Fruit, Vegetable and Cereal Science and Biotechnology ©2012 Global Science Books

Crop Physiology of Sweetpotato

Velumani Ravi* • **Raju Saravanan**

Central Tuber Crops Research Institute, Thiruvananthapuram – 695 017, India

Corresponding author: * **veluravi03@yahoo.co.in**

ABSTRACT

Sweetpotato is an important tropical tuber crop cultivated mostly under temperate and mild tropical climatic conditions. Its tubers are rich in carbohydrate and some are rich in carotene. The crop is vegetatively propagated through vines. The shoot emerging from the planted vine which grows rapidly for two months and later the growth rate slows down. Within three weeks after planting vines, tubers are formed which later develops into tuber. Soil nutrients such as nitrogen and potassium influence growth and yield of sweetpotato. Water deficit stress and high temperature are major abiotic stresses that affect sweetpotato growth and yield. Sweetpotato can tolerate low level of shade. This chapter presents recent research work done on physiological aspects that influence the growth and productivity of sweetpotato.

Keywords: Dry matter production, moisture stress, photosynthesis, respiration
Abbreviations: **ADPG**, adenosine diphosphate glucose; **ADPGPPase**, ADPG pyrophosphorylase; **CEC**, cation exchange capacity; **CGR**, crop growth rate; **chl**, chlorophyll; **CP_N**, canopy photosynthetic rate; **DM**, dry matter; **GA_3**, gibberellic acid; **HI**, harvest index; **IAA**, indole-3-acetic acid; **iP**, isopentenyl adenine; **LAI**, leaf area index; **MDA**, malondealdehyde; **NR**, nitrate reductase; **P_N**, net photosynthetic rate; **R_D**, dark respiration; **RH**, relative humidity; **R_L**, respiration in light; **SLW**, specific leaf weight; **SOD**, superoxide dismutase; **SUS**, sucrose synthase; **TBDM**, tuber dry matter; **TDM**, total dry matter; **UDPG**, uridine diphosphate glucose; **WAP**, weeks after planting; **WDS**, water deficit stress; **WP_L**, leaf water potential; **ZR**, zeatin riboside

CONTENTS

INTRODUCTION 17
SHOOT SYSTEM 18
Stem branching 18
Leaf characters 18
Leaf area 19
Photosynthesis 19
Respiration 19
Translocation 19
ROOT SYSTEM 20
Non-tubers 20
Tubers 20
STARCH SYNTHESIS 21
TUBER BULKING PATTERN 21
ENDOGENOUS GROWTH REGULATORS 21
GENE EXPRESSION DURING STORAGE ROOT FORMATION AND DEVELOPMENT 22
KNOXI genes 22
MADS-box genes 23
Spermidine synthase gene 23
Source and sink relation 23
Dry matter production and harvest index 24
RESPONSE TO STRESS 24
Water deficit 24
Flooding 25
PROPAGATION PHYSIOLOGY 25
Vine cuttings 25
Root sprouts 26
Cut root pieces 26
Micropropagation 26
Seed 26
CONCLUSION 26
REFERENCES 27

INTRODUCTION

Sweetpotato (*Ipomoea batatas* (L.) Lam., Convolvulaceae) is a herbaceous dicot, widely grown throughout the tropics and warm temperate regions of the world between latitudes 40°N and S of the equator and between sea level and 2,300 m altitude. Sweetpotato, is perennial in nature and is commonly cultivated as an annual crop. Depending on the

Received: 1 November, 2011. Accepted: 1 November, 2012.

Invited Review

Table 1 The total chlorophyll content, photosynthetic rate and tuber yield of normal green and pale green sweetpotato genotypes.

Genotype	Total chlorophyll content (mg g^{-1} fresh leaf)	Total carotene content (mg g^{-1} fresh leaf)	Photosynthetic rate (µmol m^{-2} s^{-1})	Tuber yield (g $plant^{-1}$)
Sree Bhadra* (S-1010)	1.7	0.278	18.56	587.33
Sree Vardhini* (OP-219)	1.6	0.265	17.87	496.50
S-108*	1.5	0.272	17.23	455.70
Kanhangad*	1.2	0.254	17.50	426.80
S-1267**	0.297	0.107	13.25	657.33

*normal green; **pale green
Authors' unpublished data

growing conditions and cultivars, crop growth period varies between 12-35 weeks, whereas a long duration of 25-50 weeks also has been reported for some cultivars. However most of the cultivars attain maximum tuber yield in 12-22 weeks after planting (WAP) (Sen *et al*. 1990).

Sweetpotato cultivars vary widely in their tuber yield potential. An average fresh tuber yield of about 10-25 t ha^{-1} in 16-20 weeks has been obtained in many countries (Rao and Sultana 1990; Golder *et al*. 2007). Fresh vine yield varies between 11-45.7 t ha^{-1} when harvested as whole shoots (Mukhopadhyay *et al*. 1992).

Wide variability in tuber yield among sweetpotato cultivars and individual plants of the same cultivar has been attributed to cultivar, propagation material, environment, and soil factors. Genetic and environmental factors influence leaf area, leaf production and abscission, leaf photosynthesis, tuber formation and development, total dry matter production, dry matter partitioning and tuber yield (Ravi and Indira 1999). This chapter discusses the interaction of physiological traits, gene expression and molecular aspects of tuber initiation and bulking as well as environmental and edaphic factors which determine sweetpotato yield including tuber and vine.

SHOOT SYSTEM

Stem branching

Sweetpotato has a decumbent stem and cultivars can be arbitarily categorised as either erect bushy, intermediate, or spreading, based on the length of their vines. Branching is cultivar dependent and branches vary in number and length. Normally, sweetpotato plants produce 3 types of branches: primary, secondary and tertiary at different periods of growth (Sasaki *et al*. 1993). The total number of branches varies among cultivars from 3 to 20 whereas stem length varies between 0.5-2.2 m (Jeong and Oh 1991; Rao *et al*. 1992; Rajeshkumar *et al*. 1993). However, the branching system in sweetpotato plants is heavily influenced by spacing, photoperiod, and soil moisture and nutrients. Increasing plant density decreases stem length and total number of branches per plant presumably due to increases in competition for nutrients and irradiance (Sasaki 1991; Hamid and Sasaki 2001). The increase in stem length and total number of branches per plant at decreasing plant density is primarily due to the formation of secondary branches (Somda and Kays 1990a). Stem length and total number of branches per plant increase with irrigation (Nair and Nair 1995) and soil application of N (Nayar and Vimala 1990; Nair and Nair 1995). Increase in K up to 75 kg ha^{-1} however does not significantly increase the total number of branches (Nair and Nair 1995). A long photoperiod (18 h) decreases branch number while increasing the branch length when compared to plants exposed to a 12.5 h photoperiod. A short photoperiod of 8 h increase branch number while decreasing the branch length. Light intensity does not have any clear effect on the number of branches.

Leaf characters

Sweetpotato cultivars predominantly have prostrate stems with leaves expanded into a horizontal, shallow canopy close to soil surface enabling the plant to intercept maximum solar radiation. Leaf shape varies widely among cultivars. The leaves may be round, reniform, cordate, triangular and lobed moderately or deeply. Plants have an indeterminate growth habit and continuously produce new leaves. As the number of leaves produced increases throughout the growing period, the percentage of leaves attached to the plant significantly decreases due to shedding (Somda *et al*. 1991). The number of leaves depends on the number of branches or growing points, stem and internode length, rate and duration of leaf production and leaf longevity or leaf shedding. Total number of leaves per plant among cultivars varies between 60-300 (Rajeshkumar *et al*. 1993). Number of leaves per plant increases with decreasing plant density (Somda and Kays 1990b), increasing irrigation (Indira and Kabeerathumma 1990; Holwarda and Ekanayake 1991; Nair and Nair 1995), and N application (Nair and Nair 1995). Increase in K however does not appreciably increase the number of leaves per plant. Defoliation of vine cuttings prior to planting drastically decreases the number of leaves per plant (Jayakrishnakumar *et al*. 1990).

The specific leaf weight (SLW) or leaf weight/area ratio of sweetpotato cultivars varies between 2 and 4.4 mg cm^{-2} (Nair and Nair 1995). The SLW declines at the end of growth period mainly due to translocation of dry matter from the leaves to the tubers (Somda *et al.* 1991; Nair and Nair 1995). SLW increases with increasing plant density (Sasaki 1991), and CO_2 concentration in the atmosphere (Bhattacharya *et al*. 1992). A long photoperiod (24 h) increases leaf dry weight and number as compared to short photoperiod (12 h) (Bonsi *et al*. 1992).

Stomatal density of sweetpotato leaves varies between 47-155 mm^{-2} on the adaxial side and between 151-318 mm^{-2} on the abaxial side (Bhagsari 1990; Kubota *et al*. 1992a). High yielding cultivars have greater number of stomata on the abaxial surface and lower number of stomata on the adaxial surface than low yielding cultivars (Kubota *et al*. 1993). The concentration of chlorophyll (chl) *a*, β-carotene and xanthophyll in leaves vary widely among cultivars. Chlorophyll a content varies between 5.3-7.8 mg g^{-1} dry leaf tissue while the chl *b* content varies between 2.4-3.8 mg per dry leaf tissue. The total chl (*a*+*b*) content varies between 7.6-10.6 mg g^{-1} dry leaf tissue. The leaf chl content remains relatively constant throughout the growth period while the chl *a*:*b* ratio increases with plant age (Songhai *et al*. 1994). Sweetpotato shows significant positive correlation between leaf chl and N content. However, leaf chl content does not show significant correlation with the net photosynthetic rate. A sweetpotato genotype with pale green leaves and 20% total chl content of a genotype with normal green leaves had 80% P_N rate of normal green leaf genotype (**Table 1**). The pale green genotype also had tuber yield at par with the normal green genotype (**Table 1**). Deficiency of Mn, Zn, and Cu causes interveinal chlorosis that leads to complete bleaching of the young and middle leaves. Petiole NO_3-N concentration can be a reliable indicator of current N status of the plants while total N concentration of blades appears to be a more reliable predictor of tuber yield. Nitrogen stress increases transpiration per unit leaf area and decreases water use efficiency (WUE). This was due to lower total plant DM production rather than to increased total water transpiration per plant (Kelm *et al*. 2001). Sweetpotato leaves showed typical discolouration symptom due to low P (0.04-0.12%) and K (0.63%) (Susan *et al*. 2004).

Leaf area

Leaf area per plant or the leaf area index (LAI) is the ratio of leaf area to land area. LAI varies widely among sweetpotato cultivars and at different growth periods depending on the number of leaves retained on the stem and their size. Shorter photoperiod, increasing N application (Patil *et al*. 1990), and decreasing plant density (Somda and Kays 1990b) significantly increase individual leaf area and leaf area per plant.

Changes in LAI during growth occur in three phases. LAI steadily increases from the 2nd WAP in the first phase, reaching a plateau between the 8-16th WAP in the second phase, and declines during the third phase at the end of the growth period partly due to leaf shedding, mutual shading and reduced light intensity in the lowermost leaves. The maximum LAI among cultivars during second phase varies between 2-11 (Bhagsari and Ashley 1990; Nair and Nair 1995). LAI increases with increase in air temperature (Mukhopadhyay *et al*. 1991), photoperiod (Mukhopadhyay *et al*. 1991), N application (Nair and Nair 1995), soil moisture (Chowdhury and Ravi 1990) and due to staking (Bhagsari 1990). Higher dose of K has no effect on LAI (Nair and Nair 1995).

Brown (1992) estimated that LAI of 3 to 4 is required to intercept 95% of PAR in sweetpotato. Most of the cultivars in fact maintain LAI between 3-4 between 8-16 WAP. At this LAI, maximum weekly crop growth rate (CGR) or dry matter production of cultivars varies between 106-133 g m^{-2}.

Photosynthesis

Photosynthesis of sweetpotato leaves is similar to that of C_3 plants. Net photosynthetic (P_N) rate of individual leaves varies between 12-39 mg CO_2 dm^{-2} h^{-1} among cultivars (Ravi and Saravanan 2001; Ravi 2003; Cen and Sage 2005). The P_N rate is highest during early growth period and declines at the end of growth period because the sink attains maximum size at this time. Lack of consistent P_N rate of cultivars in different seasons and at different periods of growth in the same season is primarily due to the interaction of P_N with environmental factors and plant growth period. The P_N capacity of leaf blade relates to thickening property of tubers. In reciprocal grafts between *I. batatas* cultivar and *I. trifida*, a related species which does not form tubers, P_N rate of leaf blade was greater in grafts with larger tubers than in grafts of smaller tubers. The P_N rate of individual leaves drastically declines with leaf age. The P_N rate of individual leaves negatively correlates with individual leaf size and the P_N rate per unit leaf area decreases in leaves greater than 50 cm^2. Maximum P_N rate occurs at air temperature >25-34°C (Bhagsari and Ashley 1990; Kubota *et al*. 1992a). The P_N rate of individual leaves steadily increases with an increase in CO_2 concentration up to 900 ppm in atmosphere surrounding the leaf. The P_N rate of sweetpotato leaves saturates at irradiance (I) of 750-1000 $\mu mol.m^{-2} s^{-1}$ (Ravi and Saravanan 2001; Cen and Sage 2005). The response curve of P_N /I depends upon the leaf internal CO_2 concentrations (C_i) and increase in inter-cellular CO_2 concentrations cause the P_N rate to saturate at a high level of I (Kubota *et al*. 1992b; Cen and Sage 2005). Photosynthesis of sweetpotato leaves is also influenced by stomatal resistance (S_R) because S_R regulates C_i (Kubota *et al*. 1994). High relative humidity (RH) increases P_N rate and plants grow under higher RH (85%) have greater stomatal conductance and P_N rates than those grow under low RH (Mortley *et al*. 1994). Temperature increases the CO_2 saturated rate of photosynthesis more than 5-fold between 5 and 35°C (Cen and Sage 2005).

Sweetpotato leaves show maximum photosynthetic rate between 10.00-11.00 h followed by stomatal closure and a significant decrease in P_N rate during midday (Ravi 2003). The midday depression in P_N neither relates to the accumulation of photosynthates nor to changes in CO_2 concentration of the air but closely correlates with an increase in S_R of leaves. However, under constant environmental conditions, P_N rate of sweetpotato leaves remains high and relatively stable during the morning but decreases toward the late afternoon. Under field conditions, high relative humidity and relative water content of leaves significantly influence the P_N rate of individual leaves (Ravi 2003).

It was found the P_N rate to be positively correlated with nitrogen (N) content of leaf blade. However, the P_N rate to have no significant correlation with N content of sweetpotato leaves. Photosynthesis is markedly higher in sweetpotato leaves containing >4% K on dry weight basis. This may be because K increases the rate of translocation of photosynthates from leaves which in turn accelerates photosynthetic activity. Under P-deprivation, photosynthesis and photorespriation (R_L) of isolated sweetpotato leaf cells decreased and the ratio of R_L and P_N rates increased (He *et al*. 1992). The optimum P concentration for photosynthesis of isolated leaf cells of sweetpotato is lower with 21% O_2 than with 2% O_2 and conditions favoring R_L could decrease the demand for P in photosynthesis due to release of P during the hydrolysis of phosphoglycolate to glycolate (He *et al*. 1993). Inoculation with vesicular arbuscular mycorrhizae in the root system (Potty and Indira 1990) and high concentration of CO_2 in the atmosphere surrounding the leaf increase PN rate of sweetpotato plants. The PN rate shows a negative correlation with starch content of leaves due to feedback inhibition of photosynthesis.

The P_N rate of individual leaves in sweetpotato canopy is variable and therefore P_N rate does not precisely reflect the performance of all leaves together in the canopy. Lack of correlation between P_N rate and canopy photosynthetic rate (CP_N) (Bhagsari and Ashley 1990) is presumably due to the indeterminate growth habit which results in the presence of a portion of leaves with high P_N rate while a portion of leaves have reduced P_N rate. The P_N of individual leaves also shows no significant correlation with the total dry matter production and tuber yield (Ravi 2003). Maximum CP_N rate of sweetpotato cultivars varies between 3.7-6.5 g CO_2 m^{-2} h^{-1} (Bhagsari 1990). At the end of growth period CP_N rate declines to 50% presumably due to increase in proportion of older leaves in the canopy and the decrease in P_N rate of individual leaves due to the maximum growth of tubers (Bhagsari 1990). In one study, sweetpotato cultivars differed in CP_N rates at each measurement during a 23 weeks growth period due to interaction of P_N rate with the environment (Bhagsari 1990). This makes the ranking of cultivars for CP_N difficult. Increase in plant density does not have significant effect on CP_N.

Respiration

Dark respiration (R_D) of different parts of sweetpotato plant including leaves, stem, storage and fibrous roots has not been extensively investigated. Leaves of sweetpotato plant have the highest R_D rate when compared to the stem, storage and non-tubers. The leaves also have high light dependent respiratory CO_2 efflux rate (R_L) varying between 4.9-5.7 mol m^{-2} s^{-1} (Ravi and Saravanan 2001). Throughout the growth period, leaf blades show the largest proportion (50%) of total respiration and there is no cultivar difference. The R_D rate of leaves, stems, and tubers steadily increases during the early period of growth, levels during middle of growth period, and then declines at the end of the growth period. The higher R_D of leaves, petiole, and stems than tubers may presumably decreases tuber yield when excessive vine growth occurs.

Translocation

The carbon fixed by sweetpotato leaf is translocating as sucrose out of the leaf into the stem. For sweetpotato tuber growth, high shoot growth should be combined with efficient translocation of photosynthates. Under low yielding conditions, translocation limitation is more important than sink limitation.

Translocation of ^{14}C photosynthates in rooted sweetpotato leaves (phytomodels) were studied with tubers and found that 50% of the total ^{14}C disappeared within 24 h of exposure to $^{14}CO_2$ presumably due to respiration while the rest translocated to tubers. It was reported that both apical and basal leaves on the sweetpotato stem display bidirectional transport while the lower leaves transport a major portion of their photosynthates in a basipetal direction. However, exposing the leaves in a whole plant to $^{14}CO_2$ found that essentially all of the photosynthates from the leaves on the main stem is basipetally translocated toward the roots. In that case, carbon stored as starch within the apical leaves on the main stem may be recycled for growth of the main stem apex. While acropetal translocation is negligible within the main stem, lateral branches at the base of the plant, which bear number of fully developed leaves capable of photosynthates export, exhibit acropetal translocation of some photosynthates derived from the main stem. It is not clear if the photosynthates from the main stem moves directly into the lateral branches or first moves to the root system and then translocated into the lateral branches. The significance of acropetal translocation in lateral branches is not known.

Sweetpotato leaves export greater amount of photosynthates when measured during early hours of forenoon and late hours of afternoon than the mid-day. This means basipetal translocation occurs during the dark period. Correspondingly, the export pool of photosynthates in leaves is greater in the early forenoon and late afternoon than the mid-day. In contrast to the export, storage pool of photosynthate within the leaf remains low in the early forenoon and late afternoon but increases during the mid-day. The speed of basipetal translocation of photosynthates is an important factor for tuber growth and it varies during the day and between various sites along the main stem. This may be due to influxes of photosynthates from other leaves along the stem and/or changes in the resistance to flow once the photosynthates enters the phloem tissues of the main stem.

Photosynthates translocated toward the root system are partly used for expansion of fibrous, non-tuberous roots and the rest deposited in tubers. Basipetal translocation toward underground parts increases when the tubers are initiated. High sink (tuber) potential and factors which increase tuber growth such as moderate soil moisture, RH, low soil temperature and low light intensities enhance the rate and speed of basipetal translocation. Due to increase in sink strength, subsequently decrease concentration of photosynthates in the phloem within the sink which in turn would increase the concentration gradient between the leaves and the tubers. Velocities of acropetal translocation are not much affected due to changes in the sink potential.

ROOT SYSTEM

The root system of sweetpotato plants comprises tubers, pencil roots and fibrous roots.

Non-tubers

Thin, adventitious roots arise from the internodal regions of vine cuttings or cut sprouts used for propagation. These internodal roots are typically tetrarch with a central core of xylem with no central pith and four protoxylem points with alternate phloem tissues within the stele with a broad secondary cortex and a limited amount of secondary phloem. These roots develop horizontally or obliquely in the soil. Such roots develop largely into fibrous roots. The fibrous roots are less than 5 mm thickness and are branched and rebranched with lateral roots forming a dense network throughout the root zone and constitute the water and nutrient absorbing system of the plant. The fibrous roots and tubers occupy much of the soil volume. It was found that 51 and 92% of total roots were within the top 45 and 57 cm, respectively. These roots have heavily lignified stele and very low levels of vascular cambium activity. In one study, fibrous roots accounted for 3% of the total plant dry weight (Somda *et al*. 1991). Light, dry and compact soil, high levels of N supply, low O_2 within the root zone and long photoperiod (Bonsi *et al*. 1992) are known to favor the development of non-storage, fibrous roots. The optimum pH for better root growth varies between 4.5-7.0. Whereas at pH below 3.5 no root growth occurs (Ilaava *et al*. 1995). The root cation exchange capacity (CEC) varies between 21-50 me 100 g^{-1} dry roots. Because of a strong positive correlation between root CEC and yield of tubers and lack of variation in root CEC in a particular cultivar at different seasons, the root CEC can be used as a reliable index to reflect the tuber yield. However, many of the agroclimatic factors including soil physical characters and fertility, plant spacing, soil moisture, soil and air temperature, are likely to influence the root system of sweetpotato plants.

Tubers

Tubers are capable of storing starch grains through localized lateral bulking in a specific sub-apical region of thick adventitious roots originating from the nodal region of underground portion of vine cuttings used for propagation. Such thick roots develop horizontally or obliquely in the soil. The initiation of tubers can be recognized on the basis of primary stelar structure of thick adventitious roots. The primary structure of thick roots varies. The thick roots are pentarch or hexarch or septarch at the base and tetrarch nearer to the apical meristem and contain a central pith with or without central metaxylem cells (Ravi and Indira 1996). Some roots which are tetrarch do not differentiate into tubers.

Tuber growth depends on the sink strength, the potential of leaves to export photosynthesis and on the photosynthetic efficiency of leaves (Keutgen *et al*. 2002). The initiation of tuber growth involves secondary growth by genesis of a vascular cambium as well as several anomalous circular cambia in the subapical region of thick roots (Ko *et al.* 1993; Ravi and Indira 1996). At the onset of secondary thickening, vascular cambium initials are first laid down within the parenchymatous zone lying between the xylem and phloem and are connected to form a continuous and irregular cylinder through division of the single layered pericycle. Subsequent vascular cambial activity leads to centripetal production of thin walled storage parenchyma, secondary vascular tissues and a regular cylinder of vascular cambium. Differentiation of vascular cambium is accompanied by the origin of anomalous circular cambia in the central pith around central metaxylem cell as well as around each of the discrete protoxylem elements. These meristems are referred to as anomalous primary cambia (Ko *et al*. 1993). Anomalous circular secondary cambia also originate around secondary xylem elements derived from the vascular cambium. Phellogen activity on the periphery of the tubers gives rise to the periderm. The time of initiation of tubers varies widely among cultivars and may occur during 1-13 WAP (Songhai *et al*. 1994; Ravi and Indira 1996) by which time the typical tuber number of a cultivar is determined.

Tuber growth occurs by the activity of vascular cambium as well as anomalous primary and secondary cambia. Cambial strips unassociated with vascular tissues also develop within the secondary parenchyma and contribute to tuber growth. Activity of all cambia results in the formation of thin walled, starch storing parenchyma cells. The contribution of different cambia in production of storage parenchyma varies among cultivars and appears to be cultivar characteristic. A high yielding cultivar will show extensive anomalous circular cambial activity compared to a low yielding cultivar. Cultivars with high activity of vascular cambium develop narrow uniform tubers whereas cultivars with both vascular cambium as well as anomalous cambial activity develop globular tubers (Ravi and Vimala 2001). For a detailed review on storage root formation and its molecular regulations, a detailed review is presented else-

where (Ravi *et al*. 2009).

In some tubers, cambial activity does not lead to lateral root bulking but results in uniform thickening of the entire root. Failure of further development of these tubers results from restricted activity of vascular cambium to produce a heavily lignified "pencil roots".

STARCH SYNTHESIS

Because starch is the major storage material in tubers of sweetpotato, tuber growth is influenced by the extent of starch synthesis and accumulation. Starch content of tubers also varies among sweetpotato cultivars.

Regulation of starch synthesis in sweetpotato tubers is little understood. As in other crops, starch is synthesized by starch synthase in tubers of sweetpotato. There are two forms of starch synthase, one tightly bound to the starch granule (starch granule-bound adenosine diphosphate glucose (ADPG) / uridine diphosphate glucose (UDPG) starch synthase) and the other a soluble form of the enzyme present in the amyloplasts (soluble ADPG (UDPG) starch synthase). In a developing sweetpotato tuber, starch granule-bound starch synthase activity is high during early period and it sharply declines during later periods (Babu and Nambisan 1996). Uridine diphosphate glucose (UDPG) is the predominant nucleotide during the early period while adenosine diphosphate glucose (ADPG) content is low and the latter increases during active growth. Starch granule-bound form of starch synthase prefers ADPG to UDPG as a substrate. However, the soluble form of starch synthase shows similar affinity to both ADPG and UDPG as substrates. Soluble starch synthase activity is much higher than the granule-bound enzyme activity throughout the tuber growth period. Because amylopectin makes up 70 to 80% of most starches and soluble starch synthase is responsible for its synthesis, it is likely that the soluble starch synthase activity is greater than the granule-bound starch synthase activity (Babu and Nambisan 1996). High activity of bound starch synthase during the early growth period and its sharp decrease at a later time indicates that amylose synthesis takes place early in the tuber growth (Babu and Nambisan 1996).

Although starch synthase is involved in starch synthesis, the enzyme does not account for differences in tuber dry matter and starch content among sweetpotato cultivars (Babu and Nambisan 1995). However, ADPG pyrophosphorylase (ADPGPPase) (enzyme that catalyse the synthesis of ADPG) activity shows a significant positive correlation with the dry matter and starch content of tubers (Tsubone *et al*. 1997). High ADPGPPase activity occurs in cultivars with high starch content whereas ADPGPPase activity is low in cultivars with lowest starch content. The rate of increase in starch content declines in parallel with decrease in ADPGPPase activity (Nakatani and Komeichi 1992b). Therefore the reaction catalysed by ADPGPPase appears to be more important than starch synthase in determining starch content of sweetpotato tubers. An increase in sugar concentration in the plant (stem) 27-63% increases ADPGPPase and sink activities or increase in C supply promotes starch synthesis and accumulation in roots (Kadowaki *et al*. 2001). However, activities of sucrose synthase (SUS), ADPGPPase, and starch synthase (SS) were highest in the tuber forming roots of sweetpotato rather than in thick and fibrous roots. Their activities were also greater in high yielding than in low yielding varieties (Yatomi *et al*. 1996).

TUBER BULKING PATTERN

Sweetpotato tuber yield is determined by the duration and rate of tuber growth which varies widely among cultivars. Sweetpotato tuber growth fluctuates over a long bulking period due to changes in the agroclimatic conditions. Hence, unlike cereal grains, the sweetpotato tuber can undergo periods of arrested growth during unfavorable conditions and then continues growth once conditions improve. High yielding cultivars have a high bulking rate over a long period whereas cultivars with intermediate and low tuber yield have a high bulking rate for short duration or low bulking rate for longer duration. In late bulking cultivars high bulking rate for short duration may also result in increase in tuber yield. Early maturing, short duration cultivars exhibit fast initiation and bulking of tubers whereby yields reach a maximum within a growing period of 12-16 weeks. Cultivars are classified into short duration or early maturing (12-17 weeks), medium duration (17-21 weeks) and long duration or late maturing (>21 weeks) types. The bulking rate of tubers of early maturing cultivars declines or even pauses at 12 WAP whereas for the late maturing cultivars bulking rate increases at the middle and later growth period. Short duration cultivars exhibit maximum bulking rate during 12-17 weeks period and the daily rate varies between 1.8-7.3 g plant^{-1} on fresh weight basis or 0.7-1.7 g plant^{-1} on a dry weight basis (Goswami *et al*. 1995). High and low yielding cultivars differ in their bulking rate and the period at which they exhibit the maximum bulking rate. Cooler night air temperature (11.3-26.4°C) (Mukhopadhyay *et al*. 1991), application of K (Mukhopadhyay *et al*. 1993), and 2 or 3 subsequent irrigations during 5-13th week of growth period (Goswamy *et al*. 1995) significantly increase the bulking rate of tubers. The tuber bulking rate shows a positive correlation with rainfall and relative humidity (Chowdhury 1994).

ENDOGENOUS GROWTH REGULATORS

Storage root growth (bulking) involves increase in size and weight through increase in cell number and cell size. Whereas the storage root weight increases through accumulation of photosynthates, increase in cell number and cell size in storage roots is under the control of endogenous growth regulators. Cytokinins help in the storage roots formation by developing and activating the primary cambium (Nakatani and Matsuda 1992; Tanaka *et al*. 2008). Longitudinal distribution of cytokinins in developing storage roots showed that the concentration of *trans*-ZR to be higher in parts of the proximal side than in distal parts of storage roots (Tanaka *et al*. 2008). In the transverse section of the storage roots, although *t*-ZR levels were higher in periderm (~90-140 pmol^{-1} g fresh root), moderate in primary vascular cambium (~ 80-140 pmol^{-1} g fresh root) and lower in central xylem-parenchyma region (~ 50-120 pmol^{-1} g fresh root) the differences were not significant. *Trans*-ZR content of roots increases rapidly when the thick roots begins to appear and declines later in storage roots growth. However, *t*-ZR content of fibrous roots does not change during the growth period. *Trans*-ZR content of thick storage roots is 6-7-fold greater than fibrous roots in the beginning. Developing and mature storage roots in the plant at 40 days after plantaing (DAP) showed 2.8- and 3.6-fold increase in *t*-ZR levels relative to that of fibrous roots at 14 DAP respectively (Tanaka *et al*. 2008). In a mutant with a late-storage root forming phenotype, the rapid increase in of *t*-ZR was suppressed (Nakatani *et al*. 2002). Furthermore, exogenous applications of synthetic cytokinins were reported to be effective in promoting storage root formation (Nakatani 1994). Therefore, it appears that cytokinins especially *t*-ZR participate in the activation of vascular cambium in sweetpotato roots. Cytokinin appears to be pre-requirement for proliferation of the cambial cell files in roots and stem (Nieminen *et al*. 2008)

Indole-3-acetic acid (IAA) is involved in maintaining the meristematic state of the cambial zone cells. The level of IAA was thought to be critical for pentarch or hexarch condition of the root, a prerequisite for storage roots initiation. IAA was found to be one of the phytohormone controlling the growth rate of tuber in potato but does not appear to play any direct role in storage organ formation (Menzel 1985). Application of IAA induced larger tuber formation in potato by counteracting effects of endogenous

GA (Xu *et al*. 1998). An increase in the activity of cell wall bound invertase in sweetpotato roots treated with auxin (Aux) and high levels of IAA oxidase activity in non-storage roots indicates that auxin might play a key role in storage root initiation (Acock 1984). Overexpression of genes for enzymes involved in auxin biosynthesis such as tryptophan decarboxylase and nitrilase may throw light on the role of auxin in sweetpotato storage root development. Auxin is known to regulate gene expression through targeted degradation of the short lived nuclear Aux / IAA proteins (Aux / IAA transcription repressors) that modulate the expression of wide range of genes (Leyser 2002; Dharmashree and Estelle 2004; Tan *et al*. 2007). With the recent progress in understanding the molecular mechanism of auxin signal transduction (Leyser 2002), the auxin mediated regulation of gene expression in sweetpotato storage roots warrants investigation.

The higher level of endogenous abscisic acid (ABA) in storage roots of *I. batatas* cultivar than non-storage roots of *I. trifida* indicates the involvement of ABA in storage root thickening by activating cell division, especially at the sedcondary meristem in the xylem (Oritani *et al*. 1983; Wang *et al*. 2005). Endogenous level of ABA also shows a positive correlation with the thickening potential of storage roots (Nakatani *et al*. 1987, 1988, 1989). ABA level remains much lower than that of *t*-ZR throughout the storage roots growth (Matsuo *et al*. 1988). ABA content of storage roots remains considerably greater in a cultivar with maximum root diameter than a cultivar with maximum number of thick storage roots. ABA content is higher in the vascular cambium zone than peripheral phloem and peripheral as well as central xylem (Nakatani and Komeichi 1991). These results indicate that ABA may be related to the activity of vascular and anomalous cambia and promotes cell differentiation and thickening of storage roots by itself or through interaction with cytokinin. Exogenous application of ABA stimulated tuber formation in potato (*Solanum tuberosum*) (Xu *et al*. 1998) by increasing numbers of tubers (Abdullah and Ahmad, 1980) and the earlier initiation of tubers (Menzel 1980). ABA has been proposed to be the tuber forming stimulus in potato (Menzel 1985) and the stimulation effect was proposed to be due to an antagonistic effect between ABA and GA (Krauss and Marschner 1982; Xu *et al*. 1998).

Jasmonic acid and related compounds are synthesized in leaves (Sembdner and Parthier 1993; Creelman and Mullet 1997; Mueller 1997) and roots (Abdala *et al*. 2003) and that JA is metabolized to tuberonic acid glucoside (TAG) and transported to all parts of the plant (Yoshihara *et al*. 1996). When the concentration of TAG reaches a sufficiently high level, the increase in the level of sucrose and enlargement of meristem occur before cell expansion in potato tuber formation (Takahashi *et al*. 1995). Extracts from the shoot of sweetpotato show the activity of jasmonic acid (JA) or JA-related compounds (JAs) whereas the JA activity was very high in storage roots (Nakatani and Koda 1992, 1993). In *I. batatas* cultivar, JA increases the frequency of storage roots formation as well as the diameter of storage roots (Nakatani 1994). The thickening of roots of *I. trifida* by grafting with the top organs of *I. batatas* cultivar also indicate that some substance(s) which stimulates root thickening are translocated from *I.batatas* shoot to roots of *I. trifida* (Hozyo and Park 1971). Whether JAs functions in combination with other phytohormones such as cytokinins, IAA, ABA for sweetpotato storage root formation warrants further investigation.

GENE EXPRESSION DURING STORAGE ROOT FORMATION AND DEVELOPMENT

The sweetpotato storage root formation and development is a complex process characterized by the cessation of root elongation, genesis of secondary vascular cambium, anomalous and interstitial cambia, increase in radial growth by increased rate of cell division, cell proliferation and cell expansion concomitant with the massive deposition of starch and of storage proteins such as sporamine which eventually result in enlargement of storage roots. These processes are mediated by the interaction of phytohormones such as auxins, cytokinins, jasmonic acids, abscisic acid and coordinated by the expression of several genes which are influenced by environmental and edaphic factors. There are several group of genes which are involved in the root development are discussed in detail below.

KNOXI genes

Knotted-like homeobox (*knox*) genes have been isolated from several plant species (Reiser *et al*. 2000). Recent molecular studies have identified number of these genes differentially expressed in developing sweetpotato storage roots (Tanaka *et al*. 2005). KNOXI proteins positively regulate cytokinin biosynthesis (Sakamoto *et al*. 2006) and negatively regulate gibberellin biosynthesis (Chen *et al*. 2004). Plants overproducing cytokinins exhibited higher levels of *KNAT1* and *STM* (*SHOOTMERISTEMLESS*) mRNA and overexpression of KNOX genes also led to modification of auxin and GA levels (Kusaba *et al*. 1998). The KNOXI genes are also involved in the development of sweetpotato storage root. The KNOXI genes regulate cytokinin levels in sweetpotato storage root. Tanaka *et al*. (2008) identified 3 different KNOXI gene fragments viz., *ibkn1*, *ibkn*2 and *ibkn3* in sweetpotato storage root. Expression of *Ibkn1* and *Ibkn2* were up-regulated in developing and mature sweetpotato storage roots. In sweetpotato plants, before storage root development (14 DAP), all three genes (*ibkn1*, *ibkn*2 and *ibkn3*) were highly expressed in internodes of mature stems. After storage root development (40 DAP), *ibkn*2 and *ibkn3* genes were highly expressed in developing and mature storage root as well as in stems. In developing and mature storage root, the expression of *ibkn1* was considerably lower than that in the stem. The expression patterns of *ibkn1* and *ibkn2* genes were consistent among sweetpotato cultivars. In contrast, the expression pattern of the *ibkn3* gene varied depending on the cultivar. In sweetpotato plants the expression of *ibkn1* and *ibkn3* were also observed in shoot apices. However, expression levels in shoot apices were significantly lower than those in storage roots. Expressions of *ibkn1*, *ibkn*2 and *ibkn3* were faint or undetectable in fibrous, non-storage root.

KNOXI genes (*Ibkn1* and *Ibkn2*) have functions in the storage root development process. High expression of KNOXI genes also seems to activate cytokinin biosynthesis as indicated by the high *t*-ZR content in developing sweetpotato storage roots whereas the lower *t*-ZR content in the distal end is concordant with the lower expression of KNOXI genes in this part (Tanaka *et al*. 2008). Alternatively, *t*-ZR accumulation may also induce the expression of KNOXI genes in sweetpotato storage roots, because the regulation of KNOXI genes by cytokinins has also been reported in *Arabidopsis.*

Tanaka *et al*. (2005) identified 10 storage root formation (SRF) genes, named from *SRF1* to *SRF10*, developmentally regulated during sweetpotato storage formation. Of these genes, the expression of *SRF1*, *SRF2*, *SRF3*, *SRF5*, *SRF6*, *SRF7* and *SRF9* increased during storage root formation, whereas that of *SRF4*, *SRF8*, and *SRF10* decreased. The *SRF4*, *SRF7* and *SRF8* genes were homologus to the enzymes involved in carbohydrate metabolism. The *SRF4* was thought to encode the rice cellulose synthase-like (Csl) protein putatively involved in the synthesis of *β*–linked polysaccharides. The *SRF7* appears to encode a UDP-glucosyltransferase. The *SRF1* and *SRF6* were homologus to the proteins involved in signal transduction. The *SRF1* appears to encode a transcriptional factor which is a Dof zinc finger protein. Dof zinc finger proteins have been reported to regulate variety of physiological processes, such as light response, auxin response, gibberellin response or guard cell specific gene expression (Yanagisawa 2002). The *SRF6* was homologus to the protein kinase which is involved in a wide

range of signaling processes. It encoded a receptor-like kinase (RLK) having a leucine-rich repeat (LRRs) motif in the extra-cellular domain. RLKs with LRR (LRR-RLKs) play various roles in plant development by transmitting extra-cellular signals. The *SRF6* was highly expressed around the circular primary cambium and anomalous secondary meristem in the xylem in storage roots. These tissues consist of actively dividing cells and cause the increase in root diameter during storage root formation. Since ABA promotes the thickening of the storage root by activating the meristems on the inside of the primary cambium and endogenous ABA is localized around the primary cambium and meristem in the xylem. Tanaka *et al*. (2005) proposed the possibility of ABA and *SRF6* function in the same signaling pathway, which controls storage root thickening. However, the relatively high expression of *SRF6* in stems and petioles suggests that this gene may be involved in the regulation of cell division in these organs. *SRF6*s expression was very low in leaves and not around the cork cambium. The *SRF8* appears to encode a neutral invertase-like protein while its expression decreased during storage root formation. The expression and activity of invertase has been shown to decrease during sweetpotato storage root development (Li and Zhang 2003). The *SRF5* appears to encode a heavy chain protein kinesin which is similar to KIN1 protein from maize. The maize KIN1 protein is structurally related to the human CENP-E protein which is involved in the process of cell division. This suggests that *SRF5* expression is related to active cell division during sweetpotato storage root formation. The *SRF9* was homologus to phytoene dehydrogenase, which is involved in bacterial carotenoid biosynthesis. It also showed similarity to the carotenoid isomerase of plants, which functions in the early step of plant carotenoid biosynthesis. Thus, *SRF9* was thought to encode an enzyme involved in carotenoid biosynthesis (Tanaka *et al*. 2005). The *SRF2* showed similarity to the NBS-LRR protein, a class of proteins involved in the recognition of pathogens. The *SRF3* was partially homologus to an ubiquitine conjugating enzyme, which usually works in selective protein degradation as a component of the ubiquitine / 265 proteosome pathway. However, *SRF2* and *SRF3* contained several stop codons, indicating that these genes are pseudogenes. The *SRF10* did not show significant homology to any known functional proteins, except for very weak similarities to polygalacturonase and the reverse transcriptase of *A*. *thaliana*.

MADS-box genes

MADS-box transcription factors have been found extensively controlling floral organ differentiation, MADS-box transcription factors appear to participate in divergent functions. Several MADS-box genes have been identified from sweetpotato roots, such as *IbMADS3*, *IbMADS4*, *IbMADS10*, *IbAGL20*, and *IbMADS79* (Kim *et al*. 2002, 2005b; Lalusin *et al*. 2006). These MADS-box genes derived transcription factors may contribute to root development at different stages (Kim *et al*. 2005b). The expression of *IbMADS3*, *IbMADS4* and *IbMADS79* has been detected mainly in fibrous roots before storage root formation while their expression was highest at root thickening. Transcripts of *IbMADS3* and *IbMADS4* in roots were found in the vascular cambium region where the most active cell proliferation occurs during storage root development. Recently, Ku *et al*. (2008) identified for the first time the expression of an *IbMADS1* (*Ipomoea batatas MADS-box 1*) gene (a typical MIKC type II MADS-box gene) during sweetpotato storage root formation. Among other MADS-box genes such as *IbAGL17*, *IbAGL20*, *IbMADS3*, *IbMADS4*, *IbMADS10* and *IbMADS79* identified from sweetpotato. In contrast, the expression of *IbMADS1* homologue was too low in all tissues from *Ipomoea leucantha* and *I*. *trifida*, which do not form storage roots but are the two close relatives and putative progenitors of sweetpotato. This clearly showed that the expression of *IbMADS1* was storage root organ dependant and seemed to be specifically expressed in sweetpotato among *Ipomoea* species (Ku *et al*. 2008). The *IbMADS1* expression was also tissue-specific and cell-specific and was not expressed in flowers or leaves in sweetpotato. In transverse sections of sweetpotato fibrous roots, the *IbMADS1* expression was mostly restricted to the stele, especially around the primary cambium as well as in the emerging lateral root primordium and immature vascular cells such as the protoxylem and protophloem within the root stele (Ku *et al*. 2008). Thus, active expression of *IbMADS1* appears to induce a signal-transduction pathway of cell proliferation and cell growth and activate starch biosynthetic genes to fill the storage parenchyma cells which eventually cause expansion of stele.

Spermidine synthase gene

Polyamines, spermidine (Spd, a triamine) and spermine (Spm, a tetramine) and their oblicate precursor putrescine (Put, a diamine) play important roles in plant growth, development and reproduction, plant tolerance to a wide array of environmental stresses such as low and high temperature (He *et al.* 2002), salinity and oxidative stress. Recently, Kasukabe *et al.* (2006) developed transgenic sweetpotato plants by introducing spermidine synthase gene (*FSPD1*) derived from *Cucurbita ficifolia*. The *FSPD1* – transgenic sweetpotato plants showed two fold increase in spermidine content as compared to the non-transgenic counterpart in both leaves and storage roots. The *FSPD1*-transgenic plants also had greater putrescine content in the leaves than the non-transgenic plants. The transgenic sweetpotato plants showed a similar rate of vine growth to the non-transgenic plants but the transgenic sweetpotato plants produced greater number and mass of storage roots under both stress (salinity and drought) and non-stress environments, showed greater tolerance to chilling and heat mediated damage to photosynthesis, and had enhanced oxidative stress tolerance compared to the wild type plants. Because, storage root formation depends upon active cell division in the primary cambium and the secondary meristems, polyamines may be involved in sweetpotato storage root formation. Thus, the marked increase in the spermidine content in the roots could have played a role in enhancing the potential for storage root formation in the *FSPD1*- transgenic sweetpotato plants (Kasukabe *et al*. 2006). The *FSPD1*-transgenic sweetpotato plants also had greater photosynthetic rate than non-transgenic sweetpotato plants because of higher storage root formation and the subsequent increase in the rate of assimilates flow to storage root sink. The *FSPD1*-transgenic sweetpotato plants also exhibited higher antioxidant enzyme activities in chloroplasts and showed a greater tolerance to oxidative stress (Kasukabe *et al*. 2006).

Source and sink relation

The yield of a crop depends on the production of assimilates by a “source” and the extent to which they can be accumulated in a “sink” represented by the organs which are harvested. In sweetpotato, the tubers which accumulate assimilates are the predominant sink. The shoots, mainly leaves, which produce assimilates are the source, although shoot growth is itself an important sink in the early period of crop growth. The photosynthetic rate and the leaf area can be regarded as the “source potential” while the number of tubers and the mean tuber weight can be regarded as the “sink capacity”. The source potential as well as sink potential varies widely among sweetpotato cultivars. The tuber yield is controlled not only by source potential but also by sink capacity. However, considering the wide variation in source potential and sink capacity among sweetpotato cultivars it is uncertain whether the source or the sink is limiting the tuber yield. Earlier studies were conducted to understand source and sink relations by changing the sizes of both source and sink. Source size has been varied by removing leaves while sink size has been varied either by

exposing the tubers to light or to different temperatures or by removing the tubers and by treating with growth regulators. Such treatments however, were likely to have an adverse effect on other physiological processes. To minimise interference with these processes, reciprocal grafts have been used (Ko *et al*. 1993).

Some studies indicate that in grafts between *I. batatas* and *I. trifida*, plants that had strong sink as stock accumulated dry matter much higher than plants with weak sink. Therefore, it was inferred that tuber yield of sweetpotato is determined primarily by sink capacity rather than source potential (Ko *et al*. 1992). However, both source potential and sink capacity can be factors limiting tuber yield. The relative contribution of source potential and sink capacity to tuber yield differs during the crop growth period among cultivars. The source potential is more limiting than sink during the early growth period but they are equally important in determining tuber yield at later growth period after the formation of tubers (Li and Kao 1990).

Several studies reveal a positive correlation between shoot weight and tuber weight indicating that tuber growth is closely associated with shoot growth (Mukhopadhyay *et al*. 1992, 1993). However, other studies indicate a negative correlation between shoot weight and tuber weight (Goswamy 1994). This means that tuber growth depends on the shoot growth to a certain extent. Excess shoot growth consumes greater amount of photosynthates and does not favor tuber growth. The number of branches shows negative correlation with tuber yield (Thankamma and Eswariamma 1990). LAI has a positive correlation with tuber yield (Chowdhury 1994). Sink related parameters like tuber number per plant shows positive significant correlation with tuber yield (Zang and Lian 1994). Sink characters like tuber girth and length, fresh weight per tuber (Zhang and Lian 1994) and bulking rate (Chowdhury 1994) show significant positive correlation with tuber yield.

Carbohydrate accumulates in the leaves of shoots grafted on to plants with low sink capacity (Ko *et al*. 1993). The P_N rate drastically declines when root enlargement is restrained. When grafted, the high sink capacity of high yielding cultivars increases the source potential of low yielding cultivars which in turn increases root yield (Zhong 1991). This is because higher sink capacity stimulates the translocation of photosynthates thereby reduces the carbohydrate content of the leaves and increases source potential (photosynthetic rate). The balance between source potential and sink capacity changes during the day, at different periods of growth, and due to change in environmental conditions. This makes it difficult to generalise the relative importance of either source or sink towards tuber development. Therefore, the relative contribution of source and sink towards tuber growth appears not to be constant throughout the growth period and appears to be specific to initiation and bulking period of tubers. More vine growth in cultivars represent more shoot activity which competes with tuber growth for assimilates. An active source coupled to a higher sink capacity is desirable provided that the source component should not be so active as a competitive sink.

Dry matter production and harvest index

Total dry matter (TDM) production and efficiency of dry matter (DM) allocation to tubers is an important factor determining tuber yield. The increase in TDM as well as tuber dry matter (TBDM) follows a sigmoid pattern in sweetpotato (Oswald *et al*. 1994). A few reports indicate a linear increase in TDM (Nair and Nair 1995) and TBDM (Nair and Nair 1995). The increase in TBDM is maximum during 7-23 weeks. In general, sweetpotato exhibits three growth phases based on dry matter partitioning. During the first phase, shoot growth dominates with an increasing proportion of DM diverted to shoot growth. This is followed by a second phase of constant partitioning of DM between shoot and tuber growth. During the third phase, a major portion of DM is partitioned to tubers. High soil moisture prolongs TDM production, reduces the proportion of DM allocation into tubers and diverts to shoot growth. An increase in N and K fertilizers considerably increase TDM and TBDM (Satapathy *et al*. 2005). An increase in plant population decreases TBDM and shoot DM per plant but significantly increases per hectare. Increase in shoot DM follows a hyperbolic pattern (Oswald *et al*. 1994).

The ratio between the TBDM and the TDM (harvest index, HI) indicates dry matter partitioning efficiency to tubers. Accordingly 80% HI has been estimated to equate tuber yield of the order of 46 t ha^{-1} for a 16 weeks crop or 69 t ha^{-1} for a 24 weeks crop. Sweetpotato cultivars differ in TDM production and cultivars with higher TDM divert more DM to tubers than those with lower TDM. High yielding cultivars divert more DM to tuber than low yielding cultivars. The HI among sweetpotato cultivars varies between 11-85% when harvested during 12-24 weeks (Goswami *et al*. 1995). Excess or inadequate soil moisture reduces HI (Goswami *et al*. 1995). Application of N fertilizer either has no influence or reduces HI (Nair and Nair 1992) while K increases it.

HI has a strong positive correlation with tuber yield (Bhagsari and Ashley 1990). There is a strong positive correlation between TBDM and TDM and between HI and TBDM. The correlation between HI and TDM is positive but insignificant (Li *et al*. 1991). The HI and tuber dry weight of cultivars respond differently to a change in the environment. Because, variation in HI among individual plants within cultivars is small as compared to the TBDM and HI might be influenced to a lesser extent than TBDM by change in environmental conditions (Li *et al*. 1991). HI can be used as reliable selection parameter.

RESPONSE TO STRESS

Sweetpotato production may be increased by increasing yield per unit area or increasing area under cultivation. Yield increases per unit area can be achieved by breeding and subsequent selection program. However, most of the land available in the tropics is limited in its productive capacity by either unfavorable soil properties or climatic conditions. Therefore, for increasing area under cultivation, attention must be given to developing resistant cultivars to various stress conditions.

Water deficit

Sweetpotato yields best when irrigated at 25% available soil moisture and there is no increase in storage yield by maintaining soil moisture >50%. Under typical production conditions, the crop requires 500 mm water for 16-20 weeks growth period (Chukwu 1995). However, tuber yields are affected by amount, timing and distribution of water. Tuber yield decreases under water deficit stress (WDS) particularly when the available soil moisture decreases below 20% (Nair *et al*. 1996). Irrigation less than 50% of cumulative pan evaporation rate also has been reported to decrease tuber yield (Indira and Kabeerathumma 1990; Chowdhury 1996). The tuber initiation period is the most sensitive to WDS due to its effect on tuber number (Nair *et al*. 1996; Ravi and Indira 1996). WDS during tuber initiation period induces lignification of tubers and hampers tuber growth. Lignification and reduction in tuber yield is greater in cultivars with weak sink capacity than those with higher sink capacity (Ravi and Indira 1996).

The reduction in tuber yield under WDS is also related with physiological and biochemical changes in the leaves. Under WDS conditions, water potential (WP_L) or relative water content (RWC) of sweetpotato leaves decreases (Chowdhury and Naskar 1993; Ravi and Indira 1995). Leaves permanently wilt when WP_L decreases to -1.3 MPa and at WP_L between -1.6 and -2.0 MPa the leaves senesce (Ravi and Indira 1995). The decrease in WP_L increases S_R to CO_2 exchange (Indira and Kabeerathumma 1990) causing reduction in P_N rate (Ravi and Indira 1996). Cultivars differ

in their tolerance to WDS conditions (Ravi and Indira 1996). Tolerant cultivars have greater S_R than the susceptible ones (Kubota *et al*. 1993). High S_R in tolerant cultivars may be advantageous for conserving leaf water content at the cost of reduction in photosynthesis under WDS. This helps tolerant cultivars to have lower desiccation rate in the leaf tissue than the susceptible ones (Naskar and Chowdhury 1995). Under WDS conditions, increase in CO_2 concentration surrounding the leaf improves the WP_L and the tuber yield (Bhattacharya *et al*. 1990b). Drought resistance was significantly and positively correlated with RWC and antioxidative enzyme like superoxide dismutase (SOD) activity but negatively correlated with malondealdehyde (MDA) content in leaves (Zhang *et al*. 2005). Overexpression of Cu/Zn SOD and APX in chloroplasts of sweetpotato enhanced drought tolerance. However, tuber formation in transgenic plants was poor (Lu *et al.* 2010).

The total chl, chl *a* (chl *a*), chl *b* content and ratio of chl *a* and *b* of leaves decreases in sweetpotato plants subjected to WDS (Zhang *et al*. 2002). Cultivars tolerant to WDS have lower chl and higher ATP content (Zhang *et al.* 2002) in leaves than the susceptible ones. Under WDS conditions, nitrate reductase (NR; the first enzyme of the nitrate assimilatory pathway which reduces NO_3^- to NO_2^- in the cytosol) activity decreases in sweetpotato leaves (Indira and Kabeerathumma 1990). In corn (*Zea mays* L.) and barley (*Hordeum vulgare* L.) plants, nitrate reductase (NR) activity decreased due to decrease in protein synthesis but not due to NO_3^- amount in stressed tissue. Whether the decrease in NR activity in stressed sweetpotato leaves is due to decrease in the enzyme activity itself because of decrease in protein synthesis or due to decrease in NO_3^- uptake or both, is not known. In cotton (*Gossypium hirsutum* L.) plants, during WDS, N deficiency promoted ABA accumulation which in turn induced stomatal closure and decrease in stomatal conductance at a higher WP_L than normal. However, in sweetpotato, under WDS, the interaction among low N, WP_L, ABA, and stomatal closure is not known. Because the inflow of inorganic N into plants is largely controlled by NR activity, reduction in NR activity under WDS may limit growth, development and protein synthesis. Sweetpotato cultivars tolerant to WDS have greater NR activity than the susceptible ones (Naskar and Chowdhury 1995). In 15 cultivars, the IAA, GA, ZR and iPA content in leaves decreased while ABA increased during drought (Zhang *et al*. 2002).

Drought tolerant sweetpotato cultivars accumulate greater amount of proline in the leaf and fibrous root tissues than the plants under WDS free conditions (Ravi and Indira 1997). In both tolerant and susceptible cultivars, leaves accumulate greater amount of proline than the non-storage, fibrous roots (Ravi and Indira 1996). However, some susceptible cultivars which do not yield but survive under WDS also accumulate good amount of proline in their leaf tissues (Ravi and Indira 1997). Because most of the proline accumulation occurs after growth has ceased, proline does not seem to influence sweetpotato plant growth during WDS. Free proline accumulation was also not correlated with drought resistance in sweetpotato (Zhang *et al*. 2005). The transgenic sweetpotato plants transformed with spermidine synthase gene (*FSPD1*) had 2-fold increase in foliar and tuber spermidine (Spd) content, higher photosynthetic rate, lower H_2O_2 concentrations in leaves due to higher antioxidant enzyme activity in chloroplasts, produced more number of larger tubers and showed greater tolerance to drought stress conditions (Kasukabe *et al*. 2006).

Flooding

In the tropics, waterlogging in the field during heavy rain storms or excess soil moisture in heavy soils with poor drainage, impedes the growth of plants by restricting the availability of O_2 in the root zone. Because induction and growth of tubers depend on the presence of sufficient O_2 in soil, anaerobiosis during waterlogging or surplus soil moisture reduces tuber production. Excessive vegetative growth under high soil moisture conditions results in low tuber production (Goswamy *et al*. 1995). Cultivars differ in their abilities to withstand flooding or surplus soil moisture. In rooted sweetpotato leaves flooding induces fewer tubers and increases the fibrous root dry weight. Flooding induces reduction in the number, size and diameter of tubers and increases in the shoot fresh weight, presumably due to the decrease of sink capacity which in turn inhibits the translocation of photosynthate to tubers. High temperatures during flooding also enhance leaf senescence. Plants subjected to flooding during early period of growth resumes their normal growth better than plants subjected to flooding later in the development cycle. Therefore, the reduction in storage yield is greater in plants exposed to flooding at later growth period than plants that are subjected to flooding at early growth period. Flooding resulted in less reduction of tuber yield in grafted plants with high sink capacity than those with poor sink capacity. Therefore, it appears that cultivars with high sink potential tolerate flooding than those with weak sink potential. Transient flooding (flooding two days in a week) however, increases shoot growth and tuber yield. The physiological and biochemical changes associated with flooding and the mechanism of flood tolerance needs investigation. The level of antioxidants (AOs) and AO enzyme (glutathione reductase) activities of sweetpotato leaves increase during flood stress and induce flood tolerance (Lin *et al*. 2006).

PROPAGATION PHYSIOLOGY

Sweetpotato is normally propagated vegetatively by vine cuttings. However, where vines are unavailable for planting, root sprouts and storage root pieces can be used for propagation. Micropropagation techniques and propagation from true seed have been suggested but neither of these methods is practical.

Vine cuttings

Vine cuttings are used as planting material in tropical regions. Cuttings are normally taken straight from one field being harvested to the one being planted. Adequate soil moisture, aeration, light, and heat are necessary for better establishment of vine cuttings. Portion of the vine from which cuttings are made, age of the source plants, physiological state of the cuttings, number of days the cuttings stored influence growth and subsequent storage root yield. The advantage of vine cuttings is that they are free from soil born diseases but not viral diseases (Phills and Hill 1984). Cuttings from the shoot apex are better planting material than basal or middle vine cuttings (Villamayor Jr. and Perez 1988a; Balasurya 1991; Schultheis and Cantliffe 1994). Plants grew from apical and middle cuttings accumulate maximum dry matter in the storage roots. Age of the source plants from which cuttings are taken is a critical factor. Storage root yields are significantly reduced when cuttings from older plants are used. The yield of plants from basal cuttings was 56% lower than those from apical shoot cuttings whereas yield of mixed plants was 13% lower than those from the apical vine cuttings (Villamayor Jr. and Perez 1988a). Thus for better storage root yields apical cuttings can be used. When there is scarcity of apical vine cuttings the middle or basal cuttings from any age of the source plant can be used.

The presence of leaves on vine cuttings greatly increases adventitious root production presumably due to the presence of active endogenous root promoting substances). Storage root yield is significantly higher in plants from vine cuttings with foliage than plants from cuttings without foliage (Ravindran and Mohankumar 1989). Therefore stripping of vine cuttings should be avoided if vine cuttings are to be stored.

For better storage root yield, 20-40 cm long vine cuttings should be used (Bautista and Vega 1991). Plants from

cuttings stored for 2-5 days under damp but well aerated conditions yield better than those from fresh cuttings (Ravindran and Mohankumar 1989; Nwinyi 1991; Villamayor Jr. 1991).

Root sprouts

Sprouts produced from storage roots also may be used for propagation. In temperate regions, immediately after harvest, storage roots are exposed to higher temperature about 32°C and 85% RH for about one week (curing) and then stored at about 16°C and 85% RH. During the next planting season, sound storage roots are taken from the stored lot, exposed to about 32°C and 85% RH (presprouting). Brief extension of curing and pre-sprout period induce early sprouting and increase sprout production. The pre-sprouted storage roots are then buried in moist sand or soil beds and stimulated to sprout by application of moisture. The bedded storage roots sprout within 2 weeks and about 4-6 weeks after bedding, the first batch of spouts of desirable length (20 cm) are ready for harvest. Subsequent harvests can be made at weekly intervals. Sprouts from the earlier harvests may be stored with their bases dipped into moist sandy loam soil in trays. When sufficient spouts are collected they are transplanted to the field. Cutting the storage roots transversely in to 3 or 4 sections increases sprout production. Experimental results show that ethylene chlorhydrin, thiourea or acetylene, 2,4-D, NAA, α-methoxyphenyl acetic acid, β-naphthoxyacetic acid, 3,4-dichlorophenyl α-methoxy acetic acid, dimethyl sulfoxide (DMSO), 3-IBA plus DMSO, ethephon and GA_3 (Hall 1994) increase the number of sprouts from treated storage roots with earlier sprouting in the ethephon or GA_3 treatments. However, sprouts produced through chemical treatments are not suitable for transplantation.

Cut root pieces

Several workers studied the potential of using cut storage root pieces directly as planting material (Mohankumar and Potty 1993). Cutting the storage root into pieces of 2.5 cm thickness decreases the proximal dominance and enhances sprout production. Larger root pieces produce progressively larger sprouts but these sprouts are substantially smaller than sprouts produced by intact roots. Cut roots produce more vigourous shoot growth and more adventitious roots but less uniform storage roots than vine cuttings. Smaller root pieces (6.4 cm^2) produce slightly more sprouts per cm^2 of surface area than the larger root pieces. The set size may be 20-50 g or 40-50 cm^3. Curing of cut root pieces for 24 h at 30-35°C and 100% RH or treatment with IBA and BA stimulates formation of adventitious roots and shoots. Mohankumar and Potty (1993) found no significant difference in the yield of marketable storage roots or vine, when damaged, non-marketable as well as good quality marketable roots were used as planting material. However, this technique is not yet useful in commercial production.

Micropropagation

There is an increasing interest in the micropropagation of sweetpotato through somatic embryogenesis and other *in vitro* cultures. Use of somatic embryogenesis in a seeding system offers several potential advantages e.g. the production of large quantities of propagules in limited space, maintenance of genetic uniformity, rapid propagule multiplication (Monica *et al*. 2009), and direct planting of somatic embryos in the field thus eliminating cost of transplanting and reduce incidence of disease (Bienick *et al*. 1995; Liu *et al*. 2001). Within 3-4 weeks, somatic embryos and plantlets with roots and shoots could be successfully regenerated from embryogenic callus derived from shoot apical meristem (Schultheis and Cantliffe 1992), stem and root explants, leaf explants, anther, nodal explants, petiole explants, petiole protoplasts, stem and petiole protoplasts and mesophyll cell suspension (reviewed in Ravi and Indira 1999). Such plantlets could successfully establish in the field.

Addition of salts and carbohydrates within hydroxyethyl cellulose gel increase plantlet production from somatic embryos where suspension of somatic embryos in a vicious gel supplied with growth additives was performed (Schultheis and Cantliffe 1992). Inclusion of hormones, beneficial microbes may improve embryo growth or inclusion of pesticides can prevent growth of microbes that would inhibit embryo development into plantlets. Torres *et al*. (2001) found that the number of somatic embryos increased from callus proliferation cultures when they were pulsed with 0.1 μM ABA for 14 days and addition of mannitol also improved the synchrony of sweetpotato somatic embryos.

Photoautotrophic micropropagation using sugar-free medium is an alternative to conventional method for commercial scale production of plantlets. It offers great advantages in terms of faster growth and higher biomass production *in vitro* compared to conventional tissue culture techniques. The demand for quality planting materials necessitates the scaling-up of photoautotrophic micropropagation systems. Forced ventilation photoautotrophic micropropagation systems were developed leafy stem cuttings of sweetpotato with nutrients but without sugar (Heo and Kozai 1991; Zobayed *et al*. 1999b). The inlet CO_2 concentration of the system was 1500 μmol mol^{-1} and the photosynthetic photon flux on the culture shelf was 150 μmol m^{-2} s^{-1}. The net photosynthetic rate and dry mass of sweetpotato plug plantlets from the forced ventilation treatment on day 22 were 30-40 times and 4-6 times greater, respectively, than those of the plantlets grown under the conventional, photomixotrophic micropropagation in gelled agar medium containing sugar. Zobayed *et al*. (1999a) used vermiculite mixed with 30% (w/w) paper pulp as supporting material in photoautropic micropropagation of sweetpotato and achieved higher growth performance. The shoot and root fresh mass were ×2.7 greater than that in agar; the leaf, stem and root dry mass were also greater and at least two fold. The plantlets grown photoautotrophically under forced ventilation survived better when transplanted directly into soil in the greenhouse (without e*x vitro* hardening) and grew faster. This was because they were better able to control transpiration and thus lost less water and showed no signs of wilting. In contrast, plantlets cultured under photomixotrophic conditions had open stomata which were not functional, a higher transpiration rate, and uncontrolled and rapid water loss immediately after transfer *ex vitro* (Zobayed *et al*. 2000).

Seed

Use of true seeds for sweetpotato production may simplify the planting process compared with the routine method of planting vine cuttings but genetic segregation would make true seed propagation unlikely. Many problems affect seed production in sweetpotato. Cultivars that do not flower readily can be stimulated to flower by various techniques. However, problems of incompatibility and sterility impede controlled pollination in sweetpotato. Serious physiological problems, occurring as post-pollen germination barriers to fertility, often impede seed production in sweetpotato even when a cross is compatible. Compared with vine cutting planting, storage root yield is significantly reduced in true seed planting (Schultheis and Cantliffe 1994). Storage root yield varies widely among the true seed population and cultivars tend to have higher storage root weight ratio than the true seed population. True seed method does not appear to be promising for sweetpotato propagation.

CONCLUSION

Over the past five decades understanding of the growth and productivity of sweetpotato has rapidly increased, although it still remains incomplete. Under tropical conditions,

sweetpotato can be grown throughout the year wherever water is available through rain or irrigation. Although productivity of sweetpotato is high under cool climate conditions, there is a wide gap between the potential and average yield due to vagaries of agroclimatic conditions. In view of the changing climatic conditions, sweetpotato varieties have to be developed with new potential to combat abiotic stresses such as water deficit and high temperature stresses under high CO_2 environment. The knowledge on genes identified for abiotic stress tolerance and starch biosynthesis has to be exploited for high productivity of sweetpotato in the weird climate conditions.

REFERENCES

Antony A, Inasi KA (1990) Performance of some sweet potato cultivars in Kuttanad. *Journal of Root Crops* **16**, 51-52

Babu L, Nambisan B (1995) Synthesis and turnover of starch. In: *Annual Report 1995*, Central Tuber Crops Research Institute, Trivandrum, India, pp 41-42

Babu L, Nambisan B (1996) Synthesis and turnover of starch in sweet potato. In: *Annual Report 1996*, Central Tuber Crops Research Institute, Trivandrum, India, 27 pp

Balasurya G (1991) Socioeconomic aspects of sweetpotato production in Sri Lanka. In*: Sweetpotato Cultivars of Asia and South Pacific, Proceedings of 2nd Annual UPWARD International Conference*, Los Baños, Philippines, pp 261-267

Bautista AT, Vega BA (1991) Indigenous knowledge systems on sweet potato farming among Marano Muslims in northern Mindanao. In: *Sweetpotato Cultivars of Asia and South Pacific, Proceedings of 2nd Annual UPWARD International Conference*, Los Baños, Philippines, pp 149-161

Bhagasri AS, Ashley DA (1990) Relationship of photosynthesis and harvest index to sweet potato yield. *Journal of the American Society of Horticultural Science* **115**, 288-293

Bhagsari AS (1990) Photosynthetic evaluation of sweet potato germplasm. *Journal of the American Society of Horticultural Science* **115**, 634-639

Bhattacharya NC, Bhattacharya S, Tolbert MEM (1990a) Characterization of carotene in sweet potato (*Ipomoea batatas*) grown at CO_2 enriched atmosphere under field conditions. In: Hodgson RH (Ed) *Proceedings Plant Growth Regulators Society of America 17th Annual Meetings of Plant Growth Regulator Society*, Ithaca, New York, pp 126-123

Bhattacharya NC, Ghosh PP, Hileman DR, Alemayehu M, Huluka G, Biswas PK (1992) Growth and yield of sweet potato under different carbon dioxide concentrations. In: Hill WA, Bonsi CK, Loretan PA (Eds) *Sweet Potato Technology for the 21st Century*, Tuskegee University, Tuskegee, AL, pp 333-336

Bhattacharya NC, Hileman DR, Ghosh PP, Musser RL, Bhattacharya S, Biswas PK (1990b) Interaction of enriched CO_2 and water stress on the physiology and biomass production in sweet potatos grown in open top chambers. *Plant, Cell and Environment* **13**, 933-940

Bienick ME, Harrell RC, Cantliffe DJ (1995) Enhancement of somatic embryogenesis of *Ipomoea batatas* in solid cultures and production of mature somatic embryos in liquid cultures for application to a bioreactor production system. *Plant Cell, Tissue and Organ Culture* **41**, 1-8

Bonsi CK, Loretan PA, Hill WA, Mortley DG (1992) Response of sweet potatoes to continuous light. *HortScience* **27**, 471

Brown RH (1992) Photosynthesis and plant productivity. In: Hill WA, Bonsi CK, Loretan PA (Eds) *Sweet Potato Technology for the 21st Century*, Tuskegee University, Tuskegee, AL, pp 273-281

Cen YP, Sage RF (2005) The regulation of Rubisco activity in response to variation in temperature and atmospheric CO_2 partial pressure in sweet potato. *Plant Physiology* **139**, 979-990

Chowdhury SR (1994) Environmental factors and the physiological basis of variation in yield potential in sweet potato. *Orissa Journal of Horticulture* **22**, 58-65

Chowdhury SR (1996) Effect of different irrigation treatments on water requirements in sweet potato. *Journal of Root Crops* **22**, 50-53

Chowdhury SR, Naskar SK (1993) Screening of drought tolerance traits in sweet potato: Role of relative water content. *Orissa Journal of Horticulture* **21**, 1-4

Chowdhury SR, Ravi V (1990) Effect of clipping of vines on the biomass yield in sweet potato. *Journal of Root Crops* **16**, 4-7

Chowdhury SR, Ravi V (1991) Growth analysis of five sweet potato cultivars grown in summer under Bhubaneswar conditions. *Journal of Root Crops, ISRC National Symposium Special* **17**, 104-107

Chukwu GO (1995) Crop irrigation water needs of sweet potato (*Ipomoea batatas*). *African Journal of Root Tuber Crops* **1**, 35-38

CTCRI (2006) *Tuber Crop Varieties*, Central Tuber Crops Research Institute, Technical Bulletin Series 24, 64 pp

Dasgupta M, Mukherjee A, Sahoo MR, Naskar SK, Kole PC (2006) Physiological response of orange fleshed sweet potato (*Ipomoea batatas* L.) genotypes to sodium chloride stress conditions. *Journal of Root Crops* **32**, 53-58

David PP, Trotman AA, Mortley DG, Bonsi CK, Loretan PA, Hill WA (1995) Foliage removal influences sweet potato biomass yields in hydroponic culture. *HortScience* **30**, 1000-1002

Eguchi T, Kitano M, Yoshida S, Chikushi J (2003) Root temperature effects on tuberous root growth of sweet potato (*Ipomoea batatas* Lam). *Environment Control in Biology* **41**, 43-49

El-Gamal AM (1994) Effects of paclobutrazol, a plant growth retardant levels on sweet potato yield and root quality. *Alexandria Journal of Agricultural Research* **39**, 385-397

FAO (2006) www.fao.org

Garner Jr. JO, Newell CPL, Woods FM, Silva JL (1992) Chilling and drought tolerance in selected sweet potato genotypes. In: Hill WA, Bonsi CK, Loretan PA (Eds) *Sweet Potato Technology for the 21st Century*, Tuskegee University, Tuskegee, AL, pp 318-324

Ghosh SP (1991) Growth potentials of sweet potato and cassava under different agro-ecological settings of India. *Journal of Root Crops* **17**, 130-138

Golder PC, Hossain M, Bhuiyan MKR, Ilangantileke S, Attaluri S (2007) Performance of 'Bari Sp-6' and 'Bari Sp-7' the newly released high-yielding sweet potato varieties from Bangladesh. *Journal of Root Crops* **33**, 16-19

Goswami RK (1991) Variation of growth attributes and quality parameters in some sweet potato genotypes. *Journal of Root Crops, National Symposium ISRC Special* **17**, 73-75

Goswami SB, Sen H, Jana PK (1995) Tuberization and yield potential of sweet potato cultivars as influenced by water management practices. *Journal of Root Crops* **21**, 77-81

Goswamy RH (1994) Performance of sweet potato cultivars in winter under Assam Conditions. *Journal of Root Crops* **20**, 132-134

Hall MR (1994) Early sweetpotato plant production increased by GA_3 and BA plus GA_{4+7}. *HortScience* **29**, 126

Hamid S, Sasaki O (2001) Studies on effect of planting density on the growth and yield of sweet potato (*Ipomoea batatas* Lam.). *Memoirs of the Faculty of Agriculture, Kagoshima University* **37**, 1-10

He SG, Chen SS, Li MQ (1992) Effect of P-deficiency on photosynthesis and photo-transpiration of isolated cells from sweet potato. *Plant Physiology Communication* **28**, 342-344

He SG, Chen SS, Li MQ (1993) The effect of photorespiration on phosphate metabolism during photosynthesis. *Journal of Tropical and Subtropical Botany* **1**, 64-70

Heo J, Kozai T (1999) Forced ventilation micropropagation system for enhancing photosynthesis, growth, and development of sweetpotato plantlets. *Environmental Control in Biology* **37**, 83-92

Holwerda HT, Ekanayake IJ (1991) Establishment of sweet potato stem cuttings as influenced by size, depth of planting, water stress, hormones and herbicides residues for two genotypes. *Scientia Horticulture* **48**, 193-203

Ilaava VP, Asher CJ, Blamey FPC (1995) Growth of sweet potato (*Ipomoea batatas* L.) as affected by pH in solution culture. In: Date RA, Granden NJ, Rayment GE, Probert ME (Eds) *Development in Plant and Soil Sciences*, Kluwer Academic Publications, Dordrecht, Netherlands, pp 627-630

Indira P, Kabeerathumma S (1990) Physiometabolic changes in sweet potato grown under different levels of soil moisture. *Journal of Root Crops* **16**, 28-32

Itong RB, Villamayor Jr. FG (1991) Effect of shading on some root crops. *Radix* **13**, 8-9

Jayakrishnakumar V, Shobhana S, Sheela KR (1990) Defoliation of vine cuttings on the performance of sweet potato. *Journal of Root Crops, National Symposium ISRC Special* **17**, 126-128

Jeong BC, Oh SK (1991) Effects of soil texture on growth, yield and palatability of steamed sweet potato. The Research Republic of Rural Develop Administration 33, (U & I) Suwon Republic of Korea

Kadowaki M, Kubota F, Saitou K (2001) Effects of exogenous injection of different sugars on leaf photosynthesis, dry matter production and adenosine 5'-diphosphate glucose pyrophosphorylase (AGPase) activity in sweet potato (*Ipomoea batatas* Lam.). *Journal of Agronomy and Crop Science* **186**, 37-41

Kanyo Y, Mano K (2002) The effects of night temperatures on diurnal changes in carbohydrate contents in roots and stems of sweet potaoes (*Ipomea batatas* Poir). *Journal of the Japanese Society of Horticultural Science* **71**, 747-751

Kasukabe Y, He L, Watakabe Y, Otani M, Shimada T, Tachibana S (2006) Improvement of environmental stress tolerance of sweet potato by introduction of genes for spermidine synthase. *Plant Biotechnology* **23**, 75-83

Kelm M, Bruck H, Hermann M, Sattelmaher B (2001) Plant productivity and water use efficiency of sweet potato (*Ipomoea batatas* Lam.) as affected by nitrogen supply. Scientists and farmers: Partners in research for the 21st century, Programme Report 1999-2000, pp 273-279

Keutgen M, Kubota F, Saitou K (2001) Effects of exogenous injection of sucrose solution to plant on the carbon distribution to tuberous root and tuberous root production in sweet potato (*Ipomoea batatas* Lam.). *Japanese Journal of Crop Science* **70**, 575-579

Kim SH, Mizuno K, Sawada S, Fujimura T (2002) Regulation of tuber formation and ADP-glucose pyrophosphorylase (AGPase) in sweet potato (*Ipomoea batatas*) (L.) Lam., by nitrate. *Plant Growth Regulation* **37**, 207-213

Ko JY, Chen CY, Kuo G (1992) The relationship between source-sink and photosynthates partitioning in self and reciprocally grafted leaf cuttings of

sweet potato. *Journal of Agricultural Association China New Service* **159**, 18-28

Ko JY, Chen CY, Kuo G (1993) Activity of anomalous cambium and sink capacity in self and reciprocally grafted leaf cuttings of sweet potato. *Journal of the Agricultural Association China New Service* **161**, 1-10

Kubota F, Knof R, Yatomi M, Agata W (1992a) Scoring method of stomatal aperture of sweet potato (*Ipomoea batatas* Lam.) leaf. *Japan Journal of Crop Science* **61**, 687-688

Kubota F, Yatomo M, Agata W (1992b) CO_2 exchange rate in sweet potato (*Ipomoea batatas* Lam.) leaves with and without lower epidermis. *Photosynthetica* **26**, 257-260

Kubota F, Yoshimura Y, Agata W (1993) Stomatal movement and CO_2 exchange rate of sweet potato plant (*Ipomoea batatas* Lam.) in relation to water environments - A comparison between native and improved varieties. *Journal of Faculty of Agriculture Kyushu University* **38**, 97-110

Li L, Kao CH (1990) Variations of sweet potatoes with respect to source potentials and sink capacities. *Euphytica* **47**, 131-138

Li L, Liao CH, Chin L (1994) Variability in taste and physico chemical properties and its breeding implications in sweet potatoes (*Ipomoea batatas*). *Journal of Agricultural Association China New Service* **165**, 19-31

Li L, Liao CH, Lo HF (1991) Stability of harvest index and root yield of sweet potatoes. *Journal of Agricultural Association China New Service* **154**, 3-13

Lin KHR, Tsou CC, Hwang SY, Chen LFO, Lo HF (2006) Paclobutrazole pre-treatment enhanced flooding tolerance of sweet potato. *Journal of Plant Physiology* **163**, 750-760

Liu Q, Zhai H, Wang Y, Zhang D (2001). Efficient plant regeneration from embryogenic suspension cultures of sweetpotato. *In Vitro Cellular and Developmental Biology – Plant* **37**, 564-567

Lu YY, Deng X-P, Kwak S-S (2010) Over expression of CuZn superoxide dismutase (CuZn SOD) and ascorbate peroxidase (APX) in transgenic sweet potato enhances tolerance and recovery from drought stress. *African Journal of Biotechnology* **9**, 8378-8391

Mannan MA, Bhuiyan MKR, Quasem A, Rashid MM, Siddique MA (1992) Studies on the growth and partitioning of dry matter in sweet potato. *Journal of Root Crops* **18**, 1-5

Mitsuya S, Takeoka Y, Miyake H (2000) Effects of sodium chloride on foliar ultrastructure of sweet potato (*Ipomoea batatas* Lam.) plantlets grown under light and dark conditions *in vitro*. *Journal of Plant Physiology* **157**, 661-667

Mohankumar CR, Potty VP (1993) Standardisation of nursery techniques for cassava and sweetpotato. In: *Annual Report*, Central Tuber Crops Research Institute, Trivandrum, India, pp 79-82

Monica SM, Pecota K, Yencho C, Allen G, Sosinski B (2009) Rapid shoot regeneration in industrial 'high starch' sweetpotato (*Ipomoea Batatas* L.) genotypes. *Plant Cell, Tissue and Organ Culture* **97**, 109-117

Mortley DG, Bonsi CK, Lorentan PA, Hill WA, Morris CE (1994) Relative humidity influences yield, edible biomass and linear growth rate of sweet potato. *HortScience* **29**, 609-610

Mortley DG, Lorentan PA, Bonsi CK, Hill WA, Morris CE (1991) Plant spacing influences yield and linear growth rate of sweet potatoes grown by hydroponically. *HortScience* **26**, 1274-1275

Mukhopadyay SK, Sen H, Jana PK (1990) Effects of planting materials on growth and yield of sweet potato. *Journal of Root Crops* **16**, 119-122

Mukhopadyay SK, Sen H, Jana PK (1991) Effect of time of planting on growth, yield parameters and tuber yield of sweet potato. *Journal of Root Crops* **17**, 19-25

Mukhopadyay SK, Sen H, Jana PK (1992) Effect of potassium on growth and yield of sweet potato. *Journal of Root Crops* **18**, 10-14

Mukhopadyay SK, Sen H, Jana PK (1993) Dry matter accumulation, starch and nutrient concentration in sweet potato as influenced by potassium nutrition. *Journal of Root Crops* **19**, 21-28

Mulungu LS, Mwailana DJ, Reuben SS, Tarimo JPA, Massawe AW, Makundi RH (2006) Evaluation on the effect of topping frequency on yield of two contrasting sweet potato (*Ipomoea batatas* L.) genotypes. *Journal of Applied Science* **6**, 1132-1137

Nair DB, Nair VM (1992) Nutritional studies in sweet potato. *Journal of Root Crops* **18**, 53-57

Nair GM, Nair VM (1995) Influence of irrigation and fertilizers on the growth attributes of sweet potato. *Journal of Root Crops* **21**, 17-23

Nair GM, Nair VM, Sreedharan C (1996) Response of sweet potato to phasic stress irrigation in summer rice fallows. *Journal of Root Crops* **22**, 45-49

Nakatani M (1994) *In vitro* formation of tuberous roots in sweet potato. *Japanese Journal of Crop Science* **63**, 158-159

Nakatani M, Koda Y (1993) Identification of jasmonic acid and its effects on root development in sweet potato. In: *Low Input Sustainable Crop Production System in Asia*, KSCS, Korea, pp 523-531

Nakatani M, Komeichi M (1991) Changes in the endogenous level of zeatin riboside abscisic acid and indole acetic acid during formation and thickening of tuberous roots in sweet potato. *Japanese Journal of Crop Science* **60**, 91-100

Nakatani M, Komeichi M (1992) Relationship between starch content and activity of starch synthase and ADP-glucose phosphosphorylase in tuberous root of sweet potato. *Japanese Journal of Crop Science* **61**, 463-468

Naskar SK, Chowdhury SR (1995) Genotypic variation in relative water content and nitrate reductase activity in sweet potato under field drought condition. *Journal of Root Crops* **21**, 46-49

Naskar SK, Chowdhury SR, Ravi V (1993) Breeding high yielding, better quality varieties of sweet potato. In: *Annual Report 1993*, Central Tuber Crops Research Institute, Trivandrum, India, pp 94-96

Naskar SK, Singh DP, Ravi V, Chowdhury SR, Bhat PS (1990) Breeding high yielding, better quality varieties of sweet potato. In: *Annual Report 1990*, Central Tuber Crops Research Institute, Trivandrum, India, pp 80-82

Naskar SK, Singh DP, Ravi V, Chowdhury SR, Bhat PS (1991) Breeding high yielding, better quality varieties of sweet potato. In: *Annual Report 1991*, Central Tuber Crops Research Institute, Trivandrum, India, pp 99-100

Nayar TVR, Vimala B (1990) Evaluation of some promising genotypes of sweet potato as influenced by levels of NPK fertilization. *Journal of Root Crops, National Symposium ISRC Special* **17**, 108-111

Ngeve JM, Hahn SK, Bouwkamp JC (1992) Effects of altitude and environments on sweet potato yield in Cameroon. *Tropical Agriculture (Trinidad)* **69**, 43-48

Nwinyi SCO (1991) Preplanting method and duration of storing sweet potato (*Ipomoea batatas* (L.) Lam) shoot cutting planting materials for increased tuber yield. *Tropical Science* **31**, 1-7

Nwinyi SCO (1992) Effect of age at shoot removal on tuber and shoot yields at harvest of five sweet potato (*Ipomoea batatas* (L.) Lam.) cultivars. *Field Crops Research* **29**, 47-54

O'Hair SK (1990) Tropical root and tuber crops. *Horticultural Review* **12**, 157-196

Oswald A, Alkamper J, Midmore DJ (1994) The effect of different shade levels on growth and tuber yield of sweet potato: I. Plant development. *Journal of Agronomy and Crop Science* **173**, 41-52

Oswald A, Alkamper J, Midmore DJ (1995a) Response of sweet potato (*Ipomoea batatas* Lam.) to shading at different growth stages. *Journal of Agronomy and Crop Science* **175**, 99-107

Oswald A, Alkamper J, Midmore DJ (1995b) The effect of different shade levels on growth and tuber yield of sweet potato: II. Tuber yield. *Journal of Agronomy and Crop Science* **175**, 29-40

Oswald A, Alkamper J, Midmore DJ (1996) The response of sweet potato (*Ipomoea batatas* Lam.) to inter and relay cropping with maize (*Zea mays*). *Journal of Agronomy and Crop Science* **176**, 275-287

Patil YB, Patil AA, Madalgeri BB, Patil VS (1990) Correlation studies in sweet potato (*Ipomoea batatas* (L.) Poir.) as influenced by varying levels of nitrogen and potassium and inter row spacing. *Journal of Root Crops* **16**, 98-112

Phills BR, Hill WA (1984) Sweetpotato propagation. A. Macropropagation of the sweetpotato. In: *The Sweetpotato for Space Mission*, Carver Research Foundation Tuskegee University., Tuskegee, AL, p17

Potty VP, Indira P (1990) Influence of vesicular arbuscular mycorrhiza on the photosynthesis and photorespiration of sweet potato (*Ipomoea batatas*). In: Jalali BL, Chand H (Eds) *Current Trends in Mycorrhizal Research*, *Proceedings of National Conference on Mycorrhiza*, Haryana Agricultural University, Hisar, India, p 73

Rajeshkumar SK, Sarkar, Jain BP (1993) Genotype performance and their interaction with environment in sweet potato. *Journal of Root Crops* **19**, 89-94

Rao L, Sultana A (1990) Performance of some promising sweet potato hybrids in Rajendranagar. *Journal of Root Crops* **16**, 46-47

Rao PV, Dora DK, Naskar SK, Jagdev PN (1992) Variability studies in sweet potato. *Journal of Root Crops* **18**, 126-127

Ravi V (2003) Diurnal changes in photosynthetic characteristics of sweet potato (*Ipomoea batatas* L). *Advances in Horticultural Research* **17**, 159-164

Ravi V, Indira P (1995) Investigation on the physiological factors limiting yield potential in sweet potato under drought stress. In: *Annual Report 1995*, Central Tuber Crops Research Institute, Trivandrum, India, pp 37-38

Ravi V, Indira P (1996) Anatomical studies on tuberization in sweet potato under water dificit stress and stress free conditions. *Journal of Root Crops* **22**, 105-111

Ravi V, Indira P (1996) Investigation on the physiolgical factors limiting yield potential in sweet potato under drought stress. In: *Annual Report 1996*, Central Tuber Crops Research Institute, Trivandrum, India, pp 23-24

Ravi V, Indira P (1997) Investigation on the physiological factors limiting yield potential in sweet potato under drought stress. In: *Annual Report 1996*, Central Tuber Crops Research Institute, Trivandrum, India, p 25

Ravi V, Indira P (1999) Crop physiology of sweet potato. *Horticultural Reviews* **23**, 277-338

Ravi V, Naskar SK, Makeshkumar T, Binoy B, Prakash KBS (2009) Molecular physiology of storage root formation and development in sweet potato (*Ipomoea batatas* (L.) Lam). *Journal of Root Crops* **35**, 1-27

Ravi V, Saravanan R (2001) Characteristics of photosynthesis and respiration in cassava and sweet potato. *Journal of Root Crops* **27**, 258-262

Ravi V, Vimala B (2001) Cambial activity and its relation to tuber growth in sweet potato. *Journal of Root Crops* **27**, 267-270

Ravindran CS, Mohankumar CR (1989) Effect of storage life of vines with and without leaves on the establishment and tuber yield of sweetpotato. *Journal of Root Crops* **15**, 145-146

Sahu GD, Singh J, Mehta N, Sahu TD (2005) Evaluation of sweet potato

(*Ipomoea batatas* Lam.) genotypes for Chattisgarh plains. *Journal of Intercademia* **9**, 514-517

Sasaki O, Yuda A, Ueki K (1993) Development of top system in relation to tuberous root formation in sweet potato. III. Branching characteristics and its varietal differences. *Japanese Journal of Crop Science* **62**, 157-163

Sasaki O (1991) Development of shoot system in relation to tuberous root promotion in sweet potato. II. Effects of planting density on successive development of top and tuberous root. *Bulletin of the Faculty of Agronomy, Kagoshima University* **41**, 1-6

Satapathy MR, Sen H, Chattopadhyay A, Mohapatra BK (2005) Dry matter accumulation, growth rate and yield of sweet potato cultivars as influenced by levels of nitrogen and cutting management. *Journal of Root Crops* **31**, 129-132

Schultheis J, Cantliffe DJ (1992) Growth of somatic embryos of sweetpotato (*Ipomoea batatas* (L.) Lam.) in hydroxyethyl cellulose gel amended with salts and carbohydrates. *Scientia Horticulturae* **50**, 21-33

Schultheis JR, Cantliffe DJ (1994) Early plant growth and yield of sweetpotato grown from seed, vegetative cuttings and somatic embryos. *Journal of the American Society of Horticulture Science* **119**, 1104-1111

Scott GJ, Best R, Rosegrant M, Bokanga M (2000) *Roots and Tubers in the Global Food Systems: A Vision Statement to the Year 2020*, A co-publication by CIP, CIAT, IFPRI, IITA and IPGRI, 111 pp

Sen H, Mukhopadhyay SK, Goswamy SB (1990) Relative performance of some sweet potato entries at early harvest. *Journal of Root Crops* **16**, 18-21

Shi CY, Wang ZL, Yu S (2002) Effects of soil aeration on sweet potato yield and its physiological mechanism. *Agricultural Science China* **1**, 189-194

Shoba N, Natarajan S, Kannan M, Veeraragavatham (2004) Effect of cycocel and ethephone on tuber yield of sweet potato clones COCIP-1 and IGSP-9. *Journal of Root Crops* **30**, 65-69

Somda ZC, Kays SJ (1990) Sweet potato canopy architecture: Branching pattern. *Journal of the American Society for Horticultural Science* **115**, 33-38

Songhai S, Ping HC, Ming SH (1994) Some important biochemical properties in developing sweet potato. *Acta Agronomica* **6**, 98-101

Susan JK, Shalini Pillai P, Nair GM, Chithra VG (2004) Phosphorus and potassium deficiency symptoms in sweet potato under sand culture. *Journal of Root Crops* **30**, 5-9

Tanahata Y, Noda T, Nagata T (1993) HPLC content of sweet potato cultivars and its relationships with color values. *Japanese Journal of Breeding* **43**, 421-427

Thankamma PKP, Easwariamma CS (1990) Variability in hybrid progenies of sweet potato. *Journal of Root Crops* **16**, 8-12

Tsubone M, Kubota F, Saitou K (1997) Effects of grafting on the activity of adenosine 5′-diphosphate glucose pyrophosphorylase and tuberous root production in sweet potato (*Ipomoea batatas* Lam.). *Japanese Journal of Crop Science* **66**, 509-510

Uddin MK, Mahabub ASM, Alam MJ, Hoque AKMZ (1994) Fodder yield of sweet potato as affected by different dates of vine cutting and varieties. *Bangladesh Journal of Science and Industrial Research* **29**, 47-53

Varma SP, Nedunzhiyan M (1996) Influence of cycocel on sweet potato yield under different locations. In: *International Meeting on Tropical Tuber Crops*, Indian Society of Root Crops, Trivandrum, India, p 59 (Abstract)

Varma VS, Singh KP, Singh NK, Singh JRP, Verma SP, Mishra S, Sahu MP, Kumari K, Ray R (1994) Rajendra Shakarkand 35 and Rajendra Shakarkand 43: Two high yielding selections of sweet potato. *Journal of Root Crops* **20**, 15-19

Venkatachalam R, Saraladevi D, Yassin MM, Seemanthini R (1990) An evaluation of some sweet potato types under Tamil Nadu condition. *Journal of Root Crops, National Symposium ISRC Special* **17**, 42-44

Villamayor Jr. FG (1991) Vari*etal* response of sweetpotato on storage of cutting. *Radix* **13**, 14

Villamayor Jr. FG, Perez RD (1988) Effect of mixed planting of various parts of the sweetpotato vine on yield. *Radix* **10**, 7-9

Wang QM, Zhang LM, Wang ZL (2005) Formation and thickening of tuberous roots in relation to the endogenous hormone concentrations in sweet potato. *Scientia Agricultura Sinica* **38**, 2414-2420

Watson GA, Dimyati A, Malian AH, Bahagiawati, Wargiono J (1991) Sweet potato production, utilization and marketing in commercial centres of production in Java, Indonesia. In: *Sweet potato cultures in Asia and South Pacific, Proceedings of the 2nd UPWARD International Conference*, Los Baños, Philippines, pp 361-368

Woolfe JA (1992) *Sweet Potato, an Untapped Food Resource*, Cambridge University Press, UK, 643 pp

Yatomi M, Kubota F, Saito K, Agata W (1996) Evaluation of root sink ability of sweet potato (*Ipomoea batatas* Lam.) cultivars on the basis of enzyme activity in the starch synthesis pathway. *Journal of Agronomy and Crop Science* **177**, 17-23

Zhang LY, Lian XP (1994) Studies on the yield structure of sweet potatoes. *Jiangsu Journal of Agricultural Science* **10/17**, 13-17

Zhang MS, Tan F, Zhang QT, Yang YH (2005) Physiological indices and selection of methods on rapid identification for sweet potato drought resistance. *Agricultural Science in China* **4**, 826-832

Zhang MS, Xie B, Tan F (2002) Relationship between changes of endogenous hormone in sweet potato under water stress and variety drought resistance. *Agricultural Science in China* **1**, 626-630

Zhang MS, Xie B, Tan F, Zhang QT (2002) Relationship between soluble protein, chlorophyll and ATP in drought resistant sweet potato under water stress. *Agricultural Science in China* **1**, 1329-1333

Zhong RS (1991) Studies on the source-sink relationship in sweet potato. *Jiangsu Journal of Agricultural Science* **7**, 44-48

Zobayed AF, Zobayed S, Kubota C, Kozai T, Hasegawa O (1999a) Supporting material affects the growth and development of sweet potato (*Ipomea batatas* L.) plantlets cultured photoautotrophically. *In Vitro Cellular and Developmental Biology – Plant* **35**, 450-458

Zobayed S, Kubota C, Kozai T (1999b) Development of a forced ventilation micropropagation system for large-scale photoautotrophic culture and its utilization in sweet potato. *In Vitro Cellular and Developmental Biology – Plant* **35**, 350-355

Zobayed SMA, Afreen F, Kubota C, Kozai T (2000) Water control and survival of *Ipomoea batatas* grown photoautotrophically under forced ventilation and photomixotrophically under natural ventilation. *Annals of Botany* **86**, 603-610