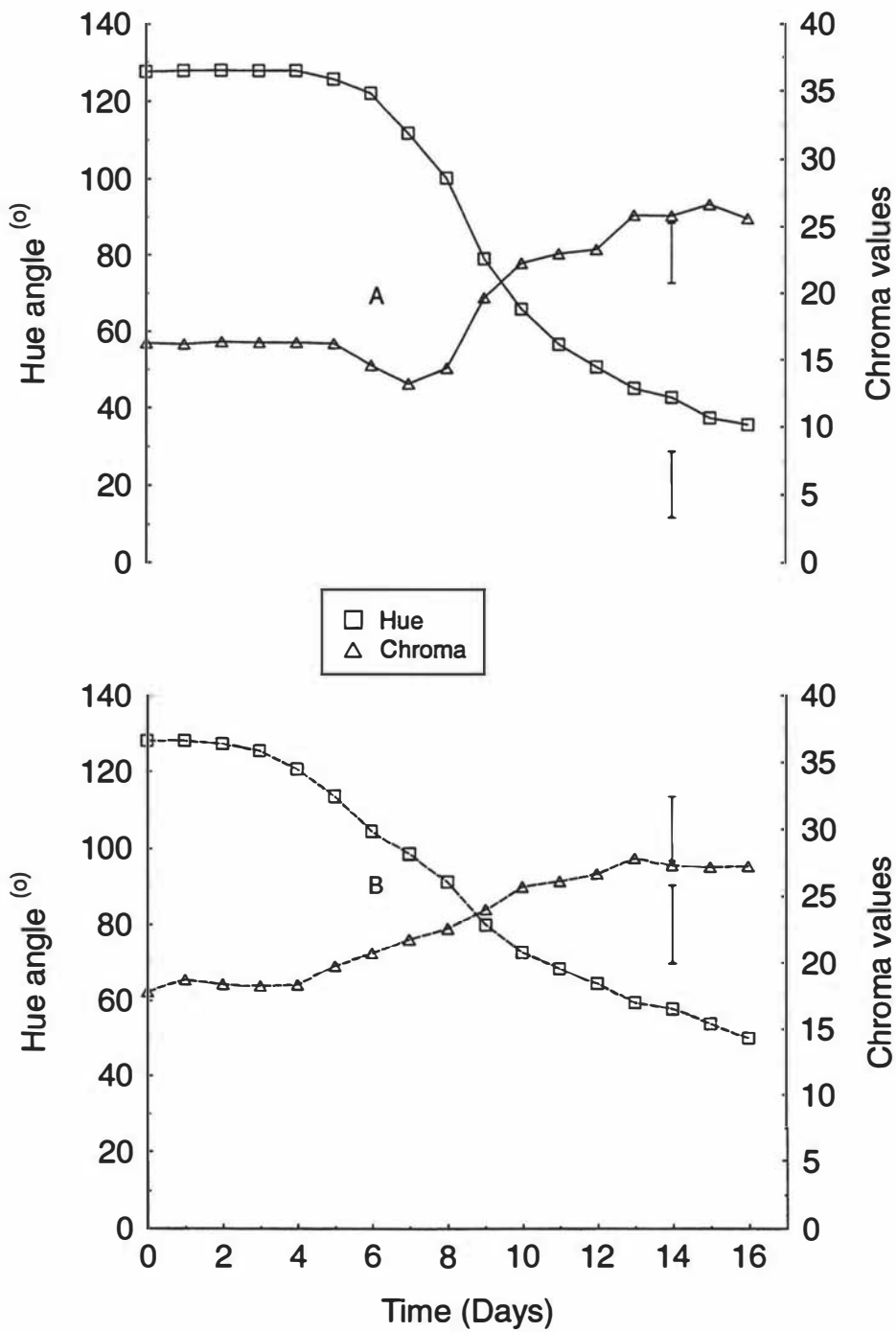


Fig.7.7: Hue angle and chroma values of attached (A) and detached (B) sweet pepper fruit. Each data point is the mean of 20 fruits. Vertical bars indicate pooled standard error of means.

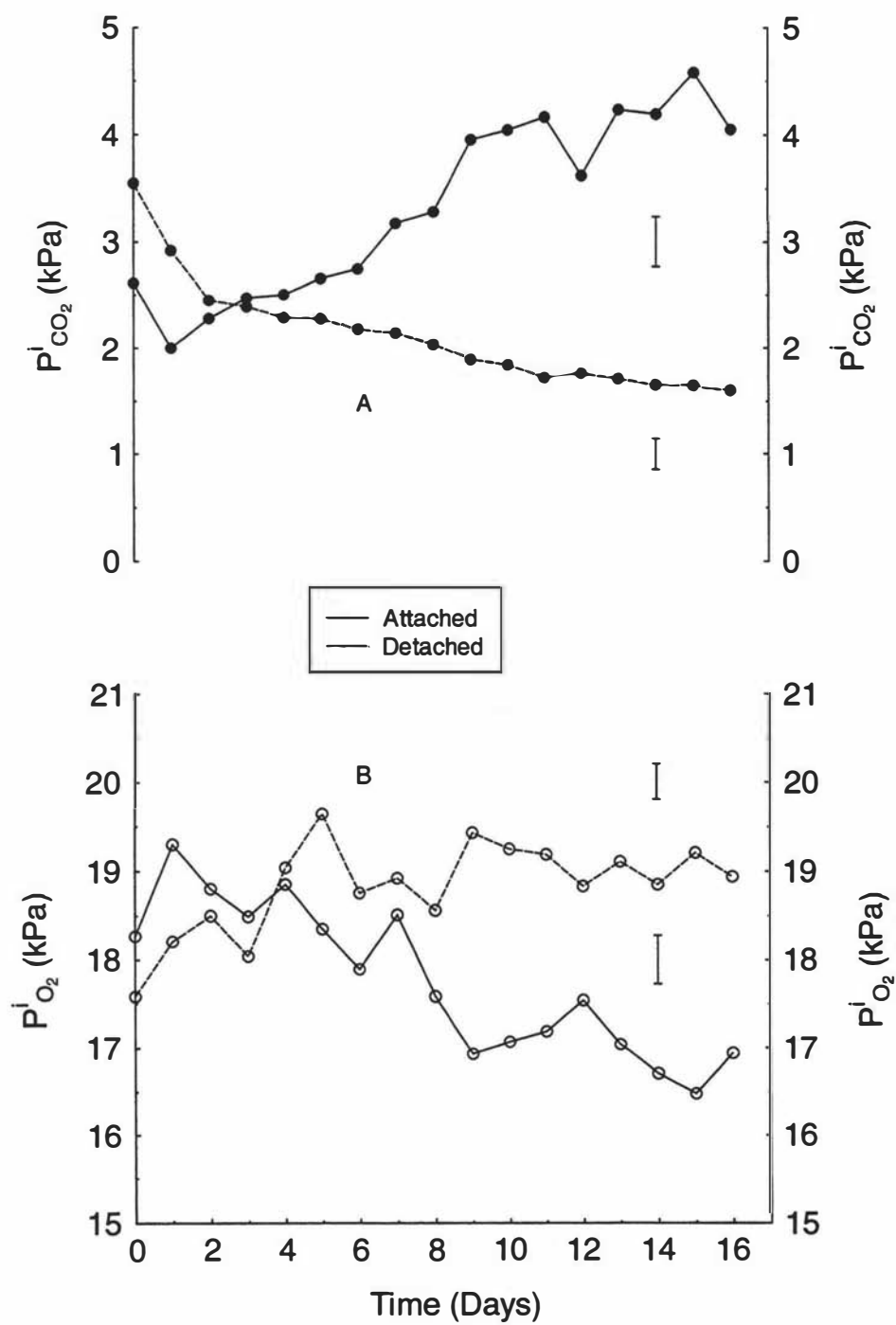


Fig.7.8: P'_{CO_2} (A) and P'_{O_2} (B) of attached and detached sweet pepper fruit. Each data point is the mean of 20 fruits. Vertical bars indicate pooled standard error of means.

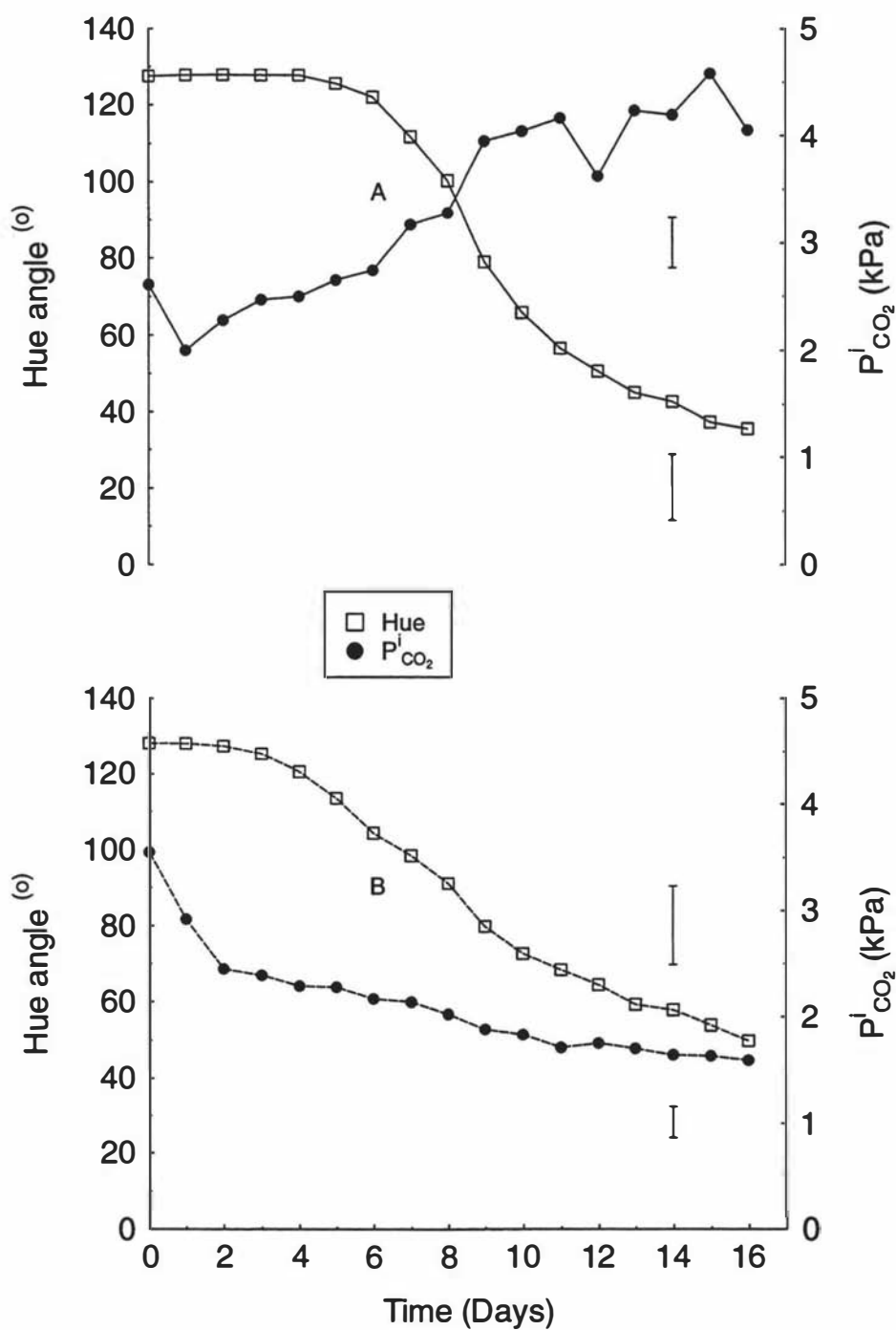


Fig.7.9 Hue angle and $P^i_{CO_2}$ of attached (A) and detached (B) sweet pepper fruit. Each data point is the mean of 20 fruits. Vertical bars indicate pooled standard error of means.

7.3.6. Changes in $P^iC_2H_4$ concentration

The internal concentration of C_2H_4 ($P^iC_2H_4$) was higher initially but rapidly declined after a day or two in both attached and detached fruit ($P \leq 0.001$) (Fig. 7.6B). It remained low for about a week and dramatically increased in attached fruit to its highest level around 8 days after measurement began. In a similar fashion, detached fruit also showed a significant increase in $P^iC_2H_4$ during the colour break stage and remained high for a few days until it gradually declined. Generally, attached fruit had higher $P^iC_2H_4$ than detached fruit ($P \leq 0.001$).

The fall in hue angle values coincided with the sharp increase in internal C_2H_4 of both attached and detached fruit (Fig. 7.10A and B). Likewise, there was a 20 fold increase in $P^iC_2H_4$ in attached fruit while detached fruit showed a 10 fold increase compared to pre climacteric phase. Furthermore, the rise $P^iC_2H_4$ was accompanied by a higher P^iCO_2 in attached fruit (Fig. 7.11A) but, this was not demonstrated by detached fruit (Fig. 7.11B).

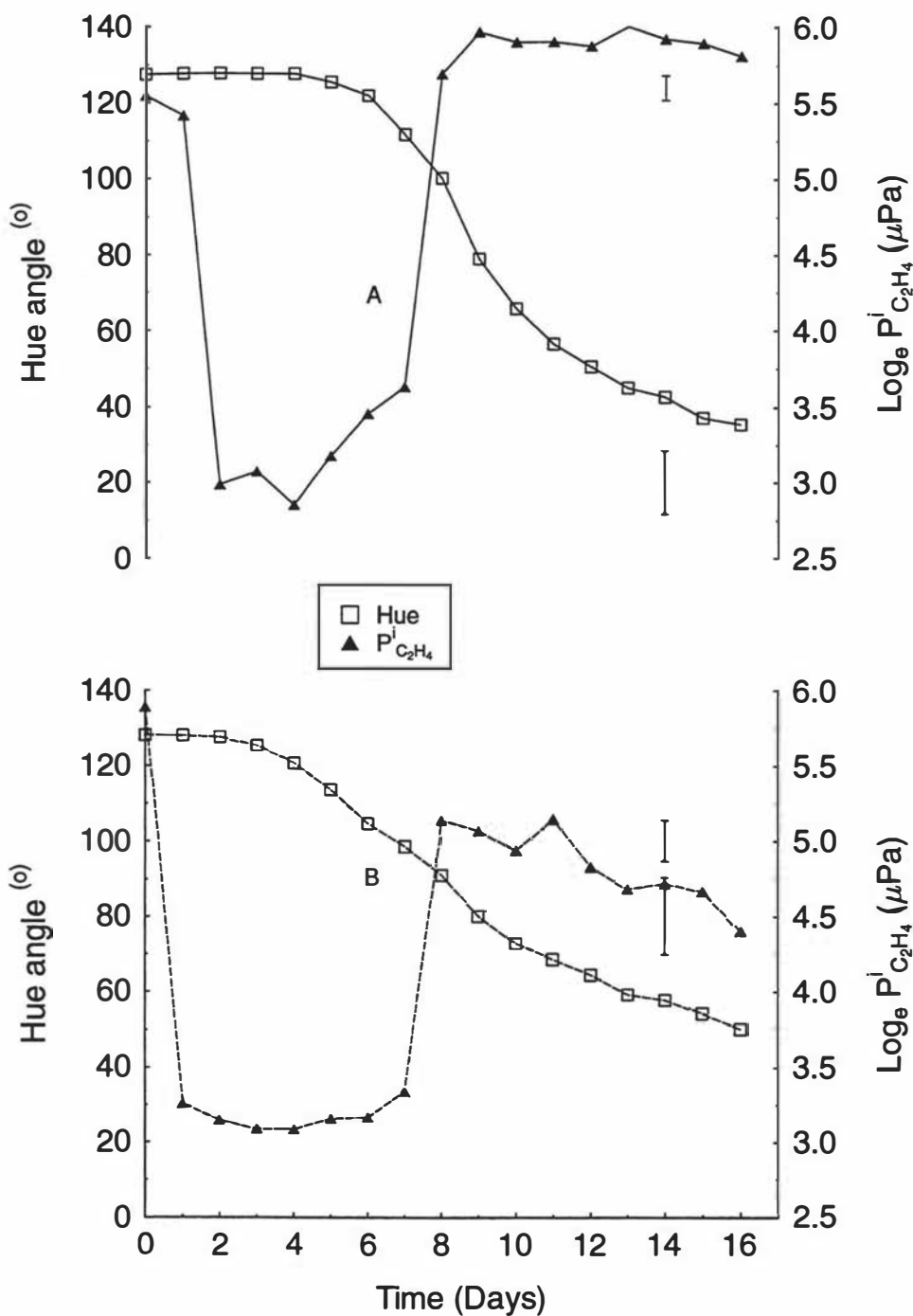


Fig.7.10: Hue angle and Log_e Pⁱ_{C₂H₄} of attached (A) and detached (B) sweet pepper fruit. Each data point is the mean of 20 fruits. Vertical bars indicate pooled standard error of means.

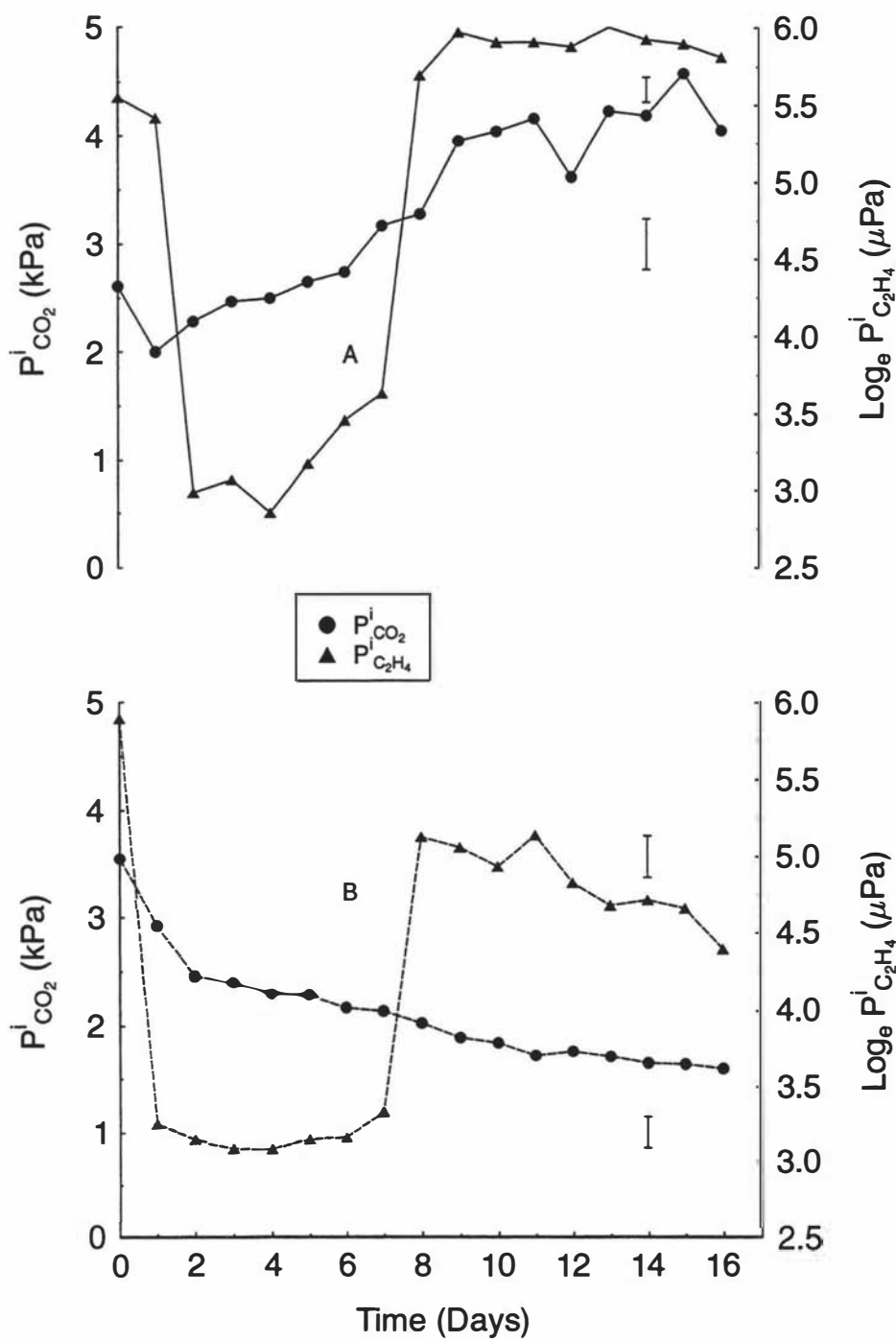


Fig.7.11: $P^i_{CO_2}$ and $\log_e P^i_{C_2H_4}$ of attached (A) and detached (B) sweet pepper fruit. Each data point is the mean of 20 fruits. Vertical bars indicate pooled standard error of means.

7.4. Discussion

7.4.1. Sampling technique

Lightness (reflectance of light), chroma (colour intensity) and hue angle (absorption of light in the visual range) (Tourjee *et al.*, 1993; Gonnet, 1995) were used to follow changes in surface colour of sweet pepper fruit.

Sampling technique had no significant effect on the colour change of the sweet pepper fruit cv. 'Evidence' presumably because there was no difference in the concentration of the ripening hormone ethylene between fruits with and without attached septa (Figs. 7.1A and B and 7.2A).

The increase in ethylene concentration after colour change had progressed may indicate a lack of involvement of ethylene in ripening of these fruit (Fig. 7.4B), while the rise in internal ethylene during the later stage of ripening may be associated with the senescence of the fruit (Matto and Suttle, 1991).

The decline in P^iCO_2 as fruit ripened from green to red suggests that the sweet pepper fruit of the cultivar "Evidence" are non-climacteric (Mizutani *et al.*, 1988). Doubling of the respiration rate from base level in these fruits concomitant with colour change (a characteristic of climacteric fruit) was not observed (Biale and Young, 1981). On the other hand, the significant difference observed in P^iCO_2 of fruits from sampling technique 2 (septa without hole) indicates that repeated sampling from such fruit induces wounding of tissues (Hoffman and Yang, 1982) and consequently led to a higher P^iCO_2 . This however, was not expressed in terms of higher $P^iC_2H_4$ as the fruit did not produce much ethylene naturally.

Although there was no significant difference between P^iCO_2 extracted by methods 1 (septa with hole) and 3 (gas extraction under water), it was slightly lower for control

fruit (Fig. 7.3a). The 'slightly' lower $P^i\text{CO}_2$ observed for water submerged system may be a result of CO_2 exchange with free water, as although the time of extraction was much faster the extracted gas was left in the water until analysis. Sestak *et al.*, (1971) indicated that if condensation or water saturated surfaces exist in the sample collection tube it may act as a source or sink for CO_2 . However, since ethylene is less soluble in water than CO_2 it may not be affected by the presence of water (Andrews, 1995).

Therefore, because the rubber sealed cavity did not increase the $P^i\text{CO}_2$ and $P^i\text{C}_2\text{H}_4$ more than the conventional system (i.e., the control treatment), then method 1 proved to be a valuable method to monitor the internal C_2H_4 and CO_2 and O_2 repeatedly from the same attached fruit during maturity and ripening.

7.4.2. Attached and detached fruit

7.4.2.1. Colour change of attached and detached fruit

Colour change with the onset of ripening was reflected in a fall in hue angle and a rise in chroma values, and is similar to the ripening of tomato fruit (Shewfelt *et al.*, 1988). The decline in hue angle was a result of a fall in the levels of chlorophylls and an increase in carotenoid synthesis in sweet pepper fruit (Pretel *et al.*, 1995), and is a result of the transformation of chloroplasts to chromoplasts (Leshem *et al.*, 1986).

Amongst the colour components (L C H) of sweet pepper fruit, lightness (L) changed very little during ripening while chroma (C) and hue angle (H) showed an upward lift and a downward drift respectively with time. The visual difference is better described by changes in hue angle followed by chroma, and with lightness the poorest indicator of colour change in sweet pepper fruit.

Detached fruit started to change colour (hue) rapidly after harvest (5 days) while

attached fruit remained green for up to 8 days. This difference could be attributed to difference in physiological changes between the two group of fruit in terms of water, nutrient and supply of assimilates. Attached fruit (unlike detached fruit) were supplied with all the necessary inputs from the plant maintaining among others their turgidity, Loss of turgidity and a decrease in fruit water potential were the primary causes of senescence of harvested sweet pepper fruit (Lurie *et al.*, 1986). On the other hand, the subsequent rapid decline in hue angle of attached fruit was probably a result of relatively higher levels of ethylene in the fruit as compared with detached fruit (Fig. 7.6b).

In attached fruit, lightness slightly increased then showed a decreasing trend during fruit ripening while detached fruit didn't change in lightness for some time before declining with ripening. The increase then decrease in lightness is due to the time gap between chlorophyll degradation and the commencement of synthesis of carotenoids (Shewfelt *et al.*, 1988). The lower values in lightness with maturity indicate higher anthocyanin accumulation in apple fruit (Singha *et al.*, 1991) and carotenoids could be the reason in case of sweet pepper.

The initial decline in chroma values in attached fruit and to some extent in detached fruit was a result of the decline in green colouring of the fruit. The subsequent increase in chroma values was attributed to a rapid decrease in hue angle and the corresponding increase in the synthesis of carotenoids (Leshem *et al.*, 1986). This change in chroma values of attached and detached fruit closely followed the changes in their respective hue angles. Accordingly, chroma values started to increase earlier in detached fruit than attached fruit.

7.4.2.2. P^iCO_2 and P^iO_2 of attached and detached fruit.

The higher P^iCO_2 and P^iO_2 of fruit measured at the beginning of the experiment is most likely related to wounding of the tissue during preparing the artificial cavity and

the subsequent harvesting and handling stress experienced by detached fruit (Hoffman and Yang, 1982). This is confirmed by high levels of ethylene measured at this time. Knee, (1995) similarly reported that insertion of tubes into tomato fruit to monitor internal gas concentration increased both the CO_2 and C_2H_4 concentrations.

The subsequent decline in P^iCO_2 of harvested fruit, (while attached fruit showed a higher rate continuously) may be a result of egress of CO_2 through the cut end (pedicel) of the fruit rather than apparent difference in the metabolism of the two groups of fruit. Burg and Burg (1965b) reported that CO_2 emanation was retarded by 60% when lanolin was applied to the pedicel end of sweet pepper fruit. Recently, De Vries *et al.*, (1996) confirmed the pedicel to be the route of emission of CO_2 and C_2H_2 in tomato and sweet pepper fruit. The lack of a respiratory climacteric in the respiration of attached fruit of sweet pepper fruit (Fig. 7.11a) was also observed in tomato (Saltveit, 1993) muskmelon (Shellie and Saltveit, 1993) and purple passion fruit (Shiomi *et al.*, 1996) which are climacteric fruit. This is in spite of producing high C_2H_4 after harvest in intact fruit. Miccolis and Saltveit (1991) also observed a decline in respiration of seven melon cultivars soon after harvest. The theory of ripening inhibitory hormone in attached fruit (Blanpied, 1993; Kays, 1991; Lau *et al.*, 1986) in apple and avocado fruit may not hold true for sweet pepper. This is because the fruit appear to ripen normally whether attached or detached as long as it is fully mature.

Saltveit (1977) noted a decline in the internal CO_2 of attached fruit in sweet pepper fruit (cv. California Wonder) in spite of showing an increase level of internal C_2H_4 . This is contrary to the current observation with respect to respiration of attached fruit. The difference may lie in the ripening behaviour of the two cultivars used. Saltveit, (1977) observed the peak ethylene concentration to be around 50 nl.l^{-1} and the increase in concentration from the lowest level to be 2 fold. He also suggested that the increase in ethylene production may be a result of deterioration and microbial infection in the ripened fruit. Unlike his observation no microbial infection was observed on fruits of this experiment and the observed rise in $\text{P}^i\text{C}_2\text{H}_4$ occurred in both

attached and detached fruit (Figs. 7.6b and 7.8a and b). This rise again was observed well ahead of possible deterioration which coincided with the change in colour of the fruit. On the other hand, the other cultivar "Evidence" examined could fall in to the category of non-climacteric fruit because both the respiration and ethylene peak were not related to ripening but probably to senescence of the fruit. Furthermore, the level of internal ethylene in "Domino" fruit was at least 5 times higher than that observed in California Wonder or Evidence fruits regardless of whether the fruit were attached or detached. In climacteric fruit there is a 10 to 100% increase in ethylene production (Pratt and Goeschl, 1969). This is similar in magnitude to what was observed in 'Domino' fruit although, the level is not as high as many climacteric fruits.

Lurie and Ben-Yehoshua (1986) also showed that the sweet pepper cultivar "Maor" had a maximum of 0.85% CO₂ during the ripening phase, an increase of only 30% from a low base level. This suggests that the fruit of the cv. Maor were not respiring as high as the cultivar Domino at the peak ripening stage of the fruit. On the other hand, Gross *et al.*, (1986) demonstrated that there was a doubling of the CO₂ production of "Chooraeahong" hot pepper during the climacteric peak which is similar in magnitude and quantity to the internal CO₂ concentration of the 'Domino' fruit.

It is likely that fruit weight increased during the sampling period of attached fruit. Hence, an increase in size could account for both the rise in CO₂ concentration of attached fruit (Saltveit, 1993) and the difference in internal C₂H₄ of attached and detached fruit. The increase in PⁱCO₂ of attached fruit could be in response to internal changes associated with ripening, which may include accumulation of the hexose sugars glucose and fructose (Nielsen *et al.*, 1991; Wall and Biles, 1993; Hubbard and Pharr, 1992). This accumulation in turn may serve as readily available substrate for respiration. Moreover, unlike attached fruit of melon which showed high internal CO₂ after fruit abscission (Shellie and Saltveit, 1993), the 'Domino' fruit exhibited the high internal CO₂ while they were ripening, as expressed by accompanying colour change.

Another feature of the difference between attached and detached fruit could be that attached fruit continues to import assimilates from the plant as growth proceeds. The type of photosynthate imported into the fruit also changes with fruit growth (Hubbard and Pharr, 1992). Czarnowski (1996) and Piechulla *et al.*, (1987) reported that sweet pepper and tomato fruit are capable of photosynthesizing. Their ability however, decreases with ripening as chlorophyll is lost (Piechulla *et al.*, 1987). Knee (1995) found that the internal CO₂ concentration of detached tomato fruit tends to decline as compared to attached fruit exposed to light. He suggested that in light, the plant supplies substrate to the fruit to maintain high CO₂ production. This enhanced CO₂ production is partially offset by photosynthesis in green fruit exposed to light (Knee, 1995). The lack of climacteric rise in attached fruit (Saltveit, 1993) and that of the 'Domino' fruit could be a result of decline in substrate import and fruit photosynthesis (Knee, 1995), and thus reduce import dependent CO₂ generation.

7.4.2.3. $P^iC_2H_4$ of attached and detached fruit.

Sweet pepper fruit of the cultivar 'Domino' whether attached or detached follow the classic pattern of climacteric ethylene production during ripening (Figs. 7.11 a and b).

Apple fruits attached to the tree contain high levels of ethylene in the pre climacteric phase (Reid, *et al.*, 1973) and the rise in concentration is more gradual than for detached fruit (Knee, 1973). In sweet pepper fruit from the current experiment however, the level was very low prior to the onset of ripening and peaked sharply at ripening.

The hot pepper fruit of the cultivar "Choorahong" showed a small but significant increase in ethylene production during ripening (Gross *et al.*, 1986). In the present experiment this increment was high compared to the hot pepper fruit examined by Gross *et al.*, (1986) and sweet pepper fruits of the cultivar California Wonder

(Saltveit, 1977) and the cultivar "Maor" (Lurie and Ben-Yehoshua, 1986).

With the climacteric rise in $P^iC_2H_4$, P^iCO_2 also showed a significant increase from its pre climacteric level in attached fruit (Fig. 7.11A). This peak in both $P^iC_2H_4$ and P^iCO_2 also coincided with a fall in hue angle and a rise in chroma values. With a rise in internal CO_2 and C_2H_4 a reduction in internal oxygen levels was also noted.

Sweet pepper fruits of the cultivar California Wonder had a low and near constant respiration and ethylene production rates during ripening (Pretel *et al.*, 1995). According to their findings the low production of ethylene during ripening was a result of the low activity of the two key ethylene biosynthesis enzymes, ACC synthase and ACC oxidase. In the current experiment the activities of the two enzymes were not measured but it is likely that the differing levels of $P^iC_2H_4$ would have been reflected in concomitant variation in these enzymes.

It is widely accepted that non-climacteric fruits show no significant increase in respiration and ethylene production during ripening (McGlasson, 1985). However, sweet pepper fruits of the cultivar 'Domino' showed a significant increase in their internal C_2H_4 concentrations, unlike other non-climacteric fruits which do not undergo much further ripening after harvest (Lurie and Ben-Yehoshua, 1986). The detached Domino fruit had essentially the same hue angle values (red ripened) at the termination of the experiment as the attached fruit, although change of colour was slightly slower than for the attached fruit. The latter might be a result of the progressive decline in $P^iC_2H_4$ resulting from egress of ethylene through the pedicel end (De Vries *et al.*, 1996).

Detached 'Domino' fruit continued to ripen in storage in spite of a steady decline in respiration and produced a significant amount of ethylene during the ripening phase. On the other hand, attached fruit exhibited both an increased respiration as well as internal ethylene concentration, concomitant with ripening of fruit.

Burdon and Sexton (1993) showed differences in ethylene production of different blackberry cultivars, and Lipe (1978) classified 'Humble' blackberry to be non-climacteric based on its level of ethylene production. This difference in ripening characteristics of 'Domino' fruit and other sweet pepper cultivars therefore, could be a result of cultivar difference and environments. It could also be a reflection of the timing of ethylene production of the cultivars examined. In raspberry fruits for instance, drupelet pigmentation changes and ethylene production changes didn't coincide at the same time for all cultivars (Burdon and Sexton, 1990). This again suggests that the developmental physiology and the role played by ethylene in inducing ripening may differ between cultivars.

Similarly, cultivar difference have been reported in melons (Pratt *et al.*, 1977) and pear (Downs *et al.*, 1991) with respect to respiration during ripening. Such examples illustrate the difficulty of defining a set criterion to be used in predicting ripening related respiratory behaviour of specific fruit. More importantly it emphasises the risk of extrapolating the data for different species and cultivars.

Thus, sweet pepper fruits (cultivar Domino) exhibited a climacteric behaviour with respect to their internal ethylene coincident with ripening. The lower peak observed in $P^iC_2H_4$ of detached fruit however, could be a result of the escape of the gas through the pedicel end (De Vries *et al.*, 1996) which otherwise would accumulate in attached fruit. The lack of a climacteric rise in respiration of attached sweet pepper fruit in this experiment and attached fruit of melons (Miccolis and Saltveit, 1991; Shellie and Saltveit, 1993) and tomato (Saltveit, 1993) although not substantiated by the results of Andrews (1995) suggests that CO_2 generation in attached fruit could be obscured by photosynthesis of the fruit (Knee, 1995).

7.5. Conclusion

Periodic sampling of the internal atmosphere composition of sweet pepper fruit is possible by preparing and sealing an artificial cavity in the fruit. Samples taken by this procedure will give as reliable result with respect to $P^i\text{CO}_2$, $P^i\text{O}_2$ and $P^i\text{C}_2\text{H}_4$ as the conventional technique of gas sampling under water.

The change in colour of sweet pepper fruit of the cv. 'Domino' was associated with a pronounced increase in its internal ethylene concentration. Detached fruit were able to ripen to the same level as attached fruit but at a slightly slower rate. Attached fruit produced higher levels of internal C_2H_4 as well as CO_2 coincident with ripening, however, $P^i\text{CO}_2$ progressively declined during ripening in detached fruit although they produced high $P^i\text{C}_2\text{H}_4$ during their ripening phase. The decline in $P^i\text{CO}_2$ and the low peak in $P^i\text{C}_2\text{H}_4$ is due to egress of these gases through the unsealed pedicel end of detached fruit rather than any inherent difference in the ripening of the two group of fruit. Based on the findings of the present study, the sweet pepper cv 'Domino' behaves like a climacteric fruit with respect to its $P^i\text{C}_2\text{H}_4$.

Chapter 8

The physiology of fruit growth, maturity and ripening of sweet pepper (*Capsicum annuum* L.) cv Domino fruit

8.1. Introduction

Sweet pepper fruit are harvested at either the green mature or colouring stage. Field grown peppers are normally commercially harvested at the mature green stage (Lin *et al.*, 1993) while greenhouse grown peppers are harvested at either the green or fully ripe stage (Bakker, 1989a).

Precise determination of the maturity of sweet pepper fruit is difficult at harvest. As a result, products are harvested at different degrees of maturity and even a proportion of the fruits may be immature. Thus, the harvesting of pepper fruits of different maturation picked at the same time is a common problem although they tend to have the same skin colour at harvest. If fruits are picked immature they may not develop acceptable flavour upon ripening (Boonyakiat *et al.*, 1987) which may lead to loss of consumer confidence. Moreover, since fruit growth continues until ripening, their size will also be smaller resulting in a loss of yield to the grower. Therefore, determining the optimum maturity will be of help to both the consumer and the grower. Most of the literature available on maturity of capsicum fruits are subjective evaluations such as visual colour (Lin *et al.*, 1993; Sanchez *et al.*, 1993; Howard *et al.*, 1994) arbitrary size, or days from anthesis (Manandhar *et al.*, 1995; Sanchez *et al.*, 1993). Thus it is important to develop different maturity and quality indices which are more reliable and correlate well with fruit maturity.

There are very few research reports on the physiology of fruit growth and maturity of sweet pepper (Biles *et al.*, 1993b; Serrano *et al.*, 1995). Some have studied the

physical or chemical changes at harvest while others have reported biochemical changes in relation to carbohydrate changes of fruit during maturation and ripening (Nielsen *et al.*, 1991; Wall and Biles, 1993). However, significant physiological changes associated with maturation and ripening may occur before or after commercial harvest and different cultivars may behave differently.

Skin colour, fruit firmness, soluble solids content, acid content, concentration of volatile compounds as well as changes in other chemical constituents have been developed for many commercial commodities as indicator of maturity. These indicators are used to determine harvest time with acceptable flavour characteristics and structural integrity (Meredith *et al.*, 1989; Wills *et al.*, 1989).

Once over harvesting of sweet pepper fruit is desirable from a production cost point of view. However, this technique requires uniform ripening of the fruit. This could be achieved by using chemical ripening agents which accelerate fruit maturity (Batal and Granberry, 1982; Sims *et al.*, 1970). One of the chemical agents which has extensively been used in ripening of capsicum fruit is ethephon (Batal and Granberry, 1982; Conrad and Sundstrom, 1987; Cooksey *et al.*, 1994). However, the drawback of using ethephon is the abscission of leaf and fruit it induces especially at higher concentrations (Conrad and Sundstrom, 1987; Cooksey *et al.*, 1994). The addition of a calcium treatment along with ethephon is required to overcome this problem (Conrad and Sundstrom, 1987) but this is not always successful (Cooksey *et al.*, 1994).

Treatment of fruits with ethylene resulted in more rapid and uniform ripening of a number of fruits (Medlicott *et al.*, 1988; An and Paull, 1990; Arjona and Matta, 1991; Burdon and Sexton, 1993; Murray *et al.*, 1993; Dominguez and Vendrell, 1994; Puig *et al.*, 1996) and degreening of citrus fruits (Hearn, 1991). However, a limited information is available on sweet pepper fruit. The available evidence indicates that ethylene gas was ineffective in degreening pimiento peppers (Lockwood and Vines, 1972).

The objectives of the experiments reported here were:

1. To define the pattern of sweet pepper fruit development and ripening
2. To determine a reliable index of maturity for the fruit.
3. To evaluate the possibility of inducing ripening in sweet pepper fruit with ethylene.

8.2. Materials and Methods

Experiment one: Fruit growth and maturity of sweet pepper fruit

8.2.1. Plant material

Sweet pepper fruit were obtained from plants grown in a greenhouse under trickle irrigation. Fruits were tagged at anthesis to determine their stage of growth and harvested at weekly interval for a total of 11 weeks to determine their growth and maturity. Fifteen fruits were assessed at each harvest period. Details of the plant growing techniques are described in chapter 4.

8.2.2. Fruit growth attributes

8.2.2.1. Fruit fresh weight

Fruit fresh weight was determined by transporting the harvested fruit in closed plastic bag to the laboratory. The weight of fruit was estimated to the nearest 0.001 g for small fruit and 0.01 g for larger ones.

8.2.2.2. Fruit diameter and length

These two attributes were determined by measuring the longest diameter and length of the fruit with digital vernier callipers.

8.2.2.3. Fruit volume

Fruit volume was measured by immersing the fruit in water filled cylinder and estimating the amount of water displaced (Lownds *et al.*, 1993), and it was also estimated by linear regression from measurement of diameter and length assuming the fruit to be a cylindrical (Marcelis and Hofman-Eijer, 1995) using the following formula:

$$V = \frac{\pi LD^2}{4}$$

[8.1]

where V is volume (cm³); π is pi (3.142); L is length (cm); D is diameter (cm).

8.2.2.4. Pericarp thickness

Fruit pericarp thickness was measured using digital vernier calliper.

8.2.3. Measurement of maturity attributes

8.2.3.1. Fruit skin colour

Fruit skin colour was measured at three positions on the fruit surface representing shoulder, equatorial and base of the external surface of the fruit. Colour was measured using a Minolta Chromameter (Model CR-100 Minolta Camera Ltd, Osaka, Japan) with LCH model calibrated with standard white plate (C Y=87.5, x=0.308, y=0.315) (Francis, 1990). Skin colour was expressed as lightness chroma and hue

angle. The three readings from each fruit were averaged prior to data analysis.

8.2.3.2. Fruit firmness

Fruit firmness (the force required to penetrate the tissue in kg) was measured at the locular space and carpel wall of the fruit at the equatorial region (Showalter, 1973). It was measured using Effegi penetrometer fitted with a 11.1 mm diameter probe and the readings were converted to Newton (N) by multiplying by 9.80665 ms^{-2} (Soule, 1985).

8.2.3.3. Total Soluble Solids (TSS)

Soluble solid concentration (%) of the expressed juice was determined using a hand-held Atago N-10 refractometer (Model N_TMcCormic Fruit Tech, brix range 0-10% at 20°C). The juice from the pericarp of whole fruit squeezed with a garlic press was used for estimation of TSS.

The refractometer was initially calibrated using distilled water and the prism was wiped with tissue paper and distilled water after each run. The data presented is an average of two readings from each fruit sample.

8.2.3.4. Titratable acidity

A 1 ml sample juice was mixed with 50 ml of distilled water. Acidity was determined by titration against 0.1 N NaOH to a pH of 8.3 end point using a Mettler DL 21 autotitrator and were expressed as % anhydrous citric acid (Mitchell *et al.*, 1992).

$$\% \text{Citric acid} = \frac{\text{ml NaOH} * \text{Normality of NaOH} * 64}{1 \text{ml juice} * 10}$$

[8.2]

64 = Molecular weight of citric acid anhydrous / 3

8.2.3.5. Fruit respiration and ethylene production

The fruit were allowed to equilibrate in air at 20°C for at least 1 h before measurements were taken. A single fruit was enclosed in a plastic jar with a capacity of 1100 ml. After the jars were sealed for 1 h at 20°C, 1 ml each of the head space gas from each of the jars was withdrawn and injected into either GC model Shimadzu (GC-8A) or photovac model 10A10 gas chromatograph for determination of CO₂ and C₂H₄ concentrations respectively.

8.2.3.6. Internal gas samples of carbon dioxide and ethylene

The internal CO₂ and C₂H₄ concentration of fruit harvested at various stages of growth was determined by immersing fruits under water and extracting gas from the fruit cavity (Saltveit, 1982). The gas samples were analyzed as described above.

8.2.4. Prediction of fruit growth

Fruit growth data from this experiment was used to develop a model predicting sweet pepper fruit fresh weight and volume from non destructive measurement of fruit diameter, length and volume. Model fitting was done as described by Myers (1990). Instead of partitioning the data into fitting and predicting samples, the whole data set

was used as the fitting sample and the data of fruit growth in chapter 6 was used for the validation.

Experiment two: Effects of ethylene treatment on respiration and colour change of sweet pepper fruit

8.2.5. Fruit materials

Sweet pepper plants of the cv Domino were grown in NFT system at an EC of 2 under standard greenhouse conditions from early March to November, 1995. Flowers were tagged at anthesis so that the stage of development of individual fruits was known accurately.

Green mature fruits were harvested between 9.00 and 11.00 hours 63 days after anthesis. Similarly, field grown half ripe (approximately 50% of the fruit skin colour red or brown) fruit of the same cv were supplied from Gisborne. On arrival at the laboratory, the fruit were sorted out to maintain uniform size and stage of ripeness. The fruit were surface treated with 0.25% (v/v) solution of Sodium hypochlorite (Rahaman *et al.*, 1993) to reduce microbial infection. No such treatment was done to the greenhouse grown green mature fruits.

In a second experiment fruit of the sweet pepper cv Evidence of different maturity class were used to determine the effect of ethylene treatment on their colour change. Fruit were hand harvested from the local greenhouse grower and transported to the laboratory within 5 h. Fruit were separated into immature green (surface colour light green weighing an average of 120 g, mature green (entire surface dark green), quarter red (1/4 of the skin colour red and the rest green), and half ripe.

8.2.6. Ethylene treatment in a static system

Ten sweet pepper fruit of the cv Domino were kept for 24 hr in a 20 l air tight chamber at 20°C to which C_2H_4 at a concentration of 1000 $\mu l.l^{-1}$ was injected (Lallu *et al.*, 1989) immediately after closure using a hypodermic needle through the serum stopper. Another batch of the same fruit were kept in ethylene free chamber containing $KMNO_4$ crystals to absorb any trace amount of ethylene in the chamber.

The field grown fruit were treated in a similar manner for 24 h at 20°C in 3 sealed containers each containing 6 fruits.

Treated and control fruits were then stored at 20°C and 50-60% RH for 1 week for further ripening.

8.2.7. Ethylene treatment in a flow system

Ten sweet pepper fruit replicate⁻¹ maturity⁻¹ of the cv Evidence were placed in a 20 l chamber at 20°C fitted with input and output ports in series. The chambers were ventilated with a constant flow of moist air (2 l min⁻¹) containing 100 $\mu l.l^{-1}$ ethylene. Ethylene was premixed in a cylinder with air and the desired concentration was diluted into the air stream by means of a fine metering needle valve (Poole and Joyce, 1993). The treatments were replicated 3 times.

Control fruits were treated continuously with ethylene free moist air in a separate room kept at 20°C. The C_2H_4 levels were monitored periodically in control chambers but were not detected.

8.2.8. Fruit Assessment

Fruits were assessed daily for colour change using a Minolta chromameter as described in section 8.2.3.1. In addition, respiration and internal CO₂ concentrations were also measured daily for greenhouse grown Domino fruits of 5 fruit treatment¹. At the termination of the experiment, TSS, fruit firmness, and acidity were also evaluated on seven fruit treatment¹.

The field grown Domino fruit were also assessed for internal ethylene and internal CO₂ concentrations at the end of the experiment.

8.2.9. Statistical Procedure

A repeated measure analysis was conducted to compare variate means of the fruit using SAS General Linear Model procedure (SAS Institute, 1988). Covariation among the variates measured for the fruit was identified by the matrix of pairwise correlation coefficients among the 60 individual fruit after maturity. Principal component analysis was made using the correlation matrix.

Difference between control and ethylene treated fruit were tested by the student's t-test for paired samples. The significance of ethylene treatment and maturity stage on fruit colour change were evaluated using a completely randomized design and SAS General Linear Model procedure (SAS Institute, 1988). Treatment mean separation was done using the Duncan's Multiple range test.

8.3. Results

8.3.1. Fruit growth pattern

Sweet pepper fruit fresh weight and volume growth was predominantly linear until 8 weeks after anthesis (Fig. 8.1A and B). The maximum size was noted 9 weeks after anthesis after which growth slowed down or stopped. Fitting Richards function to the \log_e fresh weight (Fig. 8.2A) showed a declining rate through out the growth period (Fig. 8.2B).

Fruit growth in terms of length and diameter showed that sweet pepper fruit increase in length faster than diameter in the early growth period (Fig. 8.1C and D). This in turn gave the fruit an elongated shape at an early stage of fruit growth period with L/D ratio of 1.5 (8.5D). Three weeks after anthesis the fruit has attained almost $3/4^{\text{th}}$ of its final length. The length growth however, increases with age until 10 weeks after anthesis at a reduced rate. On the other hand, the diameter growth progressed slowly at the early stage of fruit development. This continued at a constant rate until 6 weeks after anthesis. At 8 weeks after anthesis the fruit grew towards its final diameter after that it levelled off. At this stage the shape of the fruit was almost spherical to ovoid with L/D ratio ranging from 1.08 at 8 WAA to 1.18 at 11 WAA (Fig. 8.5D).

Fruit fresh weight was highly positively correlated with the physical growth attributes such as diameter, length, and volume $r=0.93, 0.81$ and 0.99 at $P \leq 0.001$ respectively. From this relationship, it was possible to estimate and predict the growth of a fruit in terms of fresh weight from the measurement of fruit diameter (Fig. 8.3 a and b). It was shown that fresh weight had a positive relationship with fruit diameter.

Fruit fresh weight could also be estimated from the measurement of fruit volume (data not shown) due to their high correlation ($r=0.99$). On the other hand since

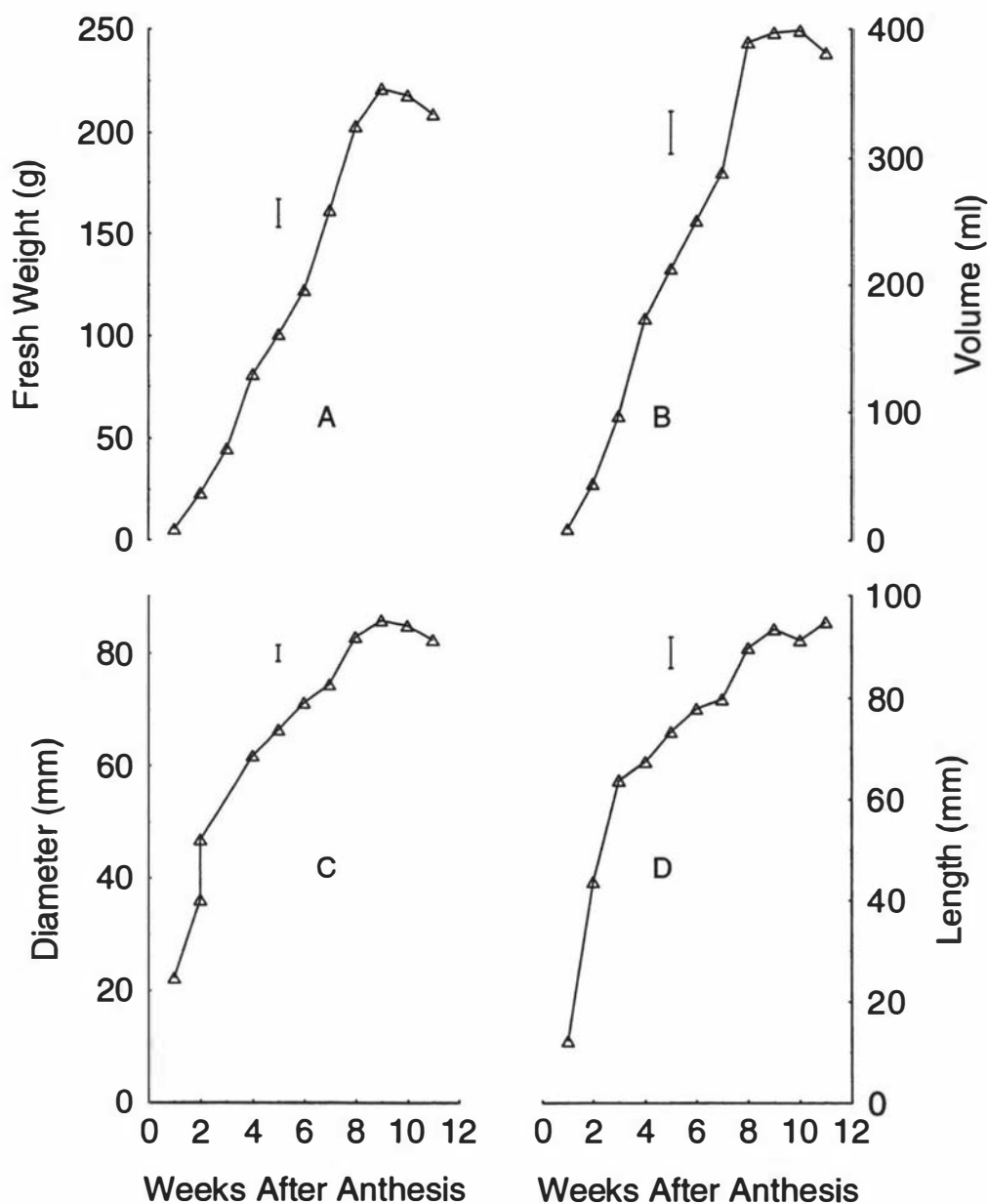


Fig. 8.1. Cumulative growth of sweet pepper fruit in terms of fresh weight (A) volume (B) diameter (C) and length (D). Each data point represents an average of 15 fruit. Vertical bars represent pooled standard error of means.

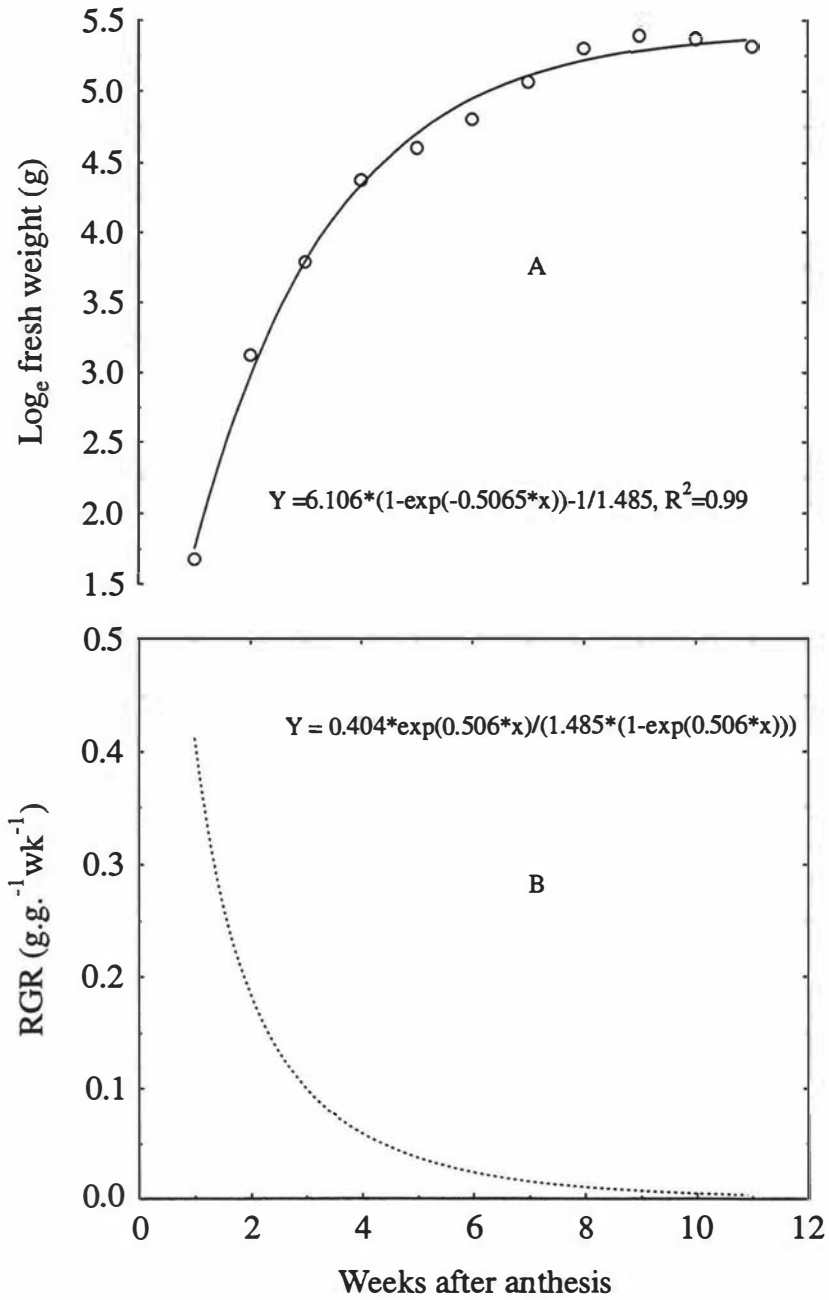


Fig 8.2: Cumulative growth of log_e Fw (A) and RGR (B) of sweet pepper fruit over time. Each data point is an average of 15 fruit. Data fitted to Richards function.

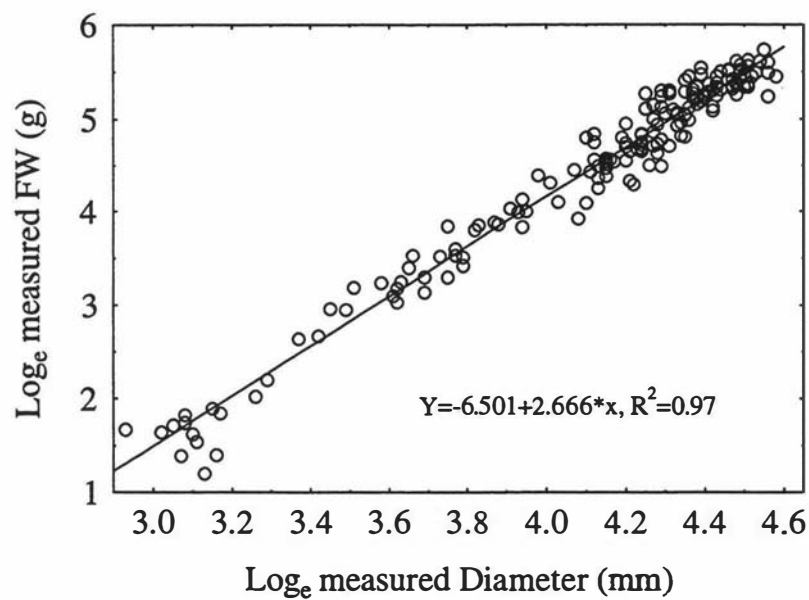


Fig 8.3a: Fitting data of fresh weight and diameter of sweet pepper fruit. Each data point represents a single fruit, n=165.

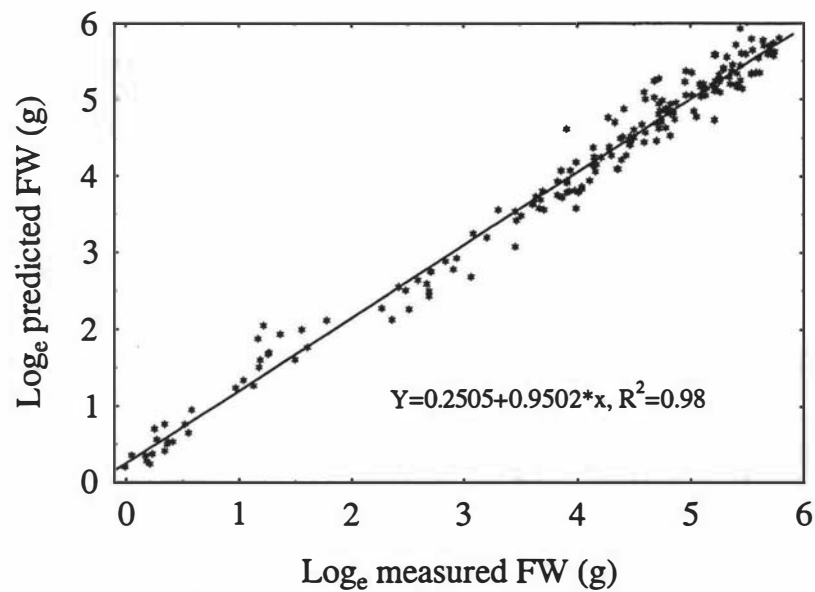


Fig 8.3b: Validation data of measured and predicted fresh weight of sweet pepper fruit calculated from diameter measurement. Each data point represents a single fruit, n=195.

volume is mathematically related to fruit length and diameter (Equation 8.1) this relationship was checked with the data of fruit volume by water displacement and it was found that there was good association between the values (Fig. 8.4a). From this relationship it was possible to estimate fruit fresh weight from calculated fruit volume (Fig. 8.4b).

8.3.2. Physicochemical changes

8.3.2.1. Fruit firmness

Fruit firmness increased with fruit size (Fig.8.5B). In this respect, the pericarp thickness which increased with fruit age (Fig. 8.5A) was closely correlated with fruit firmness ($r=0.82$). Fruit firmness showed a slight reduction towards the final harvest.

8.3.2.2. Total Soluble Solids content

The TSS remained low and essentially the same from anthesis until 7 weeks after anthesis at about 5.6 (Fig. 8.5C). There was a sharp rise in TSS at 9 weeks after anthesis which continued to increase at a reduced rate until the final measurement which reached on the average 8.2. The TSS content had a highly significant negative correlation with hue angle values ($r=-0.81$).

8.3.2.3. Colour change

Sweet pepper fruit remained green for a considerable period of time before they started to change colour. There was no change in hue angle between 1 and 7 weeks after anthesis (Fig. 8.6C). A slight reduction in hue angle was observed 8 WAA which then progressively declined. Rapid colour change was observed between 8 and

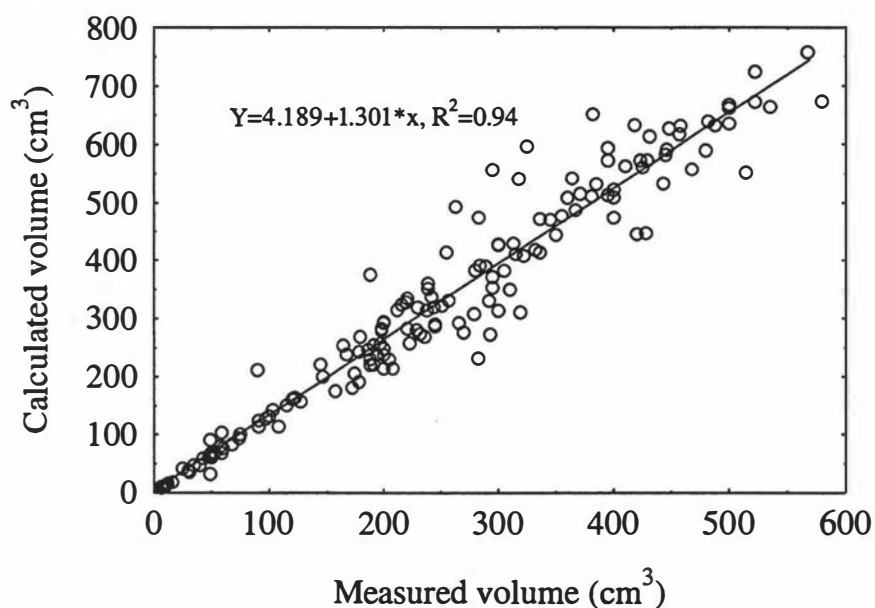


Fig 8.4a: Sweet pepper fruit volume calculated from length and diameter with measured volume by water displacement technique. Each data point represents a single fruit, n=165.

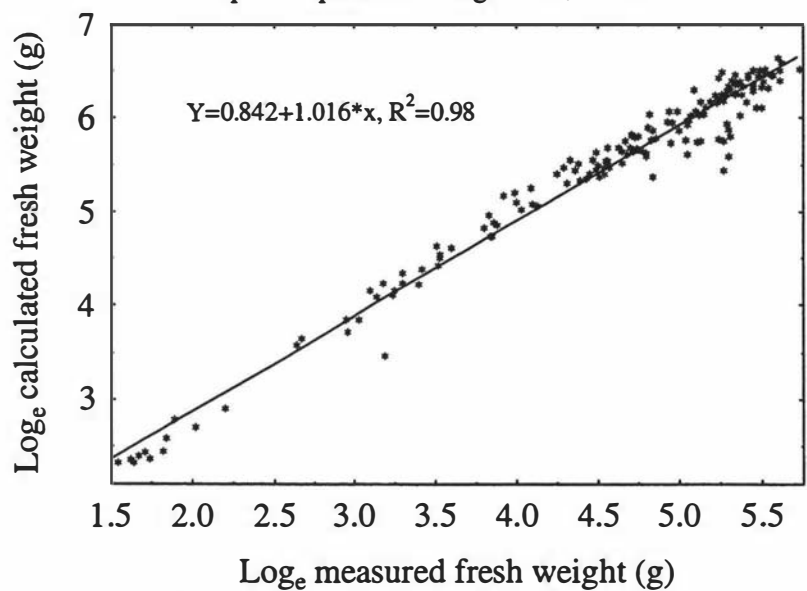


Fig 8.4b: Measured fresh weight and calculated fresh weight from length and diameter measurement of sweet pepper fruit. Each data point represents a single fruit, n=165.

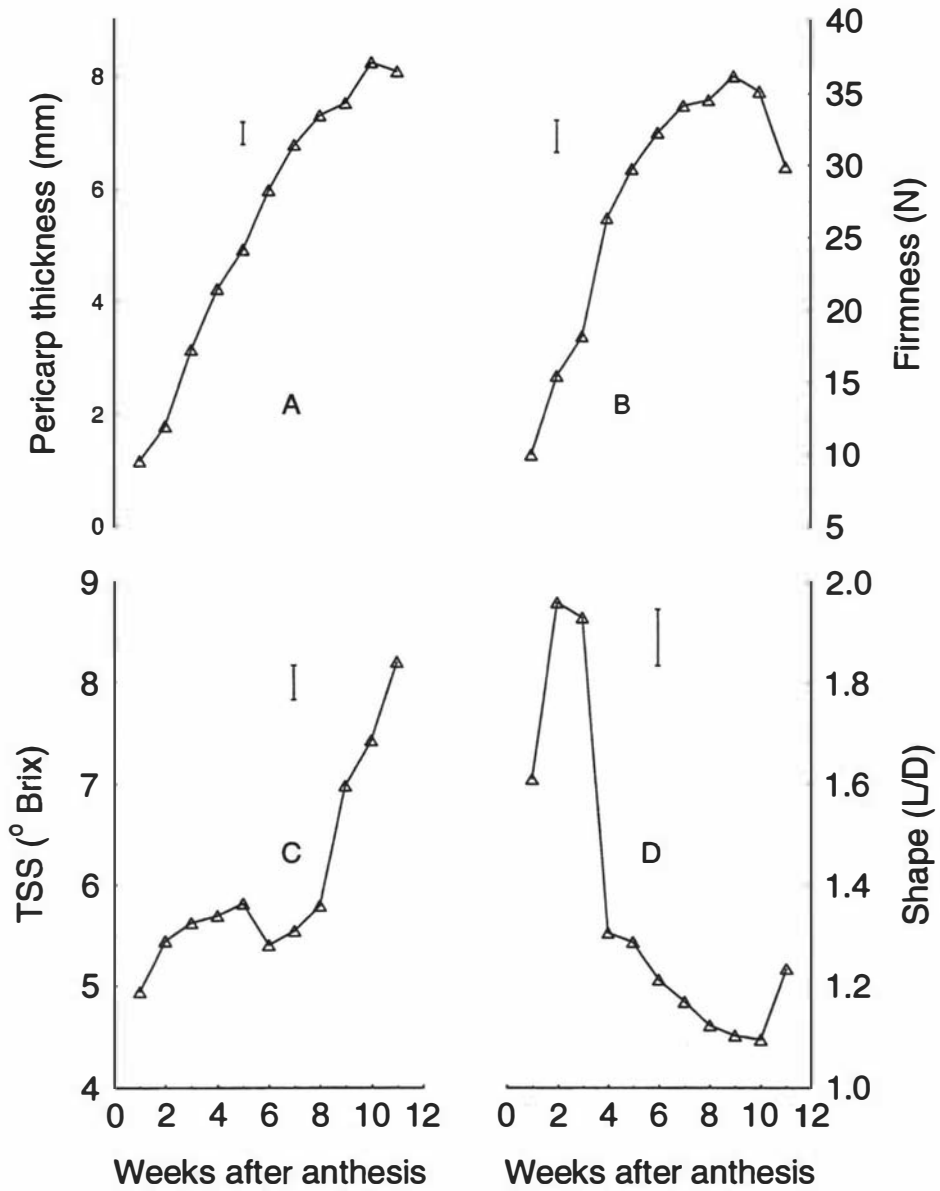


Fig. 8.5. Fruit pericarp thickness (A) firmness (B) TSS content (C) and shape (D) of sweet pepper fruit during ontogeny. Each data point represents an average of 15 fruit. Vertical bars represent pooled standard error of means.

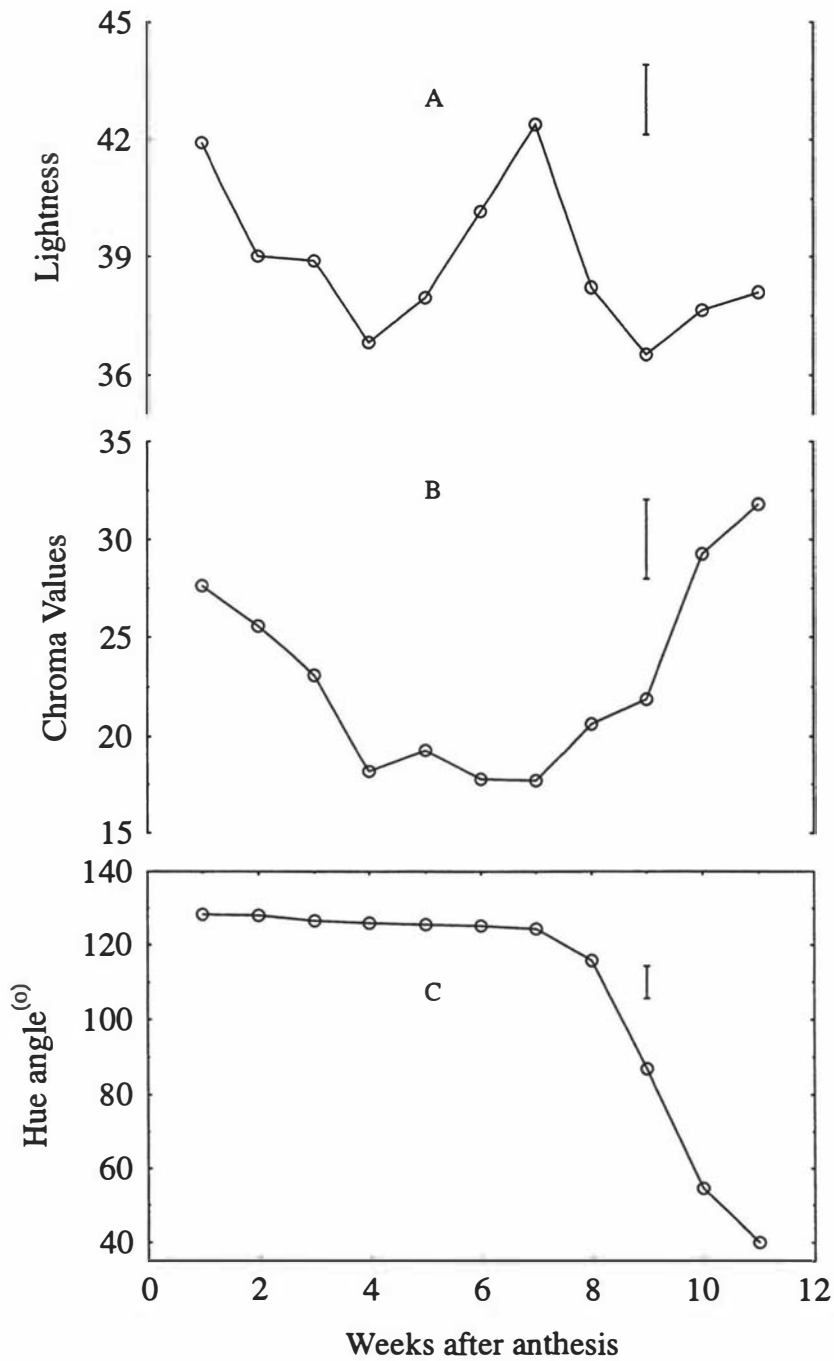


Fig 8.6: Sweet pepper fruit lightness (A) chroma (B) and hue angle (C) plotted against time. Each data point is an average of 15 fruit. Vertical lines represent pooled standard error of means.

9 WAA.

The colour intensity (chroma) of fruit was relatively higher in young fruit possibly as a result of chlorophyll build up (Fig. 8.6B). It reduced gradually until 4 WAA and remained at the same level until 7 WAA. Chroma values started to increase after 8 WAA. On the other hand, lightness of fruit colour showed very little and inconsistent change during fruit growth and development (Fig. 8.6A).

8.3.3. Physiological changes

Young sweet pepper fruit during the early stage of fruit growth were characterized by having high respiration rate and ethylene production (Fig. 8.7 A and B). As the fruit increased in size both the respiration rate and ethylene production declined up to 5 or 7 WAA respectively. The ethylene production rate remained the same between 5 to 7 WAA. Around 8 to 9 WAA there was a slight but significant increase in the level of both respiration and ethylene production of fruit before it finally declined.

Estimation of the internal concentration of CO₂ showed a similar trend to fruit respiration (Fig. 8.7 C and D). The CO₂ concentration declined steadily until 7 WAA before a minor peak at 8 WAA. On the other hand, the ethylene concentration was small during the early stage of fruit growth and development. It exhibited a sharp increase 7 WAA after anthesis with the peak concentration at 8 WAA. It declined afterwards.

8.3.4. Assessment of fruit maturity

Assessment of the relationship between the physicochemical attributes with fruit maturity was made using correlation analysis and principal component analysis

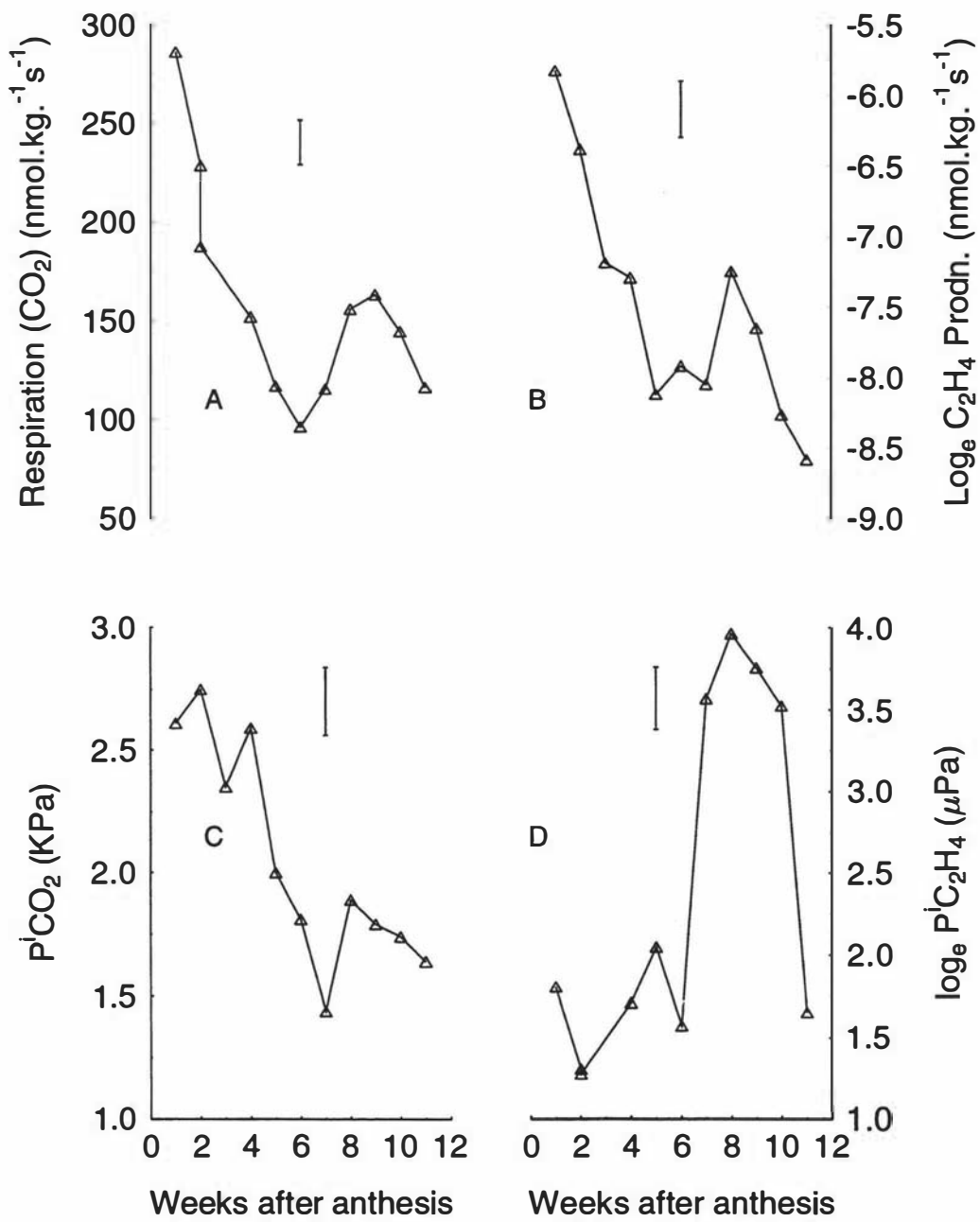


Fig. 8.7. Sweet pepper fruit respiration (A) Log_e ethylene production (B) PⁱCO₂ (C) and Log_e PⁱC₂H₄ (D) concentrations during ontogeny. Each data point represents an average of 15 fruit. Vertical bars represent pooled standard error of means.

Table 8.1. Correlation matrix between the variables analyzed, n=60

	WAA	FW	Chroma	Hue	PiC ₂ H ₄	PiCO ₂	TSS	Pericarp	Firmness
WAA	1.000								
FW	0.0426	1.000							
Chroma	0.4686 (0.0002)*	0.09104	1.000						
Hue	-0.73653 (0.0001)	-0.17728	-0.61998 (0.0001)	1.000					
PiC ₂ H ₄	-0.31469 (0.014)	0.07569	-0.0904	0.20795	1.000				
PiCO ₂	-0.1982	-0.23081 (0.076)	-0.0076	0.01655	0.25467 (0.0496)	1.000			
TSS	0.75857 (0.0001)	-0.04978	0.5172 (0.0001)	-0.79769 (0.0001)	-0.34349 (0.0072)	-0.05208	1.000		
Pericarp	0.35999 (0.0047)	0.36856 (0.0038)	0.1344	-0.32908 (0.0102)	0.10711	0.05208	0.10786	1.000	
Firmness	-0.30125 (0.019)	0.1034	0.38644 (0.0023)	0.50831 (0.0001)	0.0323	-0.02237	-0.42388 (0.0007)	-0.03485	1.000

* values in brackets are the level of significance

(PCA). PCA allows a global study of the criteria which describe the ripening process thereby reducing the number of explanatory variables of the experiment by finding a linear combinations of those variables that explain most of the variability in the data. The correlation matrix (Table 8.1) between variables shows significant correlation between, hue and WAA, hue and chroma, hue and brix, hue and firmness, and a slight but significant correlation between hue and pericarp thickness. TSS was significantly correlated with WAA, chroma, hue and slightly but significantly correlated with PC_2H_4 and fruit firmness.

Figure 8.8 shows the PCA, based on the correlation presented in Table 8.1. The length of each vector from (0, 0) is proportional to its contribution to the principal components (Camara et. al., 1993). The first two components represent more than half of the variance of the system (Table 8.2).

Table 8.3. shows the correlation coefficients of the variables with the first two axes. The values in each column give the weights of the linear combination forming each principal component. The first PC is closely related to either negatively or positively to WAA, Chroma, hue, TSS and firmness. The second PC is connected with fresh weight and, pericarp thickness.

8.3.5. Effect of ethylene treatment on colour change

Mature green greenhouse grown sweet pepper fruits treated with $1000 \mu\text{l.l}^{-1}$ changed colour more rapidly at 20°C than control fruit (Fig. 8.9C). Colour change was visible 48 h after treatment and the rate progressively increased with time until it levelled off on the 6th day when the experiment was terminated as most of the fruit were red. During the same period control fruit remained unchanged until the 4th day when it started to decline very slowly. At the end of the experiment the average hue angle values were 92 (yellow) and 55 (yellow/Red) for control and treated fruit respectively. In line with the decline in hue angle values, lightness and chroma values

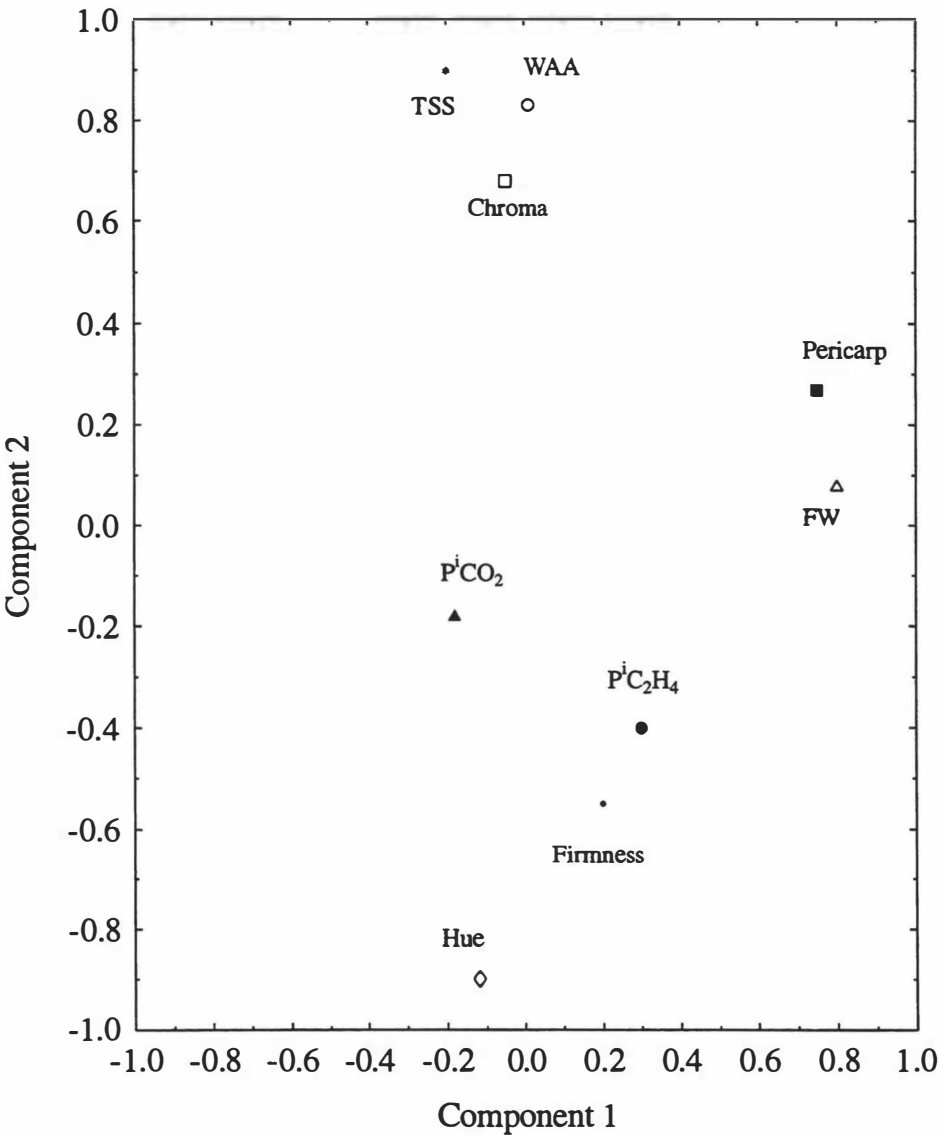


Fig. 8.8: Principal component analysis of the physiochemical and physiological attributes of sweet pepper fruit during maturity and ripening. Biplot of the first two principal components.

Table 8.2. Percentage of variance explained by each principal component

Component number	Percentage of variance	Cumulative percentage
PC 1	38.33	38.33
PC 2	16.25	54.58
PC 3	14.68	69.26
PC 4	9.32	78.58
PC 5	6.93	85.51
PC 6	6.15	91.66
PC 7	4.88	96.54
PC 8	1.94	98.49
PC 9	1.51	100.00

Table 8.3. Correlation coefficient of variables with the two principal components

	PC 1	PC 2
WAA	0.86094 (0.0001) ^x	0.04441
FW	0.11901	0.82030 (0.0001)
Chroma	0.70899 (0.0001)	-0.01430
Hue	-0.92487 (0.0001)	-0.07104
PiC ₂ H ₄	-0.34114 (0.0076)	0.34015 (0.0078)
PiCO ₂	-0.13115	-0.14999
TSS	0.87806 (0.0001)	-0.21703 (0.095)
Pericarp	0.33652 (0.0086)	0.72624 (0.0001)
Firmness	-0.56456 (0.0001)	0.26370 (0.0418)

^x values in brackets are the level of significance

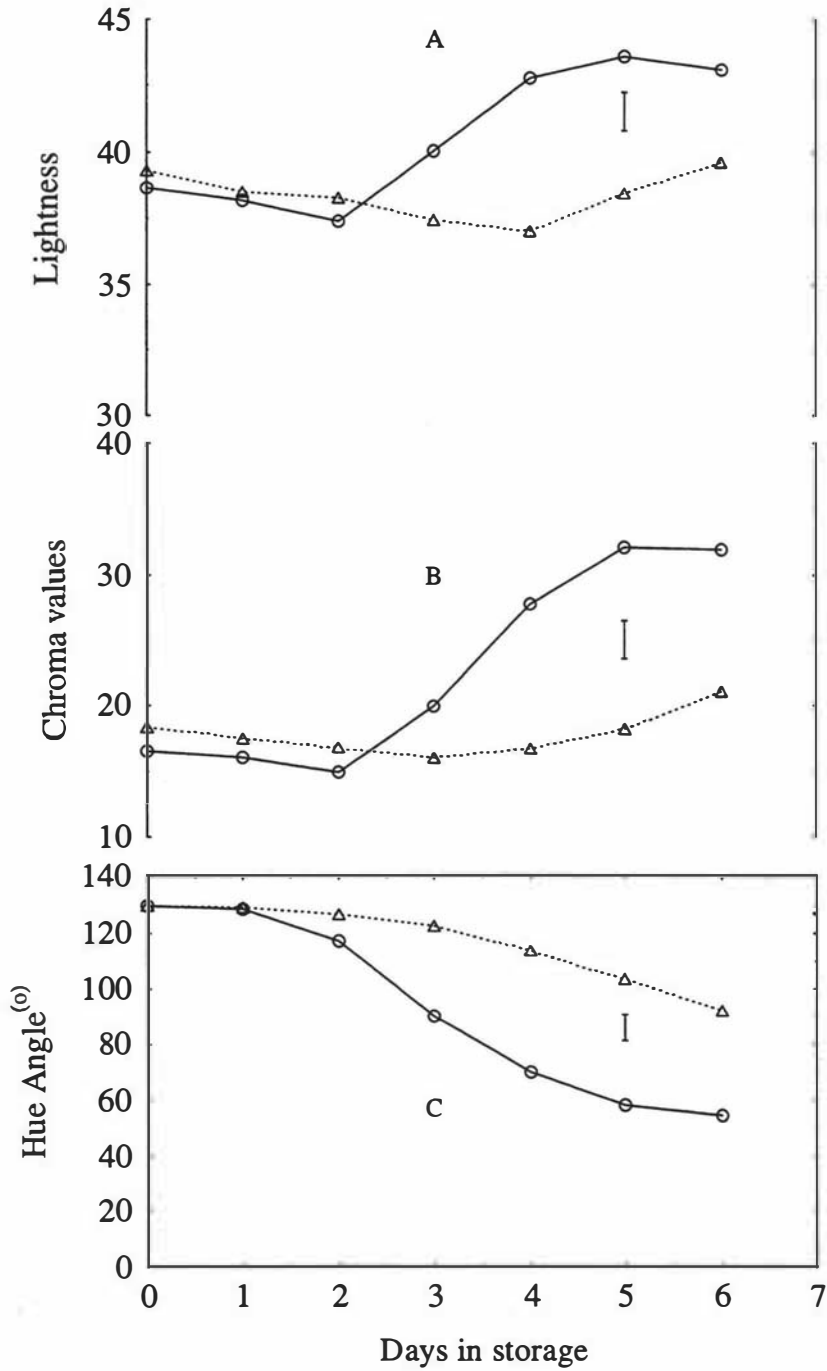


Fig 8.9: Lightness(A) Chroma (B) and Hue angle values (C) of sweet pepper fruit over time as a result of ethylene treatment. Each data point is an average of 10 fruit. Vertical lines represent pooled standard error of means. Treated (O), Control (Δ).

increased with time (Figs. 8.9A and B). The changes in lightness and chroma were more early and evident in treated fruit than control which shows an increase in the colour intensity of the treated fruit.

Comparison of ethylene treated and control fruit with plant ripened fruits of similar age revealed that plant ripened fruit appeared to be relatively less ripe than either control or treated fruit (Fig. 8.10 A B C). In terms of colour change, ethylene treated fruit showed a more advanced colour change than both control and plant ripened fruit.

In a parallel experiment half ripened field grown sweet pepper fruits of the same cultivar responded positively but with less marked effect to ethylene treatment (Fig. 8.11). It was shown that ethylene treatment didn't have a significant effect on the lightness and chroma of both treated and control fruit (8.11 A and B). The hue angle values although decreasing steadily, the difference was noted only on the 6th day after treatment (Fig. 8.11C).

Studies on the effect of ethylene treatment and fruit maturity stage on the cv Evidence revealed that ethylene treatment had no significant effect on the colour attributes (LCH) evaluated irrespective of maturity stage (Fig. 8.12). In the absence of statistically significant effect the data was pooled to evaluate the effects of maturity on colour change.

Lightness had a higher value in immature and mature green fruits implying less degradation of chlorophyll than quarter or half ripe fruit (Fig. 8.13A). Similarly, the chroma values also were higher in the latter part of the ripening phase in the more advanced group than either immature or mature fruit (Fig. 8.13B). On the other hand, the hue angle values declined relatively rapidly in half and quarter ripe fruits than mature or immature fruit (Fig. 8.13C).

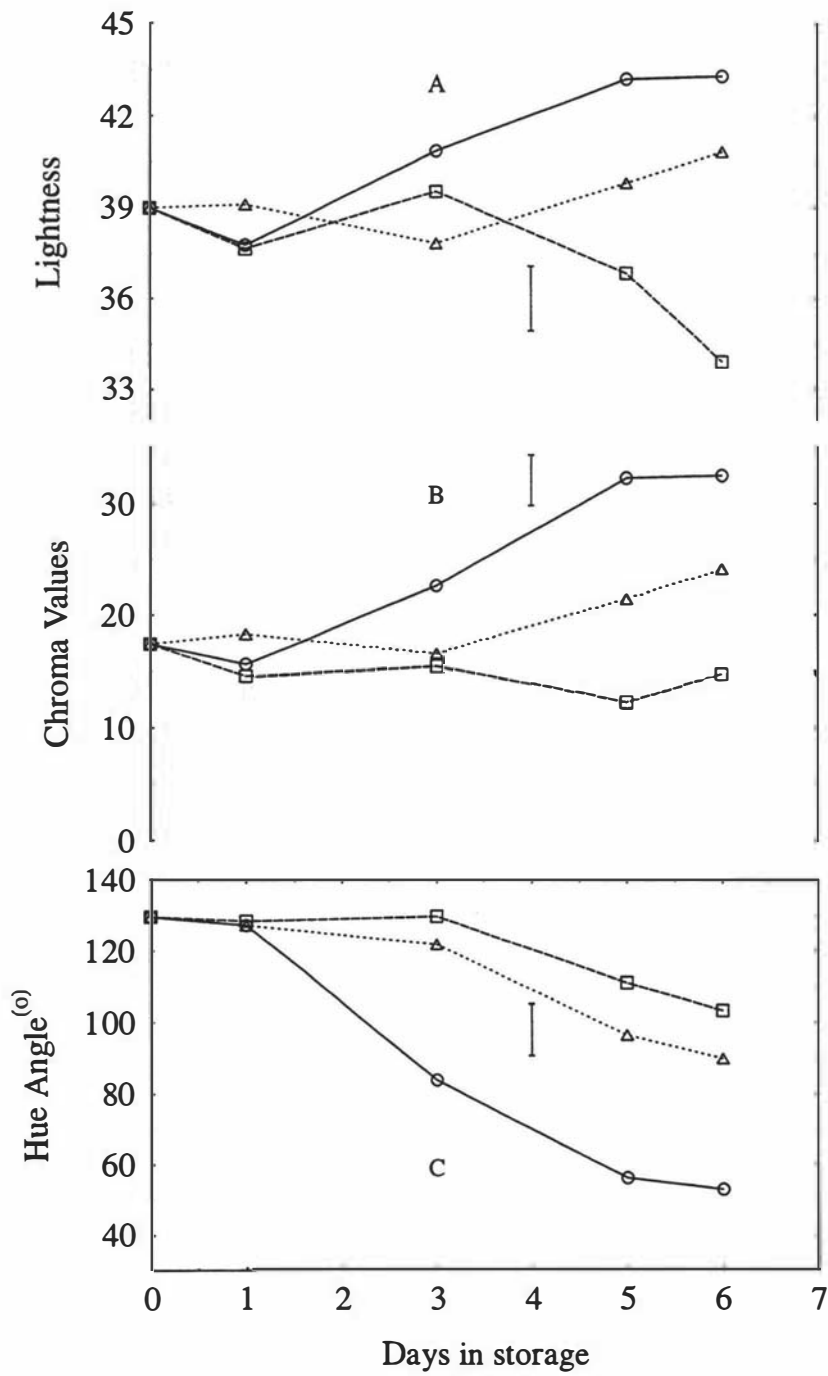


Fig 8.10: Lightness(A) Chroma (B) and Hue angle values (C) of sweet pepper fruit over time as a result of ethylene treatment. Each data point is an average of 10 fruit. Vertical lines represent pooled standard error of means. Treated (O), Control (Δ), Plant Ripe (□).

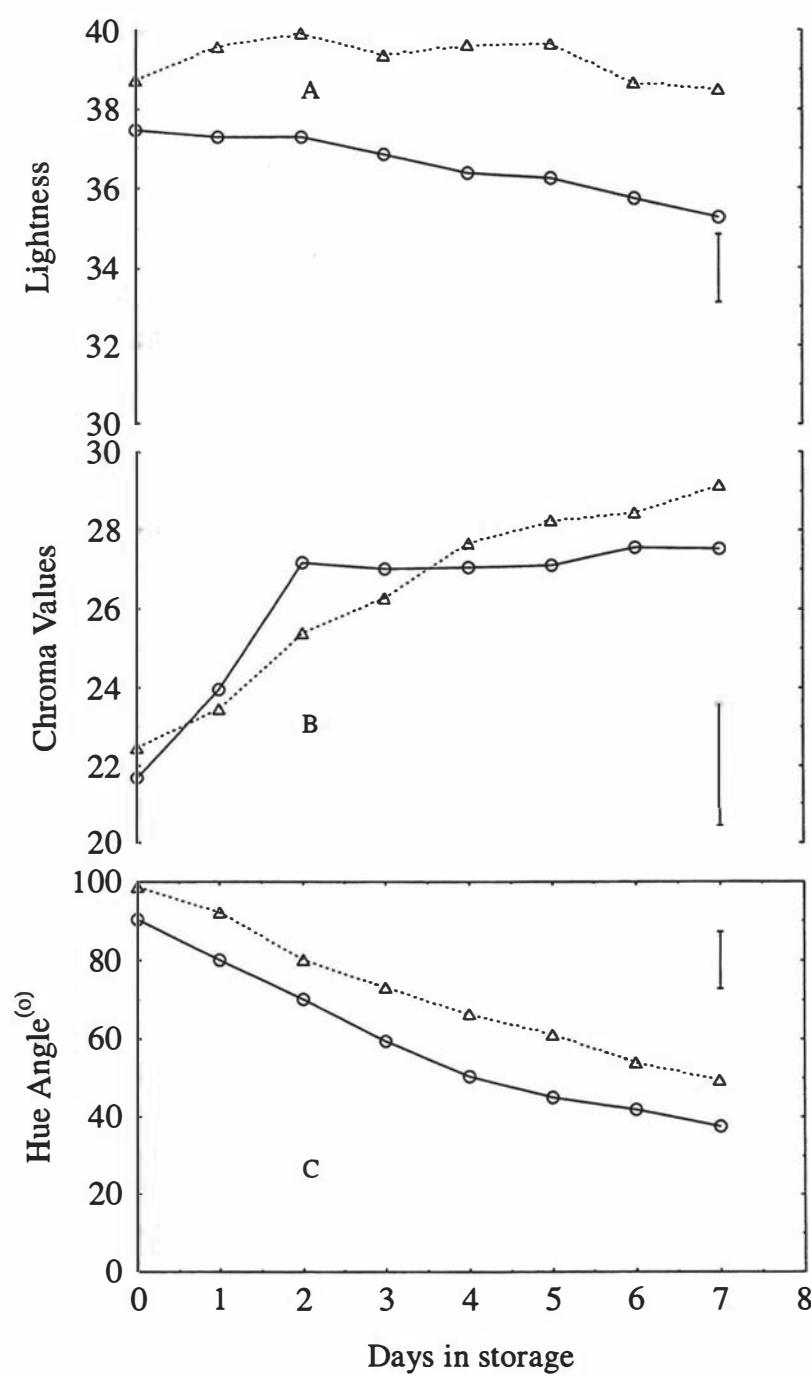


Fig 8.11: Lightness(A) Chroma (B) and Hue angle values (C) of field grown sweet pepper fruit over time as a result of ethylene treatment. Each data point is an average of 18 fruit. Vertical lines represent pooled standard error of means. Treated (O), Control (Δ).

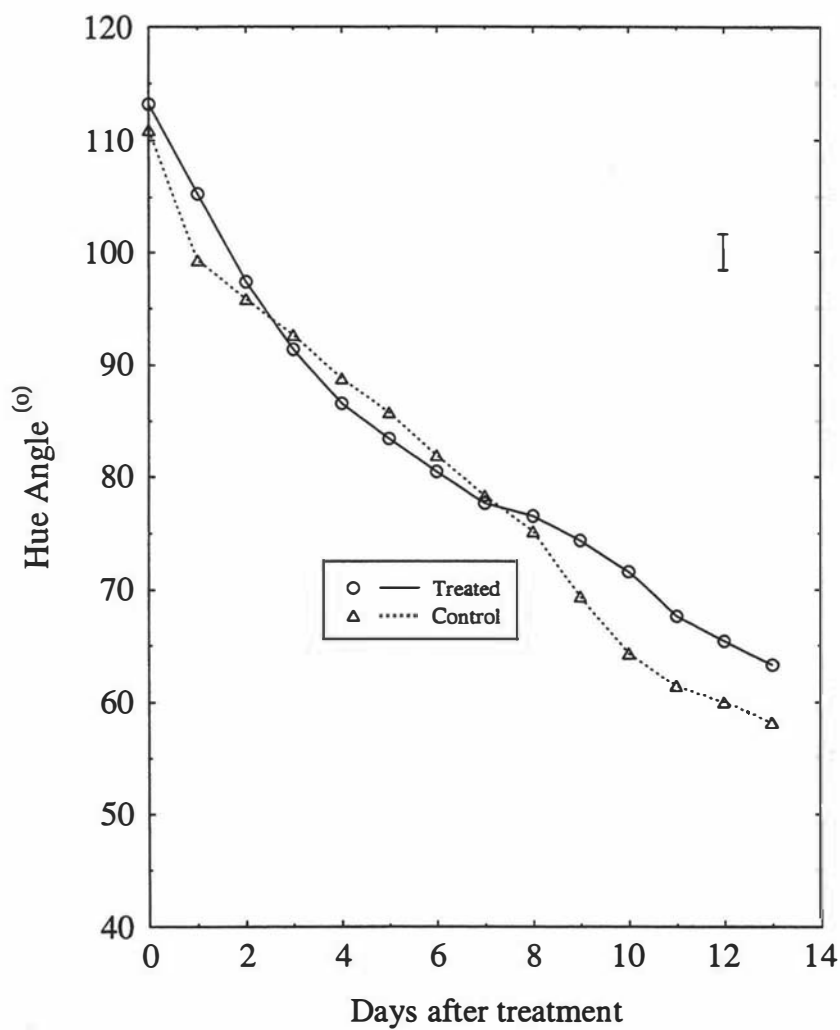


Fig 8.12: Hue angle values of sweet pepper fruit of the cv Evidence over all maturity class in time as a result of ethylene treatment. Each data point is an average of 24 fruit. Vertical bar represents pooled standard error of means.

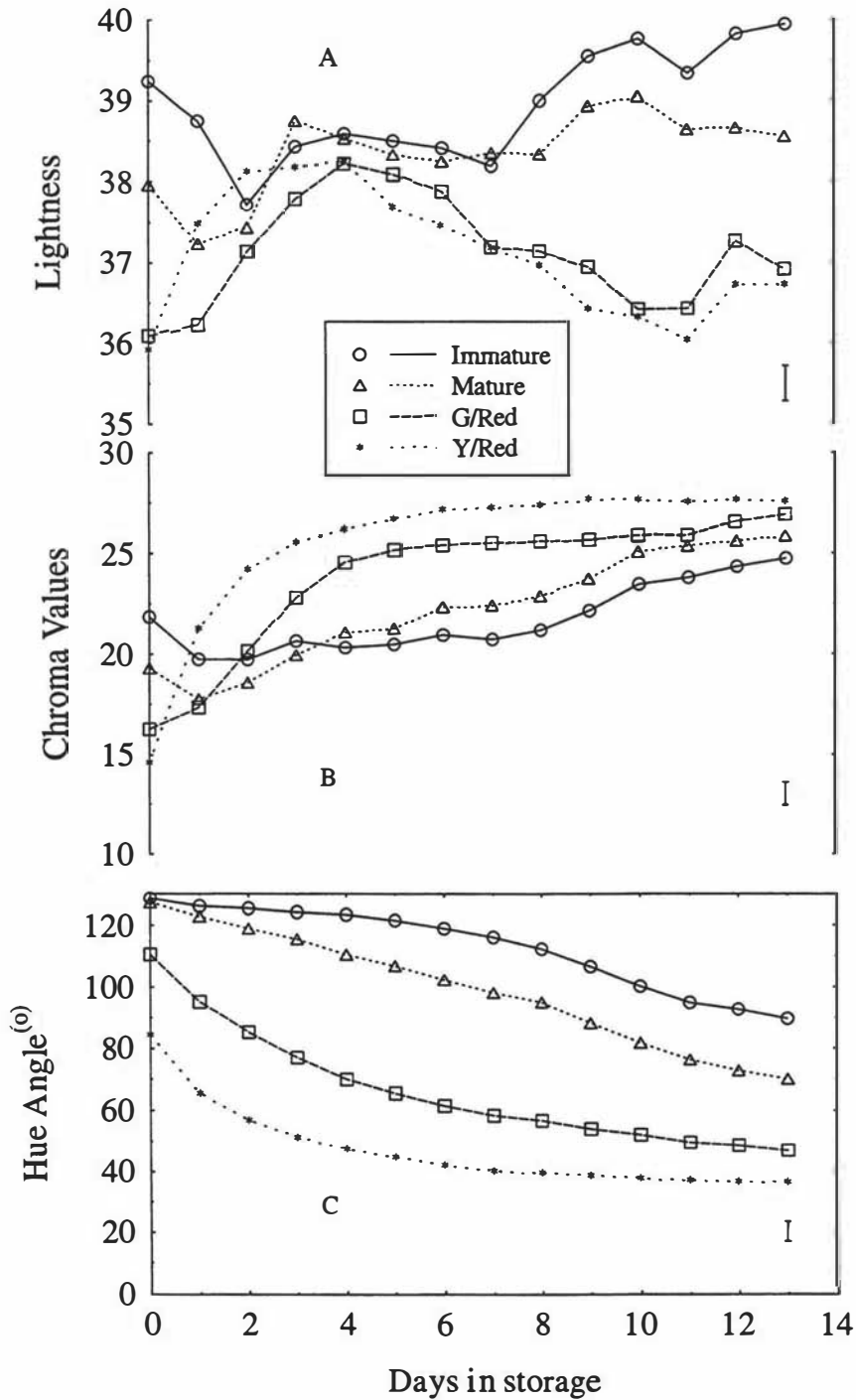


Fig. 8.13: Lightness (A) Chroma (B) and Hue angle values (C) of sweet pepper fruit over time at different maturity period. Each data point is an average of 60 fruit. Vertical lines represent pooled standard error of means.

8.3.6. Rate of Respiration

The rate of CO₂ production increased in both treated and control fruits just after harvest (Fig. 8.14a). Twenty four hours after ethylene treatment, treated fruit had almost twice the rate of respiration as the control fruit. This rate decreased gradually but still with a significant difference between treated and control fruits. Around 5 days after treatment, the two group of fruits appeared to have similar rate of respiration. Fig. 8.14b shows that the respiration rate of plant ripened fruit remained essentially the same for almost 5 days after detached fruits were removed for ethylene treatment until their respiration rate increased significantly at the last day of the experiment. The control and treated fruit on the contrary showed a declining trend after an initially high rate of respiration.

8.3.7. PⁱCO₂ and PⁱC₂H₄

The internal CO₂ concentration of mature green sweet pepper fruit of the cv Domino studied at the end of the experiment revealed that plant ripened fruit had a significantly higher concentration than both treated and control (Fig. 8.15). Likewise, treated fruit showed more PⁱCO₂ than control fruits.

On the other hand, the PⁱCO₂ and PⁱC₂H₄ of half ripe field grown Domino fruit on the last day of the experiment showed that treated fruit had significantly higher PⁱCO₂ as well as PⁱC₂H₄ (Figs. 8.16 A and B).

8.3.8. Fruit Quality

The quality of greenhouse grown ethylene treated fruits determined at the end of the experiment is presented on Table 8.4. It was shown that the change in colour of fruit

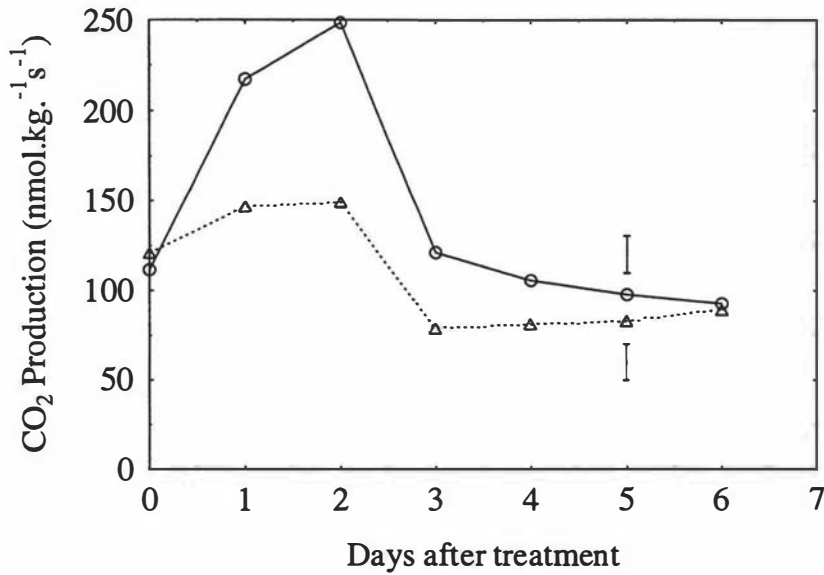


Fig 8.14a: Sweet pepper fruit respiration over time as influenced by ethylene treatment. Each data point is an average of 5 fruit. Vertical bars represent pooled standard error of means. Treated (○), Control (△).

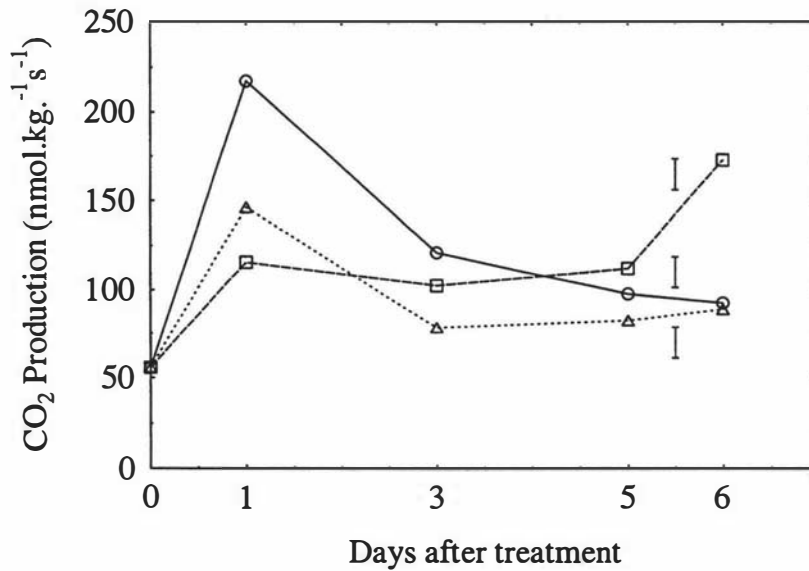


Fig 8.14b: Sweet pepper fruit respiration over time as influenced by ethylene treatment. Each data point is an average of 5 fruit. Vertical lines represent pooled standard error of means. Treated (○), Control (△), Plant Ripe (□).

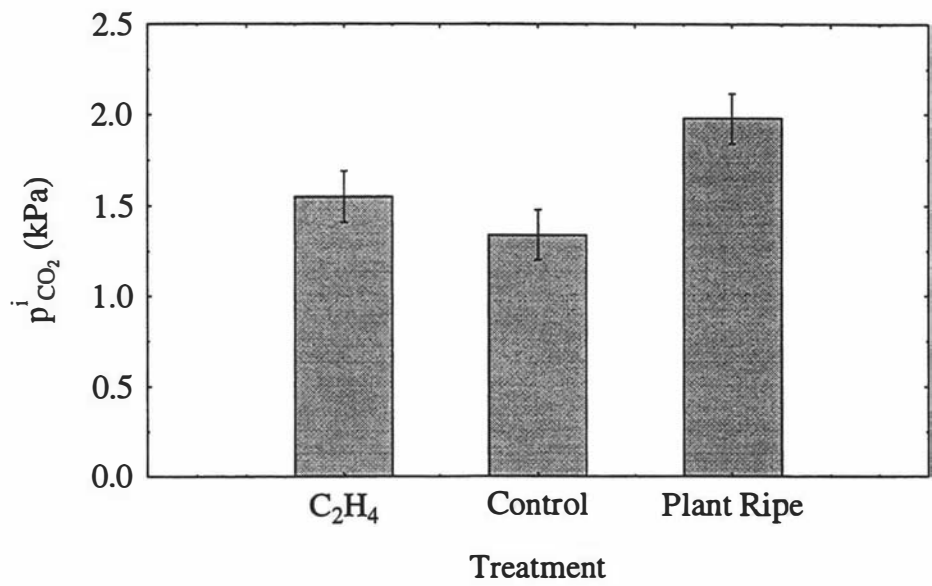


Fig. 8.15: Internal CO_2 concentration of ethylene treated, control and plant ripe greenhouse grown sweet pepper fruit. Each data point is an average of 5 fruit. Vertical bars represent standard error of means.

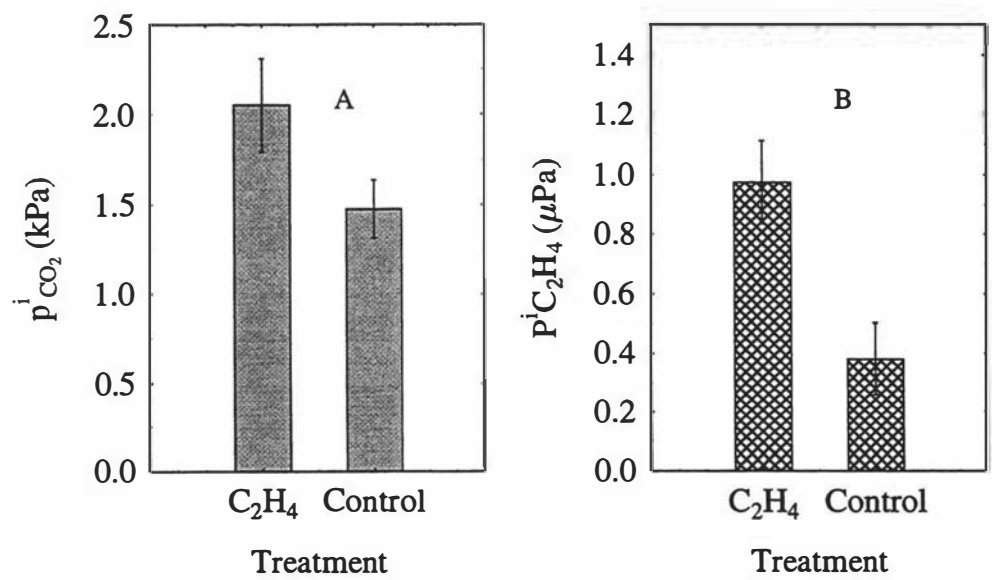


Fig 8.16: Internal CO_2 (A) and internal ethylene (B) concentrations of ethylene treated and control field grown sweet pepper fruit. Each data point is average of 7 fruits. Vertical bars represent standard error of means.

as a result of ethylene treatment was accompanied by improvement in the quality of the fruit. Accordingly, ethylene treated fruit had TSS and acidity contents as high as plant ripened fruit which in turn was significantly higher than control fruit. On the other hand, although the firmness of fruit was lower in detached fruit as compared with plant ripened fruit, both treated and control fruit had similar fruit firmness. This indicates that ethylene treatment had no adverse effect on the sweet pepper fruit quality.

Table 8.4. Fruit quality of sweet pepper fruit of the cv Domino as affected by ethylene treatment compared with plant ripened fruit.

Treatment	Firmness (N)	TSS (°Brix)	Acidity (% Citric acid)
Treated	36.39 b ^y	7.50 a	0.206 ab
Control	33.25 b	6.60 b	0.170 b
Plant ripened	40.50 a	7.58 a	0.224 a
Significant ^x	*	*	*
SEM	1.145	0.281	0.016

^x * significant at $P \leq 0.05$.

^y means followed by the same letter are not significantly different according Duncan's multiple range test.

8.4. Discussion

8.4.1. Fruit growth

Fruit growth of sweet pepper, cv. Domino followed a single sigmoid type curve which is a characteristic of many stoneless fruit (Rhodes, 1980a). There was no peak growth of fruit as such which shows that the fruit grew well until ripening. However, there was no statistically significant difference in fruit weight between those harvested at 8 Weeks After Anthesis (WAA) and later. This shows that harvesting of fruits at this stage is possible as fruit are matured enough to advance in ripening as exhibited in changes in quality of the fruit. As the current crop was grown during the winter/spring season it may appear that growth was slower. However, it is expected that a summer grown crop would grow faster and mature at least a week or two earlier. The faster growth of summer crops is because night temperatures between 18 and 20°C are suitable for pepper flowering and fruit development (Deli and Tiessen, 1969; Rylski, 1973). It is also important to note that radiation level plays an important role in determining the quality of fruits in terms of size, colour development and soluble sugar levels (Jackson, 1980). The number of fruits produced on a plant also influence the size of the harvested fruit (Ali and Kelly, 1992). This in turn is governed by the number of flowers produced and the rate of abortion of flower buds flowers and young fruits (Bakker, 1989b). According to Wein *et al.*, (1989b) environmental factors such as low light intensity, high temperature, water stress and diseases and insect pests are the major causes of flower abortion. Apart from these environmental factors, earlier formed fruit may cause the abortion of latter formed flowers and young fruits (Ruiz and Guardiola, 1994) as the fruit are strong sinks for assimilate which compete with the vegetative parts and with each other (Ali and Kelly, 1992). In the current study, since the plant was allowed to produce as many fruits as possible on a single stem, the above mentioned natural phenomenon is expected to happen which may determine the ultimate size of the harvested fruit. Thus, it may be possible that monitoring the growth of fruit on a single stem and

double stem on a plant may have produced different size group of fruits than the results presented here. However, as reported by Marcelis and Hofman-Eijer (1995) and the present result, the growth pattern is essentially the same.

In the current experiment the fresh weight of sweet pepper fruit was estimated from measurements of fruit diameter and volume. These results indicate that this procedure can successfully be employed to estimate and predict the fresh weight of the fruit using these non-destructive measurements (Fig. 8.3). It was also possible to estimate the fresh weight of fruits from calculated fruit volume due to the close association of measured and calculated volume (Fig. 8.4), but this method slightly over estimates the values. Given the difficulty of measuring fruit volume in the field it could still be used but with caution.

Fruit dimensions (diameter, length, circumference) on kiwifruit was used to estimate volume by some investigators (Prendergast *et al.*, 1987) and by Marcelis and Hofman-Eijer (1995) on sweet pepper. Volume measurement using the water displacement technique is a little cumbersome in the field and may also involves operator bias. Due to the close associations between fruit volume measured by water displacement and calculated volume ($R^2=0.97$) the latter method is more practical in the field.

The spread of the data about the regression line is attributed to the error in measurement of diameter and length, variation in fruit shape and deficiency in describing fruit shape by calculated volume. Notwithstanding this, the R^2 expressed by Fig. 8.4a suggested that it should be possible to estimate fruit volume from measurement of diameter and length and consequently to predict fruit fresh weight (Fig. 8.4b). The practical significance of this result is to predict the growth stage of the fruit in order to determine the rapid fruit growth stage and consequent sensitivity to BER. It will also predict the cessation of fruit growth which signals the approach to fruit maturity.

8.4.2. Colour change during fruit growth and development

Hue angle is an indicator of colour change from green to yellow and red (Little, 1975). This value parallels the colour change associated with the enzymatic degradation of chlorophyll (Brady, 1987).

At an early stage of fruit growth the hue angle values were very high (130), and remained high until 8 WAA after which it declined to a value of 112. As maturity and ripening progressed the hue angle values further decreased to 30 - 40 until the fruit was completely red.

Colour change corresponds to a fall in chlorophyll and an increase in carotenoid synthesis (Pretel *et al.*, 1995). This in turn shows the transformation of chloroplasts to chromoplasts (Leshem *et al.*, 1986). Accordingly, an increase in colour intensity (chroma) was observed with a fall in hue angle values. This increase in chroma values is expected to be a result of an increase in the synthesis of carotenoids. The initially high chroma values also indicate the presence of chlorophyll pigments. On the other hand, lightness appeared to change in an erratic fashion although it also had lower values (darker colour) with maturity of the fruit.

8.4.3. Changes in fruit quality

8.4.3.1. Fruit Firmness

Fruit firmness was taken as an average of two measurements over the carpel walls (which separate the locular space) and that of the locular space. As reported by Showalter (1973) the former was firmer than the latter. The results of this experiment showed that fruit firmness increased with an advance in age of the fruit. This in turn was closely related to the pericarp thickness which also increased with fruit age.

8.4.3.2. Total soluble solids

Sweet pepper fruits had a lower TSS during the early stage of growth and this increases with maturity. The sharp rise in TSS concentration was noted after fruit started to ripen. Sugars are the major components of total soluble solids (Davies and Hobson, 1981). A close positive correlation between the rise in TSS and soluble sugars was reported by Mendelinger (1992). Accordingly, the increase in TSS of sweet pepper fruit could be a result of an increase in hexose sugars which accumulate during fruit ripening (Hubbard and Pharr, 1992; Nielsen *et al.*, 1992). On the other hand, the slight fall in TSS observed 5-6 WAA could be a result of the increase in starch concentration and the corresponding decline in fructose and glucose concentrations as observed by Nielsen *et al.*, (1992).

8.4.3.3. Fruit respiration and ethylene production

The respiration rate was high in young fruit but declined steadily until 7 WAA. Similarly ethylene production was also high in young fruit but declined with fruit age until it showed an increase towards fruit ripening. The high respiration and ethylene production in young fruit is because of active growth of the fruit (Kader, 1987; Gillaspay *et al.*, 1993). Pollination of flowers at an early stage of fruit growth tends to increase ethylene production (Hall and Forsyth, 1967). On the other hand, the internal ethylene concentration was low in young fruit although the production rate was high. This could be a result of high skin permeance in young fruit to this gas. This was later confirmed by the fact that there was high accumulation of internal ethylene and relatively low production rate. The latter case is due to an increase in pericarp thickness and deposition of waxes on the surface of the fruit which leads to a lower skin permeance. Miccolis and Saltveit (1991) suggested that internal ethylene concentration better reflects the potential hormonal activity of C_2H_4 in the tissue than would rates of evolution from the fruit.

Similar high respiration and ethylene production in young fruit was reported by Pretel *et al.*, (1995) in sweet pepper cv. California Wonder and Shiomi *et al.*, (1996) in young passion fruit. However, unlike the cv. California Wonder fruit which showed a steady decline in respiration and the ethylene production, the Domino fruit exhibited an increase in CO₂ and C₂H₄ production with maturity. Pretel *et al.*, (1995) also reported that the varieties didn't respond to propylene treatment. This suggests that the two varieties of sweet pepper may have different ripening behaviour.

8.4.4. Indicators of fruit maturity

The maturity of sweet pepper fruit was determined by a combination of a number of parameters. The study identified surface colour change to predict fruit maturity because of its close association with the other parameters. To be a useful indicator of maturity the parameter must vary substantially and consistently over a range of maturities near the optimal harvest period, so that developmental stages can readily be distinguished (Brown and Walker, 1990). With this respect, ethylene and CO₂ were found to be of little value due to their generally low level production in the fruit.

Total soluble solids was shown to relate closely with colour change and could be used in combination with surface colour. Firmness also had a significant but not strong relationship with both surface colour change or TSS. It therefore, may be used in conjunction with surface colour change and TSS. It also had a strong correlation with the physical growth attributes.

Generally the close association between hue angle and brix during both the fruit growth period and maturity may suggest that these two attributes could be good indicators of sweet pepper fruit maturity and ripeness. These may be complemented with the use of fruit firmness.

8.4.5. Ethylene treatment and fruit colour change

In the present study mature green sweet pepper fruit treated with ethylene took less time to ripen than the control fruit. Treated fruit took only 6 days for fruits to fully turn red. Control fruits were still yellow at this stage. Loss of the green colour and the subsequent development of the desirable red colour was visible just 24 h after ethylene treatment and continued at a faster rate than for control fruits. Similar results were reported by various authors on different fruits (An and Paull, 1990; Arjona and Matta, 1991; Lallu *et al.*, 1989; Puig *et al.*, 1996; Reyes and Paull, 1995). Ferrarese *et al.*, (1995) also reported that exogenous ethylene at a rate of $100 \mu\text{L.l}^{-1}$ in a flow system has a strong promotive effect on the ripening of sweet pepper fruit of the cv. longum (DC.) Sendt. They reported that the change in colour was accompanied by a steep increase in cellulase activity paralleled by *de novo* synthesis of protein. The role of cellulase in fruit ripening was reviewed by Fisher and Bennett, (1991).

Pretel *et al.*, (1995) on the other hand, reported that propylene treatment of California Wonder fruit didn't affect colour development. This is similar to what was found on Evidence fruits treated under this experiment condition. This may also suggest that the sweet pepper cv Domino is different from both California Wonder and Evidence in terms of response to ethylene treatment and subsequent colour development.

Field grown sweet pepper fruit was less affected than greenhouse grown mature green fruit in terms of colour change following ethylene treatment. This may be because once ripening has been initiated by fruits having accumulated sufficient endogenous ethylene and the tissue is sensitive to ethylene, additional ethylene may not have a pronounced effect. Similar reports were also made on kiwifruit (MacRae *et al.*, 1989) and guava (Reyes and Paull, 1995). Lockwood and Vines (1972) also observed that treatment of pimienta pepper with $500 \mu\text{L.l}^{-1}$ ethylene inhibited colour development in more than 50% red colour group. However, unlike their findings no inhibitory effect of ethylene on colour development of sweet pepper fruit of the cv Domino was

observed.

Inhibition of endogenous ethylene production by exogenous ethylene treatment just after treatment was reported by Vendrell and McGlasson, (1971). Dominguez and Vendrell (1994) suggested that this may be due to the conversion of ACC to the alternative pathway of MACC (Malonyl-1-Aminocyclopropane-1-carboxylic acid) than to ethylene. According to Liu *et al.*, (1985) exogenous ethylene increases the activities of malonyl-ACC transferase much more faster than it does to ACC (Bufler, 1984).

The lack of response of ethylene treatment of sweet pepper fruit, cv Evidence suggests that this cv shows a typical non-climacteric behaviour. This is more evident by the fact that regardless of the maturity class no response was observed with respect to colour change due to ethylene treatment of the fruit. According to Serrano *et al.*, (1995) ABA concentration which tends to increase with maturation and senescence may be responsible for the ripening of sweet pepper fruit of the cv Evidence.

8.4.6. Ethylene treatment and fruit respiration

Ethylene treatment resulted in a significant increase in the respiration of treated fruit, which gradually declined with time. Ethylene treatment however, didn't result in a climacteric rise in respiration. It is not clear whether the peak respiration observed 2 days after ethylene treatment is a climacteric response. Eaks (1980) and Tucker and Laties (1984) have reported that with a higher concentration of exogenous ethylene the pulse response could merge with the climacteric. Stimulation of sweet pepper fruit respiration by exogenous ethylene was also reported by Inaba *et al.*, (1989). Pretel *et al.*, (1995) however, reported that propylene treatment of sweet pepper fruit, cv California Wonder didn't affect the respiration rate which declined steadily.

Exogenous ethylene treatment triggers an increase in fruit respiration rate in both climacteric and non-climacteric fruit (Biale, 1964). In climacteric fruit however, this increased fruit respiration appears to be a result of increased levels of endogenous ethylene (Brady, 1987). In non-climacteric fruit on the other hand, only trace amount of ethylene was found (Biale, 1964) and the level of respiration returns to the basal level upon removal of the ethylene gas (McGlasson, *et al.*, 1978).

In the present experiment the removal of ethylene didn't result in an immediate fall in the level of respiration. In fact, although ethylene production rate were not determined during this experiment the higher internal ethylene levels recorded for half ripe field grown Domino fruit indicate that endogenous ethylene production was stimulated by exogenous treatment.

8.4.7. Ethylene treatment and fruit quality

Treatment of mature green sweet pepper fruit resulted in advancement of colour change and improvement in quality of fruit in terms of TSS and acidity as plant ripened fruit. The difference in firmness of plant ripened and detached fruit either treated with ethylene or control could be a result of difference in turgidity of the fruit tissue. Accordingly, detached fruit lost some of their original water content resulting in reduced firmness of fruit. In spite of this, reduction in firmness of detached fruit however, ethylene treatment didn't affect fruit firmness as compared to control fruit. Lurie *et al.*, (1986) indicated that postharvest water loss in pepper fruit resulted in a decrease in firmness, fruit water potential and insoluble pectin and an increase in soluble pectins in the cell wall.

The improvement in the quality of ethylene treated fruit shows that fruit ripening was more advanced in treated than control fruit. Leshem *et al.*, (1986) reported that exogenous ethylene treatment of climacteric fruit leads to an autocatalytic biosynthesis of ethylene and speeds up fruit ripening. Thus, the change in colour and

improvement in quality as well as responsiveness of the fruit to ethylene treatment suggests that sweet pepper fruits of the cv Domino may behave as climacteric fruits.

8.5. Conclusion

Fruit growth in terms of fresh weight and volume increased with fruit age in a sigmoid fashion. Fruit length however, was rapid at the early stage of growth from 2-4 weeks while, diameter growth progressed slowly in young fruits and more rapidly towards maturity. Although fruit size and fresh weight and volume increased until the final harvest, there was no significant increase after 8 WAA. This was also substantiated by the RGR of the fruit which approached zero at this stage.

Measurement of other physiological maturity indicators revealed that TSS increased with fruit maturity which showed a significant increase after the onset of colour change. Fruit firmness also increased with fruit age which was closely correlated with an increase in pericarp thickness.

Fruit colour in terms of hue angle remained green for a considerable period of time until ripening was initiated at 8-9 WAA. Chroma values also increased with fruit ripening although lightness showed inconsistent results. With the onset of ripening, the internal ethylene concentration showed a pronounced increase while the internal CO₂ showed a small but noticeable increment before it started to decline. Fruit respiration and ethylene production also showed a similar trend.

Based on the present results, sweet pepper fruits of the cv Domino reach physiological maturity 8-9 weeks after anthesis. Fruit colour change, TSS and firmness were also found to be good indicators of sweet pepper fruit maturity. It was also shown that prediction of fruit growth stage was possible from measurement of fruit diameter and/or volume to determine fruit fresh weight.

The current results also demonstrate that maturity stage has a significant influence on the quality of sweet pepper fruit. For instance, fruit size, TSS, fruit firmness and pericarp thickness all increased with fruit maturity. The optimum harvest time for this product depends on the above factors as well as the colour preference of the consumer. Harvest stage not only affects the quality at harvest but also the postharvest characteristics of the product. Therefore, based on the above facts green mature pepper fruits could be harvested at 8 WAA. Coloured fruits however, may benefit in delaying the harvest by 1 or 2 weeks. However, undue delay may lead to lowering the fresh weight yield as well as loss of firmness of the fruit.

On the other hand, ethylene treatment of green mature sweet pepper fruits of the cv Domino resulted in rapid colour change, increased respiration and improved fruit quality. However, treatment of fruits of the cv Evidence of different maturity class didn't affect their rate of colour change as compared to the control treatments. It is thus, concluded that the ripening of Domino fruits was stimulated by ethylene while in the case of Evidence fruits it was not.

Chapter 9 - General Discussion

This chapter presents an integrated discussion on the results from the earlier chapters and outlines possible future experiments.

9.1. Calcium uptake and accumulation in fruit during ontogeny

Xylem water movement into both apple and tomato fruit occurs primarily only for a few weeks after fruit set; the fruit is then supplied with water and assimilates through the phloem (Wiersum, 1966). The phloem is also the principal conduit for the transport of water in citrus fruit particularly when fruit transpiration declines (Huang *et al.*, 1992). It is only a small proportion (15%) of the water input which comes via the xylem (Ho *et al.*, 1987) hence, the low Ca content of fruit.

It is known that Ca has a low mobility in the phloem as opposed to other minerals (Marschner, 1983). In this study the uptake of mineral nutrients into sweet pepper fruit revealed that Ca, Mg and K accumulate throughout the fruit growth period, with the majority of the Ca entering the fruit during early fruit development (Figs. 4.5, and 6.8). Calcium enters the fruit mainly through xylem flow (Clarkson, 1984), while the rest of the minerals are able to enter the fruit via the phloem influx (Wolterbeek *et al.*, 1987). If Ca movement into the fruit is limited to a short period after fruit set, then the increase in Ca levels up to fruit maturity implies that Ca flow through the phloem might be possible. The available evidence however, does not support this idea because only minute amount of Ca have been found in the phloem (Hendrix, 1995), however one explanation for the continued Ca input into the fruit may be night time root pressure flow (Collier and Tibbitts, 1984) when transpiration is reduced could have supplied Ca to the fruit, because there was ontogenic variation in Ca accumulation in sweet pepper fruit. Contrary to the continuous accumulation of Ca in autumn grown fruit (Fig. 4.3) there was little increase in Ca accumulation of fruit

beyond 4 weeks after anthesis in summer grown sweet pepper fruit (Fig. 5.5). This might be because the high day time temperature and light intensity resulted in a high VPD which was conducive to the movement of Ca into leaves rather than fruit. At night since the greenhouse environment had low RH, it may have inhibited the development of root pressure and xylem sap flow to deliver Ca to the fruit.

The reduction in Ca concentration during the rapid fruit growth period is due to imbalance in the supply of phloem delivered photoassimilates and water and xylem mobile Ca (Tromp, 1975). Consequently the water delivered through the phloem along with assimilates which carries little or no Ca dilutes the already available calcium delivered by xylem vessels to the fruit. Not only the Ca concentration decreases during rapid fruit development period but also the acetic acid soluble Ca compounds are also low (Chapter 5). These Ca compound (Ca pectate and Ca phosphate) are involved in cell membrane structures (Ferguson, 1984; Ho and Adams, 1989b).

Young fruit accumulate most of their Ca at night when whole plant transpiration is reduced (Ho, 1989). This may be possible because some of the calcium absorbed may be retained by absorption on the xylem conduits via cation exchange sites (Bell and Biddulph, 1963). This suggests that fruit may accumulate Ca which is transported by the transpirational stream through the action of leaves (Ho, 1989). In support of this theory Volz *et al.*, (1994) also reported that Ca content of apple fruit increased with an increase in spur leaf area and that the removal of primary leaves from clusters at bloom reduced fruit calcium and magnesium contents but not potassium. Aikman and Houter (1990) indicated that under low light levels there were reduced rates of radiative transpiration and hence less Ca flow to the growing regions. It is noteworthy that not only the presence of leaves is essential for Ca uptake and translocation but also the opening of stomata. As it is shown in Table 5.7 in this report partial closure of stomates occurred due to high stomatal resistance. This may have hindered the uptake of Ca through the transpiration stream (Clarkson, 1984) resulting in low Ca accumulation by leaves and fruit of sweet pepper grown under higher EC levels.

When less water is available in the plant as a result of high conductivity (chapter 5) the volume of the phloem sap is reduced while the concentration of the solute is increased (Ho *et al.*, 1987). Potassium which is a phloem mobile element paralleled the increase in dry matter as did Mg. On the other hand, the concentration of Ca was significantly reduced and this was more so in the distal portion of the fruit. This may be due to salinity inhibition of Ca uptake or poor xylem development (Belda and Ho, 1993).

Calcium movement is closely related to water uptake (Ho *et al.*, 1995) which in turn is influenced by solar radiation and root temperature (Adams and Ho, 1993). When the plant is under stress from low humidity (Adams and Holder, 1992) or salinity (Ho, 1989) Ca moves mainly to the leaves in preference to the fruit.

The low uptake of calcium by plants under high levels of nutrient conductivity could be due to competition between Ca and K (Kirkby, 1979); reduced osmotic potential of the solution which affects water uptake by the roots (Levitt, 1980); or salinity effects on root growth particularly damaging root tips (Cramer *et al.*, 1990) where Ca uptake takes place (Ferguson and Clarkson, 1975). Salinity also reduces leaf size which consequently decreases the amount of Ca transported to the shoot. Abd-Alla *et al.*, (1993) also observed a similar effect of salinity on cucumber.

Potassium can be translocated from leaves to fruit (Adams and Ho, 1994). On the other hand, they indicated that fruit depends solely on the supply of Ca directly from the roots through the xylem, as Ca is fixed in the leaves and cannot be retransported to the fruit via the phloem. Fruits are the strongest sinks for potassium in sweet pepper fruit as compared to Ca and Mg. The dominance of K in tomato fruit was also reported by (Voogt, 1993) who indicated that the fruit attracted over 60% of the K uptake. This suggests that maintaining a balance between Ca and the accumulation of K and Mg is of paramount importance in limiting BER.

The increase in fruit Ca levels with an increase in Ca levels in the nutrient solution

which resulted in a reduction in BER (chapter 5) is supported by the results of Adams and Holder (1992) who found that high Ca levels in the nutrient solution increased the accumulation of Ca in tomato fruit. This could be due to promoting Ca uptake by an exchange system (Harker *et al.*, 1988) in spite of the reduced Ca uptake under the high EC levels. The additional benefit of supplemental Ca could be due to the maintenance of the integrity and function of plasma membrane both in the root and shoot (Lauchli, 1990). It is therefore, suggested that providing supplementary Ca during the time of high demand by the fruit (2 - 4 weeks after anthesis) could provide the necessary Ca for new cell growth.

Calcium levels within the cytoplasm must remain low to avoid the precipitation of inorganic phosphorous, competition with Mg and the inadvertent activation or deactivation of enzyme systems (Marschner, 1986). Excessive Ca may directly inhibit cell wall growth by displacing H^+ from the Donnan Free Space near the cell wall, thus, inhibiting the action of wall loosening enzymes with acidic pH optima (Cleland *et al.*, 1990). Thus, the question of when and how much supplemental Ca is required in the nutrient solution needs further investigation.

Willumsen *et al.*, (1996) suggested that the relationship between ion activity ratios of K with Mg and Ca in the root medium and the net inflow of cations might be more important than salinity *per se* in inducing blossom-end rot. The relationship between low Ca:K and $a_k/\sqrt{a_{Ca}+a_{Mg}}$ ratios with the incidence of BER (Table 5.4) suggests that the ion activity ratio may have some effect on the physiological disorder. This relationship should be further explored in future experiments by maintaining a constant ion activity ratios in the medium.

Low relative humidity in the present studies promoted Ca uptake by the fruit particularly to the blossom-end (chapter 6). High humidity on the other hand, induced a high incidence of BER in sweet pepper fruit. Other reports also indicated that high humidity induced a calcium deficiency disorder 'Pillow fruit' at the blossom-end of cucumber fruit (Staub *et al.*, 1988). This disorder can also be increased by water

stress (Thomas and Staub, 1992). On the other hand, Adams and Holder (1992) found that high RH around the fruits of tomato increased their Ca concentration. There are several reports which indicate that low RH promotes Ca accumulation in other fruit. Perring (1979) showed that shaded apple (low transpiration rate) had a higher incidence of bitter pit, a Ca deficiency disorder, than rapidly transpiring fruit. Witney *et al.*, (1991) also found that bagging of apple fruit with brown bag increased the incidence of bitter pit by significantly reducing Ca content. This treatment also reduced fruit weight due to a decline in leaf photosynthesis of the enclosed spur by shading (Witney *et al.*, 1991). In the present study although the Ca content was reduced, fruit weight was not reduced because the enclosing polyethylene bags were transparent to light. The reports of Hopkirk *et al.*, (1990) further provide an indirect evidence for the importance of fruit transpiration in the accumulation of Ca by the fruit. According to their report, fruit which were exposed to direct sunshine had a higher Ca concentration than shaded kiwifruit.

The higher concentration of Ca found in the placenta and seeds of sweet pepper fruit (Chapter 4) suggests that the auxin produced by seeds (Bramlage *et al.*, (1990) may have promoted the uptake of calcium (Baneulos *et al.*, 1987). This indicates that good pollination might enhance Ca accumulation by the fruit. However, in order, to verify this assumption future experiments need to determine whether parthenocarpic fruit has less Ca and suffer more from BER than seeded fruit.

Recently, Saure (1996) postulated that increased root activity which can be promoted by, nitrogen dressings, excessive pruning or severe fruit thinning (Saure, 1992) will cause vigorous vegetative growth which results in increased bitter pit incidence. Saure (1996) believes that increased root activity leads to increased export of growth promoting substances such as cytokinin and gibberellin which favour vegetative growth and increase fruit size (Pharis and King, 1985). Thus, Saure (1996) suggests that the principal cause of bitter pit is high gibberellin levels late in the season rather than low Ca levels in the fruit.

Some reports indicate that the incidence of BER in tomato fruit was increased by application of GA₃ but reduced by the application of the growth retardants daminozide and chloromequat chloride (Castro and Malvavolta, 1978; Kheshem *et al.*, 1988). The reason for this was that the increased vegetative growth competes with fruit for Ca in the former case, but the reduced vegetative growth enhances fruit Ca in the latter case. This suggests that it is low Ca concentration in the fruit which causes BER rather than high GA₃ activity as suggested by Saure (1996) for bitter pit incidence. If high gibberellin levels were the cause of BER, the incidence would have been reduced with an increase in salinity or osmotic stress because GA₃ levels decrease with water stress (Torrey, 1976) or salinity (Bondok *et al.*, 1996). The results in chapter 5 however, suggest otherwise, therefore, at least in the case of BER, Ca deficiency appears to be the principal cause.

9.2. Seasonal trends in the incidence of blossom-end rot

Higher incidence of BER in the summer could be a result of increased irradiance and temperature which would increase photosynthesis (Karlsson and Heins, 1992; Heuvelink and Marcelis, 1996) thereby improving assimilate transport to the fruit (Adams and Ho, 1993), and in turn increase fruit growth.

In addition, increased irradiance tends to increase air temperature and lowers RH which promotes transpiration from the plant (Aikman and Houter, 1990), consequently promoting Ca transport into the leaves but not the fruit. As fruit size increases, unless there is a corresponding increase in Ca levels it may lead to collapse of cells (BER) at the distal end of the fruit (Ho and Adams, 1989b).

Light interception by the canopy has a marked effect on photosynthesis (Warren *et al.*, 1992). Increases in plant size effectively increase the potential photosynthetic surface area thereby increasing total assimilate production (Ho, 1995), which in turn increases the amount of sucrose delivered into the fruit (Nielsen and Veierskov,

1990). Increased irradiance is also responsible for increased air and fruit temperature which stimulates fruit enlargement (Pearce *et al.*, 1993). This environment provides ideal conditions for increased leaf transpiration by lowering air humidity and increasing the ΔVP thereby creating vapour pressure deficit, thus enhancing calcium transport to the leaves with proportionally less going into the fruit (Ho, *et al.*, 1993).

The amount of water translocated to the fruit partially determines the rate of assimilate translocation (Tromp, 1975; Schechter *et al.*, 1993) which leads to an increase in dry weight of fruits. Under low fruit growth conditions water supply through phloem is relatively low compared to xylem. Thus, under low temperature and irradiance conditions the rate of fruit growth is lower and fruit shows a higher level of Ca than at higher temperatures and irradiance. This is because by slowing the rate of water delivery into the fruit through the phloem, the fruit can benefit from the relatively rich Ca source ie xylem flow. Tromp (1975) also showed that high temperature favours phloem rather than xylem flow of water. The implication of this is that, when the time needed to reach a certain size by the fruit is long (winter crop:slow growth) the amount of Ca in the fruit will be much higher than fruits grown in a short period of time (summer crop:fast growth) for the same sized fruit. The low Ca availability in the fruit in turn predisposes the fruit to physiological disorders such as blossom-end rot. Hence, the high incidence of BER in the summer crop (Chapter 5) as compared to spring (chapter 6) autumn (Chapter 4), or winter (Chapter 3) grown plants could be seen in this way.

In addition to the seasonal effects on BER, high osmotic concentration of the nutrient solution tends to increase the incidence. Ho and Adams (1993a) reported that BER will be high if the acidity of the cell is high as it suppresses Ca availability. According to Cornish (1992) high salinity increases the acid content of fruits specially if the salinity is raised with K (Adams and Ho, 1993). In this experiment, the fruit acidity levels were not analysed (chapter 5), and thus, one can not speculate on the relationship between raised salinity, acidity and incidence of BER.

High conductivity of the nutrient solution significantly reduced Ca uptake and content of the fruit. This coupled with a reduction in fruit dry weight resulted in a substantial reduction in fruit Ca concentration. Consequently, the incidence of BER was manifested more in fruits grown under high osmotic concentration. This agrees with the reports of Adams and Ho (1993) who found that salinity reduced both fruit dry weight and Ca accumulation in tomato fruit.

The levels of calcium pectate and calcium phosphate in sweet pepper fruit under high conductivity conditions were found to be low during the rapid growth period (chapter, 5). These Ca compounds are necessary for the synthesis of cell wall and membrane (Ferguson, 1984; Ho and Adams, 1989b; Minamide and Ho, 1993), and low levels of Ca pectate and Ca phosphate results in loss of selectivity of membrane and leakage of cell contents leading to a high incidence of BER (Ho and Adams, 1993a).

The difference in the levels of Ca between the proximal and distal portions of the fruit, as demonstrated in this experiment (and others) (Ehert and Ho, 1986a), is because there are more cells and vascular bundles present in the proximal portion of the fruit (Bohner and Bangerth, 1988) which results in a higher xylem transport capacity (Brown and Ho, 1993). According to Zimmermann (1983) water flow in the xylem is related to the diameter, length and frequency of vessels. Salinity on the other hand, reduces xylem tissue development (Belda and Ho, 1993) particularly at the distal end of the fruit (Belda *et al.*, 1996) thereby aggravating the problem. Thus, the few functional xylem vessels at the distal end of the fruit will be forced to serve a larger volume of cells farther away from the source (Ho *et al.*, 1993).

A significant reduction in xylem and a major increase in phloem cross sectional area through the knuckle relative to the rest of the pedicel increases the resistance of xylem flow and transfers it to phloem, thus linking water and dry matter influx into the fruit (Lee, 1989). Since Kanahama *et al.*, (1990) identified the same vascular connection between the fruits of tomato and sweet pepper, the same principle is expected to operate with regard to the flow of water, Ca and photoassimilates in

sweet pepper.

The susceptibility of BER varies with cultivar in both tomatoes and sweet pepper, hence those with a large fruit size and heavy crop load are more prone to the incidence (Adams and Ho, 1992; Morley *et al.*, 1992). Moreover, a high leaf to fruit ratio results in vigorous growth of the plants which will increase the translocation of sugars into the fruit (Ho and Adams, 1993b) and increases its size. Since this photosynthate is transported through the phloem through which little or no Ca is transported, the fruit will be unable to cope with the extra demand of Ca for wall synthesis. Thus, the fruit will suffer from Ca deficiency and consequently BER.

The link between environmental factors with fruit growth and Ca uptake and supply of photosynthate may make the problem of BER difficult to avoid (Table 9.1), but with good crop and water management practices the problem could be minimized.

Table 9.1. A summary of environmental factors affecting calcium uptake and the incidence of Blossom-end rot (BER)***Shoot****Transpiration**

	Low	Moderately high	High
Light	x	✓	x
Temperature	x	✓	x
Air movement	x	✓	x
Humidity	✓	x	x

x reduced Ca uptake ⇒ BER

✓ increased Ca uptake

Photosynthesis

Light	✓	x
Temperature	✓	x
Carbon dioxide	✓	x

✓ a balanced growth and no BER

x ⇒ more photosynthate ⇒ increased fruit growth ⇒ less xylem and more phloem transport ⇒ less Ca delivery ⇒ BER

Root

pH	x	✓
Temperature	x	✓
Aeration	x	✓
Moisture	x	✓
Salinity	✓	x
Osmotic conc.	✓	x

x less Ca uptake ⇒ BER incidence

✓ promotes Ca uptake

* some of the environmental factors may interact with each other to promote or inhibit Ca uptake consequently, inducing BER incidence.

9.3. Dry matter production and partitioning

A plant's photosynthetic capacity and the pattern of carbon distribution among its organs are genetically controlled (Gifford, *et al.*, 1984). To sustain growth the plant should maintain dry matter accumulation against stresses imposed upon it by the environment (Boyer, 1982). Water stress affects photosynthesis by lowering stomatal conductance in response to low atmospheric humidity (Schulze, 1986b), which in turn leads to a decrease in cell turgor and cessation of growth (Geiger and Servaites, 1991). Binzel *et al.*, (1985) argues that lack of turgor is not the principal cause of the reduced cell expansion exposed to osmotic stress and Binzel and Reuveni (1994) suggest that the reduced expansion growth could be due to a limitation in carbon availability. This is a result of diversion of carbon into osmotic solutes for osmotic adjustment in order to compensate for lowered water potential (Greenway and Munns, 1980; Yang *et al.*, 1991), which depletes the carbon supply necessary for wall synthesis and cell expansion (Binzel and Reuveni, 1994).

Maintenance of phloem turgor under water stress can also limit dry matter accumulation and Giaquinta (1983) suggests that solute loading into the phloem and hence assimilate export is stimulated at lower cell turgor and that without turgor maintenance, growth slows and assimilates are diverted to sinks with less negative water potential (Robinson *et al.*, 1983). In many fruits and grain crops the fruit or grain sinks retain high water potential under moderate stress and hence growth can be sustained given an adequate supply of C and mineral ions (Patrick, 1988). Under severe stress conditions when C fixation is inhibited, sink growth may be sustained by remobilizing from the stem (Blum *et al.*, 1983).

Salinity or osmotic stress reduces plant growth by water deficit (Behboudian *et al.*, 1986) toxicity of ions (Walker *et al.*, 1983) or ionic balances (Walker, 1986). Salinity reduces fruit dry weight and affects the proportional distribution of dry matter to sweet pepper fruit by more assimilate being delivered to the vegetative parts at high salinity. This is in agreement with the reports of Ho and Adams (1994b) on cucumber

and (Ieperen, 1996) on tomato but it is in conflict with the findings of (Ehert and Ho, 1986b) on tomato.

Shoot growth may be retarded under high salinity due to reduction in the rate of leaf initiation or restriction in the expansion growth of the young leaves (Abd-Alla *et al.*, 1993), and/or by an inadequate supply of assimilates to the young leaves (Drew *et al.*, 1990) as photosynthetic rates are reduced (Bethke and Drew, 1992). Thus, a reduction in plant dry weight under osmotic or water stress is a result of lower photosynthetic activity and the lower sink strength of young leaves. Ho and Adams (1994b) reported that high salinity reduced the rate of dry matter accumulation by the plant but increased the proportion of the total dry weight in the fruit. This is because under nutrient solutions of higher conductivity, the relative water contribution of phloem increases as xylem hydraulic conductivity into the fruit is restricted (Ho *et al.*, 1987). Consequently, weak sinks such as flowers and young shoot received less assimilates. Although weak sinks were the plant parts which were less competitive under osmotic stress, it was the shoot rather than fruit which accumulated more assimilates in the current experiment.

Salinity reduces shoot and leaf dry weight and leaf area indicating that this is due to leaf osmotic adjustment (Alarcon *et al.*, 1994). They also showed that salinity reduced fruit size and number of tomatoes. The reduced weight or size of the fruit is due to a reduction in water content rather than dry matter accumulation in the tomato fruit (Adams and Ho, 1989). Salinity further induced a proportionally larger decrease in leaf area rather than leaf weight (Alarcon *et al.*, 1994).

Although the present data showed large difference between sweet pepper plants grown at low versus high EC levels (Table 5.8), the difference in leaf water potential between the different treatments was not large (Table 5.7). This may partially be attributed to an increased stomatal resistance with increases in EC (Fig. 5.17), which in turn reduced moisture loss from the plant thereby maintaining leaf water potential. Davies *et al.*, (1986) indicated that soil drying reduces transport of cytokinins and

minerals from the roots to shoots, which signalled partial closure of stomata and reduced growth before changes in leaf water potential occur. Leaf transpiration rate decreases with an increase in salinity (Al-Harbi and Burrage, 1992) due to partial stomata closure (Hoffman *et al.*, 1980) or increased stomatal resistance (Flowers and Yeo, 1989). The reduction in stomatal resistance in the present experiment suggests that both leaf photosynthesis and transpiration may have been reduced (Fig. 5.17).

Water stress affected both the diameter and length of sweet pepper fruit during the early growth period (Fig. 3.2). Similar observations were made on Asian pear fruit by Behboudian *et al.*, (1994). Fruit growth is largely dependent on the rate of net water accumulation and the water flow into the fruit in turn is dependent on the water potential difference between the fruit and the plant (Lee *et al.*, 1989).

Fruit growth is said to be less sensitive to water stress than vegetative growth (Higgs and Jones, 1991) because osmotic adjustment by the fruit enables it to maintain turgor in spite of reduced water potential (Mills *et al.*, 1996). Li *et al.*, (1991) suggest that photosynthesis is less sensitive to water stress than plant growth, hence, the strong sink activity of fruits can attract more assimilate despite reduced vegetative growth.

Water stress or osmotic stress also reduced the yield of sweet pepper due mainly to reduced fruit number and fruit size. A yield reduction of apple by water stress due to low fruit number and size was also found by Higgs and Jones (1990; 1991).

Salinity is considered to be a management tool to improve fruit quality. However, in most cases it results in reduced yield due to smaller fruit size. In the current experiment the beneficial effects of salinity was in terms of increased fruit dry matter content and advanced colour development. It may be possible that other benefits could be achieved if the plants were subjected to osmotic stress later in their growth and development. This may improve fruit quality without a significant yield reduction. This is possibly 7-8 weeks after anthesis when there is little fresh weight

gain. Future work could focus on this problem.

9.4. Fruit maturity and ripening

9.4.1. Fruit maturity

A clear distinction between growth, maturation and senescence is not always easy because the transition between these stages is always slow and indistinct (Wills *et al.*, 1989), but measurement of physical and physiological changes may give reliable estimates of the stage of physiological maturity. According to Knee *et al.*, (1989) an indicator of fruit maturity must be measurable, should correlate well with an aspect of fruit quality and be convenient to undertake.

Colour change is the most recognized criterion to determine whether a fruit is ripe or not. In sweet pepper colour changes from green to yellow and red leading to attainment of good eating quality. The loss of green colour is due to degradation of chlorophyll (Brady, 1987). This is paralleled by the synthesis of carotenoids (Leshem *et al.*, 1986).

Colour change was measured using LCH which gives an accurate measurement of colour (McGuire, 1992). The results showed that colorimeter measurement are potentially more consistent and sensitive than visual observations in giving a reliable result. It is however, important to recognize that colour development is dependent on environmental factors such as temperature and light (Lawson *et al.*, 1994). According to Faust (1989) optimum fruit colour is achieved if radiation remains > 70% of full sunlight. This shows that seasonal variation may be expected in the timing of colour change between (for instance), winter and summer grown sweet pepper fruit.

The change in TSS which became apparent after the onset of ripening may indicate the improvement in eating quality of the fruit. This was confirmed by the change in

colour particularly hue and chroma (Fig. 8.6). Luning *et al.*, (1995) further reported that when sweet pepper turned from green to red (7 to 8 weeks after fruit set) the level of flavour volatile compounds either sharply increased (7 volatiles) or drastically fell (another 7 volatiles) in concentration while another two gradually decreased. In this experiment volatile compounds were not measured owing to the practicality of it as an index of maturity. However, an assessment of flavour volatiles may have confirmed the maturity of the fruit.

Total soluble solids concentration is influenced by temperature and management conditions. Accordingly, factors which favour the production of more photosynthate available to the fruit may increase TSS (Mason *et al.*, 1989). Likewise, non shaded fruit has more TSS than shaded fruit (Tombesi *et al.*, 1993). Thus, the growing period and sampling system may affect the TSS of fruit.

The texture of sweet pepper fruit especially crispness is an important quality attribute to the consumer (Jen and Robinson, 1984). Fruits harvested early are soft while over mature fruit tend to lose water. Almela *et al.*, (1991) further reported that the vitamin A content of sweet pepper fruit is related to its moisture content at maturity and harvest. Accordingly, cultivars which conserve a higher degree of moisture at maturity had a high vitamin A content. As it has been shown in the current report (Fig. 8.6a) fruits tend to have a reduction in firmness 11 weeks after anthesis. This could be due to senescence and moisture loss. Therefore, harvesting the fruit at the optimum time could preserve its nutritional quality as well as fruit firmness.

The present result demonstrated that maturity stage has a significant influence on the quality of the harvested product. For instance, fruit size, TSS, pericarp thickness and fruit firmness all increased with fruit growth and development. However, the optimum harvest time for the product will depend not only on the above factors but also on the colour preference of the consumer. Harvest stage not only affects the harvest quality but also the postharvest characteristics of the product. Although fruit weight appeared to increase it was not statistically significant after the onset of colour

change. The lack of difference between maturity classes in chapter 3 also confirms this observation. On the other hand, the loss of firmness after prolonged storage on the plant shows that the fruit has remained on the plant too long, and that an earlier harvest would have been preferable.

Colour was the best indicator of time of harvest of sweet pepper while TSS and firmness determine its quality in terms of maturity. Additional indices of maturity would make the judgement of maturity more reliable. Although valuable information has been obtained from the current investigation, the results should be seen as a basis for future studies which should be combined with organoleptic trials in order to relate physicochemical tests to consumer acceptability. The wider applicability of colour and TSS as maturity indices for sweet pepper could also be tested by evaluating fruits grown in different season and under different management conditions.

9.4.2. Fruit ripening

The use of sensitive gas chromatography has enabled researchers to use ethylene as a criterion to differentiate climacteric from non-climacteric fruits (Abeles *et al.*, 1992). Climacteric fruits are known to exhibit increased respiration and ethylene production coincident with ripening (Wills *et al.*, 1989; Saltveit, 1993).

Non-climacteric fruits show little change in their $\text{P}^i\text{C}_2\text{H}_4$ during their development and ripening (Wills *et al.*, 1989). According to Wills *et al.*, (1989) applied ethylene enhances respiration of both climacteric and non-climacteric fruit but in the latter case the magnitude of respiration is dependent on the concentration. They also reported that the rise in respiration in response to ethylene treatment may occur more than once in non-climacteric fruits in contrast to the single increase in respiration of climacteric fruit. McGlasson (1978) also indicated that non-climacteric fruit usually lack the pronounced changes in colour and softening associated with climacteric fruit.

Japanese pear cultivars are either classified as climacteric (Kitamura *et al.*, 1981; Downs *et al.*, 1991) or non climacteric (Downs *et al.*, 1991; Tian *et al.*, 1992). Cucumber fruit are also classified as climacteric (Kanellis *et al.*, 1986) or non climacteric (Biale, 1981). There are reports which classify blackberry as climacteric (Burdon and Sexton, 1993) or non climacteric (Lipe, 1978). Burdon and Sexton (1993) even show differences in ethylene production between the different blackberry cultivars. Such difference in classification may be a result of using different cultivars and environments. It could also be a reflection of the time of ethylene production of the cultivars examined in which case the time of ethylene production and pigment changes may not coincide (Burdon and Sexton, 1990). It also illustrates the difficulty of defining a set criteria to be used to predict ripening related respiratory behaviour of a specific fruit.

Internal ethylene concentration has been considered to be a more appropriate criterion than respiration for classifying climacteric and non climacteric fruits (Spencer, 1966). According to Burg and Burg (1965a) and Miccolis and Saltveit (1991) $P^1C_2H_4$ is physiologically more important as it reflects the tissue ethylene concentration rather than the rate of ethylene synthesis.

The response of fruit to exogenously applied ethylene or propylene (an ethylene analog) was suggested as a means of distinguishing between climacteric and non-climacteric fruits (McMurchie *et al.*, 1972). In climacteric fruit ripening, respiration and ethylene production are advanced while in non-climacteric fruit it simply increases respiration without accelerating ripening.

Commercially treatments of about $1000 \mu l.l^{-1}$ are used for ripening of bananas (Inaba and Nakamura, 1988) kiwifruit (Lallu *et al.*, 1989) tomato (Sisler and Lallu, 1994). The effect of any treatment depends on the sensitivity of the fruits which increases with age, the C_2H_4 concentration used and duration of exposure (Inaba and Nakamura, 1986). The effect of C_2H_4 is said to be related to its capacity to combine to receptors present in the tissue (Whitehead and Bosse, 1991). According to Sas *et*

al., (1992) treatment of strawberries with 10, 100 or 1000 $\mu\text{L.l}^{-1}$ ethylene increased respiration of fruits at different maturity stage but respiration was returned to pre treatment levels after 48 hr. In contrast sweet pepper fruit of the cv Domino treated at 1000 $\mu\text{L.l}^{-1}$ changed colour rapidly (Fig. 8.9) with an improvement in fruit quality (Table, 8.4). On the other hand, unlike strawberry fruit the respiration of ethylene treated fruit didn't return to pretreatment levels 48 h after treatment but 72 h later. By this time colour change was well under way (Fig. 8.9). Further evidence for the higher rate of respiration of treated fruit is presented in Fig. (8.15) where at the termination of the experiment (after 8 days), treated fruit still exhibited relatively higher P^iCO_2 , but the response of ethylene treatment of fruit to C_2H_4 production was not measured in one of the experiments for technical reasons, because it could not be determined separately as it could not be differentiated from that used in the treatment (Elkashif and Huber, 1989). In future research propylene could be used to monitor ethylene production (Tian *et al.*, 1992). However, earlier examination showed that ethylene treatment of sweet pepper fruit of the cv. Domino promoted their $\text{P}^i\text{C}_2\text{H}_4$ (Fig. 8.16b). No double rise in respiration of fruit was observed as noted by Elkashif and Huber (1989) in watermelon which was the basis of classifying the fruit as non climacteric. In addition to this no extensive softening of the tissue was observed as the firmness of the treated and control fruit was similar (Table 8.4). This rules out cellular damage and no decay was observed at all in both treated and control fruit.

The decline in P^iCO_2 in detached fruit may suggest that the gas may have been leaking through the pedicel of the fruit (De Vries *et al.*, 1996) which otherwise would accumulate in the fruit of attached fruit. Moreover, when in the light, attached fruit may be supplied with substrate by the plant which would enable it to maintain high rate of carbon dioxide production (Nielsen *et al.*, 1991).

The lack of the climacteric respiration could be due to the ability of attached sweet pepper fruit to photosynthesize (Czarnowski, 1996) using CO_2 accumulated through fruit respiration (Knee, 1995). The import of substrate and photosynthesis decline as tomato fruit approaches maturity due to substantial loss of chlorophyll (Piechulla *et*

al., 1987; Knee, 1995). This in turn reduces the import dependent CO_2 generation. On the other hand, the decrease of import dependent CO_2 generation could overlap with the climacteric rise in attached fruit, and obscure the climacteric rise in respiration.

The reason for the more rapid ripening of attached fruit is that the fruit had a higher level of $\text{P}^i\text{C}_2\text{H}_4$. However, the actual drop in hue angle was closely associated with a significant increase in $\text{P}^i\text{C}_2\text{H}_4$ in both attached and detached fruit (Fig. 7.10).

Generally the association between $\text{P}^i\text{C}_2\text{H}_4$ and ripening of sweet pepper fruit cv. Domino indicates that the fruit appeared to behave as a climacteric fruit. This behaviour could however, be ascertained by studying the activities of ACC synthase and ACC oxidase in the fruit in future experiments.

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Appendix 1: Stock solution for the NFT growing system

Fertilizer nutrient	Kg.l ⁻¹
Stock solution A	
Calcium Nitrate (Ca(NO ₃) ₂ .4H ₂ O)	1.976
Chelated iron (FeNa EDTA)	0.158
Stock solution B	
Potassium nitrate (KNO ₃)	1.316
Magnesium sulphate (MgSO ₄ .7H ₂ O)	0.993
Potassium phosphate (KH ₂ PO ₄)	0.544
Manganese sulphate MnSO ₄ .5H ₂ O)	0.1231
Boric acid (H ₃ BO ₃)	3.43*
Copper sulphate (CuSO ₄ .5H ₂ O)	0.55*
Ammonium molybdate (NH ₄) ₆ Mo ₇ O ₂₄ .4H ₂ O)	0.0182*
Zinc sulphate (ZnSO ₄)	0.616*

* g.l⁻¹

Appendix 2: The parameter values for the curves fitted to Richards function

Treatment	Parameter				R ²
	a	b	c	d	
Fruit fresh weight (Fig. 5.1)					
EC 2	5.9535	0.44258	0.957926	0.917171	0.99
EC 4	5.68772	0.30022	0.939185	0.908061	0.96
EC 6	5.20417	0.143135	0.930776	0.89551	0.96
EC 8	5.16409	0.544095	1.288140	0.784074	0.98
EC 10	5.16614	0.156485	0.916319	0.906439	0.98
EC 10+	5.27491	0.17451	0.915629	0.907845	0.99