Vvgai1 mutation impacts both organogenesis and functioning in Vitis labruscana microvines

Jana Kändler, Luciana Wilhelm de Almeida, Laurent Torregrosa

Scientia Horticulturae 357 (2026) 114643

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Research Paper

Vvgai1 mutation impacts both organogenesis and functioning in *Vitis labruscana* microvines

Jana Kändler [a], Luciana Wilhelm de Almeida [b], Laurent Torregrosa [b,c,*]

[a] Centre of Vine and Wine Studies, Institut Agro, Montpellier, France
[b] UMR LEPSE, University Montpellier, INRAE, Institut Agro, Montpellier, France
[c] Experimental Unit of Pech Rouge, INRAE, Gruissan, France

ARTICLE INFO

Keywords:
Climate change
Grapevine
Dwarfism
Vegetative development
Juvenile phase
Phyllotaxis

ABSTRACT

In order to develop new genotypes to explore grapevine adaptation to climate, we introduced the *Vvgai1* mutation in *V. vinifera* x *V. labrusca* hybrids. *Vvgai1* mutation induced a strong miniaturisation of leaf and shoot length, as a result of a significant reduction of internodes size and an increase of the phyllochron. The lignification of the main shoots was delayed in the microvines in comparison to their macrovine counterparts while the leaf C assimilation rate was not impacted by the mutation. The shift from the alternate spiral (juvenile) to distichous (adult) phyllotaxis and the appearance of the first tendril occurred at lower node rank in macrovines. However, while macrovines did not produce any reproductive organs during the first vegetative cycle, microvines displayed the first perfect flowers on the main shoot from the internode 18, only a few months after embryo rescue and acclimation. The segregation of the sex type confirmed that the sex determining locus of the *V. labrusca* cv. Isabella is heterozygous. Conversely, the proportion of opposite-to-leaves organs following a *labrusca*- versus *vinifera*-type distribution suggested a more complex genetic determinism for this trait. These experiments provide a new set of microvine genotypes and phenotypic data for studying the response of *V. labruscana* to abiotic and biotic factors and open new questions about how phytohormones control the development of the grapevine liana.

1. Introduction

During the last 10 000 years, grapevine domestication (Dong et al., 2023) was mainly based on *Vitis vinifera*, a species within which thousands of varieties were selected to produce fresh and dried fruits, juice and wine (Galet, 1988). Today varieties of *V. vinifera* still represent the large majority of the grapevine genotypes across the world. However, during the last centuries, new species, particularly those found on the Asian and American continents, began to be cultivated to enable vine growing in climates where the European species *V. vinifera* was not well adapted due to the presence of pathogens. From the 19th century, interspecific *Vitis* hybrids started to be selected to combine the fruit quality of *V. vinifera* with other traits of climate adaptation or disease tolerance (Boursiquot et al., 2024). Recently, these breeding programs have become very active in order to take advantage of the cross-fertility between *Vitis* species to offer new hybrids that are better adapted to the current challenges of viticulture. *Vitis labrusca*, originated from the east coast of north America was largely used in USA, Brazil and Japan to breed varieties adapted to warm and humid summer seasons. Indeed, *V. labrusca*, a species naturally present in the states along the eastern coast of the United States, displays some tolerance to humid summer climates due to its low sensitivity to fungal diseases (Galet, 1988). This species has given rise to a wide range of hybrids through spontaneous or designed crossing with American or Asian species, as well as with *V. vinifera* (Galet, 2015). These varieties are widely cultivated for the production of table grapes, juice, still and sparkling wines, particularly in Brazil and Japan (Torregrosa, 2024a, 2024b). To mitigate certain adverse effects of climate change, particularly rising temperatures and, in some regions, increased rainfall and atmospheric humidity, the use of *V. labrusca*–derived genotypes represents a relevant alternative to pure *V. vinifera* varieties. Compared to *V. vinifera, V. labrusca* exhibits some anatomical peculiarities, including a subcontinuous to continuous arrangement of tendrils and clusters, meaning that more than two opposite-to-leaf organs can be successively present along the shoots. Because the grapevine is a non-polycyclic fruiting plant with discontinuous fruiting, genetic and ecophysiological characterization studies

* Corresponding author at: 2 Place Pierre Viala, 34060 Montpellier Cedex 2, France.
E-mail address: laurent.torregrosa@institut-agro.fr (L. Torregrosa).

https://doi.org/10.1016/j.scienta.2026.114643
Received 6 October 2025; Received in revised form 12 January 2026; Accepted 20 January 2026
Available online 23 January 2026

are very long and complicated. In practice, experiments on the response to climatic constraints take years, and the breeding of a new variety cannot be achieved in <20 or 30 years. The microvine model which results from a mutation of the *Vvgai1* gene (Boss and Thomas, 2002), an important player of the gibberellin signaling, was proposed as a model for physiological studies as well as for forward and reverse genetics (Chaïb et al., 2010).

Gibberellins (GAs) are phytohormones regulating various developmental processes in plants, including seed germination and growth, phytomer and leaf elongation and reproductive development. This signaling pathway involves DELLA proteins, which serve as negative regulators, suppressing GA-dependent growth until their degradation is triggered by GA-receptor interactions. The GAI function was initially characterized in *Arabidopsis thaliana*, where its mutant form, *gai1*, results in constitutive repression of GA responses. Mutations in GAI, make the protein less susceptible to degradation (Peng et al., 1999; Yamaguchi, 2008) disrupting the gibberellin signaling cascade, with critical phenotypic effects, such as dwarfism and reproductive reprogramming (Hedden and Sponsel, 2015; Qin et al., 2014). Plants carrying the mutation display reduced stem elongation and increased biomass allocation to reproductive structures, a trait which was exploited in semi-dwarf annual crop varieties (Ikeda et al., 2001) during the green revolution. In grapevines, GA signaling also plays a central role in vegetative expansion regulation, fruit formation and growth, seed development, and responses to environmental stimuli, particularly light. The molecular mechanisms associated with the VvGAI1, the ortholog of AtGAI1 are similar to those described for Arabidopsis (Torregrosa et al., 2019). In the spatio-temporal contexts where the gene is transcribed, the GAI1 protein is targeted to the cell nucleus where it modulates the expression of genes involved in floral differentiation and vegetative organ expansion. However, there is some diversity from species-to-species in the integration of the gibberellin signaling. For instance, in grapevine, which displays a liana behavior, under light limitation, this phytohormone promotes internode expansion to support shoot growth towards the top of the canopy as well as leaf size to increase light interception but at the same time inhibits the conversion of the opposite-to-leaf tendrils in inflorescences. In the grapevine, tendrils provide a mechanical support to the vegetative axes which are typically slender, elongated, and unbranched (Torregrosa et al., 2021). In the proximal regions of the shoots, tendrils exhibit fructiferous potential, enabling the vine to display fruits near the base of the vegetative axes, thereby minimizing mechanical stress of the main stems. But the status of opposite-to-leaf organs appears as a quantitative trait, as they can develop as a tendril, a cluster of inflorescences or a vegetative shoot.

In the grapevine, opposite-to-leaf organ fate appears as a quantitative trait which depends on the vigor of the plant, environmental conditions and plant growth regulator balance. Srinivasan and Mullins (1979) reported the conversion of tendrils in inflorescence following repeated application of 6-(benzylamino)-9-(2-tetrahydropyranyl)-9H-purine, a strong synthetic cytokinin-like compound suggesting cytokinins are promoting the differentiation of floral organs from tendrils. Gibberellins were also shown as a major negative regulator of the developmental fate of the opposite-to-leaf organs into inflorescences. For instance, it has been demonstrated that the application of anti-gibberellin compounds, like CCC (Chlormequat Chloride) can induce the conversion of tendrils into inflorescence (Coombe, 1967). Then, in *V. vinifera*, in the presence of a *Vvgai1* allele where GA signaling is disrupted, tendrils are converted into fruiting organs all along the vegetative axes and vegetative growth is inhibited resulting in a dwarf stature. However, since *Vvgai1* does not affect gametogenesis or floral development, genotypes carrying the mutation can be used in crosses as either females or males and can transmit the mutation to their offspring. The *Vvgai1* gene mechanism being semi-dominant, the phenotype is wild-type when there is no mutant allele in the L2 layer, semi-dwarf when the genetic status is heterozygous, and dwarf when the plant carries two mutant alleles (Chaïb et al., 2010). The term “macrovine” has been proposed for wild-type forms, “microvine” for genotypes heterozygous for the mutation (also called pixie vine, Peter Cousins, pers. comm.) and “picovine” for homozygous plants with both mutated alleles (Boss and Thomas, 2002; Torregrosa et al., 2019).

In *V. vinifera*, expression profiling of *GAI* isogenes has revealed their spatial and temporal regulation. For instance, *VvGAI1* shows high expression in shoots, leaves and roots, while *VvGAI2* is more specifically expressed in the fruit rather in vegetative organs (Torregrosa et al., 2019). Consequently, the mutated allele *Vvgai1* does not hinder berry development, which remains identical in microvines carrying the *Vvgai1* mutation compared to wild-type genotypes (Pellegrino et al., 2019). Moreover, the mutation does not alter the vegetative architecture (Torregrosa et al., 2021), i.e. phyllotaxis of cauline organs or the ternary rhythm of opposite-to-lead organ distribution (Bernard, 1980), meaning that a node without an opposite-leaved organ is followed by two nodes with tendrils or inflorescences (Gerrath et al., 1998; Iland et al., 2011). Thus, microvines exhibit an alternate distichous phyllotaxis and a ternary rhythm of opposite-leaved organ distribution. However miniaturising cell expansion, the mutated allele changes the aspect of the leaves which exhibit a more deep green that their wild-type counterparts, possibly due to an increase in photosynthetic pigment density with possible effects on photosynthesis functioning.

The continuous production of reproductive organs during vegetative organogenesis, is highly advantageous for research studies as it allows the interpolation of spatial data at temporal developmental points for both vegetative and reproductive organs (Dias et al., 2019; Luchaire et al., 2017; Rienth et al., 2014, 2016) facilitating the implementation of innovative experimental concepts. Dwarfism which allows plant cultivation in growth chambers under fully controlled environment combined with a very short juvenile phase makes the microvines a unique model for fruit physiology studies as well as for genetics and functional genomic programs (Costa et al., 2019; Torregrosa et al., 2019). In this study, we have introduced the *Vvgai1* mutation from a *V. vinifera* microvine into a *V. labrusca* genetic background to obtain seedlings displaying a MicroLabruscana phenotype. We have comparatively phenotyped individuals carrying the *Vvgai1* mutation against their wild-type counterparts to clarify the interactions between the *Vvgai1* allele and the main traits of vegetative and reproductive developments and the photosynthetic functioning. The miniaturization of *V. vinifera* x *V. labrusca* hybrids provides innovative material for experiments on the acclimation or adaptation to climate stresses or disease tolerance.

2. Materials and methods

2.1. Plant material

The segregating population was obtained in 2023 by crossing the 04c023V0003 female microvine (V3), with the *V. Labruscana* cv. Isabella, which corresponds to the accession 6541Mtp4 of the Grapevine Biological Resources Center of Vassal-Montpellier (https://eng-vassal.montpellier.hub.inrae.fr, France), introduced from Nepal in 1968. The V3 female genotype was chosen from previous crossbreeding experiments because of its very strong male sterility which prevents self-pollination without requiring tedious emasculation. The microvine V3 was obtained by crossing the microvine L1 line with the Grenache genotype (Chaib et al., 2010). This genotype is homozygous at the loci determining the flower sex type (f/f) and the red color of the fruit skin (B/BL1) and heterozygous at the locus responsible of the dwarfism phenotype (VvGAI1/Vvgai1).

Three 3-year-old potted plants of the female V3 were introduced in a greenhouse on day of the year (DOY) 145, one month before the expected date of pollination. On DOY 159, three 22-year-old plants of Isabella grafted on the rootstock SO4 and established in the Pierre Galet repository of Institut Agro Montpellier (France) were cane pruned in green, removing all leaves and lateral shoots to promote winter bud development. Budburst occurred 10 days after, inflorescences were

bagged on DOY 184. Bags containing inflorescences were collected from DOY 188 to 191 and oven-dried for a couple of days. Pollen was purified and conserved in a cool place in the presence of silica gel. Pollination was performed for a month at the rate of 2 inflorescences per V3 microvine plant and week, for a total of 30 pollinated inflorescences.

From DOY 258 to 279, berries were collected at the veraison stage and conserved in a fridge. After a few days, seeds were recovered and roughly cleaned in non-sterile conditions, then seeds were surface disinfected with 4 × diluted commercial sodium hypochlorite (final concentration 2.5 % NaOCl) and a few drops of Tween 20 (final concentration 0.25 ‰) for 10 min and rinsed 3 times with sterile water. Seeds were blotted onto sterile paper, let to dry under a sterile laminar flow for 1 h and then conserved in sterile petri dishes in the fridge until further use. On DOY 289 and 290 embryos were extracted and incubated according to Chatbanyong and Torregrosa (2015) with few modifications, i.e. active charcoal was reduced to 1 $g.l^{-1}$ and 2 $g.l^{-1}$ of Sigma phytagel were supplemented to the medium. We reduced the concentration of activated charcoal to limit precipitation during cooling after pouring the medium into Petri dishes. The supplementation in Phytagel aimed to increase medium firmness and facilitate the placement of embryos on the surface following their extraction from seeds. These modifications did not result in significant changes in embryo germination rates compared with the original formulation but facilitated embryo rescue manipulations.

During 8 weeks, germinating seedlings were transferred to 150 × 20 mm culture tubes containing 10 ml of MS/2 medium (Murashige and Skoog, 1962). At DOY 57 (2024, T0) *in vitro* plantlets were acclimated to non-sterile growing conditions under semi-controlled greenhouse conditions. The air temperature was regulated at 28 °C ± 5 °C from 06:00 to 21:00 and at 16 °*C* ± 5 °C from 21:00 to 06:00. Relative humidity ranged from approximately 46 % during the day to 65 % at night. Irrigation was adjusted to cover 100 % evapotranspiration demand (ETP) so as to maximise vegetative growth and photosynthetic activity. The photoperiod (15/9 d/n) was controlled by a probe and sodium lamps were automatically switched on under low natural light conditions, providing a mean daytime photosynthetically active radiation (PAR) of 250 µmol m^{-2} s^{-1} (maximum: 1010 µmol m^{-2} s^{-1}). To minimise any potential effects of acclimation on phenotypic traits, a batch of synchronised seedlings with similar shoot development (i.e. 4 ± 1 unfolded leaves) was selected for further phenotyping. These plants were subsequently managed by systematically removing sylleptic shoots to promote the growth of a single proleptic shoot per plant as previously described (Torregrosa et al., 2019).

2.2. Plant phenotyping

According to the genotype for the SDR (Sex Determining Region) of the cv. Isabella and considering the genotype of the V3 microvine for the SDR (f/f) and dwarfism (*VvGAI1/Vvgai1*), both traits, i.e. flower sex type and dwarfism were expected to segregate in the progeny. From April to June, plants were phenotyped for several developmental and architectural traits. Phyllotaxis was recorded to determine plastochron index at which seedlings transitioned from juvenile to adult patterns. Leaf area was estimated by extrapolation from the length of the main veins following Luchaire et al. (2017) for microvines and Mabrouk and Carbonneau (1996) for macrovines. The length of the proleptic shoot and the level of shoot lignification were also measured.

The position of the first apparition opposite-to-leaf organ was recorded, as well as its nature (tendril or inflorescence). Based on the distribution of opposite-to-leaf organs, plants were classified as either *labrusca*-type or *vinifera*-type. Absence and presence of opposite-to-leaf organs were coded as 0 and 1, respectively. The sequence 0–1–1–1 was assigned to the labrusca-type, whereas the sequences 0–1–1–0 and 0–1–0–1 were assigned to the vinifera-type.

In microvine, flower sex was determined by monitoring the morphology of floral organs. For traits whose expression depended on plant age, the reported duration corresponds to the delay between T0 (defined above) and the date of measurement.

The phyllochron (rate of leaf emergence) was assessed over four intervals (DOY 121–135, DOY 135–149, DOY 149–163, and DOY 163–178). It was calculated as the ratio between accumulated degree-days and the number of newly formed phytomers. Degree-day accumulation was computed assuming a 15-h photoperiod and a base temperature of 10 °C (LEBON et al., 2004), following the approach described by Luchaire et al. (2017).

Maximum photosynthesis activity was assessed measuring 4 leaves per plant for 2 macrovines (M*a*Vs) and 2 microvines (M*i*Vs) with a Licor 6800 device according to Wilhelm de Almeida et al. (2024). To compare C assimilation performance of M*a*Vs and M*i*Vs, the theoretical maximum rate of C assimilation per surface (cm^2) was multiplied by the average leaf area per phytomer.

2.3. Statistics

All statistical analyses were performed in R (R Core Team, 2021). For each trait, ANOVA assumptions (normality and homoscedasticity) were verified prior to conducting the analysis of variance. Graphical representations and data visualization were also produced using R.

3. Results and discussion

3.1. Obtaining a segregative population from V. vinifera microvine x V. labrusca

From 152 seeded berries sampled, 171 seeds were recovered. After embryo extraction and incubation in the germinating medium, 60 developing seedlings were transferred to the growing culture tubes (Fig. 1) and then acclimated to greenhouse conditions. A selection of 37 synchronised seedlings, including 11 M*a*Vs and 26 M*i*Vs were transferred in 3 L Pots (Fig. 1).

3.2. Vvgai1 impacts on the vegetative phenotypes of the seedlings

As expected from the genetic status of the progenitors, the *Vvgai1* mutation induced a pronounced miniaturization of the internodes in 50

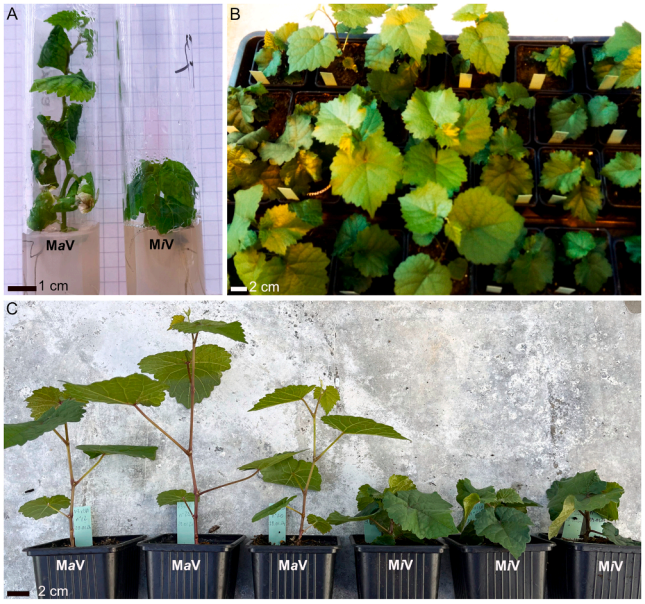

Fig. 1. - (A) Macro and microvine seedlings in culture tubes; (B) 2 months after the subculture; (C) Synchronised plant acclimatized to greenhouse conditions, before their transfer to 3 L. pots.

% of the individuals within progeny during the development in the greenhouse (Fig. 2). These so-called Microlabruscana lines showed a significant reduction in shoot growth, resulting from decreases in both internode length and phyllochron, with an average plant height of 63 cm and 39 phytometer units, compared with 339 cm and 49 in Macrovines at DOY 184 (Fig. 3A-B). This observation suggests that GA is not only involved in regulating growth via cell expansion but also impacts organogenesis via the rhythm of cauline organ differentiation. It was shown that in presence of the mutation *Vvgai1*, the microvine tends to over accumulate gibberellins, fourfold more GA1 and 12-fold more GA4 in leaves than the equivalent macrovine (Boss and Thomas, 2002). Altogether, this suggests that potentially *Vvgai1* can disturb directly growth and reproductive development by modifying the signaling pathway of GAs but also induces pleiotropic effects by disturbing the balance of other phytohormones known to regulate organogenesis through cell division and differentiation, i.e. cytokinins and auxins (Lee et al., 2019).

The quantification of the vegetative organogenesis slowing down due to the mutation Vvgai1 could be quantified by comparing the phyllochrons of the M*i*Vs vs their M*a*V counterparts not carrying the mutation. Phyllochron values were consistently higher in M*i*Vs than in M*a*Vs, with the strongest divergence early in the season (DOY 121–135; 57 vs. 32 °C·day phytomer^{-1}), then progressively decreasing across subsequent stages (approximately 28 °C·day phytomer^{-1}), in line with the differences in phytomer number (Fig. 3C). These values were slightly higher than those reported for *V. vinifera* microvines grown under standard greenhouse or growth chamber conditions (25 °C·day phytomer^{-1} at 28/15 °C day/night; Luchaire et al. (2017, 2023). The higher phyllochron values observed here may be partly due to the use of seed-derived plants rather than vegetatively propagated material. Seedlings typically develop more slowly, as resources are first allocated to root establishment and the juvenile-to-adult transition (Poethig, 2013). Despite this effect of the *Vvgai1* mutation on the rate of unfolded leaves, other vegetative organogenesis parameters (leaf and internode size, lateral shoot development) have been found equivalent to other *V. vinifera* microvines (Dias et al., 2019; Luchaire et al., 2017).

3.3. *Vvgai1 delays stem lignification with no changes in photosynthetic performances*

In perennial plants, shoot ontogenic maturation (Wareing, 1959) is a critical step to sustain the maintenance of growth during the successive vegetative and reproductive cycles (Poethig, 2013). In the grapevine, this involves several physiological features such as meristem endodormancy, starch accumulation and dehydration to increase the tolerance to abiotic factors during the vegetative rest period. Additionally, vegetative organ maturation includes anatomical changes, such meristem activity slow down, cell lignification and the development of subero-phellodermic cambium to set up protective tissues (Torregrosa et al., 2021; Bernard, 1980). Stem maturation externally manifests itself by a change in color from green to brown, and in viticulture the name of the stem changes from shoot to cane.

In the grapevine, stem maturation starts at the base of proleptic or sylleptic axes (Bouard, 1966). The change in stem maturation level is linked to a change is the status of axillary winter buds which stop further differentiation of inflorescence primordia (Dias et al., 2019), the lignification of bud scales and endodormancy (Nigon, 1961; Carolus, 1971). In this progeny, the maturation of the stem occurred approximately twice as fast in M*a*Vs compared to M*i*Vs (Fig. 4). This could be due to a better C status of the M*a*Vs resulting in an higher allocation of C for starch storage during cane maturation (Bouard, 1966). Also, this could suggest a direct function of GAs in the regulation of the maturation of the cane. In situations when GAs is needed to promote main stem growth (eg. shaded plant), this phytohormone could also play to delay the maturation of the stem, limiting C storage and cork layer differentiation to promote green organ expansion and C supply to the shoot apical meristems, in accordance with the liana-like growth pattern adopted by grapevine species. This interpretation is in agreement with Arro et al. (2017) who suggest that genes involved in the regulation of lignification could also be modulated during reproductive development.

To assess the carbon status at the plant level, leaf area and maximum photosynthetic rate in both M*a*V and M*i*V plants were assessed (Fig. 5). M*i*Vs produced significantly smaller leaves than M*a*Vs (1.57 cm^2 vs 1.96 cm^2 per phytometer, Fig. 5A). Despite this reduction in leaf size, differences in maximum photosynthetic rate between M*a*V and M*i*V leaves in this population were small, with average values of 8.2 ± 2.2 and 11.2 ± 4.4 μmol CO_2 m^{-2} s^{-1} for M*a*Vs and M*i*Vs, respectively (Fig. 5B), consistent with trends observed in other M*a*V and M*i*V populations (Figure S1). Overall, these observations suggest that M*i*Vs may assimilate a comparable amount of carbon per phytomer to their counterparts. These values are relatively low compared with other macrovine varieties grown in greenhouse conditions under well-watered regimes (Wilhelm de Almeida et al., 2024) but are consistent with previously reported values for M*i*Vs (Luchaire et al., 2023). The lower rates observed in M*a*Vs may reflect moderate water deficit, differences due to varietal background, or generally reduced light conditions in the experimental environment. Although leaf area was estimated using allometric equations developed for *V. vinifera*, which may not fully capture the specific leaf morphology of *V. labruscana* hybrids, this approach was applied consistently across all treatments. Therefore, while absolute values

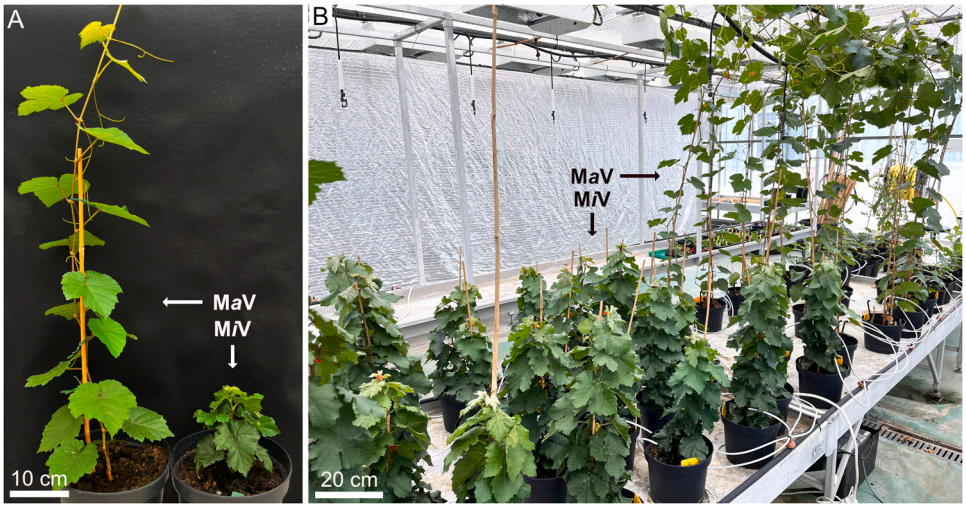

Fig. 2. - Phenotypes of the macrovine and microvine plants within the progeny at 2 (A) and 3 (B) months from T0.

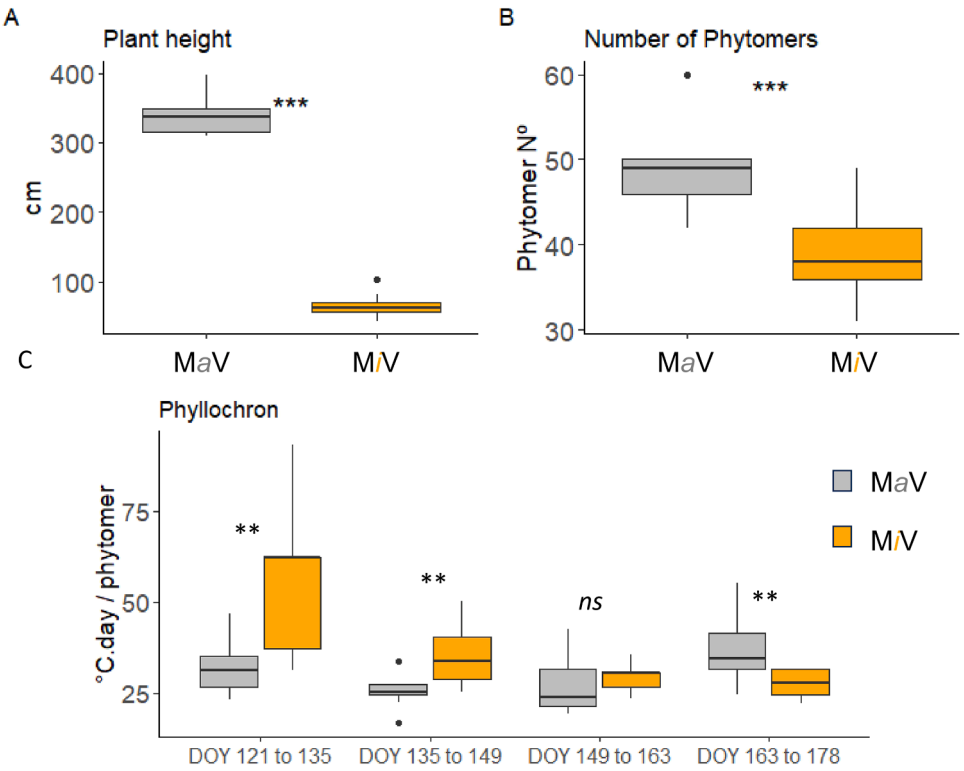

Fig. 3. - (A) Size of the main shoots; (B) number of phytomers per plant at DOY 184 and (C) phyllochron (°C·day per phytomer) accumulated for each period, DOY 121–135, DOY 135–149, DOY 149–163 and DOY 163–178).

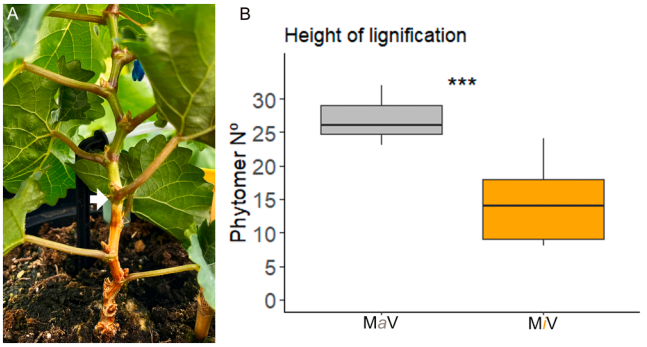

Fig. 4. - (A) Maturation of the shoot on a M*i*V plant (the white arrow shows the level of the lignification, here at the phytomer 6; (B) Level of lignification of the macrovine and microvine main shoots at DOY 184.

should be interpreted with caution, the observed differences between M*a*V and M*i*V plants are considered reliable in a comparative context.

Photosynthetic performance differences between the two models can't explain the differential behavior of cane maturation. This suggests that the mutation of *Vvgai1* gene whose expression is specifically linked to a range of vegetative organs in the grapevine, including roots, shoots, young and adult leaves (Torregrosa et al., 2019) disturb C allocation during shoot maturation. Previous observations about the effect of fruit load on shoot organogenesis and growth showed that microvines are very susceptible to fruit overloading. Recently Tournier et al. (2025) reported a significant increase of the phyllochron and even the arrest of vegetative organogenesis due to unfavorable source/sink balances when the number of bunches was not carefully controlled.

3.4. *Vvgai1 modifies the regulation of inflorescence initiation patterns and juvenile duration phase*

As expected from previous studies (Srinivasan and Mullins, 1979), the emergence of opposite-to-leaf organs was synchronised (Fig. 6) with phyllotaxis changes (Grenan and Truel, 1983). In most studies, the shift to seedling adult phyllotaxis is generally observed between the phytomers 10 and 15, depending on the environmental conditions and the plant vigour. Interestingly, in this experiment tendrils tended to appear just before the shoot apical meristem turned to the adult phyllotaxis program either on M*a*V or M*i*V plants. The transition from juvenile (spiral) to adult (distichous) phyllotaxis, as well as the emergence of the first tendrils, occurred at lower node positions in M*a*Vs than in M*i*Vs (Fig. 6). This is counter intuitive as the microvines were quicker in producing fully developed reproductive organs and exhibited some delays in the maturation of the shoots, a process which can be associated with juvenility.

Phenotyping a progeny obtained from ((*Vitis berlandieri* × *V. riparia*) × *V. biformis*) × (*V. labrusca* × *V. mustangensis*), Hartman et al. (2017) observed that location of the first node displaying an adult phyllotaxy ranged from 12 to 18, as in this study (Figs. 6 and 7). We also observed that some seedlings displayed a decrease in the quantity of tendrils at higher nodes, highlighting the phenotyping of this trait need to be done in the proximal region of the shoot. Interestingly Arro et al. (2017) who transcriptionally profiled genotypes contrasted in their quantity and distribution of opposite-to-leaf organs identified a set of DEGs associated both with tendril features and lignin pathway. These authors concluded that lignification, cell wall development and cell proliferation are processes ontologically related with shoot architecture development and likely with tendril development as well. In this study, the observed relationships between the level of lignification and the shift from juvenile to adult shoot architecture indicate an inverse association between these two developmental features in this progeny.

By crossing genotypes displaying contrasting tendril distributions,

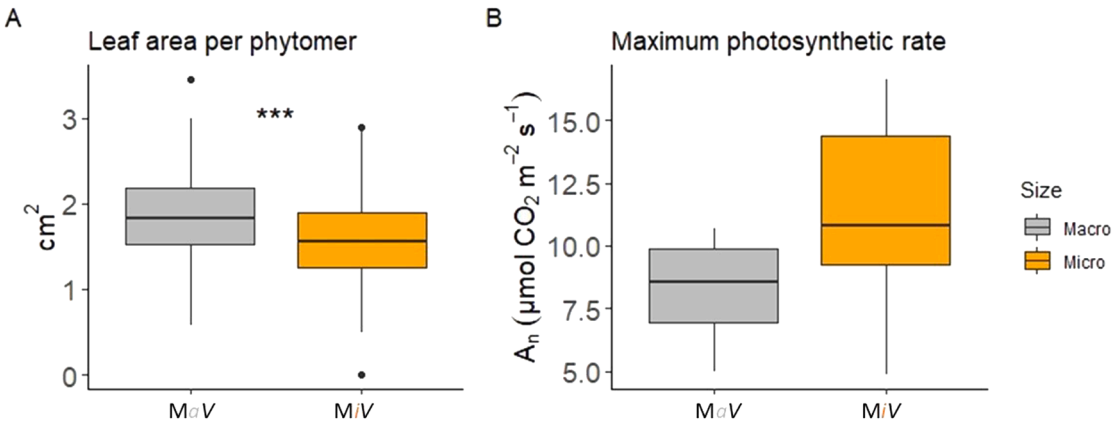

Fig. 5. - (A) Leaf area per phytomer; (B) maximum photosynthetic rate of macrovine and microvine plants.

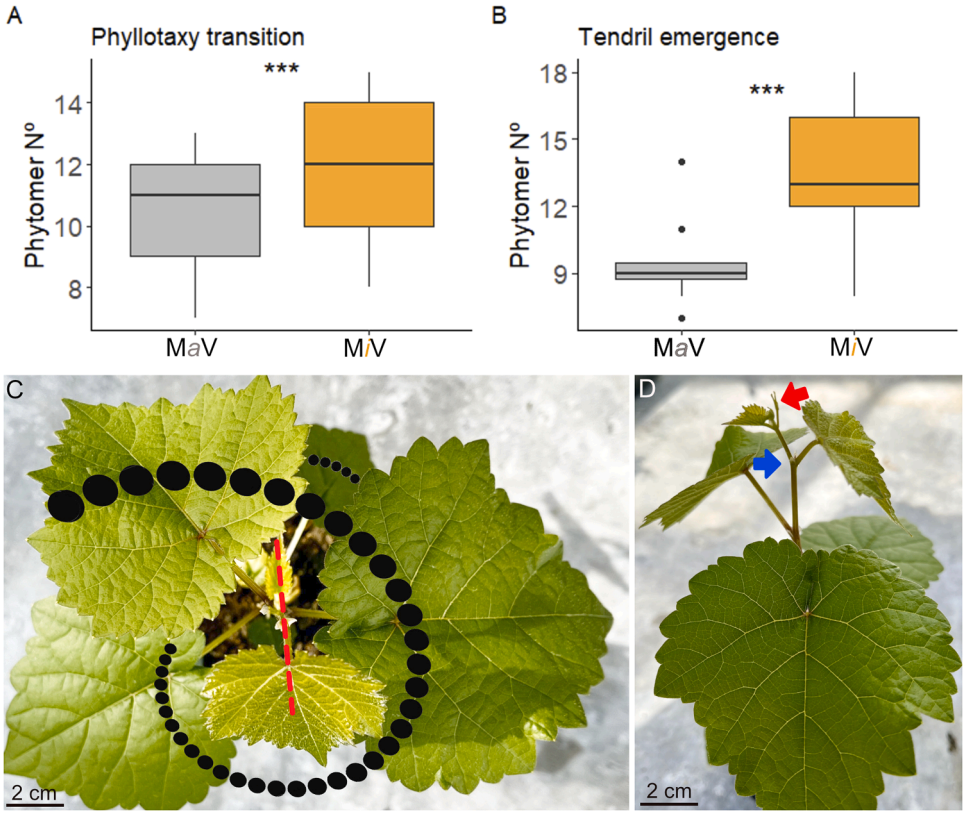

Fig. 6. - (A) Level of transition from juvenile (alternate spiral = 2/5) to adult phyllotaxis (alternate distichous = 1/2); (B) position of the first opposite-to-leaf organ (tendril) on the main shoot at X months; (C) Shift from juvenile to adult phyllotaxis on a M*a*V plant, dashed red line shows the beginning of alternate distichous distribution. (D) Apparition of the first opposite-to-leaf organ (red arrow) at the shift from juvenile to adult phyllotaxis (blue arrow).

Cousins et al. (2005, 2009) observed that the 2 tendril out of 3 nodes is the most frequent situation. However, in a self-pollinated population, Cousins and Zhong (2015) observed that 54 % of seedlings can display additional tendril-free nodes. Furthermore, Cousins and Zhong (2015) suggested that tendril distribution is under a genetic control involving dominant alleles with two loci required to produce extra tendril-free nodes. There is very little information about the genetic regulation of the labrusca-type distribution of the tendril/inflorescences, i.e. the subcontinuous production of opposite-to-leaf organs (Cousins et al., 2009). In this study crossing the *V. vinifera* with *V. labruscana* cv. Isabella, a majority of individuals displayed a labrusca type positioning of opposite-to-leaf organs, ie. 75 % vs 25 % in M*a*Vs and 65 % vs 35 % in M*i*Vs for *labrusca*- and *vinifera*-type distribution respectively. These results confirm as proposed by Cousins et al. (2009) this trait is governed by a dominant mechanism involving several independent loci in *V. labrusca*.

M*a*V plants did not initiate any reproductive organs during the first vegetative cycle. Conversely, as previously reported (Chaïb et al., 2010; Torregrosa et al., 2019) M*i*V plants produced their first flowers (Fig. 8) only a few months after embryo rescue, from the node 18 on average in this experiment. A period of 4–6 weeks after a microvine seedling is acclimated is enough to get the first flowers. However, the first inflorescences are very fragile and only display a limited number of flowers (data not shown), 2–3 more weeks of growth are required to get fully developed inflorescences suitable for cross-breeding or fruit studies.

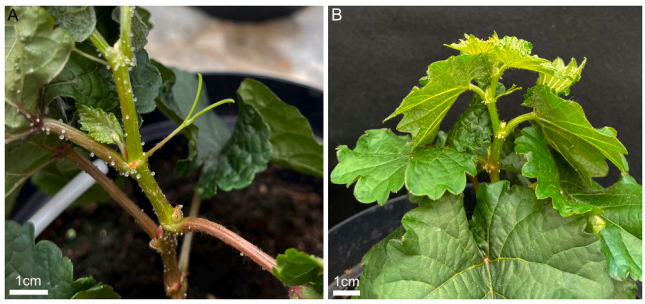

Fig. 7. - A) Development of a tendril in a M*i*V plant. B) First steps of the development of an opposite-to-leaf organ into an inflorescence in a M*i*V plant.

Fig. 8. - Development of a female (A) or a hermaphroditic (B) flower on a M*i*V plant.

3.5. *The segregation of the flower sex types*

The microvine used as female being homozygous (ff) for the recessive trait determining the flower sex type, the observed sex ratio in M*i*Vs of 49 % female and 51 % hermaphroditic (Fig. 9), suggests the *V. labrusca* progenitor be heterozygous (Hf) for the SDR locus. Consequently, all hermaphroditic microvines obtained of this progeny are heterozygous Hf, with the hermaphrodite haplotype from the cv. Isabella, while the females being homozygous (ff) associate a female allele form both parents. This can be of some importance for further cross breeding programs to select the most suitable progenitors according to expected uses. Crossing a female microvines is convenient to avoid time-consuming emasculation and selfing, while to study fruit development a hermaphroditic self pollinating ensures the development of seeded berries without extra work of pollination. Hermaphroditic M*i*Vs proved able to produce seeded fruits expressing the foxy aromatic profile of *V. labrusca* (data not shown), this specific aroma associated with the accumulation of methyl anthranilate and 2-aminoacetophenone being differentially appreciated in grape, juice or wines (Perry et al., 2019).

4. Conclusion

In this experiment, we have developed a novel set of microvine genotypes integrating *V. labrusca* genetic background. Results from phenotyping microvine and macrovine lines within the same progeny suggest that GAs are not only involved in regulating growth and reproductive program but also in the regulation of shoot maturation independently of the photosynthetic performance which remained equivalent in macro and microvines. These observations open new questions and hypotheses about how plant growth regulators control development of liana-type plants. In addition, this study provides new dwarf, rapid and continuous flowering genotypes allowing original physiological experiments and genetics dealing with grapevine climate and disease tolerance and adaptation.

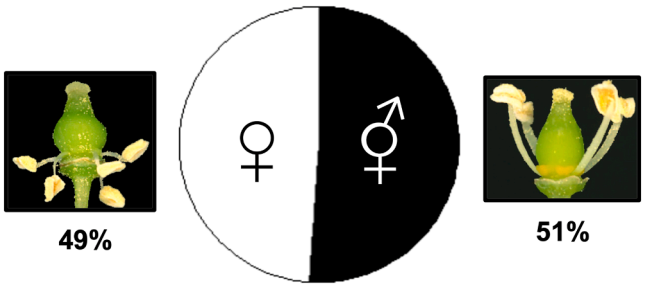

Fig. 9. - Segregation of the flower sex type within the M*i*V plants.

CRediT authorship contribution statement

Jana Kändler: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luciana Wilhelm de Almeida:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation. **Laurent Torregrosa:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Author would like to thank Thierry Lacombe and the team of the Vassal-Montpellier genetic repository (France) for advising in pollen source selection and suggesting literature references.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.scienta.2026.114643.

Data availability

Data will be made available on request.

References

Arro, J., Cuenca, J., Yang, Y., Liang, Z., Cousins, P., Zhong, G.-Y., 2017. A transcriptome analysis of two grapevine populations segregating for tendril phyllotaxy. Hortic. Res. 4 (1), 17032. https://doi.org/10.1038/hortres.2017.32.

Bernard, A.C., 1980. Contribution à L'étude De La Biologie Des Méristèmes. Montpellier Univ, France, p. 215. PhD dissertation.

Boss, P.K., Thomas, M.R., 2002. Association of dwarfism and floral induction with a grape 'green revolution' mutation. Nature 416 (6883), 847–850. https://doi.org/10.1038/416847a.

Bouard, J., 1966. Recherches physiologiques sur la vigne et en particulier sur l'aoûtement des sarments. PhD Uni. Bordeaux 344.

Boursiquot, J.M., Lacombe, T., Yobregat, Y., 2024. Histoire de l'hybridation de la vigne. Vigne Tolérantes Aux Maladies Fongiques: Des Variétés à Fruits Pour Une Viticulture En Transition Agroécologique. Edition France Agricole, Paris, France, pp. 30–52. ISBN 978285557862.

Carolus, M., 1971. Description des stades du développement des primordia inflorescentiels durant l'organogenèse des bourgeons latents de la vigne (vitis vinifera l. var. Merlot). OENO One 5 (1), 163–173. https://doi.org/10.20870/oeno-one.1971.5.1.2024.

Chaïb, J., Torregrosa, L., Mackenzie, D., Corena, P., Bouquet, A., Thomas, M.R., 2010. The grape microvine – a model system for rapid forward and reverse genetics of

grapevines. Plant J. 62 (6), 1083–1092. https://doi.org/10.1111/j.1365-313X.2010.04219.x.
Chatbanyong, R., Torregrosa, L., 2015. A highly efficient embryo rescue protocol to recover a progeny from the microvine. VITIS - J. Grapev. Res. 54 (1), 41–46. https://doi.org/10.5073/vitis.2015.54.41-46.
Coombe, B.G., 1967. Effects of growth retardants on Vitis vinifera L. Vitis 6, 278–287.
Costa, L.D., Malnoy, M., Lecourieux, D., Deluc, L., Lecourieux, F.O.-, Thomas, M.R., Torregrosa, L.J.-M, 2019. The state-of-the-art of grapevine biotechnology and new breeding technologies (NBTS): this article is published in cooperation with the 21th GIESCO International Meeting, June 23-28 2019, Thessaloniki, Greece. Guests editors: Stefanos Koundouras and Laurent Torregrosa OENO One 53 (2), 189–212. https://doi.org/10.20870/oeno-one.2019.53.2.2405.
Cousins, P., Johnston, D., Switras-Meyer, S., Meyer, C., 2009. Genetic control of tendril distribution in a grapevine rootstock hybrid population. Acta Hortic. 827, 337–340. https://doi.org/10.17660/ActaHortic.2009.827.57.
Cousins, P., Switras-Meyer, S., Vidmar, J., Boyden, L., Johnston, D., 2005. Segregation of tendril distribution patterning in grapevine populations. Acta Hortic. 689, 541–544. https://doi.org/10.17660/ActaHortic.2005.689.67.
Cousins, P., Zhong, G.-Y., 2015. Hybrid and selfed seedling progenies of *Vitis* hybrid 'Roger's Red' grape segregate for tendril distribution. Acta Hortic. 1082, 373–378. https://doi.org/10.17660/ActaHortic.2015.1082.52.
Dias, F.A.N., Torregrosa, L., Luchaire, N., Houel, C., Pellegrino, A., 2019. The microvine, a model to study the effect of temperature on grapevine latent bud development and fruitfulness. OENO One 53 (3). https://doi.org/10.20870/oeno-one.2019.53.3.2313.
Dong, Y., Duan, S., Xia, Q., Liang, Z., Dong, X., Margaryan, K., Musayev, M., Goryslavets, S., Zdunić, G., Bert, P.-F., Lacombe, T., Maul, E., Nick, P., Bitskinashvili, K., Bisztray, G.D., Drori, E., De Lorenzis, G., Cunha, J., Popescu, C.F., Chen, W., 2023. Dual domestications and origin of traits in grapevine evolution. Science 379 (6635), 892–901. https://doi.org/10.1126/science.add8655.
Galet, P., 2015. Dictionnaire Encyclopédique Des Cépages. Hachette, Paris, France, p. 1159. EdISBN 978-2847300369.
Galet, P., 1988. Cépages Et Vignobles De France: Les vignes Américaines. Dehan, Montpellier, France, p. 588. EdISBN 978-2847300369.
Gerrath, J.M., Lacroix, C.R., Posluszny, U., 1998. Phyllotaxis in the vitaceae. eds. In: Jean, R.V., Barabé, Denis (Eds.), Symmetry in Plants. World Scientific, Singapore, pp. 89–107.
Grenan, S., Truel, P., 1983. Observations sur un aspect de la variabilité constatée au cours de la multiplication végétative de variétés de vigne issues de semis de Vitis vinifera L. Agronomie 3 (7), 675–680. https://doi.org/10.1051/agro:19830709.
Hartman, L., Zhong, G.-Y., Cousins, P., 2017. Tendril quantity is positively correlated across nodes in an interspecific hybrid grapevine seedling population. Acta Hortic. 1157, 137–142. https://doi.org/10.17660/ActaHortic.2017.1157.22.
Hedden, P., Sponsel, V., 2015. A century of Gibberellin research. J. Plant Growth Regul. 34 (4), 740–760. https://doi.org/10.1007/s00344-015-9546-1.
Ikeda, A., Ueguchi-Tanaka, M., Sonoda, Y., Kitano, H., Koshioka, M., Futsuhara, Y., Matsuoka, M., Yamaguchi, J., 2001. Slender rice, a constitutive Gibberellin response mutant, is caused by a null mutation of the SLR1 gene, an ortholog of the height-regulating gene GAI/RGA/RHT/D8. Plant Cell 13 (5), 999–1010. https://doi.org/10.1105/tpc.13.5.999.
Iland, P., Dry, P., Proffitt, T., Tyerman, S., 2011. The Grapevine: from the Science to the Practice of Growing Vines For Wine. Patrick Iland Wine Promotions Pty Ltd., Adelaide.
Lebon, E., Pellegrino, A., Tardieu, F., Lecoeur, J., 2004. Shoot development in grapevine (Vitis vinifera) is affected by the modular branching pattern of the stem and intra- and inter-shoot trophic competition. Ann. Bot. 93 (3), 263–274. https://doi.org/10.1093/aob/mch038.
Lee, Z.H., Hirakawa, T., Yamaguchi, N., Ito, T., 2019. The roles of plant hormones and their interactions with regulatory genes in determining meristem activity. Int. J. Mol. Sci. 20 (16), 4065. https://doi.org/10.3390/ijms20164065.
Luchaire, N., Rienth, M., Romieu, C., Nehe, A., Chatbanyong, R., Houel, C., Ageorges, A., Gibon, Y., Turc, O., Muller, B., Torregrosa, L., Pellegrino, A., 2017. Microvine: a new model to study grapevine growth and developmental patterns and their responses to elevated temperature. Am. J. Enol. Vitic. 68 (3), 283–292. https://doi.org/10.5344/ajev.2017.16066.
Luchaire, N., Torregrosa, L.J.-M., Gibon, Y., Rienth, M., Romieu, C., Ageorges, A., Turc, O., Muller, B., Pellegrino, A., 2023. A low carbon balance triggers microvine inflorescence abscission at high temperatures. Front. Hortic. 2. https://doi.org/10.3389/fhort.2023.1267429.
Mabrouk, H., Carbonneau, A., 1996. Une méthode simple de détermination de la surface foliaire de la vigne (Vitis vinifera L.). Le Progrès Agricole et Viticole 113 (18), 392 [Publications et Actualités Vitivinicoles].
Murashige, T., Skoog, F., 1962. A revised medium for rapid growth and bio assays with tobacco tissue cultures. Physiol. Plant 15 (3), 473–497. https://doi.org/10.1111/j.1399-3054.1962.tb08052.x.
Nigon, J., 1961. Contribution à L'étude De La Dormance De La Vigne Sous Le Climat Du Languedoc. PhD Uni Paris, p. 72.
Pellegrino, A., Romieu, C., Rienth, M., Torregrosa, L., 2019. The microvine, a versatile plant model to boost grapevine studies in physiology and genetics. In: Morata, A. (Ed.), Advances in Grape and Wine Biotechnologies. IntechOpen, London, UK. EdISBN 978-1-78984-613-3.
Peng, J., Richards, D.E., Hartley, N.M., Murphy, G.P., Devos, K.M., Flintham, J.E., Beales, J., Fish, L.J., Worland, A.J., Pelica, F., Sudhakar, D., Christou, P., Snape, J. W., Gale, M.D., Harberd, N.P., 1999. Green revolution' genes encode mutant gibberellin response modulators. Nature 400 (6741), 256–261. https://doi.org/10.1038/22307.
Perry, D.M., Byrnes, N.K., Heymann, H., Hayes, J.E., 2019. Rejection of labrusca-type aromas in wine differs by wine expertise and geographic region. Food Qual. Prefer. 74, 147–154. https://doi.org/10.1016/j.foodqual.2019.01.018.
Poethig, R.S., 2013. Chapter five—Vegetative phase change and shoot maturation in plants. Eds. In: Rougvie, A.E., O'Connor, M.B. (Eds.), Current Topics in Developmental Biology, Current Topics in Developmental Biology, 105. Academic Press, pp. 125–152. https://doi.org/10.1016/B978-0-12-396968-2.00005-1.
Qin, Q., Wang, W., Guo, X., Yue, J., Huang, Y., Xu, X., Li, J., Hou, S., 2014. Arabidopsis DELLA protein degradation is controlled by a type-one protein phosphatase, TOPP4. PLoS Genet. 10 (7), e1004464. https://doi.org/10.1371/journal.pgen.1004464.
Core Team, R., 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/.
Rienth, M., Torregrosa, L., Luchaire, N., Chatbanyong, R., Lecourieux, D., Kelly, M.T., Romieu, C., 2014. Day and night heat stress trigger different transcriptomic responses in green and ripening grapevine (vitis vinifera) fruit. BMC Plant Biol. 14 (1), 108. https://doi.org/10.1186/1471-2229-14-108.
Rienth, M., Torregrosa, L., Sarah, G., Ardisson, M., Brillouet, J.-M., Romieu, C., 2016. Temperature desynchronizes sugar and organic acid metabolism in ripening grapevine fruits and remodels their transcriptome. BMC Plant Biol. 16 (164), 1–23. https://doi.org/10.1186/s12870-016-0850-0.
Srinivasan, C., Mullins, M.G., 1979. Flowering in Vitis: conversion of tendrils into inflorescences and bunches of grapes. Planta 145 (2), 187–192.
Torregrosa, L., 2024a. Principaux programmes mondiaux contemporains: le Brésil. Vigne Tolérantes Aux Maladies fongiques: Des Variétés à Fruits Pour Une Viticulture En Transition Agroécologique. Edition France Agricole, Paris, France, pp. 192–199. ISBN 978285557862.
Torregrosa, L., 2024b. Principaux programmes mondiaux contemporains: le Japon. Vigne Tolérantes Aux Maladies fongiques: Des Variétés à Fruits Pour Une Viticulture En Transition Agroécologique. Edition France Agricole, Paris, France, pp. 199–205. ISBN 978285557862.
Torregrosa, L., Carbonneau, A., Kelner, J.-J., 2021. The shoot system architecture of Vitis vinifera ssp. Sativa. Sci. Horticul. 288, 110404. https://doi.org/10.1016/j.scienta.2021.110404.
Torregrosa, L., Rienth, M., Romieu, C., Pellegrino, A., 2019. The microvine, a model for studies in grapevine physiology and genetics. OENO One 53 (3). https://doi.org/10.20870/oeno-one.2019.53.3.2409.
Tournier, M.G., Torregrosa, L., Kändler, J., Christophe, A., Boulord, R., Medici, A., Pellegrino, A., 2025. Short light/dark cycles favour photosynthetic efficiency and growth in grapevines: this article is an original research article submitted in cooperation with GiESCO 2025. OENO One 59 (3). https://doi.org/10.20870/oeno-one.2025.59.3.9274.
Wareing, P.F., 1959. Problems of juvenility and flowering in trees. Linnean Soc. Lond. Proc. Botany J. 56 (366), 282–289. https://doi.org/10.1111/j.1095-8339.1959.tb02504.x.
Wilhelm de Almeida, L., Pastenes, C., Ojeda, H., Torregrosa, L., Pellegrino, A., 2024. Water deficit differentially modulates leaf photosynthesis and transpiration of fungus-tolerant Muscadinia x Vitis hybrids. Front. Plant Sci. 15. https://doi.org/10.3389/fpls.2024.1405343.
Yamaguchi, S., 2008. Gibberellin metabolism and its regulation. Annu. Rev. Plant Biol. 59, 225–251. https://doi.org/10.1146/annurev.arplant.59.032607.092804. Volume 59, 2008.