

Prolonged phloem feeding by the spotted lanternfly, an invasive planthopper, alters resource allocation and inhibits gas exchange in grapevines

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Abstract

Spotted lanternfly (*Lycorma delicatula* White; SLF) is a phloem-feeding planthopper invasive to the Eastern United States that can feed on a range of wild and cultivated plant species. Since its 2014 introduction in the United States, large infestations and subsequent economic damage have been reported in cultivated grapevines, but no studies have detailed grapevine physiological responses to SLF phloem feeding. This study investigated grapevine-SLF interactions, detailing how different infestation densities affect leaf gas exchange and end-season concentrations of nonstructural carbohydrates and nitrogen in vegetative and perennial tissues of two *Vitis* species. Effects on fruit ripeness parameters and dormant bud freeze tolerance were examined, in addition to other year-after effects. Phloem feeding by low densities (≤ 4 SLF shoot⁻¹) had minimal effects, whereas greater densities (5–15 SLF shoot⁻¹) increasingly affected carbohydrate and nitrogen dynamics in both *Vitis* species. Phloem feeding substantially affected starch and, to a lesser extent, total nitrogen concentrations of woody roots. Prolonged exposure strongly reduced leaf gas exchange. We conclude that intensive late-season phloem feeding by large adult SLF population densities (≥ 8 SLF shoot⁻¹) can induce carbon limitation, with the potential for negative year-after effects in cases of severe belowground carbon depletion. This work presents novel insights into SLF-grapevine interactions, identifies avenues of future SLF-plant research, and assists the development of action thresholds for SLF management in vineyards.

KEYWORDS

gas exchange, invasive insect, *Lycorma delicatula*, nonstructural carbohydrates, plant-insect interactions, source-sink relationships, spotted lanternfly, *Vitis*

1 | INTRODUCTION

Insect pests are a growing challenge to agricultural systems globally as the number of invasive species increases (Paini et al., 2016;

Pyšek et al., 2020; Robinet & Roques, 2010). Indeed, insects are estimated to be among the most damaging of introduced organisms (Diagne et al., 2021), causing substantial reductions in crop yield worldwide (Paini et al., 2016) and potentially impacting pollinator

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services and biodiversity (Kenis et al., 2009; Morales et al., 2017). The spotted lanternfly (*Lycorma delicatula* White; SLF), a phloem-feeding planthopper native to China, Japan, and Vietnam, is one such example that threatens agricultural and silvicultural industries in the United States (Urban, 2020). First discovered in Southeast Pennsylvania (USA) in 2014, SLF populations have now been found in 11 states in the Eastern United States (New York State Integrated Pest Management, 2022). The threat of continued range expansion is underscored by SLF's generalist feeding habit, because it can feed on over 56 North American plant species, including economically important non-native and native perennial woody tree and fruit crop species (Barringer & Ciafré, 2020). Previously, SLF establishment was confirmed in South Korea in 2004, with reports documenting it as an invasive pest of various cultivated and landscape plants, including grapevines (Han et al., 2008; Lee et al., 2019).

To date, damage to agricultural crops in the Eastern United States has been mostly limited to vineyard systems with grape growers reporting heavy, repeated phloem feeding from adult SLF, which strongly reduced yield (up to 90%), fruit quality, and, in some instances, caused vine decline over multiple years (Urban, 2020). Generally, adult populations of SLF are more problematic than nymphs in vineyards because of high population sizes on a single plant (i.e., over 100 insect vine⁻¹; Leach & Leach, 2020) and the likelihood of reinfestation following chemical control. Therefore, total sap removal and nutrient exploitation by adult SLF in a single season can likely be substantial.

Phloem-feeding insects require significant volumes of sap to fulfill dietary carbon (C) and nitrogen (N) requirements, which can affect source-sink relationships and water dynamics of their plant hosts (Douglas, 2006). Broadly, sap-feeding insects can reduce plant C assimilation (Zvereva et al., 2010) by decreasing expression of genes involved in photosynthesis (Thompson & Goggin, 2006; Zhou et al., 2015), reducing stomatal conductance and stimulating stomata closure (Lin et al., 2021), interfering with source-sink plant dynamics, and physically damaging plant vasculature (Nabity et al., 2009). Effects of sap feeding on C allocation and metabolism can occur in tissues surrounding the feeding site (Nabity et al., 2013; Savi et al., 2019) but also in other tissues throughout the plant (Griesser et al., 2015; Kaakeh et al., 1993; Savi et al., 2021). In addition to competing directly with plant sinks for N (Girousse et al., 2005), sap-feeding insects can alter the expression of genes involved in N assimilation and translocation (Divol et al., 2005; Wilson et al., 2011). Given anecdotal observations of grapevine decline following prolonged heavy SLF phloem feeding, and the implications that disruptions in source-sink relationships have for fruit ripening and plant health, understanding the potential effects of SLF on these processes is critical. This is especially troubling as SLF is highly likely to establish in new regions, particularly those that are known for grape production (Huron et al., 2022).

Despite advances in understanding SLF distribution (Murman et al., 2020), life history (Liu, 2019), feeding habits and dietary requirements (Avanesyan & Lamp, 2020; Cooper et al., 2021; Nixon et al., 2021), and management options (Francese et al., 2020; Leach

et al., 2019), little is known about plant-SLF interactions and physiological responses to SLF feeding. In the Eastern United States, adult SLF move into vineyards late in the growing season during fruit ripening and throughout harvest (i.e., August through October). Intensive phloem feeding during this time may affect the total and relative allocation of resources to competing sinks like fruit and storage organs. The root system of perennial fruit crops comprises the bulk of the total nonstructural carbohydrates (TNC; starch and soluble sugars) and N reserves that support early season growth (Bates et al., 2002; Zapata et al., 2004a, 2004b). Significant reductions in end-of-season TNC reserves due to source-sink alterations can reduce fruitfulness the following season (Smith & Holzapfel, 2009). Soluble sugar reserves are additionally associated with plant freeze tolerance and are critical for winter survival of cold-sensitive fruit crops like grapevines (Grant & Dami, 2015). An important first step is to examine if SLF phloem feeding can alter source-sink relationships in a manner that negatively affects plant growth and health, as observed by some affected growers. This information would assist development of targeted management and mitigation strategies that can facilitate quality fruit production and sustained plant viability.

To overcome current gaps in knowledge, we explored the potential of SLF to act as a competitive resource sink in grapevine at different population densities. Our first objective was to investigate whether SLF can disrupt the allocation of TNC and total N to both above- and belowground tissues in two *Vitis* species with differing parentage, and whether above- or belowground tissues are prioritized for resource allocation in response to resource limitation. Second, we evaluated if SLF can induce source limitation by reducing overall C assimilation. Lastly, we examined whether SLF-driven resource limitation has negative implications for plant viability through analysis of bud freeze tolerance, vegetative growth, and mineral nutrient status in the dormant and growing seasons following SLF infestation.

We hypothesize that a perennial fruit crop can tolerate low populations of SLF but increasing SLF population densities will successfully compete with plant sinks for resources and significantly reduce overall N and TNC concentrations by the end of the season, with shifts in the ratio of starch to soluble sugars driving this reduction. Similarly, we expect increasing SLF densities to limit gas exchange, reduce C assimilation, and affect translocation to sink tissues. We predict that effects on TNC and N concentrations will be stronger in below- rather than aboveground tissues, as SLF, stems, and fruit outcompete roots for resource allocation (Candolfi-Vasconcelos et al., 1994; Morinaga et al., 2003; Zufferey et al., 2015). Finally, we hypothesize that a SLF-driven reduction in resources allocated to the root system will affect shoot growth and aboveground nutrient status in the following year, whereas any shifts in aboveground soluble sugars reserves may affect bud freeze tolerance during plant dormancy. Through these objectives, this study seeks to provide an understanding of plant-SLF interactions in a commercially important woody fruit crop and contribute to knowledge of herbivory-driven shifts in source-sink relationships.



2 | MATERIALS AND METHODS

The study consisted of two experiments conducted on two *Vitis* sp. The first experiment, hereafter referred to as “Experiment 1,” was conducted on field-grown *Vitis vinifera* L. grapevines in 2019 and 2020, whereas the second experiment, hereafter referred to as “Experiment 2,” was carried out on potted *Vitis* sp. interspecific hybrid vines in 2020. Experiment 2 was conducted to confirm and relate findings from a cultivar of *V. vinifera*, the most widely cultivated wine grape species worldwide, to another *Vitis* species; furthermore, the use of potted vines allowed for destructive biomass measurements. Insecticides were never applied throughout the duration of the experiments, and standard disease control practices for commercial grape production were used. Adult SLF were used for both experiments because the adult stage is typically the most present in vineyards and the stage of most concern to farmers (Leach & Leach, 2020).

2.1 | Experiment 1

2.1.1 | Study site and experimental design

The experiment was conducted at a Riesling vineyard in Coopersburg, Pennsylvania, USA (40.492644° N, 75.456533° W) during the 2019 and 2020 growing and dormant seasons. Vines were planted in the spring of 2016. In 2019, the experimental design was a randomized complete block design (RCBD) with four blocks and four SLF density treatments. Sixteen Riesling grapevines (*V. vinifera* L.) grafted on 101-14 Mgt rootstock were selected across two adjacent vineyard rows. Within each block, four vines were randomly assigned to one of the four SLF density treatments: control (0 SLF shoot⁻¹), low (4 SLF shoot⁻¹), medium (8 SLF shoot⁻¹), and high (12 SLF shoot⁻¹) density. The number of shoots of the experimental vines varied from 8 to 17, and the number of SLF per vine was between 0 and 204. These numbers were chosen based on reported levels of SLF feeding on grapevines (Leach & Leach, 2020). To avoid SLF escape and ensure treatment integrity, cages were constructed around each individual vine using a PVC pipe and wood frame and insect netting with a zipper access (AgFabric, Wellco Industries Inc., Corona, CA, USA; Figure S1). Insects were introduced in cyclical stages to mimic the nature of SLF adult infestation in vineyards where frequent insecticide applications only temporarily reduce resident SLF populations (Urban, 2020). Any insects that died following introduction were counted and replaced during each feeding cycle to maintain population densities. All SLF were manually collected from wild hosts in nearby untreated woodlands and transported using large mesh cages. At the end of each cycle, all SLF were manually removed, and the vines were not exposed to any further SLF until the beginning of the following cycle. In 2019, six SLF cycles of 4–5 days each were implemented between August 24 and October 18 (Figure S2).

In 2020, a new group of 16 Riesling grapevines from the same vineyard were used. New vines were selected to avoid cumulative effects of SLF phloem feeding over the years. In 2020, the experiment

layout was modified to a completely randomized design (CRD) with 16 population densities ranging from 0 to 15 SLF shoot⁻¹, using an increment of 1 SLF shoot⁻¹. The number of shoots of the experimental vines varied from 11 to 20 and the number of SLF per vine was between 0 and 195. The new design was selected to confirm results from 2019 and improve efforts to identify a density threshold at which SLF effects are observed. Vines were infested with adult SLF between August 19 and September 30, with three feeding cycles (Figure S2). Due to travel and labor restrictions in response to the global COVID-19 pandemic in 2020, adjustments to the feeding cycle length compared with 2019 were necessary. However, the total number of days that SLF was in the cages was similar between the two years (e.g., 26 days in 2019 and 28 days in 2020).

2.1.2 | Quantification of nonstructural carbohydrates in vegetative tissues

Woody tissue was sampled at the end of the growing season for quantification of TNC, the sum of starch and soluble sugars. On November 11, 2019, and November 17, 2020, two 1-year-old stems (i.e., canes) were collected from each vine, and three 8-cm-long stem sections were sampled from the bottom, middle, and top sections of each cane. All stem sections sampled from the same vine were combined for analysis. On the same day, lignified roots with a diameter between 1 and 4 mm were sampled from shallow soil (0–30 cm) within a 0.5 m² area around each vine trunk. Cane and root samples were placed on dry ice, transferred to the laboratory, and soaked in liquid N, and cane samples were stored at –80°C until processing. Prior to storage, root samples were rinsed with deionized water (DI-H₂O) to remove large soil particles and vortexed in 50 ml centrifuge tubes with DI-H₂O to remove smaller soil particles. Absorptive roots (<1 mm) were removed, and samples were stored at –80°C. Both cane and root samples were lyophilized for 1 week at –50°C and under 0.100 mbar pressure (FreeZone 12-liter Freeze Dryer, Labconco, Kansas City, MO, USA). To separate SLF feeding effects on phloem and xylem tissue, the bark and phloem of each cane piece were manually removed using a disposable scalpel, and all cane samples were separated into wood (including xylem tissue) and bark (including phloem tissue). Wood, bark, and root samples were milled to a fine powder (<1 mm mesh; UDY Cyclone Mill, UDY Corporation, Fort Collins, CO, USA) and stored until TNC analysis. Soluble sugar and starch concentrations were quantified in each tissue using an enzymatic assay according to Persico et al. (2021), and concentrations were expressed in glucose equivalents.

2.1.3 | Quantification of N concentrations in vegetative tissues

Total N concentration was measured on woody tissues sampled at the end of the growing season for TNC analysis and on green foliar tissue sampled at fruit harvest on September 27, 2019, and September

30, 2020. Leaf samples were collected 13 and 18 days before the beginning of the experiment in both years to ensure that leaf total N was not significantly different between vines before SLF infestation treatments took place. In both years, a composite sample of 10 leaves per vine were collected and transported to the laboratory before being washed using DI-H₂O and oven-dried for 5 days at 60°C. Leaf samples were milled according to the instructions above, and all samples were submitted to The Pennsylvania State University Agricultural Analytical Services Laboratory for N concentration analysis via combustion (Horneck & Miller, 1998).

2.1.4 | Assessment of fruit ripeness parameters

In both years, all fruit were harvested from experimental vines and used for analysis of fruit total soluble solids (TSS), pH, and titratable acidity (TA), all of which are indicators of grape ripeness (Wolf, 2008). Yeast assimilable nitrogen (YAN) was also measured as it represents the pool of fruit N that can be utilized by yeast for alcoholic fermentation (Waterhouse et al., 2016). Clusters were harvested on September 27 in 2019 and September 30 in 2020, counted, and weighed, and a subsample of five clusters per vine were placed on dry ice and transported to the laboratory for storage at -80°C until analysis. One hundred berries per vine were randomly selected for juice chemistry analysis. The berries were weighed, placed in a plastic quart-sized bag, and thawed in a water bath at 60°C until they reached room temperature. Berries were manually macerated, the juice was filtered using cheesecloth, and TSS was determined using a handheld refractometer (Master, Atago USA, Inc., Bellevue, WA). Juice pH was determined using a benchtop pH meter (Orion Star A111, Thermo Fisher Scientific, Inc., Waltham, MA, USA), and TA was determined using an autotitrator (G20, Mettler Toledo, Columbus, OH, USA). A 1 ml subsample of juice was used to assess YAN using commercial enzyme assay kits (Vintessential Laboratories, Victoria, AU).

2.1.5 | Single-leaf gas exchange measurements

Single-leaf gas exchange measurements were performed five times in 2019 and four times in 2020 on three leaves for each experimental vine (i.e., 48 leaves total per sampling timepoint). A baseline measurement was performed a week before the beginning of the experiment to assess pre-experiment biological variation among vines (no significant differences were detected, and data are not shown). Measurements were only conducted for four of the six infestation cycles in 2019 and for all three infestation cycles in 2020; it was not possible to conduct measurements following cycles five and six in 2019 due to unsuitable, poor weather conditions. The leaves were selected to represent the youngest, fully expanded leaf on a shoot. This was performed to ensure leaf uniformity across vines and to target leaves that are the most photosynthetically active within the canopy late in the season. The selected leaves were tagged at the beginning of the experiment, and gas exchange was assessed on the

same leaves throughout the study on the final day of each SLF cycle between the hours of 10:00 and 14:00. Gas exchange was measured using a CIRAS-III portable gas exchange analyzer (PP Systems, Amesbury, MA, USA) equipped with PLC3 universal leaf cuvette with an 18 × 25 mm cuvette window. The CO₂ reference was set to 400 μmol mol⁻¹, the H₂O reference at 11 mb, and the leaf temperature controlled to 25°C. Ambient light conditions (PPFD > 1200 m⁻² s⁻¹) were used for all measurements.

2.1.6 | Assessment of foliar soluble sugar concentrations via gas chromatography–mass spectrometry (GC–MS)

In 2019, all 48 leaves used for gas exchange measurement were collected on September 29 to assess SLF effects on C dynamics in source tissue. Leaves were collected prior to sunrise, between the hours of 04:00 and 06:00, to prevent any variation due to C remobilization or fixation (Goldschmidt & Huber, 1992; Halldorson & Keller, 2018). All three leaves per experimental vine were sampled together, immediately frozen in dry ice, and transported to the laboratory for storage at -80°C. Leaf samples were lyophilized, milled (<1 mm; UDY Cyclone Mill, UDY Corporation, Fort Collins, CO, USA), and soluble sugars were extracted and derivatized using a method adapted from Fiehn (2016). For each sample, 25 mg of tissue were extracted using 1 ml of labeled extraction solvent (3:3:2 isopropyl alcohol: acetonitrile: H₂O, labeled with d⁷-glucose; Thermo Fisher Scientific, Inc., Waltham, MA, USA). Samples were homogenized at 6500 rpm for 20 sec twice, with a 30 sec resting period on ice in between. Samples were placed on ice for 2 min and then centrifuged at 12,000 rpm at 4°C for 2 min. Two 450 μl aliquots of the supernatant were pipetted into separate GC–MS glass vials and evaporated using a speed vacuum evaporator. Upon drying, 10 μl of methoxamine were added, and vials were incubated at 28°C for 90 min. Following incubation, 90 μl of N-methyl-N-trimethylsilyl-trifluoroacetamide (MSTFA) + 1% TMCS (Thermo Fisher Scientific, Inc., Waltham, MA, USA) was added to each vial, and samples were incubated for 60 min at 60°C. Samples were run on a 7890 series GC coupled to a 5975 series MS (Agilent Technologies, Santa Clara, CA, USA) operated in electron ionization mode. The GC was outfitted with a 30 m Rxi-5MS capillary column (Restek Corporation, Bellefonte, PA, USA), and helium gas was used as the carrier gas. Chromatograms were analyzed using MS-DIAL v. 4.6 (RIKEN Center for Sustainable Resource Science, Yokohama City, Kanagawa, Japan), and concentrations of the major soluble sugars identified in grapevines (glucose, sucrose, fructose, and raffinose) were expressed in internal standard equivalents.

2.1.7 | Assessment of year-after effects during the dormant and growing season following SLF feeding

Bud freeze tolerance was measured twice per year to assess SLF feeding effects on the ability of grapevine bud tissue to survive low winter



temperatures. Differential thermal analysis (DTA) was used to estimate the temperature at which 50% bud death occurred, or the median low temperature exotherm (LT_{50}) (Mills et al., 2006). In both years, the first measurement occurred during vine acclimation (November 11, 2019, and November 18, 2020), and the second measurement occurred during the period of maximum hardiness (January 22, 2020, and February 5, 2021). Briefly, two canes were randomly selected from every vine at each sampling date. In the laboratory, the basal four buds of each cane were excised and used for DTA on the same day, following the protocol outlined by Smith and Centinari (2019).

Year-after effects on vine nutrient status were assessed in 2020 via analysis of leaf petiole samples at bloom (Wolf, 2008). Thirty fully expanded, basal leaves were collected per vine on June 9, 2020, and petioles were separated from leaf blades, washed, and dried at 60°C for 48 h. Petioles were submitted to The Pennsylvania State University Agricultural Analytical Services Laboratory for quantification of N by combustion (Horneck & Miller, 1998) and other macronutrient (P, K, Mg, and Ca) and micronutrient (Mn, Fe, Cu, B, and Zn) concentrations via acid digestion (Huang & Schulte, 1985). Additionally, two shoots per vine were selected in June of 2020 and used for determination of shoot growth rate. The length of each shoot was measured using a tape measure weekly from June 9 until July 7. The rate of shoot growth was calculated as the increment of growth (cm) day^{-1} . Widespread and substantial bud mortality unrelated to SLF treatments and most likely due to low winter temperatures was observed in spring of 2021 throughout the vineyard block, in both experimental and nonexperimental vines. Consequentially, vine nutrient status and shoot growth rate could not be assessed in 2021.

2.2 | Experiment 2

2.2.1 | Study site and experimental design

Experiment 2 was carried out in 2020 on 12 6-year-old Marquette (*Vitis* sp.) grapevines that were grown in 38 L pots with custom substrate (1:1:1 field topsoil, perlite, and peat moss) adjusted to a pH of 7.1. The vines were located outdoors at the Pennsylvania State University Berks Campus (Reading, Pennsylvania, USA; 40.364702° N, 75.976374° W) and arranged in two parallel rows. The experimental design was a CRD with half of the vines ($n = 6$) randomly assigned to a control treatment and the other half ($n = 6$) to an adult SLF treatment of 80 SLF vine^{-1} . This SLF density was considered high as these vines had four to six shoots each (i.e., 13–20 SLF shoot^{-1}). Each vine was individually and fully enclosed within an insect barrier netting bag with zippers (1.3 m \times 1.4 m, AgFabric, WellCo Industries, Inc., Corona, CA, USA; Figure S1). Adult SLF was released inside the enclosed vines assigned to the SLF treatment on August 19 and left on the vines until September 30. Vines were monitored three times per week, and dead insects were counted and replaced.

2.2.2 | Quantification of TNC and N in vegetative tissues

To assess if the effects of SLF feeding on plant resources storage observed in Experiment 1 would extend to another *Vitis* sp., lignified roots were selected for TNC and N analysis in Experiment 2. Root collection occurred on November 14, and a composite sample was collected from each experimental vine, prepared, stored, and analyzed using the same protocol as in Experiment 1. In addition, N concentration was also measured in aboveground vegetative tissue developed during the 2020 season (leaf blade, leaf petiole, and shoots). On September 30, 2020, the canopies of all vines were destructively harvested, and the shoots, leaves, and petioles of each vine were collected separately. All tissues were oven-dried, weighed, and analyzed using the same protocol as in Experiment 1. The N content of leaves, shoot, and petiole tissues per vine was calculated by multiplying N concentrations by the total dry mass of each tissue.

2.2.3 | Assessment of fruit ripeness parameters

Fruit was harvested from each vine on September 30, 2020, used for analysis of juice TSS, pH, TA, and YAN. Clusters were harvested, counted, and weighed before being placed on ice and transported to the laboratory for storage at -80°C until analysis. Analysis of all juice parameters were performed using the same protocol used for Experiment 1.

2.3 | Statistical analyses

All statistical analyses were performed using SAS v. 9.4 for Windows (SAS Institute, Cary, NC, USA). All 2019 data from Experiment 1, except the gas exchange and shoot growth rate data and data from Experiment 2, were subjected to analysis of variance (ANOVA) via the MIXED procedure. Significant treatment differences in Experiment 1 were assessed using Tukey's honest significant difference (HSD). Gas exchange data from 2019 and shoot growth rate data from 2020 were subjected to a repeated measures analysis using the GLIMMIX procedure. Models were fit with various covariance matrixes, and final model selection was performed following assessment of model fit statistics. Presented p -values for these data reflected the statistical significance of the selected model. For Experiment 1 data collected in 2020, PROC REG was used to plot and assess linear, quadratic, and cubic regressions. Model selection was based on evaluation of various model criteria, including p -value, r^2 , adjusted r^2 , Akaike information criterion (AIC), Bayesian information criterion (BIC), and the predicted residual error sum of squares (PRESS) statistic (Freund & Littell, 2000).

Instead of using a 5% probability value ($p = .05$) to test our experimental hypotheses, we chose to use a more liberal value ($p = .10$). A large sample size (>10 blocks) would be typically required to detect treatment differences at a 5% level ($p = .05$) in field experiments (Marini, 1999), and such a sample size was not feasible given

SLF-related constraints on the experimental design. Consequently, we decided to report exact p -values to facilitate data interpretation and data transparency. Graphs and plots were generated using OriginPro v. 2022 (OriginLab Corporation, Northampton, MA, USA), and conceptual figures constructed using BioRender (BioRender, Toronto, ON, CA).

3 | RESULTS

3.1 | SLF effects on starch and soluble sugar concentrations

Spotted lanternfly phloem feeding strongly reduced starch concentration in root tissues by the end of the growing season for both experiments (Figure 1a; Figure 2a; Table S1). In Experiment 1, starch concentration in roots of Riesling vines linearly decreased with increasing SLF density in 2020 ($r^2 = .71$; $p < .001$; Figure 1a). For example, starch concentration in the root tissues was 50.8 mg g^{-1} for the vine with 0 SLF, while it was only 17.9 mg g^{-1} for the vine with the highest SLF density (15 SLF shoot $^{-1}$). In 2019, only the medium SLF treatment had significantly lower (43.3%) root starch concentrations than the control ($p = .080$; Table S1), whereas roots of the high SLF treatment had 24.9% lower starch than control vines ($p = .415$). In Experiment 2, starch concentration in roots of Marquette vines

exposed to a high SLF density was on average 77.0% lower than that of control vines ($p < .001$; Figure 2a).

The effects of SLF feeding on starch concentrations in canes were more limited and suggested a trend opposite to that observed in the roots. In Riesling vines, starch concentration linearly increased in both cane wood ($r^2 = .51$; $p = 0.002$) and cane bark ($r^2 = .61$; $p < .001$) tissues in response to greater SLF density in 2020 (Figure 1b,c). For instance, starch concentration was 29.5 mg g^{-1} in the wood tissue of the vine with 0 SLF and 36.3 mg g^{-1} in the vine with the highest SLF density (15 SLF shoot $^{-1}$), and starch values tended to be comparable in vines exposed to SLF densities higher than 8 SLF shoot $^{-1}$. In 2019, there were no statistically significant differences in either cane bark or wood starch concentrations among treatments. However, starch concentration was 37.5% higher in the bark tissue of the high SLF treatment compared with the control vines ($p = .264$; Table S1).

Phloem feeding had negligible effects on soluble sugar concentrations in cane tissues of Riesling vines (Figure 1e,f; Table S1), whereas there was a positive, linear relationship between soluble sugar concentrations in root tissues and SLF density in 2020 ($r^2 = .22$; $p = .068$; Figure 1d). Despite this association, soluble sugar concentrations did not tend to continue increasing with SLF density higher than 8 SLF shoot $^{-1}$. Relatedly, soluble sugar concentrations in root tissues of Marquette vines exposed to high SLF density were 27.9% higher than those in control vines ($p = .093$; Figure 2b).

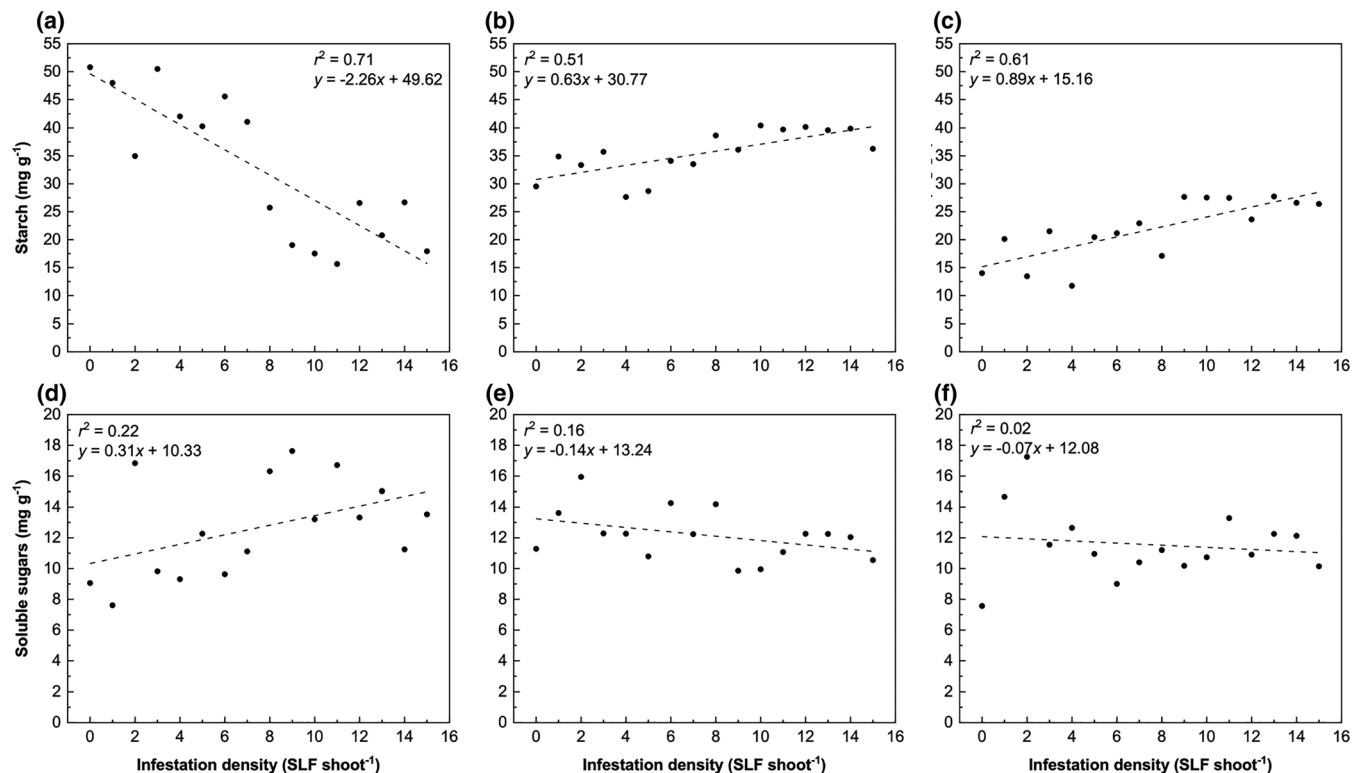


FIGURE 1 Starch (a–c) and soluble sugars (d–f) concentrations in woody root (a, d), cane bark (b, e), and cane wood (c, f) tissues collected on November 17, 2020, from Riesling vines. In all cases, linear regressions best described the relationship between tissue type and carbohydrate variable. Vines were exposed to randomly assigned infestation densities ranging from 0 to 15 SLF shoot $^{-1}$, with the same density assigned to each vine for the duration of the experiment. Concentrations are reported in milligrams of glucose equivalents per gram of dry tissue weight.

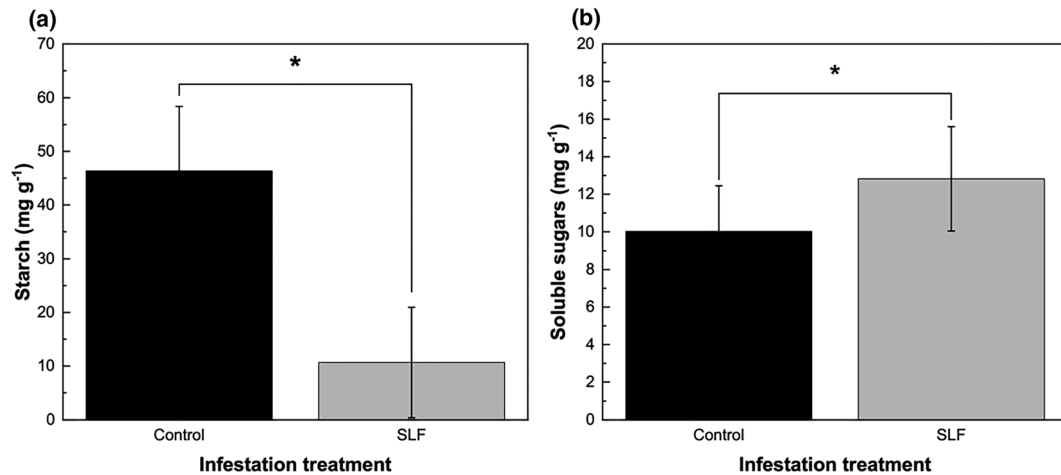


FIGURE 2 Starch (a) and soluble sugar (b) concentrations of Marquette roots sampled on September 30, 2020. Concentrations are reported in milligrams of glucose equivalents per gram of dry tissue weight. The asterisks (*) indicate a significant treatment effect (a: $p < .001$; b: $p = .093$). Control vines were assigned no SLF infestation treatment, whereas treatment vines (SLF) were assigned an infestation density of 80 SLF vine⁻¹.

3.2 | SLF effects on N concentrations

Phloem feeding from SLF affected N concentrations in root and leaf tissues by the end of the season in both experiments (Figure 3; Table 1). In Riesling vines, medium and high SLF densities significantly reduced N concentrations in leaf tissues relative to the control in 2019 ($p = .009$ and $p = .002$, respectively; Figure 3a). Further, high SLF density also reduced N concentration in root tissues ($p = .029$; Figure 3b). Compared with control vines, N was 20.9% and 26.2% lower in the leaves and 7.4% and 18.0% lower in the roots of vines exposed to medium and high SLF densities, respectively. In 2020, there were negative, linear relationships between SLF density and leaf N concentrations ($r^2 = .36$; $p = .013$) and SLF density and root N concentrations ($r^2 = .46$; $p = .004$; Figure 3c,d). In Experiment 2, Marquette vines exposed to high SLF density had 14.1% and 17.7% lower leaf ($p = .001$) and root N ($p = .058$) concentrations than control vines, respectively (Table 1). Nitrogen concentration in cane tissues did not vary between vines with zero SLF, and vines exposed to different amounts of SLF for either Riesling or Marquette (Figure S3; Table 1). Similarly, SLF phloem feeding did not decrease N content in Marquette aboveground vegetative tissues (Figure S4).

3.3 | SLF effects on fruit ripeness and growth parameters

Exposure to increasing SLF density had negative effects on fruit TSS, a proxy of soluble sugar concentrations in the fruit, at harvest in Riesling, but other fruit ripening parameters did not vary in response to SLF feeding (Figure 4; Figure S5). In 2019, TSS of vines exposed to high SLF density (12 SLF shoot⁻¹) was 13.0% lower than TSS of control vines at harvest ($p = .014$; Figure 4a). In 2020, there was a negative linear relationship between TSS and SLF density ($r^2 = .51$; $p = .002$; Figure 4c). In Marquette vines, phloem feeding had no

effect on any fruit parameter, but the presence of mild gray mold infections might have affected the fruit ripeness measurements (Figure S6). Further, there was not a clear association between YAN concentration or fruit growth parameters (e.g., berry weight) and SLF treatments for either *Vitis* species (Figure 4; Figure S6; Figure S7; Marquette data not shown). However, yield was low in both years for Riesling due to young vine age and early season frost events.

3.4 | SLF effects on leaf gas exchange

In both years, extensive vine exposure to SLF phloem feeding reduced leaf C assimilation, transpiration, and stomatal conductance in Riesling vines (Figures 5 and 6). In 2019, significant SLF treatment effects were measured in grapevines exposed to high SLF density (12 SLF shoot⁻¹) for C assimilation ($p < .001$), transpiration ($p = .008$), and stomatal conductance ($p = .005$) by the end of Cycle 2 (i.e., 8 days of SLF exposure; Figure 5b,f,j). For example, vines in the high SLF treatment vines exhibited 16.9% lower C assimilation than control vines on the final day of Cycle 2 and 68.4% at the end of Cycle 4 (i.e., 17 days of SLF exposure; $p < .001$). All gas exchange parameters of vines exposed to medium SLF density (8 SLF shoot⁻¹) were lower than those of the control vines by the end of Cycle 3 (i.e., 13 days of SLF exposure; Figure 5c,g,k; $p = .094$, $p = .007$, and $p = .056$, respectively). Effects of low SLF density were less relevant and consistent; C assimilation was significantly reduced, relative to the control, only at the end of the measurement period, following 17 days of SLF exposure ($p = .034$; Figure 5d). Transpiration and stomatal conductance were significantly lower than the control in Cycle 3 ($p = .058$ and $p = .049$, respectively; Figure 5g,k) but not in Cycle 4 ($p = .139$ and $p = .114$, respectively; Figure 5h,l).

Measurements in 2020 confirmed 2019 trends, with increasing and repeated SLF feeding significantly reducing all gas exchange parameters (Figure 6). Carbon assimilation was significantly and

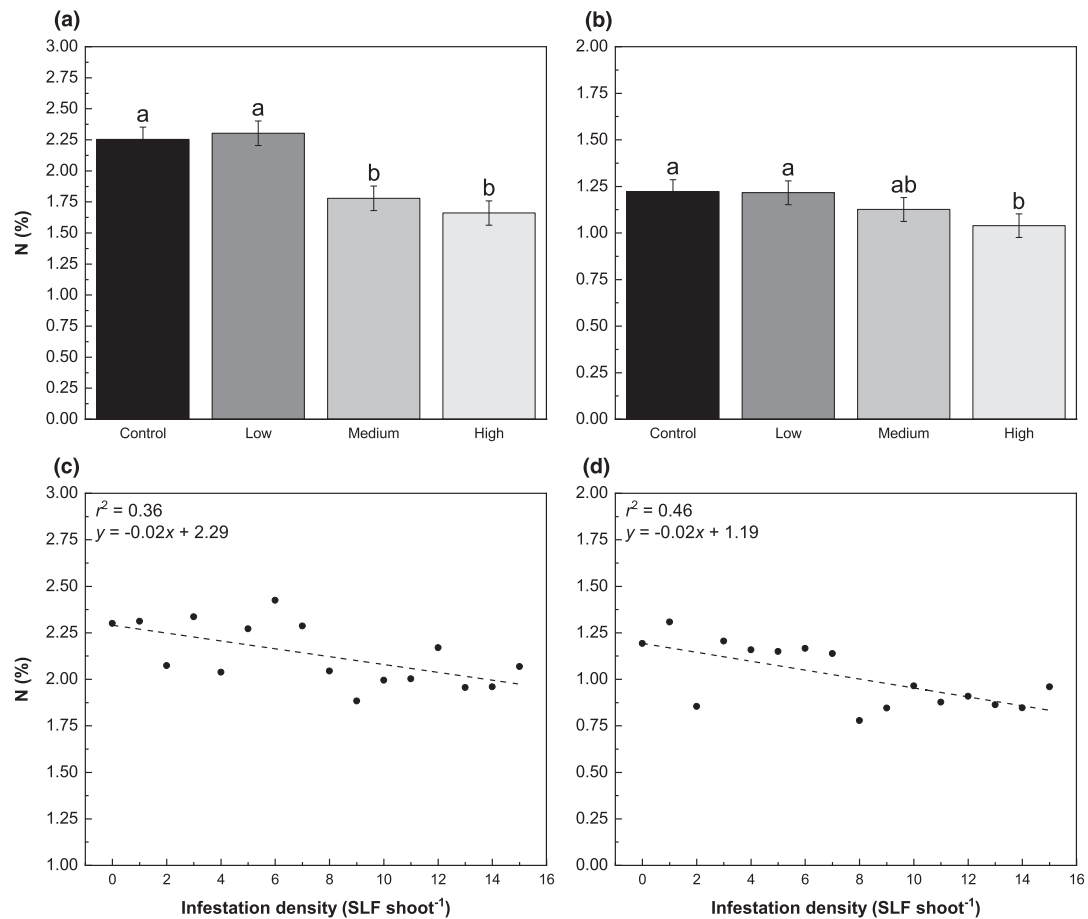


FIGURE 3 Nitrogen (N) concentrations (%) of Riesling tissues sampled in 2019 (a, b) and 2020 (c, d). Leaf tissue (a, c) was sampled prior to senescence on September 27, 2019, and September 30, 2020, whereas woody roots (b, d) were sampled on November 11, 2019, and November 17, 2020, after leaf fall. Different letters in panels (a) and (b) indicate significant differences between treatments ($p \leq .100$), and in panels (c) and (d), lines represent best-fit, significant (c: $p = .013$; d: $p = .004$) linear regressions.

TABLE 1 Nitrogen concentration (%) in the vegetative and reproductive tissues of Marquette control (0 SLF) and SLF (80 SLF vine⁻¹) vines

Treatment	Leaf blade (%)	Petiole (%)	Cane (%)	Roots (%)	Fruit (%)
Control	2.49	1.11	.91	1.26	1.04
SLF	2.14	1.15	.92	1.07	1.05
<i>p</i> -value	.001	.474	.804	.058	.932

Note: Fruit was harvested on September 11, 2020, aboveground vegetative tissues were sampled on September 30, 2020, and roots sampled on November 11, 2020.

negatively correlated to SLF density from the first cycle onwards (i.e., 6 days of SLF exposure; Figure 6a–c), whereas significant, negative correlations between SLF density and transpiration or stomatal conductance were first seen following Cycle 2 (i.e., 20 days of SLF exposure; Figure 6e,h). In all cases, correlations between gas exchange variables and SLF density strengthened following repeated exposure. Additionally, the nature of the relationship changed across the cycles. For instance, for C assimilation, the optimal model shifted from a linear fit in Cycle 1 to a quadratic fit in cycles 2 and 3. Trend lines for transpiration and stomatal conductance shifted from linear fits in cycles 1 and 2 to a quadratic fit in Cycle 3.

3.5 | SLF effects on foliar soluble sugar concentrations

Phloem feeding by SLF tended to increase foliar fructose concentrations in leaf tissues of Riesling vines exposed to high SLF density but had no effect on glucose, sucrose, or raffinose concentrations, though variation was high between samples (Table 2). Foliar concentrations of fructose in vines exposed to high (12 SLF shoot⁻¹) SLF density were, on average, 93.6% ($p = .100$) higher than those of control vines at the end of Cycle 4 in 2019 (i.e., 17 days of SLF exposure).

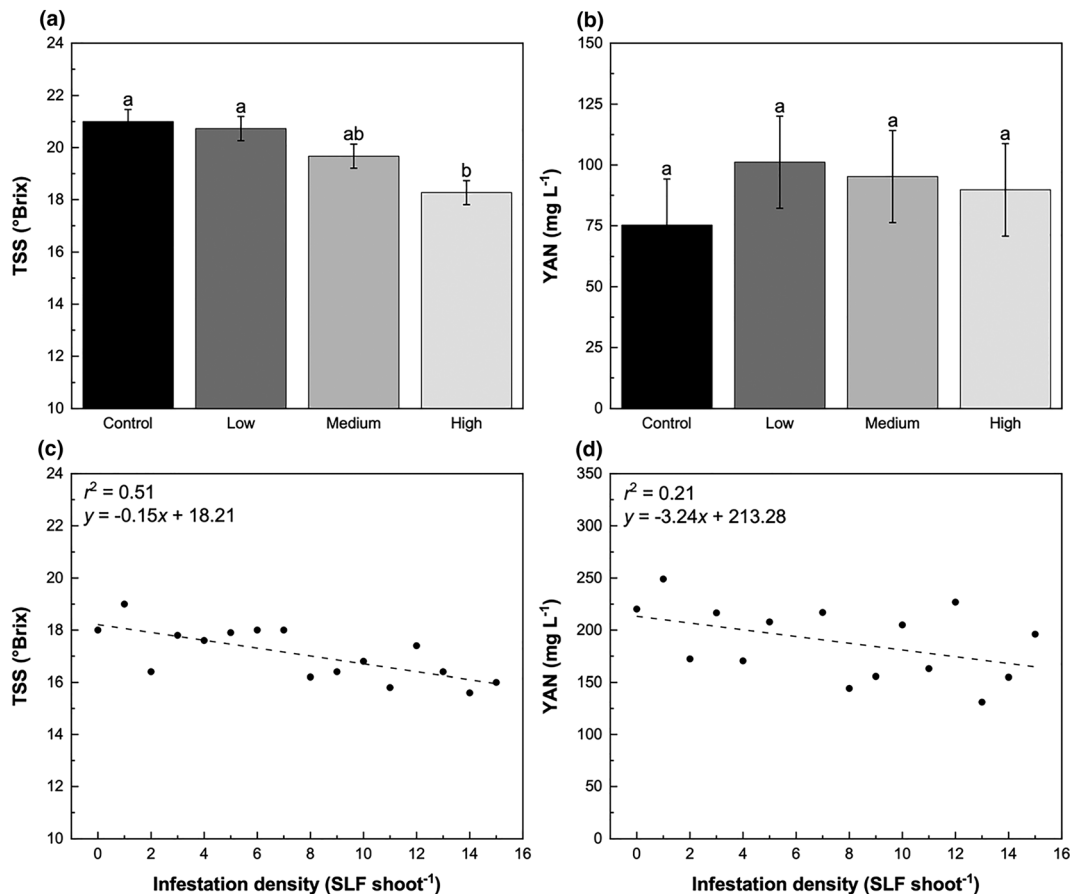


FIGURE 4 Total soluble solids (TSS) and yeast assimilable nitrogen (YAN) of Riesling grapes at harvest in 2019 (a, b) and 2020 (c, d). In 2019, mean values with different letters indicate significant treatment effects ($p \leq .100$). In 2020, linear regressions represent best-fit regressions. Both linear regression models shown are significant (c: $p = .002$; d: $p = .089$).

3.6 | SLF effects on dormant season and year-after growing season parameters

Vine exposure to adult SLF did not have a consistent effect on primary bud freeze tolerance measured in the dormant seasons following SLF exposure for Experiment 1. The only significant difference was measured during vine acclimation (i.e., November) in 2019 ($p = .011$), when the average temperature killing 50% of the buds (LT_{50}) was 2.9°C and 2.7°C higher for low and high SLF vines, respectively, than control vines ($p = .013$ and $p = .020$, respectively; Figure S8A).

Year-after effects of SLF phloem feeding on Riesling nutrient status were limited to a few macro- and micronutrients in 2020. The main effect was lower P concentrations in the SLF treatments relative to control vines ($p = .007$), regardless of density. Additionally, medium and high SLF treatment vines had higher petiolar Ca concentrations relative to control vines ($p = .028$ and $p = .005$, respectively; Table S2).

The effect of SLF phloem feeding on the year-after nutrient status of Marquette vines was similarly limited (Table S3). Contrary to the data reported for Riesling, N was the only mineral nutrient that differed between vines infested with SLF and the control ($p = .026$).

Vine exposure to SLF feeding had inconclusive effects on Riesling plant growth in the following year, due to multiple frost events in spring of 2020. Freeze damage on green shoots and inflorescences compromised accurate assessment of the effects of SLF on percent bud survival and fruitfulness (clusters shoot⁻¹). Repeated measures analysis of shoot length measurements conducted in summer of 2020 suggested no effect of SLF feeding on vine shoot growth (Figure S9). However, these results could not be confirmed in 2021 due to widespread vine and bud mortality likely associated with low winter temperatures. The main year-after effect of SLF feeding on Marquette vines was that two of the vines assigned to the SLF treatment exhibited 100% bud mortality in 2021 (Table S4).

4 | DISCUSSION

In this study, we examined the effects of an invasive insect, SLF, on gas exchange and plant resources allocation. Our experiments targeted specific aspects of perennial plant physiology that are critical for woody fruit crop longevity and management, generating new insights into plant-SLF interactions.

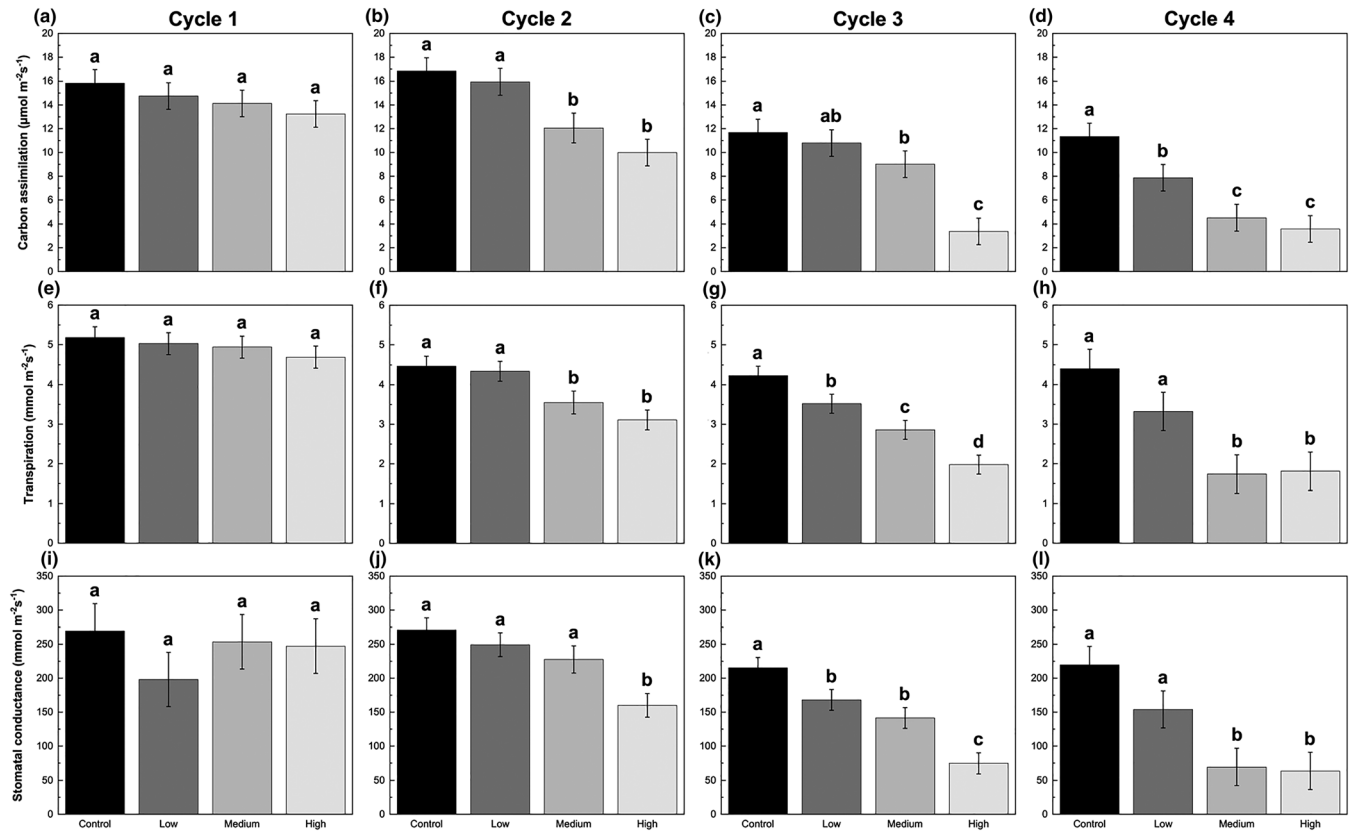


FIGURE 5 Leaf carbon assimilation (a–d), transpiration (e–h) and stomatal conductance (i–l) of Riesling vines in 2019. For each gas exchange parameter, measurements were conducted at the end of Cycle 1 (a, e, i), Cycle 2 (b, f, j), Cycle 3 (c, g, k), and Cycle 4 (d, h, l), and repeated measures analysis was performed. In each panel, mean values with different letters indicate significant treatment effects ($p \leq .100$) per cycle. Infestation treatments correspond to the following SLF densities: Control, 0 SLF shoot⁻¹; low, 4 SLF shoot⁻¹; medium, 8 SLF shoot⁻¹; or high, 12 SLF shoot⁻¹.

4.1 | Repeated SLF phloem feeding inhibits leaf gas exchange

Insect phloem feeding can either promote or reduce C assimilation in host plants (Zhou et al., 2015). Evidence of reductions in grapevine C assimilation by phloem-feeding insects has mostly involved insects that directly feed upon leaf tissues (Candolfi et al., 1993; Lamp et al., 2011; Lenz et al., 2012) or form galls (Nabity et al., 2013). In this study, we showed that prolonged exposure to SLF, an insect that feeds on the phloem of stems and trunks, can decrease photosynthetic rate, similar to other sap-feeding insect pests of woody (Zvereva et al., 2010) and herbaceous plants (Watanabe & Kitagawa, 2000). As predicted, C assimilation was initially maintained for vines exposed to relatively low populations (≤ 4 SLF shoot⁻¹); however, after extensive exposure to SLF, C assimilation was limited in all plants, although reductions were typically higher for vines exposed to ≥ 8 SLF shoot⁻¹ in both years.

Gas exchange measurements were taken more frequently in 2019, that is, four times within 17 days of SLF exposure, better pinpointing shifts in C assimilation within a few weeks of SLF infestations. Measurements conducted in 2020 confirmed that limiting SLF phloem feeding to a few days (4–6 days) did not induce a strong C

assimilation response, unless populations were extremely high (14–15 SLF shoot⁻¹). Additionally, a nonlinear response in C assimilation to SLF phloem feeding was first observed following longer exposure (i.e., 20 days), indicating that prolonged phloem feeding by densities ≥ 8 SLF shoot⁻¹ does not continue to decrease C assimilation linearly. Instead, vines exposed to higher densities appeared to remain similarly inhibited, and assimilation was not further reduced. However, measurements were conducted only on leaves within the upper canopy; it was unclear if the whole-canopy response would be as strong as the single-leaf responses detailed here, because stress responses of individual leaves may not accurately reflect the response of a canopy comprised of heterogeneous leaves (Poni et al., 2009). Further, logistical limitations and poor weather conditions prevented repeated measurement of gas exchange responses between infestation cycles when vines were not exposed to SLF phloem feeding. Because it cannot be ruled out that gas exchange responses during these periods may differ from those measured during SLF infestation, addressing this knowledge gap remains a focus of future work.

Decreases in C assimilation following SLF exposure slightly preceded those in transpiration and stomatal conductance, which in 2020 were, however, affected in a nearly identical fashion. Insect herbivores can trigger molecular signaling pathways involved in stomatal control

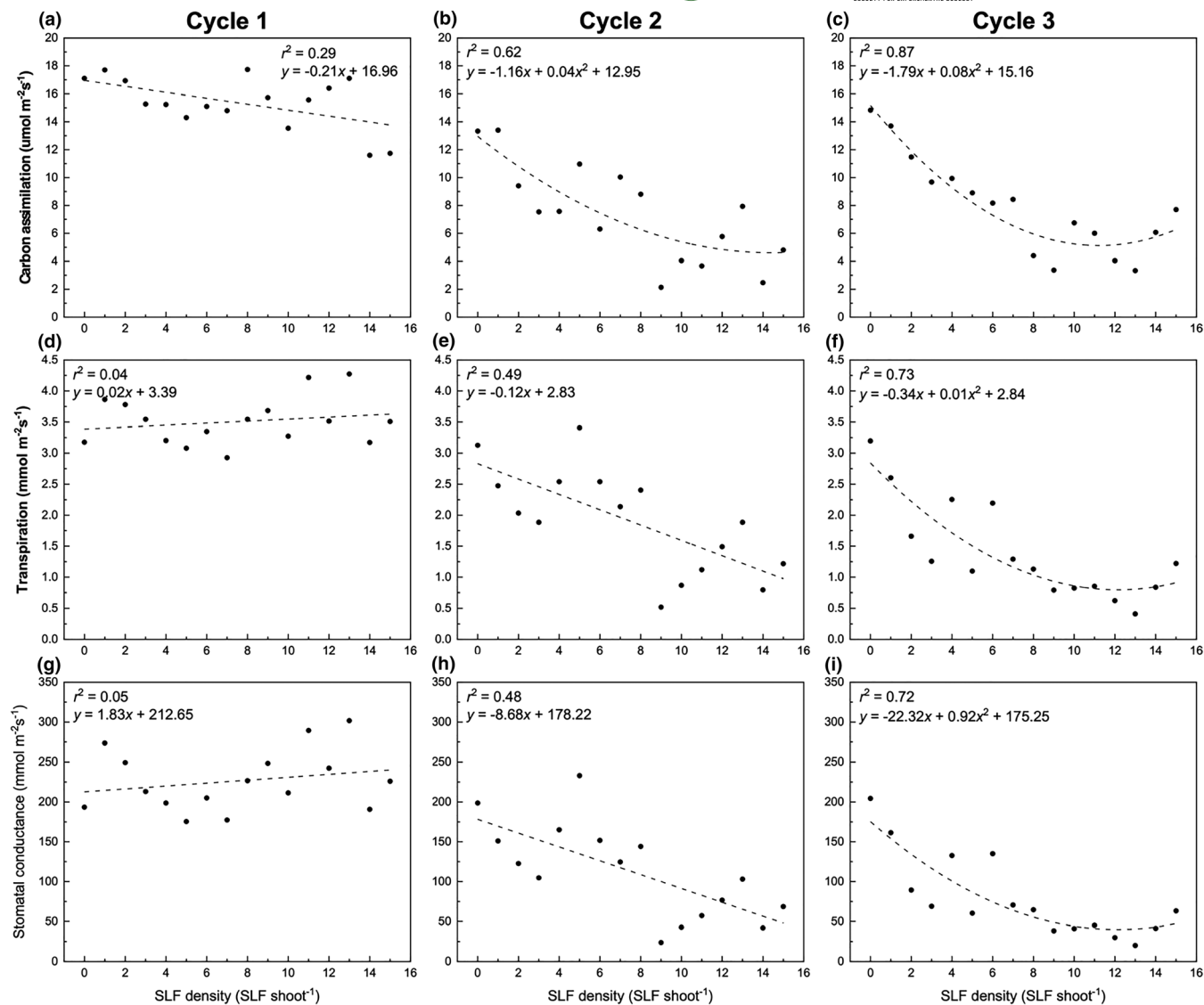


FIGURE 6 Leaf carbon assimilation (a–c), transpiration (d–f), and stomatal conductance (g–i) of Riesling vines in 2020. For each gas exchange parameter, measurements were conducted at the end of Cycle 1 (a, d, g), Cycle 2 (b, e, h), and Cycle 3 (c, f, i). Text within each panel represents the equation and strength of fit for the plotted regression lines. Regression lines were significant in panels a ($p = .032$), b ($p = .002$), c ($p < .001$), e ($p = .003$), f ($p < .001$), h ($p = .003$), and i ($p < .001$).

TABLE 2 Concentration of soluble sugars (mg g⁻¹) in Riesling leaves sampled on September 27, 2019, and quantified using GC–MS

Treatment	Glucose (mg g ⁻¹)	Fructose (mg g ⁻¹)	Sucrose (mg g ⁻¹)	Raffinose (mg g ⁻¹)
Control ^a	8.87 ^{a,b}	.48 ^b	49.88 ^a	.76 ^a
Low	6.66 ^a	.89 ^{a,b}	43.77 ^a	.65 ^a
Medium	6.29 ^a	.56 ^{a,b}	57.02 ^a	.70 ^a
High	5.45 ^a	.92 ^a	49.33 ^a	.70 ^a
p-value	.260	.057	.817	.981

Note: Concentrations are expressed in mg internal standard equivalents per gram of dry tissue weight.

^aValues within a column noted with different letters are significant at $p \leq .100$ as determined by Tukey's HSD test.

^bInfestation treatments correspond to the following SLF infestation densities: Control, 0 SLF shoot⁻¹; low, 4 SLF shoot⁻¹; medium, 8 SLF shoot⁻¹; or high, 12 SLF shoot⁻¹.

to induce stomatal closure (Lin et al., 2021). In our study, repeated SLF phloem feeding appeared to reduce transpiration via stomatal closure, but the mechanism underpinning stomatal closure is unknown and may include herbivore-associated molecular patterns (HAMPS) and/or phytohormonal (e.g., abscisic acid, ABA) interference. Stomatal regulation by ABA can also occur following foliar hexose accumulation, as hexoses involved in stomatal signaling, like glucose and fructose, can influence stomatal aperture (Kelly et al., 2013). Reduction in C assimilation and an associated increase in foliar hexose concentrations have been reported for grapevines infected with phloem-limited viral pathogens (Halldorson & Keller, 2018; Rumbaugh et al., 2021). Results from our study suggest that leaf fructose concentration might increase when vines are repeatedly exposed to high SLF densities (12 SLF shoot⁻¹), but there was no indication of changes in glucose or other soluble sugars. Therefore, it is unclear to what degree a phloem-feeding insect such as the SLF can cause hexose accumulation in leaves and mediate stomatal closure.

4.2 | Repeated SLF phloem feeding disrupts C source–Sink relationship

Spotted lanternfly phloem feeding strongly affected C source-sink dynamics of field-grown Riesling vines (Figure 7). By the end of the growing season, shifts in C resources were observed in all tissues measured, and the results support our hypothesis that SLF effects on

TNC are stronger in below- rather than aboveground tissues. Repeated phloem feeding had the strongest effect on root starch concentrations, with substantial reductions in both Riesling and Marquette vines that increased with higher SLF density. For Riesling vines, the negative root starch response to increasing SLF density was linear, indicating that vines were not able to maintain C reserves (starch) even when exposed to relatively low SLF populations for a prolonged time, approximately 26 days. Although small reductions in root starch following exposure to low SLF populations may not be biologically relevant, extreme reductions in root starch, like those measured in two SLF-infested Marquette vines with root starch concentrations at or below 1%, likely compromised plant viability and caused vine collapse. These vines likely experienced C exhaustion and had insufficient C reserves for supporting respiration during dormancy and spring growth (Kozlowski, 1992), suggesting that high SLF infestation may be able to induce fatal C deprivation in some extreme cases. However, it is unknown if older grapevines would have greater TNC reserves than the vines used in this study and how SLF-driven C competition might affect these reserves.

Decreased C allocation to the roots, and to a lesser extent, the fruit, could be related to several, potentially concomitant factors, including lower C available due to reduced C assimilation and the exploitation of available C by SLF (Watanabe & Kitagawa, 2000); a reduction in C translocation due to compromised phloem integrity (Nielsen et al., 1990; Welker et al., 2022); a shift in source-sink dynamics in response to C limitation, leading to the prioritization of

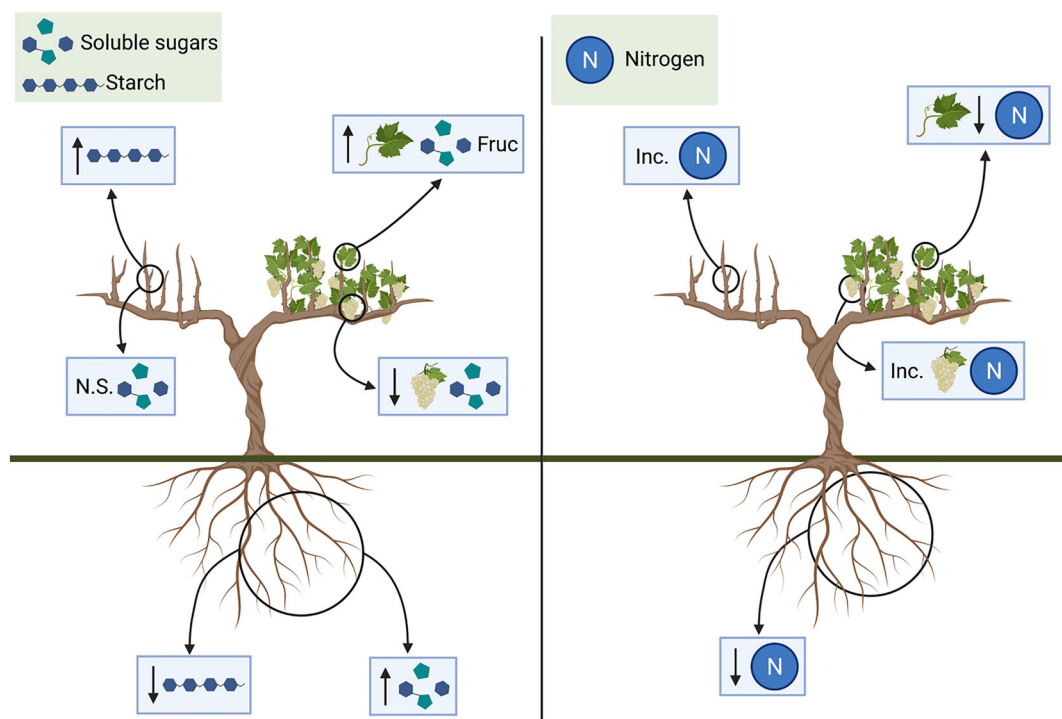


FIGURE 7 Conceptual diagrammatic summary of the effects of repeated SLF phloem feeding on Riesling grapevine (a) carbohydrate (starch and soluble sugars) and (b) nitrogen (N) resources. Inset boxes refer to measurements (concentrations of starch, soluble sugars, and N) conducted on the circled tissues (leaves, fruit, woody canes, and roots). Arrows refer to relative increase or decrease in compound of interest. Boxes with "Inc." indicate an inconsistent treatment effect. Figure created using BioRender.



one sink over another (Candolfi-Vasconcelos et al., 1994); and the catabolism of carbohydrate energy compounds (e.g., sucrose, starch) for plant defense responses, including the synthesis of antiherbivore metabolites (Zhou et al., 2015).

In our study, increasing numbers of SLF per vine progressively reduced leaf gas exchange, decreasing the pool of newly assimilated C available to sink organs. Decreased photosynthate allocation to the roots could have reduced starch concentrations, as sugar translocation is necessary for localized starch synthesis (Noronha et al., 2018). Additionally, sap flow and sugar translocation can be physically impaired by callose deposition in the phloem sieve elements (Mullendore et al., 2010). Previous studies on phloem-restricted pathogens and phloem-feeding pests have reported callose deposition in the phloem of huanglongbing-infected citrus trees (Welker et al., 2022) and in rice plants infested by brown planthopper (BPH; *Nilaparvata lugens* Stål) (Hao et al., 2008). It is plausible that SLF probing and feeding induced a similar anatomical response that reduced the total solutes translocated to sink organs such as roots or fruit. This could also be responsible for an apparent accumulation of anthocyanins in leaves of red-fruited grape cultivars with high levels of SLF feeding (Leach & Leach, 2020). Indeed, visible mechanical damage was identified on phloem tissues of stems from infested vines following removal of outer bark layers (Figure S11). These markings may be SLF-damaged cells and deposited SLF salivary sheaths, but histological and anatomical investigation may yield insights into anatomical responses (Ammar & Hall, 2012).

In contrast to observed trends for the root system and fruit, SLF phloem feeding appeared to facilitate the accumulation of starch in stems (canes), although trends were not always statistically significant and there was no effect on concentrations of soluble sugars. Adult SLF mostly feed on the phloem of the stems prior to harvest (Leach & Leach, 2020; personal observation) and, at relatively high densities, could stimulate solute allocation to feeding sites, as observed for other sap-feeding insects (Savage et al., 2016). Previous work on phylloxera (*Daktulosphaira vitifoliae* Fitch), an important galling insect pest of grapevines, reported that phloem feeding on roots can deplete the feeding site of resources (e.g., soluble sugars; Savi et al., 2019) or induce localized starch accumulation (Kellow et al., 2004; Savi et al., 2021).

Shifts in TNC allocation following biotic and abiotic stresses have been observed in woody perennials, notably in citrus trees infected by huanglongbing, where phloem disruption led to increased starch accumulation in aboveground perennial tissues and deprivation in root tissues (Etxeberría et al., 2009). Similarly, in pine trees subjected to artificial defoliation and drought, TNC concentrations were maintained or increased in stems but decreased in root tissues (Jacquet et al., 2014). Feeding by SLF may cause a similar phenomenon, as in at least one of the 2 years soluble sugars in stems were maintained, although starch tended to increase at the expense of belowground reserves. This led to an overall trend of maintained stem TNC in 2019 and increased stem TNC in 2020 in vines exposed to SLF phloem feeding, relative to vines not exposed to SLF (data not shown).

Further studies could explore the mechanisms driving these shifts, which can include catabolism of storage compounds (e.g., starch) and reallocation of soluble sugars from the roots to aboveground organs (Candolfi-Vasconcelos et al., 1994; Silva et al., 2017) to sustain plant growth, fruit ripening, and production of defense compounds. The increase in root soluble sugar concentrations in both *Vitis* species suggests an increase in starch hydrolysis in response to C limitation (Rossouw et al., 2017). However, overall TNC concentrations in woody roots were nevertheless reduced in vines exposed to SLF phloem feeding (data not shown). Reallocation of plant C resources to wounded tissues following herbivore attack is common (Schultz et al., 2013), and here, the priority of the plant might have been using C resources for synthesis of plant defense compounds (Zhou et al., 2015). However, any remobilization may not have been sufficient to sustain fruit ripening in young Riesling vines because TSS at harvest decreased as SLF density increased. It is also possible that the translocation of solutes to belowground organs was limited by a rearrangement in sink priorities following SLF-driven C limitation (Huang et al., 2021), a girdling-type effect due to phloem damage (Roper & Williams, 1989), or a combination of these and other factors. Regardless, deprivation of belowground starch reserves in woody perennials can dramatically reduce plant viability and stress resilience (Kozłowski, 1992; Landhäusser & Lieffers, 2012; Sevanto et al., 2014). Future studies should focus on resource remobilization for defense compound synthesis in response to SLF feeding in grapevines.

In both *Vitis* species, tissues used for TNC analysis were sampled during dormancy, indicating that SLF-driven effects on belowground reserves persisted post-SLF exposure. The insects were removed after fruit harvest and 24 (2019) and 42 (2020) days before root sampling for the Riesling experiment and 45 days for the Marquette experiment. In grapevines, root reserve refilling mostly occurs during fruit ripening when fruit sugar accumulation slows (Rossouw et al., 2017). Postharvest resource uptake can be important for reserve storage (Smith & Holzappel, 2009) if weather conditions suitable for gas exchange persist. Like other temperate growing regions, in Pennsylvania weather conditions and plant phenological stage (i.e., canopy senescence) may not be favorable for C assimilation and compensatory reserve refilling post-SLF exposure. In our study, SLF were present until mid-October (Riesling) and end of September (Marquette), and environmental conditions thereafter were suboptimal for photosynthesis (Figure S11). However, TNC storage might be less affected in vineyards where peak SLF presence and activity are earlier in the season and before harvest. It is unclear to what degree compensatory reserve refilling may occur if grapevines are subjected to heavy SLF feeding earlier in the season; however, this is seldom observed in current Eastern United States populations of SLF.

4.3 | SLF sink competition affects whole-plant N dynamics to a lesser extent than C

In general, relative decreases in total N concentration induced by extensive SLF phloem feeding were less prevalent than those in

starch, with effects mainly limited to leaf and root tissues in both *Vitis* species (Figure 7). This suggests that SLF infestations may, at least in the short term (i.e., within a single growing season), have more immediate consequences for plant C rather than N resources. Plant N status can quickly change when fed on by sap-feeding insects; for instance, aphid feeding can disrupt typical source-sink N relationships in alfalfa by stimulating N remobilization from apical plant sinks to damaged tissues (Girousse et al., 2005). In apple and grape, root galling induced by aphids or phylloxera can increase root N concentration relative to ungalled or uninfested root tissues (Brown et al., 1991; Eitle et al., 2017). We hypothesized that a perennial fruit crop can tolerate relatively low populations of SLF with no significant effects on tissue N, and results suggest that only vines exposed to high SLF densities (≥ 12 SLF shoot⁻¹) consistently had reductions in root N at the end of the season, compared with vines exposed to lesser SLF densities or no SLF. Unlike belowground starch resources, vines appeared to be able to tolerate low SLF populations without adverse effects on total N.

Nitrogen depletion by SLF appeared to reduce foliar N concentrations of vines subjected to relatively high SLF densities. This result was unsurprising, as previous work showed that phloem feeding by BPH reduced leaf N content and chlorophyll in rice plants (Watanabe & Kitagawa, 2000) and upregulated expression of genes involved in lipid and protein degradation, including Rubisco proteolysis (Yuan et al., 2005). Similar responses may be stimulated by heavy SLF-feeding and may in part explain the reduction in foliar total N. However, foliar N concentrations of vines exposed to SLF were comparable to those of healthy vines reported in other studies (Pérez-Álvarez et al., 2017; Schreiner et al., 2006; Williams & Biscay, 1991) and likely above deficiency or limiting levels.

Although our study showed that phloem-feeding effects on N were more limited than those on TNC, it is important to note that our measurements were limited to total N; therefore, effects of SLF phloem feeding on N metabolism are still unknown. Phloem feeding can affect amino acid composition of plant tissues and sap (Zhou et al., 2015) and nitrogenous compounds like amino acids and antinutritive proteins play roles in antiherbivore defense (Chen, 2008; Huang et al., 2011). Future efforts to characterize plant amino acid and protein responses to SLF feeding, like past proteomic analyses performed on host plant tissues and sap in response to BPH feeding (Du et al., 2015; Wei et al., 2009), may provide a molecular context for the reductions in total N reported here while providing new insights into SLF effects on N metabolism.

4.4 | After-year effects of a single season of SLF phloem feeding are likely driven by severe root starch reductions

Strong reductions in end-of-season root starch reserves can compromise plant productivity in the following year in fruit crops, such as peach (Lopez et al., 2007), sweet cherry (Loescher et al., 1990), citrus (Goldschmidt & Golomb, 1982; Jones et al., 1975; Stander

et al., 2018), and grapes (Smith & Holzzapfel, 2009). In 2020, starch concentrations in grapevines exposed to high densities of SLF (≥ 8 SLF shoot⁻¹) were only 15–25 mg g⁻¹ (or 1.5%–2.5%) for Riesling and averaged 10 mg g⁻¹ (1%) for Marquette vines. These values were much lower than minimum root starch values reported for heavy-fruited peach trees exposed to severe water stress (~7%; Lopez et al., 2007) and similar to root starch values reported for tangerine trees exhibiting symptoms of tree decline and dieback (Smith, 1976). In the study of Lopez et al. (2007), strong reductions in root starch negatively affected fruit-set in peach trees the following year, but full recovery was possible in the third year when no further stresses were applied. In 2019, roots of Riesling vines exposed to SLF tended to have higher starch concentrations (~30–40 mg g⁻¹) than in the following year; however, these concentrations were still within the range reported for plants subjected to abiotic stress and/or strong source-sink modifications (Lopez et al., 2007; Smith & Holzzapfel, 2009). Although these strong reductions in starch reserves would suggest potential year-after effects on vegetative and reproductive growth, no effects could be confirmed with field measurements due to widespread cold damage sustained by the entire Riesling vineyard block in both years. Moreover, the long-term effect of repeated SLF feeding over multiple years is unknown.

Carryover effects evaluated for experimental vines grown in plastic containers (Marquette) suggest that root starch exhaustion by extensive SLF feeding inhibited vine growth for two of the six vines assigned to the SLF treatment. Root starch concentrations for these two vines were 2.53 and 11.09 mg g⁻¹ at the end of the season, about 94.5% and 76.1% lower than the average starch concentration for control vines, respectively. Extensive vine exposure to high SLF population may have reduced starch reserves to the point of vine collapse (Kozłowski, 1992; Loescher et al., 1990; Smith, 1976). It is important to note that these values were measured on potted vines with restricted root systems, and we caution extrapolating results to field-grown vines.

Effects on Riesling nutrient status were mainly limited to decreased P concentration in leaf petiole at bloom for vines exposed to SLF feeding the previous season. Except for P, which was relatively low in all experimental vines, macro- and micronutrient concentrations were above nutrient deficiency thresholds suggested for grapevines grown in the Eastern United States (Wolf, 2008). Although not measured in our study, it is possible that C depletion in the roots may have affected fine root growth or the recruitment of arbuscular mycorrhizal fungi (AMF; Schreiner, 2003) important for grapevine P uptake (Nikolaou et al., 2003), because the bulk of seasonal AMF recruitment occurs early in the season (Schreiner, 2005). This effect on plant nutrient status was not observed for Marquette vines. However, annual fertilization of the potted Marquette vines may have affected the availability of soil P compared with the field-grown Riesling vines. Nitrogen was the only mineral nutrient that differed between control and SLF-infested Marquette vines in 2021, mirroring the reduction observed following SLF feeding. This effect was not observed in Riesling vines, but different tissues were analyzed and at different times of the season, and vines were grown in different soil types.



Feeding by SLF during the previous season had an inconsistent and limited effect on bud freeze tolerance in Riesling vines. Soluble sugar concentrations in woody stems and buds are positively correlated with tissue freeze tolerance (Jones et al., 1999; Wample et al., 1993). Although concentrations of bud soluble sugars or starch were not quantified, it is nevertheless unsurprising that bud freeze tolerance did not seem to be strongly affected by SLF infestation because stem soluble sugar concentrations were unaffected by SLF phloem feeding. We suspect that decreased bud fruitfulness and bud survival reported (Leach & Leach, 2020) after repeated and extensive SLF feeding could be more related to exploitation of TNC resources (mainly starch) by SLF than decreased cold tolerance caused by reduced soluble sugars, at least under the conditions of our study.

5 | CONCLUSION

This study illustrates how phloem feeding by an invasive planthopper, adult SLF, can alter source-sink dynamics and resource allocation in a commercially important perennial plant. Trends were observed in both *Vitis* species and largely confirmed by both experiments. Phloem feeding by large population densities (i.e., 8–15 SLF shoot⁻¹) had the greatest effect on plant C dynamics and, to a lesser extent, on plant N dynamics, at least within a single season and under our experimental conditions. The length of SLF exposure in this study is greater than what would typically be allowed in a commercial vineyard, where chemical control would be implemented soon after invasion to manage or eliminate adult SLF populations. Our results suggest that if vines are exposed to population densities <4 SLF shoot⁻¹, or populations equal to or <60 SLF vine⁻¹ for vines with 15 shoots, severe C limitation and exhaustion of belowground C resources may be avoided, at least in the first year of SLF infestation. However, providing general management guidelines is outside the scope of this work, as many factors can affect vine responses to this invasive insect, including vine age and the presence of other abiotic (e.g., water stress and nutrient deficiencies) or biotic stressors.

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CONFLICT OF INTEREST

The Authors did not report any conflict of interest.

AUTHOR CONTRIBUTIONS

Michela Centinari and Heather L. Leach conceptualized the research and acquired funding; Andrew D. Harner, Michela Centinari, Heather L. Leach, and Lauren Briggs were involved in investigation; Andrew D. Harner, Lauren Briggs, and Michela Centinari were involved in formal analysis of the data; Andrew D. Harner wrote the original draft; Michela Centinari, Heather L. Leach and Lauren Briggs reviewed and edited the original draft. Andrew D. Harner and Michela Centinari handled manuscript revisions.

DATA AVAILABILITY STATEMENT

All data supporting the findings of this study are available within the paper and within its supplemental materials published online.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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