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Evaluation of novel grapevine rootstocks for phylloxera tolerance and agronomic performance

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ABSTRACT

Since their introduction and continuous improvement, rootstocks capable of controlling phylloxera have been essential for advancing sustainable viticulture. The recently registered rootstocks, Libero and Vinto, have been rigorously evaluated within the rootstock breeding programme and across various German wine-growing regions. Their resistance mechanism is similar to that of their pollen donor, the well-established rootstock cultivar Börner. The two new rootstock varieties also display additional desirable agronomic traits, both at the propagation site and during the grafting process. In a comprehensive, multi-year, multi-site study, the two breeding lines demonstrated yield and juice quality comparable to commercial rootstocks. Furthermore, we established a pipeline for evaluating adventitious root development using rhizoboxes, which proved to be a suitable tool for assessing the early rooting behaviour of rootstock cuttings. The continued development of improved rootstocks is critical to addressing both the current and future challenges posed by climate change and the persistent threat of long-standing pests such as phylloxera. The introduction of Libero and Vinto expands the range of options available to wine-growers, enabling selection of phylloxera-withstanding rootstocks that is better suited to their specific needs, since plant material forms a cornerstone in the transition toward more sustainable agriculture.

KEYWORDS: rootstock breeding, plant improvement, rootstock testing, rhizobox, *Vitis cinerea* Arnold

INTRODUCTION

The accidental introduction of grapevine phylloxera (*Daktulosphaera vitifoliae* Fitch) into European vineyards in the 1860s created an unprecedented crisis in commercial viticulture and resulted in the widespread adoption of grafting and intense breeding of rootstocks with the purpose of controlling the invasive pest through biotechnological approaches (Ollat *et al.*, 2024). The aphid-like insect was first discovered in Germany in 1874, about ten years after the decline of vines from phylloxera infestation was first recorded in French wine-growing regions (Badia-Miró *et al.*, 2010; Tello *et al.*, 2019). As direct control of phylloxera has proven practically impossible due to its wide distribution and dual life cycles, only breeding approaches offer sustainable solutions to reduce the spread of this economically dangerous pest (Cook *et al.*, 2025; EFSA, 2014).

Rootstock breeding in Geisenheim (Rheingau, Germany) started in 1876. Through cross-breeding and systematic selection, numerous new and improved rootstock varieties for use in both German and international viticulture have emerged since then. Among the best-known are the varieties Sori and Börner, as well as the clonal variants of Kober 5 BB and Teleki 5 C Geisenheim, to name a few. The first rootstock variety crossed in Geisenheim was 26 G (*Vitis vinifera* cv. Schiava Grossa × *V. riparia* 193 G). However, it was later found to be susceptible to phylloxera rendering it ineffective for pest control and ultimately incompatible to the strict German Ordinance on Vine Pest Control (Bundesministerium der Justiz and Verbraucherschutz, 1988). The use of phylloxera-susceptible rootstock cultivars continues to pose a significant risk in modern viticulture, as repeated cases of vine decline caused by inappropriate rootstock selection has clearly demonstrated (Granett *et al.*, 1985; Heinitz *et al.*, 2019).

To date, many of the first phylloxera-tolerant rootstocks – some of which are more than a hundred years old – are still in use; these are derived from crosses of root-phylloxera-withstanding wild *Vitis* species native from North America. The vine's response to phylloxera infestation can be divided into three categories: i) susceptible: the vine is easily infested by phylloxera and suffers significant damage; *e.g.*, due to direct impairment from root injury and deformation, and especially due to secondary infections from other pathogens, ii) tolerant: the vine is infested by phylloxera but not significantly affected in its vitality; this means it can cope with a certain level of infestation without severe health deterioration, and iii) resistant: the vine exhibits defence mechanisms against phylloxera, such that reproduction is limited or prevented and the pest cannot cause damage to the host (UPOV, 1994). Additionally, *Vitis* species display different degrees of tolerance to phylloxera at both the leaf (OIV descriptor 461) and the root (OIV descriptor 462) level, which manifests itself in their ability for and the extent of gall or necrosis formation (Galet, 1979).

Grapevine resistance to phylloxera is controlled by multiple loci and differs between root and foliar infestations. Root resistance is primarily associated with the *Rdv*1 locus on chromosome 13, which is identified in the rootstock Börner and its progenies, and the *Rdv*2 locus on chromosome 14 detected in *V. cinerea* C2-50 (Hausmann *et al.*, 2011; Smith *et al.*, 2018; Zhang *et al.*, 2009). In addition, minor resistance loci have been reported on chromosomes 3, 7, and 10, implicating *Muscadinia rotundifolia* as a potential donor of phylloxera resistance (Rubio *et al.*, 2020). Foliar resistance has been mapped to *Rdv*3 on chromosome 14 and *Rdv*4 on chromosome 4 in multi-species hybrids, encompassing candidate genes associated with R-gene-mediated defence and non-responsiveness to gall formation; however, the specific species that contribute to these resistance mechanisms have still not been determined (Clark *et al.*, 2018; Yin *et al.*, 2022). Collectively, these studies underscore the polygenic nature of phylloxera resistance and provide a foundation for marker-assisted breeding in grapevine rootstock and hybrid improvement.

However, the impact of climate change, the reduced use of pesticides or the evolutionary development of phylloxera biotypes may have led to a change in grapevine response to the attack of phylloxera; *i.e.*, higher susceptibility of *V. vinifera* leaves and hybrid varieties to phylloxera leaf gall formation (EPPO, 2025; Wilmink *et al.*, 2021b).

The rootstock variety Börner (*V. riparia* 183 G × *V. cinerea* Arnold) was developed as part of the phylloxera-tolerance breeding programme initiated in 1935 by Dr. Carl Börner in Naumburg/Saale. While the initial crosses date back to that time, the selection and establishment of Börner as a rootstock variety were conducted by Prof. Dr. Helmut Becker in the 1950s: first in Neustadt/Weinstraße and later at the Institute for Grapevine Breeding and Grafting at the Geisenheim Research Center (now Geisenheim University, Department of Plant Breeding). The inheritance of the ability of the North American wild species *V. cinerea* Arnold to induce a hypersensitive response upon phylloxera attack provides the Börner rootstock (breeding line number Na 5153-54) with complete resistance in both leaves and roots (Börner, 1943). This response is a rapid, spatially-limited cell death in the affected tissue, which interrupts the pest's feeding and thus its reproduction. Börner was officially registered in 1991 and remains the only commercially important rootstock so far that is considered to have full resistance to phylloxera. Its sister varieties Rici (Na 5153-588 A9; *V. riparia* 183 G × *V. cinerea* Arnold) and Cina (Na 5004-848 C3; Kober 125 AA × *V. cinerea* Arnold) also display high phylloxera resistance at the root and leaf level, but are less favoured by winegrowers due to the low vigour conferred to the scion variety. However, these two *V. cinerea* hybrids, officially registered in 1998, are a valuable addition to the rootstock catalogue wine-growers can use for their plant material selection (Schropp *et al.*, 2002).

Due to increased pressure from climate warming, which leads to earlier and more frequent phylloxera reproductive cycles, as well as an increase in cases of insufficient vineyard hygiene – such as abandoned vineyards and rootstock suckers in production sites – phylloxera has become a timely issue for breeding programmes. This is further exacerbated by underestimating the real danger of resistance breakdown due to phylloxera. In recent years, increased phylloxera leaf

infestations have been observed in rootstock mother blocks and in vineyards planted with both fungus-tolerant and traditional grape varieties (Forneck *et al.*, 2019). Effective insecticides against the pest are limited, and their application contradicts the European Union's policy goals for pesticide reduction. The more sustainable and efficient approach to combat phylloxera than the use of biocides is preventing its development from the outset. The Geisenheim rootstock breeding programme therefore focuses exclusively on breeding lines that, like Börner, exhibit an advanced defence response to phylloxera in both roots and leaves. In addition to full phylloxera resistance, other viticulturally relevant traits are also considered in the programme, such as increased tolerance to intermittent drought, high soil lime content, and chlorosis, as well as a broad adaptability to different soil types and good graft compatibility.

Targeted crosses with resistant wild species offer a valuable opportunity to broaden genetic diversity and enhance important rootstock traits (Blois *et al.*, 2023; Riaz *et al.*, 2019). At the same time, using proven, field-tested parental varieties allows for efficient and cost-effective utilisation of existing resources (Schmid *et al.*, 2003).

In the Geisenheim rootstock breeding programme, new breeding lines first undergo resistance testing for phylloxera and mildews. The seedlings displaying proper vigour are vegetatively propagated and evaluated over several years in the field for phylloxera infestation, vigour, internode length, wood maturation, wood yield, lateral shoot formation, and compatibility in grafting, including callus formation. Additionally, in the nursery, root formation and vitality – key traits for successful plant material production – are assessed.

To evaluate the pedo-ecological range, various commercially important grapevine scion × rootstock combinations are tested in specially designed adaptation trials. These trials assess the compatibility of each rootstock and its grafting partner under varying soil types and microclimatic conditions. The scions are grafted onto selected rootstocks and evaluated in collaboration with commercial partners at sites representing diverse environmental conditions. Rootstock trials are considered the most effective method for gaining insight into rootstock performance and scion interaction under real-world vineyard conditions and allow consultation to practitioners (Dodson Peterson *et al.*, 2019).

Only the best offspring from a few crossing populations pass this rigorous and multi-year testing process.

MATERIALS AND METHODS

Two new rootstock varieties Libero (*V. berlandieri* × *V. riparia* cv. Kober 125 AA × Börner) and Vinto (*V. berlandieri* × Börner) were compared with established commercial rootstocks following the official guidelines of the German Federal Variety Office (Bundessortenamt, 1986). The testing procedure of rootstock varieties is divided into four parts: i) susceptibility to phylloxera, ii) performance at the propagation site, iii) graft affinity (*i.e.*, scion × rootstock compatibility), and iv) performance in adaptation trials.

Rootstocks for official variety registration trials were planted in the mother block in 2018. Performance at the propagation site was assessed following a two-year establishment phase (2019–2020) and a three-year production phase (2021–2023). For affinity testing, wood cuttings of the tested varieties were collected between 2021 and 2023. Official commercial-scale testing of scion × rootstock combinations at multiple sites (adaptation trials) was conducted from 2019 to 2021. In addition, this study includes data from multiple sites and periods obtained from intensive pre-testing of the breeding lines.

1. Phylloxera susceptibility and *Rdv*1 marker testing

The susceptibility of the new rootstock varieties to phylloxera was officially assessed by an independent authority. Both leaf and root infestation were evaluated over a period of at least three years using a total of twenty rooted vines per rootstock. This included four times three field replicates of each rootstock cultivar, as well as eight vines per cultivar tested under controlled greenhouse conditions. The classification of phylloxera susceptibility provided in this work was based exclusively on field-derived assessment scores, while greenhouse experiments were conducted as a complementary approach to field evaluations. According to the German Phylloxera Ordinance (Reblausverordnung), a rootstock is considered resistant to root-feeding phylloxera, if it does not develop tuberosities or only forms tuberosities clearly separated from the vascular tissue upon infestation, as determined by official testing (§ 4(2) ReblV; Table S1). For the artificial inoculation, an in-house phylloxera culture derived from susceptibility tests conducted on various rootstocks in the previous year was used. To maintain and adapt the genetic diversity of the phylloxera population, individuals from natural, not further specified, vineyard populations were added throughout the year. No further information on the phylloxera biotypes used is available. The tested rootstocks were directly compared with two tolerant reference rootstocks, namely Selektion Oppenheim 4 (SO4) and Kober 5 BB (Eder & Jung, 2025). Table S1 provides an overview of susceptibility rating scores according to Bundessortenamt (1986).

DNA was extracted from young leaves of the new varieties and Börner using a commercial plant DNA extraction kit (Macherey & Nagel, Düren, Germany). To confirm the presence of the *Rdv*1 locus in the rootstocks, genotyping was performed using 14 simple sequence repeat (SSR) markers spanning the *Rdv*1 genomic region (Table S6). PCR amplification and DNA fragment length analysis were carried out as previously described (Huber *et al.*, 2016).

2. Evaluation of the vegetative performance at the propagation site

A total of twenty plants per genotype were tested across three years of wood production at two different locations (49.9844° N, 7.9672° E, Geisenheim, Rheingau, Germany and 49.64145° N, 8.63206° E, Heppenheim, Hessian Bergstrasse, Germany). Mother vines were trained according

to the Greiner-Decker system, with 2.4 × 1.5 m spacing (3.6 m^2 per vine) and a height of 1.8 m. The rootstock cultivar Börner was used as control and was cultivated under the same growing conditions and according to best management practices at each site, respectively. To evaluate the two candidate varieties (Libero and Vinto), multiple characteristics were assessed (Table 1, Table S2). Traits were visually scored on an ordinal scale of 1 to 9, with 1 indicating the weakest and 9 the strongest expression. On five randomly selected plants, internode length and diameter (mm) were measured at internode midpoint on three representative shoots. The wood yield (hereinafter referred to as graftable lengths; *i.e.*, canes that fulfil the requirements of grafted grapevines) was determined for all plants and all their shoots based on the average number of mature, graftable rootstocks that met the criteria of a length of 32 cm, a diameter of 6.5 to 12 mm at the thinner end, and a maximum of 15 mm at the thicker end.

3. Assessment of graft ability

The compatibility of the rootstock candidates with established scion varieties was evaluated at Geisenheim University, the Department of Plant Breeding. The two candidate rootstocks, Libero and Vinto, were compared with the reference rootstocks, Kober 125 AA and SO4. Three commercially relevant scion varieties (Chardonnay, Pinot noir, and White Riesling) were used as grafting partners. For each rootstock × scion combination, 400 vines were grafted. All grafted vines were subjected to identical forcing conditions. Following forcing, vital plants were transferred to the nursery, where planting was carried out according to regional standards. Graft compatibility was assessed over a three-year period. For each combination, the percentage of shoot-producing plants during forcing and the percentage of successfully established vines in the nursery were calculated relative to the total number of grafted vines. Callus formation was evaluated by visual inspection during the quality assessment (*i.e.*, fully developed wound healing at the graft union), and the twist test was performed by applying manual force to the graft union to assess its stability. A detailed overview of the assessed traits is provided in Table S3.

4. Performance testing under commercial vineyard conditions

Adaptation trials were conducted at multiple locations across major German wine-growing regions and included various time periods and scion cultivars. Trials followed the principles of good agricultural practice at the following sites: Hattenheim, Rheingau (50.0130° N, 8.0624° E); Lonsheim, Rhine-Hesse (49.7786° N, 8.0767° E); Roschbach, Palatinate (49.2461° N, 8.1189° E); and Heilbronn, Württemberg (49.1500° N, 9.2170° E), and Heppenheim, Hessian Bergstrasse. The testing duration varied by site, with official trials lasting three years at Hattenheim and Heilbronn. For each rootstock candidate and the reference variety, twenty vines were evaluated per site. The graft combinations were planted row-wise and were not replicated in the field. Yield was measured for each of the 20 vines and extrapolated to yield per hectare. Juice quality parameters, including total soluble solids and organic acids, were analysed using Fourier-transform infrared (FTIR) spectroscopy on an FT2 Winescan spectrometer (FOSS, Hillerød, Denmark) with an in-house calibration for grape juice (Table S4).

5. Assessment of root system architecture

A total of fifteen custom-built rhizoboxes (100 cm × 50 cm × 4 cm) were used to characterise adventitious root formation in five biological replicates each of the candidate rootstock varieties Libero and Vinto, and the reference variety SO4, over a period of 66 days. Growing conditions in the greenhouse are displayed in Figure S4. Rhizoboxes were constructed from OSB-3 boards with a transparent plexiglass front and positioned at a 45° angle, with the plexiglass facing downward and covered to block light and avoid root phototropism. Rhizogenesis was induced in dormant rootstock cuttings by embedding them in a plant substrate and placing them on a heated floor (25 °C) for 21 days. Each rhizobox was filled with 18 L of a commercially available standard growth substrate (Einheitserde Typ 1; Patzer Erden, Sinntal-Altengronau, Germany). Cuttings were transplanted into rhizoboxes upon visible root emergence. Weekly RGB images were captured under standardised conditions, maintaining fixed camera angle and distance (Figure 1a–b). RootPainter (Smith *et al.*, 2022), a GUI-based software, was used to train a deep neural network for image segmentation of root tissue from background (Figure 1c–e). Root growth dynamics were quantified using RhizoVision Explorer (Figure 1f–g; Seethepalli & York, 2020). This pipeline was validated through manual reference measurements of total root length using a tape measure (Figure S1).

To assess the spatial complexity of the root systems, a customised semi-automated Sholl analysis was implemented in R (Version 2022.12.0+353) using RGB images acquired from the rhizobox-grown rootstocks. Binary root masks were processed using a custom R pipeline and combining the *imager*, *tidyverse* and *dbscan* packages. For each image, the root origin was automatically identified as the uppermost pixel in the binary matrix. Concentric semicircles were then drawn at 2.5 cm intervals (converted to pixels using a scaling factor of 4.565662 pixels mm^{-1}) from the root origin, covering 180° of the images (Figure 1h). At each radius, root-circle intersections were identified and spatially clustered using density-based clustering (dbscan, $\varepsilon = 3$ pixels) to avoid overcounting neighbouring pixels. The number of unique clusters was used as the intersection count for the respective radius Hatzig *et al.* (2015). Results were summarised as a function of distance from the origin, and overlaid plots were exported to visualise root architecture and analysis output (Figure S3a–c). Validation of the method was performed by comparing automated intersection counts to manually annotated reference images, with strong correlation observed (Figure S2). The full R pipeline is available upon request.

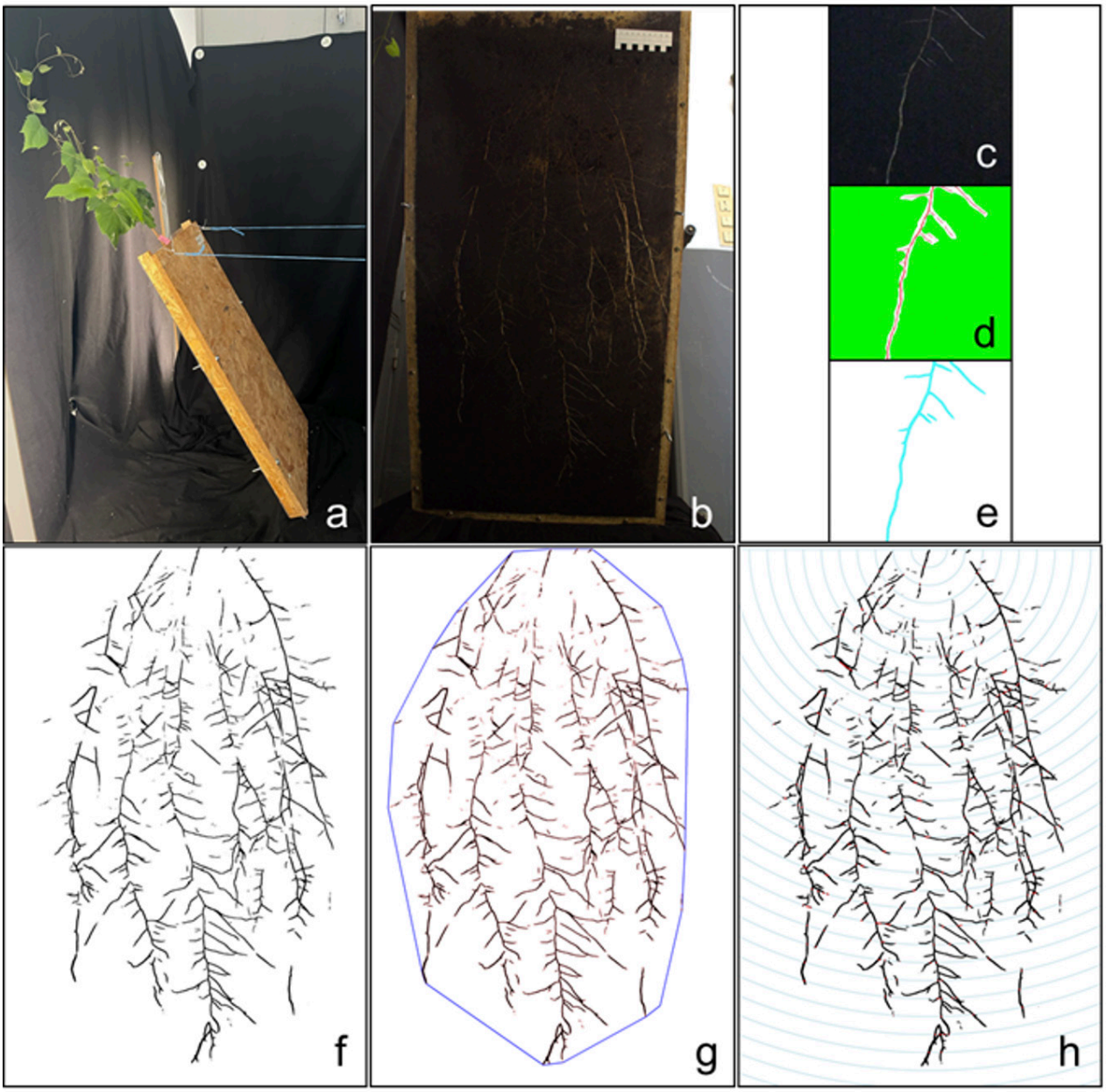


FIGURE 1. Evaluation pipeline for root system architecture assessments in rhizoboxes. Setup for imaging the boxes using RGB camera, indirect light and defined placement angles (a); original photo of the root system architecture in the rhizobox (b); training pipeline using RootPainter: original image snippet (c), manual segmentation of root and background noise for model training (d), computer-segmented image of the root (e); skeletonised black and white image output from RootPainter (f); image analysis with RhizoVision Explorer (g), and output image of customised semi-automated Sholl-analysis (h).

6. Statistical evaluation

Data was evaluated and visualised using the RStudio environment. Before analysing the data via one-way ANOVA, assumptions of normal distribution and the heterogeneity of variance were tested via diagnostic plots, such as histograms and a normal Q-Q plots. Equal variance of the groups (Rootstocks) was evaluated by plotting the residuals against fitted values. Tukey HSD post hoc-test was applied to identify statistically significant differences between the mean values of the groups for $\alpha = 0.05$. Spearman's rank correlation was used to assess the between image-derived with manually obtained data in the two image-based evaluations.

RESULTS

1. Phylloxera response

Both candidate rootstocks, Libero and Vinto, exhibited the high level of resistance inherited from the parent variety Börner and showed significantly lower susceptibility to leaf and root phylloxera compared to SO4 and 5 BB. In Vinto leaf gall formation under controlled conditions was minor (scoring: 1.6) and absent on the root level (scoring: 1). Libero showed similar resistance to leaf gall infestation (scoring of 1.8). At the root level very little colonisation was observed (scoring of 1.9), but

no tuberosities were formed, despite the presence of phylloxera (Table S1). In comparison, the reference rootstocks displayed a higher susceptibility to leaf gall formation (medium to strong; 6.1 and 5.8 for SO4 and Kober 5 BB, respectively). A low reaction to root infestations by phylloxera was described for the reference rootstocks. Tuberosities were clearly delineated from the vascular bundle in the root after infestation with phylloxera displaying a tolerant behaviour (scoring of 3.3 and 3.5, for SO4 and Kober 5 BB, respectively). Since the susceptibility to phylloxera was tested externally by an independent authority, only average values of the examination are displayed (Table 1).

Marker analyses of the *Rdv*1-associated locus confirmed the inheritance of root phylloxera resistance from Börner to its two progenies, Libero and Vinto (Table S5). In Vinto, only half of the tested markers were detected (Tables S5 and S6). Combined with the independently confirmed strong root resistance (Table 1), this indicates that Vinto is a recombinant closely linked to *Rdv*1. Consequently, the *Rdv*1 locus can be further delimited.

2. Vegetative performance in the mother block

The tested rootstocks showed no statistically significant differences for performance parameters at the propagation site, except for vegetative growth (Table 1, Table S2). Libero exhibited moderate vigour, while Vinto and the reference rootstock Börner displayed strong vigour. Libero and Vinto both showed shorter internode lengths in comparison to Börner. Although not statistically significant, Libero produced fewer graftable lengths due to narrower internode diameters, resulting in a slightly reduced wood yield compared to Börner (Table 1, Figure S5).

Additional agronomic traits of Libero and Vinto, such as lateral shoot growth, susceptibility to fungal pathogens, and wood maturation, showed no significant differences compared to the reference cultivar Börner (Table 1). Data from the second evaluation site are displayed in Table S2.

3. Rootstock and scion compatibility

The assessment of rootstock and scion compatibility during affinity testing showed no statistical differences between all parameters evaluated (Table 1, Table S3). However, affinity of rootstock varieties (displayed by the quality of callus formation) tended to vary, depending on the scion variety (Figure 2A). The total average of callus formation was slightly higher in both Libero and Vinto compared to the reference grafting combinations of Kober 125 AA and SO4.

TABLE 1. Performance comparison of new rootstock cultivars Libero and Vinto versus established cultivars Börner and SO4 on selected parameters at the propagation site of Geisenheim University. The dimensionless evaluation criteria (–) are ranked on a scale of 1 to 9, where 1 represents the lowest expression and 9 the highest. Displayed data represent the three-year averages with standard deviations. Different letters indicate statistically significant differences based on one-way ANOVA and Tukey HSD post hoc-tests ($\alpha = 0.05$).

Propagation		**Libero**	**Vinto**	**Börner**
Internode length	mm	173.7 ± 24.8 b	174.3 ± 25 b	230 ± 31.1 a
Internode diameter	mm	8.2 ± 1.1 c	9.1 ± 1.4 b	9.6 ± 1.5 a
Graftable lengths	#	33 ± 10 a	45 ± 14 a	46 ± 14 a
Vigour	–	6.5 ± 1 b	7.8 ± 0.5 a	8 ± 0 a
Lateral shoot growth	–	6 ± 0 a	6 ± 0 a	6 ± 0 a
Suscept. Plasmopara viticola	–	1 ± 0 a	1 ± 0 a	1 ± 0 a
Suscept. Erysiphe necator	–	1 ± 0 a	1 ± 0 a	1 ± 0 a
Wood maturity	–	8 ± 0 a	8 ± 0 a	8 ± 0 a

Affinity*		**Libero**	**Vinto**	**SO4**
Days until budburst	#	10 ± 1 a	10 ± 1 a	10 ± 2 a
Grafting success rate (forcing)	%	91 ± 7 a	89 ± 9 a	85 ± 12 a
Callus formation	–	8.3 ± 0.9 a	8.2 ± 0.7 a	7.6 ± 1.1 a
Survival rate (nursery)	%	82 ± 9 a	73 ± 13 a	74 ± 20 a
Total share of marketable vines	%	75 ± 12 a	65 ± 15 a	55 ± 20 a

Phylloxera testing**		**Libero**	**Vinto**	**SO4**
Leaf gall formation	–	1.8	1.6	6.1
Root gall formation	–	1.9	1	3.3

* Three-year average performance of grafted grapevines using the scion cultivars Chardonnay, Pinot noir, and White Riesling.

** Evaluation conducted by DLR Neustadt from 2019–2022 and 2020–2022 for leaves and roots, respectively. The scores reported in this assessment are explained in Table S1.

Libero showed the highest survival rate after being grown for one season in the nursery, but no statistical differences compared to Vinto and Börner were observed (Figure 2B). This also resulted in differences in the share of marketable grafted grapevines (Table 1, Table S3). Libero and Vinto showed a general tendency of fewer rejects (25 % and 35 %, respectively) compared to graft combinations of Kober 125 AA or SO4 (30 % and 45 %, respectively).

4. Commercial testing in adaptation trials

Libero and Vinto showed no negative effects on key agronomic parameters, such as yield or juice quality (Table S4). No statistically significant differences in total soluble solids or total acidity were observed between Libero, Vinto, and the reference rootstocks Börner and SO4 at any test site (Figure 3).

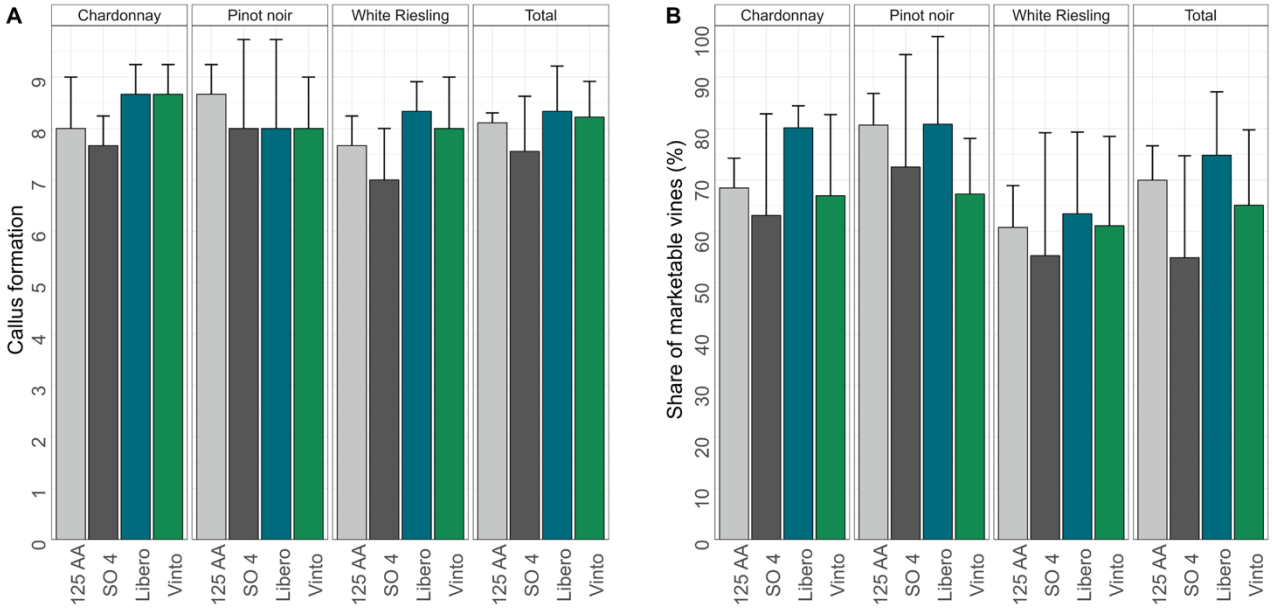


FIGURE 2. Results of rootstock × scion compatibility testing at Geisenheim Plant Breeding station: A) quality of callus formation and B) share of marketable vines (data based on post-nursery inspection and calculated from the total of 400 initially grafted vines). The plot displays the mean and standard error for each rootstock cultivar (light grey = Kober 125 AA, dark grey = SO4, blue = Libero, green = Vinto). The dimensionless evaluation criteria (–) are ranked on a scale of 1 to 9, where 1 represents the lowest expression and 9 the highest.

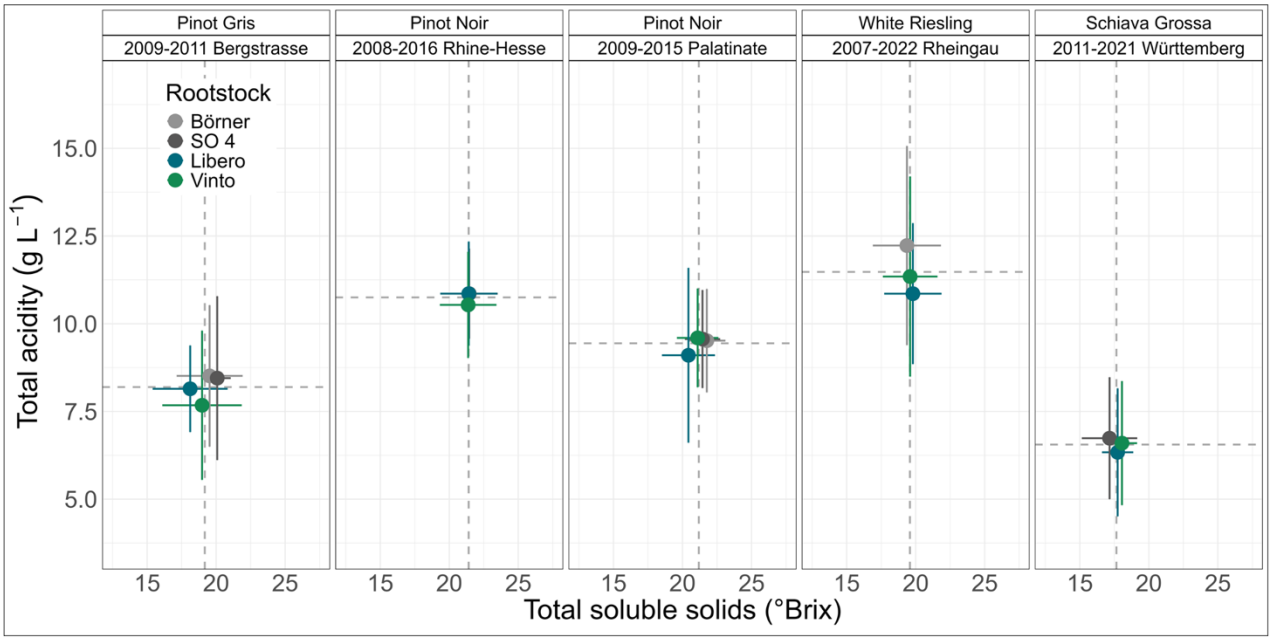


FIGURE 3. Performance comparison of the new rootstock cultivars Libero and Vinto versus the established cultivars Börner and SO4 on juice parameters across various scion varieties, wine-growing regions, and time periods. Symbols represent the mean and standard deviation of each rootstock cultivar, while dashed lines indicate the group mean of each cultivar at each site (light grey = Börner, dark grey = SO4, blue = Libero, green = Vinto).

As grafting partners, Libero confers medium vigour to the scion (between 161–49 Couderc and SO4), while Vinto imparts medium to strong vigour (between SO4 and Kober 125 AA).

5. Early rooting behaviour

No statistically significant differences were detected in the early rooting behaviour of Libero, Vinto, and SO4 within the observation period of 66 days after transplanting (DAT; Figure 4).

Considerable variation was observed within each cultivar. Nevertheless, Libero and Vinto showed a tendency for rapid soil volume exploration between 30 and 60 days after transplanting (DAT) into the rhizoboxes (Figure 4B). The dynamics of root length density (cm root length per soil volume) were more variable overall and less distinct among the rootstock genotypes (Figure 4A). Sholl analysis data indicated that both Libero and Vinto exhibited a higher branching frequency – reflected by a greater number of intersections – at 38 DAT in the upper soil layers compared to SO4. Notably, the intersection frequency of SO4 at 38 DAT compared to 21 DAT decreased in the upper 25 cm, while root growth continued between 25 cm and 50 as well as between 50 cm and 75 cm (Figure 5). While Vinto early displayed a fast root growth up to 50 cm depth (21 DAT), at 38 DAT extensive root branching could be observed in the upper soil, while few additional roots were counted below 50 cm.

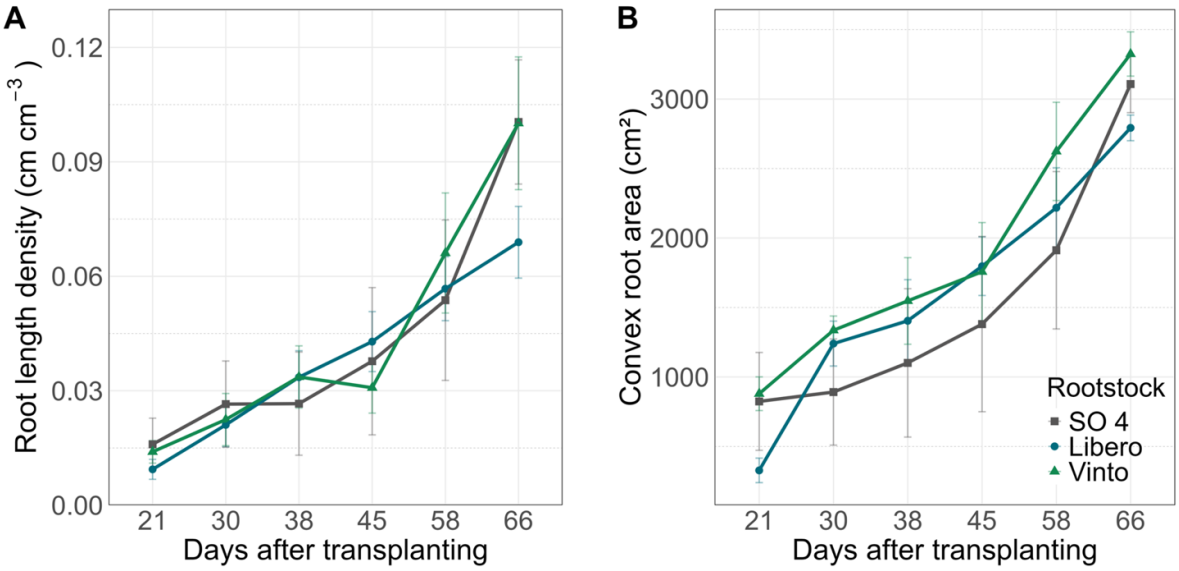


FIGURE 4. Comparison of root system architectural traits. A) Root length density development over time for three rootstock genotypes grown in rhizoboxes and B) development of the virtual convex root area as a representative for the soil exploration of the roots grown in rhizoboxes. Symbols represent the mean and standard error of each rootstock cultivar (dark grey = SO4, blue = Libero, green = Vinto).

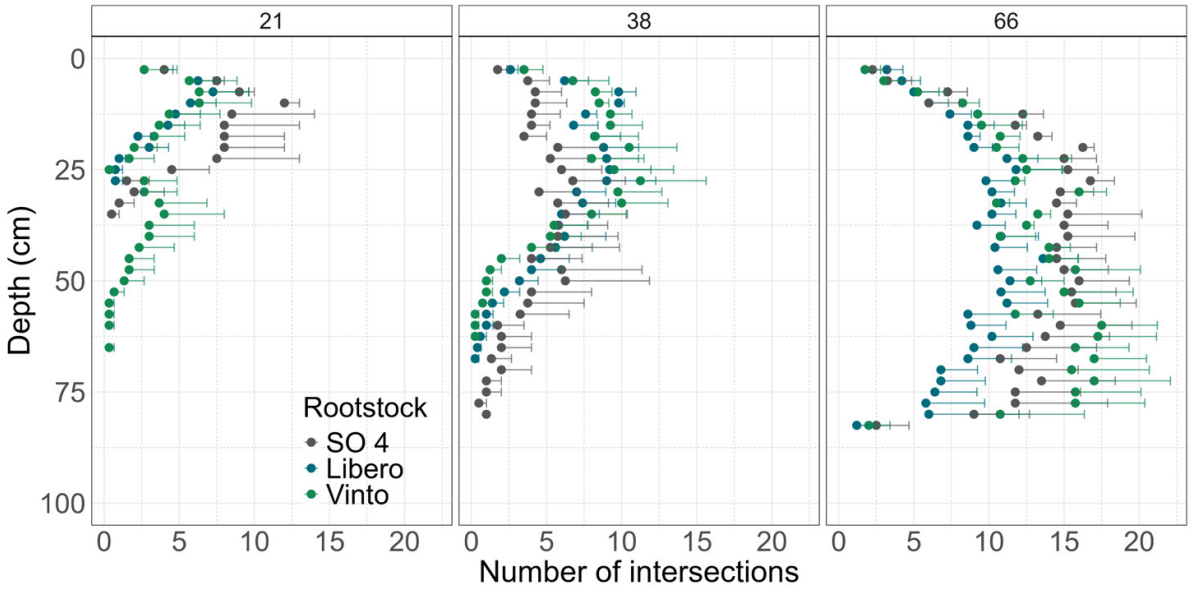


FIGURE 5. Root distribution of three rootstock genotypes as count of virtual grapevine root and concentric circle intersections within a distance of 2.5 cm and 21, 38, and 66 days after transplanting rootstock cuttings into rhizoboxes. Symbols represent the mean and standard error of each rootstock cultivar (dark grey = SO4, blue = Libero, green = Vinto).

A month later, at 66 DAT, Libero showed the lowest number of intersections, but a homogenous root distribution in the first 75 cm. Vinto exhibited an increase in root intersections from a soil depth of approximately 50 cm onward, SO4 showed the opposite trend, with a marked decline in root presence below this depth (Figure 5).

DISCUSSION

After over thirty years of crossing and extensive performance evaluations, the new rootstock varieties Libero and Vinto were officially registered by the German Federal Plant Variety Office in 2024. Libero (Kober 125 AA × Börner) and Vinto (*V. berlandieri* × Börner) display high phylloxera resistance in both the leaves and roots, good grafting compatibility, and broad adaptability to diverse sites. During the registration process and comparative variety testing, both cultivars demonstrated excellent long-term performance across a wide range of soil types and microclimates.

Significant performance differences compared to the parent Börner were observed only for Libero at the propagation site, mainly due to its reduced vigour. Libero showed smaller and shorter internodes (Table 1), despite being a cross of two typically vigorous rootstocks (Kober 125 AA and Börner). Depending on the scion variety (*e.g.*, cultivars displaying poor fruit set), soil conditions (*e.g.*, poor or highly fertile), and vineyard management system (*e.g.*, dense planting or irrigation), low- to medium-vigour-inducing rootstocks are an important means of ensuring balanced vigour, grape quality, and yield in viticulture (Dry, 2007). Under commercial production conditions, both Libero and Vinto showed a slight tendency towards lower total acidity and sugar levels (Figure 3), though these differences were not statistically significant compared to either Börner or SO4. Both new rootstock varieties demonstrated high yield levels when grafted with White Riesling and Schiava Grossa (Table S4). However, when grafted onto White Riesling, Libero and Vinto showed yield reductions of 7 % and 8 %, respectively, compared to Börner. In contrast, the high-yielding Schiava Grossa exhibited more substantial decreases of 16 % and 22 % relative to SO4 (Table S4). In varieties with high yield potential used for red wine production in particular, a natural reduction in yield is desirable, as it improves colour and decreases the need for intensive manual interventions, such as cluster thinning. Regarding compatibility during the grafting process with traditional *V. vinifera* scion varieties, such as Chardonnay, Pinot noir, and White Riesling, no statistically significant differences were detected. However, Libero showed a slightly lower loss rate in grafted grapevine production (Figure 2B). Affinity testing with new fungus-tolerant scion varieties is pending. Promoting such fungus-tolerant cultivars is a key component of sustainable viticulture and aligns with fungicide reduction targets. Nevertheless, observations and studies have reported a susceptibility of these disease-resistant hybrids to leaf gall phylloxera (Wilmink *et al.*, 2021a, Wilmink *et al.*, 2021b). Moreover, *V. vinifera* cultivars are also being increasingly affected by phylloxera at the leaf level (EPPO, 2025; Forneck *et al.*, 2019; King & Rilling, 2015; Vidart *et al.*, 2013). Using rootstocks that prevent phylloxera reproduction on the roots can significantly reduce the risk of the aerial infestation cycle of this damaging pest as well as a potential resistance breakdown (Ollat *et al.*, 2024). Resistant grapevines either do not develop tuberosities or are able to suberise cell layers close to the feeding site, and while tuberosities may not form in resistant vines, nodosities can provide a temporally limited feeding site (Granett *et al.*, 2001). Minimising population pressure in rootstock mother blocks and reducing the availability of feeding and refuge sites for phylloxera, particularly in abandoned vineyards, is essential. Thus, not only root resistance but also foliar resistance should be considered an important breeding target to limit the sexual reproductive cycle of phylloxera (Table S1). The registration of Libero and Vinto in the European varietal catalogues significantly broadens the rootstock options available to viticulturists, offering tailored solutions for diverse site conditions, microclimates, vigour management and production aims with the addition of an effective phylloxera control.

Compared to scion breeding, rootstock evaluation is more time-consuming and takes around 30 years from crossing to registration, as reliable assessments of stress tolerance and field performance can only be made once the vines are fully established in the vineyard.

For complex, polygenic traits like drought tolerance, identifying reliable performance markers remains challenging. In contrast to monogenic traits, such as resistance to biotic stressors (Torregrosa *et al.*, 2024), abiotic stress tolerance involves multiple molecular mechanisms that are still poorly understood or yet to be fully characterised (Bernardo *et al.*, 2025; Ollat *et al.*, 2025).

In contrast to the breeding of fungus-tolerant scion varieties, marker-assisted selection is rarely applied in rootstock breeding programmes. Although six root resistance and two foliar resistance markers for *Daktulosphaira vitifoliae* have been mapped to different chromosomes, the underlying genetic regions and mechanisms of resistance remain to be fully identified and understood. Efforts are ongoing to further delimit these loci and improve the reliability of existing markers. The results presented here enable the validation of both established and recently developed markers for phylloxera root resistance. However, further studies are required to fully consolidate these improvements. Within this context of incremental progress and remaining knowledge gaps, the targeted introduction of new genetic traits using modern molecular tools like Crispr/Cas9 is currently constrained by both technical and regulatory limitations, making conventional cross-breeding the dominant strategy. At the same time, given the complexity of environmental change and the diverse demands of stakeholders – from nurseries (*e.g.*, wood yield, graft compatibility), to winegrowers (*e.g.*, yield and quality parameters), and regulatory or societal actors (*e.g.*, sustainability, reduced chemical inputs) – grapevine breeding is undergoing a rapid transformation. The adoption of genomic tools, predictive methods, and the integration of multi-omics approaches now offer a powerful and holistic path toward faster and more targeted breeding outcomes (Magon *et al.*, 2023; Robinson *et al.*, 2025; Schmidt *et al.*, 2025).

Identifying elite parental genotypes will be crucial for simultaneously improving phylloxera resistance, drought and lime tolerance, as well as resistance to virus-vectoring nematodes. To support early-stage selection, high-throughput phenotyping (HTP) methods offer immense potential (Herzog *et al.*, 2025). These often allow time-independent, cost-efficient evaluation of large populations, including wild and commercial *Vitis* accessions. Digital phenotyping and smart sensing technologies have proven valuable in this context. For example, Bianchi *et al.* (2018) used thermography and reflectance spectroscopy to differentiate drought responses among 25 rootstock genotypes (Bianchi *et al.*, 2018). Similarly, UAV-based remote sensing has enabled the development of performance proxies applicable across all development stages in both mother blocks and grafted vines in commercial vineyards (Gano *et al.*, 2024; Giovos *et al.*, 2021). These tools offer considerable potential to accelerate the genetic improvement process in the face of climate change (Araus & Cairns, 2014). In particular, leaf hyperspectral reflectance datasets have shown promise for phenomic prediction, and may be integrated easily into future grapevine breeding strategies (Brault *et al.*, 2022).

In addition, root system architecture (RSA), an increasingly important target for breeding programmes, plays a critical role in stress resilience, particularly under changing precipitation patterns in traditional wine-growing regions (IPCC, 2023; van Leeuwen *et al.*, 2024). While rhizoboxes can be used to characterise root traits in both registered varieties and breeding candidates under controlled conditions (Fichtl *et al.*, 2023), this set of traits is hard to upscale and due to the limited soil volume or use of artificial substrates, the ecological validity of such experiments is constrained, requiring careful contextual interpretation. A promising strategy is to link adventitious root formation in cuttings (Figures 4 and 5) and young vines with later vineyard performance of those genotypes, allowing the development of predictive models for early-stage selection. Potential proxies, such as thermal imagery collected with UAV to assess canopy temperature, or aboveground water stress proxies of rootstock function, such as leaf water potential, stomatal conductance or leaf area index (LAI), can be used to screen large numbers of grapevine growing in the field (Burchard-Levine *et al.*, 2024). In this study, no direct comparison between greenhouse and field performance was conducted. However, early indicators (proxies) of later field performance could serve as valuable tools for improving the efficiency of rootstock breeding programmes and accelerating cultivar development. This is particularly important in the context of increasing intensity and frequency of intermittent drought periods and irregular rainfall patterns, where early and deep root development is crucial for the survival of young grapevines. Vinto in particular displayed a fast, vertical root growth within the first three weeks after transplanting into the rhizoboxes.

To ensure grower acceptance and to successfully establish improved planting material on the market over the long term, breeding lines must undergo a rigorous multi-year evaluation process. Although traits with future relevance – such as those related to climate resilience – are not yet formally required in official evaluation protocols, they are indispensable for transparent communication with the sector and for assuming responsibility for future-proof viticulture. Close cooperation with commercial winegrowers and regulatory authorities is also essential in identifying emerging issues and working collaboratively toward solutions.

The rapid global warming, especially of the European continent, which is affecting many traditional wine regions already, calls for fast and sustainable adjustments in viticultural practices. This includes the development of new scion and rootstock varieties. To accelerate the inherently lengthy breeding process, the adoption of new highly promising breeding methods is urgently needed.

To accelerate this process, innovative breeding technologies are tested in grapevine breeding programmes. Among them, genomic selection (GS) is considered particularly promising. GS combines molecular and phenotypic information to predict future genotypic performance based on estimations of breeding value for untested genotypes based on their DNA profiles (Brault *et al.*, 2024). Thus, GS offers two main advantages over conventional breeding methods: i) performance potential can be assessed at the seedling stage using only the genetic fingerprint, significantly reducing time and cost; and ii) selection accuracy is increased, as molecular data enables a much more accurate evaluation of breeding material. While GS is already well established in annual crops such as maize and cereals, its application in grapevine breeding is still in its early stages (Brault *et al.*, 2024).

CONCLUSION

The phylloxera pest remains widespread in almost all viticultural regions globally. Grafting *V. vinifera* onto tolerant rootstocks has been – and will remain – the only effective method to control phylloxera in the foreseeable future. However, given ongoing environmental changes and the narrow genetic base of currently used rootstocks, the development of fully resistant and climate-resilient rootstocks must be a central goal of future breeding efforts. With the official registration of Libero and Vinto, the Department of Plant Breeding at Geisenheim University contributes significantly to diversifying the portfolio of phylloxera-resistant rootstocks. This enables growers to make more site-, product- and profile-specific planting choices. To further accelerate rootstock development, modern breeding technologies will be essential to enhance genetic gain and breeding efficiency.

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