



Architectural Differences between Hybrid Potato Plants Grown from True Seeds and Seedling Tubers Do Not Influence Leaf Photosynthetic Traits

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Abstract

Plants grown from different propagules can develop different architectures that influence their functioning. Hybrid potato (*Solanum tuberosum*) plants grown from true seeds and seedling tubers differ in architectural development, particularly in spatiotemporal distribution of leaves, generating variations in leaf age across leaf positions and origins (main stem or branch). This may affect nitrogen distribution and leaf photosynthesis. The increasing use of true seeds in potato breeding and propagation requires a better understanding on to what extent these differences influence leaf photosynthesis and plant productivity. A greenhouse experiment was conducted, using potato plants of the same genotype grown solitarily, from true seeds and seedling tubers. Key leaf photosynthetic and physiological traits were compared between propagule types across different leaf positions, origins, and developmental stages. No significant differences were found between propagule types in leaf traits, including light-saturated net CO₂ assimilation rate (A_{sat}), dark respiration rate (R_d) and specific leaf nitrogen (SLN), and their changes across leaves over time. The decline in A_{sat} with leaf age corresponded with the decrease in SLN and stomatal conductance (g_{sw}), regardless of leaf position, origin or propagule type. We conclude that under identical environmental conditions, architectural differences between true-seed-grown and seedling-tuber-grown plants of the same genotype do not influence leaf photosynthetic traits. Leaf age is the main determinant of leaf photosynthetic properties in potato plants grown solitarily. This relationship can be used to estimate whole-plant photosynthesis yet requires accurate estimation of leaf appearance. Different architectural design may be needed for different propagule types for improved crop-level productivity.

Keywords Hybrid potato · Leaf age · Photosynthesis · Plant architecture · Propagule type · Seedling tuber · True seed

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Introduction

The timing and spatial arrangement of leaf production are key aspects of plant architectural development, which largely contribute to overall plant resource capture and allocation (Murchie and Burgess 2022). Photosynthetic properties of individual leaves vary with leaf age and position, which interact with light absorption and leaf nitrogen (N) status (Hikosaka et al. 1994; Kitajima et al. 2002; Niinemets 2016). Generally, for a solitary plant with a vertical and non-branched architecture, leaf age has a dominant effect on N distribution: younger leaves are located on higher positions and contain higher N content, compared with lower leaves, which drives a decreasing gradient of leaf photosynthetic capacity from top to bottom along the main axis (Anten et al. 1998; Field 1983; Mooney et al. 1981). In contrast, for plants with more complex architecture, such as some herbaceous species that produce numerous branches, leaves with similar ages can be scattered on different positions on the plant, which may influence N distribution within a plant, and therefore alter leaf photosynthetic properties.

Potato (*Solanum tuberosum*) is a herbaceous species with a hierarchical branched plant architecture, which exhibits a sympodial branching pattern (Struik 2007; Vos 1995). Branch development at the basal part of the main stem starts shortly after main axis extension, and continues acropetally, while sympodial branches develop basipetally after the main stem has terminated into an inflorescence (Gu et al. 2024a, b; Kacheyo et al. 2021). Such a branching pattern causes variations in leaf age at a given position on the plant: branch leaves are generally younger than main stem leaves at a same location, while some basal branch leaves can be older than some main stem leaves at higher positions, and the distribution of leaves changes with plant architectural development. Importantly, the branching pattern of potato plants also varies when the plants grow from different types of propagules (Struik 2023). For example, potato plants are commonly produced clonally from tubers which are modified stems, while they can also grow from botanical seeds, also known as true seeds, which are produced via sexual reproduction. A distinct architectural development pattern has been observed in solitary plants grown from true seeds, compared with genetically identical plants grown from seedling tubers (tubers derived from true-seed-grown plants), which mainly exist in the temporal-spatial distribution of branch and leaves along the main axis (Gu et al. 2024b). Their differences can create more variations in leaf age across positions on individual plants, which may affect N distribution and leaf photosynthetic properties between plants grown from true seeds and seedling tubers. Especially with the rapid rise in the use of hybrid true seeds in potato breeding and propagation, it is crucial to understand these differences to assess their impact on plant productivity and the potential for adopting true seeds (Bradshaw 2022; Eggers et al. 2021; Struik et al. 2023).

Previous studies have reported the change with leaf age, leaf position, and plant architecture in leaf photosynthetic capacity and related traits in potato plants grown from tubers. Light-saturated photosynthetic CO₂ assimilation rate of leaves (A_{sat}) declines with leaf age, and the trend is similar among apical

leaves located on the main stem and branches (Vos and Oyarzún 1987). Leaf nitrogen content (*LNC*; N per unit leaf mass) and specific leaf nitrogen (*SLN*; N per unit leaf area) also decrease with leaf age for main stem leaves (Vos and van der Putten 1998). Moreover, *LNC* increases with increasing leaf position on the main stem and apical branches, but such gradient is reduced with leaf ageing until levelling-off at senescence (Biemond and Vos 1992). In addition, a transgenic study has shown that enhanced cytokinin level can alter plant architecture with increased lateral branching and can increase A_{sat} and stomatal conductance (g_{sw}), although the direct causation between such architectural changes and photosynthetic capacity was not evaluated (Tao et al. 2010). Nonetheless, current knowledge on leaf photosynthetic properties and their determinants in potato plants only involves a few apical leaves on the main stem or a single sympodial branch, which does not provide an overview on how the whole-plant architectural development affects leaf photosynthetic capacity across different positions. Particularly, there is little information regarding leaf photosynthetic traits and their changes with plant architectural development for true-seed-grown potato plants. It is therefore not known if true-seed-grown and seedling-tuber-grown plants differ in leaf photosynthesis.

In this study, we aimed to quantify to what extent the differences between true-seed-grown and seedling-tuber-grown plants in plant architectural development, particularly in the spatiotemporal distribution of leaves, affect leaf photosynthetic traits. To address this question, we conducted a greenhouse experiment using solitary plants grown from the two different propagule types, true seeds and seedling tubers, of the same genotype. Key leaf photosynthetic traits were determined over time and at different positions on individual plants and compared between the two propagule types.

Materials and Methods

Plant Culture and Experimental Design

True seeds and seedling tubers of the same diploid genotype, SOLHY007, were produced from the 2021 growing season, and provided by the Dutch potato breeding company Solynta (Wageningen, the Netherlands). Before the start of the experiment, uniform plant materials from each propagule type were obtained by separately raising young plants grown from true seeds and seedling tubers for 17 days, starting from 24 June 2022. True seeds were sown individually in plugs, which contained a mixture of substrates, with 30% white peat, 50% coco peat and 20% perlite, in the greenhouse. Seedling tubers (35–45-mm square size) were taken out from cold storage (4 °C) on the same day and started sprouting (Gu et al. 2024b).

On 11 July 2022, a pot experiment was started with plantlets grown from true seeds with 4 to 5 true leaves and seedling tubers with two green sprouts per tuber of homogenous size, which were transplanted individually into 10-L pots. Each pot (about 27 cm in diameter and 21 cm in height) contained a mixture of 50% black soil and 50% potting soil and was filled up to 2 cm below the rim. Transplants were

planted at 5-cm depth below soil surface. One week after transplanting, seedling-tuber-grown plants fully emerged from soil and were thinned to maintain only one main stem per plant, which was comparable to the single-stemmed true-seed-grown plants (Supplementary Fig. S1). Additional newly emerged main stems were also removed. The experiment lasted until 12 weeks after transplanting.

The pots with solitary plants were placed in an environmentally controlled greenhouse at Wageningen University & Research, Wageningen, the Netherlands (52°N, 6°E). Our experiment used a randomised complete block design (RCBD), with propagule type as the treatment and four replicates (blocks) positioned against the incoming radiation gradient in the greenhouse. Ten pots for each propagule type were used within each block, resulting in 40 pots per propagule type and 80 pots in total. Within each block, pots were randomly placed with equal pot distance on moveable tables to prevent shading from neighbouring plants.

The temperature in the greenhouse was set at 20 °C during the day and 15 °C at night. A relative humidity of 65% and an ambient CO₂ level were maintained. The photoperiod was set at 16 h using natural light, while additional light was provided during the day by high-pressure sodium lamps when outdoor solar radiation was lower than 500 W m⁻². Nutrient solutions were applied once a week from Week 1 to Week 4 after transplanting and twice a week for the following 4 weeks. Each application contained 400 mL nutrient solution with EC (electrical conductivity)=4.4 dS m⁻¹ and pH=6.5. In total, each pot received 2.4 g N, 0.6 g P, 3.5 g K, 0.46 g Ca, 0.28 g Mg and trace elements (2.0 g MnSO₄·H₂O, 3.0 g H₃BO₃, 0.5 g ZnSO₄·7H₂O, 0.1 g CuSO₄·5H₂O and 0.1 g Na₂MoO₄·2H₂O) (Gu et al. 2024b).

Measurements of Plant Architectural Development and Leaf Traits

Plant Architectural Development

Plant architectural development was measured non-destructively upon transplanting of true-seed-grown plants and emergence of seedling-tuber-grown plants. In each block, four plants were randomly selected for each type of propagule. Measurements of leaf appearance, leaf expansion of individual leaves on the main stem and Order 1 branches, which contribute the largest proportion to whole-plant leaf area (Gu et al. 2024b; Vos 1995), were conducted every 3 days. The origins and node positions of measured leaves were recorded. Leaf origin depended on whether a leaf was originated from the main stem or branches. The node position on the main stem was based on the insertion point on the main axis of a leaf or a branch (to which the measured branch leaf was attached) (Fig. 1). Additionally, for branch leaves, both the node position on the main stem of the branch and the insertion point of the selected leaf on this branch were recorded. Leaf length was assessed from the insertion point on the main stem to the tip of the terminal leaflet. Leaf appearance was defined as the date when the leaf length reached 1 cm. The moment of leaf appearance was calculated as the time point in between the measurement date a leaf was present and the one measurement date earlier, measured by days after transplanting. When the leaf length reached its maximum length, this leaf was considered fully

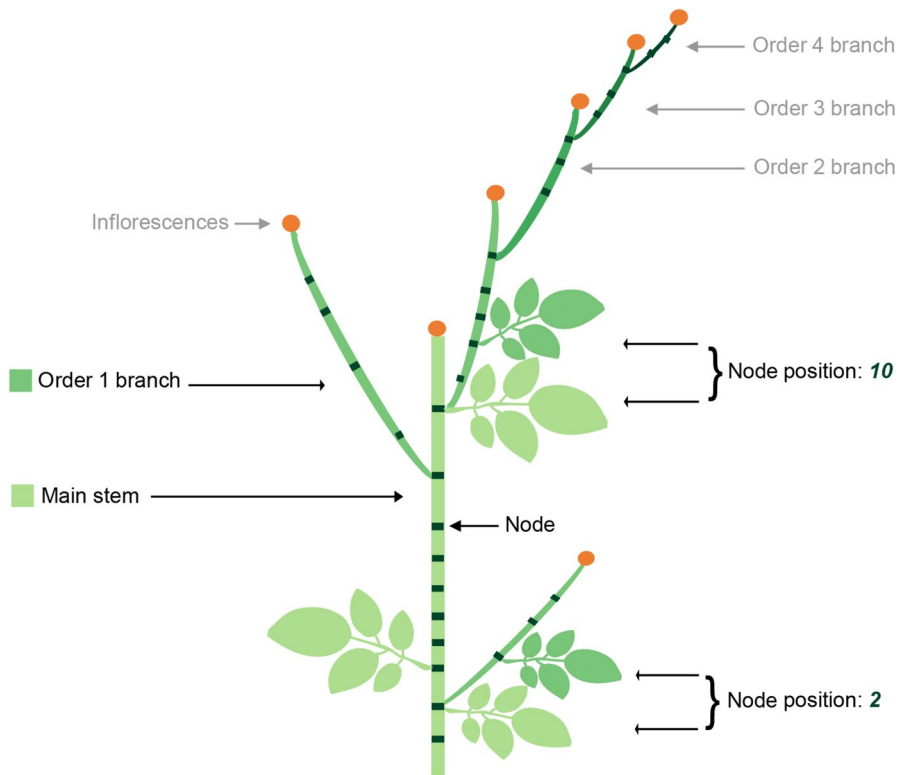


Fig. 1 Illustration of leaf origins and the node positions on the main stem of individual leaves. The stems and branches are assigned with specific branching orders, a structural pattern shared by both propagule types, as described in Gu et al. (2024b). Different leaf origins are indicated by different shades of green. This study only focused on the leaves originated on the main stem and Order 1 branches. For simplification, node position on the main stem of a branch leaf refers to the insertion point of the branch on the main stem, as shown in the example of leaves at Node positions 2 and 10

expanded. This allowed calculation of leaf age for individual leaves, defined as the difference between the day of measurement and leaf appearance.

Leaf Photosynthesis Measurements in Response to Light Intensity

Leaf photosynthesis measurements were conducted at three developmental stages (Weeks 6, 9 and 12 after transplanting), as most leaves on the main stem and Order 1 branches were fully expanded as of Week 6. Light response curves were derived from measurements of CO_2 assimilation rates using a portable gas exchange system with a 2-cm^2 leaf cuvette (LI-6800, LI-COR Biosciences, Lincoln, NE, USA). Measurements were done on the terminal leaflet of selected leaves, excluding the midrib.

On each measurement occasion, 1 plant per replicate was randomly selected (four replicates in total) for each propagule type. To ensure the leaf photosynthetic

capacity assessment covered the full range of the whole plant, every selected plant was equally divided into three leaf layers: top, middle and bottom, based on plant height. Plant height was measured from topmost leaf to soil level, using a ruler, and the height range of each leaf layer was calculated. Within each layer, one representative leaf from the main stem and Order 1 branches was randomly selected. However, due to the complex leaf structure of potato plants, a leaf was selected based on the following three criteria: (1) it was fully expanded; (2) more than 50% of its leaf area was present within a given layer and (3) the terminal leaflet was large enough for gas exchange measurement. Therefore, in each layer, a main stem leaf or a branch leaf might not be selected if it did not meet all selection criteria, which resulted in the selection of a total of five leaves per plant for each measurement occasion. In addition, to minimise plant-to-plant variation, the selected leaves on the branches with the same node rank on the main stem were closely located and the differences in their leaf appearance were minimal. The node positions of selected leaves on the main stem and/or on the branch were recorded. Leaf age of each selected leaf was then calculated as the differences between day of photosynthesis measurement and leaf appearance, using average values of four plants. The moment of appearance of selected leaves is listed in Table S1.

The measurements were conducted at a reference CO_2 concentration of $420 \mu\text{mol mol}^{-1}$, leaf temperature of 25°C , flow rate of $400 \mu\text{mol s}^{-1}$ and vapour pressure deficit (VPD) between 1.0 and 1.6 kPa. Leaf net photosynthetic rates were recorded at 11 levels of incident irradiance in a decreasing series of 2000, 1750, 1500, 1000, 500, 250, 200, 150, 100, 50 and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$. At each irradiance level, 4 to 10 min were given for leaf acclimation to reach steady state. The light response curve was fitted by using a non-rectangular hyperbola-based model (Thornley 1998):

$$A = \frac{\Phi \cdot I + (A_{\text{sat}} + R_d) - \sqrt{(\Phi \cdot I + (A_{\text{sat}} + R_d))^2 - 4\theta \cdot \Phi \cdot I \cdot (A_{\text{sat}} + R_d)}}{2\theta} - R_d \quad (1)$$

where A is the net photosynthetic rate at incident irradiance I ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$), A_{sat} is the net light-saturated photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), Φ is the apparent quantum yield of CO_2 assimilation on the basis of incident light, R_d is the dark respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and θ is the convexity of the curve. In addition, stomatal conductance to water vapour (g_{sw} ; $\text{mol m}^{-2} \text{s}^{-1}$) and transpiration rate (E ; $\text{mmol m}^{-2} \text{s}^{-1}$) were also recorded for each leaf.

In addition, for each leaf, the stomatal conductance (g_{sw}), intercellular CO_2 concentration (C_i) and ambient CO_2 concentration (C_a) were recorded at saturating irradiance, and the C_i/C_a ratio was calculated.

Leaf Transmission and Reflectance

Immediately after gas exchange measurements, a leaf punch of 6.16 cm^2 was taken around the measured position of the leaf. The leaf punch was used to measure leaf transmittance (τ) and reflectance (r) from 450 to 700 nm (PAR; photosynthetically

active radiation), with a dual-channel spectrometer and integrating spheres (Ocean Insights, Rostock, Germany) and a halogen light source (24 V/250 W, type 7748XHP, Philips, the Netherlands), after Wassenaar et al. (2022). The transmittance and reflectance of each leaf sample were used to determine leaf absorptance (Abs), calculated as $Abs = (1 - r - \tau)$. The total absorptance of each leaf for gas exchange measurement was calculated by combining the percentage of actinic light in the leaf cuvette (red: 90%; blue: 10%) with the respective spectral range (red: 615–635 nm; blue: 465–485 nm).

The maximum quantum yield of CO_2 assimilation (Φ_{max}), i.e., maximum potential light use efficiency, can be derived as:

$$\Phi_{max} = \frac{\Phi}{Abs} \quad (2)$$

Other Leaf Traits

After that, the leaf punches used for measurements of leaf transmittance and reflectance were oven-dried at 70 °C until constant weight, and their dry weights were determined. Specific leaf area (SLA ; $cm^2 g^{-1}$) was calculated as the ratio of leaf area and leaf dry weight. Then dried samples were ground to fine powder and leaf N content (LNC ; $mg N g^{-1}$ leaf) was assessed with an elemental analyser using the Micro-Dumas combustion method (model: Flash 2000, Thermo Scientific). Specific leaf N (SLN ; $g N m^{-2}$ leaf) was calculated as LNC divided by SLA . Leaf photosynthetic nitrogen use efficiency ($PNUE$), also known as photosynthetic capacity per unit N under saturating light conditions, was defined as:

$$PNUE = \frac{A_{sat}}{SLN - N_b} \quad (3)$$

where N_b refers to an estimated base leaf nitrogen content per unit area for photosynthesis (Zhou et al. 2023), derived from the x -intercept of linear regression between A_{sat} and SLN .

Intrinsic water use efficiency (WUE) was calculated as follows:

$$WUE = \frac{A_{sat}}{g_{sw}} \quad (4)$$

Statistical Analyses

Data analyses were performed in R (v.4.3.3; R Core Team 2024). A nonlinear least-squares regression was used to fit light response curves of each selected leaf to obtain leaf photosynthetic parameters A_{sat} , Φ , and R_d . To compare leaf photosynthetic traits between propagule types and developmental stages (weeks) across different leaf positions, a linear mixed effect model was used following the RCBD. In the mixed model, propagule type and week were fixed effects, and

Fig. 2 The decrease over time of average leaf photosynthetic traits per plant for true-seed-grown and seedling-tuber-grown plants. The three time points correspond to early branching (development of Order 1 branches), establishment of the whole-plant architecture, and onset of plant senescence, respectively (see Gu et al. 2024b for detailed description). Leaf traits include A_{sat} : light-saturated CO_2 assimilation rate **A**, g_{sw} : stomatal conductance **B**, R_d : dark respiration **C**, LCP : light compensation point **D**, Φ_{max} : maximum quantum yield of CO_2 assimilation **E**, and Abs : leaf absorptance based on PAR **F**. Bars represent the average values of fixed effects of the propagule types and weeks after transplanting. Error bars indicate the standard errors of the mean. Different letters indicate significant differences between weeks (capital letters), propagule types (lowercase letters) and their interactions (italic lowercase letters) ($p < 0.05$). If no lowercase letters are shown for a given time point, the difference between propagule types or the week $\times$ propagule type interaction was not significant. Detailed statistical differences for each trait are given in Supplementary Table S2

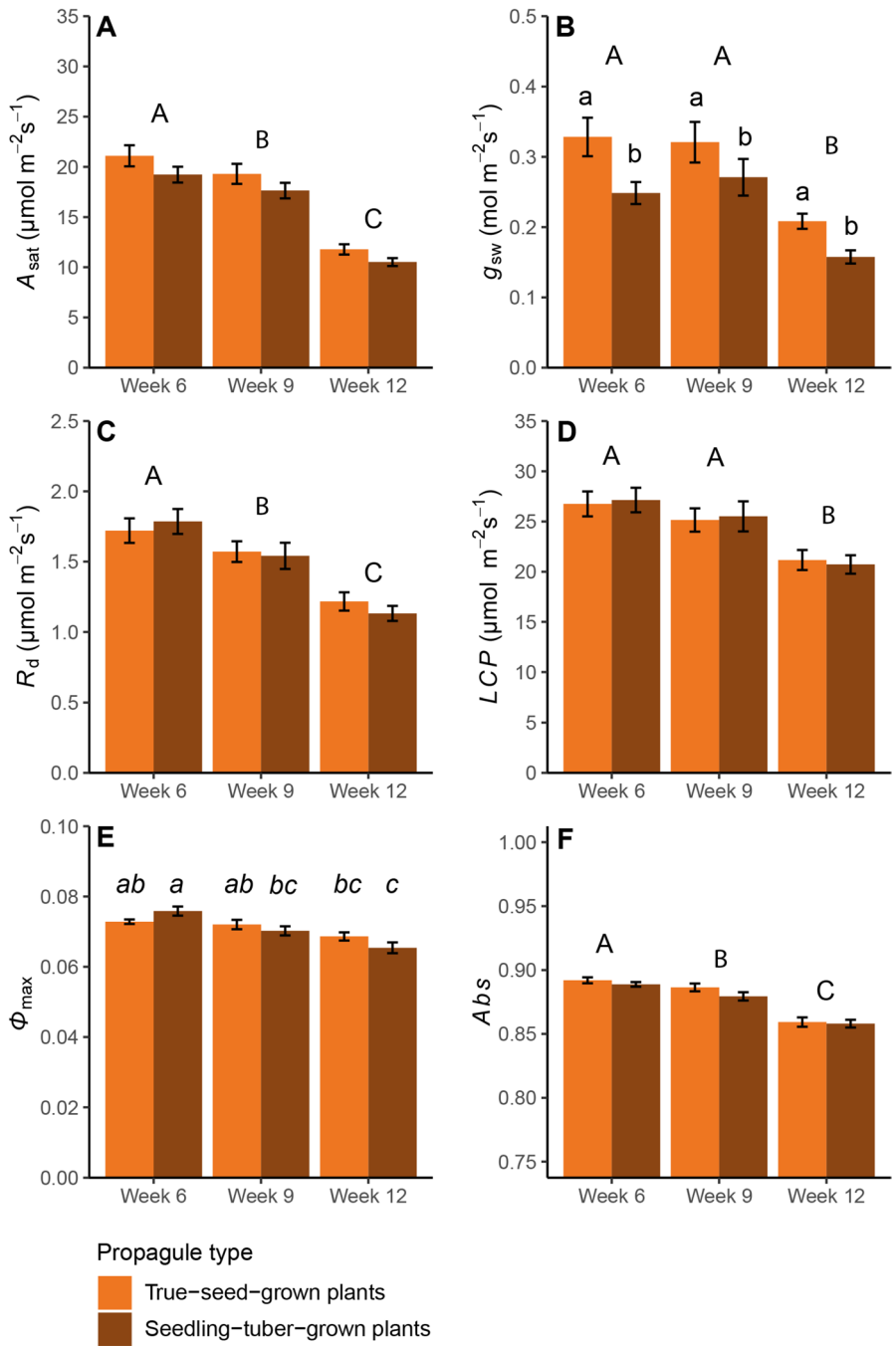
the leaf position nested within blocks was a random effect, which accounts for the random variability among leaves within each plant and avoids redundancy, as one plant per block was selected. Average values were grouped by propagule type and week. A two-way ANOVA was conducted to test the significance of fixed effects, followed by a Tukey's HSD post hoc test. To further elucidate the impact of architectural development on leaf level photosynthesis, we included leaf origin (main stem or branch) and node positions of individual leaves in the analysis. Linear regressions were applied to test the relationships between key leaf traits and leaf positions at each developmental stage and dependent on leaf origin (main stem or branch). Significant differences among slopes and among y-intercepts in linear regressions were evaluated by analysis of covariance (ANCOVA). A Pearson's correlation analysis was performed among all leaf traits for each propagule type. Key traits were selected for further linear regression analysis, and differences between propagule types were also tested by ANCOVA.

Results

Photosynthetic Traits Change with Plant Developmental Stage

As the plants aged, the average photosynthetic traits of pooled leaves per plant, including light-saturated net CO_2 assimilation rate (A_{sat}), stomatal conductance (g_{sw}), dark respiration rate (R_d), light compensation point (LCP) and leaf absorptance based on PAR (Abs), decreased consistently for plants grown from both propagule types (Fig. 2). The decreasing trend of A_{sat} was consistent with the decline in R_d and Abs (Fig. 2A, C, F), while Φ_{max} (maximum quantum efficiency of CO_2 assimilation), showed only a slight decrease over time (Fig. 2E).

Across all developmental stages, true-seed-grown plants had higher g_{sw} than seedling-tuber-grown plants, while the other traits were not significantly different between propagule types (Table S2).



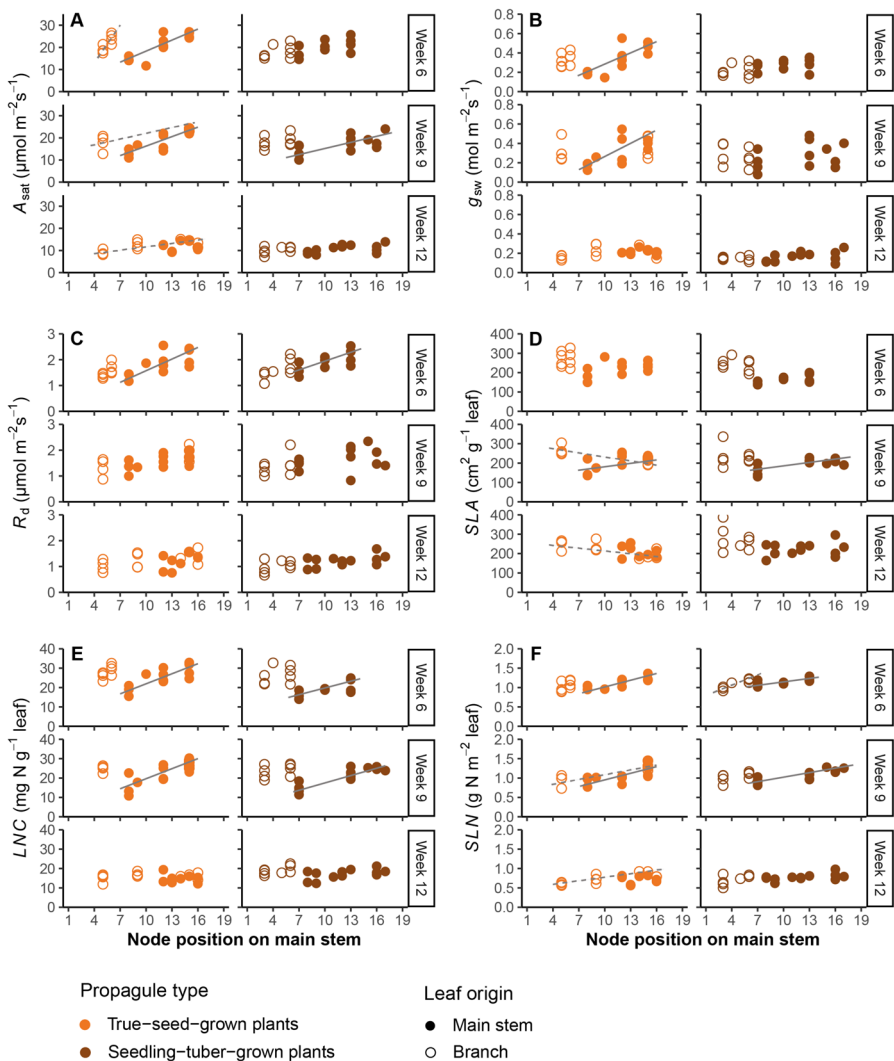


Fig. 3 Key leaf traits changes across node positions of plants grown from two propagule types at three developmental stages. Leaf traits include A_{sat} : light-saturated CO_2 assimilation rate **A**, g_{sw} : stomatal conductance **B**, R_d : dark respiration **C**, SLA : specific leaf area **D**, LNC : leaf nitrogen content **E**, and SLN : specific leaf nitrogen **F**. Filled symbols indicate main stem leaves; open symbols represent the leaves from branches of which node positions are their insertion points on the main stems. Lines denote significant linear regression ($p < 0.05$) for main stem leaves (solid lines) and branch leaves (dashed lines)

Key Leaf Traits Change with Plant Architectural Development

When introducing architectural characteristics, linear relationships were found between specific photosynthetic traits and leaf positions across developmental stages in both propagule types (Fig. 3; Table S3).

At Week 6 and Week 9, the positive relationships between node positions and the leaf traits, such as A_{sat} , R_d , LNC and SLN , were mainly significant for main stem leaves, and were not different between true-seed-grown and seedling-tuber-grown plants except for g_{sw} , and all slopes became smaller at Week 12 (Fig. 3A, C, E, F). Similar trends can be observed for branch leaves, although linear relation was found not to be significant. There were no consistent changes in g_{sw} and SLA across leaf positions (Fig. 3B, D).

For both propagule types, leaves appeared earlier at lower nodes on the main stem, which reflects decreasing leaf age with increasing leaf position on the main stem. When developed from the same node on the main stem, the leaves on the branch were younger than the one on the main stem, whereas on different nodes, basal branch leaves appeared earlier than apical sympodial leaves (Table S1).

Relationships Between Leaf Photosynthetic Traits and Leaf Age

The significant contribution of leaf age to key leaf photosynthetic traits was shown via a correlation analysis, in both propagule types (Supplementary Fig. S1). The decline in A_{sat} with leaf age was uniform across all leaf positions and regardless of leaf origin in both true-seed-grown and seedling-tuber-grown plants (Fig. 4A). A

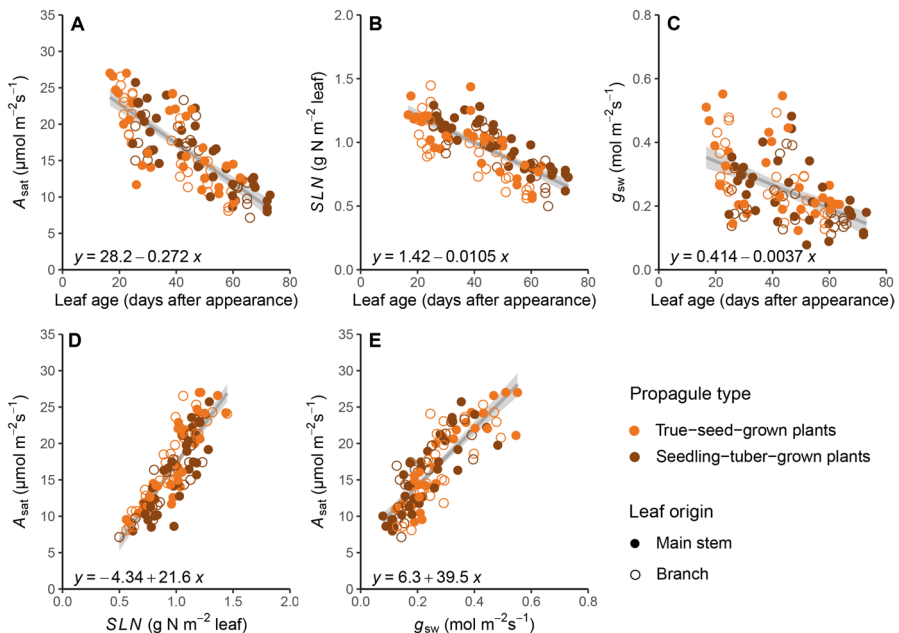


Fig. 4 Relationships between leaf age and key leaf photosynthetic traits for true-seed-grown and seedling-tuber-grown plants. A_{sat} : light-saturated CO_2 assimilation rate; SLN : specific leaf nitrogen; g_{sw} : stomatal conductance. Filled symbols indicate main stem leaves; open symbols represent the leaves originated from branches. Lines represent significant linear regression ($p < 0.05$), denoted with equations. Details on regression coefficients and p -values are shown in Table S4

Table 1 Correlation matrix (Pearson coefficient) between leaf age and key photosynthetic traits. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Bold numbers indicate highly significant correlations ($r > 0.7$)

	A_{sat}	SLN	g_{sw}	Abs	R_d	Φ_{max}	$PNUE$	WUE
Leaf age	-0.79***	-0.78***	-0.52***	-0.73***	-0.62***	-0.53***	-0.17	-0.13
A_{sat}		0.87***	0.83***	0.70***	0.66***	0.56***	0.45***	-0.12
SLN			0.58***	0.71***	0.74***	0.54***	-0.03	0.20*
g_{sw}				0.48***	0.49***	0.45***	0.59***	-0.59***
Abs					0.44***	0.46***	0.15	0.12
R_d						0.57***	-0.00	0.13
Φ_{max}							0.19*	-0.05
$PNUE$								-0.54***

consistent decrease with leaf age was also observed in SLN and g_{sw} (Fig. 4B, C), which explained over 80% of variance in the decline of A_{sat} with leaf age (Table 1; Fig. 4D, E). A stable C_i/C_a ratio was however observed (Supplementary Fig. S2).

Moreover, a highly significant correlation was also found between leaf age, Abs and R_d , respectively, and all of them were not dependent on the type of propagules, leaf position or leaf origin (Table 1). Furthermore, although Φ_{max} showed a negative correlation with leaf age, indicating reduced maximum potential light use efficiency in older leaves, this decline only became evident after about 45 days after leaf appearance (Supplementary Fig. S1). In contrast, other intrinsic resource use efficiencies, such as photosynthetic nitrogen use efficiency ($PNUE$) under saturating light intensity and intrinsic water use efficiency (WUE), were not affected by leaf age.

Discussion

Conserved Photosynthesis–Nitrogen Relationship and Intrinsic Resource Use Efficiency Between Propagule Types

In our study, no differences were found between the true-seed-grown and seedling-tuber-grown plants in the relationships among leaf photosynthetic traits such as SLN , SLA , A_{sat} , g_{sw} , R_d and Abs , across leaf position, origin and time. The intrinsic resource use efficiencies (Φ_{max} , $PNUE$, and WUE) derived from these correlations were also similar in both propagule types. This suggests that they have similar leaf structure and utilise resources for leaf photosynthesis in comparable ways. Particularly, the respective same values of Φ_{max} and $PNUE$ indicate that the physiological processes regulating photosynthetic machinery and nitrogen allocation, such as fractional nitrogen investment in Rubisco, are likely conserved within propagule types due to their shared genetic background. This aligns with findings by Hikosaka (2004), who reported that such an allocation pattern is conserved within species. Although g_{sw} and E were slightly higher in true-seed-grown plants, most likely due to the selection of younger leaves for measurement, compared to

seedling-tuber-grown plants, the WUE and C_i/C_a ratio did not differ between the two propagule types. The consistency in these physiological traits between propagule types further suggests that true-seed-grown plants have the potential to be adopted in terms of biomass production as compared to seedling-tuber-grown plants.

A Dominant Effect of Leaf Age on Photosynthetic Traits

As solitary plants were used to avoid mutual shading and ensure consistent light exposure across leaves, differences in leaf traits are considered mainly due to variations in leaf position and origin, which correlate with leaf age (Fig. 3 and Fig. 4). The observed strong negative correlations between leaf age, A_{sat} , SLN , g_{sw} and R_d were shared between the two propagule types, suggesting that leaf age has a dominant impact on leaf photosynthetic properties in potato plants regardless of propagule type. Such pattern has been reported previously in tuber-grown potato plants (Vos and Oyarzún 1987; Vos and van der Putten 1998), and other C_3 species within or beyond the Solanaceae family, such as in tobacco (*Nicotiana tabacum*) (Clarke et al. 2021) and Canada cocklebur (*Xanthium canadense*) (Anten et al. 1998). The decline of A_{sat} with leaf age is primarily attributed to the reduction in leaf nitrogen concentration, which results from the redistribution of nitrogen from old to younger leaves (Field 1983; Niinemets 2007). The parallel decrease in R_d with leaf age indicates that there are likely biochemical changes in ageing leaves, such as lower respiratory enzyme activity and the overall metabolic activity (Villar et al. 1995). Moreover, the accompanied decline in g_{sw} could be due to a decreased stomatal density as leaf ages, rather than CO_2 diffusion limitation as indicated by the stable C_i/C_a ratio, similar to findings in tobacco plants (Clarke et al. 2021). In these tobacco plants, however, a stronger linear relationship between CO_2 assimilation rate and mesophyll conductance was found, and both consistently decreased with leaf age, alongside increased leaf thickness. As this relationship is well-established in various C_3 species (Barbour et al. 2016), and may be useful for modelling whole-plant photosynthesis (Clarke et al. 2021), we suggest future study should explore whether similar patterns and leaf anatomical changes exist in potato plants. Given that measuring mesophyll conductance is time and resource demanding, the simple relationships we found between leaf age and photosynthetic traits could offer a practical proxy for modelling potato plant photosynthesis. However, accurately estimating leaf age is essential for reliable photosynthesis predictions, which is challenging in potato plants due to their sympodial growth habit. In species with monopodial growth on the main stem, such as cereals and tobacco, leaf age can be predicted through the cumulative phytomer number (the number of phytomers from the base), as leaves of the same cumulative phytomer number appear at the same time (Clarke et al. 2021; Evers et al. 2010). In potato plants, however, leaf appearance on the main stem linearly correlates with air temperature, while this relationship can be altered by onset of tuber bulking and also depends on genotype, and leaf appearance on branches is not synchronous with the main stem and therefore varies (Firman et al. 1995; Fleisher et al. 2006a, b; Oliveira

et al. 2021). The sympodial growth habit and complex interactions between branches aboveground and belowground make leaf appearance estimation difficult in potato plants, requiring alternative approaches to predict leaf age.

Impact of Architectural Development on Photosynthetic Productivity

Since the architectural development of potato plants influences the spatial and temporal distribution of leaves of varying ages, given the A_{sat} –age relationship, the impact of architectural development on whole-plant photosynthetic capacity is largely determined by the distribution of leaf age. True-seed-grown plants and seedling-tuber-grown plants likely differ in leaf age distribution due to distinct growth patterns. True-seed-grown plants, having an indeterminate growth habit, continually produce young leaves, particularly on higher order sympodial branches. These younger leaves may support higher photosynthetic rates in true-seed-grown plants than in seedling-tuber-grown plants. However, the new sympodial leaves only contribute less than 10% of the total leaf area (Gu et al. 2024b), resulting in little contribution to whole-plant photosynthesis and therefore similar amount of biomass is produced as compared to seedling-tuber-grown plants.

However, when a canopy is formed, both the distribution of leaf age and light can influence the leaf photosynthetic traits (Anten et al. 1998; Hikosaka et al. 1994; Niinemets et al. 2015). Light interception and photosynthetic rate of apical leaves contribute most to the canopy photosynthesis regardless leaf origins in tuber-grown potato plants (Fleisher et al. 2006a, b), whereas the leaves in the middle layer account for the largest leaf area, export assimilates directly to tubers and yet spend a large part of their assimilates on their own growth and maintenance (Golovko and Tabalenkova 2019). Further study is needed to investigate how leaf age and light distribution interact in a canopy and their impact on photosynthesis in crops grown from true seeds and seedling tubers. In addition, in other species with sympodial growth such as cotton (*Gossypium hirsutum*), the competition for assimilates between sympodial leaves and reproductive organs is intense when their growth period has a long overlapping duration (Chen et al. 2021; Wang et al. 2021). In the hybrid potato plants, similar competition exists between sympodial leaves and berries, and both also compete with belowground tubers. Their competition could be enhanced in true-seed-grown plants due to prolonged overlapping growth periods, which could potentially limit overall crop productivity (Gu et al. 2024a), while sympodial leaf photosynthetic performance can be potentially improved due to high plasticity of these branches (Chen et al. 2021). Therefore, managing the temporal and spatial distribution of sympodial leaves is important to develop optimised canopy structure and enhance crop productivity, which can be different for contrasting propagule types based on their distinct growth patterns. These insights are particularly relevant for developing propagation strategies and breeding programmes aimed at beneficial architectural traits of potato crops to improve production, which requires future research.

Conclusions

Our study suggests that the architectural differences between hybrid potato plants grown from true seeds and seedling tubers do not influence leaf photosynthetic properties. When grown solitarily and under identical conditions, leaf age is the main determinant of leaf photosynthetic traits in both true-seed-grown and seedling-tuber-grown plants of the same genotype, which strongly correlates with leaf nitrogen content. Leaf age can be used to estimate whole-plant photosynthesis for solitarily grown potato plants, while accurately determining leaf appearance presents a challenge due to the complex stem branching patterns. Moreover, the interaction between leaf age with light distribution in a canopy and their impact on crop photosynthesis needs further investigation. The distinct growth patterns of true-seed-grown and seedling-tuber-grown plants may require different design of architectures for improved crop productivity.

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Author Contribution J.G., S.M.D., P.C.S. and J.B.E. designed the experiment. J.G. performed the experiment, analysed the data and drafted the manuscript with input from all authors. S.M.D., P.C.S. and J.B.E. revised the manuscript. All authors approved the final version.

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Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Competing Interests P.C.S. is editor-in-chief of *Potato Research*.

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