African Journal of Agricultural Research Vol. 7(30), pp. 4236-4249, 7 August, 2012
Available online at http://www.academicjournals.org/AJAR
DOI: 10.5897/JMPR11.2178
ISSN 1991-637X ©2012 Academic Journals

Full Length Research Paper

Ontogeny of the tuber crop *Plectranthus edulis* (Lamiaceae)

Mulugeta Taye[1,2], W. J. M. Lommen[3]* and P. C. Struik[3]

[1]Hawassa University College of Agriculture, P. O. Box 5, Awassa, Ethiopia.
[2]St Mary's University College, P. O. Box 18490, Addis Abeba, Ethiopia.
[3]Centre for Crop Systems Analysis, Plant Sciences Group, Wageningen University, Droevendaalsesteeg 1, 6708 PB Wageningen, The Netherlands.

Accepted 21 June, 2012

Plectranthus edulis **(Lamiaceae) is one of the economically important tuber crops of the genus *Plectranthus*. It is grown in mid and high altitude areas in parts of Ethiopia. The structure of this plant and its development in time has not been described in detail. Two similar experiments were carried out at Awassa and Wondogenet (Southern Ethiopia) with two cultivars (Lofuwa and Chankua) and 20 harvest dates [from 14 to 280 days after planting (DAP)]. The plants were grown from seed tuber pieces and attained a maximum height of about 1.5 m. Plants produced main stems and primary, secondary and tertiary branches, with primary and secondary branches and their leaves constituting the main part of the canopy. Plant components were the seed tuber pieces, sprouts, main stems, branches, leaves, flowers, fruits, seeds, roots, stolons and tubers. Five, partly overlapping, ontogenetic vegetative phases were observed during one crop cycle: emergence, canopy development, stolon initiation and development, tuber initiation and growth, and a phase of canopy senescence. Stolons were formed on main stems and primary branches and originated below ground or above ground (aerial stolons). Aerial stolons were initiated later than below-ground stolons and were much longer (up to 2.5 m). Tubers usually were produced as a swelling on the tip of the stolon and sometimes as a swelling of the middle part of stolons. Tubers were stem tubers with pairs of "eyes" (compound buds) being arranged in the same decussate pattern as the axillary buds on stolons and stems. Tubers of cv. Lofuwa were up to 25 cm in length, those of cv. Chankua up to 20 cm, and both with a diameter of about 2 cm. The tubers in the middle of the stolon were longer than the ones at the tip. After tuber initiation, the total number of tubers increased almost linearly during 12 to 14 weeks, and maximum numbers of tubers were attained around 238 DAP, at crop senescence. Also, the number of smaller tubers (< 10 or 20 g) increased until 238 DAP. In the period of tuber initiation, the average weight per tuber increased up to 20 to 25 g per tuber. The increase in tuber fresh weight with time was therefore realized by an increase in both tuber number and in average weight per tuber. After crop maturity, farmers keep the tubers unharvested in the soil until they need them. This practice dramatically reduces tuber yield and number, because decreases of 36 to 59% were found in total tuber fresh weight and of 18 to 48% in number of tubers when tubers were kept in the soil in the 6 weeks period between 238 and 280 DAP.**

Key words: *Coleus edulis*, crop development, Ethiopian potato, leaves, morphology, *Plectranthus edulis*, stolons, crop structure, tubers, tuber crop, days after planting (DAP).

INTRODUCTION

Plectranthus edulis (Vatke) Agnew (Lamiaceae, Labiateae), syn. *Coleus edulis* Vatke, is one of the four economically important tuber crops of the genus *Plectranthus*, together with *Plectranthus esculentus* (Livingstone potato; Tindall, 1983; Allemann et al., 2003; Allemann and Hammes, 2006), *Plectranthus parviflorus* (Sudan potato; Tindall, 1983) and *Plectranthus rotundifolius* (Madagaskar potato; Jansen, 1996). *P. edulis* is an ancient Ethiopian tuber crop (Greenway, 1944; Siegenthaler, 1963; Westphal, 1975). It is locally known as Wolaita dono, Gamo dinich, Dinicha Oromo, Agew dinich, etc., and also as Ethiopian potato

(Mulugeta et al., 2007; Yeshitila, 2007). It is grown in mid and high altitude areas in the north, south and west of Ethiopia and is primarily cultivated for its tubers. These tubers are consumed after cooking. To some extent, also, the leaves are used as a cooked vegetable in some western Ethiopian regions (Westphal, 1975; Zemede and Zerihun, 1997; Mulugeta et al., 2007). The *P. edulis* crop is mainly established by planting 2 to 3 tuber pieces of a broken seed tuber in one planting hole. Cultural practices include tipping (removal of the apical stem parts) and earthing up. Tubers are usually harvested following the ceasing of the main rainy season; for instance in Wolaita and Chencha crop harvesting starts in October and November, respectively (Mulugeta et al., 2007).

Phenotypic characterizations of genotypes of this plant species were made (Yeshitila, 2007; Weyessa et al., 2009), but the full structure of this plant and its components have not been described in detail yet. Understanding its structure is essential in order to understand how to increase a crop's productivity. Struik and Wiersema (1999) underlined the importance of understanding the structure of a potato plant to influence its physiology and agronomy. Several researchers including Allemann et al. (2003) working with *P. esculentus* also carried out morphological studies as the basis for their subsequent studies. Such information is also very basic for *P. edulis.* Equally, important is the understanding of the development of a crop in time for it has both physiological (understanding the dynamics of organ appearance) and agronomic (knowing when to perform certain practices) relevance (McMaster, 2004). The sequence of the different crop stages can be considered as a series of discrete periods, each identified by a process of change in the structure, size or mass of specific organs (Squire, 1990). Temperature has profound effects on the duration of such developmental phases, for instance in cotton (Reddy et al., 1991) and enset (Admasu and Struik, 2003).

The objectives of this study were to identify the major structural components, and to describe and understand the development of the canopy and underground parts of the crop. Emphasis was on the vegetative parts of the crop. Inflorescences of *P. edulis* were earlier described by Siegenthaler (1963).

MATERIALS AND METHODS

Experimental sites

A similar experiment was carried out at two sites in the southern region of Ethiopia, that is, at Hawassa University, Awassa, from April 4, 2003 until January 9, 2004; and at Wondogenet College of Forestry and Natural Resources, Wondogenet, from April 11, 2003 until January 16, 2004. The Awassa field was located at 7° 03' N latitude and 38° 30' E longitude while the Wondogenet field was at 7° 06' N latitude and 38° 37' E longitude. Awassa is located at an altitude of 1650 m above sea level, Wondogenet at an altitude of 1850 m above sea level. Wondogenet is relatively cooler and more humid than Awassa. The daily average temperature in Awassa during the experimental period ranged between 17 to 25°C and that of Wondogenet between 14 to 24°C. Average temperatures during the experimental period were 19.9 and 18.4°C, average global radiation was 16.07 and 12.95 MJ m^{-2} day^{-1} and total rainfall 671 and 888 mm at Awassa and Wondogenet, respectively. Day length fluctuated between 11.59 h (21 December) and 12.41 h (21 June) at both sites. The soil texture at both sites was sandy loam.

Design and treatments

At both sites, a split-plot design was used with five blocks and with two cultivars as main factor and 20 harvest dates as split factor, giving 200 individual plots per experiment. The two cultivars used were Lofuwa and Chankua. Cv. Lofuwa is considered early maturing and cv. Chankua late maturing (Yeshitila, 2007). Harvests were carried out every 14 days from 14 to 280 days after planting (DAP). Each of the 200 experimental plots was 3.60 × 2.75 m, with four rows spaced at 90 cm, and 5 planting holes at a within-row planting distance of 75 cm. Plants from the middle three holes in the middle two rows (6 planting holes) were removed for observations, and plants from the remaining 14 holes were guard plants. The experimental unit therefore consisted of the plants from the inner six holes per plot.

Crop management

The experimental field was ploughed, and furrowed until a depth of 20 cm. Tuber pieces for planting were prepared by breaking a de-sprouted whole tuber of about 10 to 12 cm into about three equal pieces. Three tuber pieces were planted in a triangle with sides of about 5 cm in a planting hole in a furrow, and covered by a layer of soil of about 5 cm thick. During crop growth the soil was tilled about three times to remove and cover the weeds. Tipping, that is removing the tip (the apex plus one or two pairs of visible leaves) of the main stems and branches, was carried out when plants reached about 15 cm height, on 61 DAP in Awassa and 63 DAP in Wondogenet. Earthing up, that is piling soil around the root was done at least three times in order to cover the stolons and support the stems.

Measurements

At a harvest day, 10 samples (2 cultivars × 5 blocks), each consisting of the plants from the inner six planting holes of one plot, were carefully uprooted and transferred to the laboratory for cleaning and detailed analysis. The major above-ground and below-ground plant parts of each cultivar were visually examined and described. Numbers of main stems, branches, leaves and stolons from all six holes per plot were counted every 14 days up to the moment when no counting was possible anymore because of plant senescence. The numbers of tubers from six holes per plot were also counted every 14 days until 280 DAP. Green leaves from different stem types were counted. The number of stolons was counted for main stems and primary branches separately up to 224 to 238 DAP; thereafter counting per type stem was discontinued for it became very difficult to identify the origin of the stolons within the mass of roots present. Stolons were also grouped into aerial and below-ground stolons depending on their origin. In these

*Corresponding author. E-mail: willemien.lommen@wur.nl. Tel: +31 317 484697. Fax: +31 317 485572.

experiments, only stolons that were still connected to the stem were counted. Tubers were divided into weight classes of 10 g increments, from 0 to 10, to 80 to 90 g Tuber fresh yield per hole was determined and the average weight per tuber was calculated.

Statistical analysis

Because the objective of the study was to describe and understand the development of the crop, descriptive statistics were chosen as the appropriate method to describe the results and the variability in the results on the different harvest dates. Means and standard deviations were calculated per cultivar per harvest date using GenStat release 9.2 or Excel 2003.

RESULTS

General

The plants grown from the seed tuber pieces were ascending, herbaceous, and bushy with a maximum height of about 1.5 m. Figure 1 shows the crop (Figure 1A) and details of the plant and its structural components (Figures 1B to G). Each plant was composed of several parts: the mother tuber piece, the sprouts, the main stems, the branches, the leaves, the flowers, the fruits, the seeds, the roots, the stolons, and the tubers. The colour of the vegetative parts, stolons and tubers varied depending on the cultivar. The leaves and stems of cv. Lofuwa were green and the stolons and the skin of the tubers were creamish, with incidentally a shade of red, especially around the buds (Figure 1G). The stem, stolons and the tuber skin of cv. Chankua were reddish, while the leaves were a mixture of red and green, turning redder under high irradiation levels.

Canopy development

Sprouts

A sprout is defined as a young growth of the buds of the tuber pieces a soft stem, with or without leaves, yellowish and directly originating from a mother tuber. The soft stem might be short or lengthy, erect or crippled. More than one sprout could arise from a single eye. The first sprouts were produced between 14 and 28 DAP in both locations. They emerged between 28 and 42 DAP, developing into main stems.

Main stems and branches

The changing of colour of the sprouts from yellowish to green in cv. Lofuwa and to reddish in cv. Chankua after emergence marked the establishment of the true plant. Stems that directly originated from a mother tuber piece were considered main stems. Main stems always developed from sprouts. Branches that arose from main stems were primary branches; those from primary branches were secondary branches, etcetera. Primary branches were produced starting from the first node immediately (about 2 to 5 cm) above the bud of the seed tuber piece; their internodes increased in length as branches grew longer. In some axils of leaves more than one branch was produced. Main stems and branches were hairy, swollen at and above each node and quadrangular (Figure 1D). Branches were arranged in an opposite, decussate pattern (Figures 1C and D) following the phyllotaxis of the leaves.

After emergence, the number of main stems increased during the earlier growth stages in both genotypes at both sites but later settled to between 1 and 2 main stems per hole because some stems did not survive the intra-plant competition between main stems (Figures 2A and B).

The first primary branches appeared around 50 DAP. The number of primary branches increased thereafter to about 20 per hole in Awassa and 20 to 25 in Wondogenet (Figures 2C and D). A decrease in the number of primary branches in both cultivars took place after about 200 DAP in Wondogenet and slightly later in Awassa because of senescence of the branches (Figures 2C and D).

The first secondary branches appeared at about 70 DAP. The number of secondary branches increased substantially from about 100 DAP onwards to about 40 to 45 secondary branches per hole (Figures 2E and F). The decrease in secondary branch number started earlier than the decrease in primary branch number. In cv. Chankua the increase in the number of secondary branches was slightly slower and the decrease slightly earlier than in cv. Lofuwa.

A variable number of tertiary branches arose from some of the secondary branches and the first appeared after about 125 DAP in cv. Lofuwa and slightly later in cv. Chankua (Figures 2G and H). Maximum numbers of tertiary branches varied between 5 to 10 and about 30, with lower numbers being produced in Wondogenet than in Awassa and lower numbers being produced in cv. Chankua than in cv. Lofuwa.

The maximum total number of main stems plus branches was 80 to 100 per hole in both Awassa and Wondogenet (Figures 2 I and J).

Leaves

The leaves were oval–elliptical in shape, dentate, sessile, pubescent, slightly bent outward at the tip and on the margin, and with conspicuous veins. The phyllotaxis was opposite, with leaf pairs decussate (Figure 1B). Leaves started to appear from the 1st node of the branches. The matured leaf length was about 10 cm long and the width of the widest middle part was 5 cm.

The first green leaves appeared when the first plants emerged between 28 and 42 DAP. Thereafter, the number of green leaves from main stems increased until

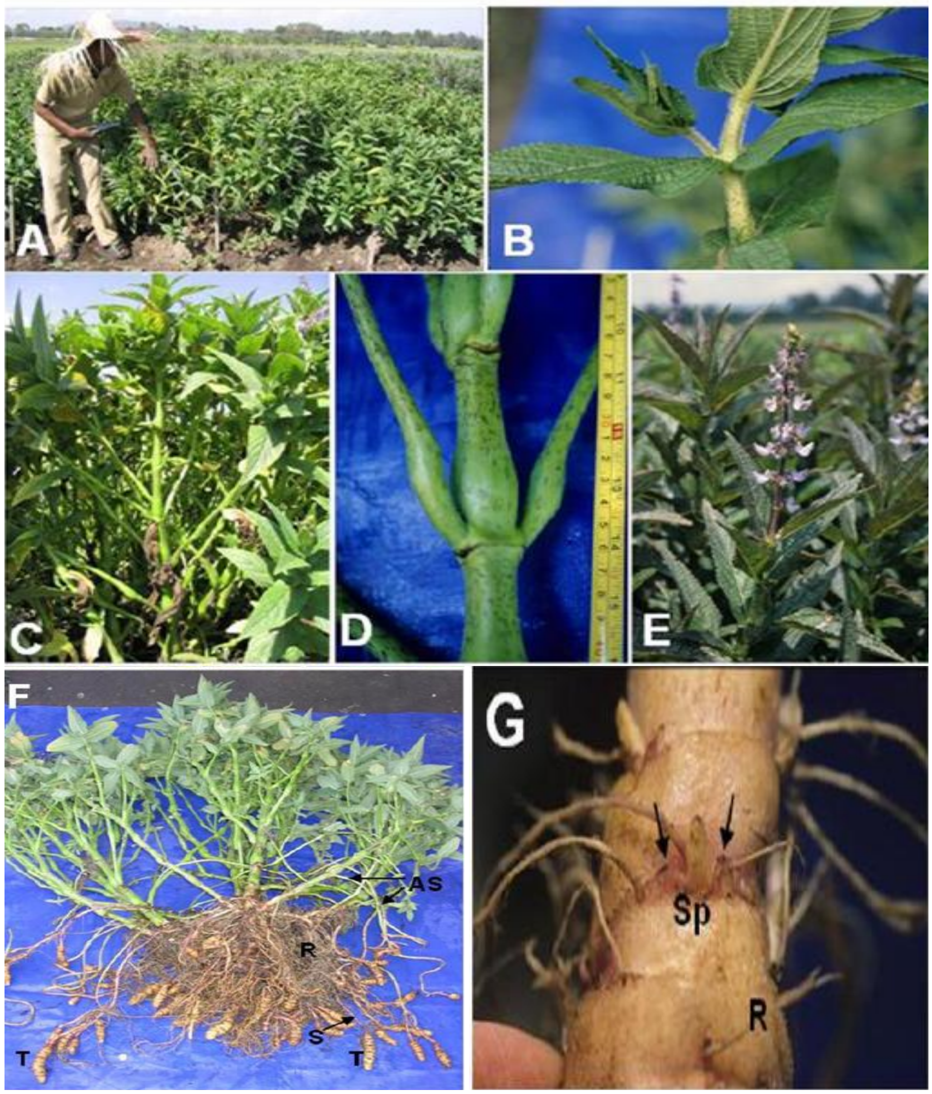

Figure 1. The *P. edulis* crop and details of the plant and its components. A, *P. edulis* crop, cv. Lufowa, in Awassa, 6.5 months after planting, crop height c. 1 m; B, upper part of a primary branch of cv. Lufowa showing sessile leaves, the opposite, decussate phyllotaxis, and a secondary branch developing in the axil of one of the two leaves of a pair; C, branching pattern in the inner part of the field crop from A; D, detail of an older part of a primary branch of cv. Lufowa showing the quadrangular stems, swollen at and above a node, and secondary branches being formed from both axillary buds at a node in an opposite decussate pattern; leaf scars are visible below the secondary branches; E, inflorescence of cv. Chankua, 6 months after planting; F, plant of cv. Lufowa dug out of the soil, 6.5 months after planting, showing tubers (T) on stolons (S), dense, fibrous roots (R), branches with leaves, and many aerial stolons (AS) arising from the primary branches, some bearing tubers. Most below-ground stolons are covered by the root mass; G, detail of a tuber of cv. Lufowa, 6 months after planting the crop, showing a tuber "eye" with the main bud producing a small sprout (Sp), small scale leaves covering the eye (arrows), roots (R) being developed at the node around the eye, and the relatively larger swelling of internodes compared to the nodes of a tuber. The tuber width is 2 cm.

about 140 DAP to about 60 per hole and then decreased when leaves senesced (Figures 3A and B). Some leaves from primary branches might have been counted as main stem green leaves because for some of the primary branches closer to the ground it was difficult to differentiate them from main stems.

The number of green leaves from the primary branches increased until about 4 weeks later than the number of green leaves on main stems in Awassa and until 0 to 2 weeks later in Wondogenet and then decreased

(Figures 4C and D). The maximum number of green leaves on primary branches was 350 to 400 per hole.

The number of green leaves from secondary branches increased up to about 400 in Awassa and 200 to 250 in Wondogenet (Figures 3E and F). The maximum number of green leaves on secondary branches was obtained at about the same moment as the maximum number on primary branches in cv. Lofuwa, but slightly later in cv. Chankua in Wondogenet. Green leaves on secondary branches stayed slightly longer around the maximum than green leaves on primary branches before they started to decrease considerably in number.

The number of green leaves on tertiary branches increased until a slightly later date than the number of green leaves on secondary branches except for cv. Chankua in Wondogenet, where the dates on which the maximum was achieved, coincided (Figures 3G and H). Maximum numbers of green leaves on tertiary branches were about 30 per hole for cv. Chankua and 40 (Wondogenet) to 100 (Awassa) per hole for cv. Lofuwa.

The maximum total number of green leaves per hole was in general higher in Awassa (*c*. 800 green leaves per hole) than in Wondogenet (*c*. 650 green leaves per hole; Figures 3 I and J). There were no green leaves present anymore at 252 DAP in Awassa and 2 weeks earlier in Wondogenet. Leaves that senesced in the later growth stages normally dropped from the plant immediately after their colour had changed to yellowish. Senescing leaves on the main stems and lower parts of the primary branches could change colour to brown and remain on the stem.

Inflorescences

Terminal inflorescences were produced at the tip of main stems and on most primary and secondary branches (Figure 1E). The panicle-like inflorescences were branched with several blue flowers in clusters of bisexual flowers. Flowers were typical for the family, with five sepals united in a calyx and five petals united to a two-lipped corolla.

Seeds and fruits

Seeds were brown/black, ovoid-shaped and smaller than 1 mm. The fruit consisted of four seeds included in the persistent calyx. We did not describe the fruits in detail.

Below-ground development

Stolons

Stolons originated from buds located in the main stems and the lower primary branches. More than two stolons could arise from one node. Stolons were hairy and could produce branches, either on one of the opposite buds of a node or on both. We call stolons that originated from main stems main stem stolons, while those from primary branches are called primary branch stolons. Stolons were also categorized as below-ground and aerial stolons, referring to whether they originated from below-ground or aerial nodes. The length of the aerial stolons varied; in some cases they grew by more than 2.5 m. Aerial stolons also were leafy and greenish or deep red depending on the cultivar. However, below-ground stolons sometimes grew above ground and became very vigorous whereas aerial stolons or branches from aerial stolons grew into the soil and formed tubers.

The first stolons appeared from below-ground nodes of main stems and primary branches about 70 DAP in Awassa and 70 to 84 DAP in Wondogenet (Tables 1 and 2). The number of below-ground stolons initially increased as time progressed but decreased later, particularly closer to maturity in Wondogenet (Table 2). Aerial stolons appeared 168 to 182 DAP, much later than below-ground stolons, also from main stems and primary branches (Tables 1 and 2). Aerial stolons were small innumber as compared to below-ground stolons in both places. The total numbers of stolons from main stems and primary branches were comparable (Figure 4). The increase in number of stolons continued longer in Wondogenet than in Awassa, and the maximum numbers of stolons were about 30 to 40 per hole in Awassa and 80 to 100 per hole in Wondogenet (Figures 5A and B). This number of stolons remained stable in Awassa until no further assessment of the number of stolons was possible anymore, but the increase in number of stolons in Wondogenet was followed by a decrease.

Tubers

Tubers (Figure 1F and G) were produced at the tip part of the stolon and sometimes also as a swelling of the middle part of stolons. The first swelling of stolons to tubers seemed to occur at the nodes, whereas later the internodes swelled and in older tubers the internodes were more swollen than the nodal parts (Figure 1G). Tubers were also produced without stolons from the mother tuber piece (sessile tubers). Tubers had pairs of "eyes" (that is, compound axillary buds) being arranged in the same pattern as the axillary buds on stolons and stems. The tuber dimensions varied. Tubers of cv. Lofuwa were up to 25 cm in length while those of cv. Chankua were up to 20 cm, both with a diameter of about 2 cm. The tubers in the middle of the stolon were longer than the ones at the tip. The flesh colour of both cultivars was creamish. Tubers from both cultivars were slender like carrots but there were also some curved ones.

Tubers started to appear about 126 DAP on stolons from main stems and from primary branches (Figure 6). Tubers of different sizes were formed but the numbers of

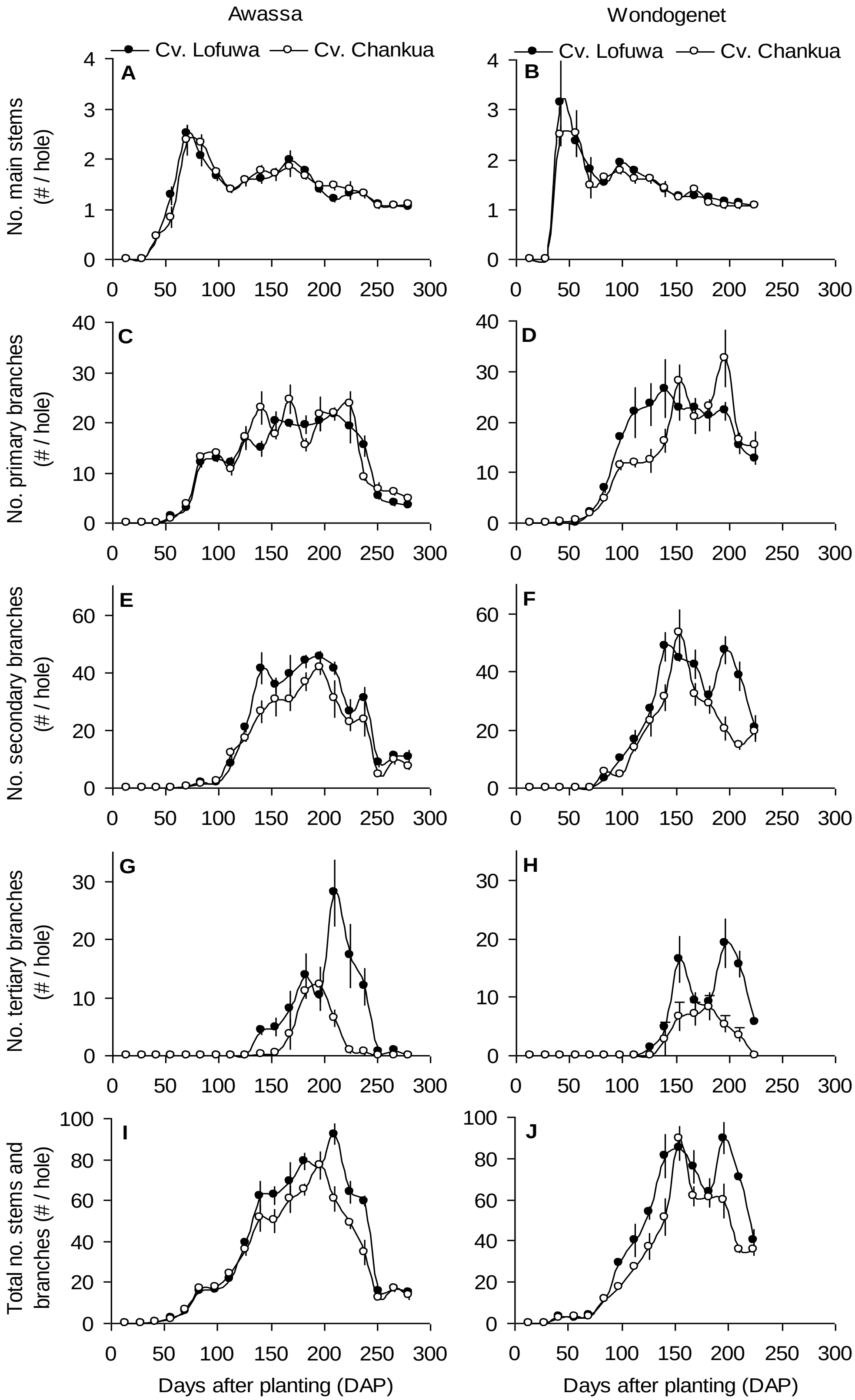

Figure 2. Number of main stems and branches per hole at Awassa and Wondogenet for cvs Lofuwa and Chankua. A, Main stems, C, primary branches, E, secondary branches, G, tertiary branches, I = total number of main stems and branches in Awassa; B, main stems, D, primary branches, F, secondary branches, H, tertiary branches; J, total number of main stems and branches in Wondogenet. Bar = standard deviation (n = 5 plots of 6 holes).

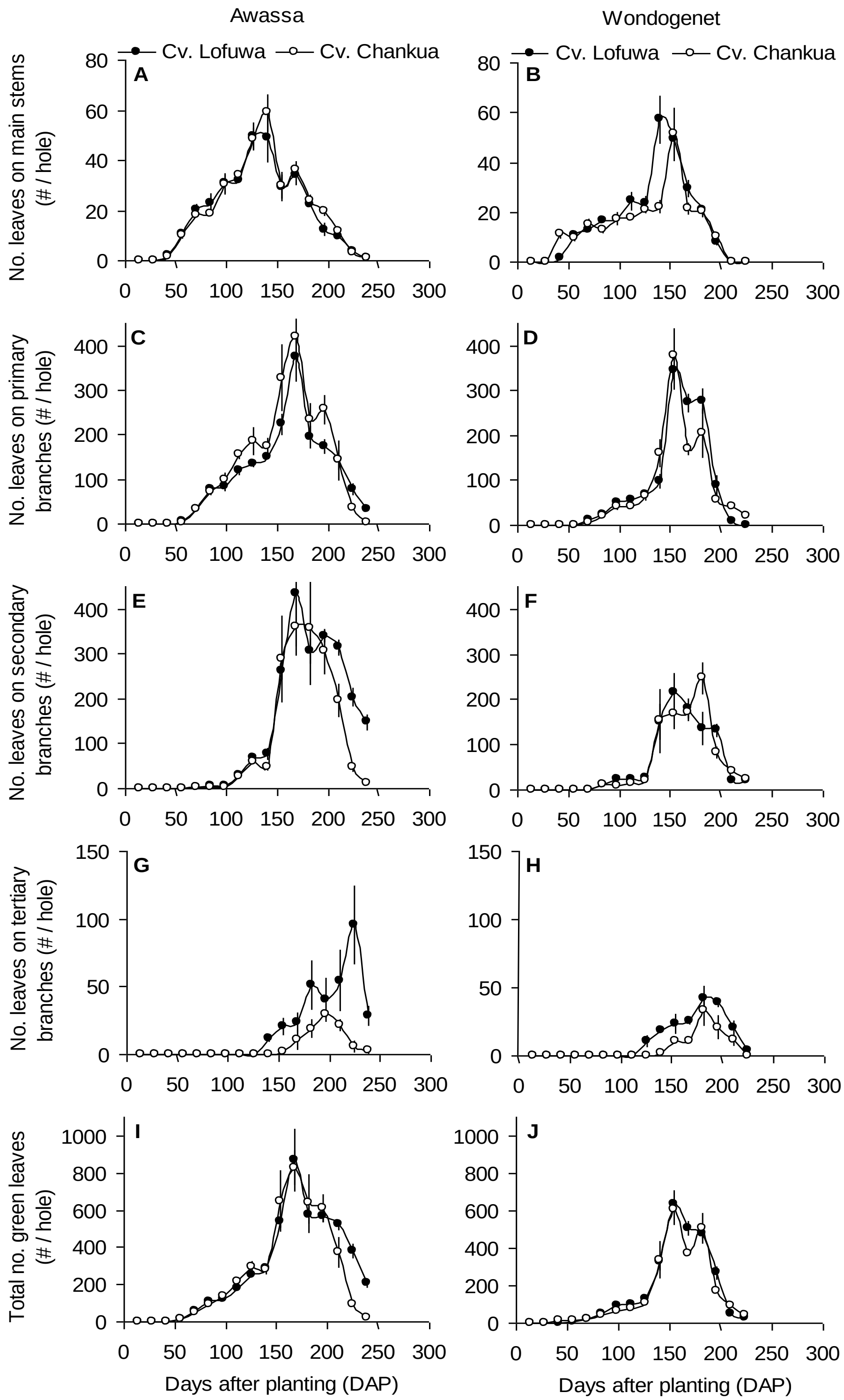

Figure 3. Number of green leaves per hole from main stems and branches at Awassa and Wondogenet for cvs Lofuwa and Chankua. A, Number of green leaves on main stem, C, number of green leaves on primary branches, E, number of green leaves on secondary branches; G, number of green leaves on tertiary branches; I, total number of green leaves on main stems plus branches in Awassa; B, number of green leaves on main stems; D, number of green leaves on primary branches; F, number of green leaves on secondary branches; H, number of green leaves on tertiary branches; J, total number of green leaves on main stems plus branches in Wondogenet. Bar = standard deviation (n = 5 plots of 6 holes).

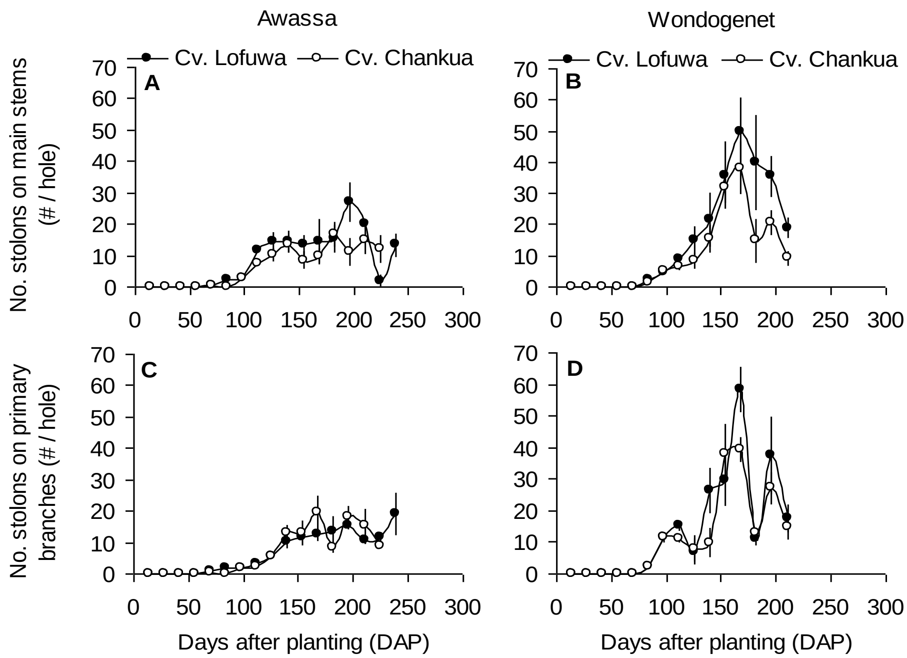

Figure 4. Number of stolons originating from main stems and primary branches per hole at Awassa and Wondogenet for cvs Lofuwa and Chankua. A, Stolons on main stems, C, stolons on primary branches in Awassa; B, stolons on main stems, C, stolons on primary branches in Wondogenet. Bar = standard deviation (n = 5 plots of 6 holes).

tubers in the weight classes 0 to 10 g and 10 to 20 g were higher than the numbers of the heavier ones (Figure 7). The heaviest tubers were found in the size class 70 to 80 g in Awassa and in the class 80 to 90 g in Wondogenet. The latter size, however, was found only now and then (1 to 2 tubers per 30 holes). The total number of tubers increased from 140 to 160 tubers per hole at about 238 DAP, but then decreased in both cultivars and places (Figures 5C and D). The average weight per tuber increased to a maximum of 20 to 25 g per tuber, as time progressed up to about 252 DAP in Awassa and 238 DAP in Wondogenet (Figures 5E and F). The tuber fresh weight per hole reached about 3000 to 3500 g in both cultivars and places at 238 DAP and thereafter decreased strongly (Figures 5G and H).

Roots

Fibrous roots were produced at the nodes of main stems, primary branches, stolons, and tubers. The roots were thin and dense and varied in length. Some were as long as 60 cm.

DISCUSSION

Structural components

The tubers of *P. edulis* are clearly stem tubers with the pairs of "eyes" (that is, compound axillary buds) being arranged in the same alternating pattern as the axillary buds on stolons and stems. *P. edulis* therefore consists of similar structural components as other crops producing stem tubers on stolons, like the Irish potato (*Solanum tuberosum*) (Beukema and van der Zaag, 1979; Struik and Wiersema, 1999). *P. esculentus* differs from *P. edulis* because *P. esculentus* produces stem tubers that are sessile and clustered around the stem (Allemann et al., 2003). The stolons of *P. edulis* were much longer than those of Irish potato and particularly the aerial stolonsbehaved differently from those of Irish potato. They were very vigorous, growing fast over the soil surface, and could achieve a length of more than 2 m. The aerial stolons produced several branches and bore tubers after the branches entered into the ground.

Tubers were formed at the tip of a stolon - as in Irish potato - or by swelling of a middle part of a stolon. In Irish potato, tubers in the middle of the stolon are only observed when secondary growth occurs, that is, the growth of the apex changes from tuber-like to stolon-like due to a switch in external conditions to those that are not conducive to tuberization and tuber bulking, for example, warm temperatures or rainfall after a dry period (Bodlaender et al., 1964; Lugt et al., 1964). For *P. edulis*, the exact nature of the tuber formation in the middle of the stolon still has to be established, but most likely it results from thickening of an existing stolon part.

P. edulis differed also in other aspects from *P. esculentus,* like the flower colour which was violet - blue

Table 1. Development with time of the numbers of below-ground and aerial stolons from main stems and primary branches for cvs Lofuwa and Chankua in Awassa.

DAP	Below-ground stolons (No. / hole)			Aerial stolons (No. / hole)		
	Main stems	Primary branches	Total	Main stems	Primary branches	Total
Cv. Lofuwa						
14	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
28	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
42	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
56	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
70	0.4 ± 0.30	0.7 ± 0.44	1.1 ± 0.33	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
84	2.4 ± 0.93	1.9 ± 0.69	4.3 ± 0.97	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
98	3.0 ± 0.85	1.9 ± 0.56	4.9 ± 1.32	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
112	11.9 ± 2.46	3.1 ± 0.64	15.0 ± 2.38	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
126	14.7 ± 6.57	5.8 ± 2.31	20.5 ± 4.71	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
140	14.5 ± 7.28	10.1 ± 4.14	24.5 ± 10.96	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
154	13.3 ± 7.19	11.9 ± 1.91	25.2 ± 8.22	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
168	14.7 ± 14.70	12.5 ± 4.53	27.2 ± 17.59	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
182	10.4 ± 5.74	4.5 ± 4.31	14.9 ± 9.93	5.0 ± 3.21	8.9 ± 6.12	13.9 ± 9.07
196	22.4 ± 12.59	8.7 ± 2.44	31.2 ± 11.43	4.6 ± 3.62	6.6 ± 3.26	11.2 ± 5.44
210	17.3 ± 3.53	4.3 ± 1.93	21.6 ± 3.77	2.6 ± 3.41	6.3 ± 1.82	8.9 ± 2.23
224	1.5 ± 3.43	6.8 ± 3.26	8.4 ± 4.46	0.4 ± 0.89	4.9 ± 1.69	5.3 ± 1.77
238	11.3 ± 5.61	14.0 ± 11.15	25.2 ± 15.50	2.1 ± 2.88	5.3 ± 3.27	7.3 ± 5.68
Cv. Chankua						
14	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
28	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
42	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
56	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
70	0.6 ± 0.48	0.7 ± 0.30	1.3 ± 0.64	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
84	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
98	2.6 ± 0.48	2.0 ± 0.53	4.6 ± 0.48	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
112	7.5 ± 2.71	2.2 ± 0.62	9.7 ± 2.80	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
126	10.3 ± 4.39	5.7 ± 2.49	16.0 ± 5.79	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
140	13.7 ± 6.18	13.0 ± 5.79	26.7 ± 11.81	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
154	8.6 ± 6.26	13.1 ± 8.60	21.7 ± 13.68	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
168	10.0 ± 5.49	19.5 ± 11.79	29.5 ± 15.08	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
182	7.7 ± 4.33	4.8 ± 2.66	12.5 ± 6.25	9.2 ± 5.13	3.5 ± 1.69	12.7 ± 6.46
196	8.9 ± 6.68	7.8 ± 3.69	16.7 ± 7.45	2.4 ± 3.36	10.5 ± 3.58	12.9 ± 3.08
210	13.4 ± 10.31	9.7 ± 12.38	23.1 ± 21.23	1.5 ± 1.18	5.6 ± 5.31	7.1 ± 4.38
224	6.9 ± 2.74	6.8 ± 2.04	13.7 ± 3.14	5.3 ± 9.24	2.0 ± 1.91	7.2 ± 8.35

Mean ± SD (n = 5 plots, from each of which plants from 6 holes were measured). DAP, Days after planting.

Table 2. Development with time of the numbers of below-ground and aerial stolons from main stems and primary branches for cvs Lofuwa and Chankua in Wondogenet.

DAP	Below-ground stolons (No. / hole)			Aerial stolons (No. / hole)		
	Main stems	Primary branches	Total	Main stems	Primary branches	Total
Cv. Lofuwa						
14	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
28	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
42	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
56	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00

Table 2. Contd.

70	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
84	2.3	±	0.64	2.5	±	0.99	4.8	±	0.69	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
98	4.6	±	0.66	11.7	±	2.10	16.3	±	2.61	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
112	8.9	±	2.75	15.1	±	2.94	24.0	±	3.03	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
126	15.0	±	9.40	7.0	±	8.66	22.0	±	17.43	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
140	21.4	±	17.92	26.4	±	14.80	47.8	±	24.67	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
154	35.9	±	22.25	29.7	±	16.99	65.6	±	38.21	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
168	43.0	±	21.98	37.6	±	10.76	80.6	±	30.87	6.7	±	3.51	20.8	±	5.99	27.5	±	6.59
182	30.5	±	25.14	4.8	±	2.22	35.3	±	26.68	9.5	±	7.30	6.5	±	3.59	16.0	±	8.97
196	31.0	±	14.84	26.3	±	14.24	57.3	±	28.65	4.5	±	3.19	11.2	±	11.77	15.6	±	11.84
210	12.0	±	2.75	12.5	±	6.63	24.6	±	8.80	6.8	±	5.91	5.0	±	3.05	11.8	±	7.51
Cv. Chankua																		
14	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
28	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
42	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
56	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
70	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
84	1.6	±	0.72	2.2	±	0.90	3.8	±	0.77	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
98	4.9	±	1.30	11.6	±	3.88	16.5	±	4.53	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
112	6.8	±	2.79	11.0	±	2.17	17.8	±	1.21	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
126	8.3	±	5.64	8.0	±	9.03	16.3	±	12.88	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
140	15.4	±	9.42	9.8	±	9.70	25.2	±	18.82	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
154	31.9	±	10.38	38.2	±	19.16	70.1	±	27.41	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
168	38.1	±	17.44	39.3	±	8.22	77.4	±	14.25	0.0	±	0.00	0.0	±	0.00	0.0	±	0.00
182	11.7	±	13.12	5.3	±	2.92	17.0	±	12.39	3.2	±	2.14	7.8	±	3.32	11.0	±	2.84
196	15.2	±	5.35	24.1	±	10.32	39.3	±	13.24	5.5	±	3.82	3.0	±	2.59	8.5	±	4.21
210	7.5	±	3.39	9.7	±	5.42	17.3	±	7.58	1.7	±	2.64	5.1	±	3.02	6.8	±	3.90

Mean ± SD (n = 5 plots, from each of which plants from 6 holes were measured). DAP, Days after planting.

in *P. edulis* (Yeshitila, 2007) while *P. esculentus* has yellow flowers (Tindall, 1983), but also by the fact that tubers of *P. esculentus* show a clear positively gravitropic growth (Allemann et al., 2003). We did not record the exact growth direction of *P. edulis* tubers and stolons, but the wide spread of the stolons suggests it was mainly plagiotropic for the stolons (with the exception of the branches from aerial stolons entering the soil).

Canopy development

Several yellowish sprouts per hole were produced from each tuber piece at the beginning of the growing period but after emergence all except a few sprouts changed to green or reddish (depending on the cultivar) and developed into main stems. The main stems were tipped at 61 to 63 DAP; tipping is a practice carried out by farmers to stimulate stem branching (Mulugeta et al., 2007, 2012). The moment of tipping was around the moment that all main stems had been formed (Figure 2). Primary branches then started to develop (Figure 2), while the number of main stems decreased to c. 1.5 per hole, likely because of inter-stem competition. This implies that at maximum half of the tuber pieces planted per hole actually produced a main stem surviving until the tuber stage. The majority of the canopy of *P. edulis* was formed by primary and secondary branches and the leaves on these branches (Figures 2 and 3). Our data on main stem numbers per hole are somewhat lower than those reported by Yeshitila (2007) and Weyessa et al. (2009), but these authors did not mention to have practiced shoot tipping or to have used seed tuber pieces, as is common practice by farmers. Canopy development was gradually arrested by the initiation of terminal inflorescences at the apices of the stems, especially the primary and secondary branches, and the ending of further initiation of new branches. First inflorescences were observed 112 DAP and 126 DAP for154 DAP for both cultivars in Wondogenet. The total number of green leaves started to decline after c. 154 to 168 DAP (Figure 3), with complete leaf senescence being attained 238 to 252 DAP. There was no prove for the assumption that cv. Lofuwa was earlier maturing than cv. Chankua.

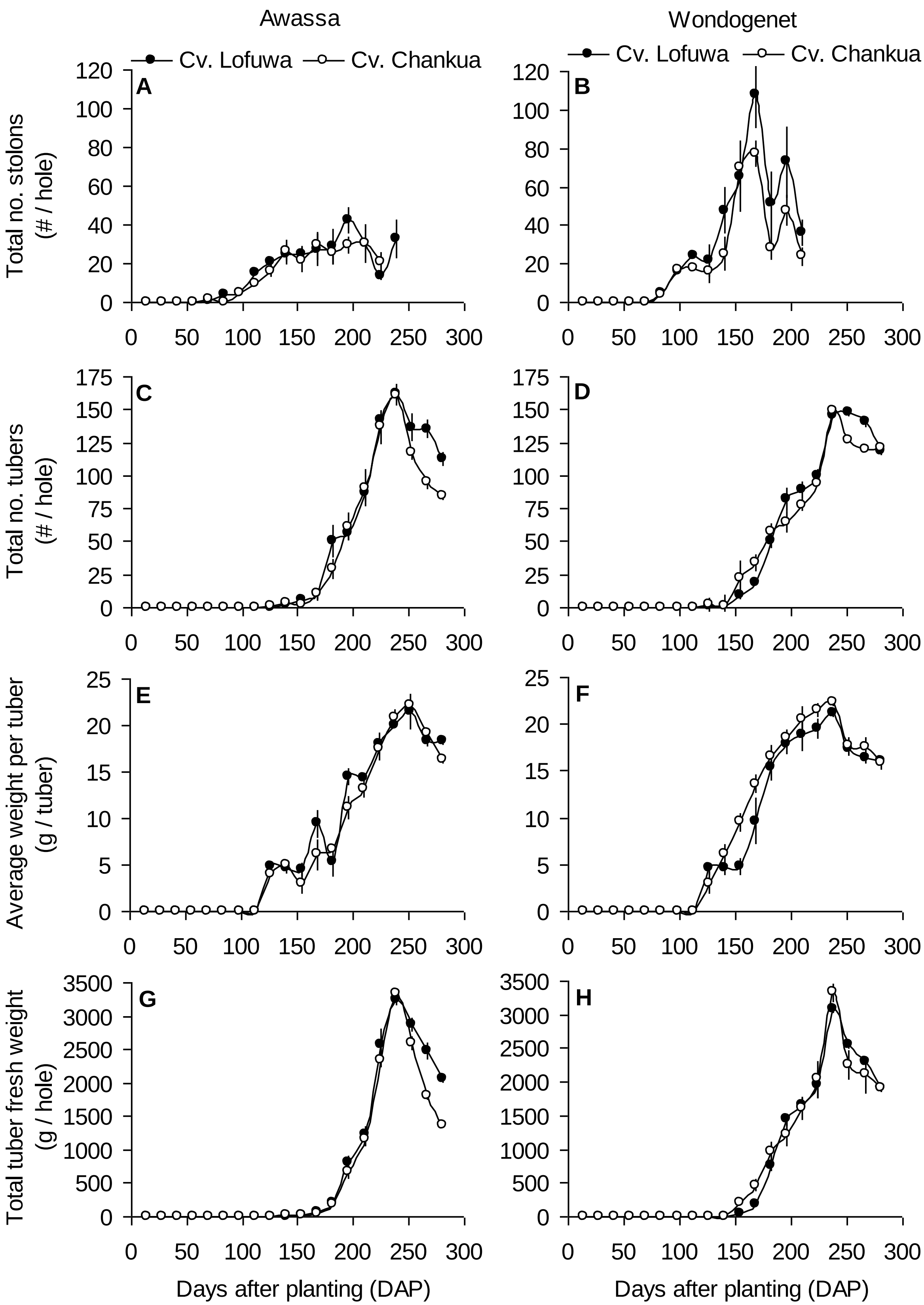

Figure 5. Total number of stolons and tubers per hole, average weight per tuber and total tuber fresh weight per hole at Awassa and Wondogenet for cvs Lofuwa and Chankua. A, Number of stolons, C, number of tubers, E, average weight per tuber, G, total tuber fresh weight in Awassa; B, number of stolons, D, number of tubers, F, average weight per tuber; H, total tuber fresh weight in Wondogenet (n = 5 plots of 6 holes).

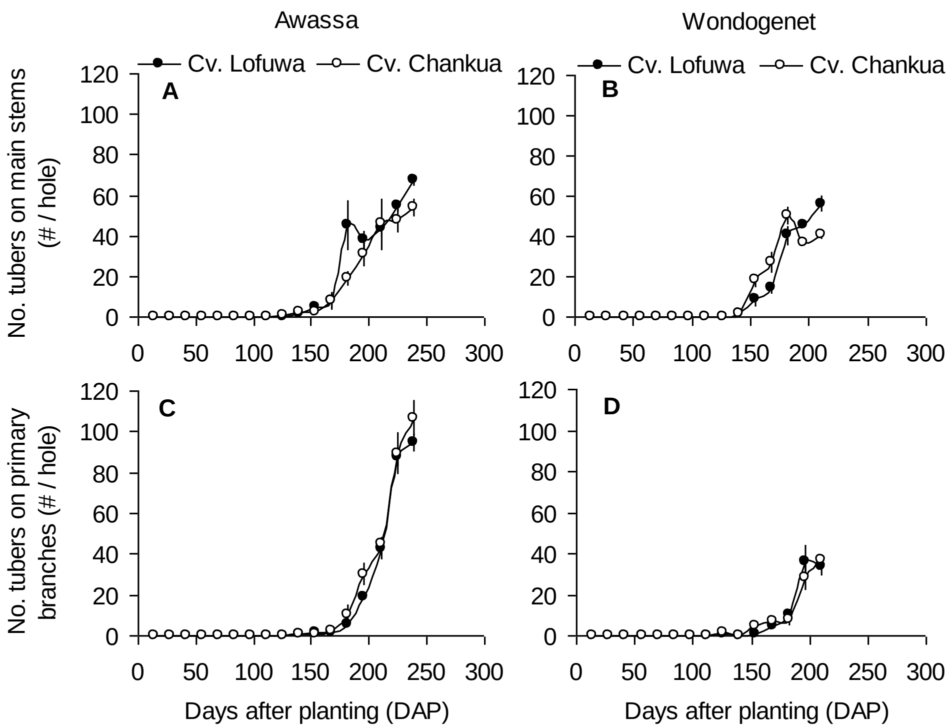

Figure 6. Number of tubers originating from main stems and primary branches per hole at Awassa and Wondogenet for cvs Lofuwa and Chankua. A, Tubers on main stems, C, tubers on primary branches in Awassa; B, tubers on main stems, D, tubers on primary branches in Wondogenet. Bar = standard deviation (n = 5 plots of 6 holes).

cvs Lofuwa and Chankua, respectively in Awassa, and

Number of stolons, number of tubers and tuber yield

The pattern of stolon formation differed greatly between sites. In Awassa, the total number of stolons levelled off after tubers were initiated (c. 150 DAP) and remained at a more or less stable level. Counting the number of stolons was difficult because some were broken while harvesting, and only those with parts that remained connected with main stems and primary branches were included in the counts. The total number of stolons in Awassa stayed around 25 to 30 per hole until 200 to 250 DAP when reliable counting of stolons was no longer possible (Figure 5A). The stable level was surprising, because aerial stolons were initiated from 182 DAP onwards, but this initiation was apparently accompanied by an overall decrease in the number of below-ground stolons (Table 1). It is unlikely that the two types of stolons were mixed because the aerial stolons were longer than the below-ground tubers, leafy and more coloured, and the two types of stolons therefore could be clearly distinguished.

In Wondogenet, the total number of stolons had increased to higher levels than in Awassa (80 to 100 versus 30 to 40 per hole) at the moment tuber initiation had started well (Figure 5). This was found for stolons from both main stems and primary branches (Figure 4). It is possible that the higher numbers of stolons were related to the overall lower temperature in Wondogenet than in Awassa. The increase in number of stolons also continued longer in Wondogenet than in Awassa, but was followed by a decrease, taking place in the period that tubers were still being initiated (Figures 5B and D). Also in Wondogenet, the appearance of aerial stolons was accompanied by a decrease in the number of below-ground stolons (Table 2). Future research will need to show the mechanisms behind these variations in stolon number.

The difference in number of stolons between sites was not reflected in the number of tubers, which at maximum was 150 to 160 per hole at both sites. After tuber initiation, the number of tubers increased almost linearly during a period of 12 to 14 weeks, and maximum numbers of tubers were attained around 238 DAP, at crop senescence. This is very unlike the common pattern of tuber formation in Irish potato, where most tubers are initiated within a period of a few weeks (after which during the tuber bulking phase the number of tubers declines due to resorption of the smallest, non-competitive tubers (Vreugdenhil and Struik, 1989; Struik, 2007). In *P. edulis* also, the number of smaller tubers (< 10 or 20 g) increased until senescence (Figure 7). In the

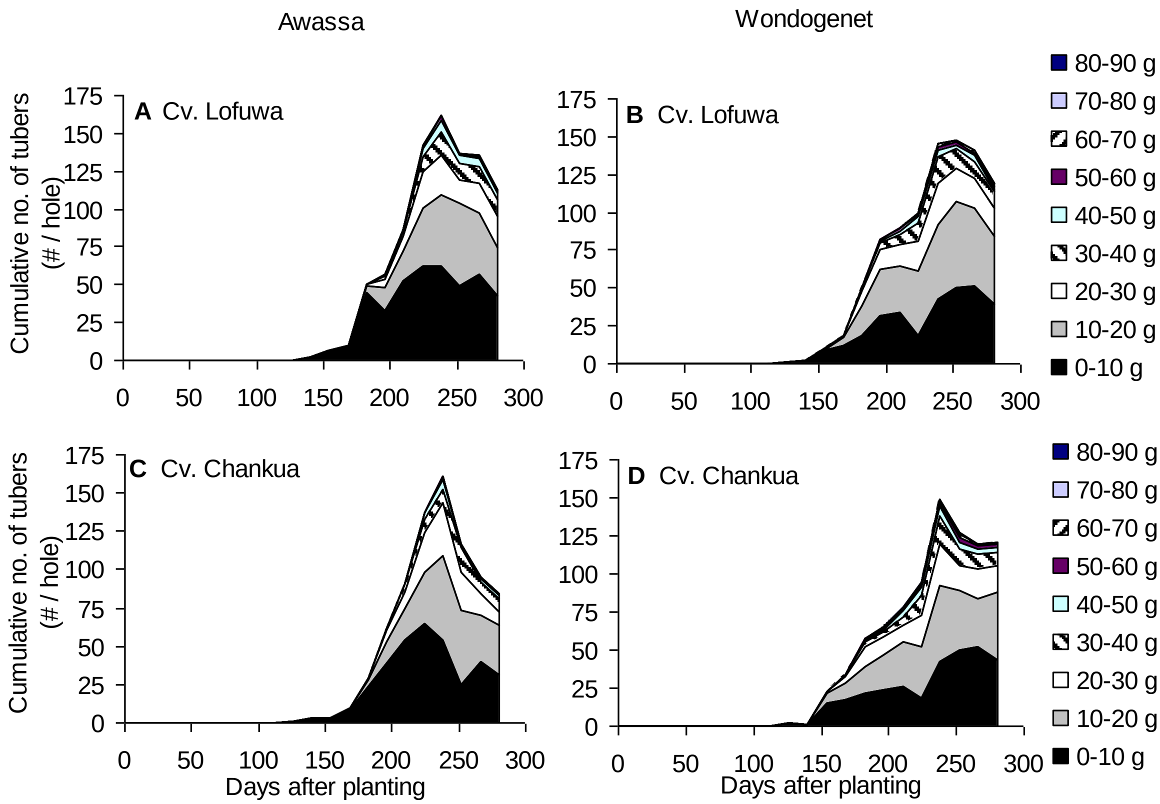

Figure 7. Cumulative number of tubers per hole in different tuber weight classes at Awassa and Wondogenet for cvs Lofuwa and Chankua. A, Cv. Lofuwa, Awassa; B, cv. Lofuwa, Wondogenet; C, cv. Chankua, Awassa; D, cv. Chankua, Wondogenet.

period of tuber initiation also the average weight per tuber increased up to 20 to 25 g per tuber around 238 DAP (Figures 5E and F). The increase in tuber yield with time until senescence was therefore realized by an increase in both tuber number and in average weight per tuber (Figure 5).

In situ storage

There was a sharp peak in number of tubers and especially in tuber fresh weight per hole at 238 DAP (Figure 5). From an agronomical point of view, it is important to identify this moment to maximize yield. Tuber yield per hole still increased before this moment, and losses occurred thereafter. It was not possible, however, to relate this moment consistently over sites and cultivars to the number of green leaves: In Wondogenet, the last counts of green leaves were made 2 weeks before this moment and at 238 DAP no green leaves were present anymore, whereas in Awassa the number of green leaves was negligible at 238 DAP in cv. Chankua but still more than 200 per hole in cv. Lofuwa (Figure 3).

After crop maturity, farmers keep the tubers unharvested in the soil until they need them (Mulugeta et al., 2007). This research shows that this dramatically reduces the number of tubers and their weight, with decreases being observed of 36 to 59% in total tuber fresh weight per hole and of 18 to 48% in number of tubers in 6 weeks (between 238 and 280 DAP; cf. Figure 5). Losses not only took place in the lightest tuber classes (<10 or 10 to 20 g) but also in the heavier tuber classes. Weight losses may have been caused by continued respiration of the tubers, by loss of water and by losses of complete tubers. Declines in the number of tubers might have been caused by resorption of the least competitive tubers, probably the smallest tubers and tubers in the middle part of the stolons. In addition, some tubers might not have been found back anymore, some of which could be lost because of rotting or by exhausting of all reserves by respiration. No obvious rotting of tubers was observed however.

Conclusions

At the onset of this research, little was known on *P. edulis* despite its long cultivation history in Ethiopia, and its stolons or type of tuber (stem tuber or root) even were not described. The present research showed that in cultivation, a plant of *P. edulis* is composed of: the mother tuber piece, sprouts, main stems, branches, leaves, inflorescences, fruits, seeds, roots, stolons, and tubers. The stolons are very long and are initiated on buds of main stems and primary branches, first only on below-ground nodes, but later also on the lower aerial nodes. Tubers are produced upon swelling of the tip or middle part of stolons. Most of the tubers that are formed along the stolon are longer than tubers formed at the stolon tip. The tubers of *P. edulis* are stem tubers, like those of Irish potato.

The crop has a long growing period of almost 8 months. Combining the results it can be concluded that the crop passes through the following ontogenetic phases during one production cycle:

1) Emergence, resulting in an established crop;
2) Canopy development, ending gradually through the initiation of terminal inflorescences;
3) A phase in which stolons are initiated and develop from below-ground and aerial buds on the main stems and primary branches, and that ends in stolon senescence;
4) A phase of tuber initiation and growth;
5) A phase of canopy senescence.

These five phases were partly overlapping each other and were not as well attuned to one another as in the Irish potato. The knowledge on the ontogenetic phases is relevant for future physiological and agronomical research and is the first step towards further crop improvement.

ACKNOWLEDGEMENT

We gratefully acknowledge the financial support from the Norwegian Agency for Development and Corporation (NORAD).

REFERENCES

Admasu T, Struik PC (2003). Growth, radiation use efficiency and yield potential of enset (*Enset ventricosum* (Welw.) Cheesman) at different sites in southern Ethiopia. Ann. Appl. Biol. 142:71−81.

Allemann J, Hammes PS (2006). Effect of photoperiod on tuberization in the Livingstone potato (*Plectranthus esculentus* N.E.Br. Lamiaceae). Field Crop Res. 98:76-81.

Allemann J, Robertse PJ, Hammes PS (2003). Organographic and anatomical evidence that the edible storage organs of *Plectranthus esculentus* N.E.Br. (Lamiaceae) are stem tubers. Field Crop Res. 83:35−39.

Bodlaender KBA, Lugt C, Marinus J (1964). The induction of second-growth in potato tubers. Eur. Potato J. 7:57-71.

Greenway PJ (1944). Origins of some of East African food plants. Part 1. East Afr. Agric. J. 10:34−39.

Jansen PCM (1996). *Plectranthus rotundifolius* (Poiret) Sprengel. In: Flach M, Rumawas F (eds) Plant Resources of South-East Asia no 9. Plants Yielding Non-Seed Carbohydrates, Backhuys Publishers, Leiden, Netherlands pp. 141-143.

Lugt C, Bodlaender KBA, Goodijk G (1964). Observations on the induction of second-growth in potato tubers. Eur. Potato J. 7:219-227.

McMaster GS (2004). Simulating crop phenology. In: Fischer T, Turner N, Angus J, Robertson M, Borrell A, Lloyd D (eds) New Directions for a Diverse Planet: Proceedings for the 4th International Crop Science Congress, Brisbane, Australia, 26 September – 1 October 2004, www.cropscience.org.au/icsc2004/poster/2/8/607_mcmaster.htm. Accessed 28 July 2011.

Mulugeta T, Lommen WJM, Struik PC (2007). Indigenous multiplication and production practices for the tuber crop *Plectranthus edulis* in Chencha and Wolaita, southern Ethiopia. Exp. Agric. 43:381-400.

Mulugeta T, Lommen WJM, Struik PC (2012). Effects of shoot tipping on development and yield of the tuber crop *Plectranthus edulis.* J. Agr. Sci. Cambridge 150:484-494.

Reddy VR, Baker DN, Hodges HF (1991). Temperature effects on cotton canopy growth, photosynthetic and respiration. Agron. J. 83:699−704.

Siegenthaler IE (1963). Useful Plants of Ethiopia. Experiment Station Bulletin No. 14. Volume I. Imperial Ethiopian College of Agricultural and Mechanical Arts, Jima Experiment Station, Alemaya, Ethiopia.

Squire GR (1990). The Physiology of Tropical Crop Production, C.A.B., Wallingford, UK.

Struik PC (2007). Above-ground and below-ground plant development. In: Vreugdenhil D, Bradshaw J, Gebhardt C, Govers F, MacKerron DKL, Taylor MA, Ross HA (eds) Potato Biology and Biotechnology: Advances and Perspectives, Elsevier, Oxford, UK; Amsterdam, Netherlands pp. 219-236.

Struik PC, Wiersema SG (1999). Seed Potato Technology, Wageningen Pers, Wageningen, Netherlands.

Tindall HD (1983). Vegetables in the Tropics. Macmillan Press, London, UK.

Vreugdenhil D, Struik PC (1989). An integrated view of the hormonal regulation of tuber formation in potato (*Solanum tuberosum*). Physiol. Plant. 75:525-531.

Westphal E (1975). Agricultural Systems in Ethiopia. Agricultural Research Reports 826. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands.

Weyessa G, Admasu T, Bezuayehu T, Hussein M (2009). Variability and association of quantitative traits in *Plectranthus edulis* (Vatke) Agnew. East Afr. J. Sci. 3:61-69.

Yeshitila M (2007). Phenotypic variation and local customary use of Ethiopian potato (*Plectranthus edulis* (Vatke) Agnew). CBM Master Theses Series 40, Swedish Biodiversity Centre, Uppsala. http://www.cbm.slu.se/eng/mastersprog/thesis2007/Yeshitila%20MekbibThesis.pdf. Accessed 16 November 2011.

Zemede A, Zerihun W (1997). Crop associations of home-gardens in Welayta and Gurage in southern Ethiopia. SINET. Ethiopian J. Sci. 20:73-90.