Final Report

Understanding tuber formation: maintaining the capability to improve tuber quality attributes including greening

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1. SUMMARY

1.1. Aim

The main aim was to quantify stolon architecture (depth from the soil surface and length) in seven varieties and relate this to the position of tubers in the soil and their susceptibility to being exposed to light, resulting in tuber greening. A further aim was to establish the influence of physiological and environmental factors (seed size, temperature, nitrogen rate) on stolon architecture. Lastly, the work aimed to survey stolon architecture and tuber greening in commercial crops.

1.2. Methodology

Seven varieties were grown in a replicated experiment in Cambridge for 3 years. Plots were sampled around the time of tuber initiation and the length and depth of every stolon was measured. In the middle of the season, stolon length and depth, and the position of each tuber were measured. Samples were taken after desiccation to assess for tuber greening. One experiment examined the effect of seed tuber size on stolon architecture and tuber greening. Two planting date experiments investigated the extent to which stolon length differed as temperatures varied and also whether the rate of nitrogen affected stolon length. 36 commercial crops were surveyed to quantify stolon architecture and tuber position and relate this to susceptibility to tuber greening.

1.3. Key findings

Significant differences in mean stolon length were observed between the varieties each year. The horizontal position of tubers was closely related to stolon length and tuber length indicating that it is possible to predict the cluster width of a crop for any given stolon length and tuber size. Stolon depth differed between varieties, but the differences were small compared to the differences in stolon length between varieties. Seed size did not affect stolon length or tuber greening. Planting date affected stolon length but the effects were inconsistent and difficult to reconcile with variation in temperature. Nitrogen rate significantly affected stolon length but the extent of the effect was small for a large difference in nitrogen rate. The survey of commercial crops found a similar range in stolon length as in the experiments and the average stolon depth was *c.* 75 % of planting depth.

At a value of £100 per tonne, tuber greening was estimated to cost the UK potato industry £25m per annum. Few green tubers were exposed at the soil surface with the majority still covered by soil indicating that cracking of the soil was important in allowing light to reach the tubers. Varieties differed in their sensitivity to light but this did not correspond to their propensity to tuber greening in the field experiments. Planting depth varied widely, both between and within crops, and influenced the amount of yield close to the soil surface. Tuber greening was most severe on sites where more tubers were close to the soil surface and tended to be more severe on soils with a higher clay content. The planter experiment indicated that hood pressure and ridge shape could influence tuber greening.

1.4. Practical recommendations

Crops grown on soils with a high clay content and planted shallowly, are particularly at risk from tuber greening, especially when yields are high and tubers are large. The optimum planting depth to limit tuber greening may be deeper on soils with a higher clay content, but may reduce overall yield. Due to the considerable range in planting depth that can occur between rows, it is advisable for growers to monitor planting depth closely and working with machinery manufacturers to reduce this variation would be beneficial. Where tuber greening is substantial, growers should investigate where the green tubers are in the ridge, e.g. exposed at the surface, growing out of the flanks or unexposed and adjust their planting depth and ridge geometry accordingly.

2. INTRODUCTION

Understanding tuber formation and development is crucial to improving the efficiency of crop production and developing new varieties. The processes that occur are relatively poorly understood in field-grown crops, because tubers are subterranean, making non-destructive measurements difficult or impossible to obtain. This work sought to improve our understanding of the fundamental processes of stolon and tuber development and relate this to tuber greening and variation in tuber size. These economically significant causes of waste, each result in, on average, *c.* 5 % of yield wasted, or diverted into lower-value products.

2.1. Stolon architecture and tuber greening

Tuber greening is a substantial cause of waste in the potato industry and is caused by tubers being exposed to light, stimulating the synthesis of chlorophyll and glycoalkaloids (Tanios *et al*. 2018). While chlorophyll is tasteless and harmless, glycoalkaloids are bitter-tasting and can occur at potentially toxic concentrations in green tubers (Friedman 2006; Nema *et al.* 2008) and consumers are aware that green tubers may be dangerous to consume and do not purchase or consume them (WRAP 2012). Factors known to influence tuber greening include row width (Bernik *et al.* 2009), planting depth (Stalham *et al.* 2002; Bohl & Love 2005; Pavek & Thornton 2009), ridge shape (Kouwenhoven *et al.* 2003; Bohl *et al*. 2014, Vučajnk *et al.* 2017), soil cracking (Kouwenhoven *et al.* 2003) and variety (Bohl *et al*. 2014). With the exception of soil cracking, the unifying mechanism behind all of these factors, is that increasing the distance between tubers and the soil surface reduces tuber greening.

2.1.1. Stolon length

Stolon length is known to vary between varieties (Kratzke & Palta 1992) but the influence of this on the position of tubers in the ridge and subsequently on the susceptibility to tuber greening has not been investigated. Kratzke & Palta (1992) grew eight varieties over two years and concluded that stolon length differed between varieties, with mean stolon length ranging from 3 to 16 cm and individual stolon lengths varying from 0 to 26 cm. Within varieties, there were no significant differences between years, so they concluded that stolon length was a consistent genetic trait. Firman (1996) measured mean tuberised stolon length in four varieties and found it ranged from 3.5 to 5.5 cm.

Pavek & Thornton (2009) found that mean stolon length was increased by *c.* 2 cm planting at 10 cm compared to at 15 cm, but they did not distinguish between tuberised and untuberised stolons. Planting deeper than 15 cm did not result in further decreases in mean stolon length. The average internode length increased as planting depth increased, but distinctions were not made between tuberised and untuberised stolons, so the effect on the depth of tuber formation is uncertain.

Authoritative book chapters on the development of potato state that stolon development begins at the most basal nodes of the stem (closest to the seed tuber; Cutter 1992; Struik 2011). This statement is based on work conducted in hydroponic conditions by Lovell and Booth (1969) and does not appear to have been validated in field-grown crops. Citing the work of Struik & van Voorst (1986), conducted in controlled environments, Struik (2011) stated that the longest stolons are found at the base of stems because they grow faster than later-initiated stolons. High temperatures and high concentrations of nitrogen have been found to promote stolon development over tuberisation in laboratory settings (Jackson 1999) but the relevance to crop development in the field is uncertain.

2.1.2. Stolon and tuber depth

Varieties have been considered to differ in the depth at which tubers develop, influencing susceptibility to tuber greening (e.g. Peters 2008) but there are no published data that support this proposition, by quantifying differences and demonstrating they are consistent. There are no reports in the literature of the average depth of tuberised stolons from the soil surface. Previous studies have measured the position of tubers in the soil and related this to the susceptibility to tuber greening (Kouwenhoven *et al.* 2003; Bernik *et al.* 2009; Vučajnk *et al.* 2017) but these studies did not relate tuber position to stolon architecture. Bohl *et al*. 2014 noted that tubers were not all orientated horizontally, but rather with the apical end closer to the soil surface than the stolon end. They suggested this was more likely to occur when stolon length was short, but only two varieties were compared and differences in tuber orientation were not quantified.

2.1.3. Commercial crops

Tuber greening occurring in commercial crops has not previously been quantified to establish where green tubers occur in the ridge and relate this to differences in agronomic practices. As a complex issue that probably has multiple, interacting causes, we considered this a vital component of the work in order to relate experimental findings to commercial practice, and to understand what actions growers may be able to take in the short-term to reduce tuber greening. Stalham & Allison (2015) found no effects of destoning (cultivation) depth on tuber greening in 20 experiments conducted in commercial crops on a range of soils.

2.2. Variation in tuber size

Variation in tuber size causes some tubers to be too small or too large to be marketable, reducing the value of crops and causing wastage (Wurr *et al*. 1993). Previous research has found nitrogen rate, harvest date, site of production and variety can affect variation in tuber size (Wurr *et al*. 1993), although more comprehensive research has found no effect of nitrogen (Allison *et al*. 2011). Further research found blackleg (*Erwinia carotovara* subspecies *atroseptica*) and *Rhizoctonia solani* infections on seed tubers can also increase variation in tuber size, but that nitrogen and irrigation did not (Firman & Shearman 2006, 2007; Firman 2004 & 2008). Stems are the true unit of population in the potato crop (Allen & Wurr 1992), but little is known about why they differ in size and how this influences variation in tuber size. Smart (2016) investigated how plant-to-plant and stem-to-stem variations in yield and number of tubers influenced variation in tuber size, but did not establish the extent to which variation in tuber size differed between varieties or whether this variation could be explained through differences in stem-to-stem variation. Data relevant to variation in tuber size are considered separately from those relating to stolon architecture and tuber greening in Section 3.11.

2.3. Experimental approach

The main component of the work was to examine stolon development, tuber position, tuber greening and stem-to-stem variation in yield and tuber size in seven varieties (Estima, Jelly, King Edward, Marfona, Maris Piper, Markies and Marfona) over three years in replicated field experiments. Results from a pilot study and the 2015 variety experiment showed a correlation between average seed tuber substrate per stem and mean stolon length, so an experiment was conducted in 2016 to examine whether larger seed tubers (with higher amounts of seed substrate per stem) would produce longer stolons than smaller seed tubers. This experiment also examined whether plant spacing could influence soil cracking, since at the same overall yield, the yield per plant (and tuber volume) is higher when spacing is wider. The influence of environmental factors on stolon architecture was investigated through two planting date experiments, consisting of three planting dates, fertilised at two highly contrasting nitrogen rates and in Estima and Markies, a determinate and indeterminate variety respectively. One hand-planted planting depth experiment was conducted, as well as a machine-planted experiment examining the influence of planting depth, planter hood pressure and ridge shape on tuber position and tuber greening.

Commercial crops encompassing a range of varieties and soil types were surveyed to quantify stolon architecture and tuber position. Crops were also assessed shortly before commercial harvesting to establish the part of the ridge in which tubers were found and to relate this to the proportion of yield affected by tuber greening.

3. MATERIALS AND METHODS

Table 1. Summary of the experiments

Expt	Variety	Seed tuber size	Treatments	Planting date(s)	Harvest dates (DAE)
1	See treatments	25-35 mm	7 varieties: Estima, Jelly, King Edward, Marfona, Maris Piper, Markies and Melody	20/4/2015	0, 12, 44, 74, 103, 124
2	See treatments	25-35 mm	7 varieties: Estima, Jelly, King Edward, Marfona, Maris Piper, Markies and Melody	26/4/2016	13, 21, 29, 70, 114
3	See treatments	25-35 mm [a] or 30-40 mm [b]	7 varieties: Estima [b], Jelly [a], King Edward [b], Marfona [a], Maris Piper [b], Markies [a] and Melody [a]	6/4/2017	7, 10, 12, 15, 17, 20, 23, 27, 84, 121
4	Jelly, Marfona, Maris Piper	See treatments	All combinations of 3 varieties and 2 seed sizes. Jelly, 25-35 mm and 45-55 mm; Marfona, 30-40 mm and 40-50 mm; Maris Piper, 30-40 mm and 50-55 mm.	19/4/16	33,120
5	Estima and Markies	25-35 mm	All combinations of 3 planting dates, 2 varieties and 2 rates of nitrogen (0 and 300 kg N/ha)	13/4/16 10/5/16 6/6/16	33
6	Estima and Markies	30-40 mm or 25-35 mm, respectively	All combinations of 3 planting dates, 2 varieties and 2 rates of nitrogen (0 and 300 kg N/ha)	30/3/17 24/4/17 16/5/17	33
7	Markies and Innovator	35-45 mm	Intended planting depths of 10, 15, 20 and 25 cm; hand planted and replicated in Markies, machine planted and unreplicated in Innovator	23/4/2015	*c.* 110
8	Russet Burbank	35-45 mm	All combinations of intended planting depths of 10 and 15 cm, bed shapes of a ridge and semi-bed, and planter hood pressures of 0 and 100 %.	4/5/2016	*c.* 120

3.1. Common methods

3.1.1. Crop maintenance

Except where stated otherwise, nitrogen was applied as ammonium nitrate at a rate of 200 kg/ha of N. Artist (flufenacet and metribuzin) was applied after planting at 2.5 kg/ha in a water volume of 200 l/ha. Irrigation was applied as required according to the CUF irrigation model. Fungicides to control late blight were applied *c.* weekly.

3.1.2. Ground cover and emergence

Emergence was recorded twice weekly for all plants in the central two rows of each plot until complete and ground cover (Burstall & Harris 1983) was recorded weekly from the central two rows throughout the season.

3.1.3. Stolon measurement

Prior to harvest, plants were spray-painted at the soil surface to determine the planting depth. Plants were dug separately, placed in polythene bags and stored at 2 ºC until analysis. Stems were separated and the above-ground stem was cut just below the spray painted line and weighed, before measuring the planting depth of the below-ground stem. Each stolon > 5 mm in length was measured. Stolon depth was defined as the distance from the top of the below-ground stem to the stolon attachment point and stolon length was defined as the distance from the stem to the end of the stolon. The type of stolon was recorded as either primary, lateral or branched and a note was made according to whether the stolon had not tuberised, had tuberised but was < 10 mm in diameter or had tuberised and was > 10 mm in diameter. Tubers > 10 mm in diameter were weighed to the nearest 0.1 g.

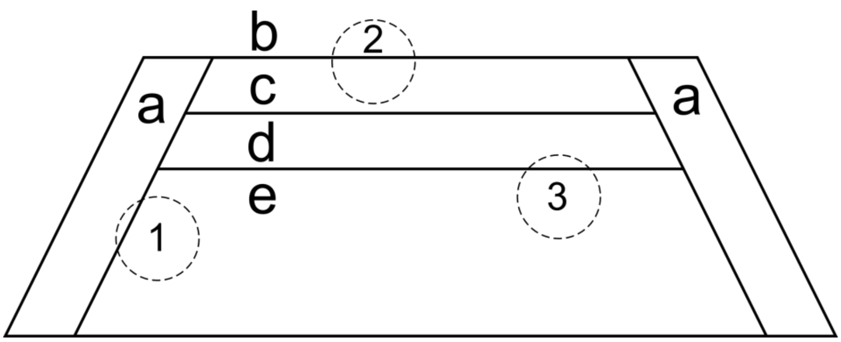
3.1.4. Tuber mapping

Above-ground stems were cut at the base and discarded to prevent further growth of the tubers and the ridge was covered with black plastic to prevent light reaching the ridge whilst assessments were made over the course of *c.* 2 weeks. A steel frame was placed above each plant in turn and positioned in the centre of the ridge with the bottom of the frame flush with the top of the ridge. A ruler attached to a digital protractor (Moore and Wright, UK) was fixed to the frame to allow the angle, distance and depth of any point from the centre of the frame to be measured. Angles were recorded to the nearest degree and all distances to the nearest 5 mm. For one plant in each plot, the ridge profile was recorded by measuring the distance from the ruler to the soil surface every 2 cm perpendicular to the centre of the ridge. The position where each stem emerged from the soil was recorded and then the soil was removed until tubers were visible. For each tuber, the position of the stolon and apical ends and the depth to the top of the tuber from the frame was recorded. When tubers were orientated more than ± 10º from horizontal, their orientation was estimated to the nearest 5º. Once mapped, the depth of the stolon from the top of the stem and the length of the stolon were measured and the stem to which the tuber was attached was recorded. Tubers were numbered with a paint pen (Grog, Italy) and the diameter, length, width, height and weight were measured in the laboratory and the incidence of tuber greening was recorded. Finally, the position of the base of each stem, the planting depth of each stem and the depth to the top of the seed tuber (when intact) were measured. The angles and distances were converted to Cartesian (x, y) coordinates and the centre of each plant was defined as the average coordinates of the base of the stems. The distance from the centre of the plant to the stolon and apical ends of each tuber were calculated. Cluster width was defined as double the mean distance from the centre of the plant to the apical end of the tuber plus two standard deviations (i.e. the width in which 95 % of tubers were found).

3.1.5. Tuber position

Tubers were harvested separately depending on their location in the ridge (Figure 1). The outermost 5 cm of soil was removed from each flank of the ridge and any tubers exposed were collected. Any tubers visible on the surface of the ridge were collected, but those visible through cracks in the soil were left in place. The top 5 cm of soil was excavated and exposed tubers were categorised according to whether they had 0-2.5 cm or 2.5-5 cm of soil coverage. Once all the tubers were collected, the number of plants, primary and secondary stems was recorded and the planting depth of 20 stems was measured to the nearest 5 mm. Tubers from each category were graded and assessed for tuber greening separately.

Figure 1. Diagram showing the different sections of the ridge from which tubers were harvested separately. (a) flank, (b) surface, (c) 0-2.5 cm, (d) 2.5-5 cm and (e) > 5 cm. Tubers were included in the section if any part was present, so that tuber 1 = flank, tuber 2 = surface and tuber 3 = 2.5-5 cm. Not to scale.



3.1.6. Tuber grading and greening

Tubers were washed and then categorised as: no greening, tubers < 40 mm with any greening, tubers > 40 mm with light-coloured greening covering < 5 %, 5-25 % or

> 25 % surface area and tubers > 40 mm with dark-coloured greening covering < 5 %, 5-25 % or > 25 % surface area. The number and fresh weight of tubers in each category was recorded. Tubers were graded into 10 mm size fractions and the fresh weight and number of tubers in each size grade was recorded.

3.1.7. Tuber size

The mean tuber size and COV of tuber size for individual plots were calculated by fitting a normal distribution to the yield of tubers within size grades using an adapted version of the method used by Travis (1987) and Wurr *et al.* (1993). Methods previously described in Smart (2016) were used to quantify mean tuber weight per stem and estimate variation in tuber size within stems.

3.2. Experiment 1 – 2015 Variety

The experiment was carried out at NIAB on a sandy loam soil. The site was ploughed in the autumn and ridges were formed by roto-ridger on 23 March. Phosphorus and potassium were applied as triple superphosphate and muriate of potash at 57 kg/ha and 249 kg/ha of P and K respectively on 27 March. Seed tubers (25-35 mm) of seven varieties (Estima, Jelly, King Edward, Marfona, Maris Piper, Markies and Melody) were planted by hand on 20 April at a within-row spacing of 30 cm and at a depth of *c*. 15 cm from the top of the seed tuber to the top of the ridge. After planting, the ridges were reformed by hand using a rake. Each plot consisted of a 9.6 m length of four rows 75 cm apart and there were four replicates of each variety arranged in randomised blocks.

Three harvests of four plants were taken beginning on 6 July, 5 August and 3 September (*c.* 44, 74 and 103 DAE) to measure the position of each tuber and length and depth of each stolon. The experiment was desiccated with Reglone, applied at 2 l/ha in a water volume of 400 l/ha on 4 September (*c.* 104 DAE). A final harvest of 12 guarded plants was dug by hand on 24 September (*c.* 124 DAE). The number of plants, main stems and secondary stems were counted and all tubers > 10 mm in diameter were collected. Any rotten tubers were replaced with tubers of a similar size and shape from discard plants. For Estima and Markies, tubers were harvested with a trowel and split into three groups depending on the distance from the top of the stem to the top of the tuber (0-5, 5-10 and 10-15 cm). Once other assessments were complete, 25 tubers from the upper- and lower-most groups of each plot were sent to the University of

Greenwich to establish whether there were any differences in mineral composition or dormancy depending on the location of tubers in the ridge. Tubers were stored at 5 ºC for 40 days before being washed and assessed for the incidence and severity of tuber greening.

Ten tubers were retained to assess their sensitivity to greening when stored in a lit and heated greenhouse (*c.* 70 µmol/m^2/s at 400-700 nm for 12 hours per day at *c.* 20 ºC). Two tubers from each plot were sampled every two days by taking a peel (*c.* 0.85 mm thick) from the upper part of the tuber and measuring the intensity of greening with a SPAD meter (Minolta, Japan) at five locations on each peel (Braun 2010).

3.3. Experiment 2 – 2016 Variety

The experiment was carried out at NIAB on a sandy clay loam soil. The site was ploughed in the autumn, re-ploughed on 31 March, followed by secondary cultivations and ridges were formed by roto-ridger on 11 April. Seed tubers (25-35 mm) of seven varieties (Estima, Jelly, King Edward, Marfona, Maris Piper, Markies and Melody) were planted by hand on 26 April at a within-row spacing of 30 cm and at a depth of *c*. 15 cm from the top of the seed tuber to the top of the ridge. After planting, the ridges were reformed by hand using a rake. Each plot consisted of an 8.1 m length of four rows 75 cm apart and there were four replicates of each variety arranged in randomised blocks.

Three harvests of four plants were taken on 14, 22 and 30 June (*c.* 13, 21 and 29 DAE) to measure stolon development. One harvest of six plants was taken following physical defoliation of plants on 10 August (*c.* 70 DAE) to measure the position of each tuber and length and depth of each stolon. The experiment was desiccated with diquat, applied at 2 l/ha in a water volume of 300 l/ha on 1 September (*c.* 92 DAE). A final harvest of 12 guarded plants was dug by hand on 23 September (*c.* 114 DAE). The number of plants, main stems and secondary stems were counted and all tubers > 10 mm in diameter were collected. Any rotten tubers were replaced with tubers of a similar size and shape from discard plants. For Estima and Maris Piper, tubers were harvested with a trowel and split into three groups depending on the distance from the top of the stem to the top of the tuber (0-5, 5-10 and 10-15 cm). Once other assessments were complete, 25 tubers from the upper- and lower-most groups of each plot were sent to the University of Greenwich to establish any differences in mineral composition or dormancy depending on the location of tubers in the ridge. Tubers were stored at 5 ºC for 19 days before being washed and assessed for the incidence and severity of greening. Ten tubers were retained to assess their sensitivity to greening as in Expt 1.

3.4. Experiment 3 – 2017 Variety

The experiment was carried out at NIAB on a sandy clay loam soil. The site was ploughed on 14-15 March, followed by secondary cultivations and ridges were formed by roto-ridger on 28 March. Seven varieties (Estima, Jelly, King Edward, Marfona, Maris Piper, Markies and Melody) were planted by hand on 6 April at a within-row spacing of 30 cm and at a depth of c. 15 cm from the top of the seed tuber to the top of the ridge. Seed tubers of Jelly, Marfona, Markies and Melody were graded 25-35 mm and those of Estima, King Edward and Maris Piper were graded 30 40 mm. After planting, the ridges were reformed by hand using a rake. Each plot consisted of a 9 m length of four rows 75 cm apart and there were four replicates of each variety arranged in randomised blocks.

Five harvests of four plants were taken on 30 May and 2, 4, 7 and 9 June (*c.* 7, 10, 12, 15 and 17 DAE). For each stem, the length of the longest stolon, the number of stolons > 5 mm in length, number of tubers (twice the diameter of the stolon) and the number of tubers > 10 mm in diameter were recorded. A further three harvests of four plants were taken on 12, 15 and 19 June (*c.* 20, 23 and 27 DAE) to measure the length and depth of each stolon as in Expt 2. One harvest of six plants was taken following physical defoliation of plants on 15 August (c. 84 DAE) and tubers were mapped over the next *c.* 2 weeks. The experiment was desiccated with diquat, applied at 2 l/ha in a water volume of 300 l/ha on 31 August (c. 100 DAE). A final harvest of 12 guarded plants was dug by hand on 21 September (c. 121 DAE), graded and assessed for tubers greening. Eight tubers were retained to assess their sensitivity to greening in the greenhouse as in Expt 1.

3.5. Experiment 4 – Seed size

Cultivations and maintenance were as for Expt 2. Treatments consisted of three varieties (Jelly, Marfona and Maris Piper) and two seed sizes (small and large; Table 2). Small seed was planted at a within-row spacing of 25 cm and large seed at 40 cm. The experiment was planted on 19 April 2016. Each plot consisted of a 6 m length of four rows 75 cm apart and there were four replicates of treatment arranged in randomised blocks.

Table 2. Size and mean weight of the seed stocks in Expt 4

	Small seed		Large seed	
Variety	Size (mm)	Mean weight (g FW)	Size (mm)	Mean weight (g FW)
Jelly	25-35	21.1	45-55	96.2
Marfona	30-40	27.3	40-50	58.0
Maris Piper	30-40	30.5	50-55	89.0

One harvest of ten plants of the small seed size, and six plants of the large seed size was taken on 28 June (*c.* 33 DAE) using the same method as for the early harvests of Expt 2-3. Stems were measured as in Expts 1-3, but only tuberised stolons were measured. The experiment was desiccated with diquat, applied at 2 l/ha in a water volume of 300 l/ha on 1 September (*c.* 98 DAE). A final harvest of 20 plants of the small seed size, and 12 plants of the large seed size was taken from the central two rows on 23 September (*c.* 120 DAE). Tubers were graded and assessed for greening as in Expt 3.

3.6. Experiment 5 – 2016 planting date

Treatments consisted of three planting dates (Early, Mid, Late; 13 April, 10 May, 6 June), two varieties (Estima and Markies) and two nitrogen rates (0 and 300 kg N/ha). Seed of both varieties was graded 25-35 mm. Each plot consisted of a 1.75 m length of four rows 75 cm apart and there were four replicates arranged in randomised blocks. Two sprinklers were placed in the central furrow of each plot at 0.38 and 1.38 m. Thermistors were placed in one plot per planting date treatment at a depth of *c.* 15 cm from the top of the ridge and the temperature was logged hourly. For plots receiving nitrogen as a treatment, 150 kg/ha N was applied as ammonium nitrate at planting, and a further 150 kg/ha N was applied just prior to emergence. Cultivations and maintenance were as for Expt 3, except that Artist was applied prior to emergence of the first two planting dates and weeds were manually controlled for the third planting date.

One harvest of six plants was taken on 22 June, 11 July or 1 August (*c.* 33 DAE) from the early, mid and late planting dates respectively. Stems were measured as in Expts 2 and 3, but only tuberised stolons were measured.

3.7. Experiment 6 – 2017 planting date

Treatments were identical to Expt 5, but the Early, Mid, Late planting dates were 30 March, 24 April and 16 May, respectively). The seed was graded 25-35 mm for Markies and 30-40 mm for Estima and each plot consisted of a 2 m length of four rows. One harvest of six plants was taken on 21 June, 4 July or 18 July (c. 33 DAE) from the Early, Mid and Late planting dates, respectively. Stolon depth and stolon length of all tuberised stolons were measured as in other experiments.

3.8. Experiment 7 – Planting depth

The experiment was carried out at Gravelly Bank near Rugeley (52.784º N, 1.942º W) on a moderately to very stony sandy clay loam soil. Seed tubers (35-45 mm) of Markies were planted by hand on 23 April 2015 at intended depths of 10, 15, 20 and 25 cm and at a within-row spacing of 30 cm. The 20 and 25 cm planting depths were achieved by removing soil from the top of the bed before planting and replacing it afterwards. Each plot consisted of a 3 m length of four rows 91.4 cm apart and there were five replicates of each of the planting depths arranged in randomised blocks. Ground cover was recorded with the CanopyCheck app on 15 June and 24 June. Unreplicated strips of Innovator were machine-planted at the same intended depths as the experiment. Fertilisers, herbicide and irrigation were applied according to local commercial practice.

A harvest of 12 plants was taken from the central two rows of each plot on 10 September. Above-ground stems were cut at the base and discarded and any tubers visible at above the soil surface were collected separately. The outermost 5 cm of soil (10 cm for one replicate) was removed from the ridge with a trowel and tubers that became exposed were collected. The remaining tubers were dug by hand separately. The number of plants and stems was recorded and the planting depth was measured on 10 stems per plot. For one plot in the 15 cm treatment, tubers from four plants were mapped using the same methods as in the Cambridge experiment. Three 3 m digs were taken in each machine-planted strip and the planting depth was measured on 10 stems. Tubers were graded and assessed for greening as in the Cambridge experiment.

3.9. Experiment 8 – Planting depth, ridge shape and hood pressure

The experiment was carried out near Thorpe Constantine (52.683º N, 1.590º W) on a sandy loam to loamy sand soil. Seed tubers (35-45 mm) of Russet Burbank were planted by machine on 4 May 2016 at a within-row spacing of 34 cm. Treatments consisted of all combinations of three factors; intended planting depths of 15 and 20 cm, bed shapes of a ridge and semi-bed, and planter hood pressures of 0 and 100 %. Each plot consisted of a 20 m length of four rows 91.4 cm apart and there were three replicates arranged in randomised blocks along one strip of the field.

Five soil samples, each consisting of a 5.5 cm diameter core of the upper 5 cm of soil, were taken from the top of the ridge or semi-bed on 20 September. The samples were bulked and dried to determine bulk density. On 21 September, three plants from one plot of each of the two planting depths and the high hood pressure and ridge shape were excavated, and the stolons measured and tubers mapped as in Expts 1-3. The experiment was desiccated on 24 September.

A harvest of 3 m of one of the central two rows was taken on 5-6 October. Above-ground stems were cut at the base and discarded. The soil surface was inspected, and the width of the widest crack and the depth of the deepest crack were measured to the nearest 5 mm using a ruler. Tubers were harvested separately according to their position in the ridge (see Section 3.1.5)

3.10. Survey of commercial crops

36 commercial crops were sampled and locations of the sites, variety and soil type were as listed in Table 3. The assessments varied at each crop, with some visited once to map the position of tubers in as in Expts 1-3, whereas others where visited once to measure the position of tubers in the ridge prior to lifting and 18 were assessed using both methods. When mapping the position of tubers, typically, four plants were sampled from two different rows and the values for tubers from each plant were averaged and the standard error of the mean value per plant was calculated. To assess the position of tubers in the ridge, six 3 m lengths of row (or 1.5 m of bed) were harvested, with tubers collected separately from different places within the ridge (Figure 1). For the crops where tuber greening was assessed, soil samples were analysed by laser diffractometry to determine their clay content.

At Workhouse, F35, F23 and Home Piece a similar method was used to that at other sites, but tubers were removed from every 2.5 cm layer rather than just the top 5 cm, and only 2 or 3 replicates were taken, with a further 3 samples taken without separating tubers according to their position. At Brandon 1, Brandon Road South and F22, it was evident that tubers had pushed soil up above the top of the bed, so prior to sampling the 0-2.5 cm section, the top of the bed was levelled and any tubers unearthed were designated as 'above'. At Brandon 1, two seed sizes (35-50 and 50-60 mm) were planted in the same field and two different planters were used, one of which did not apply hood pressure (Planter A) and the other which did (Planter B). Tubers were only mapped in the area of the small seed but final harvests were taken from areas where both the small and large seed was planted with Planter A and where the large seed was planted with Planter B. Unlike at the other sites, the 2.5-5 cm category was not harvested separately at Brandon 1. At Brandon 2, the grower had noted that some tubers had formed in the furrow, so these were harvested as a separate category and the 0-2.5 cm and 2.5-5 cm categories were combined. One of the Papplewick sites sampled was the grower's standard (ridge) and the other was where a new system of drip irrigation and a different ridge shape was used (bed). At Stackyard, some rows were misaligned so that plants emerged from the side of the ridge. The crop was sampled as for the other crops, but a further six samples were taken. Tubers were graded and assessed for greening as in the experiments.

Table 3. Details of the commercial crops sampled

Site	Location	Variety	Soil type	Sampling date(s)†
Hinstock	52.833º N, 2.466º W	Estima	Sandy silt loam	14/7/16 [a], 12/9/16 [b]
Weavers	51.993º N, 2.762º W	Estima	Clay loam	12/7/16 [a], 6/9/16 [b]
50 Acres	52.915º N, 1.212º E	Innovator	Loamy sand	18/9/17 [b]
Papplewick Bed	53.040º N, 1.166º W	Innovator	Sandy loam	21/9/16 [b]
Papplewick Ridge	53.059º N, 1.152º W	Innovator	Loamy sand	21/9/16 [b]
Gravelly Bank	52.784º N, 1.942º W	Innovator	Sandy clay loam	11/9/15 [b]
Brandon Rd South	52.389º N, 0.669º E	Jelly	Sand	1/8/16 [a], 14/9/16 [b]
Brooke	51.990º N, 2.755º W	Jelly	Clay loam	5/9/16 [a], 6/9/16 [b]
Hospital Grass 1	52.886º N, 0.031º E	Jelly	Silty clay loam	29/9/15 [b]
Icklingham	52.347º N, 0.570º E	Jelly	Loamy sand	25/9/17 [b]
Moores Belt 1	52.099º N, 0.200º E	Jelly	Sandy loam	2/7/15 [a], 30/7/15 [a]
Workhouse	52.523º N, 1.518º E	Jelly	Sandy loam	29/7/15 [a], 1/9/15 [b]
18 Acres	51.818º N, 0.289º E	King Edward	Clay loam	2/8/16 [a], 13/9/16 [b]
Bishop’s Frome	52.131º N, 2.526º W	King Edward	Clay loam	13/7/16 [a]
Brook	51.813º N, 0.287º E	King Edward	Clay loam	27/9/17 [b]
Chatteris 1	52.477º N, 0.041º E	King Edward	Peaty clay	22/7/16 [a]
Moores Belt 2	52.099º N, 0.200º E	King Edward	Sandy loam	30/7/15 [a]
Sculfers	52.835º N, 1.514º E	King Edward	Sandy silt loam	20/7/17 [a], 3/10/17 [b]
Brandon 1	52.441º N, 0.550º E	Marfona	Sand	26/7/16 [a], 29/7/16 [b]
Middle and Drain	52.645º N, 2.351º W	Marfona	Sandy loam	18/7/16 [a]
Pestels	52.815º N, 1.501º E	Marfona	Sandy silt loam	21/7/17 [a]
Wheelwrights	52.277º N, 0.687º E	Marfona	Loamy sand	30/6/15 [a], 18/7/15 [b]
F22	52.533º N, 0.462º E	Maris Piper	Peat	1/9/16 [a], 14/10/16 [b]
F23	52.532º N, 0.459º E	Maris Piper	Peat	25/8/15 [a], 15/10/15 [b]
F35	52.285º N, 0.631º E	Maris Piper	Sandy loam	1/7/15 [a], 28/8/15 [b]
Home Piece	52.513º N, 1.578º E	Maris Piper	Sandy loam	29/7/15 [a], 26/8/15 [b]
Southery	52.528º N, 0.482º E	Maris Piper	Peat	12/10/17 [b]
Aylmerton	52.913º N, 1.232º E	Markies	Sandy silt loam	8/9/16 [a], 9/9/16 [b]
Chatteris 2	52.477º N, 0.041º E	Markies	Peaty clay	21/7/16 [a]
Cricket field	52.900º N, 1.378º E	Markies	Sandy silt loam	8/10/15 [a]
High Hill 16	52.792º N, 1.486º E	Markies	Clay	9/9/16 [a], 19/10/16 [b]
Stackyard	52.904º N, 1.243º E	Markies	Sandy silt loam	18/9/17 [b]
Beezlings	52.477º N, 0.011º E	Melody	Peaty clay	20/7/16 [a], 10/10/16 [b]
Bob Cole’s	52.828º N, 1.476º E	Melody	Sandy silt loam	19/7/17 [a], 19/9/17 [b]
Hospital Grass 2	52.886º N, 0.031º E	Melody	Silty clay loam	29/9/15 [a]
Brandon 2	52.437º N, 0.553º E	Saphire	Sand	27/7/16 [a], 31/8/16 [b]

† [a] and [b] denote whether stolon architecture or tuber position were assessed, respectively.

3.10.1. Quality control data

Quality control data were supplied for 18864 loads of the varieties studied in the experiment in Cambridge (excluding Markies) that were grown from 2013-2015 and packed by Greenvale AP. Growers who supplied < 50 loads (*c.* 1000 t) across the three years were excluded leaving 16453 loads to analyse. For each load, the total wastage in a sample was assessed and if tuber greening was one of the top three defects identified, the proportion of the waste caused by tuber greening was estimated to the nearest 10 %. The total amount of waste was recorded and the percentage of yield rejected due to tuber greening was estimated from this and the proportion of waste in the sample caused by tuber greening.

3.11. Variation in tuber size

In Expt 1, seed tubers were weighed prior to planting and 50 from each variety were washed, chipped and dried individually. One harvest of 10 plants was taken as soon as each plant had emerged. A second harvest of 10 plants was taken *c.* 12 DAE and each stem in this harvest was tagged with a loop of coloured wire on the day they emerged. Roots and stolons were removed before weighing the below- and above-ground portions of each stem and bulking those from each plot before being dried. The seed tubers were washed, chipped and dried individually. Yield per stem was recorded at the tuber mapping harvests *c.* 44, 74 and 103 DAE, although in some instances the stem to which a tuber was attached could not be determined in which case the entire plant was excluded from the analysis. Due to the small sample size of the later harvests (four plants), the coefficient of variation (COV) of yield per stem was pooled across the three harvests by calculating the yield of each stem relative to total yield of the plot at each harvest.

4. Results

4.1. Experiment 1

4.1.1. Emergence and ground cover

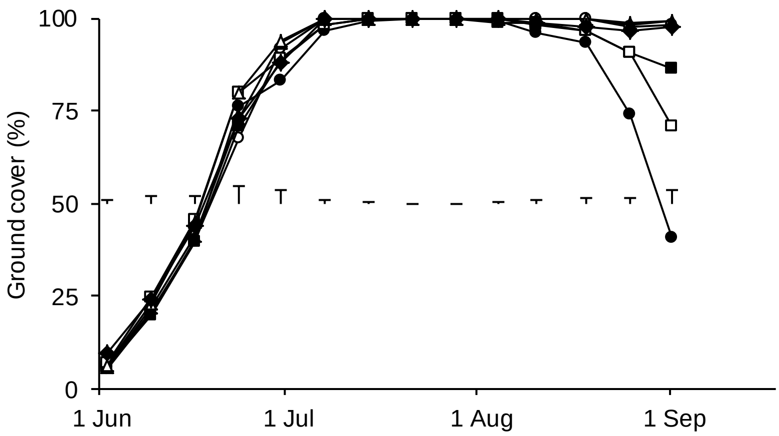
All varieties emerged between 32 and 34 days after planting with King Edward and Marfona emerging earliest and Jelly latest (Table 4). Marfona emerged most uniformly, with 20 to 80 % emergence occurring in less than two days compared with more than three days in Jelly and Maris Piper (Table 4).

Table 4. Effect of variety on the interval from planting to emergence and the rate of emergence in Expt 1

Variety	Interval from planting to 50 % emergence (days)	Interval from 20 to 80% emergence (days)
Estima	32.2	2.9
Jelly	33.5	3.2
King Edward	31.8	3.0
Marfona	31.6	1.9
Maris Piper	32.4	3.4
Markies	32.6	2.4
Melody	32.6	2.6
S.E. (18 D.F.)	0.24	0.28

Ground cover developed at a similar rate in all varieties with full canopies achieved in the first week of July. Estima began to senesce in the first week of August and King Edward and Marfona began to senesce one week later (Figure 2). The other varieties maintained full canopies until desiccation (Figure 2).

Figure 2. Foliar ground cover in Expt 1. Estima, ●; Jelly,○; King Edward, ■; Marfona, □; Maris Piper, ▲; Markies, △; Melody, ◆. Bars indicate S. E. based on 18 D.F.



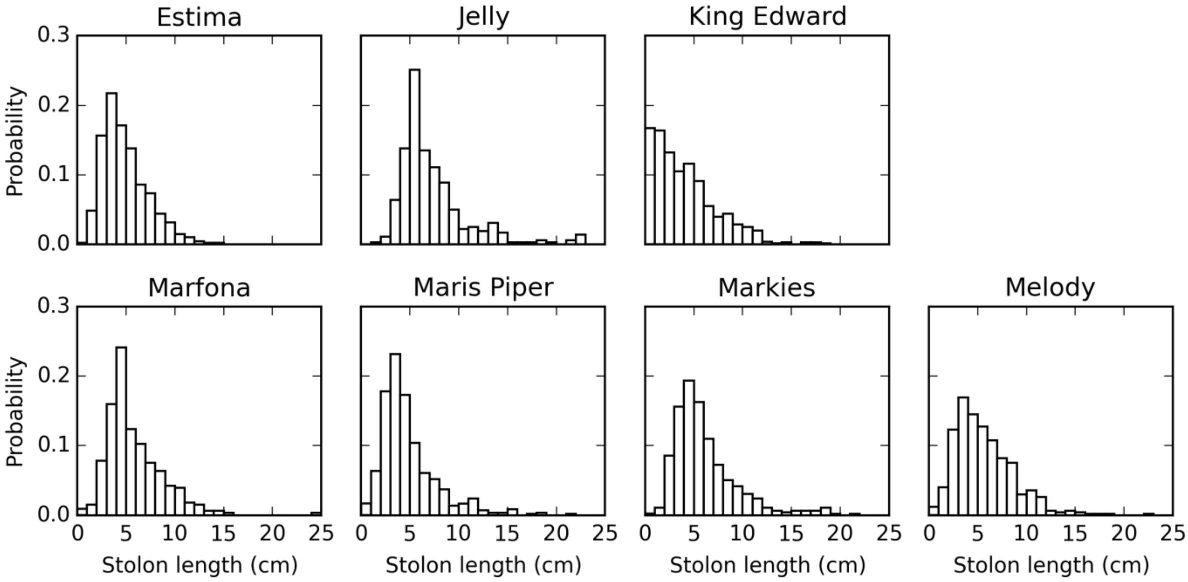
4.1.2. Stolon architecture

The mean achieved planting depth was *c.* 14 cm and there were no differences between varieties (Table 5). Minimum and maximum planting depths were *c.* 11 and 16 cm respectively and did not differ between varieties (data not shown). Mean stolon length and depth did not change significantly between harvests (data not shown) so the data from the three harvests were combined. Stolons formed, on average, *c*. 10 cm from the soil surface in all varieties, being deepest in Marfona and shallowest in Maris Piper but the differences between varieties were small (1.4 cm; Table 5), and the relative stolon depth (taking account of the slight variations in planting depth between varieties and stems) showed similar differences between varieties (Table 5). Jelly had the longest mean stolon length of 7.0 cm, King Edward had the shortest (3.9 cm) and other varieties were between 4.5 and 5.6 cm (Table 5). The median stolon length was *c.* 10 % shorter than the mean stolon length in all varieties but between varieties the two were very strongly correlated (R^2 = 0.99). This was indicative of there being a relatively small number of long (> 10 cm) stolons in all varieties (Figure 3). King Edward had *c.* 30 % of stolons < 3 cm long whereas other varieties had only *c.* 5-10 % of stolons < 3 cm long and sessile tubers (those with no stolon) only occurred in King Edward (Figure 3).

Table 5. Effect of variety on planting depth, stolon depth, relative stolon depth and stolon length in Expt 1

Variety	Planting depth (cm)	Mean stolon depth (cm)	Mean relative stolon depth (%)	Mean stolon length (cm)	Median stolon length (cm)
Estima	14.1	10.4	72.9	4.6	4.1
Jelly	14.0	11.2	80.0	7.0	6.3
King Edward	13.7	10.3	76.1	3.9	3.1
Marfona	14.5	11.4	79.0	5.6	4.8
Maris Piper	14.2	10.1	74.2	4.5	3.8
Markies	13.8	11.0	77.1	5.9	5.1
Melody	14.0	10.4	74.5	5.4	4.8
S.E. (18 D.F.)	0.25	0.22	1.11	0.26	0.23

Figure 3. Histograms of stolon length in each variety across the three harvests of Expt 1.



Stolons were clustered towards the base of the stem in all varieties and the deepest stolons shown in Figure 4 were the result of variation in planting depth between stems. Differences in the minimum stolon depth per plant were greater than the mean stolon depth with Marfona and Jelly having the deepest at *c.* 7 cm compared to other varieties at *c.* 4-5 cm (Table 6). The maximum stolon length per plant was less variable than the mean stolon length at between *c.* 9 and 13 cm in all varieties and the mean and maximum stolon lengths were not always directly related (Tables 5 and 6). While King Edward had the shortest mean stolon length, it did not have the shortest maximum stolon length (Tables 5 and 6).

Figure 4. Histograms of stolon depth in each of the varieties across the three harvests of Expt 1

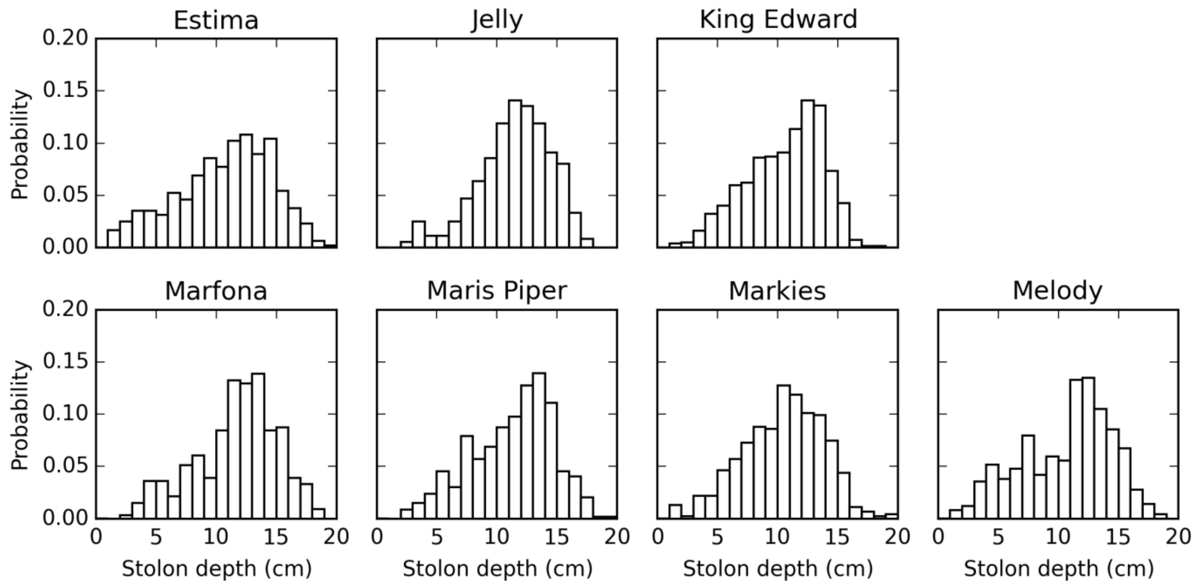


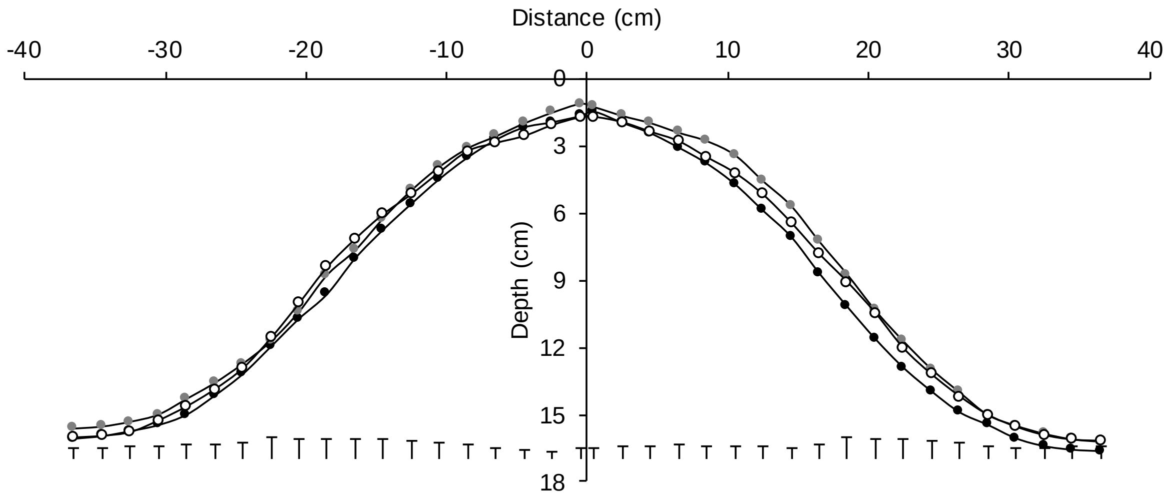
Table 6. Effect of variety on minimum stolon depth and maximum stolon length per plant in Expt 1

Variety	Minimum stolon depth (cm)	Maximum stolon length (cm)
Estima	3.9	8.6
Jelly	7.1	13.1
King Edward	4.6	10.5
Marfona	6.9	9.6
Maris Piper	5.2	10.2
Markies	5.3	12.0
Melody	4.1	10.7
S.E. (18 D.F.)	0.36	0.83

4.1.3. Ridge profile

There were no differences in the ridge profile between varieties (data not shown) and the average ridge profile remained similar between the three harvests (Figure 5). Although the frame was placed flush with the top of the ridge, the soil tended to be lower where the plant had emerged than between plants where the ridge was measured.

Figure 5. Average ridge profiles at the first (●), second (●) and third (○) harvests of Expt 1. Bars indicate S. E. based on 18 D.F. at the first harvest (this remained similar between harvests).



4.1.4. Tuber mapping

The average distance from the centre of the plant to the stolon end of tubers was between 5 and 7 cm (Table 7) and was strongly correlated and almost directly related to average stolon length (Figure 6). The distance to the stolon end did not change between the three harvests indicating that the growth of tubers did not push the tuber towards the stem. The slightly longer distance to the stolon end of the tuber than the stolon length was probably due to the stems not emerging directly above the seed tuber, resulting in the stolon attachment point being a small distance away from the centre of the plant (Figure 6). There was no evidence to indicate that tubers were further away from the seed tuber along the ridge compared to across the ridge (data not shown).

At the third harvest, the apical ends of the tubers were furthest away from the centre of the plant in Jelly, Marfona and Markies at *c*. 13 cm (Table 7). In Estima, Maris Piper and Melody, tubers were slightly closer at *c.* 11-12 cm and substantially closer in King Edward at *c*. 9 cm (Table 7). Combining the average stolon length and average tuber length accounted for a large proportion of the distance to the apical end of the tuber over the course of the season (Figure 6). The distance to the apical end was slightly shorter than the stolon length plus tuber length and this was probably due to the angle from the centre of the plant to the stolon and apical ends of the tubers not being identical and also due to the horizontal orientation of tubers varying. Considering that tuber length is related to tuber shape and mean tuber size, these results indicate that if the stolon length can be predicted, the horizontal position of tubers could also be predicted.

Table 7. Effect of variety on the distance from the centre of the plant to the stolon and apical ends of tubers at the three harvests of Expt 1.

	Distance to stolon end of tubers (cm)	Distance to apical end of tubers (cm)		
Variety Harvest	All harvests	1	2	3
Estima	4.8	9.1	10.4	11.7
Jelly	6.8	11.1	13.4	13.5
King Edward	4.6	7.3	9.0	9.4
Marfona	5.8	9.6	12.7	13.7
Maris Piper	5.0	8.4	10.5	11.0
Markies	6.2	10.6	12.4	13.0
Melody	5.7	10.1	11.3	12.1
S.E. (18 D.F.)	0.29	0.51	0.41	0.34

Figure 6. Relationships between distance to the stolon end of tubers and stolon length at all three harvests of Expt 1, ●; and between distance to the apical end of tubers and stolon length plus tuber length at the first, ○; second, ■; and third harvests, □. Line is 1:1 relationship. Relationships for each dataset are given in Table 8.

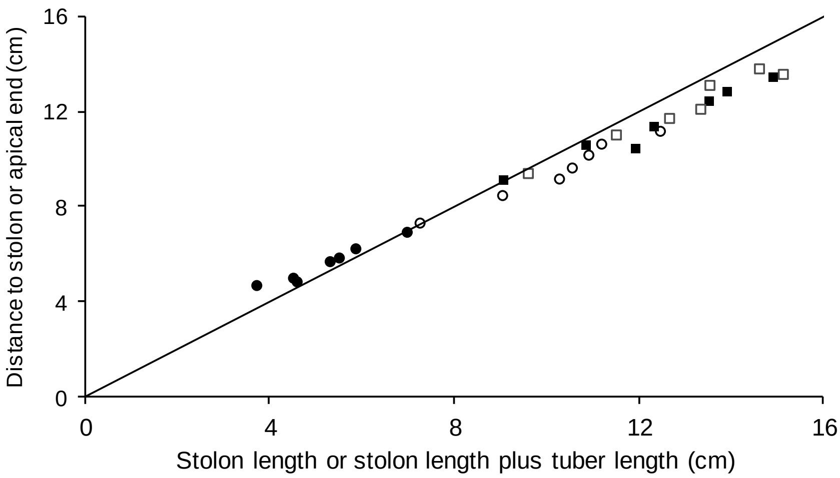


Table 8. Relationships between position of the stolon or apical end of tubers (POS, cm) and stolon length or stolon length plus tuber length (LEN, cm) in Expt 1 as shown in Figure 6: slope of relationship (*m*) and S.E., constant of relationship (*c*) and S.E., significance of relationship (*F* prob) and strength of relationship (R^2).
POS = *m* LEN + *c*

Position and harvest	*m*	S.E.	*c*	S.E.	*F* prob.	R^2
Stolon, all harvests	0.746	0.0677	1.63	0.361	<0.001	0.95
Apical, 1	0.774	0.0637	1.51	0.662	<0.001	0.96
Apical, 2	0.762	0.0689	1.92	0.864	<0.001	0.95
Apical, 3	0.808	0.0738	1.59	0.965	<0.001	0.95

Across all varieties, the average depth of the top of tubers from the top of the ridge decreased from 9.9 cm at the first harvest to 8.4 cm at the third harvest (Table 9) and this corresponded to the average increase in the vertical height of tubers between harvests (data not shown). There were no significant differences in tuber depth between varieties at the first and second harvests, but at the third harvest, Jelly had the deepest tubers at 9.7 cm and Marfona had the shallowest at 7.0 cm (Table 9). Tubers of Marfona, Maris Piper, Markies and Melody became *c.* 2 cm shallower between harvests, whereas tubers of Estima and King Edward were *c.* 1 cm shallower and for Jelly tuber depth did not change (Table 9; Figure 7). One possible cause for the consistent tuber depth in Jelly between harvests is that the combination of longer stolons (Table 5) and a low tuber population (Table 12) meant tubers were less likely to interfere with each other and be pushed towards the surface as they grew. Unlike for the horizontal position of tubers, their depth did not correlate with stolon depth at any harvest (data not shown). This was partly due to the lack of variation in stolon depth between varieties and differences in tuber size but there were also apparent differences in the vertical growth of stolons (Table 10). At the first harvest, the majority of stolons in Melody grew downwards from the stem to the tuber whereas in the other varieties they grew upwards (Table 10). In most varieties, the centres of the tubers rose closer to the surface as the season progressed, but in Estima these remained similar across harvests contributing to the relatively small change in tuber depth (Tables 9 and 10).

Table 9. Effect of variety on the depth from the top of the ridge to the top of the tubers in Expt 1

		Depth to top of tuber (cm)		
Variety	Harvest	1	2	3
Estima		9.6	9.0	8.5
Jelly		9.9	9.3	9.7
King Edward		9.5	8.4	8.1
Marfona		9.3	8.4	7.0
Maris Piper		10.4	9.2	8.7
Markies		9.6	8.1	7.8
Melody		10.8	9.3	8.7
S.E. (18 D.F.)		0.41	0.44	0.37

Figure 7. Distributions of tuber depth at the first (■) and third (■) tuber mapping harvests in Expt 1.

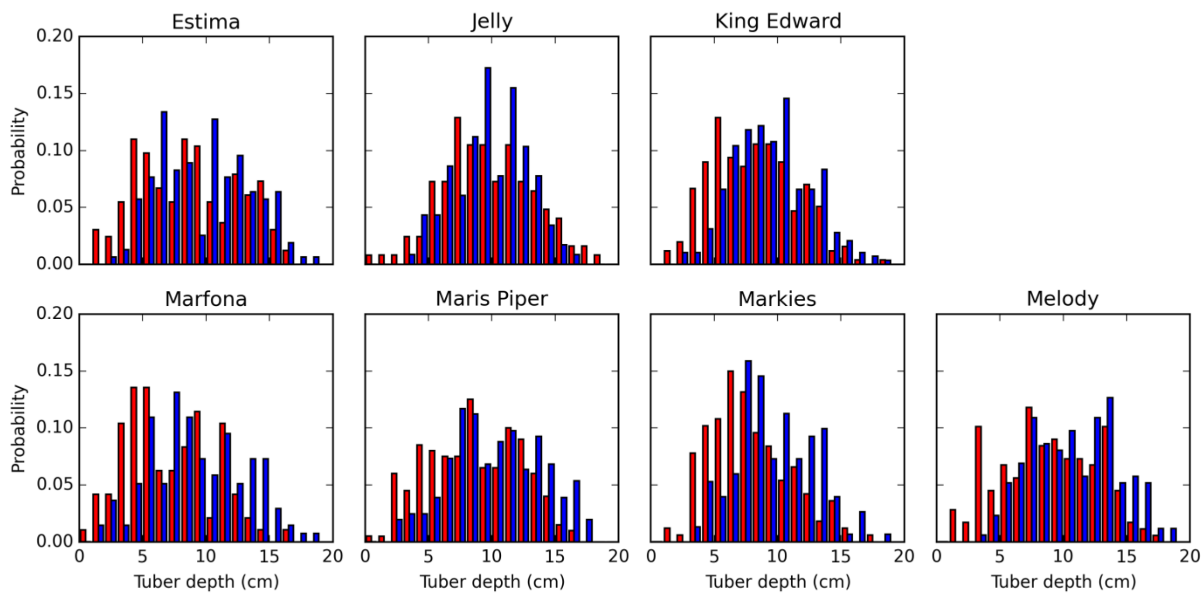


Table 10 Percentage of tubers with their centre above the stolon depth and the average difference between the stolon depth and the depth to the centre of the tuber in Expt 1

	Tubers with their centre above the stolon depth (%)			Difference between depth to centre of tuber and stolon depth† (cm)		
Variety Harvest	1	2	3	1	2	3
Estima	61	50	56	0.4	0.2	0.5
Jelly	67	71	68	0.7	1.3	1.4
King Edward	76	82	79	1.4	1.9	2.2
Marfona	63	80	71	0.8	2.2	2.1
Maris Piper	65	73	74	0.5	1.4	1.4
Markies	62	72	72	0.8	1.6	1.4
Melody	30	58	50	-0.4	0.5	0.3
S.E. (18 D.F.)	5.1	6.7	6.3	0.24	0.44	0.30

† Stolon depth values were calculated from the frame rather than measured from the top of the stem.

4.1.4.1. Green tubers

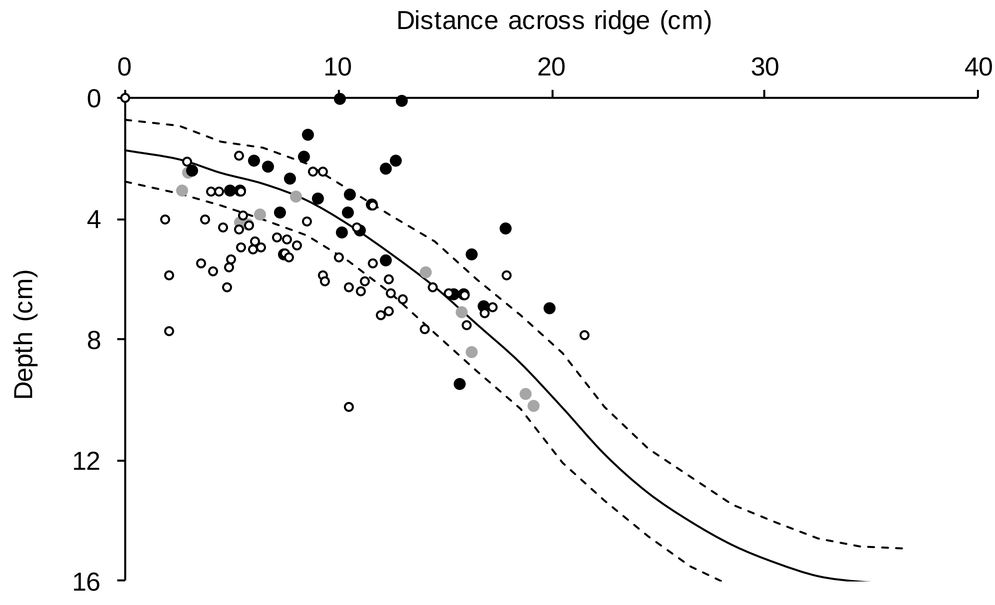
At the first harvest, no tubers were green and at the second, none or very few tubers were green with the exception of Marfona where 6 % of tubers and 4 % of yield were affected (Table 11). Tuber greening increased by the third harvest and continued to be most severe in Marfona with 21 % of tubers and 15 % of yield affected (Table 11). In Estima *c.* 9 % of yield was affected and in other varieties between 1 and 5 % of yield was affected (Table 11). The increase in yield and therefore tuber size was probably responsible for the worsening of tuber greening, either due to the apical ends of tubers growing out the side of the ridge, tubers being pushed upwards out of the ridge by their neighbours or by causing cracks to develop in the ridge.

Table 11. Incidence of and yield affected by tuber greening at the tuber mapping harvests in Expt 1

	Incidence of tuber greening (%)		Yield affected by tuber greening (%)	
Variety Harvest	2	3	2	3
Estima	2.2	9.4	1.8	8.9
Jelly	0.6	4.9	0.1	2.8
King Edward	0.7	7.8	0.6	4.7
Marfona	5.8	21.0	4.1	15.2
Maris Piper	0.0	2.9	0.0	1.4
Markies	1.5	3.6	0.8	2.9
Melody	0.0	2.2	0.0	2.0
S.E. (18 D.F.)	1.80	3.98	1.07	2.46

Across all varieties, of the green tubers at the third harvest, *c.* 30 % were visible at the soil surface and were dark green, *c.* 10 % were not visible at the surface but were dark green and the remaining *c.* 60 % were not visible at the surface and were light green (Figure 8). Tubers not visible at the surface but dark green were mostly positioned close to the surface of the average ridge profile (Figure 8). Some of the light green tubers were several cm (up to 6 cm) below the soil surface indicating that cracks in the ridge were responsible for these tubers becoming green (Figure 8).

Figure 8. Position of the upper- and outer-most part of green tubers in relation to the average ridge profile (——) and ± 2 S.E. (- - - -) at the third harvest of Expt 1. Tubers visible at the surface and dark green, ●; tubers not visible at the surface and dark green, ●; tubers not visible at the surface and light green, O.



4.1.5. Number of stems, number of tubers, yield and grading

Stem populations ranged from *c.* 90 000 to 135 000/ha, being lowest in Estima and Marfona and highest in King Edward (Table 12). Tuber populations ranged from *c.* 300 000 to 700 000/ha and were lowest in Marfona and highest in King Edward (Table 12). Yield ranged from 71-87 t/ha and was lowest in Maris Piper and highest in Melody (Table 12). The differences in tuber populations combined with relatively small differences in yield contributed to large differences in mean tuber size between varieties ranging from 58 mm in King Edward to 75 mm in Marfona (Table 12).

Table 12. Effect of variety on the number of stems and tubers and components of yield at the final harvest (124 DAE) of Expt 1

Variety	Number of stems (000/ha)	Number of tubers (000/ha)	Yield (t/ha)	Mean tuber size (mm)	Tuber shape constant
Estima	91.7	414	74.1	64.2	114
Jelly	99.1	319	79.0	70.1	112
King Edward	135.2	722	74.2	57.9	124
Marfona	91.7	308	79.6	75.3	118
Maris Piper	120.4	522	70.5	58.9	115
Markies	97.2	434	72.4	61.1	111
Melody	112.7	465	86.7	66.0	116
S.E. (18 D.F.)	6.09	22.2	2.61	0.78	1.3

4.1.6. Tuber greening

Overall, tuber greening was considerably more severe at the final harvest taken three weeks after desiccation compared to the third mapping harvest taken immediately prior to desiccation, indicating that the canopy protected the ridge from erosion and partially protected tubers from the light (Tables 11 and 1326). Marfona still had the highest incidence of greening with *c.* 40 % of tubers and *c.* 30 % of yield affected (Table 13). Estima, Jelly, King Edward and Markies were similarly affected with *c.* 20 % of yield affected while Maris Piper and Melody had < 15 % yield affected (Table 13). In King Edward, *c.* 2 % of the yield affected by greening comprised tubers < 40 mm in diameter whereas in other varieties < 1 % of yield was of small tubers (Table 13). In Estima, Jelly, King Edward and Marfona, a similar proportion of yield was affected by dark and light greening whereas in other varieties there was relatively little dark greening (Table 13). The severity of tuber greening was relatively low with on average between 1 and 4 % of surface area affected (Table 13) so for most tubers, only a small part of the tuber was affected.

Table 13. Incidence and severity of tuber greening at the final harvest (124 DAE) of Expt 1

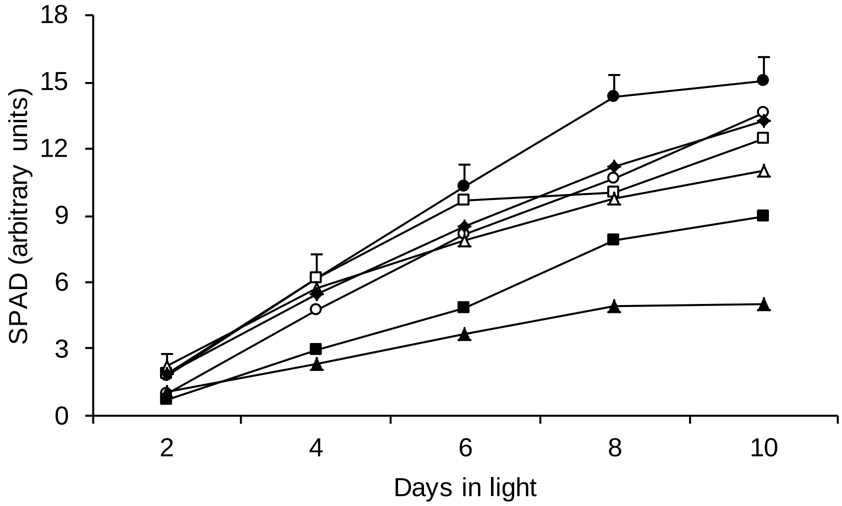
Variety	Incidence (% of tubers)	Proportion of yield (%) Total	< 40 mm	Dark green	Light green	Severity (% surface area)
Estima	23.5	21.5	0.7	9.7	11.1	2.22
Jelly	24.9	23.7	0.4	9.3	13.9	1.26
King Edward	24.7	21.4	1.8	11.2	8.4	1.72
Marfona	38.9	29.0	0.4	13.8	14.8	3.92
Maris Piper	19.4	13.9	0.9	4.2	8.9	1.11
Markies	17.6	18.3	0.5	3.3	14.4	0.81
Melody	14.9	11.8	0.4	3.3	8.2	0.92
S.E. (18 D.F.)	3.11	2.80	0.20	1.53	2.02	0.246

These results indicate that stolon architecture did not directly determine the susceptibility of varieties to greening since, for example, stolons in Marfona were the deepest of any variety and were of an average length but it had the most severe greening. Although Marfona had the deepest stolons, it also had the shallowest tubers which probably contributed to the severe greening but this was influenced by the large mean tuber size. The extensive greening in King Edward, despite having the shortest stolons, may indicate that tighter clusters of tubers do not necessarily prevent greening as they can promote the formation of cracks in the ridge.

4.1.6.1. Sensitivity to light

Varieties are known to differ in their susceptibility to tuber greening under identical lighting conditions (Reeves 1988). How this may influence the susceptibility to in-field tuber greening of the varieties studied was examined. Tuber greening increased linearly in all varieties from 2-6 days after exposure to light. There was little further change in Marfona after 6 days or in Estima and Maris Piper after 8 days, but other varieties continued to green at a similar rate (Figure 9). After 10 days, Estima was most green and Maris Piper the least (Figure 9). Melody and Marfona had similar apparent inherent susceptibility to tuber greening which suggests that the differences in sensitivity to light was of relatively little importance in determining tuber greening in the field experiment and that exposure to light was more important.

Figure 9. Development of tuber greening in the greenhouse in Expt 1. Estima, ●; Jelly,○; King Edward, ■; Marfona, □; Maris Piper, ▲; Markies, △; Melody, ◆. Bars indicate S. E. based on 18 D.F.



4.2. Experiment 2

4.2.1. Emergence and ground cover

Varieties reached 50 % emergence between 33 and 41 days after planting with Marfona emerging earliest and Jelly latest (Table 14). Emergence was close to complete in all varieties except Markies where *c.* 5 % of plants failed to emerge and in Jelly, where emergence was particularly poor with > 20 % of plants failing to emerge (Table 14). Marfona emerged most uniformly, with 20 to 80 % of plants emerging in 3 days compared with more than 6 days in Jelly and Markies (Table 14).

Table 14. Effect of variety on the interval from planting to emergence, final emergence and interval from 20-80 % emergence in Expt 2.

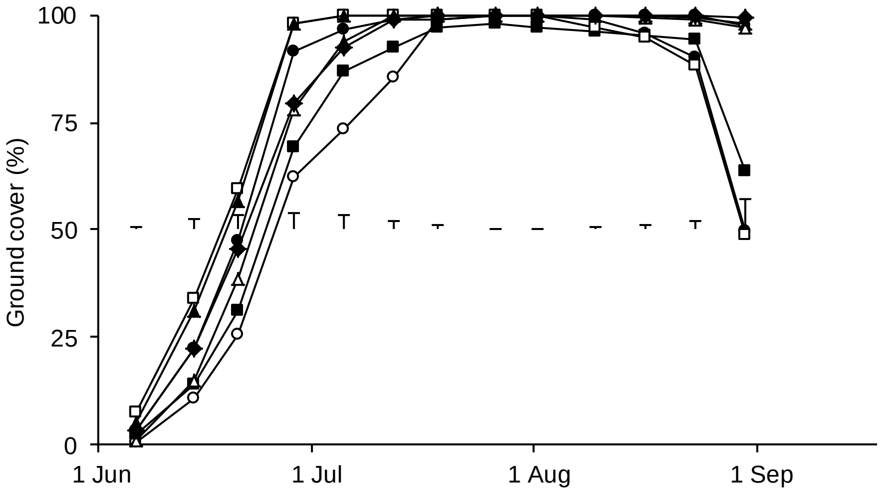
Variety	Interval from planting to 50 % emergence (days)	Final emergence (%)	Interval from 20 to 80 % emergence (days)†
Estima	34.1	99.5	3.8
Jelly	41.0	78.7	6.1
King Edward	35.4	99.5	4.7
Marfona	32.7	99.5	3.2
Maris Piper	33.5	100.0	3.4
Markies	37.7	94.0	6.3
Melody	36.2	99.1	5.3
S.E. (18 D.F.)	0.38	1.01	0.26

† Based only on plants that emerged

Ground cover developed at different rates, mainly due to differences in the date of emergence of varieties (Figure 10). Canopy development was probably delayed in King

Edward by virus Y infection and in Jelly by incomplete emergence. All varieties had developed close to full canopies by mid-July and these were maintained until mid-August (Figure 10). Estima, King Edward and Marfona began to senesce at the end of August, but the other varieties maintained full canopies until desiccation (Figure 10).

Figure 10. Foliar ground cover in Expt 3. Estima, ●; Jelly,○; King Edward, ■; Marfona, □; Maris Piper, ▲; Markies, △; Melody, ◆. Bars indicate S. E. based on 18 D.F.



4.2.2. Stolon architecture

4.2.2.1. Development

Due to the delayed emergence of Jelly, it was not sampled at the first harvest. In the other varieties *c.* 5-6 stolons had developed per stem (Table 15). Very few tubers had initiated by the first harvest and only in Marfona, Maris Piper and Melody (Table 15). By the second harvest, the number of stolons per stem had increased to *c.* 8 in all varieties, all varieties had initiated tubers and in the varieties other than Jelly, King Edward and Markies, *c.* 2 tubers > 10 mm in diameter had developed (Table 15). By the third harvest, most varieties had developed *c.* 10-12 stolons per stem, but more had formed in Melody and King Edward (Table 15). Between *c.* 5 and 9 tubers had initiated per stem, of which *c.* 3-5 had grown to > 10 mm in diameter (Table 15). Some stolons had become exposed to light and consequently turned green at the tip. Very few green stolons were recorded at the first harvest, but at the second and third harvests *c.* 10 % of stolons were affected (Table 15).

Table 15. Number of stolons per stem, tubers per stem and tubers > 10 mm at the first three harvests *c.* 13, 21 and 29 DAE of Expt 2

		Variety							
Harvest		Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	S.E. (18 D.F.)†
Stolons per stem	1	5.3	n.d.	4.5	6.6	5.5	5.2	6.0	0.36
	2	8.1	8.4	8.2	8.1	7.9	8.0	7.8	0.61
	3	10.4	12.8	19.0	10.8	11.8	11.5	16.3	1.63
Tubers per stem	1	0.0	n.d.	0.0	0.2	0.1	0.0	0.1	0.05
	2	5.9	1.3	1.7	4.7	4.4	1.7	3.6	0.38
	3	6.7	4.6	8.9	4.7	5.4	4.6	7.3	0.78
Tubers > 10 mm per stem	1	0.0	n.d.	0.0	0.1	0.0	0.0	0.0	0.03
	2	2.5	0.1	0.0	2.3	1.8	0.4	1.5	0.22
	3	5.0	4.0	3.3	2.9	3.4	3.6	4.7	0.34
Green stolons per stem	1	0.0	n.d.	0.1	0.4	0.0	0.1	0.3	0.09
	2	0.7	0.7	1.0	1.3	0.9	0.2	1.0	0.17
	3	0.7	1.5	2.5	1.4	0.9	1.2	1.3	0.28

† 15 D.F. for all variates at the first harvest, 12 D.F. for tubers > 10 mm per stem at the second harvest

The mean stolon length at the first harvest was *c.* 2-5 cm, being shortest in King Edward and longest in Jelly (Table 16). This had increased to *c*. 6-8 cm at the second harvest and there were no significant differences between varieties (Table 16). For the varieties that had appreciable numbers of tubers > 10 mm per stem (not Jelly, King Edward and Markies), the average length of tuberised stolons and stolons with tubers > 10 mm was similar to the mean stolon length (Table 16). Despite the further increases in the number of stolons between the second and third harvests, the mean stolon length remained similar in all varieties and as at the second harvest the length of all stolons, tuberised stolons and stolons with tubers > 10 mm were similar within varieties (Table 16).

Table 16. Mean length of all stolons, tuberised stolons and stolons bearing tubers > 10 mm at the first three harvests *c.* 13, 21 and 29 DAE of Expt 2

	Harvest	Variety							S.E. (18 D.F.)†
		Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	
Mean stolon length (cm)	1	2.9	n.d.	2.3	4.9	3.0	3.1	3.2	0.26
	2	6.5	7.7	7.1	7.1	5.6	7.5	7.1	0.46
	3	5.6	8.8	7.1	7.2	5.8	7.9	8.2	0.65
Mean tuberised stolon length (cm)	1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	2	6.3	8.7	7.0	6.5	5.5	7.8	6.8	0.40
	3	5.6	9.5	6.1	6.1	4.8	6.7	6.8	0.47
Mean tuberised > 10 mm stolon length (cm)	1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	2	6.5	6.4	8.2	6.3	5.3	6.9	6.0	1.42
	3	6.3	10.1	7.6	6.2	5.3	7.1	6.6	0.51

† 15 D.F. at the first harvest, 12 D.F. for measurements of stolons with tubers > 10 mm at the second harvest

Mean relative stolon depth (taking account of variations in planting depth between varieties and stems) was lowest when all stolons were included, but deeper for only tuberised stolons (Table 17). Overall, the mean relative stolon depth was slightly higher at the second harvest compared to at the first, but there was no further change, despite the number of stolons continuing to increase (Table 17). In King Edward, Markies and Marfona, there was no difference in the mean relative stolon depth between the harvests (Table 17). At the third harvest, stolons bearing tubers > 10 mm were shallowest in Estima and Markies and deepest in King Edward and Marfona (Table 17).

Table 17. Mean relative stolon depth of all stolons, tuberised stolons and stolons bearing tubers > 10 mm at the first three harvests *c.* 13, 21 and 29 DAE of Expt 2

	Harvest	Variety							S.E. (18 D.F.)†
		Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	
Mean relative stolon depth (%)	1	74.0	n.d.	62.6	68.5	73.0	61.5	70.7	1.30
	2	66.4	60.7	63.0	63.3	65.0	60.4	63.8	1.58
	3	68.8	64.0	60.0	63.4	63.8	59.6	62.0	2.55
Mean tuberised relative stolon depth (%)	1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	2	79.6	86.0	92.7	81.2	82.4	85.8	88.1	1.92
	3	79.2	84.9	75.3	82.3	82.9	79.0	77.5	1.56
Mean tuberised > 10 mm relative stolon depth (%)	1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	2	84.5	70.1	99.4	90.2	89.9	89.0	92.5	2.53
	3	80.4	83.9	86.6	86.7	84.2	79.8	81.5	1.69

† 15 D.F. at the first harvest, 12 D.F. for measurements of stolons with tubers > 10 mm at the second harvest

4.2.2.2. Fourth harvest

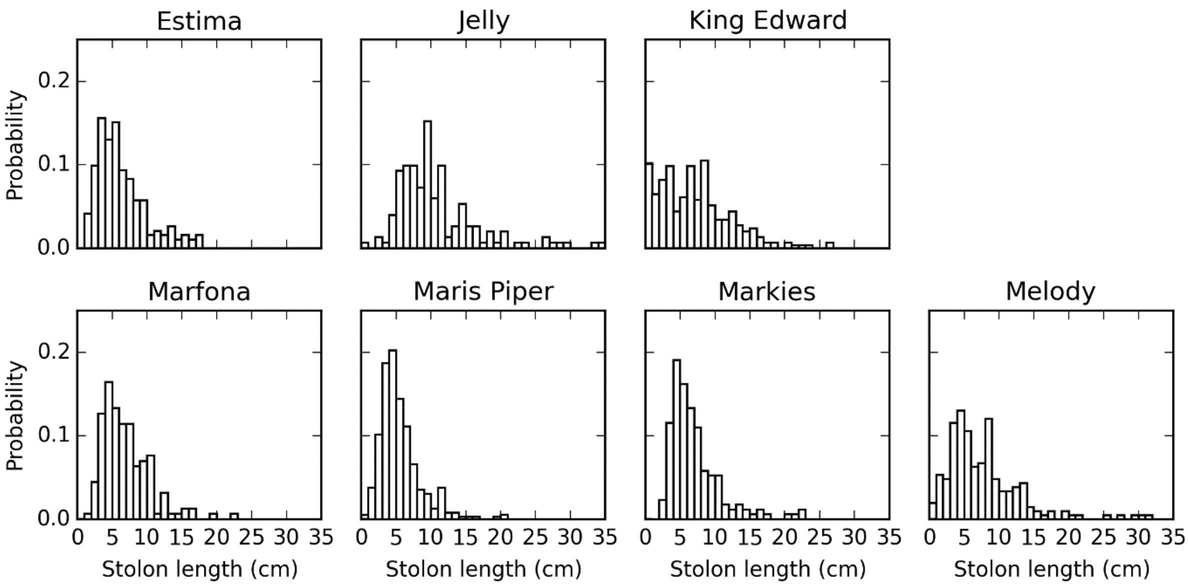
The mean achieved planting depth was *c.* 15 cm and this was similar for all varieties (Table 18). The number of tubers > 10 mm per stem was similar to the number at the third harvest in all varieties except King Edward where it had more than doubled and in Maris Piper where it increased by *c.* 30 % (Tables 15 and 18). Mean stolon depth was between *c.* 11 and 13 cm from the soil surface, being numerically deepest in Marfona and shallowest in Melody, but differences between varieties were not significant (Table 18). Relative stolon depth ranged from 75 to 85 % and Marfona and Melody remained the extreme varieties by this metric, with a significant difference between them (Table 18). In King Edward and Maris Piper, the mean relative stolon depth had decreased compared to at the third harvest, indicating that the tubers that grew > 10 mm after 29 DAE, were higher up the stem (Tables 17 and 18). A similar trend was apparent in Melody and Jelly, despite the number of tubers > 10 mm not changing appreciably between the harvest dates (Tables 17 and 18). Jelly had the longest mean stolon length, twice that of Maris Piper which had the shortest but for other varieties there was a small range (6.1-7.4 cm; Table 18). The mean stolon length was similar to at the third harvest for all varieties (Tables 16 and 18). The median stolon length was *c.* 10 % shorter than the mean stolon length in all varieties, but between varieties the mean and the median stolon length were very strongly correlated (R^2 = 0.99). This was indicative of there being a relatively small number of long (> 15 cm) stolons in all varieties

(Figure 11). King Edward had the most very short stolons (< 3 cm) and was the only variety to have sessile tubers (those with no stolon; Figure 11).

Table 18. Effect of variety on planting depth, stolon depth, relative stolon depth and stolon length at the fourth harvest (*c.* 70 DAE) of Expt 2 only for tubers > 10 mm

Variety	Planting depth (cm)	Tubers > 10 mm per stem	Mean stolon depth (cm)	Mean relative stolon depth (%)	Mean stolon length (cm)	Median stolon length (cm)
Estima	14.9	4.7	12.0	79.8	6.1	5.3
Jelly	16.0	4.2	12.6	77.9	10.6	9.6
King Edward	15.0	7.2	11.4	75.4	6.7	5.8
Marfona	14.9	2.6	13.0	84.5	6.7	6.0
Maris Piper	15.8	4.4	12.6	78.5	5.1	4.4
Markies	15.4	4.3	12.2	79.5	6.7	5.8
Melody	15.0	5.4	11.3	74.7	7.4	6.4
S.E. (18 D.F.)	0.41	0.36	0.45	1.65	0.38	0.54

Figure 11. Histograms of stolon length in each variety at the fourth harvest (*c.*70 DAE) of Expt 2.



Stolons were clustered towards the base of the stem in all varieties and the deepest stolons shown in Figure 12 were the result of stems with atypically deep planting depths. Differences in the minimum stolon depth per plant were greater than the mean stolon depth with Jelly, Marfona and Markies having the deepest at *c.* 9 cm compared to other varieties at *c.* 5-7 cm (Table 19). The maximum stolon length per plant ranged from *c.* 11 to 19 cm and was strongly correlated (R^2 = 0.75) with mean stolon length (Tables 18 and 19). Maris Piper had the shortest maximum stolon length and Jelly having the longest, although there was *c.* 5 cm difference in the maximum length between Marfona and Melody, despite the mean stolon length differing by only 0.7 mm (Tables 18 and 19).

Figure 12. Histograms of stolon depth in each of the varieties at the fourth harvest (70 DAE) of Expt 2.

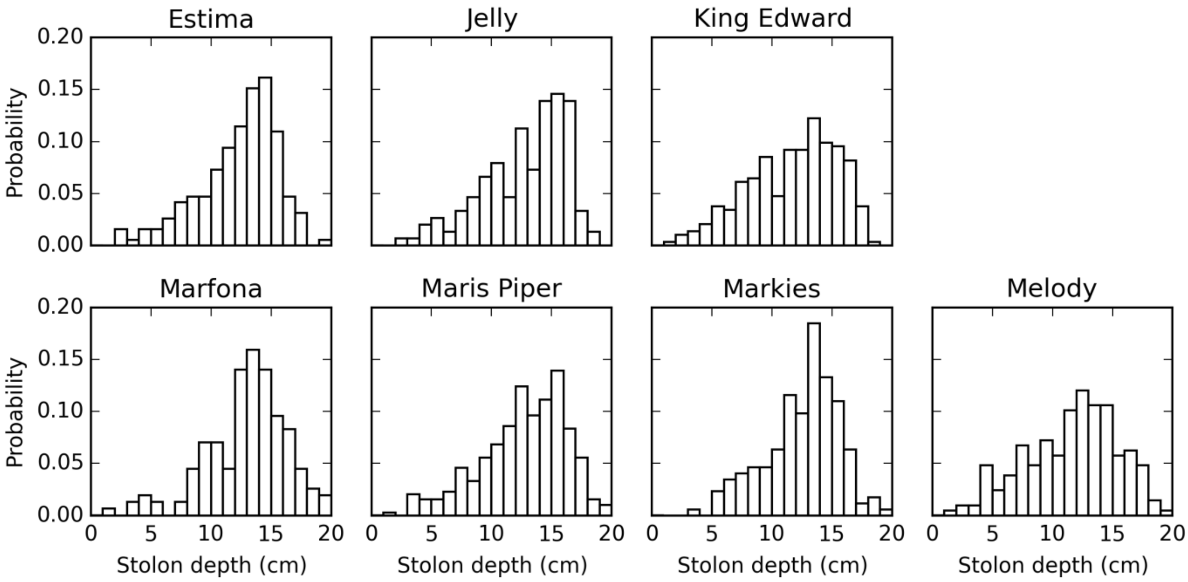


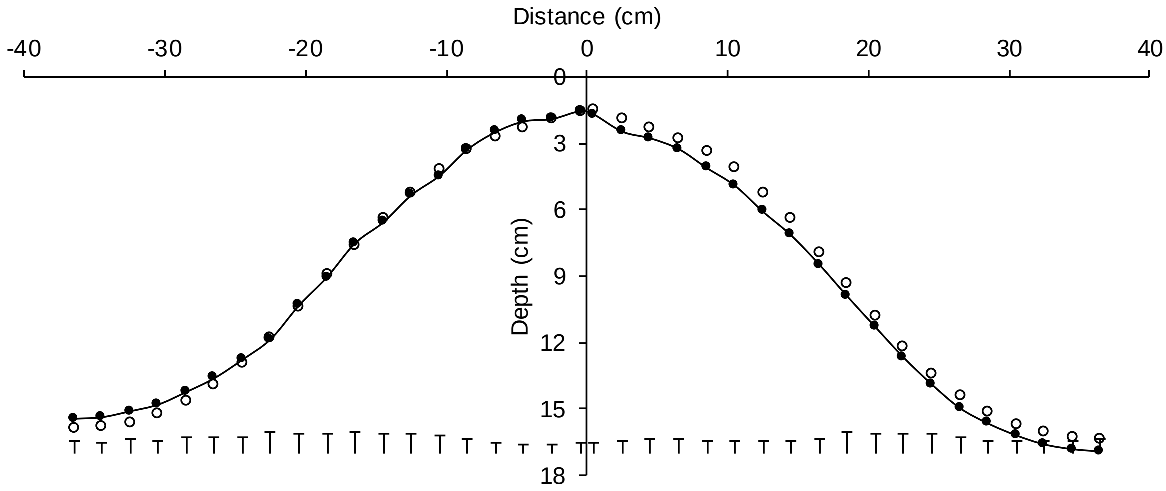
Table 19. Effect of variety on minimum stolon depth and maximum stolon length per plant in Expt 2

Variety	Minimum stolon depth (cm)	Maximum stolon length (cm)
Estima	7.1	11.7
Jelly	8.4	19.2
King Edward	5.2	15.1
Marfona	8.9	11.5
Maris Piper	5.9	11.0
Markies	8.5	12.1
Melody	5.2	16.9
S.E. (18 D.F.)	0.72	0.89

4.2.3. Ridge profile

The average ridge profile 70 DAE is shown in Figure 13, along with the average ridge profile measured at three dates in 2015 which was very similar.

Figure 13. Average ridge profiles at the fourth harvest (●; 70 DAE) of Expt 2 and the average ridge profile in 2015 (O). Bars indicate S. E. based on 18 D.F.



4.2.4. Tuber mapping

The average distance from the centre of the plant to the stolon end of tubers was between 5 and 10 cm (Table 20) and was strongly correlated and almost directly related to average stolon length (Figure 14, Table 21). The apical ends of the tubers were furthest away from the centre of the plant in Jelly, while in Estima, King Edward, Marfona, Markies and Melody tubers were all a similar distance away and Maris Piper was closest (Table 20). Combining the average stolon length and average tuber length accounted for a large proportion of the distance to the apical end of the tubers, although they were closer than expected than if the relationship was directly proportional (Figure 14). This was probably due to the angle from the centre of the plant to the stolon and apical ends of the tubers not being identical and also due to the horizontal orientation of tubers varying. On average, there was no evidence to indicate that tubers were further away from the seed tuber along the ridge compared to across the ridge (data not shown). However, when accounting for the three-dimensional position of tubers, those that were closer to the surface could be found further from the seed tuber along, than across, the ridge (Figure 15). This was probably due to stolons that grew across the ridge turning green at the tips and in turn inhibiting tuber formation (Table 15). The average tuber depth ranged from *c.* 9 to 11 cm but was unrelated to the mean stolon depth (Tables 18 and 20).

Table 20. Effect of variety on the distance from the centre of the plant to the stolon and apical ends of tubers in Expt 2

Variety	Distance to stolon end (cm)	Distance to apical end (cm)	Tuber depth (cm)
Estima	5.8	12.7	9.6
Jelly	9.6	16.2	10.2
King Edward	7.1	11.4	8.9
Marfona	6.2	13.0	9.3
Maris Piper	5.7	9.7	10.8
Markies	6.2	12.4	9.5
Melody	7.1	12.9	10.5
S.E. (18 D.F.)	0.39	0.52	0.54

Figure 14. Relationships between distance to the stolon end of tubers and stolon length, ●; and between distance to the apical end of tubers and stolon length plus tuber length, ○; in Expt 2. Line is 1:1 relationship. Relationships for each dataset are given in Table 21.

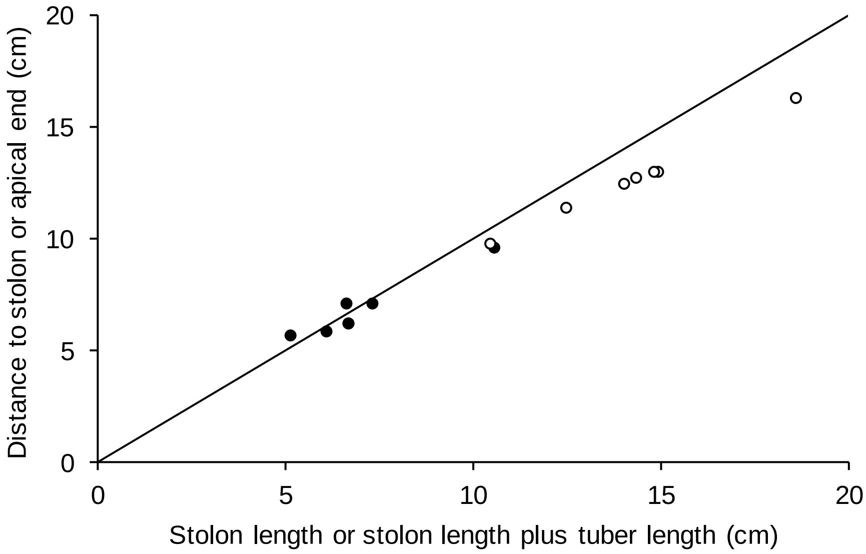


Table 21. Relationships between position of the stolon or apical end of tubers (POS, cm) and stolon length or stolon length plus tuber length (LEN, cm) as shown in Figure 14: slope of relationship (*m*) and S.E., constant of relationship (*c*) and S.E., significance of relationship (*F* prob) and strength of relationship (R^2). POS = *m* LEN + *c*

Position	*m*	S.E.	*c*	S.E.	*F* prob.	R^2
Stolon end	0.756	0.0933	1.49	0.674	< 0.001	0.92
Apical end	0.791	0.0235	1.34	0.339	< 0.001	0.99

The stolons of Estima and Melody on average grew approximately horizontally as the centres of *c.* 50 % of tubers were above and below the depth of the stolon and hence there was little difference between stolon depth and the depth to the centre of tubers (Table 22). In the other varieties, the centre of the tubers were numerically more likely to be found above the depth of the stolon and the differences were significant when the distance between the centre of the tubers and the depth of the stolons was accounted for (Table 22). Between *c.* 22 and 45 % of tubers grew at an angle > ±10º with this being least common in King Edward and Maris Piper and most common in Marfona and Jelly (Table 22). The proportion of tubers growing at an angle > ±10º increased as average tuber length increased (R^2 = 0.87; data not shown). In Maris Piper and Melody, similar proportions of tubers were angled upwards and downwards, whereas in other varieties, tubers were more likely to angle upwards (Table 22). When accounting for all tubers, Marfona had the most severely angled tubers at an average of *c.* 15º, but when only the tubers growing > ±10º were considered, all varieties except for Maris Piper and Melody had an average angle of *c.* 25-30º (Table 22).

Table 22. Percentage of tubers with their centre above the stolon depth, the average difference between the stolon depth and the depth to the centre of the tuber, the percentage of tubers with a horizontal angle > 10 % and the average orientation of all tubers in Expt 2

Variety	Tubers with their centre above the stolon depth (%)	Difference between depth to centre of tuber and stolon depth† (cm)	Tubers with a horizontal angle > ±10º (%)	Average tuber orientation angle (º)	Average tuber orientation angle of tubers > ±10º (º)
Estima	53.6	0.4	39.3	9.6	24.5
Jelly	63.2	1.3	43.9	11.2	24.4
King Edward	70.6	1.9	22.9	5.8	29.1
Marfona	70.2	1.6	45.9	14.2	29.0
Maris Piper	64.3	0.8	22.7	0.9	4.8
Markies	67.1	1.6	31.2	7.8	24.4
Melody	52.1	-0.1	33.9	-0.6	0.8
S.E. (18 D.F.)	6.74	0.43	3.96	1.90	3.80

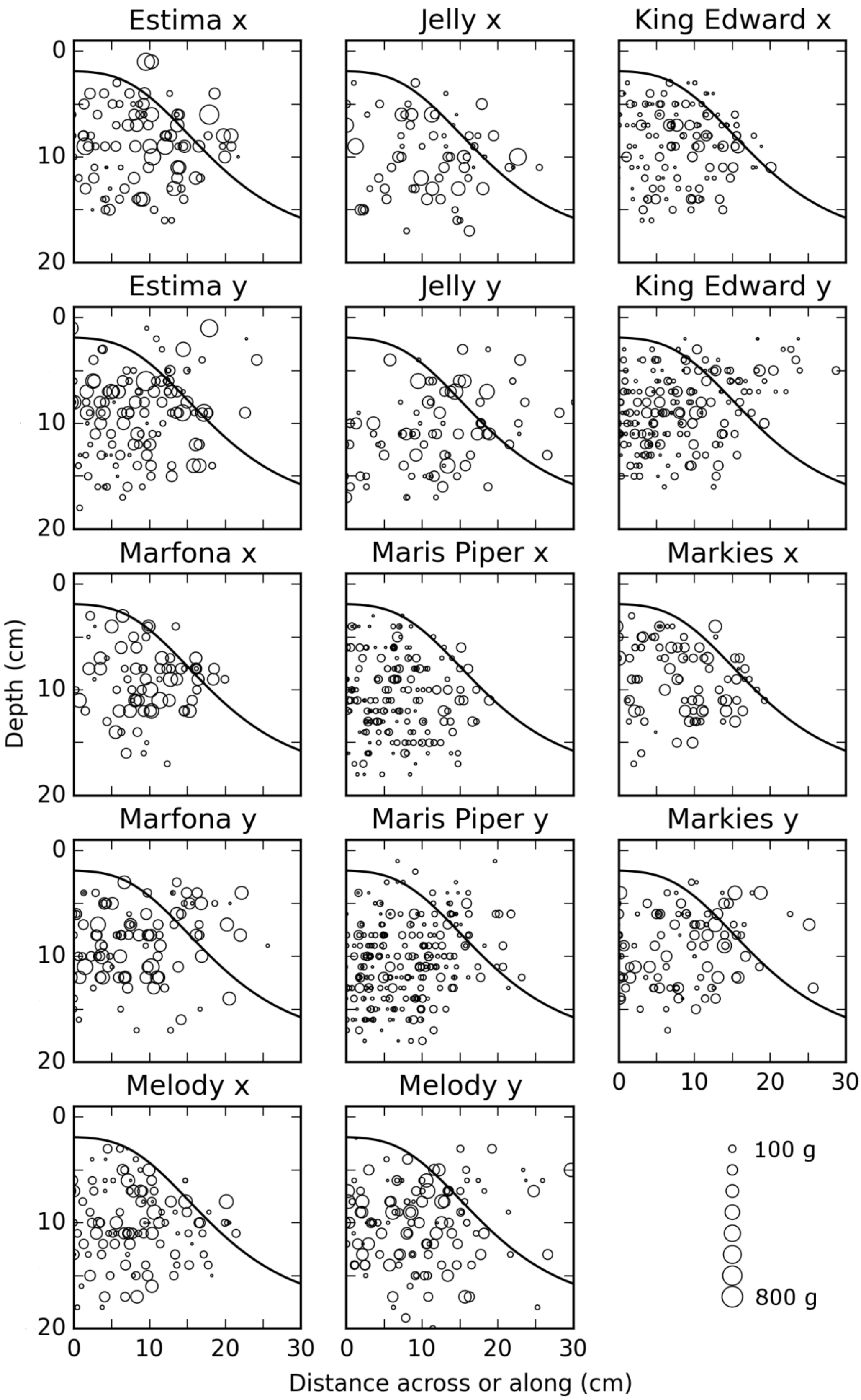
† Stolon depth values were calculated from the frame rather than measured from the top of the stem.

While all varieties had a similar proportion of tubers close to the soil surface, the amount of yield present was numerically greatest for Estima, Jelly and Marfona (Table 23, Figure 15).

Table 23. Percentage of tubers and yield within 2.5 cm of the soil surface in Expt 2

Variety	Tubers within 2.5 cm of soil surface (%)	Yield within 2.5 cm of soil surface (%)
Estima	14.9	24.3
Jelly	19.3	24.9
King Edward	18.4	19.5
Marfona	15.1	22.4
Maris Piper	11.0	9.3
Markies	18.9	11.6
Melody	15.7	14.3
S.E. (18 D.F.)	3.75	4.14

Figure 15. Diagrams showing the position of tubers across (x) and along (y) the ridge for each variety in Expt 2. Points are centred at the shallowest and furthest away point, and their diameter is proportional to tuber weight with weights of 100-800 g FW shown in the final panel. The average ridge profile is shown for reference.



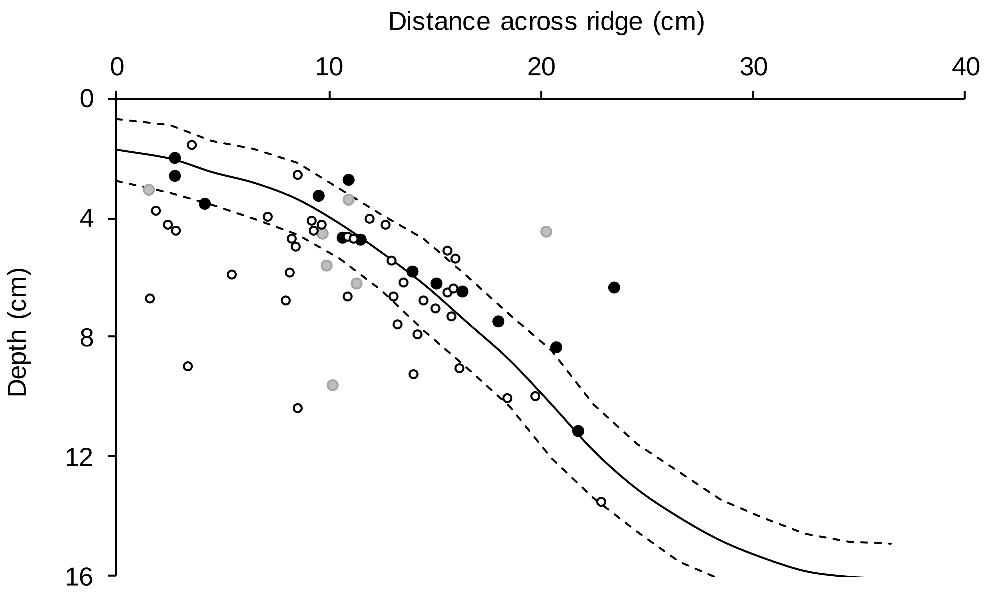
4.2.4.1. *Green tubers*

At 70 DAE, very few tubers were affected by greening with the exception of King Edward and Marfona where *c*. 5 % of yield was green (Table 24). Those that were green tended to be close to the soil surface, but in some instances were > 5 cm deeper, indicating that cracks had formed allowing light to penetrate (Figure 16).

Table 24. Incidence of and yield affected by tuber greening at the tuber mapping harvest of Expt 2

Variety	Incidence of tuber greening (%)	Yield affected by tuber greening (%)
Estima	1.7	0.7
Jelly	0.0	0.2
King Edward	10.5	5.5
Marfona	6.1	4.1
Maris Piper	0.0	0.2
Markies	0.5	0.5
Melody	1.6	0.1
S.E. (18 D.F.)	1.12	0.91

Figure 16. Position of the upper- and outer-most part of green tubers in relation to the average ridge profile (———) and ± 2 S.E. (- - - -) at the fourth harvest of Expt 2. Tubers visible at the surface and dark green, ●; tubers not visible at the surface and dark green, ●; tubers not visible at the surface and light green, O.



4.2.5. Number of stems, number of tubers, yield and grading

Stem populations ranged from *c.* 60 000 to 182 000/ha, being lowest in Jelly and highest in Maris Piper (Table 25). Tuber populations ranged from *c.* 250 000 to 700 000/ha and were lowest in Jelly and highest in Maris Piper (Table 25). Yield ranged from 55-73 t/ha and was lowest in Jelly and highest in Estima (Table 25). The differences in tuber populations combined with the differences in yield contributed to large differences in mean tuber size between varieties ranging from 52 mm in Maris Piper to 71 mm in Marfona (Table 25). The coefficient of variation (COV) of tuber size ranged from *c.* 17-21 % (Table 25) equating to marketable yields (45-80 mm) at an optimal mean tuber size of 62 mm, of between *c*. 82 and 91 %.

Table 25. Effect of variety on the number of stems and tubers and components of yield at the final harvest (124 DAE) in Expt 2

Variety	Number of stems (000/ha)	Number of tubers (000/ha)	Yield (t/ha)	Mean tuber size (mm)	COV of tuber size (%)
Estima	81.5	357	73.0	68.2	19.0
Jelly	59.3	257	55.1	69.7	16.7
King Edward	97.0	607	58.0	57.2	21.1
Marfona	110.2	291	66.4	71.2	16.5
Maris Piper	182.4	714	58.2	52.1	17.2
Markies	84.1	335	56.0	62.7	17.3
Melody	74.1	376	69.5	65.6	16.6
S.E. (18 D.F.)	6.69	25.2	2.64	1.22	0.85

4.2.6. Tuber greening

Overall, tuber greening was considerably more common at the final harvest taken three weeks after desiccation compared to at the mapping harvest taken *c.* 50 days earlier (Tables 24 and 26). Marfona and King Edward remained the varieties with the highest incidence of greening with *c.* 20 % of tubers and *c.* 17 % of yield affected (Table 26). Estima and Jelly were less affected with *c.* 14 % of tubers and a similar amount of yield affected (Table 26). The incidence of greening was lowest in Maris Piper, Markies and Melody with *c.* 6 % of tubers and *c.* 4-6 % of yield affected (Table 26). In King Edward, *c.* 3 % of the yield affected by greening comprised tubers < 40 mm in diameter whereas in other varieties < 1 % of yield was of small tubers (Table 26). This was not just due to differences in overall tuber size, since Maris Piper and King Edward both had *c.* 10 % of yield < 40 mm. In Estima, Jelly and Maris Piper, a similar proportion of yield was affected by dark and light greening, in King Edward the majority was dark greening and in the other varieties a greater proportion was light greening (Table 26). Maris Piper, Markies and Melody had very low levels of dark greening (Table 26). Less than 2 % of yield was visible at the soil surface in any variety and there were no significant differences between varieties, indicating that cracking of the ridge was important for allowing light to reach the tubers (Table 26). The severity of tuber greening was relatively low with < 1 % of surface area affected (Table 26) and this correlated strongly with the incidence of greening (R^2 = 0.85; data not shown).

As in Expt 1, the results indicate that stolon architecture did not directly determine the susceptibility of varieties to tuber greening since, for example, stolons in Marfona were the deepest of any variety and were of an average length but it had the most severe tuber greening (Tables 18 and 26). Considering tuber length as well as stolon length, Jelly and Maris Piper represented the extremes and while there was a large numerical difference in tuber greening between these varieties, this metric could not explain the large difference in tuber greening between Maris Piper and King Edward (Tables 20 and 26). The percentage of yield within 2.5 cm of the soil surface at 70 DAE was associated with the amount of tuber greening at the final harvest with Maris Piper, Markies and Melody having numerically less yield in a vulnerable position than the other varieties (Tables 23 and 26).

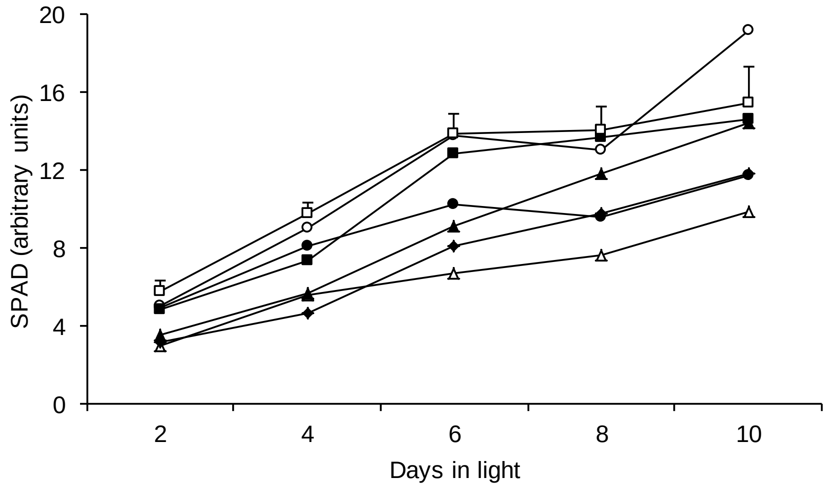
Table 26. Incidence and severity of tuber greening at the final harvest (124 DAE) in Expt 2

Variety	Incidence (% of tubers)	Yield affected (%) Total	< 40 mm	Light green	Dark green	At surface	Severity (% surface area)
Estima	13.7	14.4	0.26	8.6	5.6	1.6	0.98
Jelly	13.9	11.4	0.45	5.7	5.3	1.5	0.72
King Edward	22.5	16.2	2.74	3.4	10.0	0.9	1.00
Marfona	19.1	17.5	0.35	11.6	5.6	1.6	0.92
Maris Piper	5.6	3.5	0.97	1.8	0.7	0.3	0.13
Markies	5.9	6.3	0.30	5.1	0.9	0.2	0.08
Melody	6.3	4.1	0.30	3.7	0.2	0.4	0.24
S.E. (18 D.F.)	2.69	2.70	0.279	1.57	1.89	0.50	0.202

4.2.6.1. Sensitivity to light

As in Expt 1, tuber greening increased linearly in all varieties from 2-6 days after exposure to light began. There was little further change in Estima, Marfona and King Edward after 6 days exposure, but other varieties continued to green at a similar rate until 10 days of exposure (Figure 17). After 10 days, Jelly was most green and Markies the least (Figure 17). As in Expt 1, varieties with very different amounts of tuber greening in the field experiment had similar susceptibilities to tuber greening in the glasshouse (e.g. Maris Piper and King Edward). The average SPAD value was 2.5 higher than in Expt 1 and while Estima turned most green in Expt 1, this was not the case in Expt 2 and the correlation between years was poor (R^2 = 0.16; data not shown).

Figure 17. Development of tuber greening in a glasshouse in Expt 3. Estima, ●; Jelly,○; King Edward, ■; Marfona, □; Maris Piper, ▲; Markies, △; Melody, ◆. Bars indicate S. E. based on 18 D.F.



4.3. Experiment 3

4.3.1. Emergence and ground cover

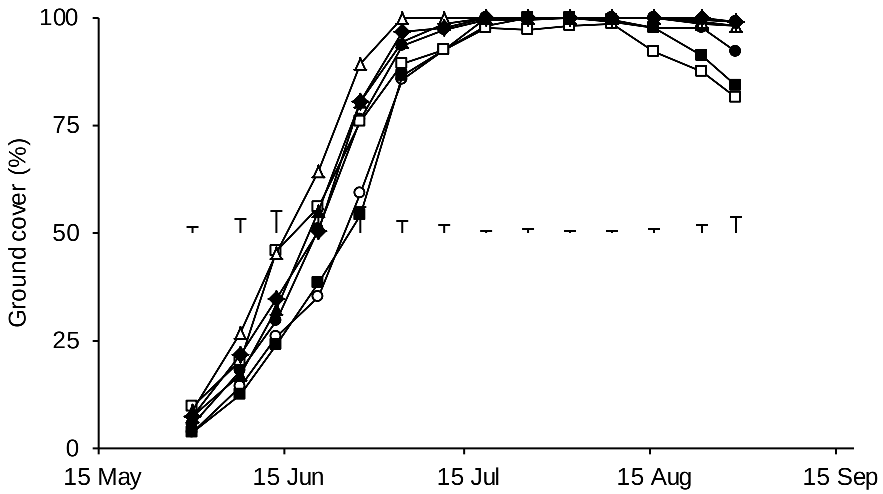
Varieties reached 50 % emergence between 43 and 50 days after planting with Marfona emerging earliest and Jelly latest (Table 27). Emergence was complete in all varieties (data not shown). The interval from 20 to 80 % of plants emerging was *c.* 4 days in all varieties (Table 27).

Table 27. Effect of variety on the interval from planting to emergence, final emergence and interval from 20-80 % emergence

Variety	Interval from planting to 50 % emergence (days)	Interval from 20 to 80 % emergence (days)
Estima	49.0	3.6
Jelly	49.9	3.7
King Edward	48.0	3.8
Marfona	43.4	3.8
Maris Piper	47.0	3.9
Markies	46.2	3.6
Melody	47.4	3.5
S.E. (18 D.F.)	0.58	0.38

Differences in ground cover development were mainly due to differences in the date of emergence of varieties (Figure 18). All varieties had developed close to full canopies by mid-July and these were maintained until mid-August (Figure 18). Estima, King Edward and Marfona began to senesce at the end of August, but the other varieties maintained full canopies until desiccation (Figure 18).

Figure 18. Foliar ground cover in Expt 3. Estima, ●; Jelly, ○; King Edward, ■; Marfona, □; Maris Piper, ▲; Markies, △; Melody, ◆. Bars indicate S. E. based on 18 D.F.



4.3.2. Stolon architecture

4.3.2.1. Development

Stolons > 5 mm long were present in all varieties at the first harvest but the percentage of stems with stolons > 5 mm ranged from *c.* 40 % in Jelly to *c.* 90 % in Marfona (Table 28). While there were differences between varieties in the percentage of stems that had stolons > 5 mm long and the number of stolons per stem, these were mainly due to the differences in emergence. When the interval from emergence was calculated separately for each variety, at *c.* 10 DAE > 90 % of stems in all varieties except King Edward had stolons > 5 mm and an average of *c.* 3 stolons per stem (data not shown). When the differences in emergence were accounted for, the number of stolons per stem was similar in all varieties except Markies at the same interval after emergence and the number of stolons increased linearly from *c.* 3 DAE (Figure 19*a*; Table 29). Apart from in Marfona and Melody, the number of stolons per stem continued to increase from 23 to 27 DAE when the last sample was taken (Table 28). Tuber initiation began at *c.* 15 DAE in all varieties and the number of tubers increased at similar rates in all varieties except for Estima where the number of tubers increased more rapidly (Figure 19*b*; Table 29). By *c.* 25 DAE, 50-60 % of stolons had tuberised in all varieties (data not shown). The development of tubers > 10 mm in diameter occurred *c.* 3 days after tuber initiation in all varieties with the majority developing between 20 and 25 DAE (Figure 19*c*). The number of tubers > 10 mm per stem developed at a similar rate in all varieties except Estima, where it occurred more rapidly (Figure 19*c*). The number of green stolons per stem was low in all varieties and increased only slightly from an average of 0.3 per stem at 20 DAE to 0.5 per stem at 27 DAE and there were no differences between varieties on any date, although Marfona had the numerically highest number at each date (Table 28).

Table 28. Number of stolons, tubers, tubers > 10 mm and green stolons per stem at the first eight harvests *c.* 7, 10, 12, 15, 17, 20, 23 and 27 DAE in Expt 3

		Variety							
	Harvest	Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	S.E. (18 D.F.)
Stems with stolons > 5mm (%)	1	47.9	37.5	63.4	88.1	79.5	80.8	63.6	8.72
	2	69.0	66.1	66.4	100.0	88.1	97.2	88.7	5.01
	3	91.4	90.0	81.0	97.5	97.5	96.9	91.9	4.77
Stolons per stem	1	0.8	0.7	2.2	3.6	2.4	3.6	1.6	0.44
	2	2.6	2.0	2.1	5.9	3.5	6.4	3.5	0.43
	3	3.6	3.5	3.4	6.2	5.2	6.9	4.6	0.46
	4	4.1	4.1	4.0	6.4	5.2	7.4	5.2	0.38
	5	5.2	4.2	4.6	7.0	7.3	8.1	6.1	0.54
	6	6.7	6.0	7.6	8.4	9.2	9.0	6.5	0.48
	7	8.1	7.3	8.6	10.0	10.2	9.7	8.4	0.61
	8	10.5	9.3	11.4	10.4	12.2	12.0	8.6	1.08
Tubers per stem	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01
	2	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.08
	3	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.04
	4	0.2	0.0	0.0	1.4	0.3	0.5	0.1	0.17
	5	0.6	0.0	0.1	2.1	0.4	1.5	0.7	0.23
	6	1.5	1.0	1.4	4.5	2.1	3.2	2.1	0.51
	7	5.0	2.0	3.2	5.2	5.0	4.7	4.0	0.72
	8	6.8	3.6	5.8	5.3	6.4	5.7	4.5	0.80
Tubers > 10 mm per stem	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	n.a.
	2	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.03
	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02
	4	0.0	0.0	0.0	0.5	0.0	0.1	0.0	0.08
	5	0.0	0.0	0.0	1.1	0.0	0.3	0.1	0.12
	6	0.3	0.1	0.1	2.5	0.3	1.1	0.6	0.24
	7	2.3	0.9	1.1	3.6	2.5	3.1	2.3	0.59
	8	3.9	2.5	3.5	3.8	4.4	4.2	3.7	0.51
Green stolons per stem	6	0.3	0.1	0.2	0.8	0.1	0.2	0.2	0.09
	7	0.3	0.2	0.4	0.9	0.2	0.2	0.3	0.17
	8	0.5	0.6	0.4	1.0	0.6	0.4	0.4	0.16

Figure 19. The number of *a)* stolons, *b)* tubers and *c)* tubers > 10 mm per stem at the first eight harvests of Expt 3 with days after emergence calculated separately for each variety. Estima, ●; Jelly, ○; King Edward, ■; Marfona, □; Maris Piper, ▲; Markies, △; Melody, ◆.

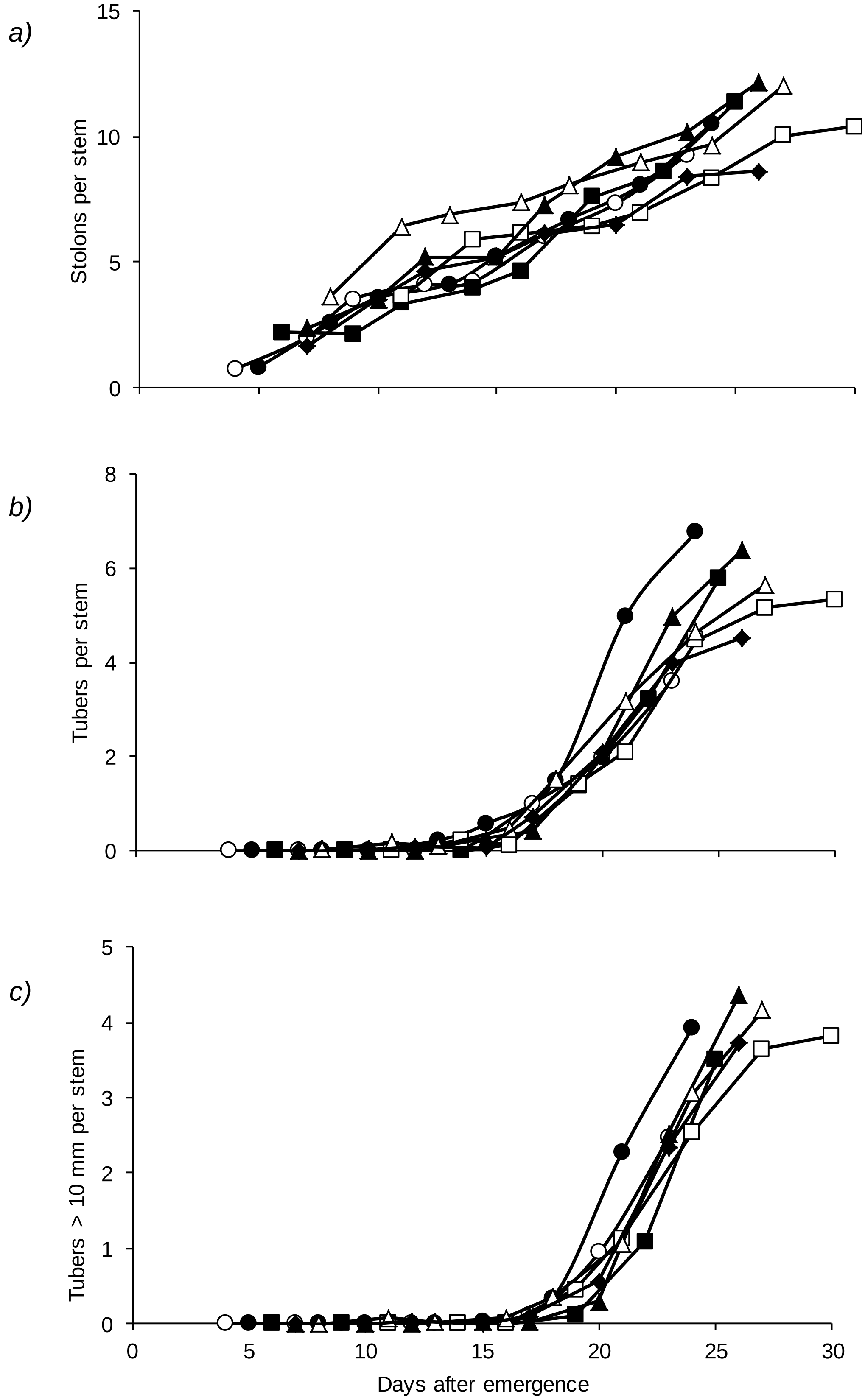


Table 29. Number of stolons, tubers and tubers > 10 mm per stem calculated at intervals from emergence for each variety in Expt 1

	DAE	Variety							S.E. (18 D.F.)
		Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	
Stolons	15	5.3	5.4	5.3	5.7	6.2	7.2	5.3	0.23
	20	7.7	7.5	7.8	7.4	8.8	9.0	7.1	0.37
Tubers	20	3.4	2.3	1.8	2.0	1.7	2.7	2.5	0.37
Tubers > 10 mm	23	3.4	2.1	1.7	2.3	2.3	2.5	2.5	0.77

The maximum stolon length per stem was between *c.* 0.5 and 4 cm at the first harvest and maximum stolon length increased linearly in all varieties at subsequent harvests but generally plateaued at *c.* 20 DAE (Table 30). At the eighth harvest there were substantial differences in the maximum stolon length per stem between varieties with Maris Piper having the shortest at *c.* 3.5 cm and Markies and Melody having the longest at *c.* 12 cm (Table 30). Unlike with the development of stolon and tuber numbers, the differences in the maximum stolon length per stem could not be accounted for by differences in emergence, indicating that the growth rate differed between varieties. At the sixth harvest, the mean length of stolons with tubers < 10 mm ranged from *c.* 2 cm in Maris Piper to *c.* 6 cm in Markies (Table 30). As more tubers > 10 mm formed, the length of stolons with tubers < 10 mm tended to decrease, indicating that tubers on longer stolons were more likely to develop into tubers > 10 mm (Table 30). At the seventh harvest, the mean length of stolons with tubers > 10 mm was similar for most varieties at *c.* 5 cm, with only Maris Piper differing appreciably at *c.* 2 cm (Table 30). Despite the number of tubers > 10 mm increasing in most varieties between the seventh and eighth harvests, the mean length of the stolons bearing these tubers did not change in any variety between the harvests (Table 30).

Table 30. Maximum stolon length of all stolons per stem at the first eight harvests *c.* 7, 10, 12, 15, 17, 20, 23 and 27 DAE of Expt 3 and the mean length of stolons bearing tubers < 10 mm and tubers > 10 mm at harvests 6-8

		Variety							
	Harvest	Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	S.E. (18 D.F.)†
Maximum stolon length (cm)	1	0.4	0.7	1.6	4.2	1.5	3.4	1.7	0.40
	2	2.2	1.5	1.4	6.6	1.4	5.6	2.9	0.31
	3	3.5	3.2	2.5	7.1	2.4	6.4	3.5	0.59
	4	5.2	3.7	3.1	7.9	2.4	8.4	4.8	0.61
	5	5.1	5.3	4.2	9.8	3.5	10.4	6.6	0.50
	6	7.5	6.7	5.5	11.3	4.2	11.0	6.3	0.42
	7	7.8	7.2	5.3	11.9	4.2	11.3	8.2	0.59
	8	7.7	8.7	8.2	11.6	3.6	12.3	7.4	0.69
Mean tuberised < 10 mm stolon length (cm)	6	4.6	5.5	3.8	4.0	2.2	5.7	4.3	0.49
	7	4.0	5.4	2.5	4.2	1.7	5.9	4.0	0.54
	8	3.1	3.4	2.2	4.7	1.1	4.0	3.0	0.51
Mean tuberised > 10 mm stolon length (cm)	6†	-	-	-	5.1	-	5.9	4.5	4.40
	7	5.6	5.7	4.1	5.5	2.1	5.7	4.9	0.45
	8	4.8	5.3	3.5	4.7	2.0	5.6	4.6	0.32

† Some values are omitted due to small sample sizes, with corresponding S.E. (4 D.F.)

Mean relative stolon depth (taking account of variations in planting depth between varieties and stems) was lowest when all stolons were included, with tuberised stolons being found closer to the seed tuber (Table 31). While there were differences in mean relative stolon depth between varieties these differences were small but changed appreciably between the sixth and eighth harvests (Table 31). At the seventh and eighth harvests, the mean relative stolon depth of stolons bearing tubers > 10 mm was *c.* 80 % in all varieties except Marfona in which it was *c.* 90 % (Table 31).

Table 31. Mean relative stolon depth of all stolons, tuberised stolons and stolons bearing tubers > 10 mm at harvests 6, 7 and 8 (*c.* 20, 23 and 27 DAE) of Expt 3

		Variety							
	Harvest	Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	S.E. (18 D.F.)
Mean relative stolon depth (%)	6	75.6	65.6	66.2	71.9	69.0	69.6	72.1	1.15
	7	72.0	66.7	69.3	68.1	69.6	67.0	70.6	1.96
	8	71.7	63.2	69.0	69.1	66.3	62.4	68.7	1.54
Mean tuberised < 10 mm relative stolon depth (%)	6	88.5	79.1	78.2	80.8	78.1	76.6	81.5	3.32
	7	80.2	75.7	83.0	75.0	81.0	72.2	75.2	4.19
	8	81.5	84.6	75.5	74.6	79.5	77.9	82.0	4.74
Mean tuberised > 10 mm relative stolon depth (%)	6†	-	-	-	89.6	-	84.6	78.7	5.61
	7	84.3	78.8	81.0	87.0	81.4	80.3	82.4	1.85
	8	82.1	81.6	82.4	89.0	79.1	76.8	79.8	1.55

† Some values are omitted due to small sample sizes, with corresponding S.E. (4 D.F.)

The majority of stolons present at the sixth harvest were primary stolons and the number of primary stolons only increased slightly between the sixth and eighth harvests, with the differences between varieties being caused mainly by differences in emergence (Table 32). Secondary stolons were present in all varieties at the sixth harvest and the number of secondary stolons increased by the eighth harvest in all varieties except Marfona which had the fewest secondary stolons (Table 32). There were generally few branch stolons across all varieties but in Marfona they were more common than secondary stolons, whilst in Estima the number was similar to the number of secondary stolons and Jelly had very few (Table 32). At the eighth harvest only *c.* 5 and 2 % of stems bore secondary or branch stolons (data not shown).

Table 32. Number of primary, secondary and branch stolons per stem at harvests 6, 7 and 8 (*c.* 20, 23 and 27 DAE) of Expt 3

		Variety							
	Harvest	Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	S.E. (18 D.F.)
Primary stolons	6	5.8	5.7	6.5	7.4	7.1	8.1	6.1	0.27
	7	6.2	7.0	7.1	7.9	8.0	8.1	7.2	0.35
	8	7.0	8.1	8.4	8.5	8.5	8.3	7.1	0.35
Secondary stolons	6	0.6	0.3	0.9	0.7	2.0	0.9	0.4	0.30
	7	0.9	0.3	1.3	0.8	2.1	1.2	0.8	0.27
	8	1.8	1.2	2.3	0.7	3.2	2.2	1.0	0.43
Branch stolons	6	0.1	0.0	0.1	0.3	0.1	0.0	0.0	0.10
	7	1.0	0.1	0.1	1.3	0.1	0.4	0.4	0.33
	8	1.7	0.0	0.5	1.3	0.4	1.6	0.3	0.58

4.3.2.2. Ninth harvest

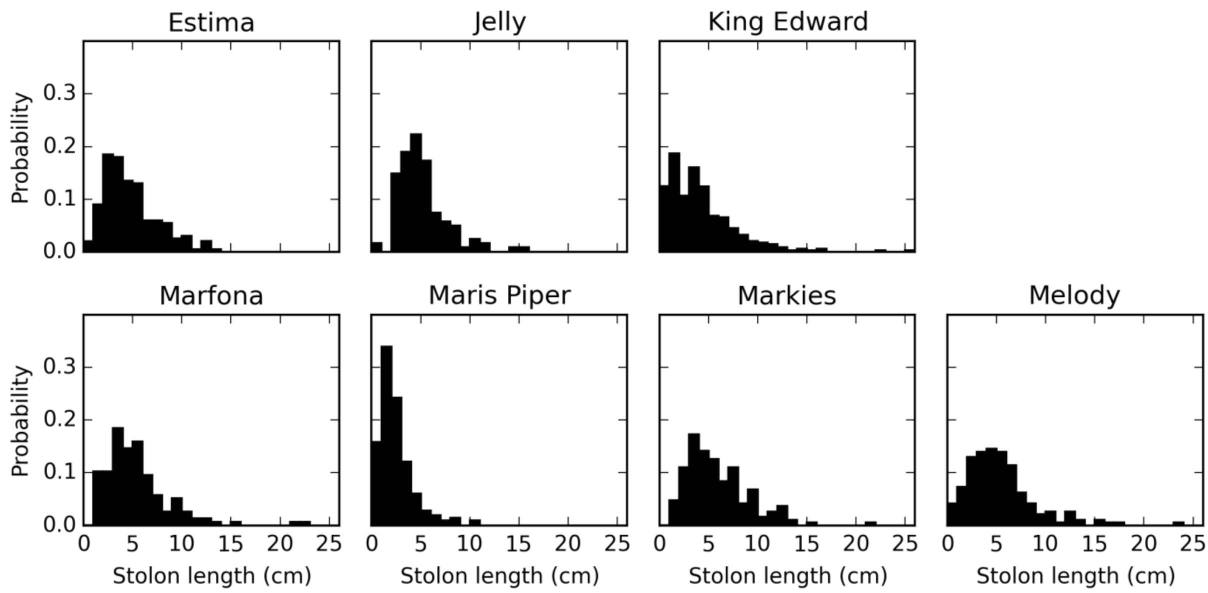
The mean achieved planting depth was *c.* 14.5 cm and this was similar for all varieties (Table 33). The number of tubers > 10 mm per stem was similar to the number at the eighth harvest in all varieties except King Edward where it had increased by *c.* 50 % and in Jelly where it had increased by *c.* 30 % (Tables 28 and 33). Mean stolon depth was between *c.* 11 and 12 cm from the soil surface, being numerically deepest in Jelly and shallowest in Estima, but differences between varieties were not significant (Table 33). Relative stolon depth ranged from 75 to 84 % and Jelly and Estima remained the extreme varieties by this metric, but the difference between them was not significant (Table 33). The relative stolon depths were slightly shallower for some varieties compared to at the eighth harvest, but this may have been due to the different methods used to measure planting depth, as the mean planting depth was *c.* 1 cm shallower at the eighth harvest than at the ninth (data not shown). Markies had the longest mean stolon length, more than twice that of Maris Piper which had the shortest but for other varieties there was a small range (4.0-5.1 cm; Table 33). The mean stolon length was similar to that recorded at the eighth harvest for all varieties (Tables 30 and 33). The median stolon length was *c.* 10 % shorter than the mean stolon length in all varieties, but between varieties the mean and the median stolon length were very strongly correlated (R^2 = 0.97). This was indicative of there being a relatively small number of long (> 10 cm) stolons in all varieties (Figure 20). Maris Piper had the most very short stolons (< 3 cm) and along with King Edward was the only variety in which sessile tubers (those with no stolon) were common (Figure 20). Overall, 98 % of tubers > 10 mm were borne on primary stolons (data not shown). In Estima, King Edward and

Maris Piper, *c.* 1-2 % of tubers > 10 mm were borne on secondary stolons, but there were none in other varieties (data not shown). In Estima, Jelly and Melody *c.* 1-2 % of tubers > 10 mm grew from branch stolons, in King Edward, *c.* 5 % of tubers did and in the other varieties, no tubers did (data not shown).

Table 33. Effect of variety on planting depth, stolon depth, relative stolon depth and stolon length at the ninth harvest (*c.* 84 DAE) of Expt 3 (stolon data for tubers > 10 mm only)

Variety	Planting depth (cm)	Tubers > 10 mm per stem	Mean stolon depth (cm)	Mean relative stolon depth (%)	Mean stolon length (cm)	Median stolon length (cm)
Estima	14.1	4.3	11.3	74.5	4.5	3.9
Jelly	14.8	3.3	12.5	83.8	4.9	4.4
King Edward	14.7	5.6	11.4	76.4	4.0	3.1
Marfona	14.9	3.4	12.3	82.6	5.1	4.2
Maris Piper	14.7	4.4	11.5	77.4	2.2	1.8
Markies	14.6	4.0	11.7	77.6	5.7	4.9
Melody	14.5	3.9	11.7	77.8	5.1	4.6
S.E. (18 D.F.)	0.31	0.21	0.37	2.45	0.37	0.31

Figure 20. Histograms of stolon length in each variety at the ninth harvest (*c.* 84 DAE) of Expt 3.



Stolons were clustered towards the base of the stem in all varieties and as in Expts 1 and 2, the deepest stolons shown in Figure 21 were the result of stems with atypically deep planting depths. Differences in the minimum stolon depth per plant were greater than the mean stolon depth with Jelly having the deepest at *c.* 10 cm compared to other varieties at *c.* 6.5-8 cm (Table 34). The maximum stolon length per plant was between *c.* 5 and 11 cm and were generally correlated with mean stolon length, with Maris Piper having the shortest, but King Edward had the longest, despite having the second shortest mean stolon length (Tables 33 and 34).

Figure 21. Histograms of stolon depth in each of the varieties at the ninth harvest (c. 84 DAE) of Expt 3.

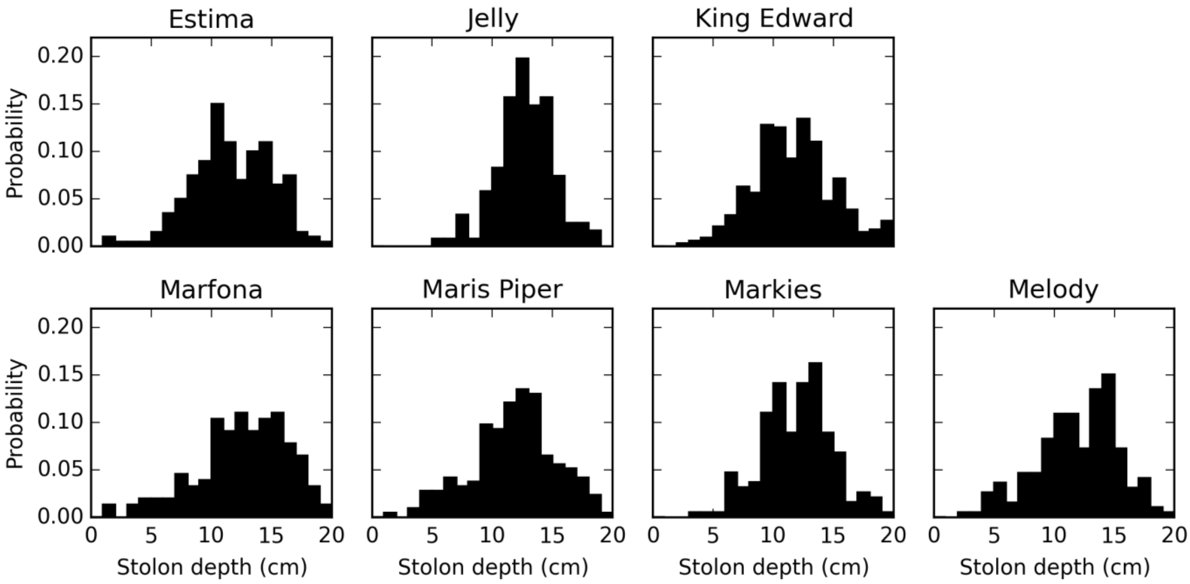


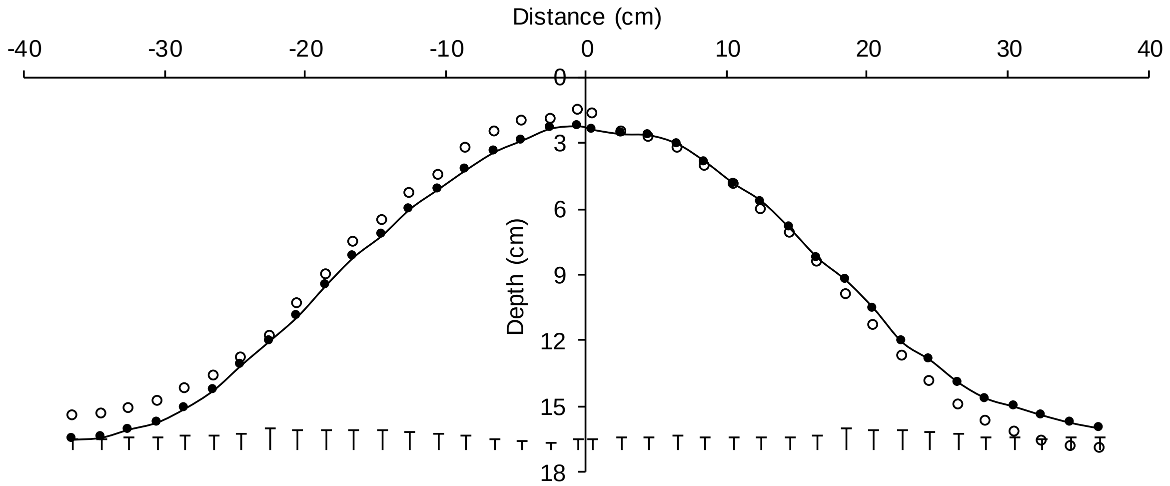
Table 34. Effect of variety on minimum stolon depth and maximum stolon length per plant in Expt 3

Variety	Minimum stolon depth (cm)	Maximum stolon length (cm)
Estima	6.7	8.8
Jelly	9.8	7.4
King Edward	6.5	11.1
Marfona	8.0	9.8
Maris Piper	7.2	5.2
Markies	7.7	10.4
Melody	6.5	10.5
S.E. (18 D.F.)	0.61	1.10

4.3.3. Ridge profile

The average ridge profile *c.* 84 DAE is shown in Figure 22, along with the average ridge profile measured in 2016 which was very similar.

Figure 22. Average ridge profiles at the ninth harvest (●; 84 DAE) of Expt 3 and the average ridge profile in 2016 (O). Bars indicate S. E. based on 18 D.F.



4.3.4. Tuber position

The average distance from the centre of the plant to the stolon end of tubers was between 3 and 5 cm (Table 35) and was strongly correlated and almost directly related to average stolon length (Figure 23, Table 36). The apical ends of the tubers were on average *c.* 12 cm from the centre of the plant in all varieties except King Edward and Maris Piper where they were *c*. 9 and 8 cm, respectively (Table 35). Combining the average stolon length and average tuber length accounted for a large proportion of the distance to the apical end of the tubers, although they were less than expected from a directly proportional relationship (Figure 23). This was probably due to the angle from the centre of the plant to the stolon and apical ends of the tubers not being identical and also due to the horizontal orientation of tubers varying. On average, there was no evidence to indicate that tubers were further away from the seed tuber along the ridge compared to across the ridge (data not shown). However, when accounting for the three-dimensional position of tubers, those that were closer to the surface could be found further away along than across the ridge (Figure 25). This was probably due to stolons that grew across the ridge turning green at the tips and in turn inhibiting tuber formation (Table 28). The average tuber depth ranged from *c.* 10 to 11 cm but was unrelated to the mean stolon depth (Tables 33 and 35). The cluster width was similar in most varieties at *c.* 26 cm and only Maris Piper differed, having a cluster width of *c.* 22 cm (Table 35). This was consistent with the relatively short mean stolon length in Maris Piper.

Table 35. Effect of variety on the average distance from the centre of the plant to the stolon and apical ends of tubers in Expt 3

Variety	Distance to stolon end (cm)	Distance to apical end (cm)	Tuber depth (cm)	Cluster width (cm)
Estima	4.5	11.4	9.8	27.4
Jelly	5.0	11.9	11.1	25.7
King Edward	5.1	9.3	10.4	25.9
Marfona	4.8	11.1	10.4	26.9
Maris Piper	3.4	8.3	10.6	21.9
Markies	5.6	11.3	11.4	26.3
Melody	5.4	11.0	10.7	27.1
S.E. (18 D.F.)	0.35	0.40	0.32	1.53

Figure 23. Relationships between distance from the centre of the plant to the stolon end of tubers and stolon length, ●; and between distance from the centre of the plant to the apical end of tubers and stolon length plus tuber length, ○; in Expt 1. Line is 1:1 relationship. Relationships for each dataset are given in Table 36.

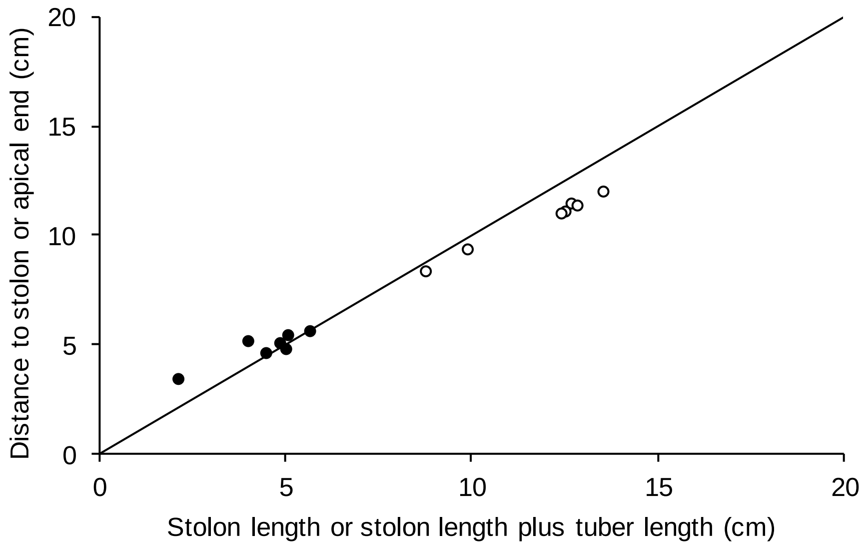


Table 36. Relationships between distance to the stolon or apical end of tubers (DIS, cm) and stolon length or stolon length plus tuber length (LEN, cm) as shown in Figure 23: slope of relationship (*m*) and S.E., constant of relationship (*c*) and S.E., significance of relationship (*F* prob) and strength of relationship (R^2). DIS = *m* LEN + *c*

	m	S.E.	*c*	S.E.	*F* prob.	R^2
Stolon end	0.56	0.122	2.32	0.565	< 0.001	0.77
Apical end	0.73	0.024	1.91	0.288	< 0.001	0.99

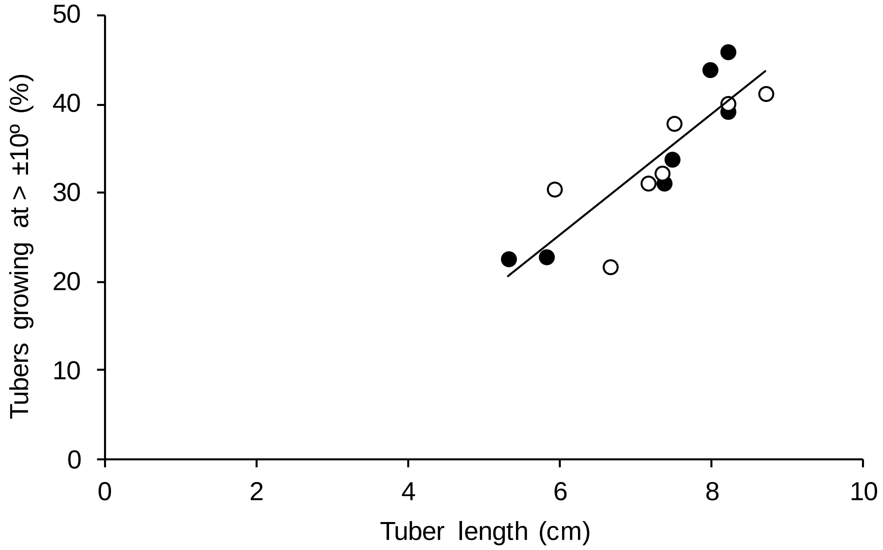
The depth to the centre of tubers was more likely to be found above than below the depth of the stolons in all varieties (Table 37). Tubers were highest relative to their stolon depth in Estima and lowest in Jelly but this difference was not significant (Table 37). Between *c.* 22 and 41 % of tubers grew at an angle > ±10º with this being least common in Maris Piper and most common in Estima, Marfona and Jelly (Table 37). The proportion of tubers growing at an angle > ±10º increased as average tuber length increased and the relationship was similar to that observed in 2016 indicating that the differences between varieties were due to differences in mean tuber size rather than genetic differences in tuber development (Figure 24). The average orientation angle was similar in all varieties except Melody where tubers on average angled downwards as opposed to upwards in the other varieties (Table 37). In Melody, this was somewhat similar to in 2016, where tubers were on average orientated horizontally, indicating that they more likely to be angled downwards.

Table 37. Percentage of tubers with their centre above the stolon depth, the average difference between the stolon depth and the depth to the centre of the tuber, the percentage of tubers with a horizontal angle > 10 % and the average orientation of all tubers in Expt 3

Variety	Tubers with their centre above the stolon depth (%)	Difference between depth to centre of tuber and stolon depth† (cm)	Tubers with a horizontal angle > ±10º (%)	Average tuber orientation angle (º)	Average tuber orientation angle of tubers > ±10º (º)
Estima	71.6	1.4	40.0	4.3	8.7
Jelly	56.7	0.4	41.3	5.1	11.7
King Edward	69.9	1.4	30.5	3.9	13.1
Marfona	58.4	1.1	37.8	5.9	13.5
Maris Piper	65.1	0.7	21.7	1.5	7.2
Markies	69.2	1.1	31.1	2.4	7.7
Melody	62.8	0.8	32.4	-6.1	-16.9
S.E. (18 D.F.)	5.96	0.27	3.16	1.76	4.81

† Stolon depth values were calculated from the frame rather than measured from the top of the stem.

Figure 24. Relationship between tuber length (TL) and the proportion of tubers growing with a horizontal angle > ±10º (HA) in 2016, ● and 2017, O. Fitted line for combined years: HA = 6.7 (±1.09) × TL -15.1 (±8.00), *p* = < 0.001, R^2 = 0.74.

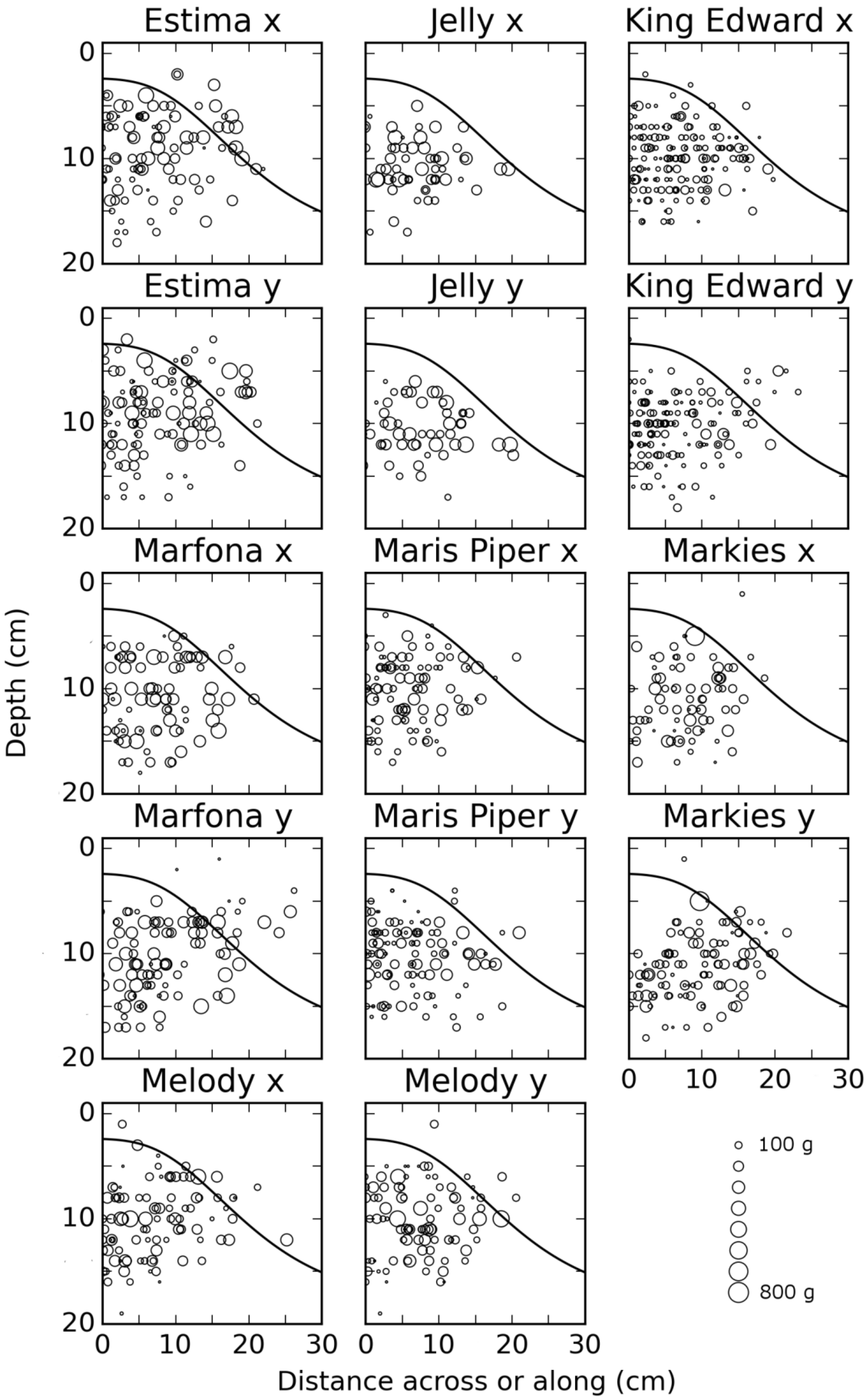


Estima and Melody had the most tubers growing close to the soil surface with approximately three times as many as Jelly. While the amount of yield present close to the surface did not differ between varieties, this was also numerically greatest for Estima and Melody (Table 38, Figure 25).

Table 38. Percentage of tubers and yield within 2.5 cm of the soil surface in Expt 3

Variety	Tubers within 2.5 cm of soil surface (%)	Yield within 2.5 cm of soil surface (%)
Estima	11.8	17.3
Jelly	4.3	5.3
King Edward	5.7	5.6
Marfona	9.1	5.9
Maris Piper	8.8	6.6
Markies	6.1	7.6
Melody	12.0	13.0
S.E. (18 D.F.)	1.70	3.53

Figure 25. Diagrams showing the position of tubers across (x) and along (y) the ridge for each variety in Expt 3. Points are centred at the shallowest and furthest away point, and their diameter is proportional to tuber weight with weights of 100-800 g FW shown in the final panel. The average ridge profile is shown for reference.



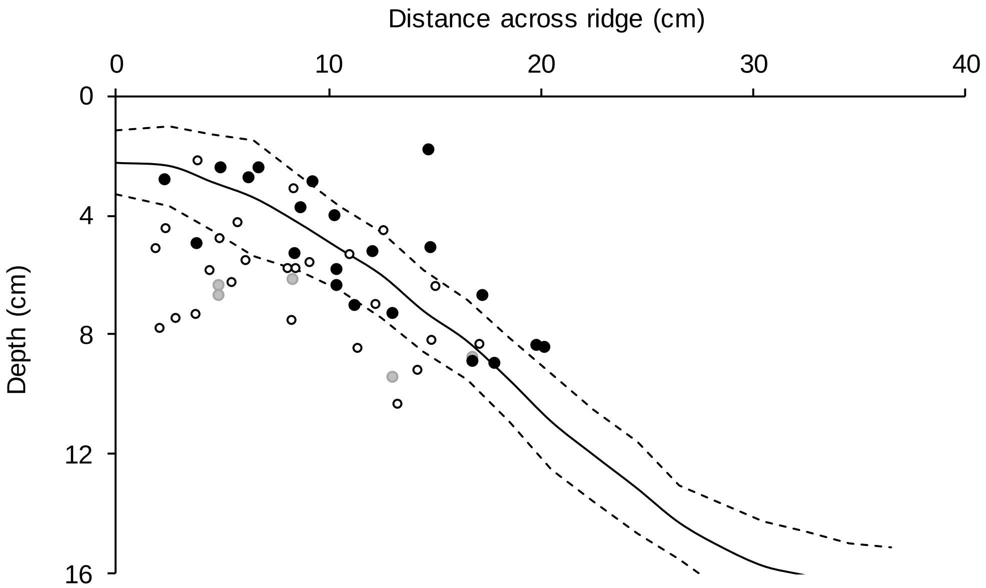
4.3.4.1. Green tubers

At 84 DAE, very few tubers were affected by greening with the exception of King Edward and Marfona where *c*. 6-7 % of tubers were green (Table 39). The amount of yield that was green was more variable than the number of tubers with King Edward having four times as much yield affected as Marfona, despite the incidence being similar (Table 39). Tubers that were green tended to be close to the soil surface, but in some instances were > 5 cm deeper, indicating that cracks had formed allowing light to penetrate (Figure 26).

Table 39. Incidence of and yield affected by tuber greening at the tuber mapping harvest

Variety	Incidence of tuber greening (%)	Yield affected by tuber greening (%)
Estima	6.0	4.2
Jelly	0.0	0.0
King Edward	7.4	8.0
Marfona	6.1	2.0
Maris Piper	1.4	1.1
Markies	0.6	0.2
Melody	2.1	1.1
S.E. (18 D.F.)	1.60	1.57

Figure 26. Position of the upper- and outer-most part of green tubers in relation to the average ridge profile (———) and ± 2 S.E. (- - - -) at the ninth harvest of Expt 3. Tubers visible at the surface and dark green, ●; tubers not visible at the surface and dark green, ●; tubers not visible at the surface and light green, O.



4.3.5. Number of stems, number of tubers, yield and grading

Stem populations ranged from *c.* 70 000 to 120 000/ha, being lowest in Jelly and highest in King Edward (Table 40). Tuber populations ranged from *c.* 200 000 to 700 000/ha and were lowest in Jelly and highest in King Edward (Table 40). Yield ranged from 49-69 t/ha and was lowest in Maris Piper and highest in Estima (Table 40). The differences in tuber populations combined with the differences in yield contributed to large differences in mean tuber size between varieties ranging from 50 mm in King Edward to 70 mm in Jelly (Table 40). The coefficient of variation (COV) of tuber size did not differ between the varieties but ranged from *c.* 15-18 % (Table 40) equating to marketable yields (45-80 mm) at an optimal mean tuber size of 62 mm, of between *c.* 89 and 94 %.

Table 40. Effect of variety on the number of stems and tubers and components of yield at the final harvest (121 DAE) in Expt 3

Variety	Number of stems (000/ha)	Number of tubers (000/ha)	Yield (t/ha)	Mean tuber size (mm)	COV of tuber size (%)
Estima	91.7	408	69.4	62.4	17.0
Jelly	72.2	214	53.0	69.5	14.7
King Edward	120.4	677	51.5	49.8	17.7
Marfona	80.6	281	54.1	67.7	17.0
Maris Piper	103.7	436	48.7	57.2	16.7
Markies	80.6	363	51.6	59.0	15.5
Melody	82.4	346	61.9	66.9	17.0
S.E. (18 D.F.)	4.59	29.7	1.84	0.94	0.78

4.3.6. Tuber greening

Overall, tuber greening was considerably more common at the final harvest taken three weeks after desiccation than at the mapping harvest taken *c.* 40 days earlier (Tables 39 and 41). Estima, King Edward and Marfona remained the varieties with the highest incidence of tuber greening with *c.* 17-23 % of tubers affected but, the range in the amount of yield affected was greater, indicating that small tubers were more likely to be green in Marfona, but not in Estima (Table 41). Maris Piper and Jelly were less affected with *c.* 10 % of tubers and a similar amount of yield affected (Table 41). Markies had the lowest incidence, but a higher proportion of yield affected, whereas Melody had the lowest amount of yield affected despite having a higher incidence than Markies (Table 41). In King Edward, *c.* 3 % of the yield affected by greening comprised tubers < 40 mm in diameter whereas in other varieties < 1 % of yield was of small tubers (Table 41). In most varieties, a similar proportion of yield was affected by dark and light greening, but in King Edward a greater proportion was dark greening and in Markies and Melody there was very little dark greening (Table 41). Numerically, Maris Piper had the most yield visible at the soil surface at *c.* 2 %, Markies and Melody had almost no yield visible at the surface and the other varieties had *c.* 1 % (Table 41). The severity of tuber greening was relatively low with < 2 % of surface area affected (Table 41) and this correlated strongly with the incidence of tuber greening (R^2 = 0.83; data not shown).

As in previous years, the results indicate that stolon architecture did not directly determine the susceptibility of varieties to greening since, for example, Estima and Melody had very similar mean stolon lengths and depths (differing by 6 mm and 3 mm, respectively), but Estima had more than four times as much yield affected by tuber greening than Melody (Tables 33 and 41). Considering tuber length as well as stolon length, Jelly and Maris Piper represented the extreme varieties, but both had similar amounts of yield affected by tuber greening (Tables 35 and 41). The percentage of yield within 2.5 cm of the soil surface at 84 DAE was not associated with the amount of tuber greening at the final harvest with Estima and Melody having a similar proportion of tubers in susceptible positions, despite the large difference in tuber greening (Tables 38 and 41).

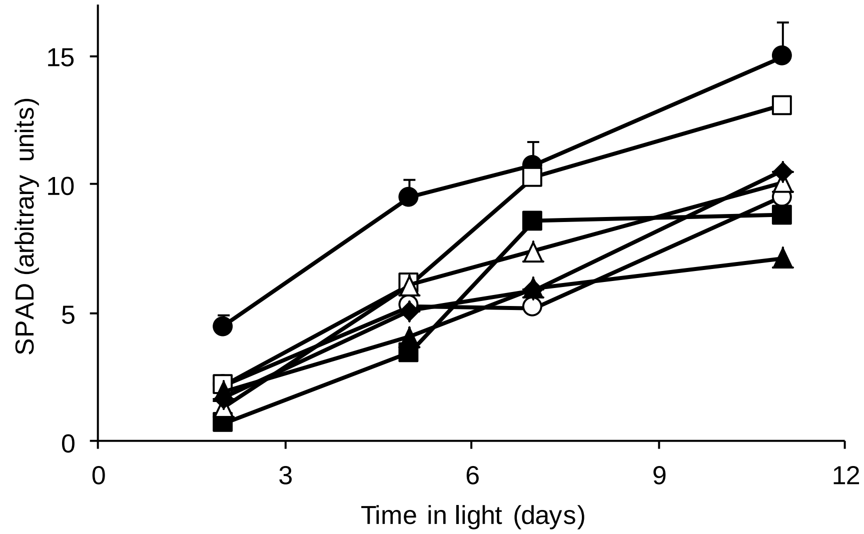
Table 41. Incidence and severity of tuber greening at the final harvest (124 DAE) in Expt 3

Variety	Incidence (% of tubers)	Yield affected (%)					Severity (% surface area)
		Total	< 40 mm	Light green	Dark green	At surface	
Estima	22.6	22.6	0.7	12.8	9.1	0.8	1.8
Jelly	11.1	10.1	0.1	6.1	3.9	0.8	0.7
King Edward	20.7	18.9	3.3	5.5	10.1	1.2	1.3
Marfona	17.3	13.8	0.4	7.9	5.6	1.1	1.9
Maris Piper	10.8	11.0	0.6	5.4	5.0	2.2	0.6
Markies	5.1	8.8	0.0	8.0	0.8	0.1	0.3
Melody	7.7	5.3	0.4	4.5	0.3	0.1	0.2
S.E. (18 D.F.)	2.49	3.18	0.23	2.46	1.54	0.43	0.30

4.3.6.1. Sensitivity to light

As in the previous two years, tuber greening increased linearly in all varieties from 2-7 days after exposure to light began. There was little further change in King Edward after 7 days exposure, but other varieties continued to green at a similar rate until 11 days of exposure (Figure 27). After 11 days, Estima was most green and Maris Piper the least (Figure 27). As in Expts 1 and 2, varieties with very different amounts of tuber greening in the field experiment had similar susceptibilities to greening in the glasshouse (e.g. Markies and King Edward). The average SPAD value after 11 days was similar to that in Expt 1 after 10 days, and the values for varieties were correlated with those from Expt 1 (R^2 = 0.63), but not with those from Expt 2 (R^2 = 0.00).

Figure 27. Development of tuber greening in a glasshouse in Expt 3. Estima, ●; Jelly,○; King Edward, ■; Marfona, □; Maris Piper, ▲; Markies, △; Melody, ◆. Bars indicate S. E. based on 18 D.F.



4.4. Summary of variety experiments

Stolons were shorter nearer the base of stems than towards the soil surface in all varieties in each year (Figure 28). Although relatively little of variation in stolon length was accounted for by variation in relative stolon depth (Average R^2 = 0.21; range 0.02-0.49), with the exception of King Edward in 2016, the correlations in Figure 28 were all significant at $p = < 0.001$.

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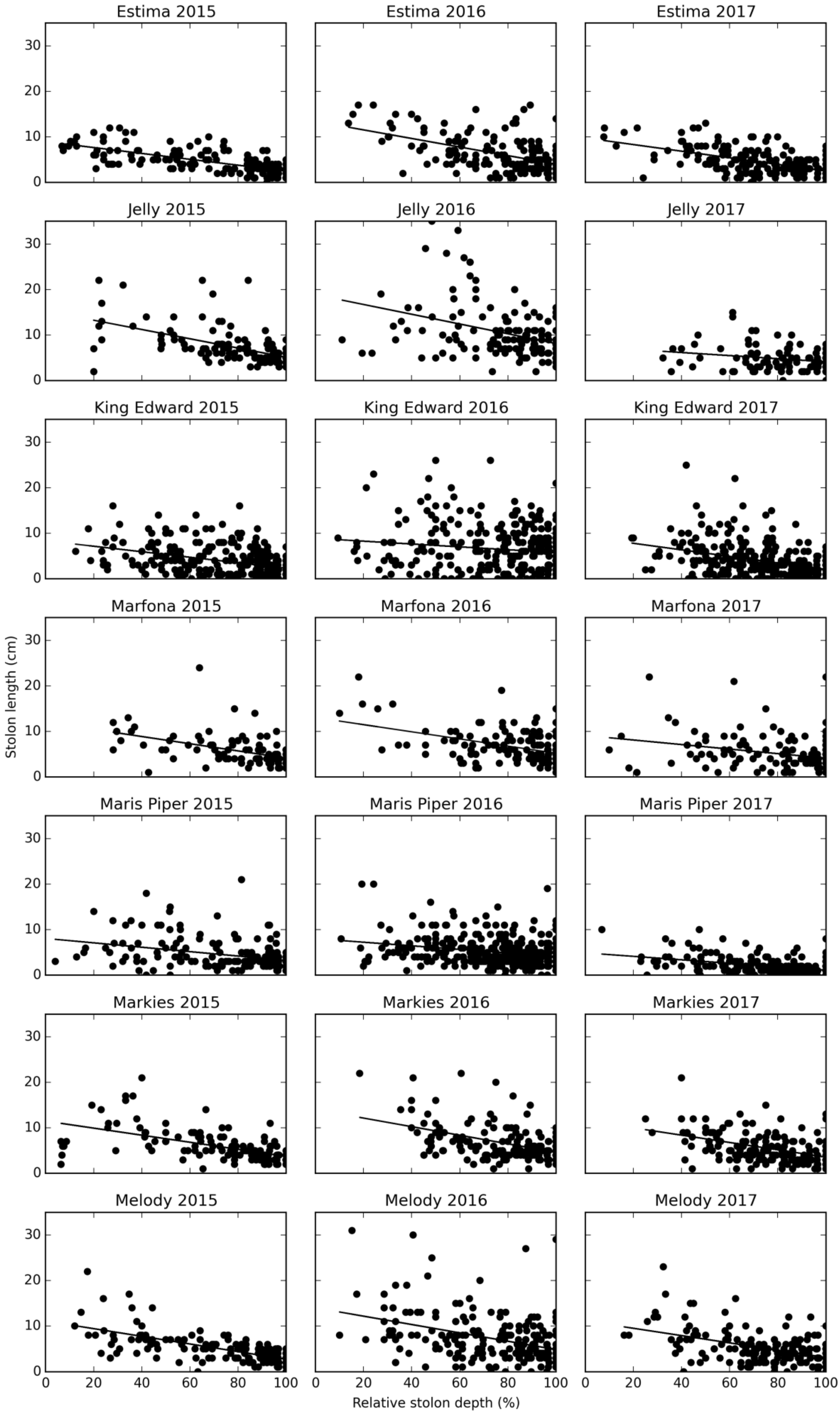
Figure 28. Relationships between relative stolon depth and stolon length in Expts 1-3.



Mean stolon length was on average 2.5 cm longer in Expt 2 than in Expt 1 and Expt 3 (Table 42) and these differences between years were relatively consistent between varieties, except Jelly, where stolons were *c.* 6 cm longer in Expt 2 than in Expt 1 and Expt 3 (Figure 29*a*). Seed tuber health of Jelly in Expt 2 was poor, and may have influenced stolon development. In Jelly and Maris Piper, mean stolon length in Expt 3 was *c.* 2.5 cm shorter than in Expt 1, but in other varieties, there was less than a 0.5 cm difference between these experiments. On average Jelly had the longest mean stolon length of *c.* 8 cm and Maris Piper had the shortest of 4 cm, but there was little variation between the other varieties, where mean stolon length was between *c.* 5 and 6 cm.

Relative stolon depth varied very little between years, ranging from *c.* 76 to 80 % of planting depth and averaged across the 3 years, the range in values for varieties was similar (Table 42). In most varieties, there were no differences between years and the largest difference occurred in Estima, where relative stolon depth was *c.* 8 % deeper in Expt 2 than in Expt 1 (Figure 29*b*). The average cluster width varied from *c.* 24 cm in Maris Piper to *c.* 31 cm in Jelly and there was a *c.* 5 cm range between years (Table 42). These differences in cluster width were mainly caused by differences in stolon length between varieties (R^2 = 0.77; data not shown).

Figure 29. Summary of *(a)* mean stolon length and *(b)* relative stolon depth in Expt 1, ■; Expt 2, ■; and Expt 3, ■. Bars indicate S. E. based off 18 D.F.

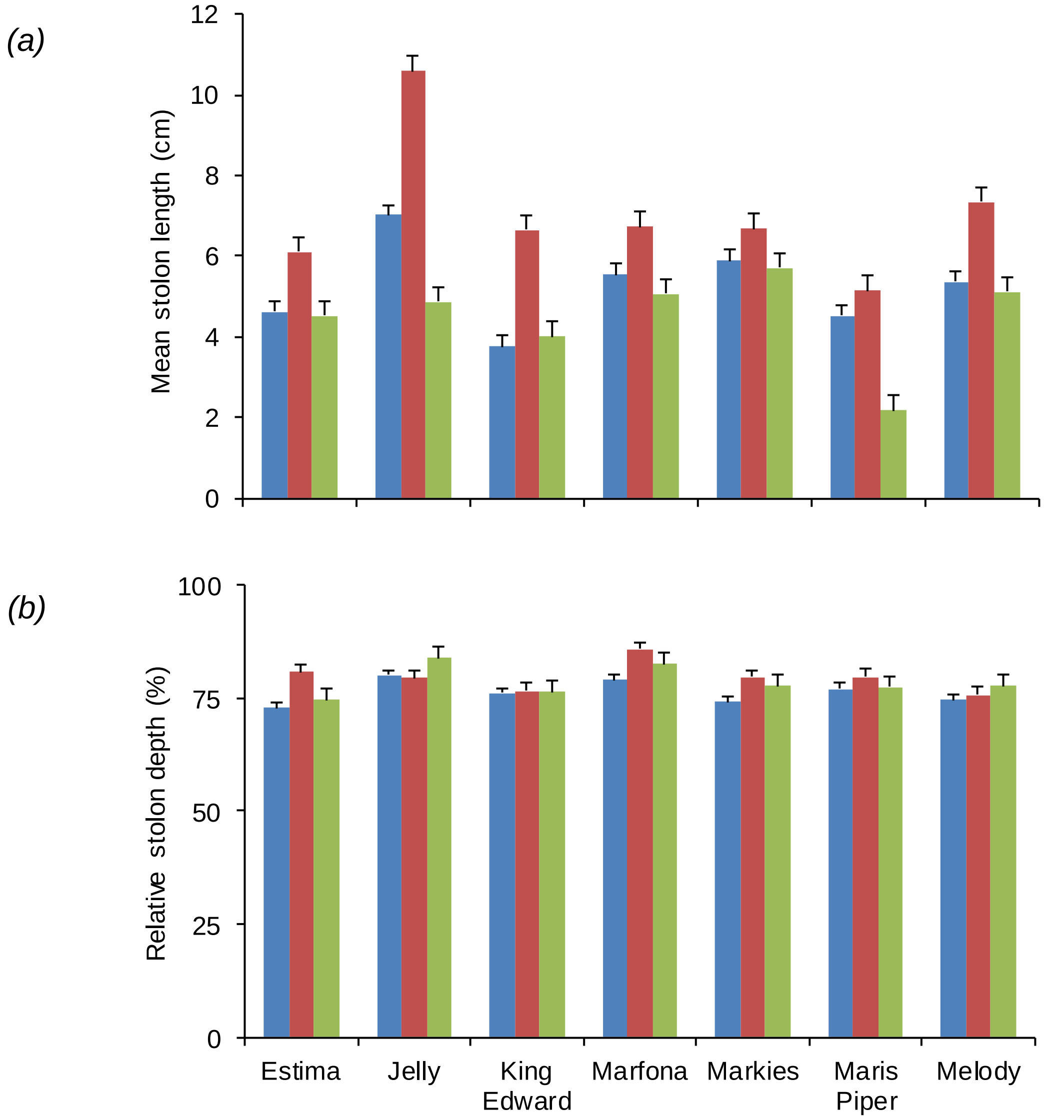
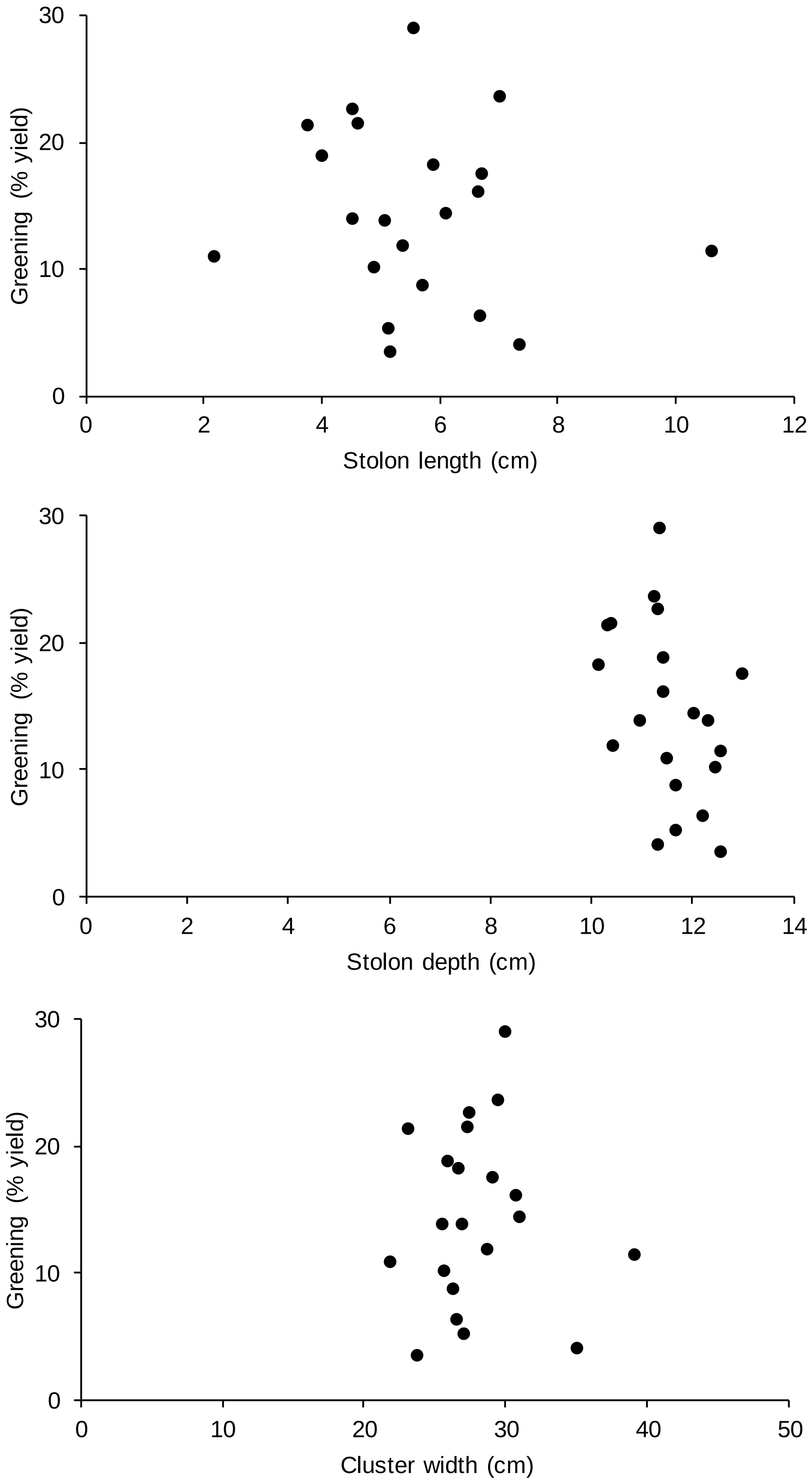


Table 42. Average mean stolon length, relative stolon depth, tuber depth, cluster width and tuber greening in Expts 1-3

	Mean stolon length (cm)	Relative stolon depth (%)	Tuber depth (cm)	Cluster width (cm)	Tuber greening (% yield)
Variety					
Estima	5.1	76.1	9.4	28.6	19.5
Jelly	7.5	81.1	10.2	31.4	15.1
King Edward	4.8	76.4	9.2	26.6	18.8
Marfona	5.8	82.5	9.4	28.7	20.1
Maris Piper	3.9	78.1	9.6	23.7	9.5
Markies	6.1	77.1	10.2	26.5	11.1
Melody	5.9	76.0	10.2	30.3	7.1
S.E. (54 D.F.)	0.20	1.27	0.26	0.78	1.94
Year					
2015	5.2	76.3	8.8	27.3	19.9
2016	7.0	79.7	9.8	30.8	10.5
2017	4.5	78.6	10.6	25.9	12.9

Combined, the results of Expts 1-3 indicate that differences in stolon architecture had limited influence on the susceptibility of varieties to tuber greening since there was no relationship between either stolon depth or stolon length and tuber greening (Figure 30). Even when differences in tuber length were accounted for by calculating the cluster width, this could not explain differences in tuber greening between the varieties (Figure 30*c*).

Figure 30. Relationships between *(a)* stolon length, *(b)* stolon depth, *(c)* cluster width and tuber greening in Expts 1-3. Each point represents one variety in each experiment.



4.5. Experiment 4

4.5.1. Emergence and ground cover

The interval from planting to emergence was *c.* 4 days shorter in Marfona and Maris Piper than in Jelly (Table 43). Emergence was complete in both seed sizes of Marfona and Maris Piper and the large seed of Jelly, but in the small seed of Jelly *c.* 3 % of plants failed to emerge (although this was substantially better than the emergence of the same seed stock in Expt 2; Tables 27 and 43). Emergence was more protracted in the small seed than the large seed in all varieties, but particularly in Jelly for which there was a large difference between the seed sizes (Table 43).

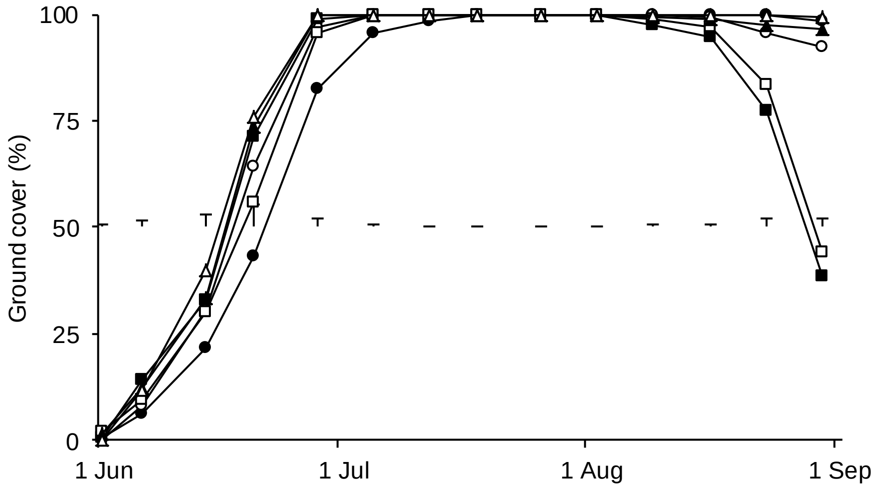
Table 43. Effect of variety and seed size on the interval from planting to emergence, final emergence and the interval from 20-80 % emergence in Expt 4

Variety	Jelly		Marfona		Maris Piper		S.E.
Seed size†	Small	Large	Small	Large	Small	Large	(15 D.F.)
Interval from planting to 50 % emergence (days)	39.2	39.2	35.0	36.0	35.4	36.1	0.39
Final emergence (%)	97.4	99.2	100	100	100	100	0.45
Interval from 20-80 % emergence (days)	6.1	3.1	3.3	2.8	3.6	2.5	0.19

† Small seed at spaced at 25 cm, large seed spaced at 40 cm

Canopies expanded at a similar rate for both seed sizes of Maris Piper, but for Marfona, the large seed was slower to develop than the small seed and in Jelly the small seed had a slower rate of expansion than the large seed (Figure 31). Except for the small seed of Jelly, all treatments produced full canopies by the last week of June (Figure 31). Marfona began to senesce in mid-August, but the other varieties maintained full canopies until desiccation (Figure 31).

Figure 31. Foliar ground cover in Expt 4. Small Jelly, ●; Large Jelly, ○; Small Marfona, ■; Large Marfona, □; Small Maris Piper, ▲; Large Maris Piper, △. Bars indicate S. E. based on 15 D.F.



4.5.2. Stolon architecture

Planting depths were between *c.*13 and 14 cm and the small seed tubers were shallower than the large tubers, although this was mainly in Marfona and Maris Piper rather than Jelly (Table 44). This may have been due to seed being planted at a similar distance from the top of the ridge, but stems that emerged from the bottom of the large seed tubers had a deeper effective planting depth. Mean stolon length was *c.* 3 cm in Maris Piper, *c.* 6 cm in Marfona and *c.* 9 cm in Jelly (Table 44). Seed size had no effect on stolon length, so the hypothesis that larger seed would produce longer stolons can be rejected (Table 44). Mean stolon depth was deepest in Marfona and shallowest in Jelly and consistent with the difference in planting depth, large seed had deeper stolons (Table 44). Once planting depth was accounted for, Marfona still had the deepest stolons and Jelly the shallowest and in these varieties there was no effect of seed size, but in Maris Piper, the small seed had deeper stolons than the large seed (Table 44).

Table 44. Effect of variety and seed size on planting depth, stolon length, stolon depth and relative stolon depth in Expt 4

Variety	Jelly		Marfona		Maris Piper		S.E.
Seed size†	Small	Large	Small	Large	Small	Large	(15 D.F.)
Planting depth (cm)	12.6	12.8	12.9	14.0	12.8	14.3	0.41
Mean stolon length (cm)	9.0	9.4	5.9	6.6	3.9	3.1	0.32
Mean stolon depth (cm)	10.1	10.3	11.0	12.1	10.9	11.4	0.32
Relative stolon depth	80.8	81.8	87.5	85.4	86.1	80.2	1.37

† Small seed at spaced at 25 cm, large seed spaced at 40 cm

4.5.3. Yield and tuber greening

At the different plant spacings, stem populations were very similar for both seed sizes in Maris Piper, but numerically higher in the large seed than small seed of Jelly and in the small seed than large seed of Marfona (Table 45). The number of tubers per stem was similar between the seed sizes in Jelly, but the larger seed of Marfona and the small seed of Maris Piper had numerically higher numbers of tubers per stem (Table 45). Yield ranged from *c.* 60 70 t/ha and was highest in Marfona, but similar in Jelly and Maris Piper and there were no differences between seed sizes (Table 45). Mean tuber size was largest in Marfona, followed by Jelly and Maris Piper. There was no numerical difference in mean tuber size between seed sizes in Marfona, but the mean tuber size from small seed of Jelly was numerically *c.* 4 mm larger than large seed and the mean tuber size from large seed of Maris Piper was numerically *c.* 5 mm larger than from small seed (Table 45). There were no significant differences in the COV of tuber size between varieties or seed sizes (Table 45).

Table 45. Effect of variety and seed size on components of yield in Expt 4

Variety	Jelly		Marfona		Maris Piper		S.E.
Seed size†	Small	Large	Small	Large	Small	Large	(15 D.F.)
Number of stems	95.3	117.4	132.0	102.8	184.7	185.4	11.82
Number of tubers	282	353	267	244	613	534	33.0
Yield (t/ha)	62.1	60.4	69.9	66.9	59.1	62.8	1.91
Mean tuber size (mm)	67.8	63.9	74.2	74.2	53.6	58.9	1.33
COV of tuber size (%)	16.0	15.9	16.6	16.0	16.4	18.2	1.07

† Small seed at spaced at 25 cm, large seed spaced at 40 cm

Maris Piper had the lowest amount of tuber greening with *c.* 5 % of yield affected but there was no difference between Jelly and Marfona which both had *c.* 15 % of yield affected (Table 46). Seed size had no significant effect on the total amount of tuber greening in any variety (Table 46), although numerically, in Maris Piper, the large seed had approximately twice as much tuber greening as the small seed, in Marfona the large seed had *c.* 50 % more than the small seed and in Jelly, the small seed had *c.* 33 % more than the large seed. Of the yield affected by tuber greening, *c.* 10-20 % was visible at the surface, but there were no significant differences in the percentage of yield visible at the surface between treatments (Table 46). The proportion of yield affected by light greening was significantly higher in the large seed size of Marfona compared to the small seed size (Table 46), which supports the hypothesis that, when other factors (e.g. yield, mean tuber size, stolon length) are equal, wider spacing can increase cracking of the ridge due to higher tuber volumes per plant. Interpreting these results is complicated by the numerical differences in planting depth and mean tuber size between seed sizes, which may have confounded effects of the treatments, and by the relatively high errors associated with the estimates of tuber greening.

Table 46. Effect of variety and seed size on tuber greening in Expt 4

Variety	Jelly		Marfona		Maris Piper		S.E.
Seed size†	Small	Large	Small	Large	Small	Large	(15 D.F.)
< 40 mm diameter (% yield)	0.4	0.6	0.2	0.2	0.7	0.9	0.18
Light greening (% yield)	6.7	5.3	5.4	12.2	1.5	2.9	1.35
Dark greening (% yield)	9.6	6.5	6.5	6.1	1.5	2.8	1.39
Visible at surface (% yield)	3.3	1.7	1.6	1.9	0.5	0.8	0.88
Overall greening (% yield)	16.7	12.5	12.1	18.5	3.6	6.5	2.23

† Small seed at spaced at 25 cm, large seed spaced at 40 cm

4.6. Experiment 5

4.6.1. Meteorology

Average air and soil temperatures in the 4 weeks after emergence increased with delay in planting, but there were periods at which at the same interval after emergence, soil temperatures were not higher for later planting dates than earlier planting dates (Table 47, Figure 32). When considering temperatures from 0-3 weeks (from emergence to the start of tuber initiation) or 1-4 weeks (the period over which most stolon development would be expected to occur), differences between planting dates were less consistent than from 0-4 weeks. For example, there was little difference between average soil temperatures from the Early and Mid-planting dates over 1-4 weeks, nor between the Mid and Late planting dates over 0-3 weeks (Table 47). Differences in the amount of incident radiation between planting dates were generally similar to those between air and soil temperature (Table 47).

Figure 32. Daily average soil temperatures from the date of 50 % of emergence for Estima at the Early (———), Mid (— — —) and Late (········) planting dates in Expt 5.

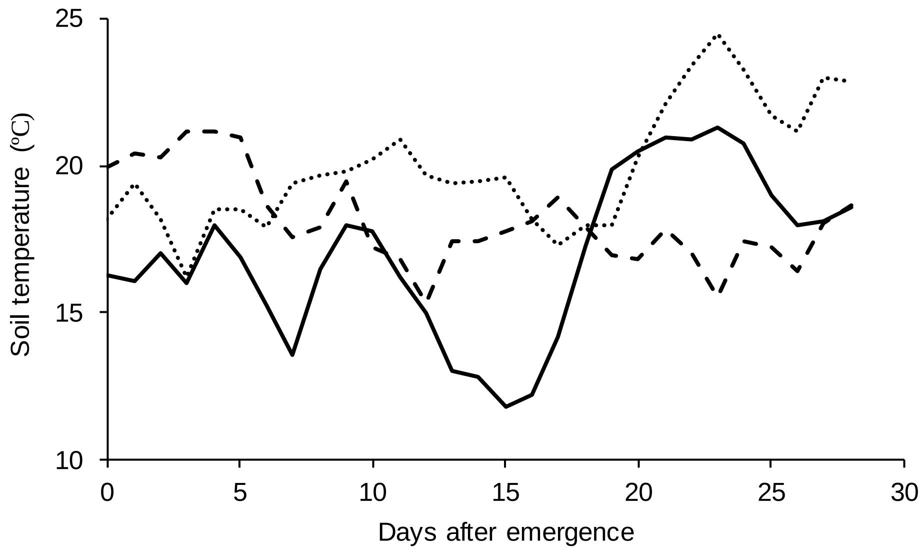


Table 47. Total incident radiation, average air temperatures and average soil temperatures from the date of 50 % emergence until 3 or 4 weeks later and from 1-4 weeks after emergence in Expt 5

		Radiation (MJ)		Average air temperature (ºC)		Average soil temperature (ºC)	
	Variety	Estima	Markies	Estima	Markies	Estima	Markies
	Planting date						
0-3 weeks	Early	323	327	17.4	17.8	16.2	16.8
	Mid	347	336	20.0	19.5	18.5	18.1
	Late	387	403	21.0	22.3	19.0	19.7
0-4 weeks	Early	429	425	17.9	17.9	17.0	17.0
	Mid	476	471	19.9	19.7	18.2	18.0
	Late	522	518	22.1	22.5	20.0	20.1
1-4 weeks	Early	314	297	18.3	18.2	17.1	17.2
	Mid	359	358	19.5	19.6	17.5	17.5
	Late	393	380	23.1	23.3	20.6	20.6

4.6.2. Emergence and ground cover

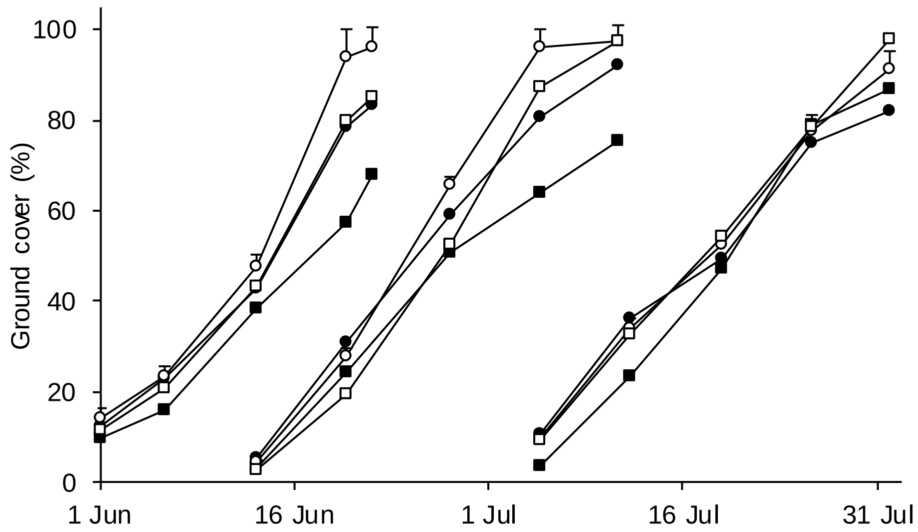
The interval from planting to emergence decreased as planting dates became later such that despite the intervals between planting dates differing, there was *c*. 20 days between the dates of 50 % emergence of consecutive planting dates (Table 48). Estima consistently emerged 2-3 days earlier than Markies and had closer to complete emergence (Table 48). With the exception of the Mid planting date, Estima emerged more uniformly than Markies, and at the Late planting date, emergence was particularly protracted in Markies (Table 48). Canopies took longest to reach 50 % ground cover at the Early planting date, but did not differ between the Mid and Late planting dates (Table 48). The canopies of Markies reached 50 % ground cover more rapidly than Estima and treatments with high rates of nitrogen reached 50 % ground cover more rapidly than those that received no nitrogen, but the differences were small in comparison to those between planting dates (Table 48).

Table 48. Effect of planting date, variety and nitrogen rate on the interval from planting to emergence, final emergence, the interval from 20 to 80 % emergence and the interval from 50 % emergence to 50 % ground cover in Expt 5

	Variety	Estima		Markies		
	Nitrogen	0	300	0	300	Mean
Interval from planting to 50 % emergence (days)						
Planting date	Early	35.8	35.7	39.5	39.1	37.5
	Mid	27.4	28.0	30.0	30.1	28.9
	Late	21.1	21.3	24.6	24.1	22.8
	S.E. (33 D.F.)		0.19			0.09
Final emergence (%)						
Planting date	Early	100.0	99.1	94.6	95.5	97.2
	Mid	99.1	98.2	96.4	90.2	96.0
	Late	97.3	94.6	88.2	86.6	91.7
	S.E. (33 D.F.)		-			-
Interval from 20 to 80 % emergence (days)						
Planting date	Early	3.5	3.3	4.7	5.1	4.2
	Mid	3.3	3.4	2.5	4.1	3.3
	Late	4.3	3.9	9.7	5.9	5.9
	S.E. (33 D.F.)		0.49			0.24
Interval from 50 % emergence to 50 % ground cover (days)						
Planting date	Early	26.8	25.5	25.6	23.6	25.4
	Mid	19.1	17.8	18.9	18.4	18.5
	Late	21.8	20.7	18.8	17.8	19.8
	S.E. (33 D.F.)		0.69			0.34

At the date of the Early and Mid harvests, Estima and the high nitrogen treatments had higher ground cover than Markies and those that received no nitrogen (Figure 33). At the Late harvest, there was no difference in ground cover between varieties, but the high nitrogen treatments again had higher ground cover (Figure 33).

Figure 33 Effect of planting date, variety and nitrogen rate on foliar ground cover in Expt 5. Estima 0 N, ●; Estima 300 N, ○; Markies 0 N, ■; Markies 300 N, □. Bars indicate S. E. based on 9 D.F.



4.6.3. Stolon architecture

Planting depth varied by *c.* 3 cm between planting dates but was similar for treatments within planting dates (Table 49). Consistent with the difference in planting depth, the mean stolon depth differed between planting dates (Table 49). Mean relative stolon depth was deeper when the planting depth was shallower across planting dates (Table 49). The relative stolon depth of Markies that received no nitrogen was consistently *c.* 3 % shallower than the high nitrogen treatments, but nitrogen had no effect on the mean relative stolon depth in Estima (Table 49). At the early planting date, mean stolon length was *c.* 2 cm longer in Markies than in Estima (Table 49). Mean stolon length was *c.* 50 % longer at the mid planting date than at the first planting date, but there was no difference between varieties (Table 49). At the late planting date, mean stolon length was on average similar to the early planting date, but was only *c.* 1 cm longer in Markies than in Estima (Table 49). These differences in mean stolon length between planting dates are difficult to explain, considering the differences in soil temperature and canopy development. While the increase in stolon length at the mid date compared to the early date was consistent with higher temperatures favouring stolon growth, it was either a similar or higher average temperature at the late date compared to the mid date, but stolon length was similar to the first date, which is inconsistent with the hypothesis. High nitrogen significantly increased stolon length compared to when no nitrogen was applied, but the difference was small (0.4 cm) and inconsistent between planting dates and varieties (Table 49). Considering the large difference between treatments in comparison to those used in practice, it is unlikely that nitrogen rate has any substantial influence on stolon length in these varieties.

Table 49. Effect of planting date, variety and nitrogen rate on planting depth, stolon depth, relative stolon depth and stolon length in Expt 5

	Variety	Estima		Markies		
	Nitrogen	0	300	0	300	Mean
Planting depth (cm)						
Planting date	Early	13.6	13.5	14.3	14.4	14.0
	Mid	12.9	12.9	13.4	12.2	12.9
	Late	15.9	15.8	15.7	16.1	15.9
	S.E. (33 D.F.)		0.75			0.37
Stolon depth (cm)						
Planting date	Early	11.0	10.8	11.0	11.5	11.1
	Mid	10.5	10.5	10.5	10.3	10.5
	Late	12.6	12.5	11.9	12.8	12.4
	S.E. (33 D.F.)		0.63			0.31
Relative stolon depth (%)						
Planting date	Early	81.1	80.6	77.3	80.1	79.8
	Mid	81.5	80.8	78.7	83.6	81.2
	Late	79.2	79.4	75.7	79.0	78.4
	S.E. (33 D.F.)		1.54			0.77
Stolon length (cm)						
Planting date	Early	3.5	4.1	5.3	6.4	4.8
	Mid	7.0	7.5	7.4	7.2	7.3
	Late	4.1	4.7	5.6	5.4	5.0
	S.E. (33 D.F.)		0.25			0.13

4.7. Experiment 6

4.7.1. Meteorology

Average air and soil temperatures in the 4 weeks after emergence increased with delay in planting, but there was relatively little difference between planting dates, particularly between the Mid and Late planting dates (Table 50). There were also periods at which at the same interval after emergence, soil temperatures were not higher for later planting dates than earlier planting dates (Figure 34). When considering soil temperatures from emergence to tuber initiation (from 0-3 weeks) differences between planting dates were similar to those from 0-4 weeks, but for 1-4 weeks (the period over which most stolon development occurred in Expt 3), differences between planting dates were smaller than from 0-4 weeks (Table 50). Unexpectedly, the amount of incident radiation from 0-4 weeks after emergence did not increase at later planting dates, and from 1-4 weeks, the Late planting date received the least incident radiation (Table 50).

Figure 34. Daily average soil temperatures from the date of 50 % of emergence for Estima at the Early (———), Mid (— — —) and Late (········) planting dates in Expt 6.

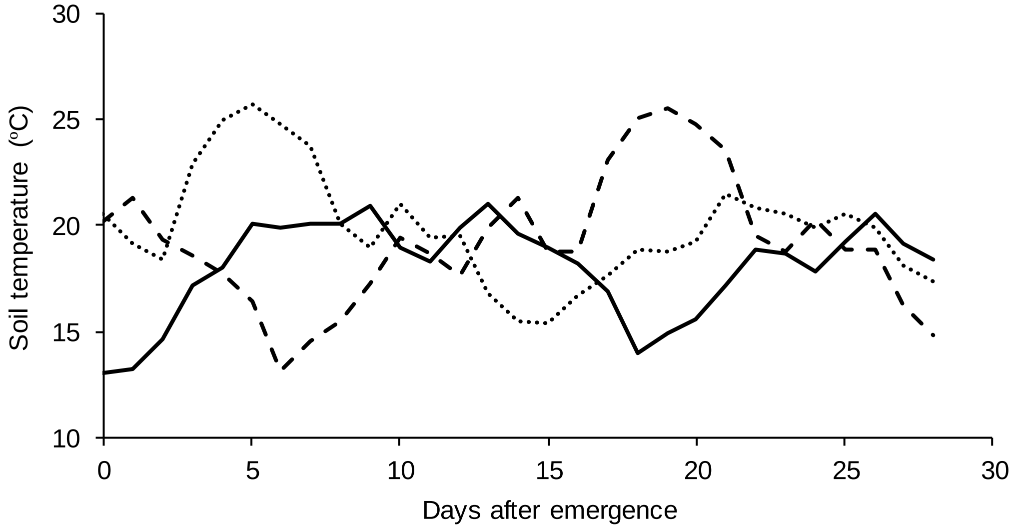


Table 50. Total incident radiation, average air temperatures and average soil temperatures from the date of 50 % emergence until 3 or 4 weeks later and from 1-4 weeks after emergence in Expt 6

		Radiation (MJ)		Average air temperature (ºC)		Average soil temperature (ºC)	
	Variety	Estima	Markies	Estima	Markies	Estima	Markies
	Planting date						
0-3 weeks	Early	392	373	16.4	16.4	17.8	17.7
	Mid	416	393	18.1	17.3	19.4	18.5
	Late	363	373	18.5	18.3	19.9	19.9
0-4 weeks	Early	546	493	16.8	16.2	18.0	17.4
	Mid	501	515	17.8	18.1	19.4	19.5
	Late	491	512	18.7	18.7	20.0	19.9
1-4 weeks	Early	390	390	16.9	16.9	18.5	18.5
	Mid	387	396	18.5	18.4	19.8	19.5
	Late	329	354	17.7	18.5	19.2	20.0

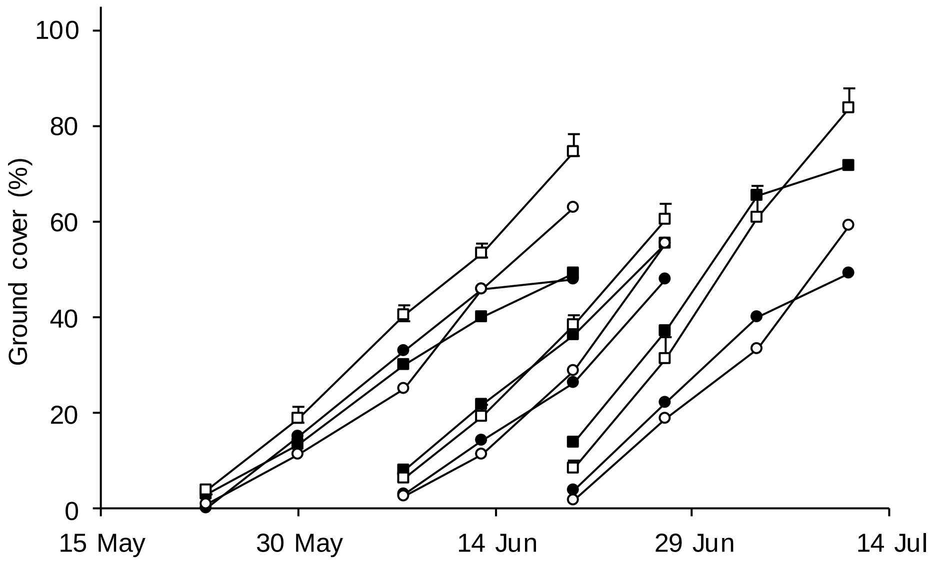
4.7.2. Emergence and ground cover

The interval from planting to emergence decreased as planting dates became later such that despite the intervals between planting dates differing, there was *c*. 12 days between the dates of 50 % emergence of consecutive planting dates (Table 51). Markies consistently emerged *c.* 3 days earlier than Estima (Table 51). Emergence was close to complete in all treatments except in Markies at the Late planting date where 5-10 % of plants failed to emerge (Table 51). The duration of emergence was similar between treatments, with the exception of at the Mid planting date, where Markies emerged more uniformly than Estima (Table 51). The interval between 50 % emergence and reaching 40 % ground cover was similar for the Early and Mid planting dates but was shorter for the Late planting date (Table 51). At the Early planting date, the canopy of Markies developed more rapidly than Estima, at the Mid planting date the varieties were similar and at the Late planting date, Markies developed more rapidly than Estima (Table 51; Figure 35). Nitrogen did not affect the interval from emergence to 40 % ground cover, but at the Early and Late planting dates, nitrogen increased ground cover at the last date that ground cover was recorded (Table 51; Figure 35).

Table 51. Effect of planting date, variety and nitrogen rate on the interval from planting to emergence, final emergence, the interval from 20 to 80 % emergence and the interval from 50 % emergence to 50 % ground cover in Expt 6

	Variety	Estima		Markies		
	Nitrogen	0	300	0	300	Mean
Interval from planting to 50 % emergence (days)						
Planting date	Early	51.3	51.5	48.1	47.6	49.6
	Mid	38.4	39.2	35.3	35.5	37.1
	Late	30.2	31.0	27.2	28.0	29.1
	S.E. (24 D.F.)		0.38			
Final emergence (%)						
Planting date	Early	99.3	99.3	99.3	99.3	99.3
	Mid	99.2	100.0	100.0	99.2	99.6
	Late	100.0	98.4	94.5	89.1	95.5
	S.E. (24 D.F.)		1.23			
Interval from 20 to 80 % emergence (days)						
Planting date	Early	4.7	6.0	5.0	3.7	4.8
	Mid	4.4	4.9	2.0	3.7	3.7
	Late	4.4	4.0	4.1	5.7	4.5
	S.E. (24 D.F.)		0.36			
Interval from emergence to 40 % ground cover (days)						
Planting date	Early	20.7	21.8	27.8	21.2	22.9
	Mid	23.4	20.7	22.8	21.9	22.1
	Late	18.7	19.5	15.5	16.7	17.6
	S.E. (24 D.F.)		1.18			

Figure 35 Effect of planting date, variety and nitrogen rate on foliar ground cover in Expt 6. Estima 0 N, ●; Estima 300 N, ○; Markies 0 N, ■; Markies 300 N, □. Bars indicate S. E. based on 9 D.F.



4.7.3. Stolon architecture

Planting depth varied by *c.* 3 cm between individual treatments, but these differences were not significant (Table 52). Mean stolon depth did not differ between planting dates but was slightly deeper in Markies than Estima (Table 52). Mean relative stolon depth was similar at the first two planting dates at *c.* 80 % of planting depth, but was *c.* 4 % shallower at the final planting date (Table 52). The mean relative stolon depth was *c.* 2 % deeper in Markies than Estima, but nitrogen had no effect (Table 52). At the Early planting date, mean stolon length was 5.4 cm and stolons were *c.* 1.5 cm longer in Markies than in Estima (Table 52). At the Mid planting date, stolons were *c.* 1 cm shorter than at the Early planting date and there was no difference between varieties (Table 52). Stolons were longest at the Late planting date at 6.1 cm and were *c.* 0.5 cm longer in Markies than Estima (Table 52). Considering the trend for soil and air temperatures to increase as the planting date became later, these results do not support the hypothesis that stolon length increases as temperature increases, however, the range in soil and air temperatures was relatively small in this experiment and larger differences in temperature might result in clearer effects. High nitrogen significantly increased stolon length compared to when no nitrogen was applied, but the difference was only 1 cm (Table 52). Considering the large difference between treatments in comparison to those used in practice, it is unlikely that nitrogen rate has any substantial influence on stolon length in these varieties.

Table 52. Effect of planting date, variety and nitrogen rate on planting depth, stolon depth, relative stolon depth and stolon length in Expt 6

	Variety	Estima		Markies		
	Nitrogen	0	300	0	300	Mean
Planting depth (cm)						
Planting date	Early	12.0	13.5	14.2	14.1	13.5
	Mid	14.0	13.8	13.5	12.7	13.5
	Late	13.7	15.1	15.0	14.7	14.6
	S.E. (24 D.F.)		0.52			0.36
Stolon depth (cm)						
Planting date	Early	9.4	10.7	11.5	11.5	10.8
	Mid	11.1	11.3	11.0	10.7	11.0
	Late	10.3	11.1	11.5	11.8	11.2
	S.E. (24 D.F.)		0.48			0.26
Relative stolon depth (%)						
Planting date	Early	80.0	78.7	81.2	81.5	80.3
	Mid	81.7	81.4	81.2	82.5	81.7
	Late	75.2	73.7	76.2	80.6	76.4
	S.E. (24 D.F.)		1.55			0.38
Stolon length (cm)						
Planting date	Early	4.3	5.1	5.4	6.8	5.4
	Mid	4.0	5.0	4.0	5.5	4.6
	Late	5.7	6.1	5.9	6.9	6.1
	S.E. (24 D.F.)		0.31			0.20

4.8. Experiment 7

The 10 and 15 cm planting depths were achieved satisfactorily, but the 20 and 25 cm depths were shallower than intended, particularly the 25 cm depth which was only 19 cm deep (Table 53). There were no differences in ground cover on either of the sampling dates, which was surprising since it was expected that deeper planting would delay emergence and consequently canopy development. All treatments maintained a full canopy until harvest (data not shown). Planting depth had no effect on the number of stems and tubers (Table 53) or on the tuber size distribution (data not shown).

Yield was numerically 6 t/ha lower at a planting depth of 19 cm than at 10 cm which was unexpected given the absence of any difference in canopy development, but consistent with previous planting depth experiments (e.g. Stalham *et al.* 2002, Stalham 2003). At the shallowest depth, 5 % of yield was visible at the surface and nearly all of these tubers were green, whereas at the deeper depths, < 1 % of yield was visible at the surface (Table 53). Including that found on the surface, 50 % of yield was found in the outer 5 cm of the ridge at 10 cm planting depth and while planting at 15 cm decreased this to *c.* 23 %, further increases in planting depth did not significantly decrease the proportion of yield close to the soil surface (Table 53). Tuber greening was most severe at the shallowest depth with 16 % of yield affected but increases in planting depth beyond 15 cm did not significantly decrease tuber greening (Table 53). Combined with the numerical differences in yield, the highest yields of non-green tubers occurred at the intermediate planting depths (Table 53). The majority of tuber greening occurred within 5 cm of the soil surface although the presence of some at greater depths indicated that cracks in the ridge allowed light to penetrate > 5 cm (Table 53).

Table 53. Effects of planting depth on components of yield and tuber greening in Expt 8

	Target planting depth (cm)‡				S.E.
	10	15	20	25	(12 or 9† D.F.)
Planting depth at harvest (cm)	9.8	14.6	17.6	18.8	0.41
Ground cover on June 15 (%)	25.4	35.0	33.4	34.4	8.50
Ground cover on June 24 (%)	66.6	73.6	67.8	72.7	7.23
Number of stems (000/ha)	86.3	108.8	98.5	96.0	7.14
Number of tubers (000/ha)	354	368	363	327	20.1
Total yield (t/ha)	62.6	60.7	59.6	56.5	1.86
Yield visible at soil surface (%)	5.1	0.7	0.1	0.3	0.78†
Yield in outer 5 cm of ridge (%)	45.0	23.4	21.7	17.4	2.42†
Green tubers (% of yield)	16.1	4.5	2.4	1.6	-
Green tubers (ANG)*	23.4	11.3	7.5	6.1	2.18
Dark green tubers (% of yield)	5.4	0.8	0.2	0.6	-
Dark green tubers (ANG)*	12.8	3.8	1.2	2.7	1.75
Light green tubers (% of yield)	10.3	3.7	2.2	1.0	-
Light green tubers (ANG)*	18.6	10.1	7.2	4.9	1.92
Yield of non-green tubers (t/ha)	52.5	57.9	58.2	55.6	1.69
Green tubers on surface (% of yield)	4.4	0.8	0.1	0.2	-
Green tubers on surface (ANG)*	11.9	4.2	0.7	1.8	1.42†
Green tubers in top 5 cm (% of yield)	10.3	2.7	2.0	0.5	-
Green tubers in top 5 cm (ANG)*	18.4	8.5	6.5	3.4	2.34†
Green tubers below 5 cm (% of yield)	0.7	1.1	0.0	0.4	-
Green tubers below 5 cm (ANG)*	2.3	3.1	0.0	2.3	2.13†

‡ For actual planting depth, see table in table. † One replicate was excluded from these analyses.
* ANG indicates angular transformed data.

4.8.1. Stolon architecture and tuber mapping

Tubers were only mapped from one plot of the 15 cm treatment. Mean stolon length was 5.8 cm, almost identical to that observed for Markies in Expt 1. Mean stolon depth was deeper than in Expt 1 at 13.1 cm but this was associated with a deeper planting depth while the relative stolon depth was very similar at 76 %. Despite the mean stolon depth being *c.* 3 cm deeper than in Expt 1, the tubers were only 1.2 cm deeper compared to the third harvest of Expt 1.

4.8.2. Machine-planted strips

As in Expt 7, the 10 and 15 cm treatments were achieved satisfactorily, but the deeper treatments were shallower than intended (Table 54). Due to the lack of replication no firm conclusions can be drawn, but the same trends were apparent as in the planting depth experiment with yields being numerically lower at deeper planting depths, tuber greening not decreasing beyond 15 cm and optimum yields of non-green tubers being achieved at the intermediate depths (Table 54).

Table 54. Effect of planting depth on yield and greening in unreplicated, machine planted strips of Innovator

		Target planting depth (cm)†			
		10	15	20	25
Planting depth at harvest (cm)	Mean	10.2	14.9	17.4	21.3
	S.D.	1.01	0.46	1.22	1.96
Total yield (t/ha)	Mean	60.2	57.7	55.3	54.9
	S.D.	3.23	2.50	3.39	2.45
Green tubers (% of yield)	Mean	15.0	7.9	3.0	2.6
	S.D.	4.23	6.65	2.16	3.17
Yield of non-green tubers (t/ha)	Mean	51.2	53.2	53.6	53.4
	S.D.	5.33	4.66	2.11	0.61

† For actual depths, see data in table.

4.9. Experiment 8

4.9.1. Stolon architecture and tuber mapping

The planting depth of the two plots where stolon architecture was measured were *c.* 17 cm for the intended depth of 15 cm and 23 cm for the intended depth of 20 cm (Table 55). Mean stolon length was *c.* 7 cm in both treatments (Table 55). Mean stolon depth was deeper at the deeper planting depth, but the mean relative stolon depths were both *c.* 70 %, indicating that deeper planting increased the distance between nodes, but did not influence the relative distance between them (Table 55). Consequently, the absolute difference in tuber depth was less than the difference in planting depth (Figure 36, Table 55). As in Expts 1-3, the average distance from the centre of the plant to the stolon and apical ends of tubers was consistent with the average stolon length and stolon plus tuber length, respectively (Table 55).

Figure 36. Ridge profile and tuber position in the (a) shallow planting depth and (b) deep planting depth, for high hood pressure and ridge bed shape treatments only in Expt 8. Green tubers indicate those with any tuber greening. See Table 55 for achieved planting depths. Scale bar = 10 cm.

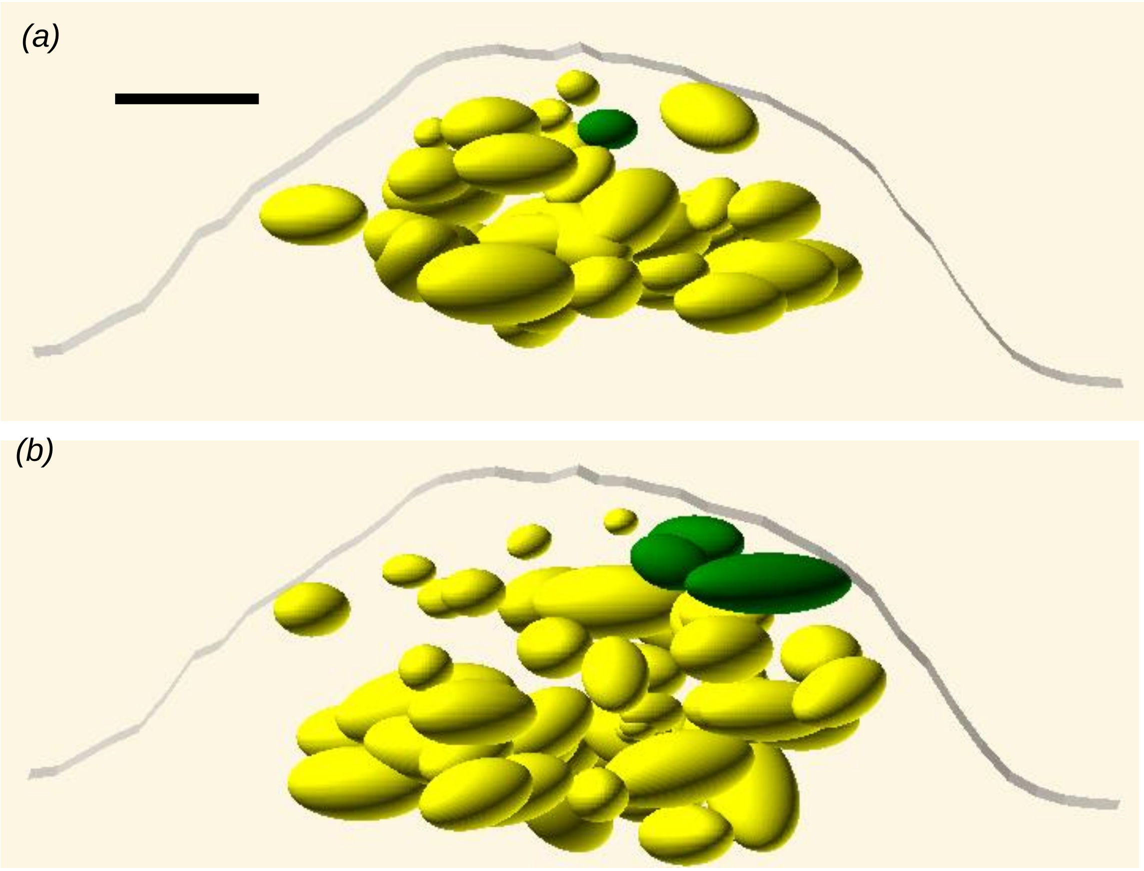


Table 55. Stolon architecture and tuber mapping for two plots at the two planting depths, for high hood pressure and ridge bed shape treatments only in Expt 8

	Intended planting depth			
	15		20	
	Mean	S.E. (2 D.F.)	Mean	S.E. (2 D.F.)
Achieved planting depth (cm)	16.8	0.95	23.3	0.42
Mean stolon length (cm)	6.7	1.13	7.7	0.85
Mean stolon depth (cm)	11.4	1.35	15.8	0.50
Mean relative stolon depth (%)	69.3	6.85	69.6	3.59
Distance to stolon end (cm)	6.8	1.11	8.1	0.47
Distance to apical end (cm)	14.4	1.00	15.0	0.88
Tuber plus stolon length (cm)	15.3	0.97	15.9	1.42
Mean tuber depth (cm)	10.6	1.59	14.2	0.40

4.9.2. Planting depth and soil properties

The 20 cm planting depth was achieved as planned, but the 15 cm planting depth was *c.* 2 cm deeper than intended (Table 56). Neither hood pressure nor ridge shape had any effect on the achieved planting depth (Table 56). Bulk density of the top 5 cm and the maximum depth and width of cracks were unaffected by any treatment, although numerically, cracks were wider and deeper in the ridge than in the semi-bed (Table 56).

Table 56. Achieved planting depth, soil bulk density and maximum depth and width of soil cracks in Expt 8

	Depth		Pressure		Shape		S.E.
	15	20	High	Low	Ridge	Semi-bed	(14 D.F.)
Achieved planting depth	17.3	20.6	19.3	18.6	18.8	19.1	0.42
Soil bulk density (g/cm^3)	1.13	1.13	1.14	1.12	1.12	1.13	0.013
Maximum crack width (cm)	3.3	3.6	3.5	3.3	4.1	2.8	0.49
Maximum crack depth (cm)	6.8	6.2	6.5	6.6	7.4	5.7	0.70

4.9.3. Number of stems, number of tubers, yield and grading

There was no effect of any treatment on the number of plants, main stems or tubers (Table 57). The number of secondary stems was high, but was unaffected by any treatment (Table 57). Yield was *c.* 6 t/ha lower in the semi-bed than in the ridge and numerically lower at the deeper than at the shallower planting depth, but hood pressure had no effect (Table 57). The effect of planting depth was as expected from previous work, and the difference between ridge shapes could potentially have been caused by slower emergence in the semi-bed. Consistent with the difference in yield, mean tuber size was larger in the ridge than the semi-bed (Table 57). Variation in tuber size was greater when high hood pressure was used compared to when low pressure was used, but it is uncertain what mechanism could account for this effect (Table 57).

Table 57. Effects of planting depth, hood pressure and ridge shape on components of yield in Expt 8

	Actual depth (cm)		Pressure		Shape		S.E.
	17.3	20.6	High	Low	Ridge	Semi-bed	(14 D.F.)
Plant population (000/ha)	27.4	28.3	27.7	28	28.6	27.1	1.01
Main stems (000/ha)	72.3	80.8	76.9	76.3	78.4	74.8	2.88
Secondary stems (000/ha)	64.4	59.9	60.2	64.1	63.5	60.8	7.29
Tuber population (000/ha)	477	491	494	474	473	495	15.8
Yield (t/ha)	65.3	60.5	62.0	63.8	65.8	60.0	1.91
Mean tuber size (mm)	57.5	56.8	57.2	57.1	58.5	55.8	0.77
COV of tuber size (mm)	15.4	16.3	16.7	15.0	15.9	15.8	0.49

4.9.4. Tuber position and tuber greening

The semi-bed had approximately half the amount of yield present in the flank, consistent with that shape having half the amount of flank (Table 58). Very little yield (*c.* 0.2 %) was exposed at the surface and *c.* 4 % of yield was found in the top 2.5 cm. The amount of yield in either location was unaffected by any treatment (Table 58). The shallower planting depth had *c.* 50 % more yield present at 2.5-5 cm than the deeper planting depth but the other treatments had no effect on the amount of yield in this location (Table 58). Overall > 80 % of yield had > 5 cm of soil coverage (Table 58).

Relatively little yield was affected by tuber greening in any treatment (Table 58). Planting depth did not have a significant effect on tuber greening, but high hood pressure had more greening compared to low pressure, and the ridge had more tuber greening than the semi-bed (Table 58). High hood pressure caused a greater proportion of yield in the flanks and in the top 0-2.5 cm to be affected by tuber greening compared to when low hood pressure was applied (Table 58), and this may have been caused by increased cracking of the ridge. The difference in tuber greening between the ridge shape treatments was consistent with the difference in the amount of yield present in the flanks (Table 58). The majority of tuber greening occurred within 5 cm of the soil surface although the presence of some tuber greening at greater depths indicated that cracks in the ridge allowed light to penetrate > 5 cm, consistent with the maximum depth of cracks present (Tables 56 and 58). Similar proportions of the green tubers were light and dark coloured in all treatments and *c.* 10 % of the yield affected by tuber greening was of tubers < 40 mm (Table 58).

Table 58. Effects of planting depth, hood pressure and ridge shape on the amount of yield and tuber greening present in different parts of the ridge, and the overall amount of tuber greening in Expt 8

	Actual depth (cm)		Pressure		Shape		S.E. (14 D.F.)
	17.3	20.6	High	Low	Ridge	Semi-bed	
Yield (%)							
Flanks	6.0	4.3	5.4	4.9	7.2	3.0	0.75
Surface	0.2	0.2	0.2	0.2	0.4	0.1	0.20
0-2.5 cm	4.3	3.7	4.5	3.5	3.6	4.5	0.43
2.5-5 cm	10.4	6.7	9.0	8.1	8.1	9.0	0.81
> 5 cm	79.2	85.1	80.9	83.5	80.8	83.5	1.10
Tuber greening (%)							
Flanks	1.7	1.2	2.0	0.9	2.3	0.6	0.40
Surface	0.2	0.2	0.2	0.2	0.4	0.1	0.20
0-2.5 cm	1.4	1.4	2.2	0.7	1.5	1.4	0.32
2.5-5 cm	1.8	0.5	1.1	1.2	1.7	0.6	0.44
> 5 cm	0.3	0.2	0.2	0.4	0.3	0.2	0.12
< 40 mm	0.6	0.4	0.6	0.4	0.6	0.4	0.12
Light green	2.7	1.7	2.9	1.5	2.9	1.4	0.62
Dark green	2.2	1.5	2.3	1.5	2.7	1.0	0.41
Overall	5.5	3.6	5.8	3.3	6.2	2.9	0.75

4.10. Commercial crops

4.10.1. Stolon architecture

Mean stolon length ranged from *c.* 3 to 12 cm between sites and was highest in the Workhouse crop of Jelly and shortest in the Moores Belt crop of King Edward (Table 59). This range was very similar to that reported by Kratzke & Palta (1992) who examined eight North American varieties over two years, and to the range observed in Expts 1-3. At most sites, the maximum stolon length was < 20 cm (Figure 37). Stolons > 30 cm were uncommon and the longest stolon occurred in Saphire at Brandon 2, being *c.* 47 cm (Figure 37). There was no correlation between planting depth and mean stolon length (Table 59).

Mean stolon depth ranged from *c*. 9 to 16 cm, being shallowest in the Cricket Field crop of Markies and deepest in the Chatteris 1 crop of King Edward (Table 59). Mean stolon depth was positively correlated with planting depth (R^2 = 0.61, p = < 0.001; data not shown) but planting depth had very little effect on the proportion of stolons < 5 cm from the surface (R^2 = 0.12, p = < 0.05.; data not shown) meaning that deeper planting did not prevent tubers from forming close to the surface. Relative stolon depths ranged from *c.* 55 to 80 % which was a greater range than seen in Expts 1-3, but the majority of crops were within the range of *c.* 70 to 80 %, similar to in Expts 1-3 (Table 59). The four crops of Markies had the shallowest relative stolon depths and this was due to very few stolons being present at the base of the stem and at Aylmerton and High Hill 16, was associated with the bases of some stems being necrotic.

Table 59. Mean stolon length and depth in the commercial crops

Site	Variety	Mean stolon length (cm)		Mean stolon depth (cm)		Mean relative stolon depth (%)		Planting depth (cm)	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Gravelly Bank	Innovator	5.8	0.31	11.9	2.28	79	4.3	15.1	2.06
Hinstock	Estima	5.3	0.68	9.3	0.93	76	2.1	12.1	1.14
Weavers	Estima	5.7	0.42	15.8	1.26	72	3.2	21.8	0.92
Brandon Rd South	Jelly	11.2	1.79	10.9	0.91	75	0.8	14.5	1.18
Brooke	Jelly	6.6	0.50	12.5	0.20	69	4.8	18.3	1.26
Hospital Grass 1	Jelly	6.0	0.44	15.8	0.75	77	3.0	20.4	0.97
Moores Belt 1	Jelly	7.4	0.77	12.1	0.54	57	1.6	19.2	0.74
Workhouse	Jelly	11.6	0.67	13.4	0.78	81	1.4	16.5	1.21
18 Acres	King Edward	6.6	0.24	12.3	0.29	73	0.9	17.0	0.26
Bishop’s Frome	King Edward	9.4	0.56	14.4	1.05	81	4.3	18.2	0.84
Chatteris 1	King Edward	6.8	0.31	16.1	0.67	77	1.9	20.9	0.92
Moores Belt 2	King Edward	3.4	0.49	14.0	0.74	75	1.3	18.8	0.55
Sculfers	King Edward	3.4	0.51	12.6	0.98	74	3.9	17.0	0.55
Brandon 1	Marfona	10.8	0.52	15.7	1.38	81	2.3	19.4	1.49
Middle and Drain	Marfona	7.2	0.88	9.6	1.14	70	4.5	13.8	1.30
Pestels	Marfona	8.2	1.53	13.6	1.75	71	7.8	19.5	2.15
Wheelwrights	Marfona	9.1	0.80	13.1	0.30	77	2.4	17.2	0.48
F22	Maris Piper	6.3	0.32	13.8	0.92	65	5.6	21.7	1.39
F23	Maris Piper	4.8	1.15	14.1	0.70	69	3.3	20.4	1.64
F35	Maris Piper	4.4	0.17	12.8	0.83	74	2.0	17.6	0.59
Home Piece	Maris Piper	4.9	0.69	9.4	0.52	69	4.2	13.7	0.65
Aylmerton	Markies	6.8	0.43	10.4	1.29	55	9.1	18.9	0.70
Chatteris 2	Markies	5.9	0.55	14.1	0.80	65	3.2	22.0	0.85
Cricket Field	Markies	6.2	1.64	8.8	1.81	52	7.8	16.5	1.51
High Hill 16	Markies	5.4	0.66	11.9	0.86	61	3.4	19.5	1.01
Beezlings	Melody	4.5	0.25	15.1	0.77	72	1.7	20.8	0.85
Bob Cole’s	Melody	8.2	1.79	13.0	0.90	74	4.2	17.5	0.69
Hospital Grass 2	Melody	4.8	0.42	13.2	0.64	72	2.4	18.4	1.03
Brandon 2	Saphire	10.9	2.15	13.8	1.24	72	1.4	19.2	1.58

Figure 37*a*. Relationship between stolon length and relative stolon depth in the commercial crops.

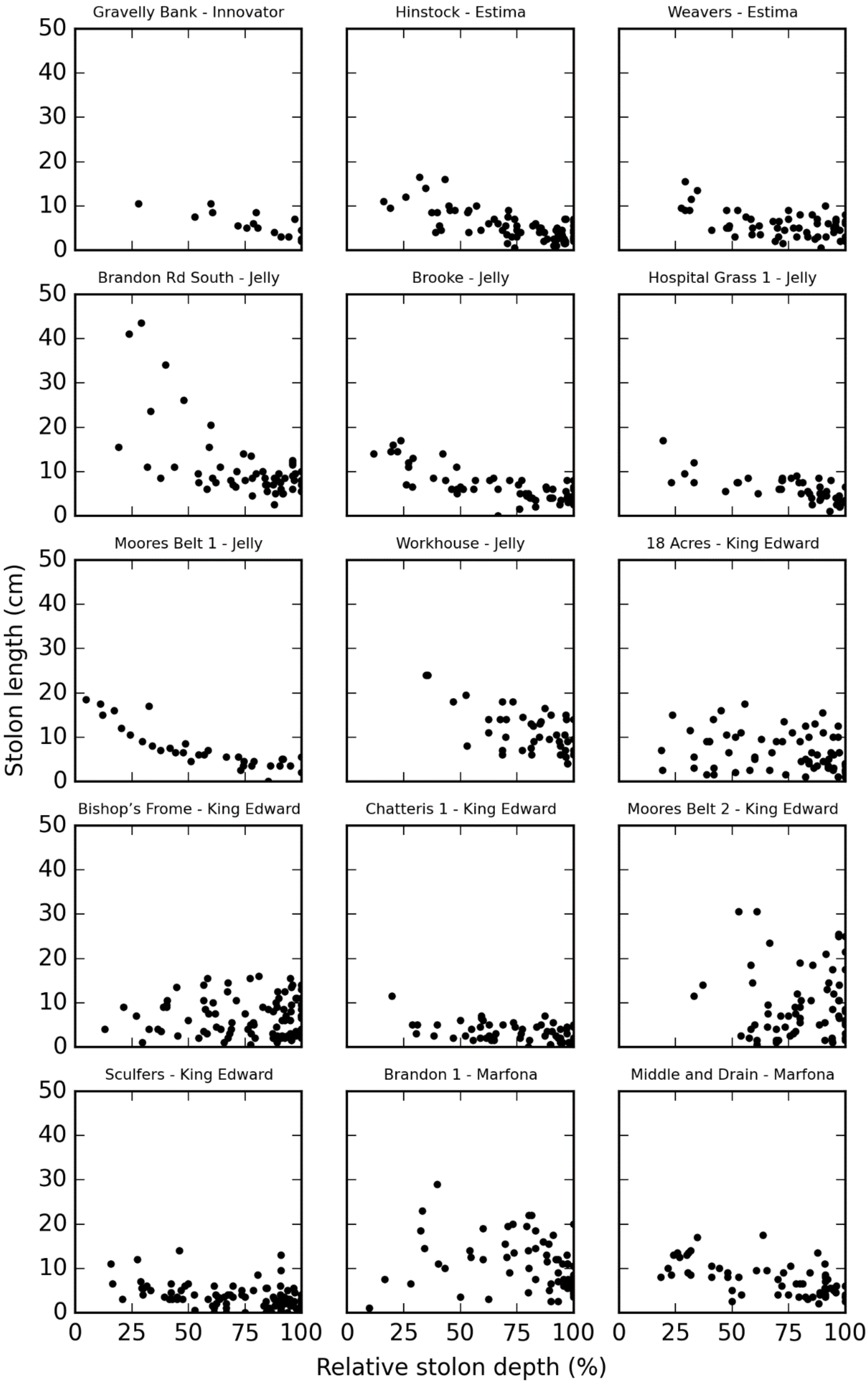
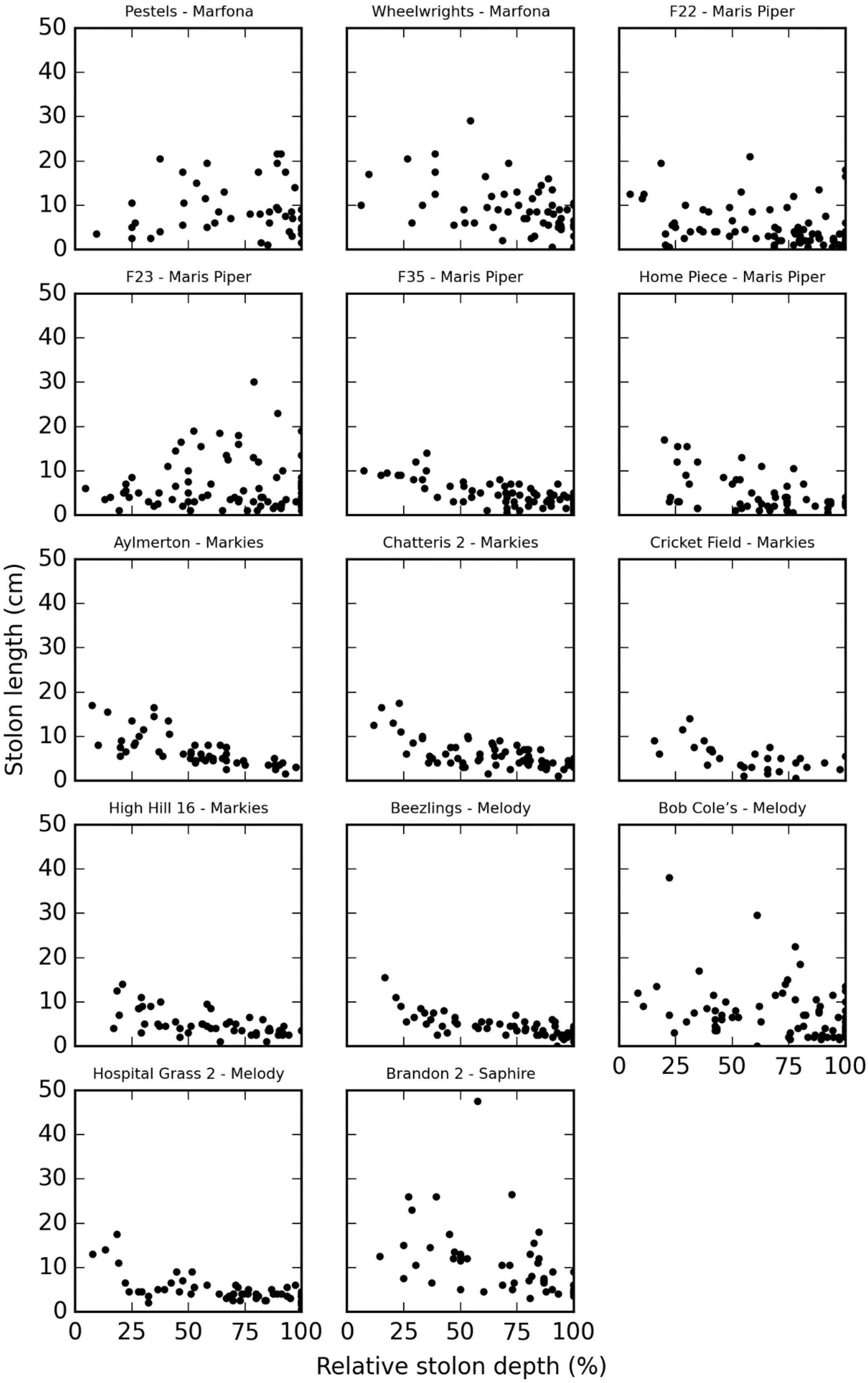


Figure 37*b*. Relationship between stolon length and relative stolon depth in the commercial crops.



4.10.2. Tuber mapping

Tubers were furthest from the centre of plants at the three Brandon sites, Pestels and Workhouse, and closest at Sculfers, Weavers, Chatteris 2 and Beezlings (Table 63), although this was mainly due to earlier sampling of these crops when tubers were relatively small. As in Expts 1-3, the distance to the stolon end of the tubers was strongly correlated with mean stolon length and the distance to the apical end of the tubers was strongly correlated with the mean stolon length plus tuber length (Figure 38, Table 62). This demonstrates that if the mean stolon length can be established then the horizontal position of tubers could be predicted. There was a moderate correlation (Table 60) between mean tuber depth and mean stolon depth, and also between mean planting depth and mean tuber depth (Table 60). Accounting for differences in tuber size between sites by considering mean tuber length, explained 66 % of the variation in tuber depth (Table 60), suggesting that any varietal differences in stolon architecture were of minor importance compared to planting depth and tuber size. Tuber height would be a more relevant variate than tuber length, but was not measured at some sites in 2015, and at sites where both were measured, there was a very strong correlation between the two (R^2 = 0.95, data not shown).

Tubers were on average *c.* 3 cm shallower than the stolons as would be expected due to the stolon being attached to the centre of the tuber. The difference was more pronounced at Brandon 1 with the mean tuber depth *c.* 7 cm shallower than mean stolon depth and this was associated with the tubers being large and *c.* 60 % of them being orientated > ± 10º, with angled tubers on average orientated at *c.* 50º (Table 63).

Table 60. Relationships between the mean stolon depth (SDP, cm), mean planting depth (PDP, cm), mean tuber length (TLN, cm) and the mean tuber depth (TDP, cm) in the commercial crops. TDP = *m* SDP + *c* or TDP = *m* PDP + *n* TLN + *c*

SDP	PDP	TLN	*m*	S.E.	*n*	S.E.	*c*	S.E.	*P*	R^2
●			0.80	0.141	n.a.	n.a.	-0.5	1.84	< 0.001	0.53
	●		0.64	0.113	n.a.	n.a.	-1.6	2.07	< 0.001	0.52
	●	●	0.57	0.098	-0.48	0.139	2.6	2.15	< 0.001	0.66

Table 61. Mean position of tubers in the commercial crops

Site	Variety	Mean distance to stolon end (cm)		Mean distance to apical end (cm)		Depth to top of tuber (cm)	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
Gravelly Bank	Innovator	7.7	0.65	12.6	1.45	7.3	2.63
Hinstock	Estima	5.7	0.67	10.5	0.44	7.1	0.51
Weavers	Estima	6.7	0.30	9.9	0.43	13.7	1.11
Brandon Rd South	Jelly	10.8	1.69	18.2	1.69	8.1	0.86
Brooke	Jelly	7.1	0.28	13.5	0.28	9.8	0.76
Hospital Grass 1	Jelly	6.3	0.71	14.0	0.33	10.5	1.23
Moores Belt 1	Jelly	7.3	0.65	13.2	0.57	9.5	0.41
Workhouse	Jelly	10.8	0.58	18.2	0.95	9.1	0.61
18 Acres	King Edward	7.6	0.27	12.5	0.42	9.0	0.18
Chatteris 1	King Edward	6.9	0.38	10.0	0.46	13.4	0.92
Bishop’s Frome	King Edward	9.5	0.25	12.8	0.40	10.7	0.43
Moores Belt 2	King Edward	4.3	0.50	9.1	0.40	11.8	1.23
Sculfers	King Edward	5.1	0.24	8.3	0.52	10.6	0.73
Brandon 1	Marfona	11.1	0.66	17.6	0.97	8.8	1.92
Middle and Drain	Marfona	7.1	1.14	12.5	0.89	5.6	0.63
Pestels	Marfona	10.1	0.61	16.2	0.54	8.9	1.10
Wheelwrights	Marfona	9.5	1.17	15.6	0.96	8.7	0.55
F22	Maris Piper	6.0	0.45	13.0	0.60	9.1	0.73
F23	Maris Piper	5.6	0.88	10.7	0.75	11.6	0.82
F35	Maris Piper	5.5	0.15	9.5	0.17	10.9	0.85
Home Piece	Maris Piper	5.8	0.42	12.8	0.52	7.1	0.55
Aylmerton	Markies	7.3	0.68	13.1	0.47	9.0	0.79
Chatteris 2	Markies	6.5	0.65	9.9	0.60	13.6	0.87
Cricket field	Markies	7.2	0.69	14.0	1.79	6.1	2.14
High Hill 16	Markies	6.1	0.48	13.2	0.73	10.9	0.62
Beezlings	Melody	4.9	0.32	8.7	0.30	14.1	0.70
Bob Cole’s	Melody	8.1	1.72	13.0	1.84	10.1	0.69
Hospital Grass 2	Melody	6.0	0.24	12.7	0.66	10.0	0.44
Brandon 2	Saphire	11.2	1.73	17.6	2.25	11.5	1.10

Figure 38. Relationships between distance to the stolon end of tubers and stolon length in the commercial crops, ●; and between distance to the apical end of tubers and stolon

length plus tuber length, O in the commercial crops. Line is 1:1 relationship. Relationships for each dataset are given in Table 62.

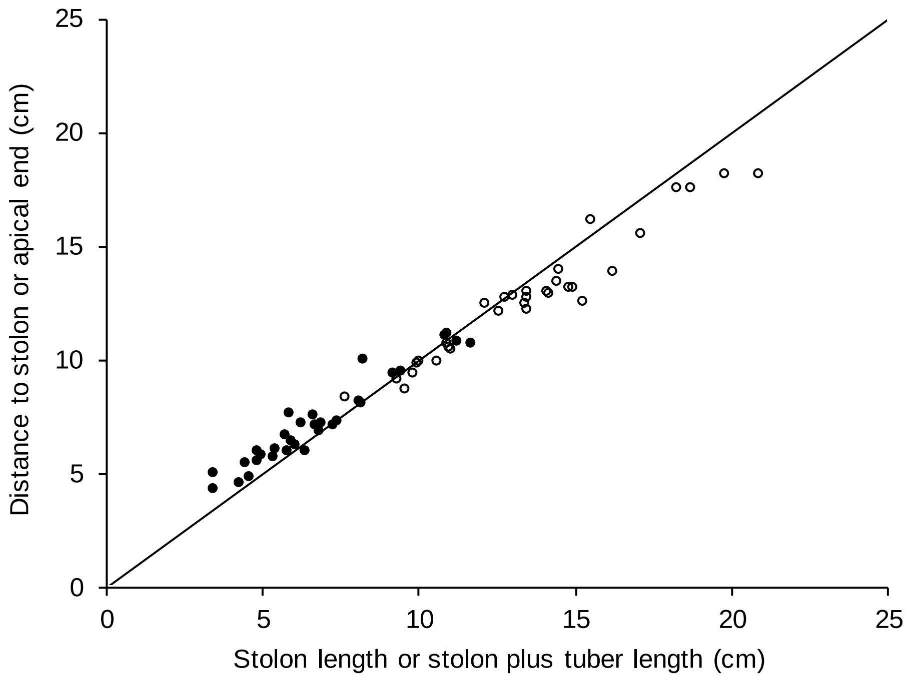


Table 62. Relationships between position of the stolon or apical end of tubers (POS, cm) and stolon length or stolon length plus tuber length (LEN, cm) as shown in Figure 38: slope of relationship (*m*) and S.E., constant of relationship (*c*) and S.E., significance of relationship (*F* prob) and strength of relationship (R^2). POS = *m* LEN + *c*

Position	*m*	S.E.	*c*	S.E.	*F* prob.	R^2
Stolon	0.838	0.0439	1.66	0.316	< 0.001	0.93
Apical	0.828	0.0376	1.59	0.528	< 0.001	0.95

Table 63. Tuber orientation in the commercial crops (some sites are omitted due to the variates being undetermined)

Site	Variety	Tubers with a horizontal angle > ±10º (%)		Average tuber orientation angle (º)		Average tuber orientation angle of tubers > ±10º (º)	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
Gravelly Bank	Innovator	38	12.5	19	12.2	45	17.5
Hinstock	Estima	34	5.8	9	1.5	27	3.8
Weavers	Estima	10	0.6	4	2.8	40	26.2
Brandon Rd South	Jelly	58	6.4	16	4.2	26	3.7
Brooke	Jelly	41	7.4	11	0.3	25	3.3
Hospital Grass 1	Jelly	37	11.6	2	1.5	19	13.2
Moores Belt 1	Jelly	21	9.6	4	5.6	28	21.3
18 Acres	King Edward	26	2.6	5	1.4	18	4.9
Bishop’s Frome	King Edward	15	4.8	7	2.9	48	8.0
Moores Belt 2	King Edward	13	8.7	6	4.2	46	8.7
Sculfers	King Edward	12	0.7	4	0.8	35	9.6
Brandon 1	Marfona	64	3.8	29	3.4	45	4.0
Middle and Drain	Marfona	33	3.9	9	2.1	27	4.0
Pestels	Marfona	57	5.8	19	3.3	32	2.9
F22	Maris Piper	2	1.2	-1	0.4	-37	5.3
F23	Maris Piper	24	8.6	5	1.6	17	2.7
Aylmerton	Markies	24	8.2	1	1.6	3	5.2
Chatteris 2	Markies	14	1.9	0	2.2	0	13.5
Cricket Field	Markies	34	12.6	1	0.9	7	4.4
High Hill 16	Markies	49	4.6	11	3.2	21	5.0
Beezlings	Melody	15	8.8	0	1.9	4	13.7
Bob Cole’s	Melody	27	9.1	2	1.0	9	2.8
Hospital Grass 2	Melody	15	4.1	1	1.4	4	11.1
Brandon 2	Saphire	17	4.8	5	3.0	28	21.3

Ridge profiles varied considerably between sites with some being trapezoid with a *c.* 30 cm flat top (e.g. F35) whereas others were more triangular (e.g. Bishop’s Frome, Figure 39). The ridges of crops grown on three-row beds (e.g. Brandon crops) had a relatively shallow profile compared to those grown on two-row ridge systems (Figure 39). Of the four crops grown on three-row ridge systems, the middle row had a similar profile to the outer row at Sculfers and High Hill 16, but at Pestels and Bob Cole’s it was considerably smaller (Figure 39). The apical ends of tubers were generally well-accommodated within the ridge profiles, but tuber greening could be expected to be higher at those sites where tubers were shallower or the apical ends were closer to the edge of the ridge profile (Figure 39).

Figure 39. Ridge profiles in the commercial crops. Inset boxplots show the position of the apical ends of tubers, positioned at the average tuber depth and with a height twice the standard deviation of tuber height. Dotted lines represent ridge profiles from the central row at three-row sites.

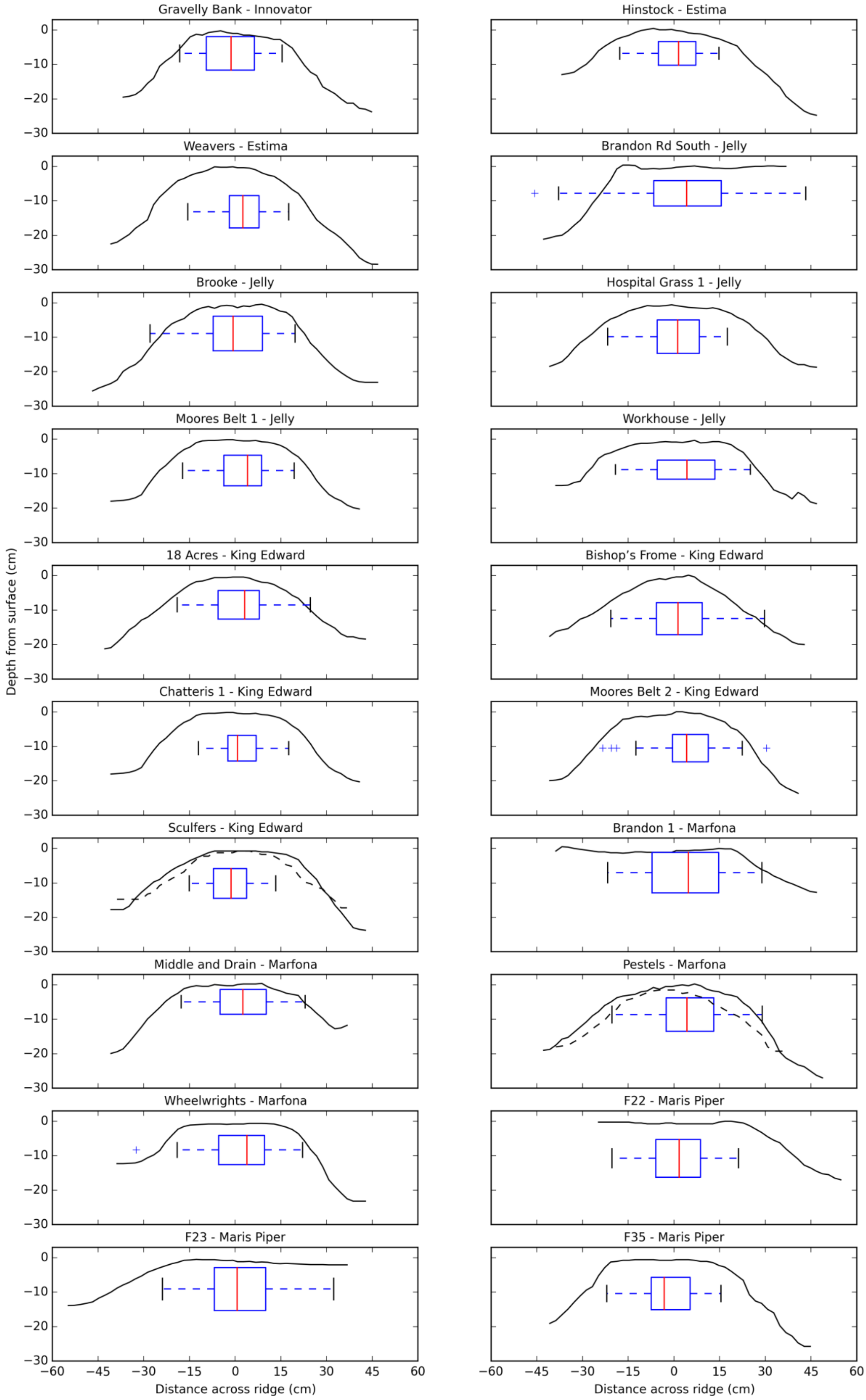
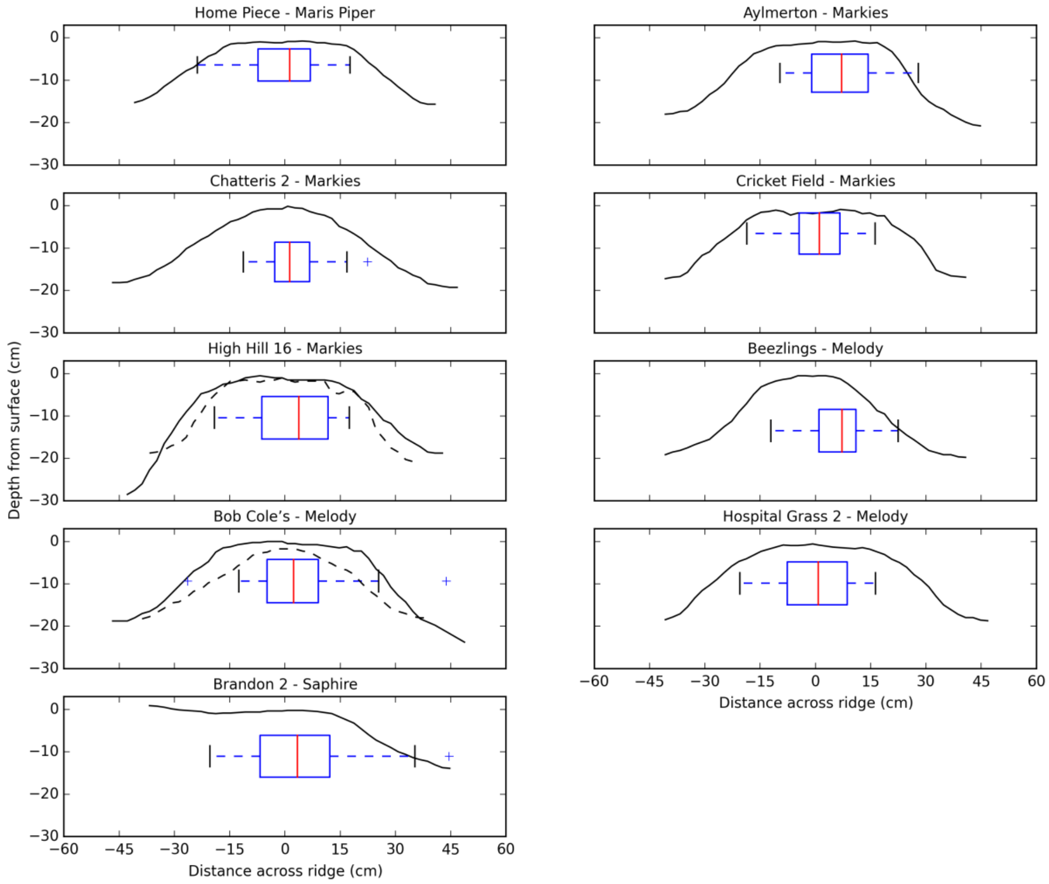


Figure 39 continued



4.10.3. Number of stems, number of tubers, yield and grading

Plant populations ranged from *c.* 18,000 to 41,000/ha and were lowest in Southery and highest in Aylmerton (Table 64). Stem populations ranged from *c.* 70,000 to 220,000/ha and were lowest in Brandon 2 and highest in Sculfers (Table 64). Tuber populations ranged from *c.* 260,000 to 1,060,000/ha and were lowest in Papplewick Ridge and highest in Sculfers (Table 64).

Table 64. Number of plants, stems and tubers in the commercial crops

		Number of plants (000/ha)		Number of stems (000/ha)		Number of tubers (000/ha)	
Site	Variety	Mean	S.E.	Mean	S.E.	Mean	S.E.
Hinstock	Estima	35.3	2.03	130	6.5	537	30.3
Weavers	Estima	27.4	0.82	113	7.5	508	24.7
50 Acres	Innovator	39.5	1.46	101	9.6	360	12.7
Papplewick Bed	Innovator	38.9	1.11	165	2.1	341	11.7
Papplewick Ridge	Innovator	31.1	1.65	106	8.2	263	14.2
Brandon Rd South	Jelly	28.0	1.54	114	9.1	433	16.1
Brooke	Jelly	23.7	0.82	115	7.8	433	10.5
Icklingham	Jelly	32.8	1.88	123	8.0	503	30.9
Workhouse	Jelly	24.4	0.38	78	3.1	424	16.6
18 Acres	King Edward	26.1	0.61	90	1.7	671	17.2
Brook	King Edward	28.0	1.54	80	4.3	553	37.7
Sculfers	King Edward	34.8	0.81	219	11.1	1058	56.6
Brandon 1	Marfona	32.2	0.61	101	5.2	422	17.9
Wheelwrights	Marfona	n.d.	n.d.	83	2.4	372	16.7
F22	Maris Piper	31.1	1.11	122	6.3	433	22.1
F23	Maris Piper	37.2	2.00	161	10.5	673	42.3
F35	Maris Piper	20.8	0.51	83	3.4	489	14.7
Home Piece	Maris Piper	30.5	0.79	95	6.0	738	21.4
Southery	Maris Piper	17.8	1.41	103	3.5	449	24.3
Aylmerton	Markies	41.3	1.22	170	11.1	610	31.7
High Hill 16	Markies	30.8	1.49	91	6.7	458	29.4
Stackyard	Markies	40.1	1.88	131	5.3	460	17.7
Beezlings	Melody	29.8	1.12	105	6.7	444	28.5
Bob Cole's	Melody	33.6	2.12	92	3.6	494	13.2
Brandon 2	Saphire	32.8	0.94	74	5.8	497	17.3

Yields ranged from *c.* 39 t/ha at Brook to *c.* 92 t/ha at High Hill 16 (Table 65) and were on average 66 t/ha, considerably above the estimated average UK yield for the three years of *c.* 45 t/ha. Mean tuber size was close to the optimum of 62 mm for marketable yield (45-80 mm) in the majority of the packing crops, but was lower at Hinstock and in the three crops of King Edward (Table 65). There was substantial range in the COV of tuber size, which at the optimum mean tuber size equated to *c.* 98 % of yield being marketable at Brandon 2 compared with *c.* 86 % at Weavers (Table 65). Combined, marketable yield ranged from 28 to 78 t/ha or 72 to 97 % of total yield and was on average 57.8 t/ha or 87 % of total yield (data not shown).

Table 65. Yield, mean tuber size and COV of tuber size in the commercial crops

Site	Variety	Yield (t/ha)		Mean tuber size (mm)		COV of tuber size (%)	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
Hinstock	Estima	58.3	2.33	54.2	0.91	17.0	0.43
Weavers	Estima	73.6	2.52	63.9	0.76	19.0	0.76
50 Acres	Innovator	68.6	6.63	63.2	1.53	16.3	0.54
Papplewick Bed	Innovator	60.2	2.58	63.7	1.13	17.1	0.46
Papplewick Ridge	Innovator	58.4	2.76	67.0	1.22	18.9	0.95
Brandon Rd South	Jelly	72.6	3.69	62.6	0.57	14.1	0.70
Brooke	Jelly	68.6	2.11	65.6	0.77	17.8	0.51
Icklingham	Jelly	83.3	2.52	61.8	0.94	15.0	0.57
Workhouse	Jelly	59.5	1.52	59.9	0.87	14.1	0.30
18 Acres	King Edward	49.1	1.45	50.4	0.72	17.1	0.71
Brook	King Edward	38.8	2.12	49.7	0.89	16.6	0.71
Sculfers	King Edward	79.7	2.44	55.7	0.82	21.0	0.71
Brandon 1	Marfona	67.0	1.34	61.9	0.55	14.9	1.03
Wheelwrights	Marfona	55.7	2.02	59.4	1.50	14.1	0.56
F22	Maris Piper	61.3	2.37	60.6	1.16	17.7	0.97
F23	Maris Piper	61.8	2.24	54.5	1.14	18.8	0.49
F35	Maris Piper	69.2	1.76	59.8	0.86	15.5	0.32
Home Piece	Maris Piper	72.7	2.08	61.8	0.39	15.6	0.44
Southery	Maris Piper	54.4	4.14	59.5	1.20	19.4	0.76
Aylmerton	Markies	62.0	2.54	52.6	0.48	16.3	0.46
High Hill 16	Markies	91.8	3.47	65.9	1.07	18.7	0.74
Stackyard	Markies	75.0	2.16	59.9	1.22	13.8	0.66
Beezlings	Melody	61.9	2.68	62.6	0.78	18.3	0.65
Bob Cole's	Melody	70.9	2.59	64.5	0.45	19.7	0.63
Brandon 2	Saphire	72.7	3.29	59.7	0.93	12.5	0.69

4.10.4. Planting depth

Mean planting depths ranged from *c.* 12 to 21 cm, being shallowest at Icklingham and deepest at Beezlings (Table 66). The average COV of planting depth within rows ranged from *c.* 7 to 20 % (Table 66) which at the average planting depth of 17.1 cm equated to 95 % of stems having a planting depth between 14.7 and 19.5 cm for the least variable crops but between 10.3 and 23.9 cm for the most variable. There were substantial differences in planting depth between rows, with the maximum difference between samples ranging from *c.* 1.8 to 4.5 cm (Table 66). The variation between rows did not correlate to variation within rows, e.g. at Brandon Road South, variation within rows was high, but there was low variation between rows, whereas the opposite occurred at F22 (Table 66). This suggests that the variation in planting depth within and between rows had different causes.

Table 66. Mean and variation in planting depth at the yield and tuber position harvests of commercial crops

Site	Variety	Planting depth (cm)		COV of planting depth (%)		Difference between shallowest and deepest mean planting depth of rows (cm)‡
		Mean	S.E.	Mean	S.E.	
Hinstock	Estima	12.3	0.61	13.2	0.76	4.0
Weavers	Estima	20.8	0.35	10.3	0.50	2.0
50 Acres	Innovator	15.0	0.99	11.7	1.56	5.2
Papplewick Bed	Innovator	13.7	0.66	13.9	1.12	4.0
Papplewick Ridge	Innovator	14.8	0.42	12.4	0.68	2.8
Brandon Rd South	Jelly	13.8	0.26	19.7	2.20	1.8
Brooke	Jelly	18.9	0.67	10.1	0.61	4.1
Icklingham	Jelly	11.5	0.57	19.1	1.97	3.6
Workhouse	Jelly	18.7	0.12	6.7	0.10	n.d.
18 Acres	King Edward	15.5†	0.66	12.8	2.84	3.7
Brook	King Edward	17.1	0.49	10.3	1.10	3.1
Sculfers	King Edward	16.6	0.56	13.2	1.01	4.1
Brandon 1	Marfona	18.3	0.61	14.3	0.94	4.1
Wheelwrights	Marfona	n.d.	n.d.	n.d.	n.d.	n.d.
F22	Maris Piper	17.8	0.66	9.5	0.60	4.5
F23	Maris Piper	19.6	0.86	8.6	0.36	n.d.
F35	Maris Piper	18.3	1.95	11.6	2.54	n.d.
Home Piece	Maris Piper	14.7	0.40	8.3	0.42	n.d.
Southery	Maris Piper	21.8	0.71	9.0	0.78	4.1
Aylmerton	Markies	18.4	0.29	9.3	0.79	2.1
High Hill 16	Markies	17.5	0.62	13.3	0.77	3.7
Stackyard	Markies	14.0	0.70	12.3	1.30	4.8
Beezlings	Melody	21.4	0.26	9.5	0.74	1.9
Bob Cole's	Melody	17.8	0.50	14.3	1.36	3.2
Brandon 2	Saphire	20.1	0.42	11.9	1.48	2.8

‡ Values are omitted for crops sampled in 2015 as there were only three replicates. † At 18 Acres due to flailing prior to sampling, planting depth could only be determined for three replicates.

A model was created to estimate the typical differences in planting depth that would occur between rows given that the planting depth of plants and stems varies within rows. For each of three seed sizes (20-30, 30-40 and 40-50 mm), random seed tuber diameters and numbers of stems per plant were generated. The planting depth of each seed tuber was generated as 17.5, 18.5 or 19.5 cm for respective seed sizes, equivalent to the set depth of the planter, minus 1.5 ± 0.75 cm to simulate some soil falling back behind the planter. For each stem, the planting depth was calculated as the seed planting depth minus the seed diameter ± 0.5 × seed diameter. Six samples of 10 plants were generated and the largest difference in the mean planting depth between the six samples was calculated. Across 10 simulations, the average maximum difference in planting depths between the six samples was *c.* 1.5 cm, indicating that the differences observed between rows in the survey were only partially caused by chance variations in planting depth within rows. Consequently, while in some crops the observed variation between rows was similar to what would be expected by chance, in others there was a *c.* 2 to 4 cm range in planting depth between rows.

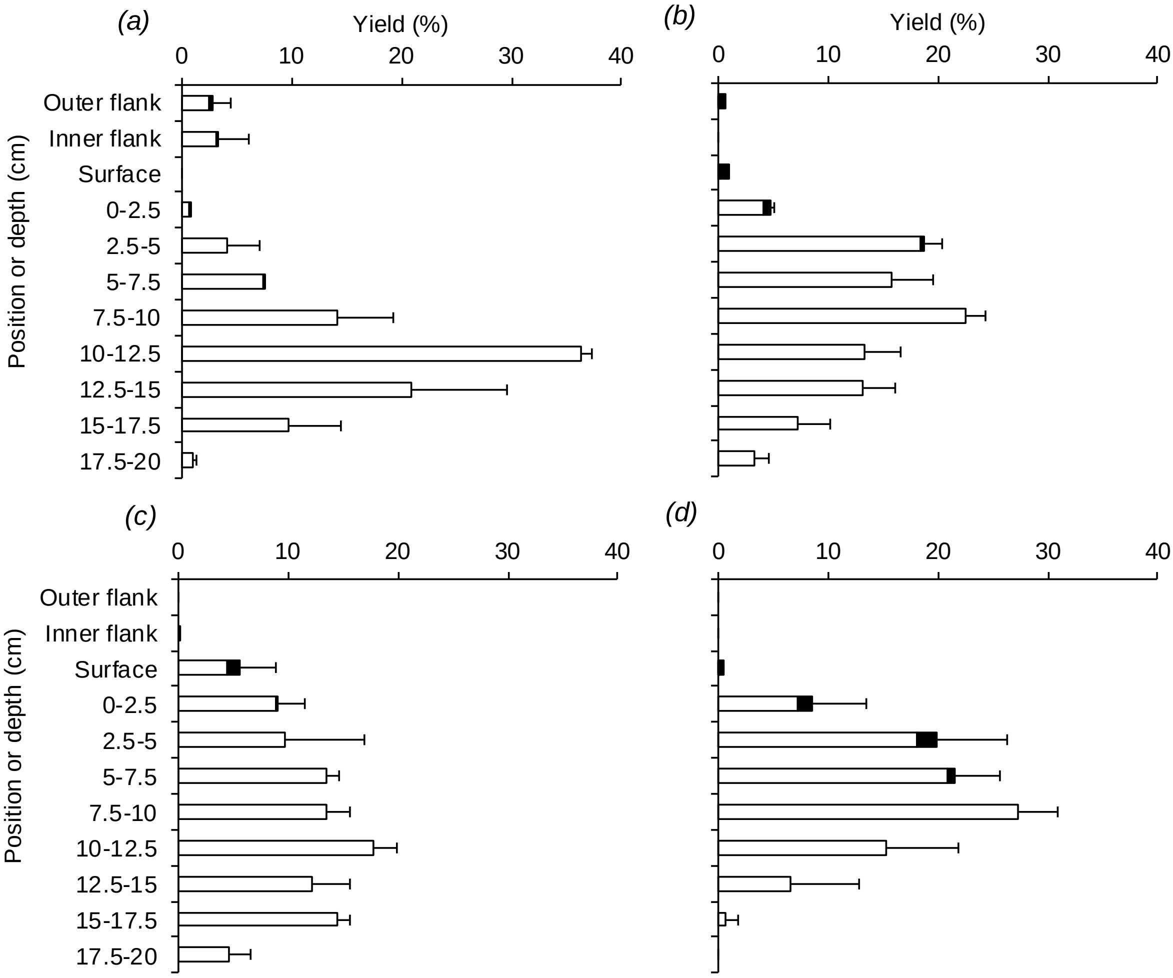
4.10.5. Tuber position and tuber greening

4.10.5.1. 2015

At Workhouse, consistent with the long mean stolon length, *c.* 5 % of yield was found in the outer 5 cm of the flanks of the ridge, but only a small proportion of this was affected by tuber greening (Figure 40*a*). Almost no yield was found in the top 2.5 cm of soil, *c.* 4 % in the next 2.5 cm section and > 50 % of yield was found between 10 and 15 cm. In contrast to Workhouse, in all three crops of Maris Piper, almost no yield was present in the flanks of the ridge and a greater proportion of yield was found in the upper 5 cm of soil (Figure 40). At F23 this included *c.* 5 % of yield being present above the top of the ridge although despite this, only one fifth of that yield was affected by tuber greening as the peat soil had been pushed upwards along with the tubers and they were shielded from sunlight (Figure 40*c*). Tuber greening was more severe at Home Piece where *c.* 30 % of yield was found in the top 5 cm and the presence of green tubers below 5 cm indicated that cracks formed in the ridge allowing light to penetrate (Figure 40*d*). Unlike at Workhouse, in the crops of Maris Piper yield was distributed relatively evenly throughout the depth profiles (Figure 40). At F35 and F23 nearly all tubers with > 5 % S.A. affected by common scab were found > 10 cm from the surface, but at Home Piece they were found throughout the profile (data not shown).

Figure 40. Proportion of yield within different parts of the ridge of non-green tubers, ☐; and green tubers, ■; at *(a)* Workhouse (Jelly); *(b)* F35 (Maris Piper); *(c)* F23 (Maris Piper) and *(d)* Home Piece (Maris Piper). Tubers were included in the class nearest the

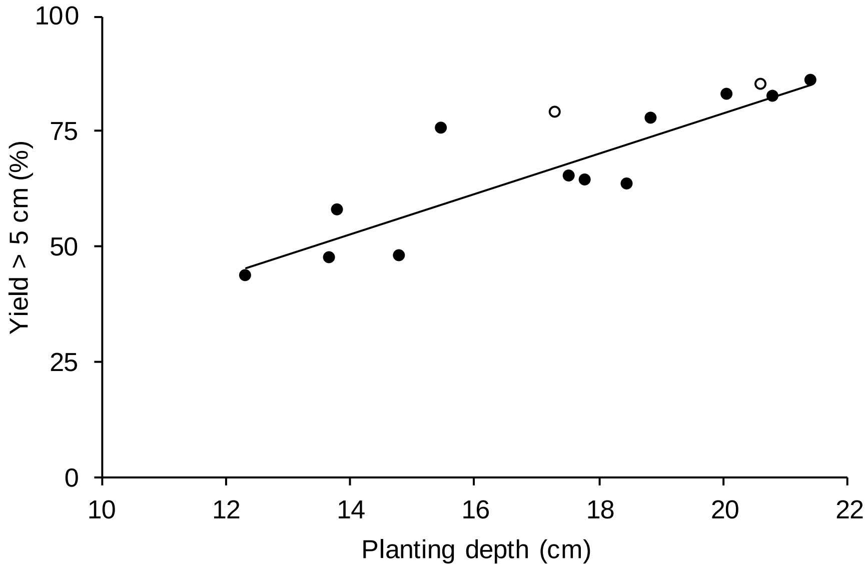
surface in which any part of the tuber was found. Bars indicate S.D. of non-green tubers.



The amount of yield present in the flanks of the ridge ranged from *c.* 0.5 % at F22 to *c.* 9 % at Papplewick Ridge and Brandon Road South (Table 67). At F22 this was associated with a 2 m wide bed containing two rows, so plants emerged far from the flank. Papplewick Ridge was grown on 1 m wide rows, but within the row, plants were arranged in a diamond arrangement and were *c*. 7.5 cm from the centre of the row and consequently closer to the flank. Brandon Road South was grown on 1.8 m beds containing three rows, with plants emerging *c.* 10-15 cm from the flanks. The amount of yield visible at the surface was < 0.6 % at six sites, 0.9-2.5 % at five sites and only appreciably high at the Papplewick sites where *c.* 8 % was visible (Table 67). At both Papplewick sites this was associated with tubers being orientated such that their apical ends were above the soil surface although their stolon ends were substantially deeper, but this was not quantified.

At the three sites where tubers had pushed soil above the top of the bed, *c.* 5-7 % of yield was located there (Table 67). Across all sites, between *c.* 3 and 22 % of yield was present in the upper 2.5 cm of soil and between *c.* 8 and 26 % in the next 2.5 cm of soil (Table 67). Consequently, the amount of yield with > 5 cm of soil coverage ranged from *c*. 46 to 86 %. Deeper planting depths were associated with a greater proportion of yield having > 5 cm of soil coverage and the findings were consistent with those found in Expt 8 (Figure 41). 18 Acres had more yield with > 5 cm of soil coverage than expected from the planting depth, and this may have been due to the recorded planting depth being a poor estimate due to flailing of the stems.

Figure 41. Relationship between planting depth (PDEP) and the percentage of yield with > 5 cm of soil coverage (YL5) for the crops surveyed (●) and for the two planting depths in Expt 8 (○). Fitted line for surveyed crops: YL5 = 4.38 (±0.720) × PDEP -8.5 (±12.5), *p* = < 0.001, R^2 = 0.77.



The amount of tuber greening present in the flanks varied considerably despite the relatively similar amounts of yield present in the flanks. For example at Aylmerton, *c.* 2 % of the yield in the flanks was green, whereas at Papplewick Bed, *c.* 62 % of the yield in the flanks was green (Tables 67 and 68). As expected, almost the entire yield exposed at the surface was green (Table 67). At the four sites where tubers were present above the level surface of the beds, but not visible, only *c.* 10-20 % of the yield was green and this was probably because at these sites, soils were either very sandy or peat, and they deformed rather than cracking (Table 67). Substantial amounts of tuber greening were found at depths of 0-2.5 cm at 18 Acres, Hinstock, High Hill 16 and Weavers with > 50 % of the yield present in that section being green, compared to

< 10 % of the yield present at Brandon Road South, Brandon 1 and F22, even when the yield present above the surface of the bed at these sites was included (Table 67).

Less of the yield at a depth of 2.5-5 cm was green than at a depth of 0-2.5 cm and generally the sites that had a greater proportion of the yield present at 0-2.5 cm had a greater proportion affected at 2.5-5 cm (Table 67). However, 18 Acres and Hinstock had substantially less tuber greening at 2.5-5 cm than at 0-2.5 cm (Table 67). Seven of the 15 sites had some green tubers present in the section with > 5 cm soil coverage indicating that cracks penetrated the soil to at least this depth. However, only at High Hill 16 and Weavers was > 1 % of the overall yield affected by tuber greening in that section (Table 67). At Bob Coles, tuber greening was numerically twice as high (21 *vs* 12 %) in the central rows and this was associated with the central row having a smaller ridge profile than the outer rows (data not shown, Figure 39)

Figure 42. Percentage of yield and tuber greening in different part of the ridge in commercial crops. Flank, not green, ; flank, green, ; surface, not green ; surface, green ; 0-2.5 cm, not green ; 0-2.5 cm, green ; 2.5-5 cm, not green ; 2.5-5 cm, green ; > 5 cm, not green ; > 5 cm, green . For standard errors see Tables 67 and 68

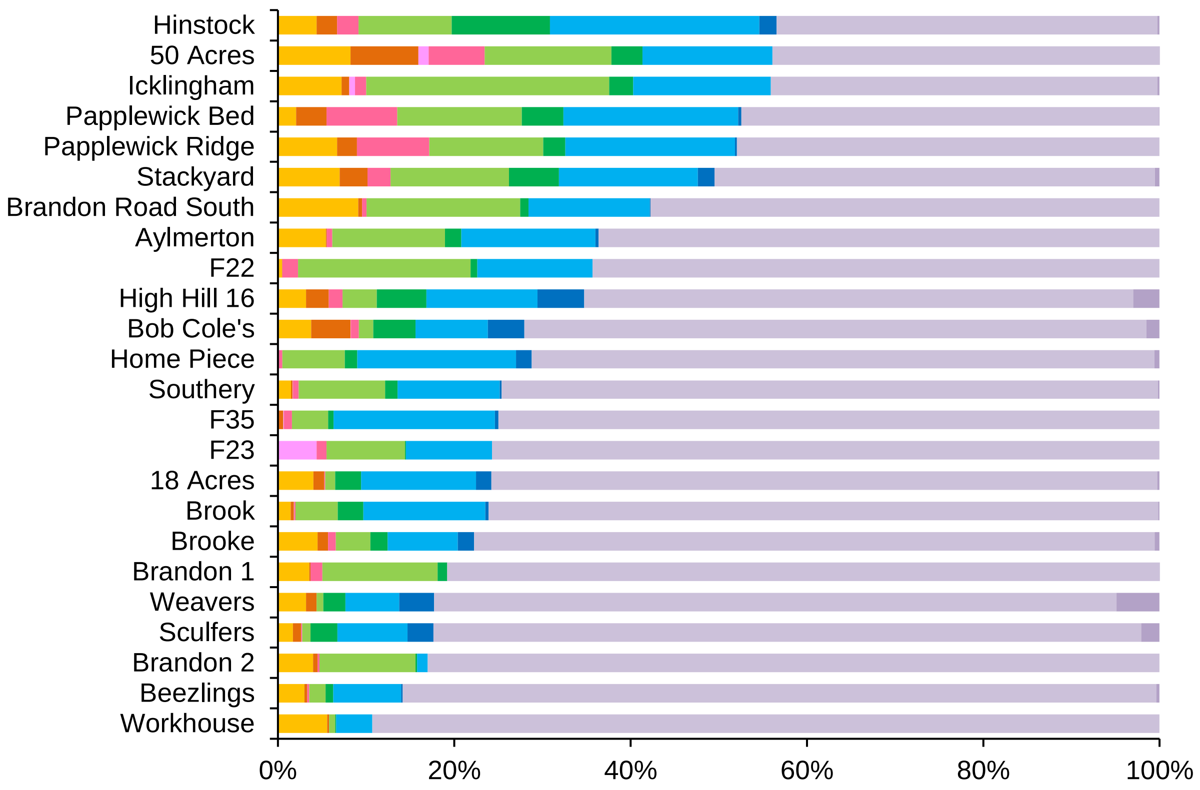


Table 67. Percentage of yield in different parts of the ridge in the commercial crops. n.d. = not determined

	Section	Flanks		Surface		Above		0-2.5 cm		2.5-5 cm		> 5 cm	
Site	Variety	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Hinstock	Estima	6.7	0.67	2.4	0.87	n.d.	n.d.	21.7	2.74	25.7	0.96	43.4	4.13
Weavers	Estima	4.4	1.28	0.0	0.00	n.d.	n.d.	3.3	1.02	10.1	2.10	82.3	3.39
50 Acres	Innovator	15.9	3.90	7.5	2.31	n.d.	n.d.	17.9	3.33	14.8	1.73	43.9	7.35
Papplewick Bed	Innovator	5.5	1.16	8.0	1.58	n.d.	n.d.	18.8	2.53	20.2	1.54	47.4	3.20
Papplewick Ridge	Innovator	9.0	1.33	8.2	1.26	n.d.	n.d.	15.4	2.30	19.5	3.38	48.0	4.25
Brandon Rd South	Jelly	9.5	1.20	0.5	0.17	5.6	1.07	12.8	1.02	13.8	2.06	57.8	1.61
Brooke	Jelly	5.7	1.81	0.9	0.31	n.d.	n.d.	5.9	0.70	9.8	2.14	77.8	3.41
Icklingham	Jelly	8.1	1.32	1.9	0.85	13.8	0.73	16.4	1.73	15.6	1.18	44.1	4.01
Workhouse	Jelly	5.8	3.19	0.0	0.00	n.d.	n.d.	0.8	0.17	4.1	2.12	89.4	5.48
18 Acres	King Edward	5.2	0.42	0.1	0.07	n.d.	n.d.	4.0	0.85	14.8	2.43	75.8	3.15
Brook	King Edward	1.8	0.58	0.2	0.11	n.d.	n.d.	7.7	1.04	14.2	1.19	76.1	1.95
Sculfers	King Edward	2.7	0.51	0.1	0.05	n.d.	n.d.	4.0	0.59	10.9	0.71	82.4	1.26
Brandon 1	Marfona	3.7	0.92	1.4	0.72	4.6	0.79	9.6	1.61	n.d.	n.d.	80.8†	1.61
F22	Maris Piper	0.5	0.29	1.8	0.35	7.1	1.17	13.2	1.73	13.1	1.25	64.3	2.23
F23	Maris Piper	0.0	0.01	5.5	2.49	n.d.	n.d.	9.0	1.62	9.8	4.11	75.7	3.19
F35	Maris Piper	0.6	0.55	1.0	0.70	n.d.	n.d.	4.7	0.55	18.7	0.88	75.0	1.37
Home Piece	Maris Piper	0.0	0.00	0.5	0.27	n.d.	n.d.	8.5	3.60	19.8	5.21	71.2	4.24
Southery	Maris Piper	1.7	0.98	0.7	0.43	n.d.	n.d.	11.2	1.38	11.8	1.53	74.6	2.14
Aylmerton	Markies	5.5	1.09	0.6	0.34	n.d.	n.d.	14.6	1.69	15.6	0.89	63.6	2.36
High Hill 16	Markies	5.5	0.96	1.5	0.26	n.d.	n.d.	9.0	0.79	16.9	1.84	67.1	2.47
Stackyard	Markies	10.2	3.93	2.6	1.04	n.d.	n.d.	19.1	2.29	17.7	0.96	50.5	4.59
Beezlings	Melody	3.3	0.95	0.2	0.17	n.d.	n.d.	2.7	0.73	7.9	1.42	85.8	2.10
Bob Cole's	Melody	8.2	0.71	0.9	0.17	n.d.	n.d.	6.4	0.96	12.4	0.91	72.0	1.42
Brandon 2	Saphire	4.5	1.39	0.2	0.15	n.d.	n.d.	11.1†	0.69	1.2†	0.51	83.0	1.90

† For Brandon 1, > 5 cm = > 2.5 cm; for Brandon 2, 0-2.5 cm = 0-5 cm and 2.5-5 cm = yield in the furrow.

Table 68. Percentage of yield in different parts of the ridge affected by tuber greening in the commercial crops. n.d. = not determined

	Section	Flanks		Surface		Above		0-2.5 cm		2.5-5 cm		> 5 cm	
Site	Variety	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Hinstock	Estima	2.3	0.76	2.4	0.88	n.d.	n.d.	11.1	2.34	2.0	0.95	0.2	0.23
Weavers	Estima	1.2	0.34	0.0	0.00	n.d.	n.d.	2.5	0.72	4.0	1.19	4.9	1.82
50 Acres	Innovator	7.7	2.67	6.4	1.59	n.d.	n.d.	3.5	1.22	0.0	0.00	0.0	0.02
Papplewick Bed	Innovator	3.4	1.29	8.0	1.58	n.d.	n.d.	4.7	1.42	0.3	0.34	0.1	0.08
Papplewick Ridge	Innovator	2.2	0.95	8.2	1.27	n.d.	n.d.	2.5	1.02	0.2	0.20	0.0	0.00
Brandon Rd South	Jelly	0.4	0.15	0.5	0.17	0.7	0.32	0.2	0.15	0.1	0.05	0.0	0.00
Brooke	Jelly	1.2	0.53	0.9	0.31	n.d.	n.d.	2.0	0.78	1.8	0.61	0.6	0.35
Icklingham	Jelly	0.9	0.32	1.3	0.38	2.4	0.70	0.3	0.22	0.0	0.00	0.2	0.25
Workhouse	Jelly	0.2	0.22	0.0	0.00	n.d.	n.d.	0.1	0.14	0.0	0.00	0.0	0.03
18 Acres	King Edward	1.2	0.46	0.2	0.14	n.d.	n.d.	2.9	0.67	1.7	0.81	0.3	0.18
Brook	King Edward	0.4	0.22	0.2	0.11	n.d.	n.d.	2.9	0.73	0.4	0.23	0.2	0.10
Sculfers	King Edward	1.0	0.34	0.1	0.05	n.d.	n.d.	3.0	0.61	2.9	0.64	2.1	0.90
Brandon 1	Marfona	0.1	0.11	1.0	0.50	1.0	0.30	0.1	0.10	0.0	0.00	0.0†	0.01
F22	Maris Piper	0.0	0.02	1.6	0.44	0.7	0.24	0.1	0.03	0.0	0.00	0.0	0.00
F23	Maris Piper	0.0	0.00	1.1	0.35	n.d.	n.d.	0.1	0.13	0.0	0.00	0.0	0.00
F35	Maris Piper	0.6	0.55	0.9	0.62	n.d.	n.d.	0.6	0.30	0.4	0.43	0.0	0.00
Home Piece	Maris Piper	0.0	0.00	0.4	0.27	n.d.	n.d.	1.4	0.50	1.8	0.54	0.6	0.65
Southery	Maris Piper	0.2	0.18	0.6	0.41	n.d.	n.d.	1.4	0.59	0.2	0.22	0.2	0.13
Aylmerton	Markies	0.1	0.06	0.6	0.34	n.d.	n.d.	1.9	0.68	0.4	0.26	0.0	0.00
High Hill 16	Markies	2.5	0.38	1.4	0.27	n.d.	n.d.	5.4	0.38	5.0	0.61	2.9	0.94
Stackyard	Markies	3.2	1.59	2.6	1.03	n.d.	n.d.	5.6	1.55	1.9	0.83	0.5	0.23
Beezlings	Melody	0.3	0.33	0.2	0.17	n.d.	n.d.	0.9	0.40	0.2	0.15	0.4	0.38
Bob Cole’s	Melody	4.5	0.51	0.9	0.17	n.d.	n.d.	4.8	0.73	4.1	0.73	1.5	0.49
Brandon 2	Saphire	0.5	0.27	0.2	0.15	n.d.	n.d.	0.2†	0.15	0.0†	0.00	0.0	0.00

† For Brandon 1, > 5 cm = > 2.5 cm; for Brandon 2, 0-2.5 cm = 0-5 cm and 2.5-5 cm = yield in the furrow.

The overall amount of yield affected by tuber greening ranged from *c.* 1-18 % being lowest at F23 Brandon 2 and highest at 50 Acres, Hinstock and High Hill 16 (Table 69). For the crops where stolon architecture had been assessed, there was no significant relationship between the proportion of yield affected by tuber greening and either mean stolon length or depth (data not shown). The lack of any correlation between stolon length and tuber greening was particularly apparent for the three Brandon sites where the mean stolon length was > 10 cm, but only 1-2 % of yield was affected by tuber greening. This was particularly surprising since these crops were all grown in three-row beds with plants emerging *c.* 10-15 cm away from the flank (Figure 39) which, combined with the long stolon length, should have resulted in tubers initiating close to the flank, erupting as they grew and subsequently turning green. While neither the proportion of yield with < 5 cm of soil coverage nor the clay content of soil could account for the variation in tuber greening, together these two factors accounted for *c.* 50 % of the variation in tuber greening (Table 70). This suggests that deeper-planted crops on sandy soils are the least susceptible to tuber greening and that shallower-planted crops on clay soils are most susceptible.

Overall, 10 % of the yield affected by greening occurred in tubers < 40 mm and *c.* 45 % occurred as both light and dark coloured greening, but there were considerable differences between sites. Except at Hinstock and in the crops of King Edward, the proportion of yield affected by greening of tubers < 40 mm was low. At both Papplewick sites, tuber greening was severe with *c.* 13 and 16 % affected and *c.* 75 % of it occurred as dark green tubers, which was consistent with the high proportion of tubers that were exposed at the surface (Tables 67 and 69).

Table 69. Amount of yield affected by tuber greening in the commercial crops

		< 40 mm (% yield)		Light green (% yield)		Dark green (% yield)		Total (% yield)	
Site	Variety	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
Hinstock	Estima	1.3	0.30	10.5	1.87	6.3	1.22	18.1	2.68
Weavers	Estima	0.7	0.11	8.3	1.42	3.5	0.98	12.5	2.09
50 Acres	Innovator	0.9	0.20	5.0	1.76	11.7	3.45	17.6	4.63
Papplewick Bed	Innovator	0.4	0.06	3.4	0.88	12.8	1.38	16.6	2.11
Papplewick Ridge	Innovator	0.4	0.14	3.0	1.19	9.7	2.02	13.1	1.86
Brandon Rd South	Jelly	0.3	0.09	0.6	0.27	1.1	0.25	1.9	0.28
Brooke	Jelly	0.3	0.10	3.8	0.60	2.3	0.56	6.4	0.97
Icklingham	Jelly	0.3	0.11	1.8	0.78	3.0	0.53	5.1	0.98
Workhouse	Jelly	0.0	0.00	0.6	0.27	0.8	0.56	1.4	0.79
18 Acres	King Edward	2.5	0.44	1.8	0.53	2.0	0.88	6.3	1.66
Brook	King Edward	1.7	0.40	1.7	0.38	0.6	0.30	4.0	0.83
Sculfers	King Edward	2.2	0.33	2.3	0.49	4.6	1.47	9.1	2.05
Brandon 1	Marfona	0.3	0.06	0.9	0.41	1.0	0.41	2.2	0.81
Wheelwrights	Marfona	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	2.8	1.04
F22	Maris Piper	0.6	0.15	0.4	0.19	1.4	0.44	2.3	0.55
F23	Maris Piper	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	0.9	0.29
F35	Maris Piper	0.4	0.11	2.3	0.93	1.2	0.46	3.8	1.32
Home Piece	Maris Piper	0.3	0.08	4.3	0.69	0.9	0.31	5.5	0.95
Southery	Maris Piper	0.3	0.12	0.9	0.43	1.4	0.31	2.6	0.52
Aylmerton	Markies	0.2	0.12	2.3	0.85	0.4	0.23	2.9	1.05
High Hill 16	Markies	0.5	0.10	11.1	1.31	5.6	0.51	17.2	1.71
Stackyard	Markies	0.6	0.11	8.5	2.53	4.8	1.61	13.8	3.84
Beezlings	Melody	0.3	0.14	1.0	0.62	0.7	0.48	2.0	1.04
Bob Cole's	Melody	1.3	0.27	7.6	0.90	6.9	1.00	15.8	1.65
Brandon 2	Saphire	0.1	0.08	0.5	0.26	0.3	0.17	0.9	0.42

Table 70. Relationships between the proportion of yield with < 5 cm of soil coverage (YL5, %), clay content of soil (CLA, %) and the proportion of yield affected by tuber greening (GRE, %) in the commercial crops. GRE = *m* YL5 + *n* CLA + *c*

YL5	CLA	m	S.E.	n	S.E.	c	S.E.	P	R^2
●		0.24	0.073	n.a.	n.a.	0.0	2.55	< 0.01	0.30
	●	n.a.	n.a.	0.16	0.102	5.3	2.00	n.s.	0.06
●	●	0.28	0.064	0.22	0.078	-4.7	2.74	< 0.001	0.47

4.10.5.2. Brandon 1 planters

There were no differences in tuber position or the amount of tuber greening for the two seed sizes at Brandon 1 planted with Planter A (Tables 67 and 71; data not shown). Of the two planters however, Planter B had approximately three times as much yield affected by tuber greening as Planter A (Table 71). This was mainly due to the amount of tuber greening being higher in the portion of tubers that had protruded above the top of the bed, despite similar proportions of yield being in that section in both areas of the crop (Table 71). Although not significantly different, the *c*. 2 cm numerical difference in planting depth between the areas cannot be ruled out as having contributed to the difference in tuber greening (Table 71). At the time of sampling, it was noticeable that for Planter B, tubers protruding above the surface had caused the soil to crack, whereas for Planter A, the soil had deformed (Figure 43). This was consistent with the higher amount of light green tubers found in the area of Planter B compared to Planter A (Table 71). Soil bulk density of the top 10 cm of the beds was measured in order to try to quantify this apparent contrast between the areas, but no differences were apparent (data not shown), suggesting that only the top *c.* 2-3 cm of the soil was affected. As an un-replicated comparison, it is impossible to draw conclusions from these observations, but they are consistent with the findings of Expt 8 and highlight the need for further work. The results suggest that cracking of the soil can be important for causing tuber greening even on very sandy soils. As well as the differences in tuber greening, variation in planting depth and variation in tuber size were both higher for Planter B than Planter A (Table 71).

Table 71. Planting depth, location of tubers and tuber greening in two areas of the Brandon 1 Marfona crop planted with different planters, one of which did not apply hood pressure (A) and one which did apply hood pressure (B)

Planter	A		B		
	Mean	S. E. (5 D.F.)	Mean	S. E. (5 D.F.)	*p*-value
Planting depth (cm)	18.6	0.37	16.5	0.49	n.s.
COV of planting depth (%)	15.7	1.50	19.5	0.90	< 0.05
Yield (%)					
Flanks	4.3	1.25	3.5	0.84	n.s.
Above	5.3	1.15	7.6	1.44	n.s.
Surface	1.0	0.23	1.6	0.59	n.s.
0-2.5 cm	10.5	0.66	15.3	1.85	< 0.05
> 2.5 cm	78.8	2.07	72.0	1.54	n.s.
Tuber greening (%)					
Flanks	0.6	0.15	0.5	0.23	n.s.
Above	0.4	0.18	3.5	0.95	< 0.05
Surface	1.0	0.22	1.6	0.60	n.s.
0-2.5 cm	0.4	0.17	1.3	0.69	n.s.
> 2.5 cm	0.0	0.00	0.0	0.02	n.s.
< 40 mm	0.4	0.15	0.5	0.12	n.s.
Light	0.7	0.22	4.4	1.27	< 0.05
Dark	1.3	0.38	2.0	0.63	n.s.
Overall	2.3	0.37	6.9	1.50	< 0.05
COV of tuber size (%)	12.8	0.48	14.9	0.34	< 0.01

Figure 43. Photographs showing typical examples of the beds created with *(a)* planter A or *(b)* planter B at Brandon 1. Field of view in each photograph = *c.* 50 cm.

(a)

(b)

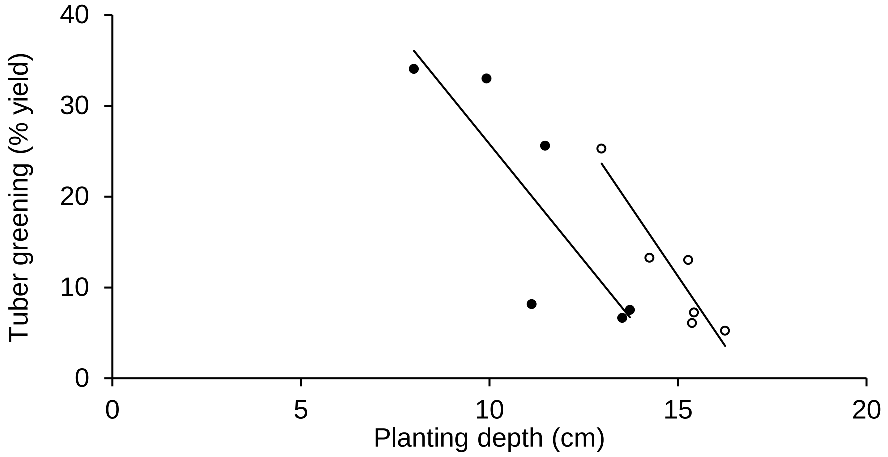
4.10.5.3. Misaligned ridges in Stackyard

In rows where stems had emerged *c.* 10 cm from the centre of the ridge due to the misalignment of seed tubers, the planting depth was *c.* 4 cm shallower than where stems had emerged in the centre (Table 72). The number of tubers was unaffected by the difference in plant alignment, but yield was *c.* 9 t/ha lower where stems had emerged from the side of the ridge (Table 72). Although where planting was misaligned it resulted in a numerical increase in the amount tuber greening, this was not significant (Table 72). This was probably due to planting depth varying substantially in addition to alignment. Surprisingly, at similar planting depths, the misaligned rows had less tuber greening than those that were well-aligned and this was probably due to the seed tubers having greater vertical soil coverage due to the stems emerging from the side of the ridge (Figure 44).

Table 72. Influence of planting misalignment on crop parameters in Stackyard

	Well-aligned		Misaligned		
	Mean	S.E.	Mean	S.E.	*p* value
Planting depth (cm)	14.9	0.47	11.3	0.88	< 0.01
Number of tubers (000/ha)	446	17.3	418	23.2	n.s.
Yield (t/ha)	76.6	1.81	68.0	2.04	< 0.05
Tuber greening (% yield)	11.7	3.06	19.2	5.38	n.s.

Figure 44. Relationship between planting depth and tuber greening in Stackyard for well-aligned (○) and misaligned (●) rows.



4.11. Commercial quality control data

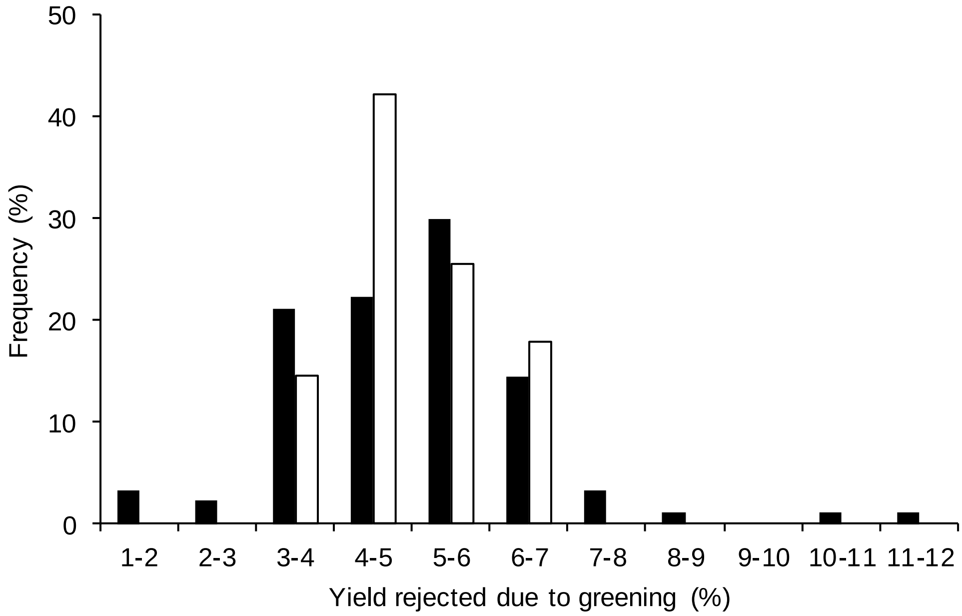
The total proportion of yield rejected by the packer during 2013-2015 ranged from *c.* 22 % in Marfona to *c.* 32 % in Maris Piper (Table 73). The amount of tuber greening was highest in Estima where *c.* 7 % of yield was rejected and lowest in Maris Piper where *c.* 4 % of yield was rejected (Table 73). Variations between years were small, ranging from 4.6-5.0 % suggesting that, on a national scale, seasonal variations had little influence on the amount of tuber greening. Amongst individual growers, the amount of tuber greening varied substantially from 1.4-11.5 %, with the majority between 3 and 7 % (Figure 45). Overall, much of this variation was due to differences in the varieties grown by individual growers, as those growing high proportions of Estima would be expected to have higher amounts of tuber greening than those growing a high proportion of Maris Piper (Figure 45). For individual growers however, the correlation between the amount of tuber greening and the amount expected from their variety mix was weak (R^2 = 0.26) suggesting that factors other than variety are important.

The average amount of yield rejected due to tuber greening was approximately one third less than in the survey of commercial crops in this work, at 4.8 % compared to 7.4 % (Tables 69 and 73). This difference could be because the survey of commercial crops was unrepresentative, differences in the methodologies used to assess tubers, or because some green tubers were removed prior to delivery to the packer. Estimating the financial cost of tuber greening to the UK potato industry is complicated by differences in the value of crops and whether there are alternative markets for tubers affected by greening. Using conservative values of 5 % of yield affected of the 5 million tonnes produced (AHDB 2017) and sold at £ 100 per tonne, the loss is estimated at £ 25m per annum.

Table 73. Estimated amount of yield rejected by a packer for six varieties over 2013-2015

Variety	Number of loads	Wastage (% yield)		Tuber greening (% yield)	
		Mean	S.E.	Mean	S.E.
Estima	2248	29.2	0.29	6.8	0.13
Jelly	2864	26.1	0.20	4.9	0.08
King Edward	1500	27.4	0.35	6.4	0.13
Marfona	1367	22.6	0.28	5.5	0.12
Maris Piper	7222	32.4	0.18	3.8	0.05
Melody	1252	27.3	0.31	4.6	0.12

Figure 45. Average amount of yield rejected due to tuber greening for individual growers, ■; and for the same growers, the average amount of greening based on their varietal mix, □.



4.12. Variation in tuber size

4.12.1. Establishment

At emergence, the dry weight of the seed tubers had decreased by between *c*. 15 and 40 % compared to at planting, with the decrease greatest in Marfona and smallest in Maris Piper (Figure 46). Approximately half of the dry weight lost from the seed tubers prior to emergence was not recovered in the stems indicating this was either lost through respiration or present in the roots (Figure 46). The below-ground stems of Melody were heavier than the other varieties but this was not linked with a greater decrease in dry weight of the seed tuber (Figure 46). Although the dry weight of above-ground stems was very low, there were differences between varieties and these were related to the amount of dry weight lost from the seed tuber (Figure 46). The dry weight of seed tubers continued to decrease after emergence with all varieties except Maris Piper decreasing by *c*. 70 % at 12 DAE compared to at planting, whereas Maris Piper decreased by only *c*. 50 % (Figure 46). The below-ground stems increased in weight by 30-50 % and the weight at 12 DAE correlated strongly with their weight at emergence. The above-ground stems grew rapidly from emergence making up > 50 % of the total dry weight 12 DAE in all varieties except Maris Piper. The total weight of the plants 12 DAE was similar to that of the seed tubers at planting but it was not possible to determine the relative contributions of seed tuber substrate and photosynthesis to growth of the above-ground stems. Across all of the plots, the amount of dry weight lost from the seed tuber correlated strongly with the above-ground stem weight and when variations in the date of emergence were taken into account, 74 % of the variation could be accounted for (Table 74).

Figure 46. Plant dry weight in each variety at planting (first column), emergence (second column) and 12 DAE (third column). Seed tuber, ■; below-ground stem, ■; above-ground stem, ■. Bars indicate S.E. based on 18 D.F.

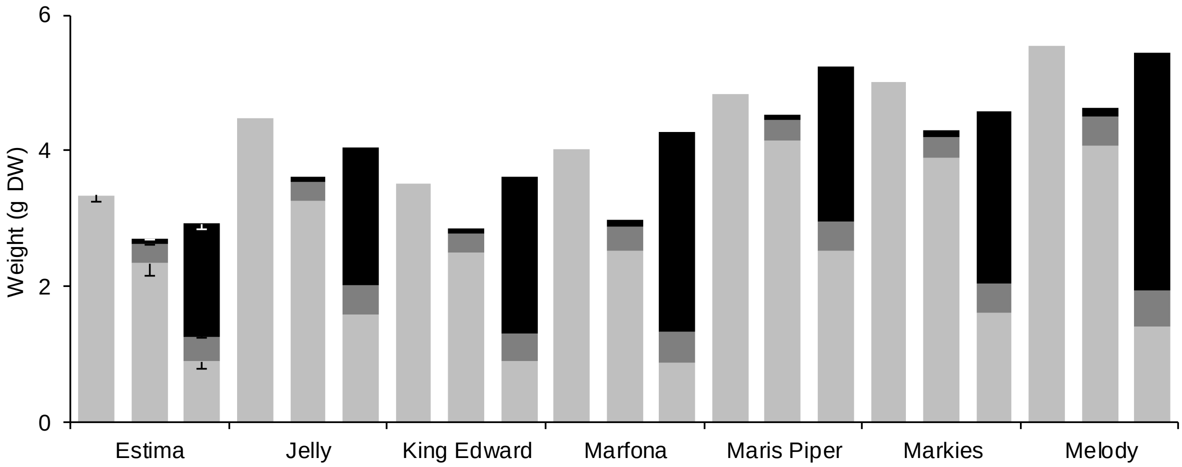


Table 74. Relationships between above-ground stem weight per plant (AG, g DW) and dry weight lost from the seed tuber (WL, g DW) and days after emergence (EM) at 12 DAE in Expt 1. AG = *m* WL + *n* EM + *c*

Explanatory variable(s)	*m*	S.E.	*n*	S.E.	*c*	S.E.	*P*	R^2
WL	0.75	0.126	n.a.	n.a.	0.25	0.380	< 0.001	0.56
EM	n.a.	n.a.	0.35	0.125	-1.3	1.36	< 0.01	0.20
WL, EM	0.72	0.098	0.31	0.072	-3.0	0.814	< 0.001	0.74

For individual plants, the total proxy below-ground stem diameter increased as seed tuber weight and the number of stems per plant increased (Table 75). For individual stems, the above-ground stem weight increased as the proxy below-ground stem diameter increased and as they increased in age (Table 76). Altogether, the relationships in Tables 74-76 indicate that initial differences in the development of stems are the result of how seed tuber substrate is allocated between sprouts and stems as they develop.

Table 75. Relationships between proxy below-ground stem diameter per plant (PSD, g FW/cm) and seed tuber at planting (ST, g FW) and number of stems per plant (NS) at 12 DAE in Expt 1. PSD = *m* ST + *n* SN + *c*

Explanatory variable(s)	*m*	S.E.	*n*	S.E.	*c*	S.E.	*P*	R^2
ST	0.0148	0.00093	n.a.	n.a.	0.066	0.0226	< 0.001	0.48
SN	n.a.	n.a.	0.0785	0.00722	0.215	0.0195	< 0.001	0.30
ST, SN	0.0128	0.00080	0.0585	0.00535	-0.035	0.0210	< 0.001	0.63

Table 76. Relationships between above-ground weight per stem (AG, g FW) and proxy below-ground stem diameter per stem (PSD, g FW/cm) and days after emergence (EM) at 12 DAE in Expt 1. AG = *m* PSD + *n* EM + *c*

Explanatory variable(s)	*m*	S.E.	*n*	S.E.	*c*	S.E.	*P*	R^2
PSD	76.2	2.46	n.a.	n.a.	-1.39	0.441	< 0.001	0.58
EM	n.a.	n.a.	1.84	0.075	-6.26	0.764	< 0.001	0.48
PSD, EM	57.2	1.96	1.39	0.052	-11.64	0.536	< 0.001	0.77

4.12.2. Stem-to-stem variation

Variation (COV) in the number of stems per plant did not differ significantly between varieties in 2015, but variation was significantly different in 2016 and 2017 (Table 77). Overall, Maris Piper had the least variation in stems per plant and King Edward had the most, but the difference between them was relatively small (Table 77). Variation in the number of stems per plant had a modest effect on variation in yield per stem but did not correlate with any other variate (Table 78). This was unexpected as simplistically, higher variation in the number of stems per plant could increase variation in the amount of seed tuber substrate available to each stem during establishment, which may in turn be expected to result in greater variation in yield per stem. One explanation for this is that the number of stems per plant is a poor descriptor of how seed substrate is shared between stems growing from the same seed tuber because the relative size of stems can vary substantially, i.e. a two-stemmed plant could consist of two stems of equal size or of one very large stem and one very small stem.

Differences between varieties in the COV of above-ground stem weight early in the season occurred each year, but in some varieties there were substantial differences between years, indicating that physiological or pathological factors may influence this (Table 77). Overall, Jelly, Marfona and Melody had the least variable-sized stems and King Edward had the most variable-sized stems (Table 77). Since the weight of above-ground stems correlates with leaf area, larger stems intercept more radiation over the course of the season and thus produce higher yields (Smart 2016). Variation in yield per stem differed significantly between varieties, in 2015, but not in 2016 and 2017; however this was probably related to the smaller sample size in those years (Table 77). Averaged across the 3 years, variation in yield per stem differed between varieties and was generally similar to the variation in above-ground stem weight averaged across the 3 years (Table 77).

The number of tubers per stem increased as the yield per stem increased in all varieties each year, but there were substantial differences between the varieties. In Estima, Jelly, Marfona and Markies, the relationship tended to have a shallow slope, such that the number of tubers per stem increased relatively little as yield per stem increased (Figure 47). Contrastingly, in King Edward and Maris Piper, the slope was steeper and the number of tubers per stem responded markedly as yield per stem increased (Figure 47). Melody responded intermediately to the other varieties (Figure 47). These relationships are consistent with the relationships between number of stems and number of tubers per hectare, previously derived in order to calculate seed rates (Firman & Daniels 2011; Firman 2014). In Marfona and Markies for example, the number of tubers per stem is relatively constant at different stem densities, whereas in King Edward and Maris Piper, the number of tubers per stem is relatively plastic. This consistency between these relationships indicates that the response of tuber population to stem population could be predicted from small samples, early in the variety selection process. The mean tuber weight per stem increased as yield per stem increased and the slopes of the relationships were inversely related to the relationships between yield per stem and number of tubers per stem (Figure 48). The different slopes of these relationships determine how variation in yield per stem affects variation in mean tuber weight per stem and thus how variation in yield per stem influences uniformity.

Figure 47. Relationships between yield per stem and number of tubers per stem in Expts 1-3.

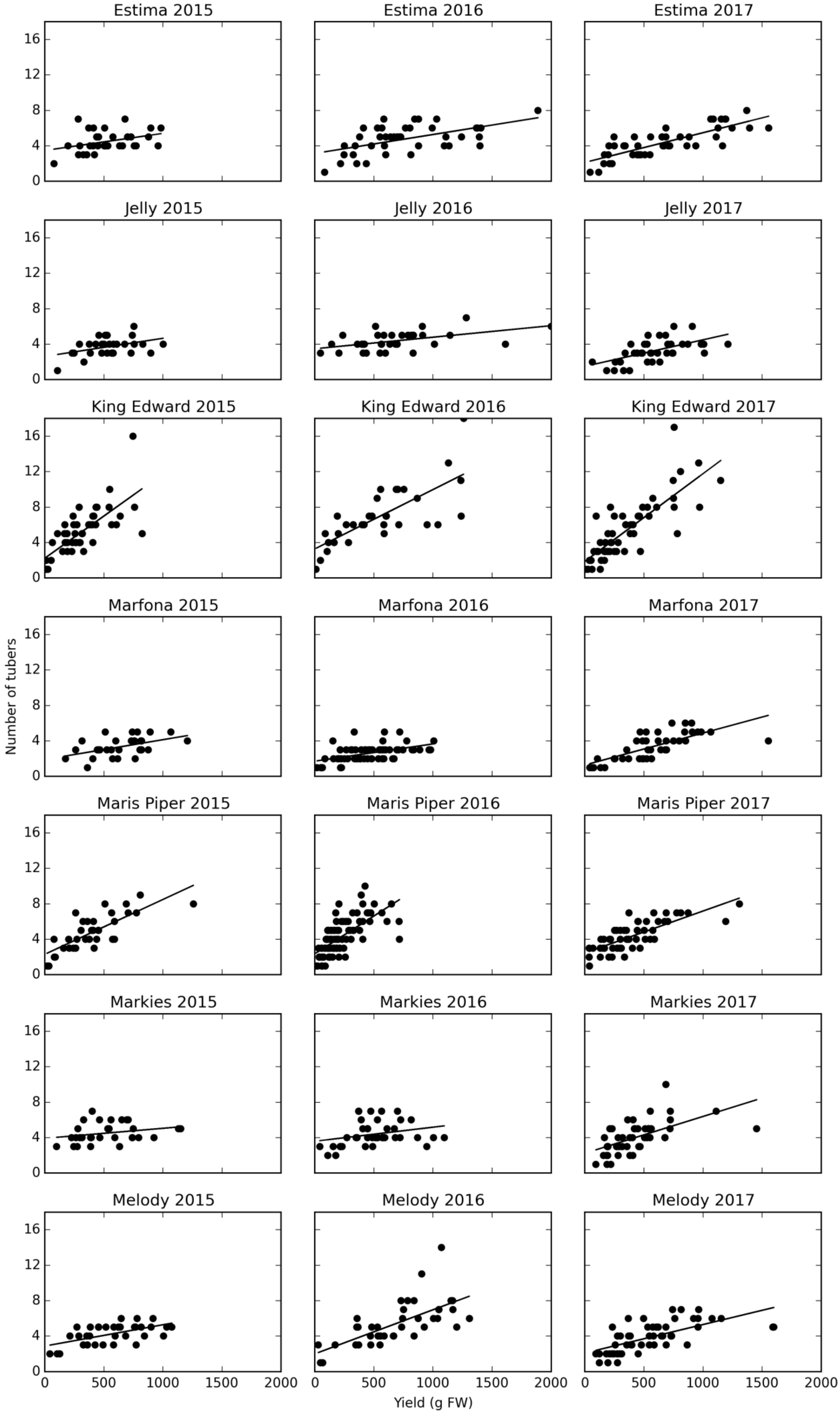
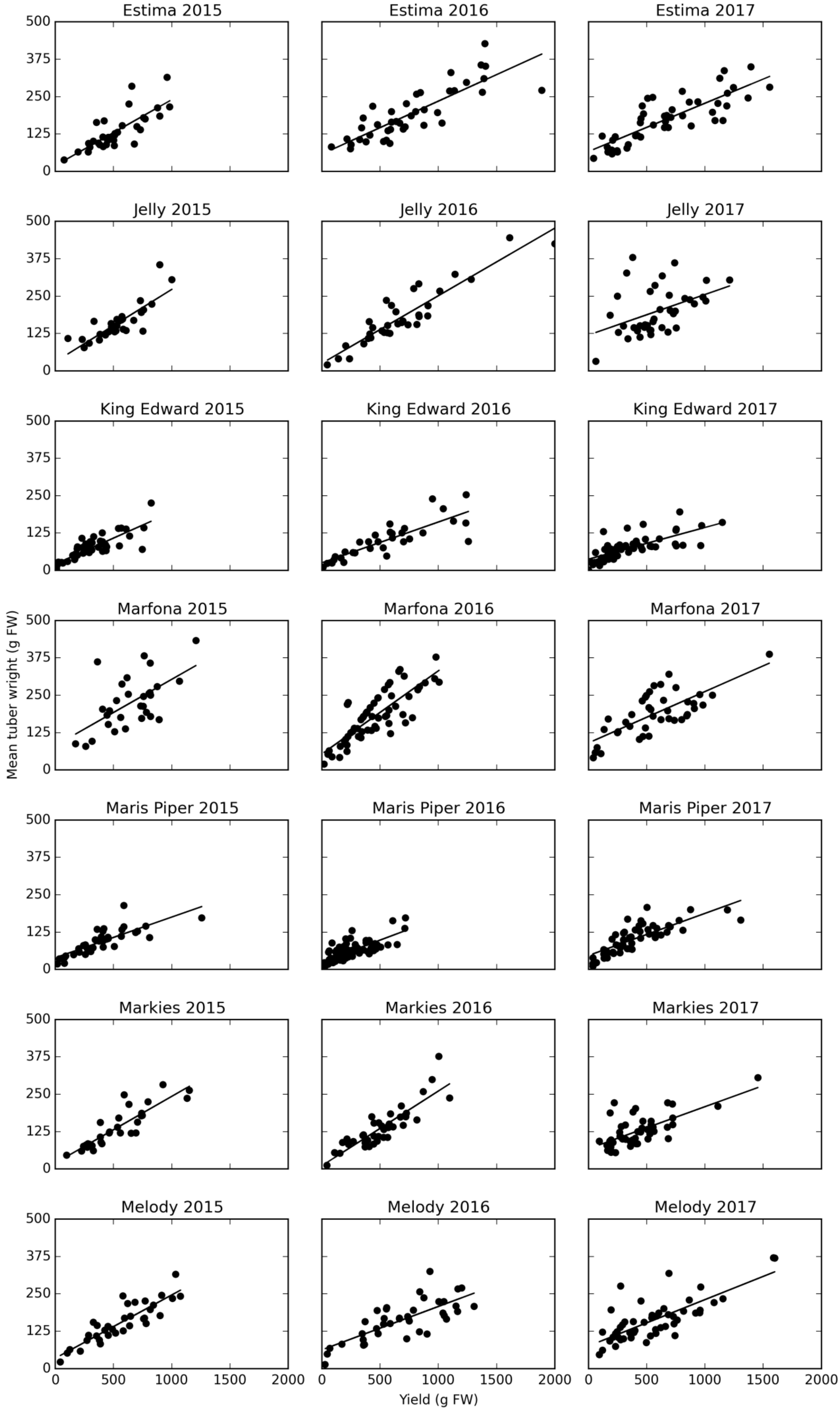


Figure 48. Relationships between yield per stem and number of tubers per stem in Expts 1-3.



Within-stem variation in tuber size was substantially lower than the overall COV of tuber size indicating that if there was less variation in yield per stem, then overall variation in tuber size would be lower (Table 77). There were significant differences in the within-stem COV of tuber size between varieties in 2015 and 2017 but not in 2016 (Table 77). Overall Jelly and Markies had the least variation in tuber size within stems and King Edward had the most (Table 77). Within-stem variation in tuber size tended to increase with increase in number of tubers per stem (R^2 = 0.33), but a larger number of varieties would need to be studied to determine whether this is a consistent trend. Within-stem variation in tuber size was also higher when the yield per stem was more variable (Table 78), which was unexpected since these could theoretically vary independently of each other. There were considerable differences in within-stem variation in tuber size per year indicating that environmental or pathological factors may affect within-stem variation (Table 77).

Mean tuber weight per stem increased as yield per stem increased in all varieties (data not shown) and consequently, the variation in mean tuber weight per stem increased as the variation in yield per stem increased (Table 78). While King Edward had the most variation in mean tuber weight per stem, the extent of the variation was less than expected from the variation in yield per stem, compared to the other varieties (Table 77).

Averaged across the 3 years, the percentage of marketable yield (45-80 mm) at an optimum mean tuber size (62 mm) ranged from 94 % in Jelly to 85 % in King Edward. The overall variation in tuber size increased as variation in yield per stem, mean tuber weight per stem and within-stem variation in tuber size increased (Table 77). A greater proportion of the variation in the overall COV of tuber size could be accounted for by a combination of variation in mean tuber weight per stem and within-stem variation in tuber size (Table 70). Accounting for variation in yield per stem did not further improve the relationship, due to it being a major determinant of variation in mean tuber weight per stem (data not shown).

Table 77. Coefficients of variation of the number of stems per plant, above-ground stem weight, yield per stem, within-stem tuber size, mean tuber weight per stem and overall tuber size

	Year	Variety							S.E. (18 D.F.)†
		Estima	Jelly	King Edward	Marfona	Maris Piper	Markies	Melody	
COV of stems per plant (%)	2015	32.6	30.2	34.3	35.7	35.7	33.1	36.1	3.85
	2016	32.2	37.4	43.1	32.0	28.6	39.6	38.0	2.78
	2017	39.0	33.5	46.4	39.5	31.4	32.6	33.4	2.54
	Mean	34.6	33.7	41.3	35.7	31.9	35.1	35.8	1.79
COV of above-ground stem weight (%)	2015	62.7	44.4	78.2	55.2	73.9	60.1	55.4	5.93
	2016	44.4	50.5	62.2	51.5	64.4	70.4	40.5	4.77
	2017	68.0	46.1	88.2	46.8	67.8	52.2	54.5	4.62
	Mean	58.4	46.9	76.2	51.2	68.7	60.9	50.1	2.97
COV of yield per stem (%)	2015	42.7	36.7	71.7	54.8	59.0	47.7	57.1	5.92
	2016	52.5	49.6	78.3	49.7	71.3	46.1	50.7	8.61
	2017	59.4	42.3	76.8	58.7	62.1	55.6	56.1	7.91
	Mean	51.5	42.9	75.6	54.4	64.2	49.8	54.6	4.37
Within-stem COV of tuber size (%)	2015	10.4	7.7	15.1	10.4	10.9	7.8	9.5	1.29
	2016	11.8	10.3	11.8	8.9	11.7	10.7	14.3	1.30
	2017	10.4	7.8	12.5	10.7	12.6	8.7	12.1	0.94
	Mean	10.9	8.6	13.1	10.0	11.7	9.1	12.0	0.68
COV of mean tuber weight per stem (%)	2015	40.8	33.2	51.3	36.2	45.5	48.2	41.4	4.54
	2016	43.0	45.3	66.1	43.3	56.2	46.9	41.8	7.59
	2017	43.3	39.3	51.3	40.7	47.4	39.2	38.1	5.05
	Mean	42.4	39.3	56.2	40.1	49.7	44.8	40.4	3.30
COV of tuber size (%)	2015	17.2	13.4	19.4	15.9	17.1	14.4	14.5	0.54
	2016	19.0	16.7	21.1	16.5	17.2	17.3	16.6	0.85
	2017	17.0	14.7	17.7	17.0	16.7	15.5	17.0	0.78
	Mean	17.7	15.0	19.4	16.5	17.0	15.7	16.0	0.42

† S.E. based on 54 D.F. for the means of the 3 years

Table 78. Correlation matrix between the average values of the variates listed in Table 77. SPP = COV of stems per plant; AGW = COV of above-ground stem weight; YPS = COV of yield per stem, WTS = COV of within-stem variation in tuber size; MTW = COV of mean tuber weight per stem; OTS = COV of the overall tuber size distribution. Values are the R^2 of linear regressions and asterisks indicate the significance of the relationship: * for p = < 0.05; ** for p = < 0.01 and ***for p = < 0.001

	SPP	AGW	YPS	WTS	MTW
AGW	0.09				
YPS	0.15*	0.34*			
WTS	0.04	0.10	0.34**		
MTW	0.08	0.25*	0.54***	0.13	
OTS	0.12	0.11	0.42***	0.47***	0.46***

Table 79. Relationships between within-stem variation in tuber size (WTS, %), variation in mean tuber weight per stem (MTW, %) and overall variation in tuber size (OTS, %). OTS = *m* WTS + *n* MTW + *c*

WTS	MTW	*m*	S.E.	*n*	S.E.	*c*	S.E.	*P*	R^2
●		0.62	0.142	n.a.	n.a.	10.1	1.56	< 0.001	0.47
	●	n.a.	n.a.	0.166	0.0394	9.3	1.78	< 0.001	0.46
●	●	0.44	0.125	0.117	0.0340	6.8	1.58	< 0.001	0.66

These results show that there can be large differences in uniformity between varieties and that they can be explained by variation in other traits. Considering those traits, Jelly was the least variable variety overall and King Edward was the most variable and this was consistent with the overall variation in tuber size. This increased understanding of the mechanisms underlying variation in tuber size could assist breeders in selecting for more uniform varieties earlier in the selection process, however, considerable effort was required to describe the variation in these varieties and further work would be required to streamline the process.

5. Discussion

5.1. Stolon architecture and tuber position

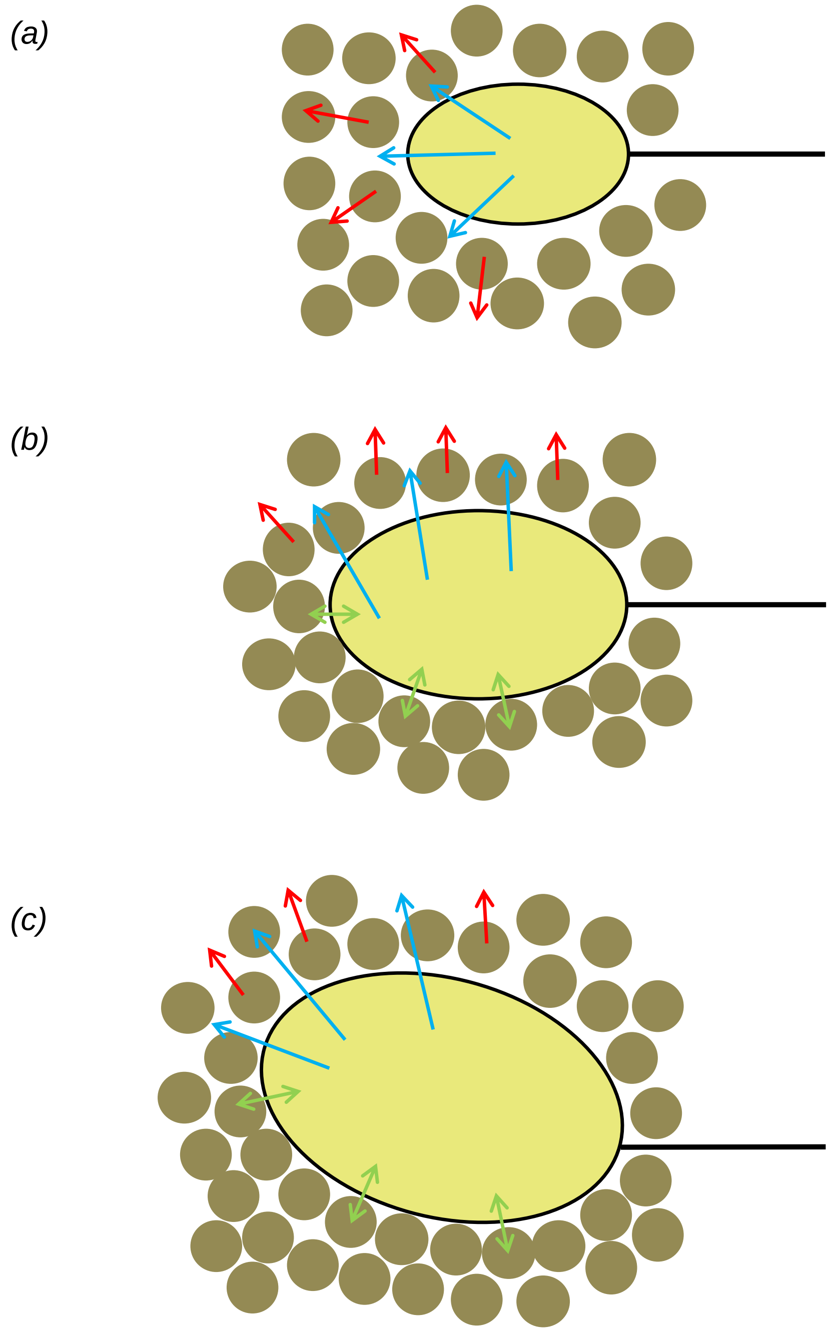
Patterns of stolon architecture observed in this work were typically in contrast to those described by Struik (2011), in that stolons tended to be shortest at the base of the stem and longest closer to the soil surface. The reason for this difference is unclear, but the wide range of soil types and varieties measured in this work, suggest that these patterns are typical for field-grown crops grown in temperate climates, whereas Struik's data were derived from plants grown in controlled environments. The range in mean stolon length, both in the experiments and commercial crops, was similar to those reported by Kratzke & Palta (1992). The distributions of individual stolon lengths were also of a similar shape, although the maximum length recorded was *c.* 45 cm rather than 26 cm by Kratzke & Palta (1992). Unlike the data of Kratzke & Palta (1992) this study found up to two-fold variation in mean stolon length within varieties, between years and between sites. Nitrogen fertiliser significantly increased mean stolon length indicating that it may have slightly delayed tuber initiation (Jackson 1999), but the effect was so small as to be of no practical importance.

Bohl *et al*. (2014) considered that non-horizontal orientation of tubers was associated with short stolons as they were more common in Defender than in Summit Russet with mean stolon lengths of 2.9 and 6.4 cm, respectively. This hypothesis is not supported by this study, as there was no relationship between stolon length and either the proportion of tubers growing non-horizontally, or the average angle of tubers. Instead, tubers were more likely to grow at an angle as the mean tuber length increased. In light of this, it is worth noting that Bohl *et al*. (2014) reported the average tuber weight was higher in Defender than in Summit Russet, indicating that the tubers were longer as well, which would be consistent with the findings of this work.

A model to explain the non-horizontal orientation of tubers is presented in Figure 49. This incorporates findings from Expt 1 that indicated that tuber depth decreased over time in proportion to tuber height, and findings from Expts 1-3 that the distance to the stolon end of tubers was consistently similar to stolon length (i.e. the expansion of tubers did not compress the stolon). These patterns of tuber growth are consistent with the results of Reeve *et al.* (1973) who found that the cells in tubers of Russet Burbank were smaller and younger at the apical end than the stolon end, suggesting that tubers grow from the apical end, rather than expanding in all directions. At tuber initiation, the bulk density of soil surrounding the tuber is relatively low, with large pore spaces between soil aggregates, so the tuber can expand freely in all directions (Figure 49*a*). As the tuber expands, soil aggregates become more tightly packed, and the aggregates on the basal side and apical end of the tuber eventually reach their maximum packing density. Aggregates above the tuber are comparatively free to move, so the tuber moves towards the soil surface (Figure 49*b*). As expansion continues, the resistance provided by the already packed soil forces the apical end of the tuber upwards, consequently making the tuber orientated with the apical end higher than the stolon end (Figure 49*c*).

At planting, the bulk density of soil in potato ridges is typically *c.* 1.0 to 1.4 g/cm^3 at 25 cm depth and tends to increase by *c.* 0.2 g/cm^3 during the season (Stalham & Allison 2015). These values are still far less than the density of soil particles of 2.65 g/cm^3 (Hall *et al*. 1977), but some degree of porosity will always remain, and the maximum packing density of soil is *c.* 2 g/cm^3 (Reichert *et al.* 2009). The increase in bulk density with depth found by Stalham & Allison (2015), may explain why tubers tend to orientate with the apical end towards the surface, as there will be less resistance on the upper side of the tuber. While the precise values are uncertain and will depend on the soil type and initial bulk density, a 300 g tuber that developed in a soil with a bulk density of 1.2 g/cm^3 at planting, and with a maximum packing density of 1.8 g/cm^3, would cause 900 cm^3 of soil at planting to be compressed into 600 cm^3 at harvest. It is likely however, that not all the soil would reach the maximum packing density and thus, a greater volume of soil would be compressed to a lesser degree, or displaced. Kouwenhoven *et al.* (2003) noted that the volume of tubers was small (*c.* 1 % per 10 t/ha of yield) in comparison to the total ridge but, plants with relatively short stolons and a yield of 2 kg would cause large disturbances in the soil surrounding them.

Figure 49. A proposed model to explain how changes in soil bulk density surrounding the tuber may cause them to orientate non-horizontally as they expand (*a* to *c*). Blue arrows indicate the direction of tuber movement during expansion. Red arrows indicate the movement of soil aggregates. Green arrows indicate where the soil provides resistance to tuber expansion. Not to scale.



5.2. Tuber greening

Kouwenhoven *et al.* (2003) considered that cluster width was an important factor in determining the susceptibility of crops to tuber greening. In this study however, differences in the cluster width of varieties did not account for any of the differences in tuber greening. In most of the commercial crops, less than 5 % of yield was found in the flanks of the ridge, indicating that in those crops, the ridge was sufficiently large to accommodate the cluster width of the crops. The high amounts of tuber greening in

Expts 1-3 were probably partly caused by the crops being grown on 75 cm wide rows, which Bernik *et al*. (2009) found resulted in more severe tuber greening compared to 90 cm rows. In some commercial crops however, there was severe tuber greening despite them being grown on 91 cm wide rows, indicating that row-width is not the only important factor in determining tuber greening.

The results of the planting depth experiments were broadly similar to previous work (Stalham *et al.* 2002; Bohl & Love 2005; Pavek & Thornton 2009), with the highest yield of non-green tubers occurring at planting depths between 15 and 20 cm. In the survey of commercial crops however, planting depth ranged from 12 to 22 cm, suggesting that growers may be reducing marketable yield by planting too shallow or too deep. Considering that the proportion of yield within 5 cm of the soil surface decreased as planting depth increased, and that this, in combination with the clay content of soil influenced tuber greening, further research is required to establish whether the optimum planting depth differs depending on soil type.

Booth & Allen (1990) surveyed three commercial crops where different seed sizes had been planted and measured the depth of planting, defined as the length of non-pigmented stem. The average COV of planting depth was 15.9 % and was not consistently related to the variation in seed tuber size. Hogge (1991) also surveyed planting depth in commercial crops and the average COV of planting depth was 17.5 %. The COVs of planting depth reported in this study were generally lower than those reported by Booth & Allen (1990) and Hogge (1991) but are not directly comparable as within- and between-row variations were considered separately in this study, resulting in the within-row COV being lower than if all rows were considered together. Some of the variation in planting depth between rows may have been due to differences in slumping caused by differences in bulk density at planting. The increase in ridge bulk density reported by Stalham & Allison (2015) indicates that planting depth, as defined by the length of the below-ground stem, will underestimate the original planting depth. Kouwenhoven *et al.* (2003) found that the height of ridges decreased by *c.* 10 % during the season.

Cracking of the ridge was found to be an important contributor to causing tuber greening. The finding that clay content influenced soil cracking is consistent with basic knowledge of soil cracking (Yong & Warkentin 2012) and was also noted by Kouwenhoven *et al.* (2003). Although not investigated in relation to tuber greening, soil organic matter (Sharma *et al*. 1995) and water content (Morris *et al.* 1992) are both known to influence soil cracking. These general theories of soil cracking may only be of limited relevance to soil cracking of potato ridges however, since the deformation and displacement of soil by developing tubers may be an important and exceptional factor. If this is indeed the case, then short stolons and wide within-row spacings could influence the extent of soil cracking.

The varieties studied in this work differed in their sensitivity to light when placed in a greenhouse, consistent with the findings of Reeves (1988). The linear increase in tuber greening, quantified by SPAD, over time was also consistent with the findings of Braun *et al*. (2010). The relative importance of the sensitivity of tubers to light for preventing in-field tuber greening is unclear, but in this work, the sensitivity to light did not correlate with the amount of yield affected by tuber greening. Thus, it would appear that preventing tubers becoming exposed to light is more important than their sensitivity. It is conceivable however, that on soils where cracking is more prevalent, varieties that are less sensitive to light would be less affected by tuber greening. Non-greening clones of *Solanum microdontum* have been identified (Bamberg *et al.* 2015) and may lead to the development of greening-resistant potato varieties in the long-term, but in the short- and medium-term, reductions in tuber greening will be achieved by preventing tubers being exposed to light.

5.3. Uniformity

The results of this work demonstrate that earlier conclusions (Smart 2016) based on observations made in a smaller number of varieties apply more widely, and that there are significant differences in traits which contribute to uniformity between varieties. Differences in above-ground stem weight during establishment are predominantly caused by differences in the amount of seed tuber substrate that each stem receives (Tables 74-76). Stems with a relatively low above-ground stem weight during establishment remain smaller throughout the season and produce a lower yield and smaller tubers than relatively large stems. Varieties differ in the relationship between yield and number of tubers per stem and these are consistent with relationships previously described between the number of stems and number of tubers per hectare (Firman & Daniels 2011; Firman 2014). This similarity is because at different stem populations, but a similar yield, the average yield per stem differs. Theoretically, these differences between varieties may influence how varieties respond to variable within-row spacing and emergence. In varieties such as Maris Piper and King Edward, where the number of tubers per stem increases as yield per stem increases, if a stem emerges early or has more space, the effect on mean tuber size of the stem is compensated for the increase in number of tubers, whereas in varieties such as Jelly or Marfona, the number of tubers increases less, so mean tuber size of the stem will increase. Consequently, Maris Piper and King Edward would be relatively insensitive to decreases in uniformity caused by variable within-row spacing and emergence, whereas Jelly and Marfona would be relatively sensitive.

6. Conclusions

6.1. Stolon architecture

Stolons began to initiate within 5 DAE and the number of stolons per stem increased linearly until *c.* 30 DAE, after all tubers had initiated. Once differences in the date of emergence were accounted for, the initial development of stolons and tubers per stem occurred at a similar rate in all varieties. Mean stolon length ranged from *c.* 2 to 11 cm in the variety experiments and from *c.* 4 to 12 cm in the commercial crops. The shapes of the distributions of stolon length were similar in all crops, with the majority being relatively short (< 10 cm) and long stolons being comparatively rare. Nitrogen had a significant effect on mean stolon length, but the effect was so small as to be of no practical importance. The role of temperature is less certain, because while there were differences in mean stolon length between planting dates, the differences were inconsistent with differences in soil and air temperatures. The differences in soil and air temperatures in these experiments were however, relatively small compared to those that occur in practice. Seed tuber size did not affect stolon length.

In the variety experiments, mean stolon depth was consistently 70-80 % of planting depth and while there were differences between varieties these were generally small. Stolons bearing tubers > 10 mm were clustered towards the base of the stem. The range in relative stolon depth was greater in the commercial crops at 52-80 % of plant depth, but the average was similar to in the variety experiments. In some of the crops with shallower stolons this was associated with pathological problems. In the commercial crops, planting depth did not influence the relative stolon depth. Neither planting date, nitrogen rate nor seed tuber size had any consistent effect on relative stolon depth.

6.2. Tuber position

Across the 3 years this work has shown that while stolon architecture influences tuber position, the differences between varieties were less than expected. Differences in mean stolon length were relatively small compared to differences in tuber length and it was the combination of stolon length and tuber length which determined the cluster width of crops. In the commercial crops, cluster width did not appear to be an important factor affecting tuber greening at the majority of sites, as relatively little yield was found in the flanks of ridges, where it would occur if cluster widths were too large. While some small differences in stolon depth were observed between varieties, these did not directly influence tuber depth. As with the influence of tuber length on cluster width, larger tubers were found closer to the surface than their stolon depth would suggest. Secondly, as tubers grew longer, they were more likely to become orientated with their apical ends pointing towards the surface. In Melody, however, tubers were more frequently orientated downwards than upwards, and the cause of this is uncertain. In the commercial crops, the major determinant of tuber depth was planting depth because the relative stolon depth varied relatively little between them, whereas planting depth varied substantially.

6.3. Tuber greening

Tuber greening differed between varieties each year, but could not be accounted for by differences in stolon length, stolon depth or cluster width. In both the experiments and the commercial crops, few tubers were exposed at the soil surface, with the exception of crops of Innovator where this was associated with tubers being orientated with their apical end above the stolon end. In the commercial crops, the proportion of yield affected by tuber greening ranged from *c.* 1 to 18 %. At some sites, green tubers were found with > 5 cm of soil coverage indicating that light penetrated the soil to at least this depth, consistent with the findings of Kouwenhoven *et al.* (2003). Tuber greening was higher where the proportion of yield with < 5 cm of soil coverage was high and where the clay content of soils was relatively high. These findings are consistent with clay soils being more susceptible to cracking and with cracks penetrating deeper on soils with a higher clay content than with a lower clay content. The relatively weak relationships between tuber greening, soil coverage and clay content indicates that other factors are important. Planting depth was found to vary considerably within and between rows which probably contributes to increasing tuber greening and decreasing total yield. The optimum planting depth for maximising non-green yield is a balance between producing higher total yields, but more green yield at shallower depths and lower total yields, but less green yield at deeper depths. While determining where the optima lies on different soil types is important, tuber greening could be readily reduced if planting depth variation between rows could be reduced.

In Expt 4, seed size and spacing had no significant effect on total tuber greening, although numerically it was twice as high in larger seed of Maris Piper and light-coloured tuber greening was higher in larger seed of Marfona. In Expt 8, tuber greening was higher when a ridge shape rather than a semi-bed was used and also when the hood pressure applied with the planter was higher. At Brandon 1, the area of the field where a planter that applied hood pressure had been used also had higher amounts of tuber greening than where a planter that did not apply hood pressure was used.

6.4. Further research

6.4.1. Stolon and tuber development

Although the planting date experiment was conducted over 2 years, the range in temperatures that crops were exposed to during stolon development was relatively small. Further work could examine the length of stolons in crops growing in environments with larger differences in temperature to establish the extent to which this can explain within-variety variation in stolon length. The 2016 and 2017 results from Cambridge showed a consistent relationship between average tuber length and the proportion of tubers growing at an angle. Some of the commercial crops diverged from this trend and had more tubers growing at an angle than expected and the causes of this could be investigated.

There is undoubtedly scope for increasing our understanding of stolon and tuber development through the use of x-ray computed tomography (Ferreira *et al.* 2010 and Perez-Torres *et al.* 2015). Due to the short interval of time over which tubers develop and stem-to-stem variations that occur within samples, elucidating the precise sequence and timing of development is impossible in field experiments with relatively small sample sizes as used in this work. Fundamental questions that remain uncertain after this work, but which could be studied using x-ray computed tomography include: How does the time of sprout emergence from the seed tuber influence date of emergence of the stem? Do sprouts elongate at different rates prior to emergence depending on the seed tuber substrate per stem and diameter of the sprout? How does the timing of individual stolon initiation influence the timing of tuber initiation? Over what interval do tubers initiate on individual stems and how does this influence variation in tuber size on the stem? How does the timing of tuber initiation influence final tuber size? Does the relative growth rate of tubers on the same stem vary? At present the cost of measuring a plant once using x-ray computed tomography is £50-100 (Gerth, personal communication), approximately 50 times the cost of measuring a plant destructively. A comprehensive investigation would require *c.* 20 measurements per plant during the season and thus collecting data on 4 plants in a replicated variety experiment over 3 years as in Expts 1-3 would cost *c.* £ 0.5m.

6.4.2. Tuber greening

The results suggest that the optimum planting depth may vary on different soil types because on sandy soils, tubers can be closer to the surface without becoming affected by tuber greening than on heavier soils. Since it is generally important to plant as shallow as possible in order to expedite emergence and therefore maximise yield, establishing where the optima lie is vital. While numerous planting experiments have been conducted previously (Stalham *et al.* 2002; Bohl & Love 2005; Pavek & Thornton 2009) there have been no comprehensive economic studies, that account for differences in the cost of planting at different depths, in terms of the speed of cultivation and harvesting operations, as well as crop value due to differences in yield and tuber greening. Considering the increases in bulk density that occur in potato ridges over the course of the season (Stalham & Allison 2015), the influence of this on decreasing planting depth should be evaluated.

Cracking of the soil is a substantial cause of tuber greening and yet is a relatively poorly understood phenomenon. Clay content is undoubtedly a major determinant, but soil organic matter, cultivations, planter hood pressure and irrigation could all influence the extent to which a soil cracks. In contrast to most research conducted on soil cracking, where soils crack as they dry and shrink, observations made in the commercial crops indicated that cracking was influenced by the volume of tubers increasing, causing compression and deformation of the soil. Ridges with a lower bulk density and with a more stable structure should in theory be more resistant to this form of cracking. The effect of plant spacing was examined in Expt 4, and there was evidence that wider spacing may result in more tuber greening, due to the less even distribution of tubers along the row causing more soil cracking. The conclusions from Expt 4 were limited however, because of differences in mean tuber size of the crops between treatments. Further work could compare seed sizes planted at different spacings but to achieve similar stem densities and thus mean tuber size, in order to make the comparisons more valid and practically relevant. Plant spacing is unlikely to be an important factor in all varieties and all soil types however, with it being more likely on heavier soils and in varieties with shorter stolons.

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