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Opening Eyes on Seedling Tuber Quality in Potato: Size Matters

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Abstract
For potato, diploid hybrid breeding is a novel breeding technique that speeds up the development of new varieties. A consequence of hybrid breeding is the introduction of hybrid true potato seeds as starting material. From these seeds, seedling tubers can be produced in one field season, to use as starting material for a seed or a ware crop in the following year. For breeding purposes as well as for seed crop and ware crop production, it is essential to produce seedling tubers of high quality. The production of seedling tubers is a new step in the potato production chain; therefore, we investigated the effect of tuber quality traits on plant development and yield. With similar seedling tuber weight, more eyes per seedling tuber led to more stems per plant. This was compensated by a lower number of tubers per stem resulting in an equal total tuber number and weight per plant at the end of the growing season. A higher seedling tuber weight led to a higher soil cover in the field. Hybrid potato plants grown from larger seedling tubers produced a greater total tuber weight per plant than plants grown from smaller tubers, while number of eyes and stems per tuber had no effect on final yield when using equal seedling tuber weight.

Keywords Hybrid potato · Number of eyes · Seedling tuber quality · Tuber weight

Introduction

Recently, potato breeding was revolutionized by the introduction of diploid hybrid breeding (Stokstad 2019). Whereas genetic gain in conventional breeding is low and targeted breeding is difficult due to large variation in tetraploid material, diploid hybrid breeding enables stacking of desired traits and a more predictable outcome

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of the breeding process (Lindhout et al. 2011; Jansky et al. 2016; Lindhout & Struik 2023). Through self-compatibility and the simpler genetics of diploids, homozygous parent lines can be produced by performing self-pollinations (Lindhout et al. 2018; Eggers et al. 2021;). By crossing two of these homozygous parent lines, a diploid hybrid is produced that can be planted in the field (de Vries et al. 2023). Besides more efficient breeding, parent lines as well as hybrids can be used in research to understand traits and perform, for example, mapping studies (Meijer et al. 2018; Prinzenberg et al. 2018; Endelman and Jansky 2016; Korontzis et al. 2020).

A hybrid variety of potato is the result of the cross between two homozygous parent lines; therefore, the starting material is hybrid true potato seed (HTPS). Advantages of HTPS compared to conventional seed tubers are the small size of the seeds which makes them easy to store and to transport. In cool conditions, they can be stored for more than 40 years when dried and stored in good conditions (Pallais 1987), and, contrary to seed tubers, HTPS are usually disease-free. Moreover, starting material can be scaled up very fast and made available to end-users (Kacheyo et al. 2023). In one crossing season, millions of HTPS can be produced, which can in turn be used to produce seedling tubers in the following season (de Vries et al. 2023). When starting with a single seed tuber, multiplication takes many years until a new variety can be released.

With HTPS as starting material, there are different cultivation pathways to grow ware tubers (van Dijk et al. 2021). Seedlings can be produced in greenhouse conditions from HTPS, after which they can be transplanted into the field for ware tuber production. When using HTPS instead of seed tubers to start a ware crop, a disadvantage can be a longer growing season (van Dijk et al. 2022). This can lead to lower yield in temperate climates such as the Netherlands. In East Africa, however, using HTPS as starting material can be an advantage due to high disease pressure when grown from seed tubers (de Vries et al. 2016; den Braber et al. 2023). Another pathway is to grow seedling tubers from seedlings produced in a greenhouse and use these as starting material for a ware crop or another generation of seed tubers in the subsequent year (Stockem et al. 2020; van Dijk et al. 2021). Especially in medium or high tech-cropping systems, the production of seedling tubers would be a desirable step, as the whole production chain is optimized for growing from seed tubers.

To introduce diploid hybrids into the potato production chain with seedling tubers as starting material, it is essential to produce high-quality seedling tubers. High-quality starting material is needed to produce a vigorous crop in the field with a high potential yield (Caldiz 2009). Additionally, in breeding programmes, it is important to have high-quality starting material, because selections are based on the results of field trials. As breeders want to select the hybrids with the highest genetic potential, high-quality trials where yield differences are the result of genetics rather than of other sources of variation such as field gradients (Stockem et al. 2022) or seed-tuber quality are important.

Important quality traits in seed tubers that affect the number and vigour of stems, plant development and yield are the physiological age, seed tuber weight and number of eyes per seed tuber. These traits are interrelated (Struik & Wiersema 1999). The physiological age of seed tubers is affected by chronological age, as well as by environmental conditions during the growing season of the seed, the conditions during storage and by genotype (Struik & Wiersema 1999; Struik 2007; Kwambai et al. 2023). During the growing season, an important determinant for the physiological age of the produced seed tubers is temperature, and besides that, factors such as water availability and light conditions can play a role (Caldiz 2009; Struik and Wiersema 1999). This means that seed tuber lots produced in different locations are often of different physiological ages (Kwambai et al. 2023), resulting in variation in plant development and yield when planted together in one field.

The development of the crop in the field is affected by the physiological age of the mother tuber (Caldiz 2009). An important difference between seedling tubers and conventional seed tubers is the physiological age of the material. Conventional seed tubers usually are multiplied over several generations where mother and grandparent tubers affect the development of the subsequent crop (Went 1959). Seedling tubers, on the other hand, are produced in one single season from true seed; as a result, the physiological age only is affected by the conditions of one growing and storage season.

Besides physiological age, the tuber weight and number of eyes per tuber are important quality traits of seed tubers. Larger seed tubers usually lead to earlier emergence, more stems and faster ground cover, and yields are higher due to more tubers produced per plant (Struik & Wiersema 1999; Ebrahim et al. 2018). In tetraploid varieties, positive effects of larger seed tubers produced from seedlings were found even in subsequent generations of tuber multiplication (Maris 1986; Brown 1988). Moreover, there is a positive relation between seed tuber size and eye number (Reeves & Hunter 1980; Struik & Wiersema 1999). Each eye can develop into one or more sprouts, affecting the number of stems per plant in the field. Number of stems per plant is one of the components that determine the yield of the crop, and often farmers adjust plant density to seed tuber size to achieve a stem density that is optimal for the crop's purpose or market outlet. As the proportion of eyes producing a sprout, the number of sprouts per eye, and the proportion of sprouts that develop into tuber-bearing stems are all affected by the physiological quality of a seed tuber, it is important to assess how seedling tubers behave that have been produced by TPS-grown plants and therefore are not affected by the physiological age of seed tubers as is the case for seed tubers from seed-tuber grown plants.

In this research, we aimed to determine the effect of quality traits in seedling tubers on plant development in the field and on yield parameters to understand to which extent selections in a breeding programme are the result of seedling tuber quality rather than genetics. We formulated the following sub-questions:

1) What is the variation in number of eyes and weight of tubers in diploid hybrid seedling tubers within and among hybrids?
2) What is the effect of number of eyes, plant and crop development and production origin on plant development and yield?

It is expected that more eyes per seedling tuber will result in more stems per plant, and with that in more tubers and higher yield per plant. Also, higher seedling tuber weight will probably result in higher yield per plant. With the results of this research, we will be able to improve the selection process in hybrid potato breeding to select for highest yielding genotypes. Moreover, we will improve the cropping system for a ware crop grown from seedling tubers by understanding the effect of seedling tuber traits on ware yield.

To answer the above-described questions, seedling tubers of four different hybrids and different origins were selected for number of eyes and weight of individual seedling tubers. The different tuber classes were used to perform two field trials in which we compared the tubers differing in number of eyes, weight and production origin.

Material and Methods

Two trials were performed to determine the effect of quality traits in seedling tubers on the development of potato plants in the field and on yield parameters. In Trial 1, the effect of number of eyes was examined in four different diploid hybrids (H1, H2, H3, H4). In Trial 2, we investigated the effect of seedling tuber weight and production location of seedling tubers of the same hybrids as in Trial 1.

Trials 1 and 2 were performed on the same field back-to-back. The field was located at Grebbedijk (Wageningen, NL, 51°57′08.2″N, 5°38′09.0″E), on a light clay soil (Table 1). Seedling tubers of both trials were planted on 02.05.2022, haulm killing was done on 29.08.2022 and the trials were harvested on 23.09.2022.

Planting Material

Both trials were performed with four diploid test hybrids (H1, H2, H3, H4) that were produced in a diploid hybrid breeding programme as described by Lindhout et al. (2011, 2018). All hybrids produce medium–high yields. They contrasted for tuber shape, with H1 and H2 producing long-oval tubers, H3 producing long tubers and H4 producing round-oval tubers. Seed production of hybrid seeds was performed in 2020 in a greenhouse (Ressen, NL). Seedling tubers were produced in 2021 under field conditions as described by Stockem et al. (2020). For Trial 1, all seedling tubers were produced in Garsthuizen (GAR) (NL, 53°23′17.8″N, 6°44′46.8″E). In Trial 2, production location of the seedling tubers was one of the experimental factors. Seedling tubers for this trial were produced in Emmeloord (EMM) (NL, 52°44′00.0″N, 5°42′29.1″E), Garsthuizen and Anna Paulowna (ANN)

Table 1 Physical composition of the soil at the production sites of the seedling tubers

Location	Clay (%) <2 µm	Silt (%) < 2–50 µm	Sand (%) > 50 µm	pH
Emmeloord	11	31	49	7.4
Garsthuizen	13	38	45	7.4
Anna Paulowna	19	30	39	7.5
Grebbedijk	26	48	19	7.3

(NL, 52°50′23.9″N, 4°55′43.6″E), all located in the Netherlands. The number of growing days in the field was 128, 93 and 110 days for Emmeloord, Garsthuizen and Anna Paulowna, respectively. Soil characteristics of these sites can be found in Table 1. The crop was irrigated adequately and kept disease-free by preventive spraying with fungicides. To avoid virus infection, insecticides were applied, and roguing was done. Tubers were sent for testing for the presence of viruses, ring rot and brown rot, and found disease-free.

Quality of Starting Material

To compare the physiological quality of seedling tubers at the moment of planting, a sprouting test was performed with seedling tubers of all treatments. Tubers for these trials were selected based on the same criteria as for the field trials ("Treatments and trial design" and "Selection of seedling tubers" sections). The sprouting test was designed as a complete randomized block design with 10 replicates and one tuber per replicate.

Sprouting tests were performed as described by Van der Zaag and Van Loon (1987). Seedling tubers were placed in a dark climate room in the same week as the field trials were planted. Temperature was set at constant 18°C with a relative humidity of 85%. The sprouts were measured after 24 days in these conditions.

At the start of the test, seed tubers were de-sprouted, and tuber weight and number of eyes were assessed per tuber. At the end of the sprouting test, the number, length (mm) and fresh weight (g) of the sprouts were recorded per seedling tuber. The sprouting capacity was calculated by dividing the fresh weight of the sprout by the initial fresh weight of the tuber.

Treatments and Trial Design

Trial 1

The goal of Trial 1 was to determine the effect of number of eyes in seedling tubers on plant development in the field and on yield parameters. This was done in the diploid hybrids H1, H2, H3 and H4. Seedling tubers were divided into a treatment with a high and a low number of eyes per tuber, while seedling tuber weight was kept as equal as possible between the eye number classes. This was done for each hybrid separately because the ranges differed among the hybrids. The selection procedure of seedling tubers is explained below.

The trial was designed as a split-plot trial with hybrid as main plot and number of eyes as sub-plot with three replicates. Plot size and shape were determined based on earlier work, with each net plot consisting of 20 plants planted on two ridges, with a planting distance of 20 cm within the ridge and 75 cm between the ridges (Stockem et al. 2022). On either side of the plot, one border row was placed containing the same genotype in the same planting arrangement.

Trial 2

In Trial 2, we investigated the effect of production origin and tuber weight of seedling tubers from the hybrids H1, H2, H3 and H4. Seedling tubers were divided into a high and a low weight while keeping number of eyes as equal as possible (Table 2) between the two treatments. Origins of the seedling tubers were the production locations Emmeloord, Garsthuizen and Anna Paulowna (Table 1). The trial was laid out as a split-split-plot trial with hybrid as main-plot, origin as sub-plot and seedling tuber weight as sub-sub-plot, with a net plot size of 20 plants per plot and three replicates. The plot layout was equal to plots in Trial 1.

Selection of Seedling Tubers

To determine the variation for number of eyes and tuber weight, a batch of 420 seedling tubers per hybrid in the size class 35–45 mm was scored for these traits. Additionally, a seedling tuber weight of 200 tubers per hybrid was scored for a batch of size class 28–35 mm. Based on the variation that was found, we determined the treatments for both trials.

For Trial 1, we selected seedling tubers with the largest possible difference between high and low number of eyes. This was done per hybrid, and within each eye class, not more than a difference of one eye was allowed (Table 2). Seedling tuber weight was kept as equal as possible within the hybrid.

For Trial 2, seedling tubers of the size class 28–35 mm and 35–45 mm were used. Per size class and per hybrid seedling tubers were collected that had a similar tuber weight to reduce variation within the treatment (Table 3). So for these treatments, seedling tuber size as well as seedling tuber weight is known. For Replicate 1, number of eyes was counted for all treatments.

Table 2 Properties of seedling tubers per hybrid in the different treatments in Trial 1

Hybrid	Eye class	Average number of eyes	Range of number of eyes per class	Average seedling tuber weight (g)	Range of seedling tuber weight in treatment (g)
H1	High	5.3	5–6	47.9	40–55
H1	Low	2.8	2–3	46.1	40–58
H2	High	7.3	7–8	51.9	40–62
H2	Low	4.8	4–5	50.6	44–61
H3	High	6.3	6–7	54.9	41–66
H3	Low	3.8	3–4	54.4	41–70
H4	High	6.3	6–7	41.7	35–49
H4	Low	4.6	4–5	40.8	36–48

Table 3 Average number of eyes per tuber and seedling tuber weight (g/tuber) of Replicate 1 in Trial 2 (n=20). Abbreviations of production origins are *ANN*, Anna Paulowna; *EMM*, Emmeloord; *GAR*, Garsthuizen

Hybrid	Origin	Size class (mm)	Number of eyes per seedling tuber	Seedling tuber weight (g)
H1	ANN	28–35	3.2	24.5
H1	ANN	35–45	3.3	38.2
H2	ANN	28–35	3.7	26.9
H2	ANN	35–45	4.5	39.8
H3	ANN	28–35	4.1	29.0
H3	ANN	35–45	4.0	54.0
H4	ANN	28–35	3.9	22.5
H4	ANN	35–45	4.4	45.9
H1	EMM	28–35	3.8	25.7
H1	EMM	35–45	4.0	39.8
H2	EMM	28–35	4.7	26.3
H2	EMM	35–45	5.0	41.5
H3	EMM	28–35	3.9	29.6
H3	EMM	35–45	4.6	57.1
H4	EMM	28–35	3.9	21.8
H4	EMM	35–45	4.7	46.4
H1	GAR	28–35	3.9	25.3
H1	GAR	35–45	4.4	39.6
H2	GAR	28–35	5.0	26.8
H2	GAR	35–45	5.2	39.5
H3	GAR	28–35	4.3	28.6
H3	GAR	35–45	4.8	56.3
H4	GAR	28–35	5.0	22.4
H4	GAR	35–45	5.2	46.5

Measurements and Statistical Analysis

The same measurements were done in both trials. During the growing period, we measured emergence and soil cover over time; number of stems was counted at 65 days after planting (DAP). Ground cover was measured thirteen times between 28 and 119 DAP. This was done using a grid (75 × 75 cm), which was divided into 100 squares (7.5 × 7.5 cm). A square was counted as 1% groundcover if it was filled for at least 50% with canopy. At harvest, tuber weight and tuber number were measured per plot. To compare soil cover among the treatments, the area under the canopy cover progress curve (AUC) was calculated using the R package DescTools (Signorell et al. 2017).

In Trial 1, yield was decomposed into different components that determine yield to reveal the effects of number of eyes on plant development and yield. This was done using the following function: yield (g/plant) = number of eyes/seed tuber × number of stems/eye × number of tubers/stem × average single tuber weight.

For statistical analysis, R (R Core Team 2021) was used. For Trial 1, the ANOVA for split-plot trials was used from the Agricolae package (Felipe de Mendiburu 2020), and for Trial 2, the ANOVA for split-split-plot trials. For these trials, Fisher's LSD was used as a post-hoc test. In all trials, residuals were tested for normal distribution. Log or square root transformations were applied when residuals were not distributed normally. The relation between yield components in Trial 2 was calculated using Pearson's chi-squared tests.

Data of the sprouting tests were partly not distributed normally, even after transformation. Therefore, the non-parametric Kruskal-Wallis test was performed. This was done per hybrid separately; the treatments were separated according to Trials 1 and 2. For the treatments of Trial 2, Dunn's test was used as a post-hoc test. Here, we compared per hybrid separately the effect of number of eyes on the one hand and the effect of seedling tuber size and production origin on the other hand.

Results

Sprouting Test

A sprouting test was performed to compare the physiological age of the starting material. Tubers were collected using the same criteria as tuber selection for Trials 1 and 2, and data were analyzed per hybrid separately.

Effect of Number of Eyes

Number of eyes affected only sprout length in hybrid H3, where more eyes led to a higher sprout length (Table 4). The rest of the traits that were measured in the sprouting test was not affected by number of eyes; as a result, the physiological age in tubers with high or low number of eyes was assumed to be similar.

Effect of Size and Origin

Several traits in the sprouting test were affected by tuber size and production origin. Number of sprouts and total sprout fresh weight were higher in the larger seedling tubers in hybrid H3 produced in ANN. Seedling tubers of hybrid H4 of size class 35–45 mm produced in EMM produced more sprouts and had a higher total sprout fresh weight than those in the size class 28–35 mm (Table 4). Also in H4, larger seedling tubers produced in ANN led to a higher sprout fresh weight. Sprout length was not affected by any of the tuber size or origin treatments. Number of sprouts per eye was only affected in hybrid H3 from EMM, where larger tubers produced more sprouts per eye.

As an indication of physiological age, sprouting capacity (total sprout fresh weight/tuber fresh weight) was calculated from seedling tubers in the different treatments. In the hybrids H1 and H3, sprouting capacity was higher in seedling tubers with a lower tuber weight (Table 4); in the other two hybrids, no effect was found.

Table 4 Average values of traits measured in the sprouting test. Significant differences calculated with the Kruskal-Wallis test, followed by Dunn's post-hoc test, are indicated with letters. When no letters are present, the value differs from no other value in that group. Significant differences were calculated separately per hybrid and for the eyes and the size and origin treatments, so values presented in different horizontal lines were statistically compared with each other. Abbreviations of production origins are *GAR*, Garsthuizen; *ANN*, Anna Paulowna; *EMM*, Emmeloord

Hybrid	Origin	Treatment	Sprouting capacity	Number of sprouts	Sprout length (mm)	Sprout fresh weight (g)	Sprouts per eye
H1	GAR	eyes-high	0.021	4.3	176.7	0.98	0.95
H1	GAR	eyes-low	0.017	4.4	133.9	0.76	1.32
H2	GAR	eyes-high	0.017	3.7	140.3	0.87	0.57
H2	GAR	eyes-low	0.022	2.8	159.4	1.14	0.64
H3	GAR	eyes-high	0.013	5.3	149.3 a	0.74	0.98
H3	GAR	eyes-low	0.011	4.5	108.5 b	0.61	1.14
H4	GAR	eyes-high	0.014	4.4	136.3	0.61	0.78
H4	GAR	eyes-low	0.015	5.1	143.5	0.62	1.16
H1	ANN	size_28–35	0.024 a	3.7	126.6	0.59	1.21
H1	ANN	size_35–45	0.014 b	3.4	93.6	0.58	1.13
H1	EMM	size_28–35	0.026 ab	3.7	162.0	0.66	0.94
H1	EMM	size_35–45	0.020 ab	4.5	152.3	0.77	1.26
H1	GAR	size_28–35	0.024 ab	2.9	122.0	0.64	0.77
H1	GAR	size_35–45	0.013 b	3.3	110.3	0.50	0.80
H2	ANN	size_28–35	0.024	2.7	114.0	0.61	0.67 ab
H2	ANN	size_35–45	0.017	3.0	112.7	0.72	0.75 ab
H2	EMM	size_28–35	0.031	2.5	152.2	0.87	0.46 b
H2	EMM	size_35–45	0.024	3.3	183.0	1.00	0.85 a
H2	GAR	size_28–35	0.027	2.4	139.7	0.68	0.55 ab
H2	GAR	size_35–45	0.024	3.5	191.4	0.94	0.63 ab
H3	ANN	size_28–35	0.012 ab	3.4 b	77.3	0.35 b	1.01

Table 4 (continued)

Hybrid	Origin	Treatment	Sprouting capacity	Number of sprouts	Sprout length (mm)	Sprout fresh weight (g)	Sprouts per eye
H3	ANN	size_35–45	0.011 ab	5.6 a	120.3	0.61 a	1.20
H3	EMM	size_28–35	0.013 ab	3.9 ab	102.4	0.42 ab	1.06
H3	EMM	size_35–45	0.010 b	4.7 ab	126.2	0.57 ab	1.05
H3	GAR	size_28–35	0.015 a	4.3 ab	108.2	0.43 ab	1.00
H3	GAR	size_35–45	0.010 b	5.4 ab	131.3	0.60 ab	1.05
H4	ANN	size_28–35	0.019	4.2 ab	122.5	0.42 bc	1.08
H4	ANN	size_35–45	0.017	4.7 ab	126.2	0.85 a	1.13
H4	EMM	size_28–35	0.014	3.3 b	95.5	0.32 c	0.76
H4	EMM	size_35–45	0.017	5.4 a	147.1	0.82 a	0.99
H4	GAR	size_28–35	0.019	3.5 ab	106.5	0.43 bc	0.76
H4	GAR	size_35–45	0.014	4.6 ab	130.5	0.65 ab	0.82

Variation Within Seedling Tuber Batches

In seed tuber production, it is common practice to sort seed tubers based on square measure of the tubers. The size class 35–45 mm is often used for seed tubers. To determine the variation of tuber weight and number of eyes within this size class, these traits were measured in 420 tubers of each hybrid in the size class 35–45 mm (Fig. 1). The range in number of eyes per seedling tuber was different among the hybrids. The largest range was found in H3 with a minimum of 2 and a maximum of 14 eyes per tuber. H1 had the smallest range with a number of eyes between 1 and 8. H3 also had the largest difference in tuber weight, with values between 31 and 143 g. In H4, the smallest difference was found with seedling tuber weights between 28 and 106 g.

So, although seedling tubers were sorted based on square measure, large variations for number of eyes (factor 4–8 difference between high and low eye number) and seedling tuber weight (factor 3.8–7 difference between high and low seedling tuber weight) were found.

Field Results Trial 1: Number of Eyes

In this trial, we investigated the effect of number of eyes in seedling tubers on plant development in the field and on yield parameters.

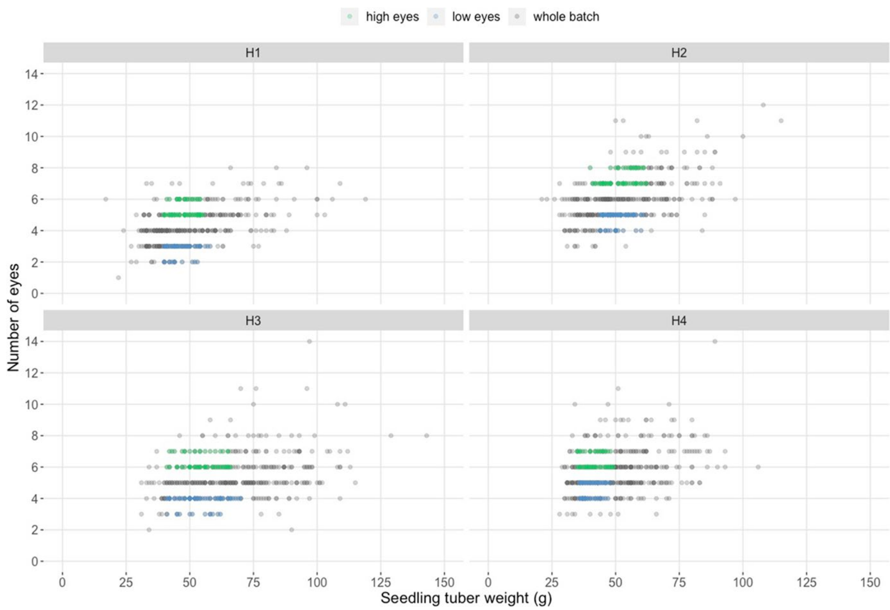

Fig. 1 Seedling tuber weight and number of eyes per tuber of a batch of 420 tubers per hybrid in the size class 35–45 mm of the hybrids H1, H2, H3 and H4. Tubers that were selected for the high and low eyes treatments of Trial 1 are shown in green (high) and blue (low)

Total tuber weight per plant as well as number of tubers per plant were only affected by genotype, not by number of eyes in the seedling tuber. To reveal the effect of number of eyes on plant development and yield, a calculation of the contribution of different components to total yield was made, and in these components, significant differences between the high and low eye classes were found.

All genotypes produced more stems per eye in the low eye class than in the high eye class. Number of stems per eye was also affected by genotype, and an interaction between eye number and genotype was found, where H1 produced 1.6 times more stems per eye in the low eye class compared to the high eye class and H4 only 1.1 times more. (Table 5, Fig. 2). In total, however, seedling tubers with more eyes resulted in more stems per plant, and this was only affected by number of eyes, not by genotype (Table 5, Fig. 2). Despite the higher number of stems per plant, no difference between treatments or genotypes was found for groundcover when comparing the area under the curve (AUC) of groundcover measurements.

Number of tubers per stem was higher (on average up to 0.4 tubers extra) in plants grown from seedling tubers in the low eye class; this variable was also affected by genotype with H1 and H2 producing more tubers than H3 and H4. Together with the lower number of stems per plant, the higher number of tubers per stem in the low eye class led to a lack of difference in number of tubers per plant between seedling tubers with high and low number of eyes (Table 5).

Tuber size was slightly higher in plants grown from seedling tubers with a low number of eyes (Table 5). Moreover, tuber size was affected by genotype. Overall, a higher number of stems per eye, combined with more tubers per stem and a slightly larger tuber size in seedling tubers in the low eye class, resulted in no difference in total tuber yield or number of tubers per plant between the high and low eye class. So, for total yield and number of tubers, the difference in number of eyes between the seedling tubers was compensated for by other yield components.

Field Results Trial 2: Seedling Tuber Size and Origin

In the second trial, the effects of seedling tuber size and production origin on plant development and yield were investigated. Seedling tubers of size class 28–35 and 35–45 mm were selected.

A larger seedling tuber size led to an increase in number of tubers per plant, while there was no effect on average weight per tuber. This resulted in a higher total tuber weight per plant (Table 6). Total tuber weight, average weight per tuber and number of tubers per plant all were affected by genotype, and no significant interactions between seedling tuber size and genotype were found (Table 6). Despite the effect of seedling tuber weight on total tuber number, no significant effects of genotype, production origin, or seedling tuber size on number of tubers per stems or number of stems per plant were found. The area under the curve (AUC) of ground cover was used as a measure for total ground cover during the season. AUC was significantly higher when larger seedling tubers were used.

Also for this trial, we calculated different yield components that contributed to total yield. Figure 3 shows the interrelations between these yield components of

Table 5 *P*-values of ANOVAs on yield and yield components from Trial 1, AUC is area under the canopy cover progress curve

	Tuber weight per plant	No. of stems per eye	No. of stems per plant	No. of tubers per stem	No. of tubers per plant	Tuber size	AUC
Hybrid	0.001**	2.3 x10^−5***	0.17	0.003**	0.001**	0.0008***	0.17
Eye class	0.73	9.1x10^−6***	0.0098**	0.03*	0.24	0.17	0.10
Hybrid × eye class	0.75	0.004**	0.84	0.52	0.56	0.82	0.40

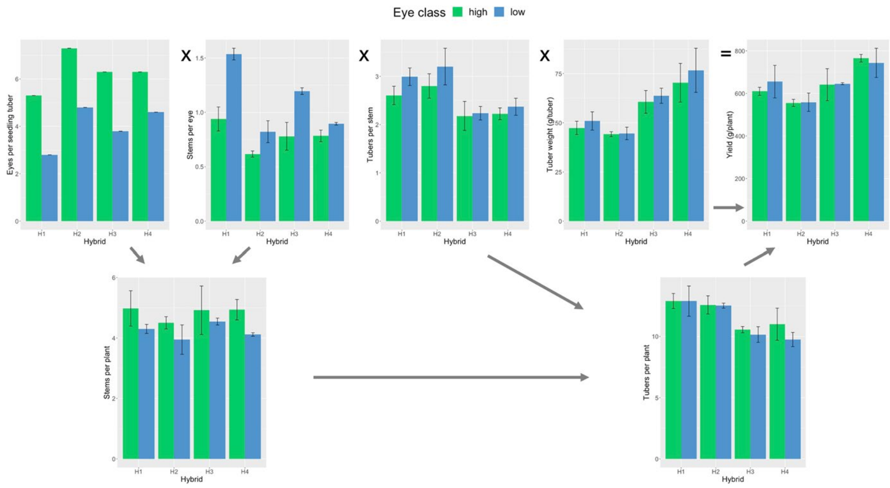

Fig. 2 Bar plots of yield and yield components of four hybrids grown from seedling tubers with high or low eye number per seedling tuber

both seedling tuber size classes of H1. A negative correlation was found between number of tubers per stem and number of stems per plant for both seedling tuber size classes. No significant relation was found between number of tubers per stem and number of tubers per plant for both size classes. In the size class 35–45 mm, a positive relation was found between number of tubers per plant and tuber weight per plant, while this relation was not significant in the size class 28–35 mm (Fig. 3). In both size classes, no relation was found between tuber weight per plant and number of stems per plant.

To estimate the impact of differences in seedling tuber weight on yield, the increase in tuber yield per extra gram of seedling tuber weight was calculated (Table 7). To determine the possible variation in yield due to seedling tuber weight when sorting seedling tubers based on square measure, we used the variation that was found in the batch of 420 seedling tubers in size class 35–45 mm (Fig. 1) for multiplying with the tuber yield increase per extra gram of seedling tuber (Table 7). Based on this calculation, the variation in seedling tuber weight within the size class 35–45 mm can lead to a variation in yield of up to 16.1 Mg/ha, depending on the genotype (Table 7).

Discussion

To understand the impact of seedling tuber quality on plant and crop development and tuber yield, we performed two field trials in which we determined the effects of number of eyes, tuber size and production origin. Moreover, a sprouting test was performed to compare the physiological age of seedling tubers of the different treatments that were used.

Table 6 *P*-values of ANOVAs performed for Trial 2, size and origin, AUC is area under the canopy cover progress curve

	Tuber weight per plant	Tuber weight per tuber	No. of tubers per plant	No. of tubers per stem	No. of stems per plant	Yield per seedling tuber weight	AUC
Name	8.4 ×10^−5 ***	3.4×10^−6 ***	0.0009***	0.1	0.2	4.1 × 10^−5 ***	0.3
Origin	0.2	0.07	0.7	0.7	0.9	0.5	0.1
Hybrid × origin	0.07	0.07	0.2	0.06	0.1	0.05	0.3
Size class	0.0008***	0.3	2.2 × 10^−6***	0.1	1	2.2* 10^−16	4.7 × 10^−7***
Size class × hybrid	0.7	0.9	0.5	0.8	0.8	2.8*10^−7	0.5
Size class × origin	0.09	0.2	0.4	0.4	0.4	0.03	0.9
Size class × hybrid × origin	0.6	0.05*	0.09	0.2	0.3	0.5	0.7

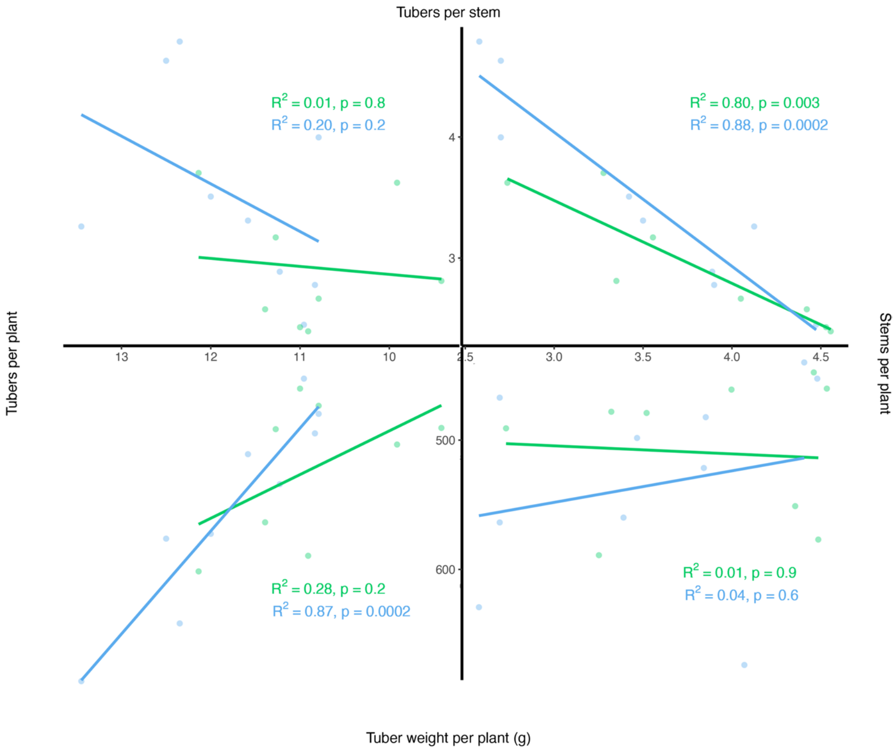

Fig. 3 Interactions between yield components for seedling tubers of size class 28–35 (green) and 35–45 (blue) of H1. R^2 and P-values, calculated using Pearson's chi-squared test, are indicated corresponding to the color of the plots

Effect of Number of Eyes, Production Origin and Size of Seedling Tubers

In Trial 1, we determined the effect of number of eyes in seedling tubers on plant and crop development and yield. As sprouts and eventually stems develop from the eyes of a seed tuber (Struik & Wiersema 1999), a tuber with more eyes potentially can develop more stems per plant. Indeed, we found that a higher number of eyes resulted in a higher number of stems per plant in the field. Previous research in tetraploid as well as diploid potato has shown that a higher number of stems lead to a higher number of stolons, and more stolons result in more tubers (Haverkort et al. 1990, Stockem et al. 2020).

In our research, the higher number of stems per plant did not result in more tubers per plant. An explanation might be the competition for resources among the stems. Previous research has shown that number of eyes per tuber and seed tuber size are positively related (Struik & Wiersema 1999). In the beginning of the growing period, the stems share the resources from the mother tuber (Struik 2007), where plants with more stems probably came from a larger seed tuber, with more resources. Later in the season, the stems become independent units that compete for resources such as light and nutrients (Struik 2007).

Table 7 Calculation of potential variation in yield due to differences in seedling tuber weight (STW) in the size class 35–45, based on measured variation (highest and lowest tuber weight within the size class) in the seedling tuber batch (Fig. 1) and yield difference due to seedling tuber weight in Trial 2

Hybrid	Size class (mm)	Average STW (g)	Difference in STW between size classes (g)	Max. difference in STW measured within size class 35–45 mm (g) (Fig. 1)	Tuber yield Trial 2 (Mg/ha)	Difference in yield between size classes (Mg/ha)	Tuber yield increase (Mg/ha) per extra gram seedling tuber	Potential variation in Mg/ha in size class 35–45
H1	28–35	25.2	14.0	-	32.0	2.2	-	-
	35–45	39.2		102	34.2		0.16	16.1
H2	28–35	26.7	13.6	-	29.5	1.8	-	-
	35–45	40.3		94	31.2		0.13	12.2
H3	28–35	29.1	26.8	-	35.0	3.1	-	-
	35–45	55.8		112	38.1		0.12	13.0
H4	28–35	22.2	24.1	-	45.0	2.7	-	-
	35–45	46.3		78	47.8		0.11	8.8

In our study, we selected seedling tubers that only differed in number of eyes, and not in tuber weight, so plants from tubers with more eyes that developed more stems did not have the advantage of larger initial resources. Indeed, no difference in ground cover was found between the two groups, so the plants with more stems were not able to capture more light than the plants with fewer stems. In our trial, no difference in total tuber weight or in number of tubers per plant was found between plants grown from seedling tubers with high or low number of eyes. The yield component analysis has shown that the higher number of stems was compensated for by a lower number of tubers per stem, resulting in an equal number of tubers between the two groups.

In a second field trial, we investigated the effect of seedling tuber weight with a similar number of eyes between the two tuber size classes. Seedling tubers of the size class 28–35 mm and 35–45 mm were selected as two treatments in Trial 2. A higher seedling tuber weight resulted in a higher total tuber weight and more tubers per plant. Also, ground cover increased in the size class 35–45 mm, while the number of stems per plant and the number of tubers per stem did not differ between the size classes. So with a higher seedling tuber weight, rather than with more stems, plants develop faster which results in an increased ground cover, more tubers per plant and a higher total tuber weight. These results suggest that a higher number of eyes in a seedling tuber only is advantageous when accompanied by a higher seedling tuber weight to result in an increase in ground cover and in more yield.

Production origin from three locations in the Netherlands did not affect the yield or yield components that were measured, and also soil cover was not affected by production origin of the seedling tubers. Differences would be expected as growing days differed in the different locations. Also, trials with seed tubers have shown that the production location affects the seed tuber quality (Kwambai et al. 2023). Differences may be small because the production locations all were in the Netherlands and relatively close together. Also, the soil compositions and pH values of the fields were comparable. Moreover, seedling tubers that were used in the trial were selected for similar weight; this selection could have played a role as well. Recently, Zou et al. (2024) showed that a function based on sprouting behaviour as total sprout dry weight per tuber at different time points during storage was a more accurate method to quantify physiological age. Such a method can be applied to discriminate among small differences in physiological age, such as found in this study.

Implications for Breeding and Ware Crop Production

Understanding how yield components interact and which component is limiting to gain higher yield is important for breeding as well as for ware crop production (Stockem et al. 2020). For breeding, it gives direction on which traits need to be improved, and in ware crop production, it can help optimizing the crop management for higher yield. A higher number of eyes did result in more stems per plant, but not in more tubers or a higher yield. Therefore, when making selections for tuber number or yield, number of eyes in seedling tubers is not an important quality trait that affects the selections. When the number of stems per plant, however, is part of the selection criteria, variation in number of eyes can lead to unwanted variation in the data.

A higher seedling tuber weight resulted in increased yield (Table 6). Within the seedling tuber lots, large variation in weight was found for all hybrids in the size class 35–45 mm, as shown in Fig. 1. Tuber shape affects the variation in tuber weight within a size class, because the square measure of a size class was measured on the lowest diameter of the tuber. So, longer tubers can have a larger tuber weight than shorter tubers, while belonging to the same size class.

We calculated that the tuber weight variation that was found in size class 35–45 mm can lead to yield differences up to 8.9 to 16.1 Mg/ha for the hybrids that were used in this study. This is between 18 and 45% of the average yield of the hybrids in size class 35–45 mm over all locations. As these effects were calculated based on the seedling tubers with the highest and lowest weight, it is important to note that the effect of variation in seedling tuber weight in the size class 35–45 mm is an estimation and not an actually measured value. In breeding, this effect of seedling tuber weight on yield can lead to selecting varieties for high yield that is the result of a higher seedling tuber weight rather than better genetics. Therefore, it is important to use similar seedling tuber weights rather than the same size class of seedling tubers in breeding trials, especially because different tuber shapes are present in breeding trials. Moreover, seedling tuber weight could be considered as a selection trait itself, as the seedling tubers of hybrids that produce large tubers have a higher yield potential.

In ware crop production, planting density partly is based on the size class of the seed tubers to optimize crop management for high yield. However, the variation that we found in seedling tuber weight and the large effect on yield lead to the question whether plant density can be optimized better for high yields when using tuber weight instead of size class to classify seed(ling) tubers.

Conclusions

In this research, we investigated the effect of number of eyes, tuber size and production origin of seedling tubers on plant growth and tuber production in the field. No effect of production origin was found; this might be due to the relatively small distance between the production sites, or because we selected seedling tubers for the trials based on similar tuber traits.

A higher number of eyes per tuber led to a higher number of stems per plant; however, this did not result in an increase in soil cover. Besides that, the higher number of stems was compensated for by a lower number of tubers per stem, resulting in no difference in total number of tubers per plant or tuber weight per plant between plants grown from seedling tubers with a high or a low number of eyes.

In all hybrids, a higher seedling tuber weight led to higher yield. A variation in seedling tuber weight up to factor seven between low and high weight was found within the size class 35–45 mm. This variation can lead to a yield difference up to 16.1 Mg/ha, which is 45% of the average yield, based on the results of Trial 2.

With these results, we can design trials with lower variation that result in more precise results and lead to better selections.

Appendix

Table 8 Mean values of traits measured in sprouting trials of Trial 1: eyes and Trial 2: size and origin. Abbreviations of production origins are *GAR*, Garsthuizen; *ANN*, Anna Paulowna; *EMM*, Emmeloord

Trial	Hybrid	Origin	Treatment	Number of sprouts	Sprouts per eye	Sprout length (mm)	Total fresh weight sprouts (g)	Fresh weight per sprout (g)	Sprouting capacity
Trial 1: eyes	H1	GAR	eyes-high	4.3	0.95	176.7	0.98	0.23	0.021
Trial 1: eyes	H1	GAR	eyes-low	4.4	1.32	133.9	0.76	0.20	0.017
Trial 1: eyes	H2	GAR	eyes-high	3.7	0.57	140.3	0.87	0.27	0.017
Trial 1: eyes	H2	GAR	eyes-low	2.8	0.64	159.4	1.14	0.47	0.022
Trial 1: eyes	H3	GAR	eyes-high	5.3	0.98	149.3	0.74	0.15	0.013
Trial 1: eyes	H3	GAR	eyes-low	4.5	1.14	108.5	0.61	0.14	0.011
Trial 1: eyes	H4	GAR	eyes-high	4.4	0.78	136.3	0.61	0.15	0.014
Trial 1: eyes	H4	GAR	eyes-low	5.1	1.16	143.5	0.62	0.15	0.015
Trial 2: size and origin	H1	ANN	28–35	3.7	1.21	126.6	0.59	0.17	0.024
Trial 2: size and origin	H1	ANN	35–45	3.4	1.13	93.6	0.58	0.23	0.014
Trial 2: size and origin	H1	EMM	28–35	3.7	0.94	162.0	0.66	0.20	0.026
Trial 2: size and origin	H1	EMM	35–45	4.5	1.26	152.3	0.77	0.18	0.020
Trial 2: size and origin	H1	GAR	28–35	2.9	0.77	122.0	0.64	0.23	0.024
Trial 2: size and origin	H1	GAR	35–45	3.3	0.80	110.3	0.50	0.15	0.013
Trial 2: size and origin	H2	ANN	28–35	2.7	0.67	114.0	0.61	0.25	0.024
Trial 2: size and origin	H2	ANN	35–45	3.0	0.75	112.7	0.72	0.26	0.017
Trial 2: size and origin	H2	EMM	28–35	2.5	0.46	152.2	0.87	0.44	0.031
Trial 2: size and origin	H2	EMM	35–45	3.3	0.85	183.0	1.00	0.30	0.024

Table 8 (continued)

Trial	Hybrid	Origin	Treatment	Number of sprouts	Sprouts per eye	Sprout length (mm)	Total fresh weight sprouts (g)	Fresh weight per sprout (g)	Sprouting capacity
Trial 2: size and origin	H2	GAR	28–35	2.4	0.55	139.7	0.68	0.30	0.027
Trial 2: size and origin	H2	GAR	35–45	3.5	0.63	191.4	0.94	0.27	0.024
Trial 2: size and origin	H3	ANN	28–35	3.4	1.01	77.3	0.35	0.11	0.012
Trial 2: size and origin	H3	ANN	35–45	5.6	1.20	120.3	0.61	0.13	0.011
Trial 2: size and origin	H3	EMM	28–35	3.9	1.06	102.4	0.42	0.11	0.013
Trial 2: size and origin	H3	EMM	35–45	4.7	1.05	126.2	0.57	0.12	0.010
Trial 2: size and origin	H3	GAR	28–35	4.3	1.00	108.2	0.43	0.11	0.015
Trial 2: size and origin	H3	GAR	35–45	5.4	1.05	131.3	0.60	0.13	0.010
Trial 2: size and origin	H4	ANN	28–35	4.2	1.08	122.5	0.42	0.13	0.019
Trial 2: size and origin	H4	ANN	35–45	4.7	1.13	126.2	0.85	0.21	0.017
Trial 2: size and origin	H4	EMM	28–35	3.3	0.76	95.5	0.32	0.11	0.014
Trial 2: size and origin	H4	EMM	35–45	5.4	0.99	147.1	0.82	0.16	0.017
Trial 2: size and origin	H4	GAR	28–35	3.5	0.76	106.5	0.43	0.16	0.019
Trial 2: size and origin	H4	GAR	35–45	4.6	0.82	130.5	0.65	0.14	0.014

Table 9 Mean values of traits measured in the field Trials 1 and 2. Abbreviations of production origins are *GAR*, Garsthuizen; *ANN*, Anna Paulowna; *EMM*, Emmeloord

Trial	Hybrid	Origin	Treatment	Tuber weight (g/plant)	Stems per eye	Stems per plant	Tubers per stem	Tubers per plant	Tuber size (g/tuber)	Area under the curve of soil cover (%.d)
Trial 1: eyes	H1	GAR	eyes-high	609.7	0.9	5.0	2.6	12.9	47.4	6833
Trial 1: eyes	H1	GAR	eyes-low	655.3	1.5	4.3	3.0	12.9	50.9	6720
Trial 1: eyes	H2	GAR	eyes-high	555.3	0.6	4.5	2.8	12.6	44.2	6604
Trial 1: eyes	H2	GAR	eyes-low	558.5	0.8	3.9	3.2	12.5	44.6	6636
Trial 1: eyes	H3	GAR	eyes-high	640.9	0.8	4.9	2.2	10.6	60.6	6665
Trial 1: eyes	H3	GAR	eyes-low	645.7	1.2	4.5	2.2	10.2	63.7	6404
Trial 1: eyes	H4	GAR	eyes-high	765.6	0.8	4.9	2.2	11.0	70.3	6640
Trial 1: eyes	H4	GAR	eyes-low	743.4	0.9	4.1	2.4	9.8	76.7	6558
Trial 2: size and origin	H1	ANN	28–35	472.7	1.1	3.7	2.9	10.5	45.3	6490
Trial 2: size and origin	H1	ANN	35–45	481.2	1.2	4.1	2.7	11.0	43.7	6686
Trial 2: size and origin	H1	EMM	28–35	564.0	1.2	4.5	2.5	11.2	50.6	6366
Trial 2: size and origin	H1	EMM	35–45	530.2	0.7	2.9	4.0	11.8	45.0	6669
Trial 2: size and origin	H1	GAR	28–35	509.2	0.9	3.5	3.3	11.0	46.2	6370
Trial 2: size and origin	H1	GAR	35–45	600.5	0.8	3.4	3.8	12.5	48.0	6650
Trial 2: size and origin	H2	ANN	28–35	414.4	1.0	3.7	2.9	10.3	40.2	6259
Trial 2: size and origin	H2	ANN	35–45	443.4	0.9	3.9	3.0	10.5	42.4	6604
Trial 2: size and origin	H2	EMM	28–35	482.6	0.8	3.9	3.1	11.4	42.4	6318
Trial 2: size and origin	H2	EMM	35–45	491.9	0.9	4.6	2.7	12.0	40.9	6393
Trial 2: size and origin	H2	GAR	28–35	454.3	1.0	5.0	2.3	10.9	41.6	6229
Trial 2: size and origin	H2	GAR	35–45	470.2	0.8	4.4	2.9	11.9	39.8	6372
Trial 2: size and origin	H3	ANN	28–35	561.5	0.9	3.5	3.1	10.6	52.9	6462
Trial 2: size and origin	H3	ANN	35–45	608.0	1.0	3.9	2.9	10.9	56.6	6689
Trial 2: size and origin	H3	EMM	28–35	529.4	0.9	3.6	2.7	9.2	57.3	6243

Table 9 (continued)

Trial	Hybrid	Origin	Treatment	Tuber weight (g/plant)	Stems per eye	Stems per plant	Tubers per stem	Tubers per plant	Tuber size (g/tuber)	Area under the curve of soil cover (%.d)
Trial 2: size and origin	H3	EMM	35–45	526.7	0.8	3.8	3.0	11.1	47.6	6535
Trial 2: size and origin	H3	GAR	28–35	542.3	0.9	3.8	2.6	9.9	54.9	6439
Trial 2: size and origin	H3	GAR	35–45	616.6	0.7	3.2	3.6	11.3	54.6	6769
Trial 2: size and origin	H4	ANN	28–35	684.4	0.9	3.4	2.6	8.8	78.0	6402
Trial 2: size and origin	H4	ANN	35–45	709.7	0.9	3.9	2.9	10.3	69.4	6810
Trial 2: size and origin	H4	EMM	28–35	705.6	0.9	3.4	2.7	9.1	77.7	6281
Trial 2: size and origin	H4	EMM	35–45	758.5	0.8	3.6	2.7	9.5	80.0	6713
Trial 2: size and origin	H4	GAR	28–35	655.7	0.7	3.5	2.5	8.3	79.4	6181
Trial 2: size and origin	H4	GAR	35–45	711.8	0.7	3.6	2.6	8.6	83.1	6454

Declarations

Conflict of Interest PCS is the editor-in-chief of Potato Research.
JES, MDB and MED are employees of Solynta.

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