Preliminary study of the spatial distribution of sweet potato storage roots

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Abstract

Sweet potato (*Ipomoea batatas*) plants produce adventitious roots that may swell to form localised carbohydrate storage structures as the growing season advances. These sections of the root are known as storage roots and are the part commonly harvested for human consumption. A storage root is a morphologically defined segment of an adventitious root, characterised by its distinctive lateral growth, which represents a region of marked meristematic activity and carbohydrate deposition. The storage root is attached to the sweet potato plant at the proximal end by a variable length of relatively unthickened root, known as the root stalk. At the distal end of the storage root, the unthickened root continues to extend, performing typical root functions such as absorption of water and minerals, and plant anchorage. The length of the root stalk is generally considered cultivar-specific and is used as a formal morphological feature in cultivar descriptors. This study demonstrates that the root stalk length of a cultivar may be modified by manipulating the sweet potato propagule and its interaction with the environment. The region in which the storage function occurs can be moved down the length of an adventitious root, increasing the root stalk length at its proximal end. This may be useful in developing plug-based propagation systems that eliminate the coiling of storage roots initiated within the physical constraints of a plug tray.

Additional keywords: *Ipomoea batatas*, lignification, plug propagation, root stalk

Introduction

The sweet potato (*Ipomoea batatas* (L.) Lam.), also known as kumara, is a herbaceous dicotyledonous perennial plant grown in New Zealand as an annual root crop. Factors influencing the *in situ* growth and spatial distribution of its roots are an important area of study. The plant is propagated on a commercial scale through the use of unrooted cuttings (Coleman, 1972), so all initial roots are adventitious in derivation (Esau, 1977). Sweet potato stem cuttings readily develop adventitious roots, possibly due to the presence of pericycle and endodermal tissue in the stem

(Onwueme, 1978; Caveness *et al*., 1983). Lateral roots arise directly from the adventitious roots, significantly increasing the overall root volume with primary, secondary and occasionally tertiary laterals (Weaver and Bruner, 1927).

The initial adventitious roots originate from pre-formed root primordia that are commonly visible on the aerial stem at the time of cutting (Hahn and Hozyo, 1983; Belehu *et al*., 2004). These root primordia typically form in pairs either side of the stem just below the point of petiole insertion (Togari, 1950). Sweet potato plants have a 2/5 phyllotaxis, meaning that leaves in the same vertical plane are separated by two revolutions of the stem comprising five leaves inserted in a spiral (Onwueme, 1978; Huamán, 1992). As the leaves are arranged in this spiral pattern, the adventitious roots derived at the nodes are effectively arrayed in three dimensional space without mutual interference. Further adventitious roots may develop within the callus tissue that forms on the buried end of the transplanted stem cutting (Sirju-charran and Wickham, 1988).

Swollen edible storage roots develop from the initial adventitious roots, primarily those pre-formed at nodes prior to transplanting rather than those initiated later in the stem-end callus. A storage root is a length of adventitious root that forms a localised carbohydrate storage structure. It is morphologically defined by its distinctive lateral growth, which represents a region of marked meristematic activity and carbohydrate deposition. Storage roots are the principal carbohydrate storage organ in sweet potato. Storage root growth begins with the deposition of carbohydrates at the distal end of the developing storage root and then proceeds upward to the proximal end (Kays *et al*., 1982). A relatively unthickened root stalk attaches the proximal end of the storage root to the plant's stem, while at the distal end the unthickened fibrous root continues down into the soil, performing typical root functions such as absorption of water and minerals, and plant anchorage. Both the root stalk and fibrous root delimit the storage root, and may become lignified as the storage section develops (Wilson, 1982).

The width of a storage root is due to the contribution of cells from two distinct types of cambia. In a cross sectional view, the normal vascular cambium within a developing storage root eventually forms a circle, with xylem forming on the inner face gradually displacing the cambium outward, while phloem forms to the outside (Esau, 1977). The secondary xylem also contains a large proportion of parenchyma storage cells. However, anomalous cambia are a common characteristic in sweet potato storage roots and occur within various tissue types. The anomalous cambia may form around protoxylem groups, the central metaxylem cell, within secondary xylem derived from the vascular cambium, within xylem derived from previous anomalous cambia, around protophloem groups, or even independently of vascular groups (Artschwager, 1924; Wilson and Lowe, 1973). The anomalous cambia mainly develop in the parenchyma cells around individual secondary xylem vessels or vessel groups, producing a few tracheary elements (xylem) towards the vessels, a few sieve tubes (phloem) and laticifers

(latex ducts) away from the vessels, and considerable storage parenchyma in both directions. So phloem elements may form within tissue that originally differentiated as xylem tissue (Esau, 1977). The relative importance of the different cambia is cultivar-specific. Storage roots thickened primarily by the activity of the normal vascular cambium tend to be uniformly narrow along their length while the involvement of anomalous cambia leads to more globular storage roots (Wilson, 1982).

A root developmental series based on root diameter can be broadly predicted. The first formed adventitious roots tend to have a pentarch or higher polyarch stele anatomy (McCormick, 1916; Wilson and Lowe, 1973) and may develop into 'fibrous roots' (< 5 mm diameter), then 'pencil roots' (< 15 mm diameter) and finally into 'storage roots' (> 15 mm diameter). It should be noted that roots may change anatomically from a pentarch or hexarch structure to tetrarch along their length (Wilson, 1982). The vascular structure of later-formed adventitious roots tends to be tetrarch, and they are developmentally limited to the early categories such as fibrous roots or possibly pencil roots.

Any event that limits carbohydrate deposition, or the cambial activity associated with development of a fully formed storage root, will temporarily or permanently obstruct the progress of a root along the developmental series (Togari, 1950; Kays, 1985). Some environmental switches are reversible, for example exposure of a root system to light inhibits storage root formation until the root is returned to the dark (Tsuno and Fujise, 1965; Hozyo and Kato, 1976). While the capacity of a plant to form storage roots is not permanently impaired by limited anoxic soil conditions (Chua and Kays, 1981; King, 1985), exposure to prolonged oxygen deficiency in the root zone, through waterlogged or high bulk density soils, can permanently disrupt cambial activity through lignification of the vascular stele (Togari, 1950; Watanabe *et al*., 1968; Ravi and Indira, 1996). Permanent fibrous roots, rather than those going through a transitory stage, are incapable of further lateral growth as lignification of the vascular stele permanently impairs the ability of the cambium to provide secondary thickening (Wilson and Lowe, 1973). Permanent pencil roots have a limited carbohydrate storage function as the stele may be only partially lignified, allowing some secondary lateral thickening (Wilson, 1970).

The effect of propagation system on carbohydrate distribution to plant components has been discussed previously (Lewthwaite, 1999). This study examines the location of root carbohydrate storage, with reference to storage root stalk length. It represents a preliminary contribution to a more comprehensive investigation into the location and development of sweet potato carbohydrate storage structures.

Materials and Methods

Sweet potato sprouts were produced by bedding storage roots of the cultivar 'Owairaka Red' in trays of commercial potting mix in an unheated glasshouse. The sprouts produced were passed through various pre-planting treatments to determine their effect on crop establishment and growth (Table 1). The treated sprouts were transplanted into a commercial sweet potato field at

Dargaville, New Zealand, on 28 November 1997 and thoroughly watered in by a tractor-drawn tanker.

The soil at the field site consisted of Kaipara clay, to which superphosphate (NPK 0-10-0) had been broadcast (1 t ha^{-1}) 6 months prior to transplanting. One month before planting muriate of potash (NPK 0-0-50) at 0.5 t ha^{-1} and urea (NPK 46-0-0) at 0.1 t ha^{-1} were broadcast and incorporated. The soil was sampled on the day of transplanting with the following analysis: phosphorus 74 g ml^{-1}, potassium 1.83 me 100 g^{-1}, calcium 18.9 me 100 g^{-1}, magnesium 3.08 me 100 g^{-1}, sodium 0.20 me 100 g^{-1}, cation exchange capacity 31.3 me 100 g^{-1}, available nitrogen 86 kg ha^{-1}, pH 5.9, and a volume:weight ratio of 0.95 for dried ground soil.

Weed control was by hand weeding and application of Gramoxone® at 0.5 l ha^{-1} (paraquat dichloride, 25% active ingredient), 30 days after transplanting (Lewthwaite and Triggs, 2000).

The field experiment was laid out in a modified-alpha row and column design (Williams and John, 1989), comprising 48 plots arranged in a rectangular array of 12 rows and 4 columns. There were 16 treatments each with 3 replicates, and each plot consisted of 4 rows of plants with only the 2 middle rows being harvested. The harvested portion of each plot was 3.5 m long by 1.5 m wide and contained 20 plants arranged in 2 rows of 10 plants, at a 30 cm within-row plant spacing. Plants at either end of the plot were discarded so plots were fully buffered, leaving 16 datum plants in each plot.

Storage roots (above 15 mm in diameter) were hand harvested on 20 January 1998 (53 days after transplanting). Storage root stalk length was measured at full extension, from the point of stalk attachment on the underground stem to the shoulders of the storage root. Stalks of any storage roots broken during harvest or with poorly defined storage root shoulders were not measured. Of all the storage roots produced, 84% had their stalk length measured. The root stalk length data was analysed using the GenStat®: ANOVA procedure (with and without storage root number as a covariate).

Storage root stalk samples were fixed in formalin-acetic acid-alcohol (FAA). The FAA solution consisted of formalin (13 ml), glacial acetic acid (5 ml) and 50% ethanol (200 ml). Sections for lignin staining were immersed overnight in 50% ethanol prior to sectioning at approximately 90 μm, using a vibratome. Lignin was stained using acidified phloroglucin (Sass, 1951).

Table 1: Sweet potato cv. 'Owairaka Red', plant propagule treatments.

Treatment	Description
Control	Sprouts of commercial size (30 cm long, with 6 nodes), transplanted with 4 nodes inserted into the soil the day following cutting
Held-1	As for the control, but held for 3 days under moist conditions at ambient temperature prior to transplanting
Held-2	As for the control, but held for 6 days under moist conditions at ambient temperature prior to transplanting
Held-3	As for the control, but held for 9 days under moist conditions at ambient temperature prior to transplanting
Sand-1	As for the control, but held for 3 days with 4 nodes inserted into river sand prior to transplanting
Sand-2	As for the control, but held for 6 days with 4 nodes inserted into river sand prior to transplanting
Sand-3	As for the control, but held for 9 days with 4 nodes inserted into river sand prior to transplanting
Anti-1	As for the control, but with leaves dipped in an anti-transpirant solution (Vaporgard® at 2% v/v) just prior to transplanting
Anti-2	As for the control, but with leaves dipped in an anti-transpirant solution (commercial fish oil (NPK 5-1-1) at 1% v/v) just prior to transplanting
Start-1	As for the control, but watered in with 200 ml sprout^{-1} of monopotassium phosphate (NPK 0-52-34) in a 1% w/v solution
Start-2	As for the control, but watered in with 200 ml sprout^{-1} of monoammonium phosphate (NPK 12-61-0) in a 1% w/v solution
Mould	As for the control, but transplanted into a protective groove formed along the top of the soil ridge, to reduce exposure
Size-1	Small sprouts (4 nodes) with 1 node inserted into the soil the day following cutting
Size-2	Small sprouts (4 nodes) with 2 nodes inserted into the soil the day following cutting
Size-3	Small sprouts (4 nodes) with 3 nodes inserted into the soil the day following cutting
Plug	Small sprouts (3 nodes) with 1 node inserted into 45 ml plugs, 23 days before transplanting

Results and Discussion

The number of storage roots produced under the various treatments at 53 days after transplanting differed significantly ($P<0.01$), so a covariate analysis of stalk length on storage root number was conducted. However, any apparent covariate effect was due solely to the high numbers of storage roots and long stalk lengths within the plug treatment alone. As there was no significant relationship between storage root number and stalk length across the other 15 treatments, a standard ANOVA was used. The treatments Start-1 and Size-2 produced storage root stalk lengths just significantly longer than the control ($P<0.05$). However, the plug treatment produced much longer storage root stalks ($P<0.001$), on average over twice the length of the control treatment (Figure 1). By selectively staining transverse sections of storage root stalk and storage root tissue for lignin, it was demonstrated that there was greater lignification in the stalks relative to tissue at active storage sites.

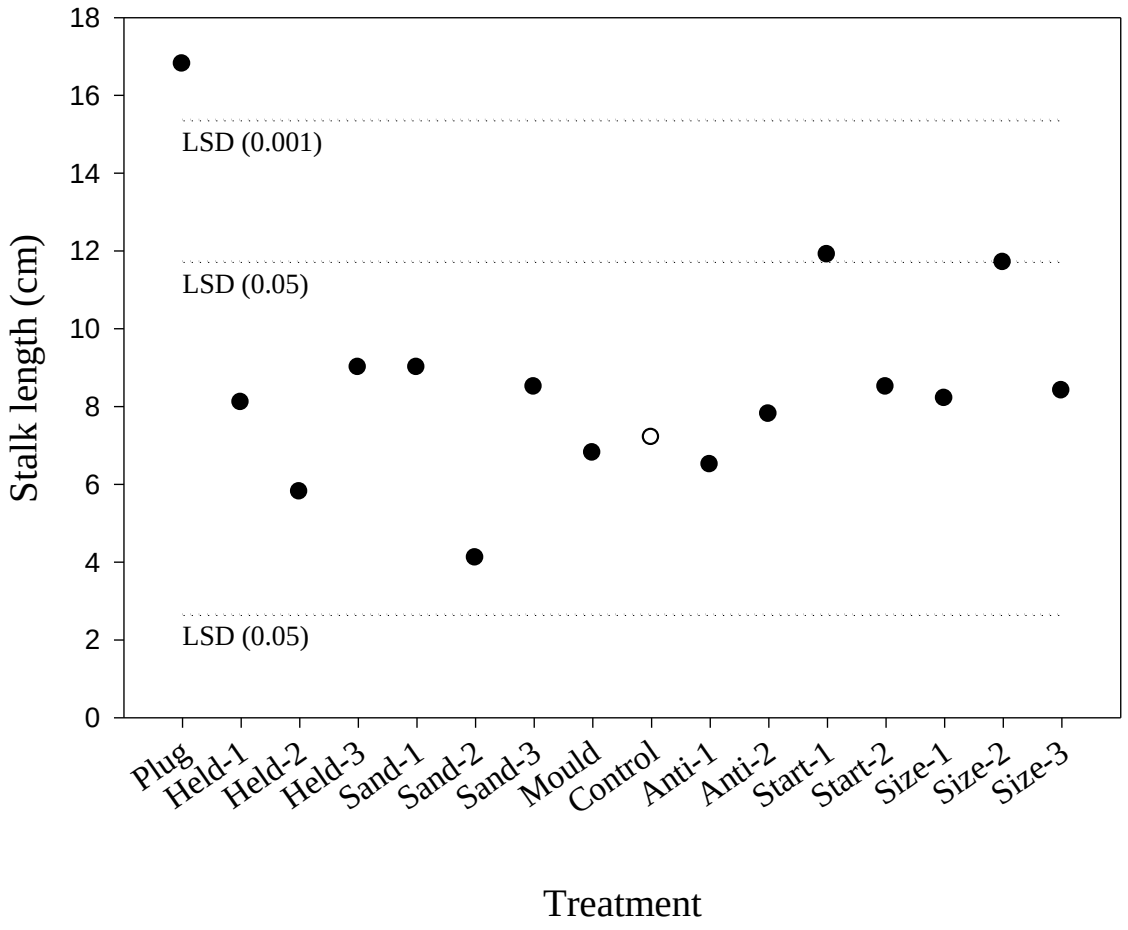

Figure 1: The average length of sweet potato cv. 'Owairaka Red' storage root stalks under various transplant treatments, following 53 days of field growth. The open circle represents the control treatment. Least significant differences (LSD) relative to the control are shown at 0.1 and 5% levels.

Interest in the conservation and utilization of international plant resources has led to the development of systematic descriptor lists for a wide range of plant species (Gotor *et al*., 2008). For sweet potato germplasm various characterisics are considered useful, allowing identification of specific cultivars and the classification of cultivars by individual morphological traits (CIP *et al*., 1991). A cultivar's storage roots may be classified *in situ* by their arrangement on the underground stem, depending on the relative proximity of their point of attachment, with states ranging from a closed to extremely dispersed storage root cluster. A further characteristic is storage root stalk length, where a 10-point scale is used, ranging from the complete absence of a stalk where storage root attachment to the underground stem is sessile, to very long root stalks (> 12 cm) (CIP *et al*., 1991). The predominant New Zealand cultivar 'Owairaka Red' typically has root stalks which are considered short (2-5 cm) on the sweet potato descriptor scale (CIP *et al*., 1991). However, in this experiment longer root stalks developed. Although the length of the root stalk is generally considered cultivar specific and is used as a formal morphological characterisation feature, this study demonstrates that root stalk length may be profoundly influenced by the interaction of the sweet potato propagule with its environment.

Sweet potato plug transplants have become an area of research interest in the last decade, both as a potential means to propagate the crop (Lewthwaite, 1999; Lewthwaite and Triggs, 1999; Tateishi and Murase, 2000; Islam *et al*., 2002; Islam *et al*., 2006) and as a research tool (Afreen-Zobayed *et al*., 1999; Zobayed *et al*., 2004). There have been reports that sweet potato storage roots initiated during plug transplant production may grow on in a coiled state to become abnormally shaped in the field (Islam *et al*., 2002; Islam *et al*., 2006). However, this is not consistent with local experience (Lewthwaite and Triggs, 1999). In this trial, the plug treatment did not produce abnormal storage roots due to lignification (Wilson and Lowe, 1973) of the roots coiled within the plug. Only the unlignified extensions from these roots, developing outside the plug volume, had the capacity for a storage function. This process effectively moved the storage function down the root's length, leaving an extended root stalk (Figure 1). Storage root formation occurred at the same soil depth for all the treatments, as the stalks in the plug treatment were coiled. Root lignification in this trial was a natural consequence of particularly warm, and dry, seasonal conditions (Figure 2), especially in the ridged soil profile. However, artificially contrived root lignification may provide a method for relocating storage root initiation sites.

Sweet potato roots are categorised as feeder, pencil, or storage roots, depending primarily on root thickness but also on their anatomy (Kays, 1985). These categories define roots by their most developed state, but under-represent the complexity within an individual adventitious root, which may exhibit all three states simultaneously. As demonstrated by this study, lignification is a mechanism that may delimit the specific location and degree of carbohydrate storage along the length of an individual root. That lignification

may act in a highly localised way is borne out by examination of comprehensively conjoined roots, one component classified as pencil and the other storage, both roots confined to simultaneous growth and adjacent positions within the soil (S.L. Lewthwaite, unpubl.). When the tissues of these conjoined roots are stained with acidified phloroglucin, the pencil component consistently shows a high degree of lignification relative to the storage component.

The spatial distribution of storage roots *in situ* is an important issue for sweet potato production. Storage roots that are widely dispersed within the soil ridge may be exposed to light, pathogens, pests, or be damaged by harvesting. Sweet potato phyllotaxis is significant to the production of well-shaped storage roots, as demonstrated by the mutual interference of roots when fasciated stem transplants are used for propagation. Finally, an understanding of the effect of anoxic soil conditions on root lignification is critical to optimising sweet potato propagation, yield and quality.

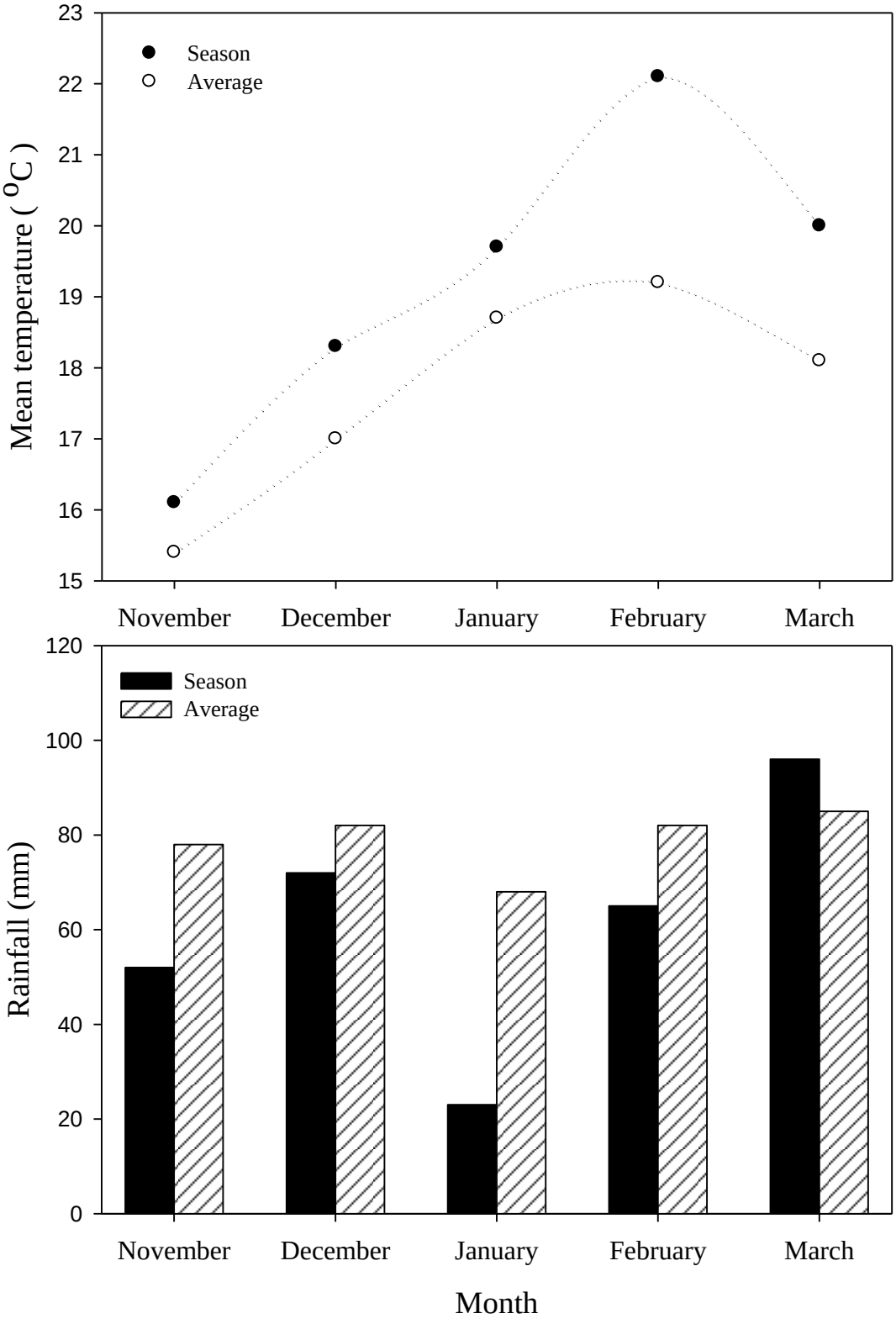

Figure 2: Mean monthly temperature (°C) and monthly rainfall (mm) at Dargaville in the 1997-1998 growing season, contrasted with long term averages (50-55 years). Data courtesy of the National Institute of Water and Atmospheric Research Ltd.

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References

Afreen-Zobayed, F., Zobayed, S.M.A., Kubota, C., Kozai, T. and Hasegawa, O. 1999. Supporting material affects the growth and development of *in vitro* sweet potato plantlets cultured photoautotrophically. *In Vitro Cellular & Developmental Biology – Plant* 35: 470-474.

Artschwager, E. 1924. On the anatomy of the sweet potato root, with notes on internal breakdown. *Journal of Agricultural Research* 27: 157-166.

Belehu, T., Hammes, P.S. and Robbertse, P.J. 2004. The origin and structure of adventitious roots in sweet potato (*Ipomoea batatas*). *Australian Journal of Botany* 52: 551-558.

Caveness, F.E., Hahn, S.K. and Alvarez, M.N. 1983. Sweet potato, yam and cocoyam production. pp. 23-31. *In*: Global workshop on root and tuber crops propagation. Ed. Cock, J.H. CIAT, Cali.

Chua, L.K. and Kays, S.J. 1981. Effect of soil oxygen concentration on sweet potato storage root induction and development. *HortScience* 16: 71-73.

CIP, AVRDC, IBPGR. 1991. Descriptors for sweet potato. Ed. Huamán, Z. International Board for Plant Genetic Resources, Rome. 134 pp.

Coleman, B.P. 1972. Kumara growing. New Zealand Department of Agriculture, Bulletin 294, A.R. Shearer, Wellington. 44 pp.

Esau, K. 1977. Anatomy of seed plants. John Wiley & Sons, New York. 550 pp.

Gotor, E., Alercia, A., Rao, V.R., Watts, J. and Caracciolo, F. 2008. The scientific information activity of Bioversity International: the descriptor lists. *Genetic Resources and Crop Evolution* 55: 757-772.

Hahn, S.K. and Hozyo, Y. 1983. Sweet potato and yam. pp. 319-340. *In*: Symposium on potential productivity of field crops under different environments. Eds Smith, W.H. and Banta, S.J. International Rice Research Institute, Los Baños, Laguna.

Hozyo, Y. and Kato, S. 1976. Thickening growth inhibition and re-thickening growth of tuberous roots of sweet potato plants (*Ipomoea batatas*). *Proceedings of the Crop Science Society Japan* 45: 131-138.

Huamán, Z. 1992. Systematic botany and morphology of the sweet potato plant. Technical Information Bulletin 25. International Potato Center, Lima. 22 pp.

Islam, A.F.M.S., Kubota, C., Takagaki, M. and Kozai, T. 2002. Sweet potato growth and yield from plug transplants of different volumes, planted intact or without roots. *Crop Science* 42: 822-826.

Islam, A.F.M.S., Kubota, C., Takagaki, M. and Kozai, T. 2006. Effects of ages of plug transplants and planting depths on the growth and yield of sweet potato. *Scientia Horticulturae* 108: 121-126.

Kays, S.J. 1985. The physiology of yield in the sweet potato. pp. 19-133. *In*: Sweet potato products: A natural resource for the tropics. Ed. Bouwkamp, J.C. CRC Press, Florida.

Kays, S.J., Chua, L.K., Goeschl, J.D., Magnuson, C.E. and Fares, Y. 1982. Assimilation patterns of carbon in developing sweet potatoes using ^{11}C and ^{14}C. pp. 95-118. *In*: Sweet Potato: Proceedings of the First International Symposium. AVRDC Publication No. 82-172, Tainan.

King, G.A. 1985. The effect of time of planting on yield of six varieties of sweet potato (*Ipomoea batatas* (L.) Lam.) in the southern coastal lowlands of Papua New Guinea. *Tropical Agriculture* 62: 225-228.

Lewthwaite, S.L. 1999. Field establishment of sweet potato transplants. *Proceedings Agronomy Society of New Zealand* 29: 51-57.

Lewthwaite, S.L. and Triggs, C.M. 1999. Plug transplants for sweet potato establishment. *Proceedings Agronomy Society of New Zealand* 29: 47-50.

Lewthwaite, S.L. and Triggs, C.M. 2000. Weed control in sweet potatoes. *New Zealand Plant Protection* 53: 262-268.

McCormick, F.A. 1916. Notes on the anatomy of the young tuber of *Ipomoea batatas* Lam. *Botanical Gazette* 61: 388-397.

Onwueme, I.C. 1978. Origin, classification, genetics and botany of sweet potato. pp. 167-195. *In*: The tropical tuber crops: yams, cassava, sweet potato, cocoyams. Ed. Onwueme, I.C. John Wiley & Sons, Chichester.

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

Sass, J.E. 1951. Botanical microtechnique. The Iowa State College Press, Iowa. 228 pp.

Sirju-charran, G. and Wickham, L.D. 1988. The development of alternative sink sites in sweet potato *Ipomoea batatas*. *Annals of Botany* 61: 99-102.

Tateishi, M. and Murase, H. 2000. Development of transplant production in closed system - irrigation scheduling based on evapotranspiration rate. *In*: ASAE Annual International Meeting, Milwaukee, July 9-12 2000. 9 pp.

Togari, Y. 1950. A study on tuberous root formation in sweet potato. *Bulletin of the National Agricultural Experiment Station, Tokyo* 68: 1-96.

Tsuno, Y. and Fujise, K. 1965. Studies on the dry-matter production of sweet potato. *Bulletin of the National Institute for Agricultural Science (Japan)* D13: 1-131.

Watanabe, K., Ozaki, K. and Yashiki, T. 1968. Studies on the effect of soil physical condition on the growth and yield of crop plants 7. Effect of soil air composition and soil bulk density on the growth of sweet potato. *Proceedings of the Crop Science Society Japan* 37: 65-69.

Weaver, J.E. and Bruner, W.E. 1927. Root development of vegetable crops. McGraw-Hill, New York. 341 pp.

Williams, E.R. and John, J.A. 1989. Construction of row and column designs with contiguous replicates. *Applied Statistics* 38: 149-154.

Wilson, L.A. 1970. The process of tuberization in sweet potato (*Ipomoea batatas* (L.) Lam.). Volume 1, pp. 24-26. *In*: Proceedings of the 2nd

International Symposium of Tropical Root and Tuber Crops. Hawaii.

Wilson, L.A. 1982. Tuberization in sweet potato (*Ipomoea batatas* (L.) Lam.). pp. 79-94. *In*: Sweet Potato: Proceedings of the First International Symposium. AVRDC Publication No. 82-172, Tainan.

Wilson, L.A. and Lowe, S.B. 1973. The anatomy of the root system in West Indian sweet potato (*Ipomoea batatas* (L.) Lam.) cultivars. *Annals of Botany* 37: 633-643.

Zobayed, S.M A., Afreen, F., Xiao, Y. and Kozai, T. 2004. Recent advancement in research on photoautotrophic micropropagation using large culture vessels with forced ventilation. *In Vitro Cellular & Developmental Biology – Plant* 40: 450-458.