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VITICULTURE ORIGINAL RESEARCH ARTICLES

First characterisation of the restricted spring growth syndrome affecting grapevines in Chile

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ABSTRACT

Restricted spring growth (RSG) is a poorly documented grapevine syndrome that compromises vegetative development, fruit production, and vineyard longevity. Here, we provide the first formal report and characterisation of RSG in commercial vineyards of Vitis vinifera cv. Sweet Globe in Central Chile. Across three affected sites and one control vineyard, we compared vegetative traits, nutritional reserves, and vascular anatomy of symptomatic (Sy) and asymptomatic (As) vines. Field observations revealed that Sy plants developed significantly shorter and thinner basal internodes than As plants, leading to reduced cane vigour. Although leaf nutrient concentrations did not differ between groups, analyses of root reserves indicated that Sy vines tended to accumulate fewer reserves during dormancy, suggesting impaired reserve dynamics.

Histological analyses provided critical evidence of vascular impairment, showing that Sy plants developed smaller vessel elements, irregular xylem rays, and disorganised, underdeveloped phloem, frequently associated with callus formation. Screening for potential biotic causes found no association with mites, Pseudomonas, or grapevine trunk diseases. All vineyards tested positive for common viruses (GVA, GRSPaV, GFLV). Hence, pathogens and buds are unlikely to be the cause of the syndrome. Our findings point to an abiotic origin of RSG, shaped by the combined effects of reserve dynamics, cold stress, and vascular tissue damage. Collectively, these results indicate that RSG is a multifactorial disorder that disrupts vascular functionality and reserve accumulation, with consequent impacts on both shoot and fruit development.

KEYWORDS: *Vitis vinifera*, restricted spring growth, vascular anatomy, frost damage, dormancy, non-structural carbohydrates

INTRODUCTION

Climate change, along with abiotic and biotic stressors, poses a significant challenge to agricultural production systems. Under stress conditions, plants allocate fewer resources to growth and development, increasing their susceptibility to physiological disorders and pathogen attacks, ultimately compromising food security (Fahad *et al.,* 2017; Seleiman *et al.,* 2021; Savary, 2020). Intensive agricultural practices, driven by the rising demand for highquality products, increasingly rely on fertilisers, growth regulators, and biostimulants to maximise yield (Zahid *et al.,* 2023; Basile *et al.,* 2020; Van Oosten *et al.,* 2017). However, such practices push vines to their physiological limits, thereby exacerbating the effects of abiotic and biotic stress. These conditions may contribute to the development of physiological disorders and syndromes, encompassing restricted spring growth (RSG).

Restricted spring growth (RSG), also known as delayed spring growth or, in some cases, shoot stunting, are terms that describe similar conditions but with subtle differences in symptomatology. Whereas shoot stunting allows for some degree of recovery and structural development during the growing season, RSG exhibits a persistent growth arrest. The condition has been recognised since 1990; however, its detailed characteristics have not yet been formally published, and the data remain unavailable (Bernard *et al.,* 2005; AWRI, 2010); the only official article is that of Hackett and Holzapfel (2002), which provides a descriptive synthesis of information compiled during a seminar but non-quantitative data. Although technical reports and presentations have described aspects of RSG, they lack explicit empirical data.

Hackett and Holzapfel (2002) schematically propose factors that define a plant's condition, distinguishing between vigorous and healthy individuals (VSG) and those exhibiting restricted growth (RSG). They further outline three potential scenarios for these plants: productive and healthy plants, disabled plants, and infected plants. Additionally, they explain that RSG constitutes a multifactorial syndrome characterised by disrupted budburst and retarded shoot growth, with causes associated either with grapevine pathologies or with environmental interactions.

Furthermore, a three-season study conducted in Australia by Bernard *et al.* (2005) identified *Calepitrimerus vitis* and *Colomerus vitis* as common causes of RSG. This research evaluated leaf distortion, shoot length, and the presence of Eriophyid mites (Eriophyidae) in Chardonnay and Cabernet-Sauvignon grapevines. According to their results, acaricide treatments mitigated the syndrome's severity, as evidenced by increased shoot length and reduced bud necrosis. However, the Australian Wine Research Institute (AWRI, 2015) suggests that RSG may, in some cases, be misdiagnosed, with symptoms mistakenly attributed to Eriophyid mite infestations.

Most technical reports describe RSG as widespread delays and asynchrony in budburst, accompanied by underdevelopment of both vegetative and reproductive structures (Kultural *et al.,* 2021; AWRI, 2015). This condition disrupts vine vigour, reducing yields and consequently compromising fruit quality. Furthermore, RSG increases pathogens' susceptibility and shortens the longevity of commercial vineyards. The syndrome is most frequently observed in young vineyards, especially during the first three years in vines grown under an excessive fruit load (Kultural *et al.,* 2021; AWRI, 2010).

Studies indicate that RSG expression is more pronounced in vigorous plants exhibiting active late-season growth, often driven by excessive fertilisation and irrigation. As a result, vigorous rootstocks have been associated with a higher incidence of RSG (Tian, 2022; Kultural *et al.,* 2021). Late-season vigour may interfere with dormancy and acquisition of cold hardiness in plant tissues, thereby increasing susceptibility to frost damage (De Rosa *et al.,* 2021; Ferguson *et al.,* 2014). According to Esau (1948), the state of dormancy is only fully established after the occurrence of the first frost. Moreover, Zabadal *et al.* (2007) reported that winter frosts can damage the vascular cambium, leading to callus formation that disrupts vascular function and results in disorganised, underdeveloped phloem. Additionally, Gonzalez Antivilo *et al.* (2020) demonstrated that cold-induced damage to the phloem and cambium can cause phloem necrosis, further disrupting bud break in grapevines.

Late-season vigour may also decrease carbohydrate and nitrogen reserves before winter. This reduction in reserve accumulation is linked to low vigour in the following season and increases susceptibility to pathogens (Claverie *et al.,* 2025). Additionally, reduced reserve levels have been suggested as a possible contributing factor in the development of RSG (Kurtural *et al.,* 2021). In perennial plants, the storage of non-structural carbohydrates (NSC), such as sugars and starches, before dormancy is critical for winter survival and uniform budburst in spring (Tixier *et al.,* 2019).

Environmental conditions influence the accumulation and consumption of NSC; therefore, unstable winters increase the rate of reserve depletion (Tixier *et al.,* 2019; Chamberlain & Wolkovich, 2021). Furthermore, in plants, arginine is the primary nitrogen reserve and plays a crucial role in vine vigour. It has been demonstrated that vines with lower arginine reserves exhibit a lower bud fruitfulness (Monteiro *et al.,* 2022) and reduced sprouting vigour (Falginella *et al.,* 2022; Verdenal *et al.,* 2021; Winter *et al.,* 2015). Furthermore, research on other plant species suggests that insufficient reserve accumulation can alter phenological development (Roxas *et al.,* 2021).

This phenomenon has also been observed in both table and wine grape vineyards and has been reported in both traditional and newly bred varieties, regardless of their ripening period (Kurtural *et al.,* 2021; Tian, 2023). Due to its variable occurrence and multifactorial nature, RSG is considered a syndrome with erratic patterns and complex underlying causes (AWRI, 2015; Zhuang & Fidelibus, 2022). The objective of this study was to characterise restricted

spring growth in commercial vineyards by integrating field observations, climatic data, anatomical analyses, and reserve assessments to explore potential abiotic mechanisms underlying the syndrome.

MATERIALS AND METHODS

1. Experimental design and plant material

The study was conducted in four commercial vineyards of *Vitis vinifer*a cv. Sweet Globe and is located in Central Chile. Three vineyards: Los Andes (32° 52' 03.3" S 70° 38' 43.8" W; grafted onto 1103 Paulsen), Rancagua (34° 08' 30.2" S 70° 51' 39.3" W; grafted onto Harmony), and Lampa (33° 19' 05.0" S 70° 52' 07.9" W; grafted onto Ramsey) displayed varying degrees of RSG expression. The remaining vineyard, San Vicente (34° 27' 22.7" S 71° 06' 27.4" W; grafted onto 1103 Paulsen), exhibited no symptoms of RSG and was designated as the absolute control, serving as a baseline to represent normal vine growth. Details regarding vineyard management practices are provided in Table S1.

During January 2022 (summer), vineyard growers guided us through their fields and indicated the zones where the syndrome had been expressed. Within these zones, we identified symptomatic vines using the following criteria: shortened basal internodes, reduced cane thickness, diminished vegetative vigour, and reduced fruit presence. Based on symptom expression, vines were subsequently classified into two groups: asymptomatic (As), which showed no visible symptoms of RSG, and symptomatic (Sy), which exhibited clear reductions in vegetative growth and fruit production.

In each vineyard, six plants per category were marked for monitoring throughout the season. From each plant, we obtained three samples for histological study, five shoots for measuring basal internode traits, a pooled set of four young leaves displaying potential viral or bacterial symptoms, and two spurs intended for fungal pathogen assessment. This sample size is appropriate for capturing the main differences among conditions, although it may offer limited power to detect very subtle effects. Figure 1 presents representative examples of asymptomatic and symptomatic plants, with additional images in Figure S1.

2. Climatological data

Temperature and relative humidity data were recorded using meteorological stations installed at each vineyard. These stations collected hourly readings from May 2021 to July 2022, which were subsequently aggregated into daily data, enabling precise monitoring of environmental conditions, including frost events. Data from winter 2021 provided information on the environmental conditions that could influence dormancy and bud development, whereas data from winter 2022 provided insights into the weather conditions that influenced shoot emergence and growth. In each vineyard, the number of frost events from May to October was recorded. Moreover, the chill hours were calculated from May, 1st to September, 1st using a 7.2 °C threshold. Additionally, heat accumulation was assessed from August, 1st, 2021, to May, 1st, 2022, to evaluate potential influences on budbreak and early-season growth.

3. Vegetative characterisation

3.1 Basal internodes length and thickness measurements

To assess vegetative growth, we measured shoot development at the onset of winter 2022. Using a digital calliper (Shahe IP54, China), the length and thickness of the internodes in the first six basal nodes were recorded. Measurements were taken from five shoots per plant, using the same six plants per condition (asymptomatic and symptomatic) that had been previously marked in each vineyard for monitoring.

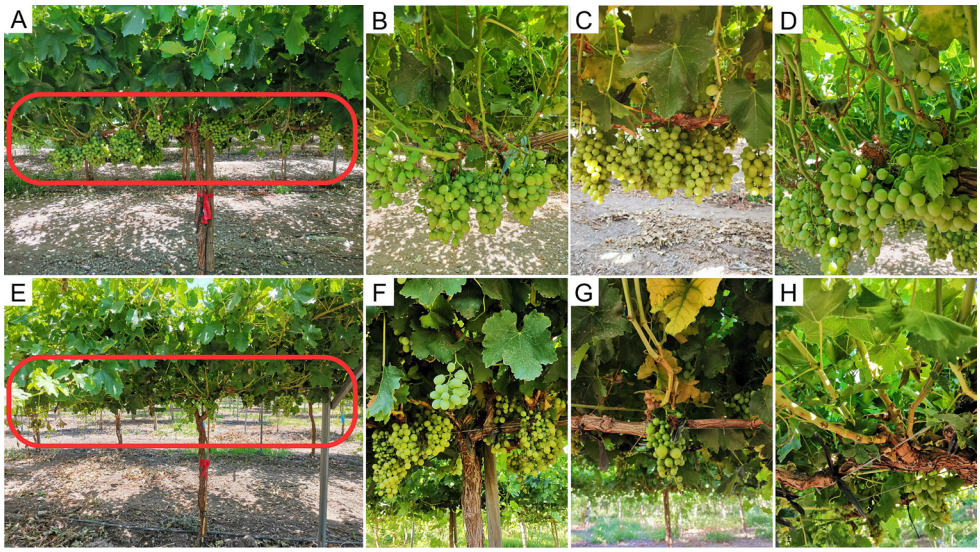


FIGURE 1. Different points of view on representative images of asymptomatic plants (A, B, C and D) and symptomatic plants (E, F, G and H).

*The red square indicates the fruit production area.

3.2 Histological protocol

For anatomical analysis, cuttings from the first two basal internodes of canes were collected. Random samples were obtained from the previously marked plants in each vineyard, following the first frost in May 2022. Due to the destructive nature of sampling, four samples per condition were systematically collected from the marked plants in each vineyard to ensure sufficient material for histological sectioning. Canes samples were collected to assess damage caused by frost on vascular tissues; three samples were collected, each conducted after a distinct frost event. Cane samples were fixed in FAA solution (50 % ethanol, 35 % distilled water, 10 % formalin, 5 % glacial acetic acid) and stored for at least two weeks prior to processing.

Following fixation time, samples were placed in labelled cassettes, and dehydrated through a double ethanol series (50 %, 70 %, 85 %, 95 %, and 100 %) and subsequently placed in a double Xylol/Alcohol series (30 %, 50 %, 70 %, and 100 %). The tissue was then embedded in Leica® Paraplast (USA) using a double Paraffin/Xylol series (35 %, 65 %, and 100 %). Each step of the three series lasted 1 hour, except for the final step (100 %), where samples were left overnight to ensure adequate embedding. Finally, the samples were embedded in paraffin blocks, which were then sectioned to a thickness of 15 µm using a microtome (Olympus® CUT 4060, Japan). Sections were stained with blue aniline, following the protocol described by Gärnet and Schweingruber (2013), and mounted on glass slides using an Entellan/Xylol (90:10) mixture. Microscopic examination was performed with a Nikon® Labophot-2 (Japan), and histological images were captured with a digital camera (Canon® EOS Rebel 7T, Japan).

3.3 Analysis and processing of anatomical images

Histological images were analysed using ImageJ 1.53k. Comparisons of vascular tissue were conducted among absolute control, asymptomatic, and symptomatic plants. Measurements of xylem and phloem dimensions were conducted and supplemented with a detailed visual description. These measurements encompassed various aspects, including the cross-sectional area (CSAV) and mean perimeter (PVE) of primary vessel elements. Additionally, the radial length of phloem tissue (RLP) was measured from the vascular cambium to the phloem cusp. To ensure standardisation, measurements were performed within the area enclosed by the three central vascular rays, with particular attention to cambium integrity and xylem and phloem deformation.

3.4 Nutritional status

A foliar nutritional analysis was conducted to evaluate the nutrient status of asymptomatic and symptomatic plants. Leaf samples (lamina) were collected on March 16, 2022 (late summer) and analysed for total nitrogen (N) and phosphorus (P) concentrations, as well as ammonium (NH_4^+) and nitrate (NO^{3-}) levels. Additionally, root reserve analysis was performed on samples collected on July 15, 2022, focusing on arginine, starch, and dry matter accumulation. All nutritional analyses were conducted by Agroanálisis UC (www.agroanalisis.uc.cl).

3.5. Pathogen and pest analysis

To assess whether RSG was associated with biotic agents, the presence of Eriophyid mites, viruses, fungal pathogens (with a focus on grapevine trunk diseases), and *Pseudomonas spp*. was evaluated. Viral and *Pseudomonas* screenings were conducted on both mature and young leaves exhibiting varying degrees of symptom expression. At the same time, samples of woody tissues were taken from distal spurs of each vine to detect potential trunk disease pathogens. All samples were collected on 26 January 2022.

The screen for Eriophyid mites was conducted through bud dissections, using canes collected concurrently with the samples for histological analysis. Bud dissections were performed under a bench magnifying glass using fine dissection tools, including scalpels and dissecting needles. Virus detection was performed on symptomatic and mature leaves by RNA extraction followed by polymerase chain reaction (PCR), following the protocols established by Tobar *et al.* (2020). The analysis targeted key grapevine viruses, including *grapevine leafroll-associated virus 3* (GLRaV-3), *grapevine fleck virus* (GFkV), *grapevine virus A* (GVA), *grapevine rupestris stem-pitting associated virus* (GRSPaV), and *grapevine fanleaf virus* (GFLV). Fungal testing was performed on distal spur samples, which were surface sterilised, isolated, and incubated at 20 °C for 15 days, following the methodology described by Díaz and Latorre (2014). After incubation, samples were examined macroscopically and microscopically to identify fungal pathogens associated with grapevine trunk diseases. *Pseudomonas spp*. were assessed by isolating samples and culturing them on King medium A (Becton Dickinson, Difco™ 244910), a fluorescence-selective medium specifically formulated for the detection of *Pseudomonas*.

4. Statistical analysis

The absolute control vineyard was used to establish reference values for each measured variable; however, no direct statistical comparisons were made between the control and the affected vineyards. Instead, the analysis focused on comparing asymptomatic and symptomatic plants within the affected vineyards, with each plant treated as an experimental unit.

A completely randomised design (CRD) was adopted, with vineyards treated as randomised blocks. The software JMP® 13.0 (SAS Institute Inc.) was used to perform the analysis. Outliers were identified through Mahalanobis and Jackknife distance metrics. Additionally, the normality of the residuals was assessed using the Shapiro–Wilk test. Moreover, Levene's and Bartlett's tests were applied to assess the homogeneity of variance. To analyse the data, a linear mixed-effects model was fitted using the restricted maximum likelihood (REML) method. Plant condition (asymptomatic vs symptomatic) was used as a fixed effect, and vineyard as a random effect. Statistical significance was determined at $p < 0.05$, and post-hoc

comparisons were conducted using *t*-tests. Graphical outputs were generated using R software (R Core Team, 2025).

RESULTS

The climatic conditions of the 2021–2022 season were consistent with a typical Mediterranean pattern. Notably, late autumn (May) was characterised by temperature fluctuations, which led to a significant drop in temperatures. Early winter (June) was cold, whereas mid-winter (July–August) included several consecutive days of unusually high maximum temperatures, reaching up to 30 °C in Los Andes (Figure S2). Spring 2021 exhibited pronounced temperature fluctuations across all vineyards, accompanied by a consistent warming trend.

In contrast, regarding frost occurrence, the absolute control vineyard recorded only seven frost events in 2021 and four in 2022. In 2021, the first frost was recorded on 10 May (autumn) in the Lampa vineyard. Through the winter, this field registered the highest number of frost events (71), followed by Rancagua (40) and Los Andes (19). In 2022, all the vineyards exhibited a similar pattern, although with reduced intensity and frequence of frost events (Table 1). Thus, confirming that Lampa is the coldest field, with mean minimum temperatures of –3.7 °C in July 2021, followed by Rancagua at -0.8 °C. Figure S3 presents histograms showing the frequency distribution of minimum temperatures for each vineyard, corresponding to the final month of autumn and the onset of winter. These data support the occurrence of frost events in May across the vineyards, with Lampa emerging as the coldest site.

TABLE 1. Climate overview, variables according to trial timeline.

	◄ Winter 2021			– Timeline –		Winter 2022 ►		
Field	< 0 °C	< –2 °C	< –4 °C	Chill H.	Heat R.	< 0 °C	< –2 °C	< –4 °C
SV*	7	1	0	989	1,867	4	2	0
LA	19	3	0	1079	2,091	10	1	0
RA	40	14	0	981	1,647	35	10	3
Lam	71	47	23	821	1,624	27	17	4

SV: absolute control, LA: Los Andes, RA: Rancagua and Lam: Lampa. Number of frost events in each vineyard per year (May-October). The number of events below 0 °C, -1 °C, -2 °C, and -4 °C is listed. In the centre, chill hours (Chill H.) of winter 2021 and heat hours (Heat H.) of the 2021-2022 season.

All vineyards accumulated at least 800 chilling hours during the winter of 2021, and during that growing season, they reached a total accumulation of no less than 1,600 heat hours. Additionally, despite the differences in frost frequency between all the vineyards, chilling hours and heat accumulation were similar among all (Table 1). Thus, the fluctuating and elevated winter temperatures did not appear to compromise the accumulation of chilling hours. Consequently, based on the accumulated chill and heat accumulation, an adequate budburst would theoretically be expected, as neither factor seems to be limiting.

Differences in growth and development between asymptomatic (As; Figure 1A–1D) and symptomatic (Sy; Figure 1D–1F) plants were revealed through a characterisation of cane growth, with Sy plants generally exhibiting reduced cane growth (Figure 2). The absolute control exhibited a growth pattern similar to that of As plants, although internodes were slightly longer. This difference may be associated with

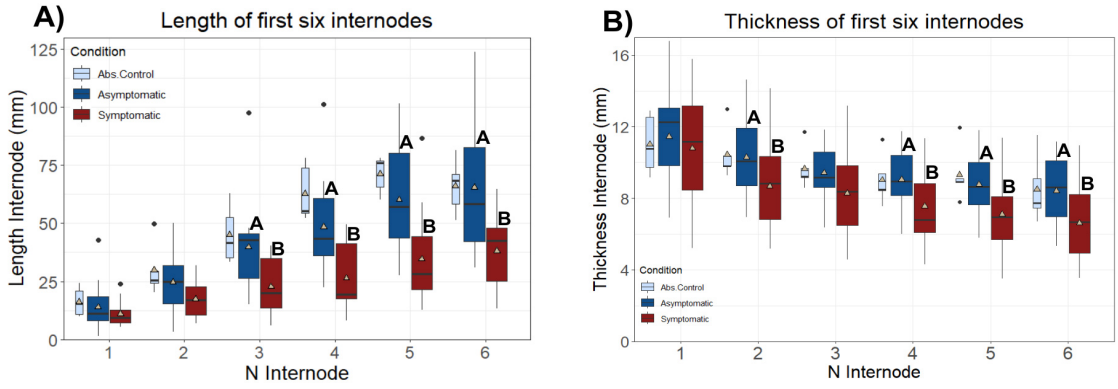


FIGURE 2. Cane growth characterised by condition.

*A) Length of the first six internodes. B) Thickness of the first six internodes. Absolute control (grey), Asymptomatic (blue), and Symptomatic (red), the inner triangle of each box is its average by condition. The box represents the interquartile range; the horizontal line indicates the median; the whiskers extend to 1.5 × IQR; and black dots represent outliers. Statistical analysis does not consider absolute control; statistically significant differences for each node position are indicated by letters A and B (α: 0.05).

the invigorating effects of the Freedom rootstock. As plants consistently developed longer basal internodes, Sy plants had significantly shorter internodes from the third basal node onward, 42.0–49.2 % shorter than those of As plants (Figure 2A). Vineyards generally do not show significant differences in internode length; however, the Los Andes site tends to exhibit the shortest internodes overall (Figure S4).

Internode thickness, for its part, exhibited substantial variability across the evaluated plants; however, from the fourth basal node onward, As plants produced thicker canes, with internodes at least 12.5–21.4 % thicker than those of Sy plants (Figure 2B). Internode thickness tended to vary among vineyards; in this regard, the Los Andes site exhibited the greatest internodal thickness, whereas Lampa consistently showed the thinnest internodes. Furthermore, upon evaluation of this parameter, asymptomatic vines displayed a markedly irregular pattern, the expression of which appeared to be strongly influenced by fieldspecific conditions (Figure S4). In Figure S5, a representative image of a standard RSG shoot is provided, along with representative shoot images corresponding to each vineyard and condition.

Leaf nutritional analysis conducted in late summer, near harvest, revealed no dietary imbalances associated with the syndrome, and no statistically significant differences were observed for any measured variables (Table 2). In contrast, analysis of root reserves during winter dormancy showed that symptomatic (Sy) plants accumulated lower levels of arginine and starch under the conditions of this study. The absolute control exhibited significantly higher arginine levels compared to the asymptomatic (As) plants. No statistically significant differences were found in dry matter accumulation (Table 3).

TABLE 2. Foliar nutritional analysis by condition. Foliar analysis of total nitrogen (%) and total phosphorus (%), ammonium (mg/kg), and nitrate (mg/kg).

	Nitrogen (%)	Phosphorus (%)	Ammonium (mg/kg)	Nitrate (mg/kg)
Absolute control	2.4 ± 0.06	0.21 ± 0.006	91 ± 4.7	630 ± 11.7
Asymptomatic plants	2.4 ± 0.05	0.25 ± 0.055	194 ± 32.8	488 ± 10.6
Symptomatic plants	2.5 ± 0.14	0.21 ± 0.145	189 ± 31.8	502 ± 15.5
p-value	0.3886	0.3222	0.7701	0.4668
D.f.	14	14	14	14

*Values are average ± standard error. Statistical analysis does not consider absolute control. REML significances are indicated; in case of statistically significant differences (*p*-value ≤ 0.05), the *p*-value is highlighted with a *, and a Student's t-test is performed. Degrees of freedom (D.f) are given. The differences provided by the student are presented by different letters.

TABLE 3. Nutritional analysis of root reserves by condition. Root analysis of arginine (mg/g), starch (%), and dry matter (%).

	Arginine (mg/g)	Starch (%)	Dry matter (%)
Absolute control	27.3 ± 1.96	42.2 ± 1.03	40.5 ± 1.72
Asymptomatic plants	20.6 ± 3.35 A	43.3 ± 2.98 A	40.4 ± 0.63
Symptomatic plants	16.9 ± 2.50 B	40.5 ± 3.62 B	41.8 ± 0.54
p-value	0.0468*	0.0309*	0.1199
D.f.	13	13	13

*Values are average ± standard error. Statistical analysis does not consider absolute control. REML significances are indicated; in case of statistically significant differences (*p*-value ≤ 0.05), the *p*-value is highlighted with a *, and a Student's *t*-test is performed. Degrees of freedom (D.f) are given. The differences provided by the student are presented by different letters.

The anatomical characterisation of absolute control, asymptomatic (As), and symptomatic (Sy) plants included descriptions of vascular structures in histological sections and statistical analyses of the cross-sectional area of vessels (CSAV), mean vessel perimeter (PVE), and radial phloem length (RLP). The absolute control showed the highest values for all variables, with CSAV nearly twice that of As plants. Sy plants exhibited significantly lower CSAV and PVE compared to As plants, while no statistically significant differences were found in RLP (Table 4).

Histological sections of the absolute control revealed well-developed conductive tissues. The xylem contained large-diameter vessels evenly distributed across the cross-section, with clearly defined xylem rays. The phloem displayed at least three distinct layers of sieve tube elements and phloem fibres, along with well-structured phloem rays, indicating the absence of cold damage (Figure 3A).

Asymptomatic (As) plants exhibited greater vascular tissue development compared to symptomatic (Sy) plants (Figure 3B–3C). Their xylem contained significantly larger-diameter vessels

TABLE 4. Characteristics of vascular tissues in spurs.

	CSAV (µm²)	PVE (µm)	RLP (µm)
Absolute control	14,117 ± 1,596	408 ± 20.9	552 ± 20.8
Asymptomatic plants	6,990 ± 650 A	275 ± 16.1 A	299 ± 9.85
Symptomatic plants	3,917 ± 476 B	177 ± 9.10 B	274 ± 15.5
p-value	0.0001*	0.0001*	0.1559
D.f.	25	25	25

*As column headers, the cross-sectional area of the vessel (CSAV), the mean perimeter of the vessel elements (PVE), and the radial length of the phloem (RLP). Values are average ± standard error. Statistical analysis does not consider absolute control. RMEL significances are indicated; in case of statistically significant differences (*p*-value ≤ 0.05), the *p*-value is highlighted with a *, and a Student's t-test is performed. Degrees of freedom (D.f) are given. The differences provided by the student are presented by different letters.

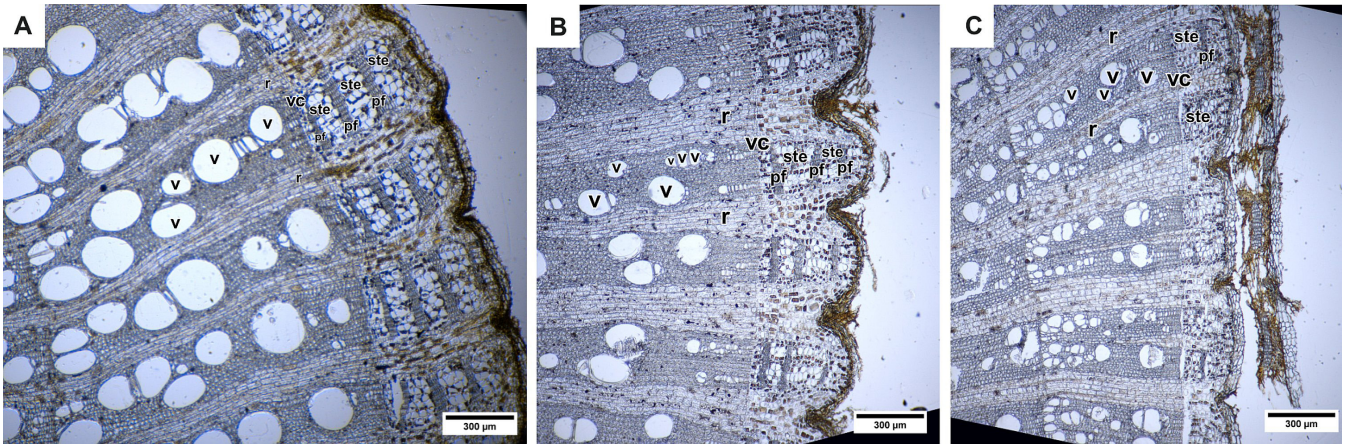


FIGURE 3. Representative histological sections of vascular tissues from control, asymptomatic, and symptomatic spurs.

*A) Absolute control. B) Asymptomatic. C) Symptomatic. Magnification X4, scale bar of 300 µm. The notations are vc: vascular cambium, v: vessels, r: rays, ste: sieve tube elements, and pf: phloem fibres.

distributed throughout the section, with well-defined xylem rays, although some areas showed variations in thickness. The phloem consisted of at least two layers of sieve tube elements. Still, it appeared somewhat underdeveloped and deformed, with interruptions in the sieve tube layers occasionally replaced by phloem fibres or possible callus formation (Figure 3B).

Conversely, Sy plants showed a generalised vascular underdevelopment. More specifically, its vessel elements are low in diameter and display an uneven distribution, while its xylem rays exhibit irregular thickness (Figure 3C). In certain cases, Sy plants present callus formation and disrupted xylem vessels, providing evidence of cold damage to the vascular cambium. Moreover, its phloem is underdeveloped, no distinct layers of sieve tubes were observed, and the phloem rays appeared poorly defined or irregularly shaped. These characteristics are associated with cold damage to vascular cambium, phloem, or both (Figure 3B–3C).

Furthermore, vascular tissue deformations in the xylem and phloem were detected in both asymptomatic (As) and symptomatic (Sy) plants, and were more frequent in Sy plants. More specifically, in the xylem, the most frequently observed features were the callus formation and vessels within the xylem rays, usually accompanied by a distortion of vessel elements distribution (Figure 4B). In the phloem, deformations mainly consisted of underdeveloped tissue with disorganised, poorly formed sieve tube elements or of extensive callus formation throughout the phloem region (Figure 5B). Additional examples of these deformations are provided in Figure S6.

No leaf symptoms associated with Eriophyid mites were observed in any vineyard, nor were mites detected in dissected buds. In contrast, leaf virus testing revealed widespread infections with *grapevine virus A* (GVA), *grapevine rupestris stem pitting-associated virus* (GRSPaV), and *grapevine fanleaf virus* (GFLV) across all vineyards and conditions (Table S2). Fungal isolations identified environmental fungi, including *Cladosporium spp*., *Penicillium spp*., *Alternaria spp*., and *Rhizopus spp*.; no wood-pathogenic fungi were detected. Tests for *Pseudomonas spp*. on leaves were negative in all vineyards and conditions. These findings suggest no clear biotic cause for the observed symptoms, prompting further consideration of climatic and anatomical factors in plant performance.

DISCUSSION

In this study, the climatic conditions of the 2021–2022 season were consistent with what is expected for a Mediterranean climate. However, the occurrence of early autumn frost and warm periods during winter may have affected plant

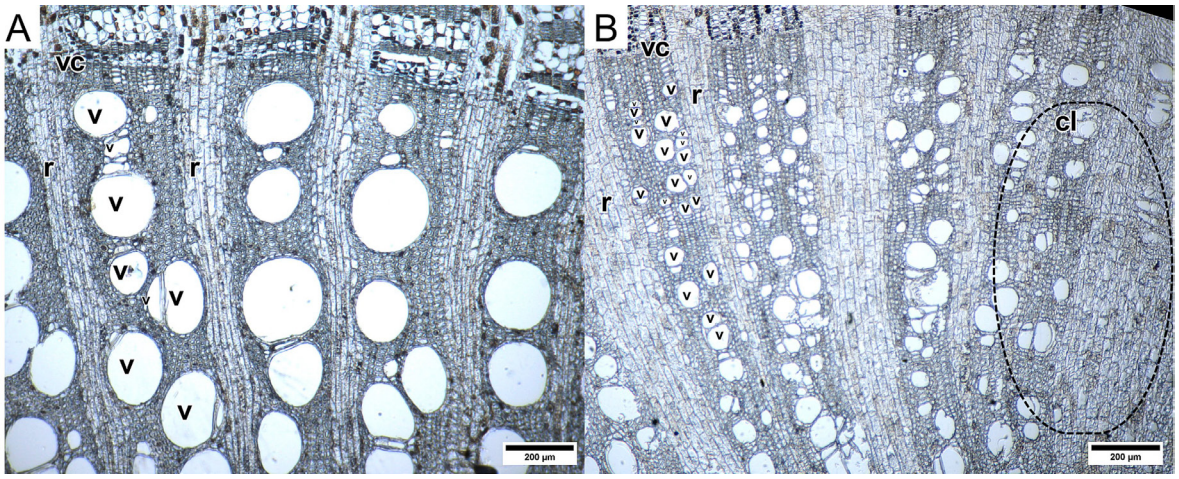


FIGURE 4. Comparison of the principal deformations detected in the xylem.

*A) Normal development of xylem on spurs. B) Deformations on the spur xylem. The deformed area is marked in red. In both cases, a scale of 300 µm is shown. The notations are vc: vascular cambium, v: vessels, cl: callus-derived tissue.

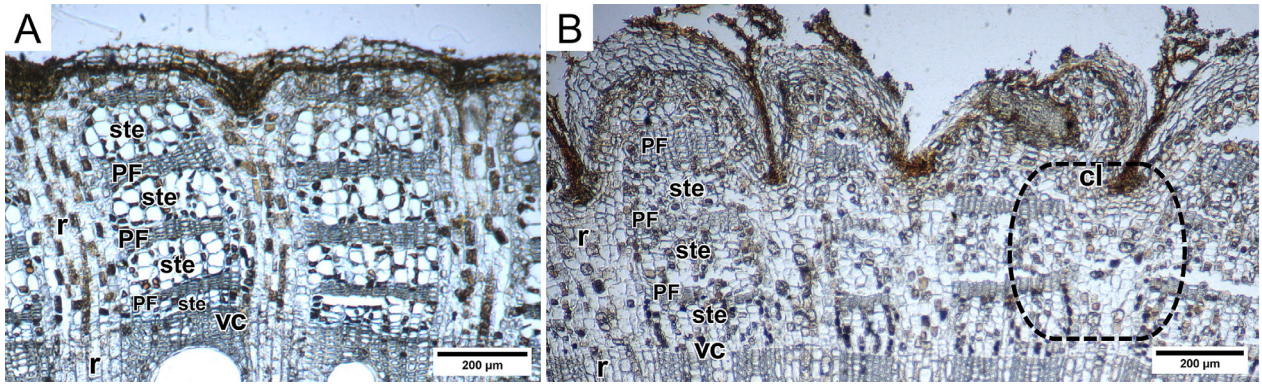


FIGURE 5. Comparison of the deformations detected at the phloem.

*A) Normal development of phloem in spurs. B) Deformations and callus on phloem. The deformed area is marked in red. The notations are ste: sieve tube elements, pf: phloem fibres, vc: vascular cambium, r: rays, and cl: callus-derived tissue.

development (Figures S3 and S4). Despite these climatic fluctuations, chill hour accumulation was not limiting in any of the vineyards (Table 2). Furthermore, heat accumulation values were within the expected range, which is sufficient for normal grapevine development. Nevertheless, these vineyards exhibited clear manifestations of the syndrome.

Leaf nutritional analysis at harvest revealed no significant differences between asymptomatic (As) and symptomatic (Sy) plants for any measured variables (Table 3). Nitrogen and phosphorus levels were within adequate ranges (Coombe & Dry, 1992; Ruiz, 2019), and ammonium concentrations fell within acceptable limits across all vineyards. Although nitrate levels were slightly below the optimal 500–600 mg/kg range (Coombe & Dry, 1992; Ruiz, 2019), they remained within expected values for the assessment period, suggesting nitrate availability was not a limiting factor (Verdenal *et al.,* 2021; Goldspink *et al.,* 2000).

In contrast, winter root reserve analysis showed that the absolute control accumulated more arginine than the other vines. In comparison, Sy plants had lower arginine and starch levels than As plants, which may partly correlate with the syndrome's expression (Table 4). Starch levels were within or slightly above the optimal range across all vineyards (Zapata *et al.,* 2004; Ruiz, 2019). While the vineyard with absolute control maintained optimal arginine levels, the other vineyards exhibited slightly lower accumulations. Although no established standards exist for this variety, the arginine deficiency may be considered mild (Ruiz, 2019), and the plants nevertheless exhibited normal shoot development.

These findings indicate a potential role of reserve dynamics in grapevine physiology and may help to explain the observed syndrome. Reserve accumulation begins after veraison, with the final phase occurring between harvest and leaf fall (Verdenal *et al.,* 2021; Goldspink *et al.,* 2000; Coombe & Dry, 1992). In this study, non-structural carbohydrate (NSC) dynamics were assessed through root starch accumulation. During winter, stored starch supplies energy for basal metabolism (Sperling *et al.,* 2015) and contributes to the elimination of reactive oxygen species (ROS) (Martínez-Lüscher & Kurtural, 2021; Roxas *et al.,* 2021). In addition, adequate starch reserves, combined with proper tissue maturation, enhance structural protection against cold stress (Charrier *et al.,* 2018; Zabadal *et al.,* 2007).

The accumulation of reserves and their relationship to cold hardiness may be linked to seasonal climatic conditions, which likely influence grapevine physiology. The tissue damage

caused by early autumn frost can lead to the accumulation of reactive oxygen species (ROS), molecules that the plant can remove using stored starch and arginine as energy sources. The reserves play a critical role in tissue cold hardiness; moreover, both starch and arginine are heavily consumed to mitigate damage generated by ROS during the winter, which could eventually lead to their depletion (Beil *et al.,* 2021; Chamberlain & Wolkovich, 2021; Tixier *et al.,* 2019). The dynamics of NSC could explain why asymptomatic plants show a stable nutritional balance: throughout the growing season, they maintain nutritionally adequate levels and enter winter with sufficient reserves. In contrast, symptomatic plants exhibit normal nutrient levels during the growing season; however, by the onset of winter, their starch and arginine levels are reduced (Table 4).

Frost damage and reserve depletion by cold stress in the syndrome have been discussed as potential contributors to syndrome expression; their roles remain speculative based on the current evidence. Under this rationale, one would expect the Lampa and Rancagua vineyards, which are the sites most affected by autumn frosts (Figure S3), to exhibit the highest expression of the syndrome. Interestingly, internode length did not differ among vineyards; however, notable differences were observed in internode thickness. Specifically, Lampa tended to produce shoots with internodes of intermediate length but with the narrowest diameters, followed by Rancagua, which displayed a comparable pattern (Figure S4). These findings suggest that increased exposure to frost events may be associated with the formation of shoots characterised by thinner internodes, which could, in turn, contribute to a more pronounced visual expression of the syndrome.

Some authors have proposed that invigorating rootstocks may also trigger RSG expression (Kurtural *et al.,* 2021; Tian, 2023; Hackett & Holzapfel, 2002). However, our data do not support the notion that syndrome expression is solely linked to rootstock vigour, as RSG symptoms were observed in vines grafted onto 1103 Paulsen, Harmony, and Ramsey (Table S1), which are considered medium- to high-vigour rootstocks (Migicovsky *et al.,* 2021). Additionally, despite the presence of several rootstocks across vineyards, internode length did not differ among sites, whereas internode thickness did. From a physiological standpoint, one would expect Lampa and the absolute control in San Vicente, both of which are grafted onto highly vigorous rootstocks, to be the sites most affected by the syndrome. However, this was not the case. In contrast, Rancagua, which uses the leastvigorous rootstock, exhibited substantial variability in internode thickness yet remained broadly comparable to the absolute control (Figure S4). What clearly distinguishes these sites is that Lampa is the coldest vineyard, which again highlights the relevance of low autumn temperatures in the expression of RSG.

One limitation of this study is the lack of continuous monitoring of root starch and arginine levels throughout the entire growing season, which restricts our discussion on the sampling conducted after the harvest period. Specifically, additional sampling during key phenological stages such as budburst, when the pool of NSC is crucial for sustaining the early spring growth. Future research should assess the seasonal dynamics of NSC and arginine reserves in asymptomatic (As) and symptomatic (Sy) plants over a complete growing cycle, to clarify whether the low reserve levels observed in symptomatic plants are a cause or a consequence of symptom development.

The direct impact of the winter accumulation of reserves is reflected in cane growth at the end of the season. Asymptomatic plants (As) exhibit higher internode lengths from the second node onward. Similarly, absolute control plants follow an internode length growth trend comparable to that of As plants (Figure 2A). For internode thickness, a similar pattern was observed, where asymptomatic plants showed better growth, particularly from the fourth node onward; these plants developed thicker internodes (Figure 2B). The seasonal dynamics of non-structural carbohydrates (NSC) likely contributed to differences in vine vigour and growth capacity (Roxas *et al.,* 2021), which may explain the reduced internode length and thickness observed in symptomatic plants, as well as their underdeveloped vegetative and reproductive structures (Figure 1; Figure S1).

The reduced internode elongation observed in Sy plants could be attributed to limitations in carbohydrate availability during the period of active shoot growth, thereby constraining cell expansion and secondary thickening. Tombesi *et al.* (2022) also reported that delayed leaf area development in plants can lead to carbon starvation, ultimately reducing growth. Furthermore, elevated temperatures between budburst and flowering intensify competition among shoot formation, leaf area expansion, and the differentiation of reproductive structures (Pagay & Collins, 2017) (Figure S2). In this context, the underdevelopment of shoots in Sy plants likely increases their exposure to excessive radiation and high temperatures, thereby intensifying stress conditions (Migicovsky *et al.,* 2024). Collectively, the cited works highlight that these factors could explain why symptomatic plants develop shorter and thinner internodes (Figure 2; Figure S5).

On the other hand, histological cuts reflected the differences detected in the shoot development between asymptomatic (As) and symptomatic (Sy) plants. The anatomical analysis provided key information about the syndrome, indicating that the problem lies in their vascular structure. The primary differences between As and Sy plants clearly reside in the distribution and diameter of their main xylem vessels, as well as in the degree of phloem development. In general, Sy plants exhibited an abnormal thickness of their xylem rays. Additionally, affected plants fail to fully develop their phloem, showing fewer than three layers of sieve elements, which according to Esau (1948), this number of layers is characteristic of table grapevines growing in Mediterranean conditions. In contrast, the absolute control fulfils this condition and displays a well-organised distribution of transport tissues, in agreement with the anatomical patterns described by Pouzoulet (2014).

Another important aspect to consider is that the vascular deformations and presence of callus were observed in As and Sy plants; however, they were almost absent in the absolute control vineyard (Figure 3). This could be associated with the low number and intensity of frosts in the absolute control vineyard; therefore, the degrees of vascular deformation could be related to varying levels of frost damage in the affected vineyards (Table 1; Figure S3). These vascular abnormalities are likely associated with early autumn frosts, particularly in vigorous plants that fail to initiate natural senescence and cold hardening. Callus formation is a known response to cold damage in the vascular cambium, along with cellular injury and phloem necrosis caused by frost (Goffinet, 2000; Zabadal *et al.,* 2007; Gonzalez Antivilo *et al.,* 2020). However, the presence of xylem conduits within the xylem rays or abnormally thickened xylem rays, as observed here (Figure 5B), has not been previously reported. Therefore, based on the literature, this could be a consequence of cold injury or might represent a specific symptom of RSG, indicating that further investigation is required.

Examining the expression of RSG alongside the degree of vascular deformation and reserve accumulation provides new insights into their potential interactions. In line with the findings described above, both asymptomatic and symptomatic plants exhibit a certain degree of vascular distortion, which could limit tissue functionality and trigger RSG expression earlier in the spring growing. In some cases, plants with sprouting irregularities can recover as the season progresses (Kurtural *et al.,* 2021; AWRI, 2015; Peacock, 2007; Hackett & Holzapfel, 2002). However, not all plants recover. Our findings suggest that recovery depends on the extent to which vascular tissues regain functionality and may be constrained by both the level of reserve accumulation and the severity of vascular deformation, which together limit the plant's capacity to overcome the syndrome fully. Elucidating this hypothesis in future studies will be crucial for developing effective strategies aimed at mitigating and potentially resolving the syndrome.

The expression of RSG during the first two or three years of the vineyard establishment could be related to the anatomical characteristics and reserve accumulation observed in symptomatic (Sy) plants. These variables may be influenced to some extent by the frequency and timing of frost events, especially during periods of tissue formation and reserves remobilisation, though this remains a tentative interpretation that requires further investigation. A possible explanation is that plants grown under intensive production systems are saturated with fertilisers and water to enhance their vegetative growth and accelerate canopy and wood development. As a result, these plants maintain active shoot apices until the end of the season, resulting in incomplete dormancy. Furthermore, this prolonged activity could hinder the remobilisation of nutrients, leading to insufficient starch and arginine accumulation (Verdenal *et al.,* 2021; Winter *et al.,* 2015; Zapata *et al.,* 2004). Consequently, these plants may enter spring with reduced reserves for sprouting. In addition, their canes may exhibit lower cold hardiness, making them more vulnerable to autumn frost damage (Zabadal *et al.,* 2007; Hackett & Holzapfel, 2002), and helping to explain the extensive vascular deformities observed in this study (Figures 4 and 5).

Frost damage to the cambium in young vines can compromise the development of conductive tissues, leading to the formation of callus that obstructs vascular continuity. This structural disruption impairs the transport of nutrients, minerals, and growth regulators, potentially resulting in long-term consequences for vine health and vineyard longevity (Gonzalez Antivilo *et al.,* 2020; Zabadal *et al.,* 2007). According to Esau (1948), early-season growth relies on the spring cambium reactivation, a process that is modulated by hormonal signalling. Because the vascular cambium serves as a key pathway for auxin transport from developing tissues, its damage can hinder growth reactivation and the formation of functional conductive tissues (Beck, 2010). Auxins play a central role in the development and differentiation of these tissues (Pérez-de-Lis *et al.,* 2016; Sorce *et al.,* 2013). Furthermore, a reduction in reserve balance may compromise spring budburst by limiting non-structural carbohydrate (NSC) availability or impairing xylem refilling, which in turn restricts the formation of new shoots and other structures. Consequently, symptomatic plants exhibit reduced internode growth (Figure 2).

In addition to frost damage, environmental stressors–such as unstable spring and autumn temperatures and extreme summer heat–can disrupt dormancy transitions, ultimately affecting budburst timing and uniformity (De Rosa *et al.,* 2021; Fidelibus, 2021). According to Pérez-de-Liz *et al.* (2016), seasonal temperature variations in spring can influence vascular differentiation processes. These stresses may also reduce photosynthetic capacity and promote the accumulation of reactive oxygen species (ROS), further impairing tissue development, NSC storage, and overall plant resilience, while increasing susceptibility to pathogens (Malyshev, 2020; Yu *et al.,* 2010).

In line with previous studies (AWRI, 2015; Peacock, 2007) and our analysis of biotic agents, there is no evidence to support a pathogenic origin for the syndrome. Affected plants showed no leaf symptoms associated with Eriophyid mites, nor were these mites detected in bud dissections from any vineyard. All vineyards and conditions studied tested positive for the presence of *grapevine virus A* (GVA), *grapevine rupestris stem pitting-associated virus* (GRSPaV), and *grapevine fanleaf virus* (GFLV), which suggests that these viruses probably originated in nurseries where vines were propagated, a scenario previously suggested by Hackett and Holzapfel (2002). Moreover, the possibility that RSG expression resulted from *Pseudomonas* infection was dismissed, given that all tests were negative across vineyards and conditions. On the other hand, fungi isolations detected only environmental fungi, which were not associated with pathogenic species.

Finally, the findings contribute to identifying the key factors responsible for RSG expression and recovery, which is

particularly complex since management strategies intended to restore plant vigour may promote late-season growth, consequently increasing their susceptibility to chilling injury. Hackett and Holzapfel (2002) proposed a cycle that explains the syndrome stages and the different factors that influence its expression; nevertheless, they do not consider the extent of cold-induced vascular damage, which, depending on its severity, may be irreversible. An extreme manifestation of the syndrome is shown in Figure S7. From our perspective, future investigations of this syndrome should encompass tissue histology, reserve dynamics, and dormancy acquisition, since such integration will be essential to elucidate its underlying mechanisms and to establish effective management practices for its control.

CONCLUSION

Restricted spring growth (RSG) is a complex syndrome that impairs the development of both vegetative and reproductive structures. Affected plants exhibit reduced internode length and thickness by the end of the season, often accompanied by significant yield losses and diminished reserve accumulation. Our findings suggest that the restriction of shoot growth may be linked to significant deformation of vascular tissues, which could impair the translocation of hormones and nutrients, thereby potentially explaining why shoots fail to grow. Moreover, according to the literature, such deformations are consistent with damage associated with frost events. Under the conditions of our study, this type of injury could be related to the earlyautumn frosts reported to affect immature shoots or tissues with low cold hardiness. Nevertheless, further research is required to clarify the extent to which frost injury contributed to the observed anatomical alterations.

The degree of vascular tissue deformation may help explain why the syndrome becomes evident in spring. A damaged cambium in the canes would be unable to supply the resources required by emerging shoots, and depending on the extent of this injury, some shoots may still be able to recover and resume growth. Under our study conditions, the pathological analyses performed appear to rule out a biotic origin for this syndrome. Although biotic factors can reduce vine vigour, our data suggest that, in this case, the syndrome is more likely to be associated with environmental factors. We consider histological analysis of vascular tissues a fundamental approach for the identification and characterisation of RSG syndrome. Particularly in the context of climate change, future research should focus on dormancy acquisition, non-structural carbohydrate dynamics, and the impact of environmental conditions on dormancy transitions throughout autumn and winter. Investigating seasonal fluctuations in non-structural carbohydrates in young vines could provide critical insights into the expression of the syndrome and support the development of vineyard management strategies to mitigate its effects.

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AUTHORS' NOTES

During the preparation of this manuscript, the authors used ChatGPT-5 and Grammarly exclusively to improve the English translation of our ideas and enhance the text's cohesion and coherence, ensuring fluent readability and clear comprehension. The use of these tools adhered to ethical standards and best practices for responsible AI-assisted writing. All sections of the manuscript were carefully reviewed and edited by the authors to ensure accuracy and clarity.

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