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Branching response to stem density and its impact on yield in hybrid potato grown from true seeds and seedling tubers

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ABSTRACT

Context: Hybrid potato crops can be grown from true potato seeds or from seedling tubers. True-seed-grown plants produce lower marketable tuber yield than seedling-tuber-grown plants, because of their low early vigour and distinct growth and development patterns, notably in term of main stem number and stem branching. These differences are pivotal for yield formation but their impacts on crop performance and yield are not well understood.

Objectives: We quantified the differences between the propagule types (true seeds vs seedling tubers) in their branching responses to stem density and assessed to what extent these differences contribute to differences in crop development and tuber production.

Methods: Two field experiments were conducted in different years, planting transplants from true seeds and pre-sprouted seedling tubers from the same genotype, while controlling their stem density per unit area. Responses in stem branching and biomass partitioning to stem density were quantified on individual main stems, followed by an evaluation of the impact of these responses on crop performance.

Results: On individual main stems in both propagule types, higher stem density decreased branch development, decreased the number of branches above- and belowground, resulted in shifts in aboveground branch distribution towards lower branching orders, and led to smaller tuber sizes. However, such branching responses were stronger in true-seed-grown plants than in seedling-tuber-grown plants. At crop level, differences between propagule types were significant in canopy duration, number of tubers, tuber size distribution and marketable yield, but there was no stem density effect.

Conclusion: Our results emphasized the differences between propagule types in branching and its impact on crop development and tuber yield, due to the absence of stem density effects. Propagule type effects could be attributed to intrinsic differences between propagule types in branching control, growth habit and source-sink relations. These effects are relevant for hybrid potato breeding and require further research. Management practices were partly responsible for year-to-year differences in branching and yield formation, which highlights their significance for hybrid potato production.

1. Introduction

Potato, the largest non-cereal food crop worldwide, is conventionally grown from seed tubers, which are vegetatively generated storage organs. Since the recent development of the diploid hybrid potato breeding technology, multiple types of propagules have been introduced into potato production systems, such as true potato seed (TPS or true seed), TPS transplants and seedling tubers (de Vries et al., 2023; Eggers et al., 2021; Lindhout et al., 2018). True seeds are botanical seeds produced via sexual propagation, and seedling tubers are the seed tubers derived from plants grown from true seeds. The use of true seeds brings advantages: they are almost entirely free from seed-borne diseases, have a high multiplication rate and are easy to store and transport (Almekinders et al., 2009; Bradshaw, 2022; de Vries et al., 2016; Struik et al., 2023). However, true-seed-grown plants exhibit distinct growth and development patterns that vary from regular tuber-grown plants. There is limited understanding of the impact of these growth and developmental differences on tuber yield and of the underlying mechanisms. This hampers the adoption of true seed in commercial potato production (Almekinders et al., 1996; Çalışkan et al., 2009; de Vries

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et al., 2023; Kacheyo et al., 2021; Struik et al., 2023).

Currently, seedling tubers derived from hybrid true seeds or tubers of later generations are introduced in production systems, where some hybrid cultivars show comparable crop development and yield potential, compared to conventional cultivars (Benz et al., 1995; Stockem et al., 2020; Struik and Wiersema, 1999; Wiersema, 1984). However, (trans)plants grown from true seeds generally have smaller canopy or slower canopy development and produce a lower marketable yield, compared to seedling-tuber-grown plants, even when they belong to the same genotype and are planted at similar density (Almekinders et al., 1996; Benz et al., 1995; de Vries et al., 2023). These studies also report that smaller tubers but more tubers per production area are produced from true-seed-grown plants than those grown from seedling tubers, which results in different market values. Yet, our understanding of the causes of these differences is limited.

An obvious difference between true-seed grown plants and tuber-grown plants is the number of main stems per plant. A true seed produces a single-stemmed plant, whereas a seedling tuber can produce multiple main stems, each stem becoming an independent production unit sometime after emergence (Moorby, 1978). The main stems may also differ between the two propagule types, especially in branch production. In single-stemmed independent plants grown from true seeds and seedling tubers, the main stems produce divergent temporal-spatial distribution of branches above- and belowground, which influences plant architectural development and biomass partitioning (Gu et al., 2024; Kacheyo et al., 2021). When growing these plants as crops, their differences in branching can affect crop yield, as proven in many other crop species (e.g., Tian and Jiao, 2015). In potato crops, particularly, the aboveground branches with leaves that are photosynthetically active provide assimilates to belowground branches, which are stolons (hooked, horizontally growing branches) and tubers (swollen stolons), but they also compete with each other and with other types of stem structures, which influences crop development, biomass partitioning and yield (Almekinders and Struik, 1996; Oparka, 1985). Therefore, quantifying differences in branching between the true-seed-grown and seedling-tuber-grown plants is fundamental to elucidate their different performances at crop level.

Moreover, branching is highly plastic in potato crops (Ewing and Struik, 1992; Steward et al., 1981). The production of different types of branches can be influenced by various external factors, including plant and stem density. For a crop grown from seedling tubers, each plant produces a collection of multiple main stems with branches. In contrast, a crop grown from true seed should have more plants per unit area, as all plants are single-stemmed, with specific patterns of branching. Stem density is one of the yield components in potato crops, which influences canopy development, tuber yield and tuber size distribution in both propagule types (Almekinders, 1995; Knowles and Knowles, 2016; van Dijk et al., 2021a). The intrinsic differences between the two propagule types can interact with the impact of stem density, which may give rise to divergent responses in crops grown from these propagule types regarding branching above- and belowground and thus yield formation.

Previous research showed the response of branching to stem density in qualitative terms, for each of the two types of propagules. For example, increased stem density in true-seed-grown plants enhanced total tuber yield and shifted tuber size distribution towards smaller size (Çalışkan et al., 2009; van Dijk et al., 2021a). In seedling-tuber-grown plants, the number of aboveground branches per stem was lower with increasing stem density, but canopy cover duration and tuber yield were higher at higher stem density (Engels et al., 1993a, 1993b). While in other research using seed tubers as planting material, tuber yield increases, no changes or even reductions have been reported (Allen and Wurr, 1992; Bussan et al., 2007; Fleisher et al., 2011; Knowles and Knowles, 2016; Love and Thompson-Johns, 1999). There is a lack of systematic understanding of how branching above- and belowground responds to stem density and how these responses to density impact tuber production, which makes it difficult to evaluate differences in branching and yield formation in potato crops grown from the two propagule types.

Therefore, we aimed to 1) quantify to what extent the propagule types differ in their branching responses to stem density on individual main stems; 2) assess to what extent these differences contribute to differences in crop development and tuber production. We conducted two field experiments in different years, using true-seed-grown and seedling-tuber-grown plants from the same genotype, while controlling their stem density. Their responses in branching and biomass partitioning to stem density were quantified on individual main stems, followed by an evaluation of the impact of these responses on crop performance.

2. Materials and methods

2.1. Experimental site and plant materials

The field experiments were carried out in 2021 and 2022 at the experimental farm (UNIFARM) of Wageningen University & Research, Wageningen, the Netherlands (51° 59’ N, 5 ° 39’ E). The soil of the experimental sites was sandy with a pH of 5.6 and 3.5 % organic matter. The meteorological data were recorded daily by a weather station (https://veenkampen.nl/data/), including global incoming radiation (MJ m^{-2}), average air temperature (°C) and precipitation (mm) during the growing seasons (Supplementary Fig. S1). The growing season ran from 18 May to 4 October (139 days) in 2021 and from 12 May to 26 September (137 days) in 2022.

Plant materials were produced by the Dutch potato breeding company Solynta (Wageningen, the Netherlands) in the year preceding each experiment. Two types of propagules, i.e., true seeds and seedling tubers, of the genotype SOLHY007 were used, the most advanced genotype at that time. To synchronize development and avoid night frost damage, pre-sprouted seedling tubers and transplants from true seeds were raised separately before the start of the field experiments. Seedling tubers with square size of 35 – 45 mm harvested in the previous growing season were stored at 4 °C. To control the number of main stems per plant, seed tubers were taken out of storage and pre-sprouted on 29 March 2021 and 28 March 2022 for six weeks, as described by Struik and Wiersema (1999). On 12 April 2021 and 11 April 2022, true seeds were sown individually in plug trays (plug dimensions: 28 mm diameter, 32 mm height) with a mixture of 30 % peat, 50 % coco peat and 20 % perlite and grown in the greenhouse for about four weeks. After that, young transplants were hardened off for one week in a screenhouse with open sides, which made true-seed-grown transplants adapted to outdoor environment and reduced the transplanting shock in the field. The greenhouse settings and cultivation protocols were as described by van Dijk et al. (2021b). Two days before (trans)planting, seedling tubers with one or multiple green sprouts of 1 cm and young plants grown from true seeds with 6 – 8 true leaves and of homogenous size were selected. On 18 May 2021 and 12 May 2022, all propagules were (trans)planted into the field.

2.2. Experimental design and crop management

A randomized complete block design (RCBD) was used for both experiments. Each block contained six plots in which the six combinations of two propagule types and three stem densities were randomly applied. There were three replications in 2021 and four in 2022. To be able to compare propagule types, the stem density treatments were realized by keeping a constant spacing between planting holes per row while manipulating the number of main stems in each planting hole. The row distance was 0.75 m, and within-row spacing between holes was 0.20 m. The three stem densities were: one (D1), two (D2) and three (D3) main stems per hole, which resulted in 6.7, 13.3 and 20 main stems per m^2, respectively. For seedling-tuber-grown plants, one tuber was planted in each planting hole and the number of sprouts per tuber was controlled:

one, two or three sprouts per tuber were maintained for the respective stem densities. For true-seed-grown plants, to simulate clustering of main stems as grown from seedling tuber, one, two or three transplants were planted into one hole to realize the respective stem densities. The number of stems per plant was checked after full emergence and excess stems were removed to maintain the intended stem densities accordingly. The achieved stem densities are shown in Supplementary Table S1.

For both years, small ridges were made before transplanting, and the ridges were hilled up two to three times until the seedling tubers and the plugs of true-seed-grown plants were covered by about 10 – 15 cm of soil. Fertilization was applied homogeneously in the field one month before (trans)planting, with 150 kg ha^{-1} N, 60 kg ha^{-1} P_2O_5 and 150 kg ha^{-1} K_2O. Weed control was done manually to avoid herbicide damage. Other crop management practices such as crop protection measures were conducted according to Dutch potato cultivation standards. Additional irrigation was applied when necessary.

2.3. Measurements and calculations

2.3.1. Thermal time, destructive harvests, and non-destructive measurements

Thermal time (°Cd) was calculated from daily air temperature from the (trans)planting date until the harvest date for both propagule types, following the method of Khan et al. (2019). The base temperature was set to 0 °C (van Dijk et al., 2021b). Two intermediate harvests and a final harvest were done in 2021, while an additional intermediate harvest was conducted in 2022. The development of aboveground branches was assessed twice and non-destructively as branch count, from the beginning of branch appearance until canopy closure. The dates of each measurement and the respective thermal days are listed in Table 1.

Non-destructive measurements were conducted in each plot, in which two representative main stems from two planting holes were selected and marked. The number of aboveground branches on individual main stems were counted, separated based on their assigned branching order (Fig. 1 A). A detailed description of branching orders can be found in Gu et al. (2024).

At each intermediate harvest, entire plants, including aboveground and belowground parts, were sampled separately from four planting holes per plot. The number of main stems was counted in each planting hole. A sub-sample of two main stems was randomly selected from two different plants to determine the aboveground branching pattern. For each main stem, the characteristics of main stem and branching were quantified, including main stem height, number of nodes and leaves on the main stem and individual leaf area, the number of branches, their branching order and node position on the main stem, as well as the summed branch leaf area for each branching order.

Aboveground main stem nodes were counted acropetally from the soil level, thus identifying the main stem node position, called node rank. To eliminate differences in the final number of main stem nodes between the two propagules and between-stem variations within each propagule, the relative node position was defined as the main stem node rank of a specific branch divided by the total number of nodes of that main stem. By definition, the relative node position of 1.0 refers to the topmost node, as illustrated in Fig. 1B. The branch count and the branch leaf area of each branching order were determined based on the relative node positions on the main stem of the branches. The total number of branches per branching order was then grouped into five position ranges: 0.0 – 0.2, 0.2 – 0.4, 0.4 – 0.6, 0.6 – 0.8, 0.8 – 1.0. The number of branches and leaf area per branching order per position range were determined by the average values of two observations in each plot.

As the main stem origin of belowground parts was difficult to assess, belowground structures were pooled per planting hole and separated into branches (including stolons and tubers), and roots. Tubers from each planting hole were scanned using a tuber phenotyping machine SmartGrader (GeJo Grading Services B.V., Luttelgeest, the Netherlands). Individual tuber fresh weight and square size were recorded. Square sizes of tubers were assessed based on their transverse diameter, and tubers were categorized into six size classes: 0 – 25, 25 – 35, 35 – 45, 45 – 55, 55 – 65 and 65 – 75 mm.

After that, biomass partitioning within individual main stems was determined for each plot. The aboveground parts from each selected main stem were separated into main stem leaves and stem, branch leaves and stems, and berries. These parts were oven dried at 105 °C to constant weight, and the biomass of each part per main stem was recorded using an electric balance. The belowground biomass of stolons, roots and tubers from each planting hole was taken separately, and then divided by the number of main stems per planting hole to obtain their biomass per main stem.

At final harvest, only tubers remained, and all samples were collected at plot level. Tubers from 10 (2021) or 12 (2021) planting holes per plot were collected. Individual tuber fresh weight, square size and total fresh weight per plot were assessed. A sub-sample of tubers of about 1 kg was taken from each plot to assess tuber dry-matter concentration after drying at 105 °C. Tuber dry weight per plot was then calculated as the product of total fresh weight per plot and dry-matter concentration.

2.3.2. Canopy cover measurement and model

At crop level, green canopy cover was determined weekly for each plot from (trans)planting until haulm senescence. A camera frame was used with the dimensions 0.75 m × 0.99 m, which produced photos that captured an area of 5 planting holes. Within each plot, two photos were taken of the two inner rows, with fixed locations in the field during the whole growing season. The percentage of green area from each photo observation was analysed in MATLAB, using the photo processing software Canopeo (Oklahoma State University App Center; https://canopeoapp.com/). The canopy cover percentage per plot was then determined by the average values of two observations in each plot.

The measured canopy cover development over thermal time per plot was fitted into the canopy cover model, as described by Khan et al. (2019). This model describes the canopy development pattern which

Table 1
Harvest date and the respective days (d) and thermal time (°Cd) after (trans)planting.

Year	Non-destructive measurements and harvests	Date	Days after (trans)planting (d)	Thermal time (°Cd)
2021	Branch count 1	17 June	30	420
	Branch count 2	2 July	45	660
	Intermediate harvest 1	19 July	62	954
	Intermediate harvest 2	16 August	90	1440
	Final harvest	4 October	139	2180
2022	Branch count 1	10 June	29	434
	Intermediate harvest 1	20 June	39	586
	Branch count 2	4 July	53	812
	Intermediate harvest 2	18 July	67	1035
	Intermediate harvest 3	15 August	95	1460
	Final harvest	26 September	137	2063

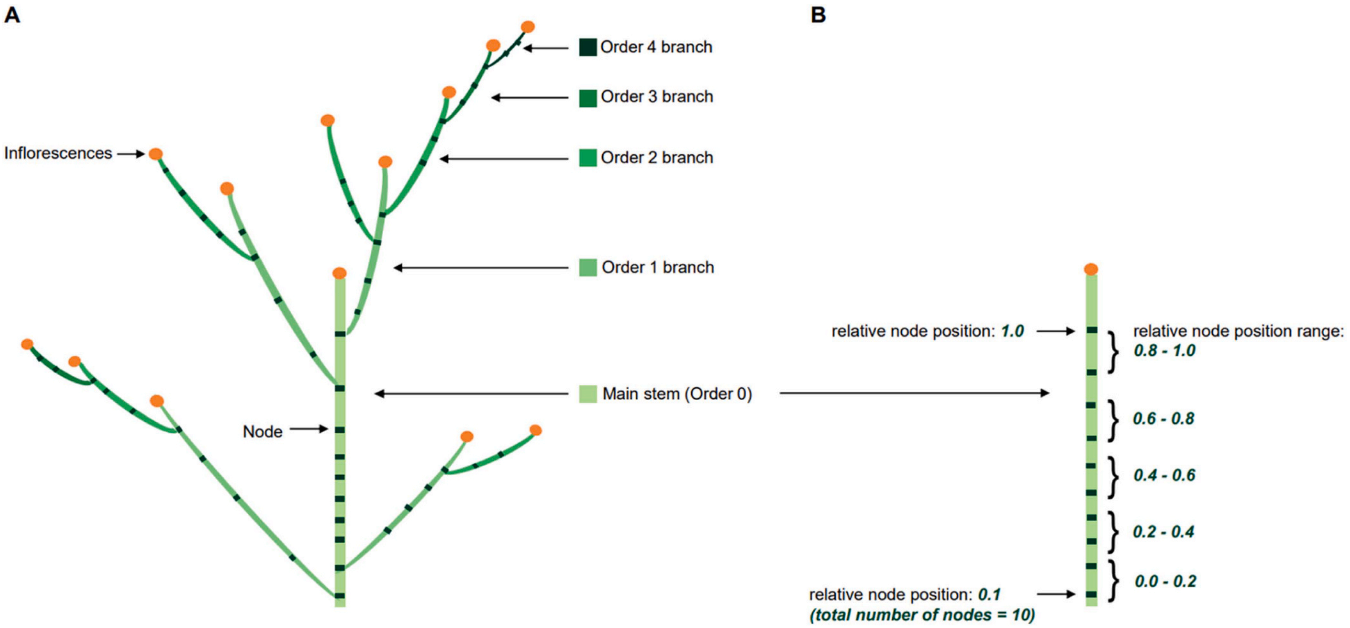

Fig. 1. Illustration of stems and branches assigned with specific branching orders and relative node positions. A) Branching orders are indicated by different shades of green. B) An example of relative node position for the lowest node is calculated as 1 / 10 = 0.1, which belongs to the position range 0.0 – 0.2.

mainly contains three phases, namely the buildup phase (1), the maximum canopy cover phase (2) and the senescence phase (3). Five model parameters were used: t_{m1} defines the moment of the highest canopy build up rate and t_1 is the moment that canopy cover reaches its maximum v_{max}; t_2 defines the start of canopy senescence and t_e is the end of senescence with zero canopy cover. The equations of the three phases of the model are:

$$v = v_{\max}\left(1+\frac{t_1-t}{t_1-t_{m1}}\right)\left(\frac{t}{t_{m1}}\right)^{\frac{t_1}{t_1-t_{m1}}} \text{ with } 0 \le t \le t_1 \tag{1}$$

$$v = v_{\max} \text{ with } t_1 \le t \le t_2 \tag{2}$$

$$v = v_{\max}\left(\frac{t_e-t}{t_e-t_2}\right)\left(\frac{t+t_1-t_2}{t_1}\right)^{\frac{t_1}{t_e-t_2}} \text{ with } t_2 \le t \le t_e \tag{3}$$

The model parameters were estimated using Nonlinear Least Squares regression, applying the Gauss method. Two secondary parameters, t_2 - t_1 and t_e - t_2, were then derived to describe the duration of the maximum canopy cover phase and of the senescence phase, respectively.

2.3.3. Light interception and RUE_{tuber} calculations

The daily photosynthetically active radiation (PAR) was first calculated as 50 % of the global incoming radiation. Daily canopy cover was estimated from the model for each plot, which was then converted into the estimated fraction of daily PAR intercepted (fPAR), using a linear relationship given by Haverkort et al. (1991) as fPAR(%) = 0.895 × canopy cover (%) + 0.043. Estimated total light interception was then calculated over the whole growing season as multiplying the daily incoming PAR by the daily fPAR and summing up the daily values. The efficiency of radiation use for the formation of tuber biomass (RUE_{tuber}) was calculated as the slope of the linear regression between tuber biomass per m^2 and cumulative light interception at all harvests.

2.4. Statistical analysis

Data collected in the two years were analysed separately. The data were assessed for normal distribution using the Shapiro-Wilk normality test. In cases in which the data were not normally distributed, such as percentage data, an arcsine square root transformation was applied. However, if the transformed data continued to deviate from normality, the original data were retained. To evaluate the performance of the canopy cover model, root mean squared error (RMSE) was calculated as a measure of goodness of fit. Average value and standard error of the mean of each measured (e.g., number of branches per main stem) and estimated (e.g., canopy cover model parameters, estimated total light interception, RUE_{tuber}) variable were first calculated for each plot. Then a two-way ANOVA was performed based on the RCBD design, across all treatments (propagule types and stem densities) and their interaction. A significance level of 0.05 was used to evaluate differences between treatments. Multiple comparisons of means for significant treatment effects were conducted using Tukey HSD test. All data were processed and analysed in R 4.3.1 (R Core Team, 2023).

3. Results

3.1. Branching responses to stem density on individual main stems

3.1.1. Branch development

The general trend of the change in number of branches over thermal time was similar for the two years (Fig. 2). At low stem density (D1), branches appeared faster and were more abundant than at higher stem densities (D2 and D3), both aboveground (Fig. 2 A, 2B, 2E and 2 F) and belowground (Fig. 2 C, 2D, 2 G and 2 H). Although this pattern was similar for the two propagule types, differences between stem densities were larger in true-seed-grown plants than in seedling-tuber-grown plants. Moreover, the development of branches started earlier and lasted longer in true-seed-grown plants than in seedling-tuber-grown plants, both aboveground and belowground. The decrease in branch number at later stage suggested plant senescence.

The aboveground plant architecture was established between 1000 – 1500 °Cd, while the production of tubers belowground was complete around 2250 °Cd. At any stem density, true-seed-grown plants produced a more branched and compact architecture than seedling-tuber-grown plants, with on average shorter main stems (23 vs. 48 cm), fewer main stem nodes (12 vs. 16 nodes), and more branches both aboveground (24 vs. 18) and belowground (11 vs. 6) (Supplementary Table S2). Within each propagule type, higher stem density did not affect the number of main stem nodes, but increased main stem height and decreased the

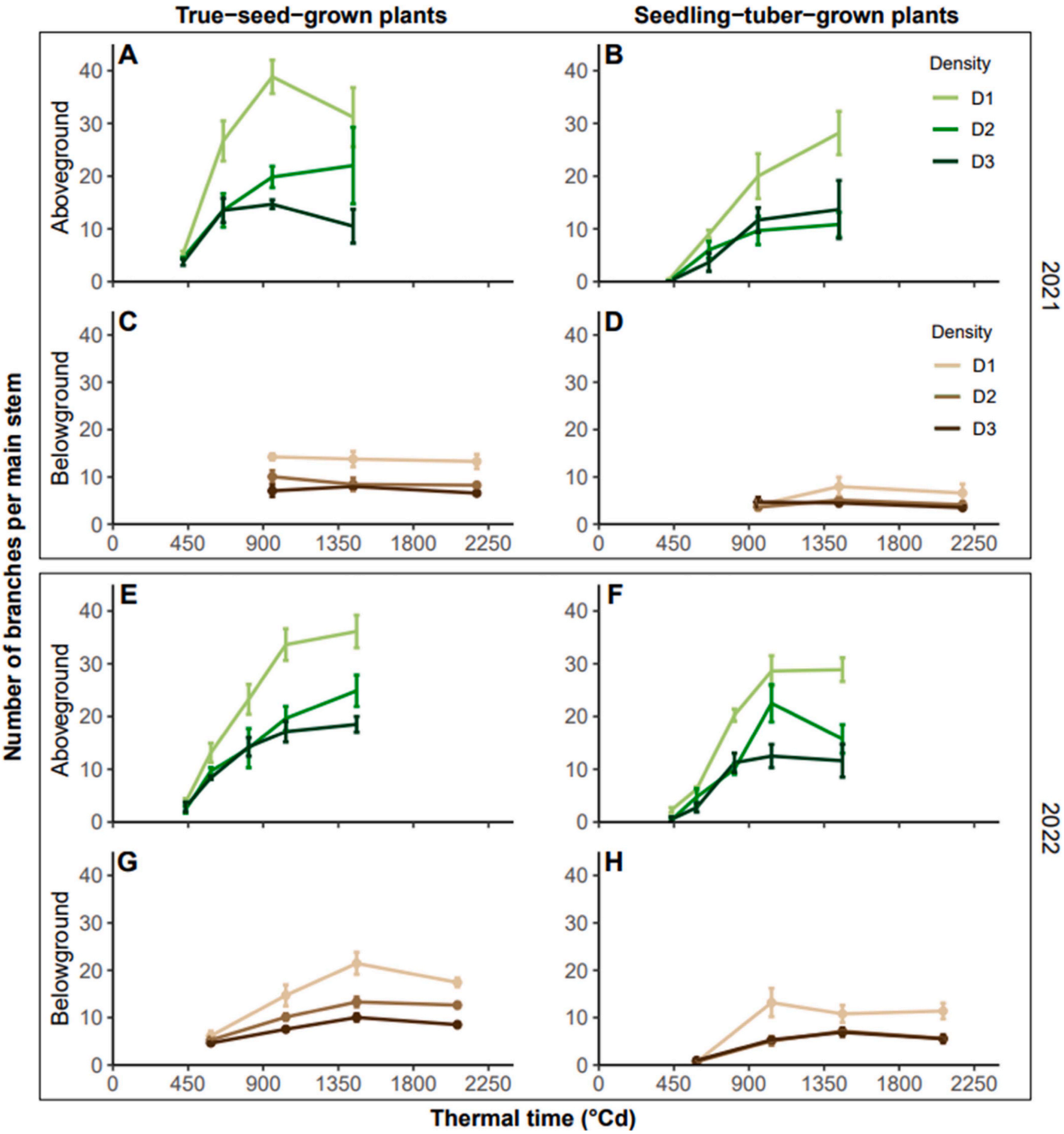

Fig. 2. The change in thermal time (°Cd) of the number of branches aboveground (green) and belowground (brown) for three stem densities of true-seed-grown plants and seedling-tuber-grown plants in 2021 and 2022. The symbols represent average values, and the whiskers show the standard errors of the means (n = 3 in 2021 and n = 4 in 2022). Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

total number of branches per main stem.

3.1.2. Distribution of branches along main stems

Aboveground, the contribution of branches from different branching orders (Table 2) and their spatial distribution along the individual main stems responded differently to stem density in two propagule types, which was evaluated on 954 and 1035 °Cd in 2021 and 2022, respectively (Fig. 3).

The higher number of branches in true-seed-grown plants was mainly caused by more sympodial branches, including order 1 branches at the apical part of the main stems, and order 2, 3 and 4 branches, than in seedling-tuber-grown plants. In addition, the reduction of these sympodial branches with increasing stem density led to fewer branches per main stem, which can be observed at most node positions on the main stem, especially at the basal part (relative node position 0.0 – 0.6) (Fig. 3 A, 3B, 3 C, 3 G, 3 H, 3I). This pattern was visible in both years.

In contrast, fewer sympodial branches developed in seedling-tuber-grown plants, especially from high branching order (orders 3 and 4)

Table 2
Average number of aboveground branches per main stem in total (mean ± standard error) and the average percentage of branch number attributed to each branching order ($n = 3$ in 2021 and $n = 4$ in 2022). Capital letters represent the significant differences between propagule types, and lower-case letters indicate differences between densities. Lower-case letters in bold reflect interactions between propagule type and density. Significance levels are shown as $p < 0.001$ ***, $p < 0.01$ ** and $p < 0.05$ *. n.a. means test is not applicable.

		Total branch number per main stem	Contribution of branching order to total branch number (%)			
			Order 1	Order 2	Order 3	Order 4
2021						
	D1[a]	38.8 ± 3.2 Aa	25.1 B	50.8	22.0 **a**	2.0
True-seed-grown plants	D2	19.8 ± 2.0 Ab	41.4 B	46.8	11.8 **ab**	0
	D3	14.7 ± 0.8 Ab	51.4 B	46.6	2.0 **b**	0
	D1	20.0 ± 4.3 Ba	51.8 A	46.7	1.5 **b**	0
Seedling-tuber-grown plants	D2	11.6 ± 2.8 Bb	61.0 A	39.0	0.1 **b**	0
	D3	11.7 ± 2.3 Bb	61.1 A	36.8	2.1 **b**	0
Propagule (P)		0.002 **	0.022 *	0.319	< 0.001 ***	n.a.
Density (D)		< 0.001 ***	0.144	0.684	0.008 **	n.a.
P × D		0.054	0.614	0.945	**0.006** **	n.a.
2022						
	D1	33.2 ± 3.1 a	34.1	58.0	7.1 A	0.8
True-seed-grown plants	D2	19.2 ± 2.5 b	45.5	44.6	8.8 A	1.1
	D3	17.0 ± 1.9 b	48.1	42.5	8.3 A	1.1
	D1	28.4 ± 2.9 a	49.5	48.6	1.9 B	0
Seedling-tuber-grown plants	D2	22.1 ± 3.5 b	49.6	46.7	3.7 B	0
	D3	10.9 ± 1.6 b	60.1	39.9	0.0 B	0
Propagule (P)		0.263	0.075	0.433	0.024 **	n.a.
Density (D)		< 0.001 ***	0.221	0.087	0.759	n.a.
P × D		0.263	0.697	0.533	0.837	n.a.

[a] Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

(Table 2). The reduced total number of branches with increasing stem density was mainly attributed to the absence of order 1 branches, without which the sympodial branches from higher branching orders could not be produced, and this reduction occurred mainly at the basal part of the main stems, whereas the apical part (relative position 0.8 – 1.0) was less affected (Figs. 3D, 3E, 3 F, 3 J, 3 K, 3 L). The differences in lower nodes between two years were mainly due to the variations in hilling practices, with more lower nodes covered by soil in 2021 which resulted in a shift of branch distribution towards upper nodes. Nonetheless, the composition of branch number in different branching orders and their responses to stem density was consistent between the two years.

The distribution of branches also influenced the distribution of leaf area within the different stems, which was determined at the same time (Table 3 and Fig. 4).

In true-seed-grown plants, branch leaves accounted for over 95 % of total leaf area per main stem in both years, mainly contributed by order 1 and 2 branches (Table 3). Although the number of order 1 branches was not strongly affected by stem density, the leaf area on these branches reduced significantly with increasing stem density, particularly at the basal part of the main stems (Fig. 4 A, 4B, 4 C, 4 G, 4 H, 4I).

In seedling-tuber-grown plants, however, the total leaf area per main stem was mainly distributed over the leaves from main stems and order 1 branches, taking up on average 11 – 31 % and 50 – 70 % of the total leaf area, respectively (Table 3). The spatial distribution of main stem leaves almost did not change with stem density, while the leaf area on branches decreased largely with increasing stem density (Figs. 4D, 4E, 4 F, 4 J, 4 K, 4 L).

Belowground, the distribution of tubers per main stem was based on tuber size at the end of growing season, which shifted with changing stem density (Fig. 5).

The higher number of tubers in true-seed-grown plants was mainly attributed to the tubers from small size classes, such as 0 – 25 and 25 – 35 mm, accounting for over 70 % of the total number of tubers at any stem density in both years, compared with seedling-tuber-grown plants in which small tubers comprised about 42 – 56 % of the total number of tubers (Table 4).

Moreover, fewer tubers were larger than 35 mm at higher stem density in both propagule types, resulting in a reduction of total number of tubers and a shift in size distribution towards smaller tuber sizes. A larger reduction was observed in true-seed-grown plants, with only 16 – 23 % tubers bulking to large size at higher stem densities D2 and D3, whereas there were still 44 – 58 % of tubers produced in these size classes in seedling-tuber-grown plants.

3.1.3. *Biomass production and partitioning*

The different patterns in branching responses to stem density between the two propagule types were also reflected in biomass production and partitioning (Fig. 6).

The total biomass per main stem decreased with increasing stem density for both propagule types. In true-seed-grown plants, the decline was consistent between the two years. At around 1450 °Cd, plants produced the highest amount of total biomass per main stem at stem density D1, followed by a 44 – 51 % reduction at D2 and 56 – 65 % decline at D3 (Supplementary Table S3). A similar trend was also observed in seedling-tuber-grown plants, but large differences between years made it less obvious, with about 56 % and 41 – 61 % reduction in biomass at stem densities D2 and D3 compared to D1.

A tendency of changes in biomass partitioning to different plant parts aboveground with stem density was shared between the two propagule types (Supplementary Table S3). At higher stem density, a shift of aboveground biomass from branch stems and leaves to main stems was observed, resulting in a reduced production of berries. Nonetheless, the extent of this shift in partitioning was different between propagule types. In true-seed-grown plants, the main stems only comprised about 4 % of total biomass, while a significantly higher proportion of biomass was allocated to berries (23 %), compared to seedling-tuber-grown plants, in which 11 % and 14 % of total biomass was invested in main stems and berries, respectively.

Biomass partitioning among the belowground parts did not show a

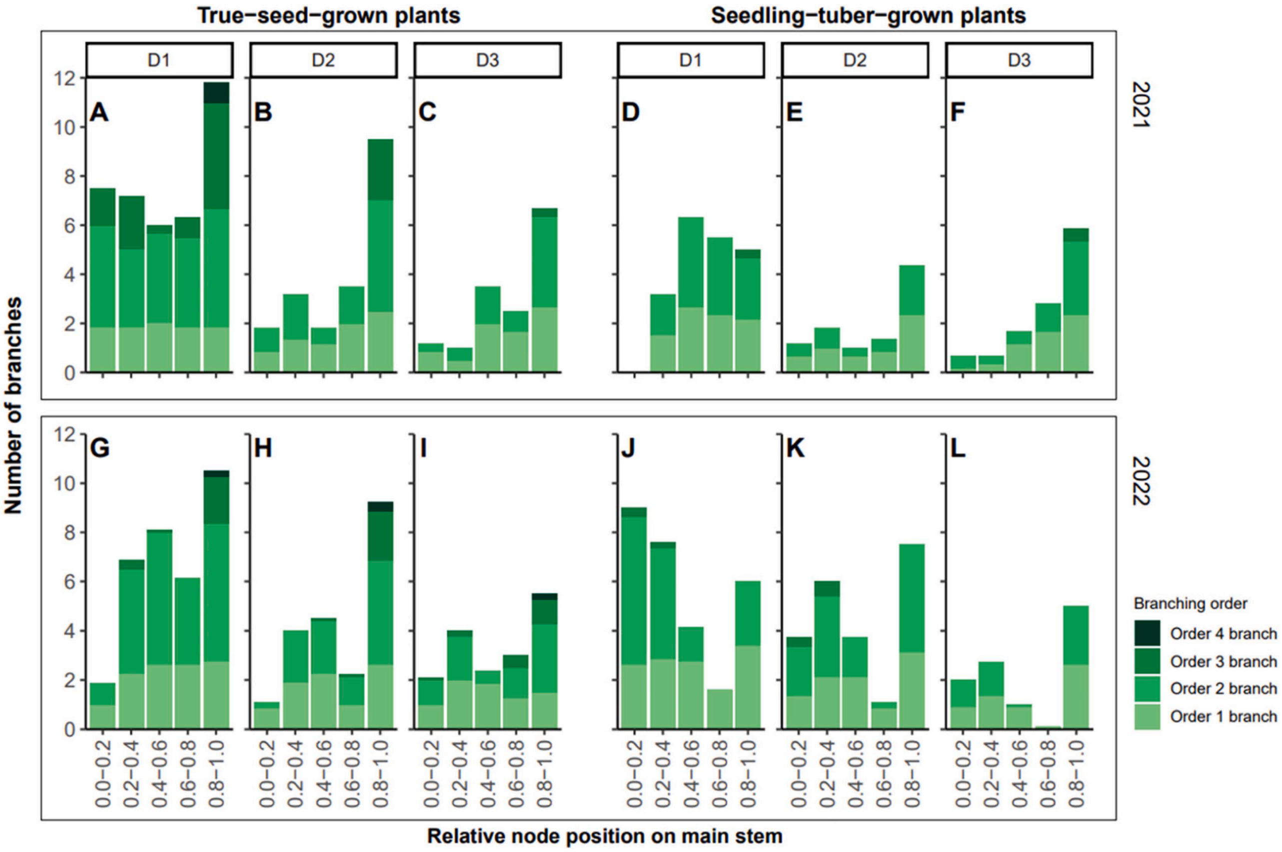

Fig. 3. The distribution of the average number of aboveground branches per main stem for three stem densities, for true-seed-grown plants and seedling-tuber-grown plants in two years (n = 3 in 2021 and n = 4 in 2022). The average branch count per branching order was grouped based on the range of branch relative node positions inserted on the main stem. Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

Table 3
Average leaf area per main stem (mean ± standard error) and the average percentage of leaf area attributed to each branching order (n = 3 in 2021 and n = 4 in 2022). Samples were evaluated at 954 °Cd in 2021 and 1035 °Cd in 2022. Capital letters represent the significant differences between propagule types, and lower-case letters indicate differences between densities. Lower-case letters in bold reflect the interactions between propagule type and density. Significance levels are shown as p < 0.001 ***, p < 0.01 ** and p < 0.05 *. n.a. means test is not applicable.

		Total leaf area per main stem (cm^2)	Branching order contribution to total leaf area (%)				
			Order 0 (main stem)	Order 1	Order 2	Order 3	Order 4
2021							
True-seed-grown plants	D1[a]	7016 ± 769 Aa	0.6 **c**	57.9 **ab**	34.4 A	6.5 **a**	0.6
	D2	3900 ± 274 Ab	4.9 **c**	61.3 **ab**	30.3 A	3.6 **ab**	0
	D3	3330 ± 44 Ab	0.6 **c**	75.3 **a**	23.8 A	0.2 **b**	0
Seedling-tuber-grown plants	D1	4335 ± 345 Ba	11.3 **bc**	69.5 **ab**	19.0 B	0.2 **b**	0
	D2	2502 ± 940 Bb	40.6 **a**	50.9 **b**	8.5 B	0.0 **b**	0
	D3	3059 ± 330 Bb	28.6 **ab**	60.6 **ab**	10.6 B	0.2 **b**	0
Propagule (P)		0.012 *	< 0.001 ***	0.237	< 0.001 **	0.003 **	n.a.
Density (D)		0.002 **	0.011 *	0.060	0.115	0.043 *	n.a.
P × D		0.165	**0.044 ***	**0.028 ***	0.599	**0.043 ***	n.a.
2022							
True-seed-grown plants	D1	6678 ± 705 Ba	2.4 Bb	61.3	33.4 A	2.7 A	0.2
	D2	3299 ± 356 Bb	3.1 Bab	61.1	31.4 A	4.3 A	0.1
	D3	3095 ± 221 Bb	5.0 Ba	68.9	22.3 A	3.6 A	0.3
Seedling-tuber-grown plants	D1	8093 ± 498 Aa	16.3 Ab	63.5	19.9 B	0.3 B	0
	D2	5106 ± 606 Ab	20.2 Aab	62.4	16.9 B	0.5 B	0
	D3	3078 ± 214 Ab	32.5 Aa	52.9	14.6 B	0.0 B	0
Propagule (P)		0.012 *	< 0.001 ***	0.356	0.019 *	0.013 *	n.a.
Density (D)		< 0.001 ***	0.046 *	0.961	0.346	0.806	n.a.
P × D		0.142	0.165	0.189	0.801	0.865	n.a.

[a] Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

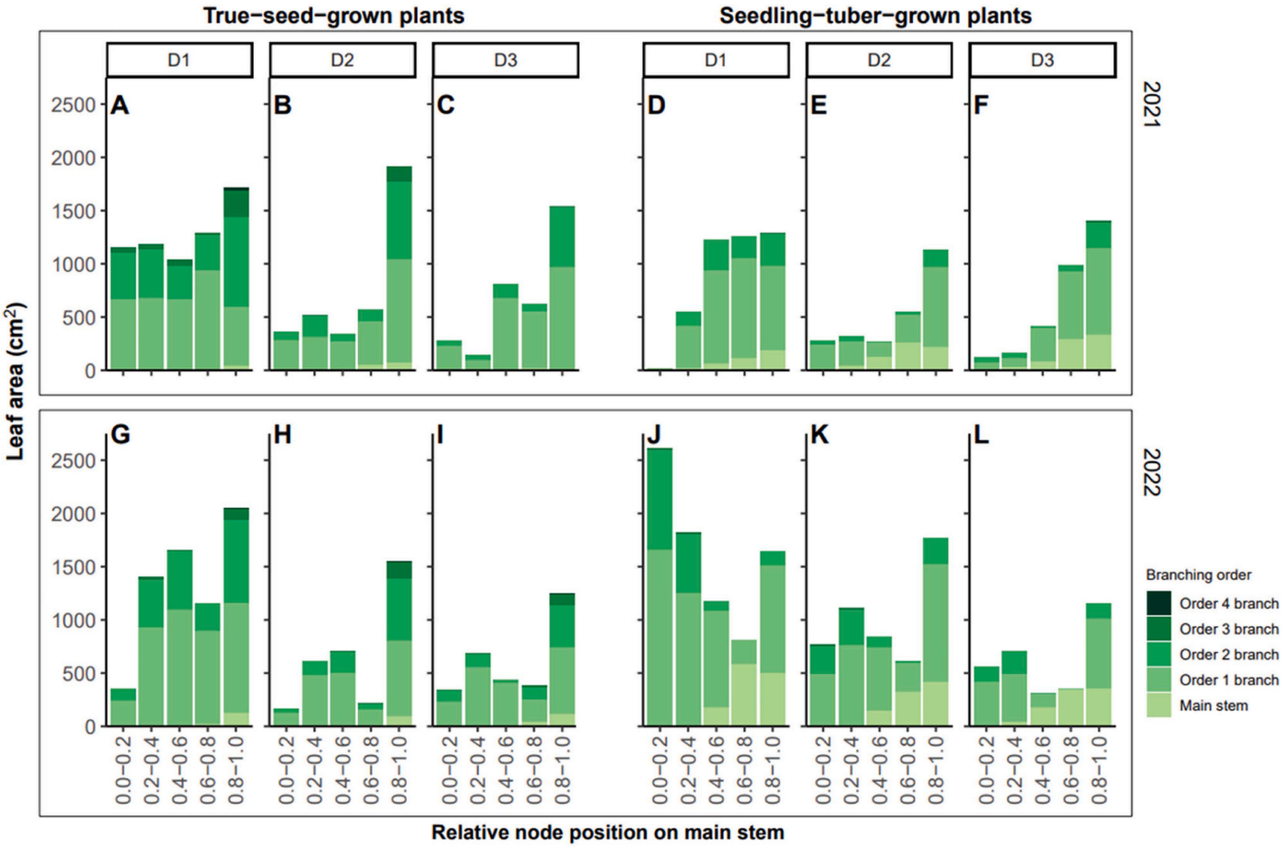

Fig. 4. The distribution of average leaf area per main stem at three stem densities, for true-seed-grown plants and seedling-tuber-grown plants in two years (n = 3 in 2021 and n = 4 in 2022). Samples were evaluated at 954 °Cd in 2021 and 1035 °Cd in 2022. The average leaf area per branching order was grouped based on the range of branch relative node positions inserted on the main stem. Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

clear pattern. A common trend in both years showed that biomass allocation into tubers started earlier (around 950 °Cd) but at a slower rate in true-seed-grown plants than in seedling-tuber-grown plants, which eventually constituted almost the same percentage of biomass allocated to tubers for the two propagule types.

3.2. *Consequences on crop development and growth*

3.2.1. *Canopy development*

Aboveground, the different spatial and temporal distributions of leafy branches on individual main stems influenced architectural traits of the canopies from the two propagule types, reflected in different temporal dynamics of canopy development (Fig. 7).

The development of canopy over the whole growing season, estimated by the canopy cover model, showed similar trends for both years. Canopy development was only slightly affected by stem density at an early stage, before most sympodial branches started to develop. For both propagule types, canopy developed faster at high stem density D3, followed by D1 and D2, which was also described by the model fitted parameters t_{m1}, the lower the values, the faster the canopy developed (Supplementary Table S4).

At later stages, the significant propagule effect was dominant on most model fitted parameters. The maximum canopy cover was maintained for longer in seedling-tuber-grown plants (t_2 - t_1), whereas the canopy senesced slower in true-seed-grown plants (t_e - t_2).

3.2.2. *Light interception, radiation use efficiency in tubers and yield*

Total light intercepted by the canopy over the whole growing season showed the same tendency against stem density for both propagule types in both years: highest values at high stem density D3, followed by D2 and D1 (Table 5). The response in radiation use efficiency based on tuber biomass (RUE_{tuber}) to stem density was consistent in both years (Supplementary Fig. S2) for each propagule type. Seedling-tuber-grown plants had a higher average RUE_{tuber} (1.71 g MJ^{-1}) compared to true-seed-grown plants (1.34 g MJ^{-1}) across stem density; within each propagule type, RUE_{tuber} was highest at stem density D3 in seedling-tuber-grown plants (2.05 g MJ^{-1}), whereas it was lowest in true-seed-grown plants (1.22 g MJ^{-1}).

Because of their effects on total light interception and RUE_{tuber}, tuber biomass production showed strong interactions between propagule type and stem density. Seedling-tuber-grown plants produced largest tuber biomass per unit area at highest stem density D3, 870.5 and 836.4 g m^{-2} in 2021 and 2022 respectively, whereas the lowest tuber biomass was produced at stem density D3 in true-seed-grown plants, which was 485.7 and 648.7 g m^{-2} in two years, respectively.

The total tuber fresh yield was slightly higher in seedling-tuber-grown plants than in true-seed-grown plants, which was only statistically different in 2021. True-seed-grown plants produced, however, significantly more tubers per unit area than seedling-tuber-grown plants, which resulted in a much lower average tuber fresh weight, 24 g and 45 g per tuber, respectively.

Furthermore, the tendency of average tuber fresh weight decreasing with increasing density was shared by both propagule types, but such effect was stronger in true-seed-grown plants. Especially in 2022, about 24 – 34 % reduction of average tuber weight at higher stem density was observed in true-seed-grown plants, compared to low stem density D1, while the reduction was only 6 – 18 % in seedling-tuber-grown plants. This response was reflected in the tuber fresh yield distribution, where a larger proportion of tuber fresh weight was shifted to small tuber sizes (0 – 25 and 25 – 35 mm) at high stem density in true-seed-grown plants,

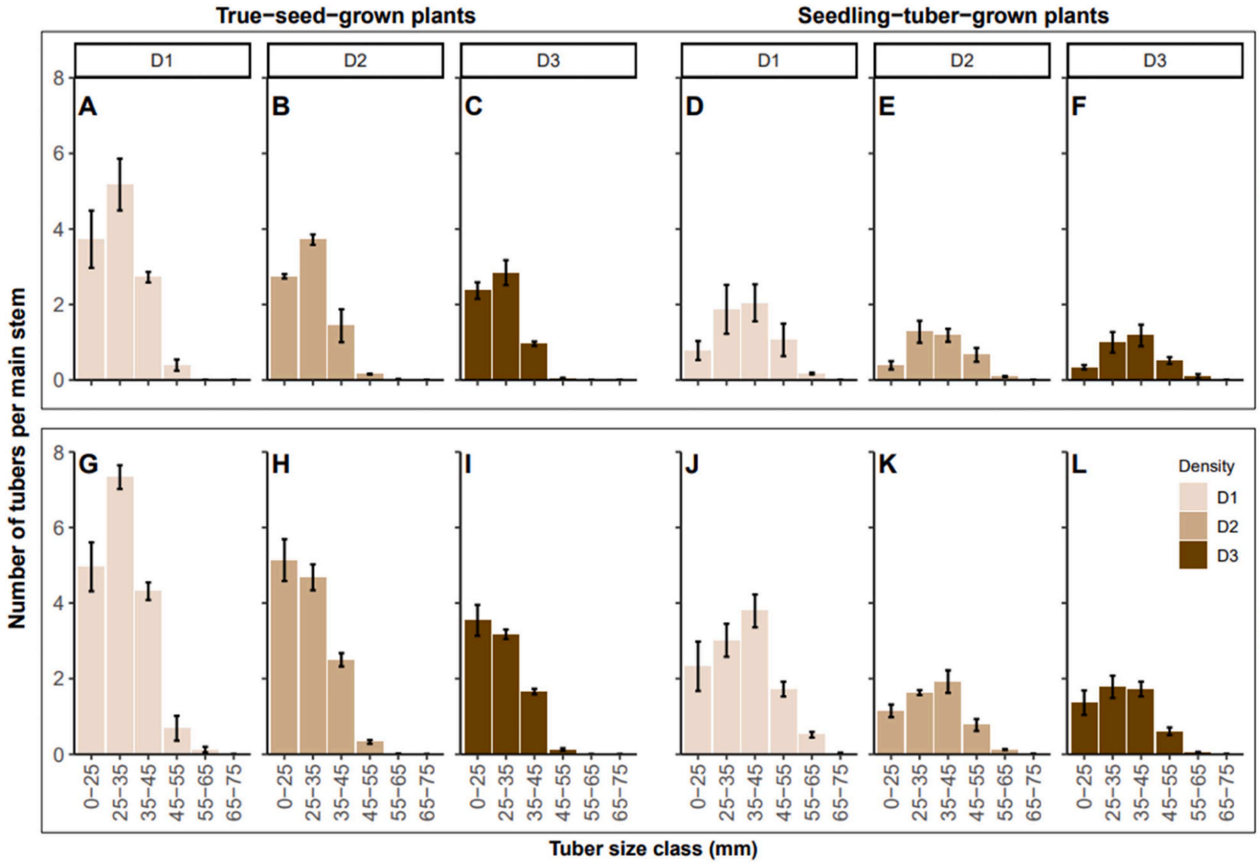

Fig. 5. The distribution of average number of tubers per main stem over six size classes at three stem densities for true-seed-grown plants and seedling-tuber-grown plants in both years (n = 3 in 2021 and n = 4 in 2022). Samples were evaluated at 2180 °Cd in 2021 and at 2063 °Cd in 2022. Error bars represent standard errors of the means. Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

Table 4
Average number of tubers per main stem distributed over six size classes (mean ± standard error) and the average percentage of number of tubers attributed to each size class (n = 3 in 2021 and n = 4 in 2022). Samples were evaluated at 2180 °Cd in 2021 and at 2063 °Cd in 2022. Capital letters represent the significant differences between propagule types, and lower-case letters indicate differences between densities. Lower-case letters in bold reflect the interactions between propagule type and density. Significance levels are shown as $p < 0.001$ ***, $p < 0.01$ ** and $p < 0.05$ *. n.a. means test is not applicable.

		Number of tubers per main stem	Size class contribution to number of tubers (%)					
			0 – 25 mm	25 – 35 mm	35– 45 mm	45 – 55 mm	55 – 65 mm	65 – 75 mm
2021								
True-seed-grown plants	D1[a]	13.3 ± 1.5 Aa	30.4 A	42.9 A	23.1 B	3.6 B	0.0 B	0
	D2	8.2 ± 0.5 Ab	34.3 A	46.2 A	17.4 B	2.0 B	0.2 B	0
	D3	6.6 ± 0.0 Ab	38.2 A	45.6 A	15.4 B	0.8 B	0.0 B	0
Seedling-tuber-grown plants	D1	6.6 ± 1.9 Ba	13.5 B	30.3 B	35.3 A	17.7 A	3.2 A	0
	D2	4.1 ± 0.7 Bb	11.2 B	34.7 B	33.3 A	18.1 A	2.7 A	0
	D3	3.5 ± 0.3 Bb	11.6 B	30.8 B	36.7 A	17.5 A	3.4 A	0
Propagule (P)		< 0.001 ***	< 0.001 ***	0.002 **	< 0.001 ***	< 0.001 ***	0.005 **	n.a.
Density (D)		< 0.005 **	0.649	0.608	0.470	0.897	0.966	n.a.
P × D		0.317	0.349	0.907	0.406	0.916	0.903	n.a.
2022								
True-seed-grown plants	D1	17.4 ± 0.9 Aa	28.1 Ab	42.5 A	24.8 B	3.9 Ba	0.7 **c**	0
	D2	12.4 ± 0.6 Ab	40.4 Aa	36.9 A	19.9 B	2.6 Bab	0.1 **c**	0
	D3	8.5 ± 0.6 Ac	41.3 Aa	37.5 A	19.7 B	1.5 Bb	0.0 **c**	0
Seedling-tuber-grown plants	D1	11.4 ± 1.7 Ba	19.1 Bb	26.5 B	34.0 A	15.7 Aa	4.6 **a**	0.2
	D2	5.6 ± 0.4 Bb	20.5 Ba	29.7 B	33.9 A	13.4 Aab	2.3 **b**	0.2
	D3	5.5 ± 0.9 Bc	23.7 Ba	32.2 B	32.0 A	11.0 Ab	1.1 **bc**	0.1
Propagule (P)		< 0.001 ***	< 0.001 ***	< 0.001 ***	< 0.001 ***	< 0.001 ***	< 0.001 ***	n.a.
Density (D)		< 0.001 ***	0.009 **	0.780	0.276	0.039 *	< 0.001 ***	n.a.
P × D		0.056	0.111	0.072	0.544	0.666	**< 0.001** ***	n.a.

[a] Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

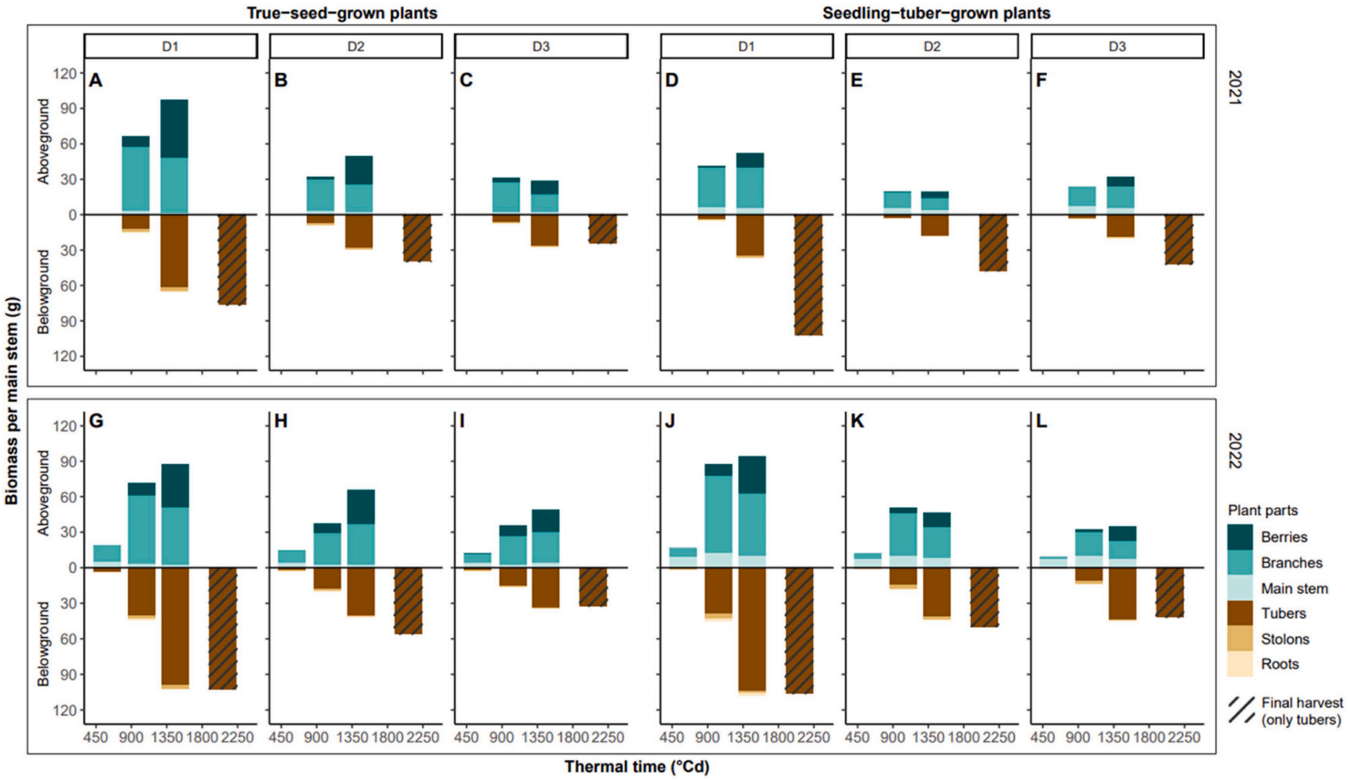

Fig. 6. Average biomass accumulation (g) and partitioning into different plant parts per main stem on different harvest dates (thermal time) for true-seed-grown plants and seedling-tuber-grown plants in two years (n = 3 in 2021 and n = 4 in 2022). Biomass allocation was separated into the aboveground (above zero line) and belowground part (below zero line). Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

compared to seedling-tuber-grown plants (Supplementary Fig. S3). It therefore caused a 4 – 6 % reduction of marketable yield (tuber size > 25 mm) in true-seed-grown plants when the stem density was higher than D1, whereas there was almost no change in marketable yield in seedling-tuber-grown plants.

4. Discussion

4.1. The distribution of aboveground branches along the stem depends on agronomic practices

Differences between years were observed in the distribution of branches along the main stems, especially on the aboveground basal node positions (relative node position within the range 0.0 – 0.4) (Fig. 3 and Fig. 4). Other than the year-to-year environmental variations, we surmise that the small variations in crop management practices had significant impacts, such as the duration of the transplant nursery period, the moment of hilling and its frequency, as well as seedling tuber quality.

The duration of the greenhouse nursery period affects transplant age for true-seed-grown plants (van Dijk et al., 2022). During this stage, plants initially grow exponentially, and basal branches normally start to develop about 20 days after sowing (Kacheyo et al., 2021). In our experiment, the transplants stayed for 5 days less in the nursery in 2022 (22 days), due to higher outdoor temperatures than in 2021 (27 days). The basal branches may not have developed yet or were just at their initial stage in 2021, and therefore their growth could have been restrained by the transplanting shock and by the burial by soil in the field (Kacheyo et al., 2023). After (trans)planting, hilling was conducted. The more often hilling was conducted, the more basal nodes were limited in developing branches. In our study, hilling was done one time less in 2022 than in 2021. The combination of these minor variations could lead to the discrepancy observed in the development of the basal branches in true-seed-grown plants (Fig. 3 A, 3B, 3 C, 3 G, 3 H, 3I). Similarly, in seedling-tuber-grown plants, many more basal branches developed in 2022 (Fig. 3 J, 3 K, 3 L) because of less frequent hilling. Moreover, the relatively poorer quality of seedling tubers in 2021, as shown by slight infection by *Rhizoctonia solani*, could induce stem and stolon canker and thus inhibit branch development (Tsror, 2010), resulting in fewer basal leafy branches, stolons and tubers, compared to the second year. The integration of these variations in branch distribution on individual main stems further influences canopy structure, which could account to a certain extent for the year-to-year differences in total light interception and tuber yield.

On the other hand, although the distribution of branches varied between years, the contribution of branch number and leaf area from different branching orders to their total amounts as well as their responses to stem density were consistent. In addition, the belowground branching was not significantly different between the two years. Van Dijk et al. (2022, 2021b) also showed that transplant age and hilling do not affect total tuber yield or number in a wide range. Therefore, the observed common trends in branching responses and their impacts on crop performance are still valid for further discussion. Nonetheless, here we emphasize the importance of agronomic practices when studying branching in field conditions, including transplant age and hilling. Other factors such as transplanting shock, tillage systems and fertilization are also crucial to successful field transplanting of true-seed-grown plants (Kacheyo et al., 2023), while their effect on branching and impact on yield formation still requires further research.

4.2. Different branching responses to stem density between propagule types may result from differences in branching control and assimilate competition between branches

Our results showed that per individual main stem, the branching response to increasing stem density differed between true-seed-grown

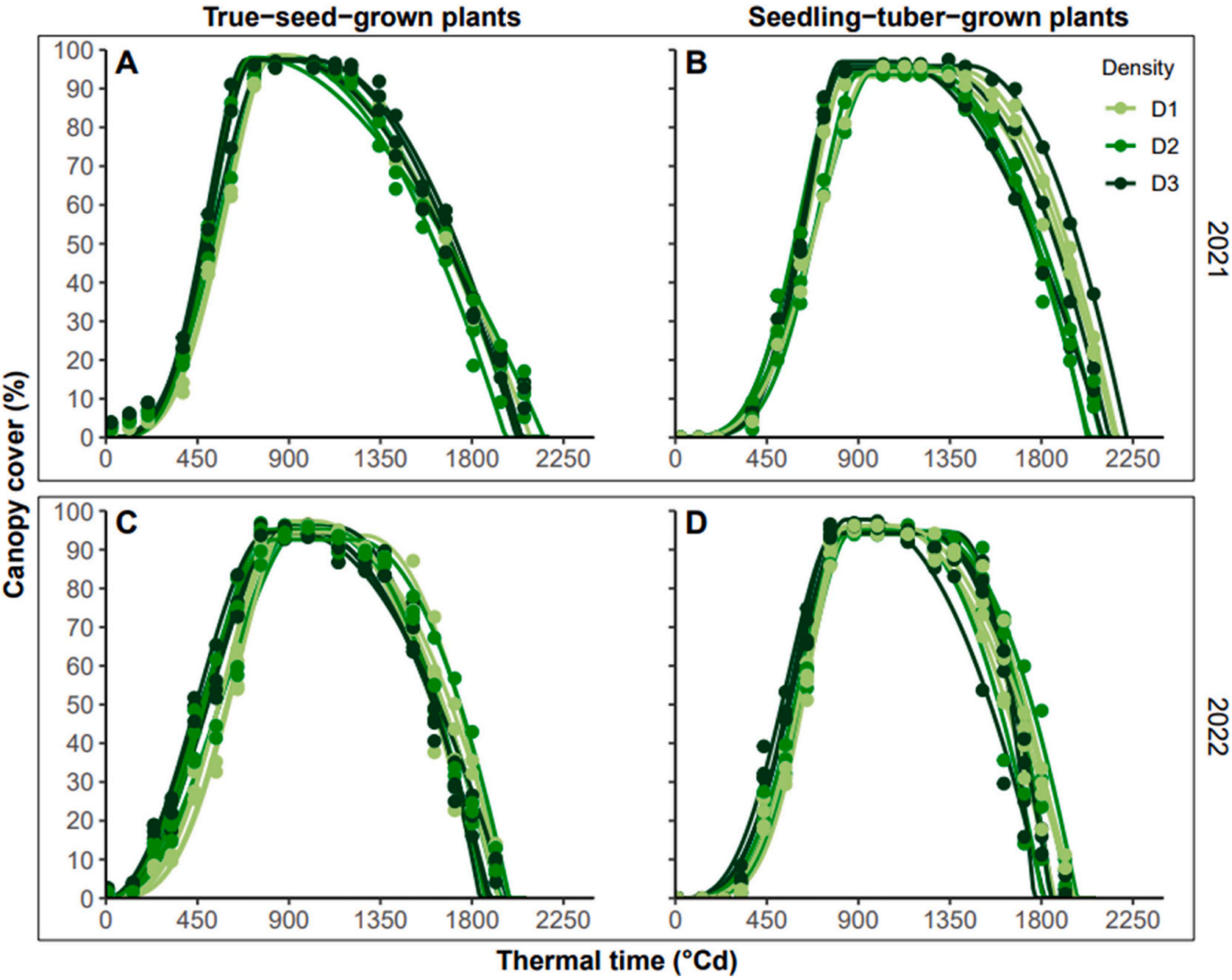

Fig. 7. Modelled canopy cover over thermal time per plot at three stem densities for true-seed-grown plants (A, C) and seedling-tuber-grown plants (B, D) in two years. Each treatment included 3 plots in 2021 and 4 plots in 2022. Lines represent the model fitted values per plot. Observed data points are shown in closed circles. Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

plants and seedling-tuber-grown plants. First, at any stem density, branching patterns per main stem differed between the two propagule types. In true-seed-grown plants, a more branched and compact architecture, and a continuous production of branches per main stem were observed, than in seedling-tuber-grown plants. This effect may result from differences in meristem development, especially in the number and the position of axillary meristems, regulation of bud break and the subsequent branch production (Teichmann and Muhr, 2015). Our results corroborate previous observations (Benz et al., 1995; Gu et al., 2024; Wiersema, 1984), which indicate such distinct branching pattern in true-seed-grown plants may be controlled by weaker apical dominance. In potato plants, apical dominance-regulated branching control mainly involves several phytohormones such as cytokinin, auxin, strigolactone and gibberellin (Saidi and Hajibarat, 2021; Vreugdenhil and Struik, 1989), which are also found in other crop species (e.g., Arite et al., 2009; Kebrom et al., 2010; Li et al., 2019). Specifically, shoot branching and tuber number both above- and belowground are promoted by cytokinin in potato plant (Tao et al., 2010), but suppressed by auxin, strigolactone and gibberellin (Roumeliotis et al., 2012; Saidi and Hajibarat, 2021). Research on the differences in the roles of these phytohormones in branching control between the propagule types is needed to improve mechanistic understanding of the development of potato plant architecture.

Second, in both propagule types, the number of branches decreased significantly with increasing stem density, which can be due to the change in light environment near axillary meristems. For example, with increasing stem density, light intensity and red:far-red ratio decrease, both of which can inhibit bud outgrowth (Leduc et al., 2014). However, in true-seed-grown plants, a larger reduction with increasing stem density was found in traits such as number of branches, branch leaf area, especially of sympodial branches, number of tubers and average tuber weight per main stem in true-seed-grown plants than in seedling-tuber-grown plants. The highly branched nature of true-seed-grown plants may change light environment to a larger extent under high stem densities, which induces a higher level of inhibition in bud outgrowth than less branched seedling-tuber-grown plants.

In addition, we also surmise that a stronger competition for assimilates existed between both above- and belowground branches as well as among aboveground branches in true-seed-grown plants. Sexual reproduction was pronounced in true-seed-grown plants, via production of flowers and berries. This can influence competition for biomass between tubers and sexual organs resulting in a slower biomass accumulation in tubers, compared to seedling-tuber grown plants. This finding in is line with Almekinders and Struik (1996) who stated that a large number of sympodia, terminating in inflorescences and infructescences, can increase competition for assimilates and reduce the rate of shift in assimilate partitioning to tubers. Additional studies should be done to elucidate branching control and assimilate allocation in different types

Table 5

Average values of crop traits per unit area (mean ± standard error) (n = 3 in 2021 and n = 4 in 2022). Capital letters represent the significant differences between propagule types, and lower-case letters indicate differences between densities. Lower-case letters in bold reflect the interactions between propagule type and density. Significance levels are shown as $p < 0.001$ ***, $p < 0.01$ ** and $p < 0.05$ *. [a] Per planting hole, there were either one (D1), two (D2) or three (D3) main stems.

		Total light interception (MJ m^{-2})	RUE_{tuber} (g MJ^{-1})	Tuber biomass (g m^{-2})	Tuber dry matter content (%)	Tuber fresh yield (g m^{-2})	Tuber number per m^2	Average tuber FW (g per tuber)	Marketable yield (tuber size > 25 mm)	Percentage marketable yield of total fresh yield (%)
2021										
True-seed-grown plants	D1[a]	513.7 ± 6.4 ab	1.47 ± 0.07 B	511.2 ± 7.8 **b**	19.6 ± 0.1	2607 ± 29.3 B	92.2 ± 6.5 A	28.6 ± 2.3 B	2413 ± 47.5 B	91.6 **b**
	D2	524.7 ± 4.7 b	1.47 ± 0.21 B	530.3 ± 70.3 **b**	20.0 ± 0.7	2664 ± 371.4 B	116.0 ± 9.2 A	22.7 ± 1.6 B	2355 ± 370.7 B	87.7 **bc**
	D3	549.8 ± 4.9 a	1.25 ± 0.09 B	485.7 ± 19.0 **b**	19.9 ± 0.3	2447 ± 99.7 B	123.8 ± 4.3 A	19.8 ± 0.4 B	2121 ± 86.3 B	85.7 **c**
Seedling-tuber-grown plants	D1	545.3 ± 8.5 ab	1.76 ± 0.09 A	705.0 ± 41.6 **ab**	20.3 ± 0.3	3463 ± 181.4 A	71.8 ± 7.9 B	49.0 ± 3.6 A	3394 ± 170.1 A	97.9 **a**
	D2	505.8 ± 7.7 b	1.74 ± 0.14 A	635.3 ± 31.7 **b**	20.0 ± 0.6	3191 ± 257.3 A	68.0 ± 4.7 B	47.3 ± 4.5 A	3142 ± 267.0 A	98.2 **a**
	D3	553.1 ± 22.3 a	2.15 ± 0.07 A	870.5 ± 64.6 **a**	20.7 ± 0.5	4223 ± 407.4 A	79.0 ± 2.4 B	53.4 ± 4.5 A	4169 ± 390.7 A	98.6 **a**
Propagule (P)		0.629	0.001 **	< 0.001 ***	0.216	< 0.001 ***	< 0.001 ***	< 0.001 ***	0.001 ***	< 0.001 ***
Density (D)		0.018 *	0.696	0.164	0.799	0.356	0.052	0.578	0.38	0.072
P × D		0.087	0.066	**0.039** *	0.676	0.116	0.138	0.204	0.092	**0.025** *
2022										
True-seed-grown plants	D1	675.0 ± 13.6 A	1.27 ± 0.12	682.7 ± 41.2 **a**	19.4 ± 0.3	3521 ± 231.3	116.1 ± 6.2 **b**	30.4 ± 1.4 Ba	3295 ± 217.5 B	93.6 **a**
	D2	705.3 ± 18.1 A	1.44 ± 0.21	747.5 ± 50.2 **a**	19.6 ± 0.3	3816 ± 273.4	164.7 ± 4.4 **a**	23.2 ± 1.9 Bb	3401 ± 295.7 B	88.8 **b**
	D3	706.2 ± 7.0 A	1.19 ± 0.34	648.7 ± 51.4 **a**	19.8 ± 0.1	3277 ± 272.6	165.6 ± 12.4 **a**	20.0 ± 1.8 Bb	2867 ± 239.3 B	87.5 **b**
Seedling-tuber-grown plants	D1	658.9 ± 9.2 B	1.36 ± 0.32	707.6 ± 37.6 **a**	19.1 ± 0.3	3711 ± 201.9	85.0 ± 2.8 **c**	44.0 ± 3.6 Aa	3602 ± 219.0 A	97.0 **a**
	D2	669.5 ± 17.6 B	1.34 ± 0.05	661.7 ± 63.7 **a**	18.9 ± 0.1	3506 ± 331.6	85.4 ± 9.0 **c**	41.2 ± 1.2 Ab	3379 ± 312.0 A	96.4 **a**
	D3	677.6 ± 16.0 B	1.95 ± 0.28	836.4 ± 49.8 **a**	19.6 ± 0.5	4272 ± 206.3	118.9 ± 7.6 **b**	36.1 ± 1.5 Ab	4083 ± 175.9 A	95.7 **a**
Propagule (P)		0.016 **	0.245	0.32	0.097	0.185	< 0.001 ***	< 0.001 ***	0.028 *	< 0.001 ***
Density (D)		0.126	0.59	0.618	0.276	0.819	< 0.001 ***	< 0.001 ***	0.942	< 0.001 ***
P × D		0.724	0.231	**0.048** *	0.706	0.066	**0.001** **	0.506	0.068	**0.016** *

of propagules.

4.3. *Differences in crop performance between propagule types are greater than between stem densities*

Despite main stem branching responses having been altered by stem density within each propagule type, the consequences of branching responses were not significant for crop traits, such as canopy development and total tuber fresh yield. At early stages of development, the canopy developed slightly faster at higher stem density in both propagules, while the differences between stem densities narrowed down after the highest developmental rate was reached (t_{m1}). This could be attributed to plasticity in branching. The increased stem density may have enhanced competition for light and assimilates among branches, leading to individual plants or main stems having reduced production of branches, while maintaining total light interception and biomass production. Such a strategy of regulating aboveground branching based on density is also observed in other potato studies (e.g., Engels et al., 1993a; Fleisher et al., 2011), as well as in other crop species, such as rice (Kumar et al., 2016), wheat (Evers et al., 2006), sweet potato (Somda and Kays, 1990a, 1990b), peanut (Gao et al., 2023), and cotton (Zhou et al., 2023). In potato crops, a unique trait is that tubers, as parts of belowground branches, undergo a shift in size distribution, as a consequence of changes in aboveground branching. This phenomenon of an increased number of tubers in smaller sizes with higher stem density and the consequent reduced average tuber weight have been consistently reported in the two propagule types, regardless of increases, decreases or no changes in total tuber yield (e.g., Allen and Wurr, 1992; Çalışkan et al., 2009; Knowles and Knowles, 2016; van Dijk et al., 2021a).

Importantly, the differences between propagule types outweighed the effects of stem density at crop level. This is reflected in the aboveground canopy cover duration, and belowground number of tubers, tuber size distribution and marketable yield (Table 5). Our results are in agreement with Benz et al. (1995) who observed a similar pattern when comparing genetically identical true-seed-grown and seedling-tuber-grown plants, and they concluded that such differences were inherent to the type of planting material which differed physiologically. One of the reasons could be their different growth habits, with true-seed-grown plants having indeterminate growth while seedling-tuber-grown plants having determinate growth (Gu et al., 2024) . The excessive and continuous production of branches in true-seed-grown plants resulted in more tubers, a stronger inter-tuber competition and therefore lower average tuber weight (cf. Wiersema, 1986). Our study showed that although increasing stem density largely increased the total number of tubers per unit area in true-seed-grown plants, yet these extra tubers could not bulk to large sizes, thus did not increase total tuber yield, and even reduced marketable yield. Such result is in line with Çalışkan et al. (2009), who found that the increase in number of tubers compensated for the decrease in average tuber weight but did not contribute to total tuber yield. A possible explanation is that the tubers in true-seed-grown plants are weaker sinks to compete with aboveground sink branches (van Dijk et al., 2021a; Wiersema, 1984). Particularly, these aboveground sinks include vegetative branches and berries in true-seed-grown plants. Tekalign and Hammes (2005a) found a reduced biomass allocation in tubers and decreased tuber yield in true-seed-grown plants with fruits (berries), compared to the non-fruiting plants of the same genotype; they postulated that the developing berries could be stronger sinks compared to developing vegetative organs such as tubers and leaves. We also observed a higher biomass partitioning in berries and a lower allocation in tubers and leafy branches in true-seed-grown plants, compared to seedling-tuber-grown plants.

Weaker sinks in tubers in true-seed-grown plants could also potentially explain the less efficient conversion of radiation intercepted into tubers ($\text{RUE}_{\text{tuber}}$) than in seedling-tuber-grown plants. However, an increased source output was reported in fruiting plants which have higher stomatal conductance, higher rate of net leaf photosynthesis and leaf transpiration than the non-fruiting ones (Tekalign and Hammes, 2005b). In addition, the differences between fruiting and non-fruiting plants are also genotype dependent. Applying these findings to our case, an enhanced source output may be produced in true-seed-grown plants due to higher production of berries, compared to seedling-tuber-grown plants. However, it is not clear to what extent the source capacity is different between plants grown from true seeds and those from seedling tubers, and how much it can influence source-sink relations in hybrid potato. We recommend future research should focus on source-sink relations between different types of propagules and more genotypes should also be included, which can bring more insights in hybrid potato breeding from various types of propagules.

5. Conclusion

Our study quantified and compared branching response to stem density and its impact on tuber production using true seeds and seedling tubers of the same genotype. The results emphasized differences in stem branching, crop development and tuber production between propagule types which outweighed the effect of stem density. The intrinsic differences between true seeds and seedling tubers may cause differences in branching control, growth habit and source-sink relations, which are important for hybrid potato breeding and require further research. Moreover, management practices were partly responsible for year-to-year differences in branching and yield formation, which highlights their significances for hybrid potato production.

CRediT authorship contribution statement

Jiahui Gu: Data curation, Methodology, Formal analysis, Writing-Original draft preparation. **Jochem B. Evers:** Writing- Reviewing and Editing, Supervision. Steven **M. Driever:** Writing- Reviewing and Editing, Supervision. **Ke Shan:** Data curation, Writing- Reviewing and Editing. **Paul C. Struik:** Conceptualization, Writing- Reviewing and Editing, Supervision.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Paul C. Struik is editor of Field Crops Research. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2024.109548.

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