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Fine root dynamics in response to early and late shoot tip management practices in *Vitis vinifera* L. cv. Cabernet franc

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ABSTRACT

Shoot tip management practices can influence the balance between aboveground canopy and belowground root systems in grapevines, yet their long-term effects on fine root dynamics remain poorly understood. This study evaluated the effects of shoot wrapping (SW), shoot tucking (ST), and conventional hedging (Control, C), applied either early or late in the growing season, on fine root production, fine root age structure, vertical fine root distribution, and fine root lifespan of *Vitis vinifera* L. cv. Cabernet franc grafted onto 3309C rootstock. Fine root dynamics were monitored using minirhizotrons over three growing seasons (2017–2019). Responses varied with shoot tip management practice, application timing, phenological stage, and year. Early shoot wrapping (SWE) increased fine root production at selected phenological stages, particularly in 2018. When application timings were pooled, shoot wrapping was associated with deeper fine root distribution and greater proportions of older root cohorts at specific phenological stages. In contrast, ST showed responses more similar to the control treatment, whereas the effects of application timing were less consistent across years. Shoot tip management practices did not affect fine root lifespan, indicating that canopy manipulation influenced fine root production and distribution rather than root survival. Together, these findings demonstrate that shoot tip management practices can modify belowground root development and provide new insight into the physiological coordination between canopy and root systems in grapevines.

KEYWORDS: canopy architecture, minirhizotron, belowground plant development, grapevine phenology

INTRODUCTION

Grapevine growth is often vigorous in cool-climate wine regions with high precipitation, resulting in excessive vegetative growth that reduces fruit-zone light exposure and airflow, increases disease pressure, and negatively affects fruit ripening (Zoecklein *et al*., 1992; Valdés-Gómez *et al*., 2008; Austin & Wilcox, 2011). To manage excessive grapevine vigour, growers commonly employ management practices such as cover cropping (Klodd *et al*., 2016), root pruning (Centinari *et al*., 2016), and top hedging (Wolf, 2008).

Fine roots play a critical role in water and nutrient acquisition and may use up to 50 % of the daily photosynthates for growth and maintenance (Lambers, 1987). Because fine root growth depends on carbohydrates supplied by aboveground source tissues, canopy management practices can influence belowground development (Eissenstat & Duncan, 1992; Comas *et al*., 2005). Hence, changes in fine root production, longevity, and distribution may reflect shifts in whole-vine resource allocation and influence vine performance.

Few studies have evaluated the effects of aboveground management practices on grapevine root dynamics (Anderson *et al.,* 2003; Morinaga *et al.,* 2003; Hunter *et al*., 1995). Hunter *et al*. (1995) reported that selective partial defoliation increased light intensity above the cordon from 13 % of ambient light in control vines to 26 % and 32 % in the pea-size and veraison treatments, respectively, and increased photosynthetic activity of basal and middle leaves. The authors concluded that increased photosynthetic activity of the remaining leaves was sufficient to sustain root growth despite partial leaf removal. In contrast, canopy reduction through hedging decreased root length density and increased root mortality in citrus, likely due to temporary reductions in photosynthetic source capacity during canopy regrowth (Eissenstat & Duncan, 1992). Together, these studies suggest that modifications of canopy architecture can influence belowground root dynamics, although the magnitude and direction of these responses depend on the nature and intensity of canopy modification.

The timing of canopy management practices may also influence fine root responses. Hunter and Roux (1992) reported that grapevine defoliation performed one month after budbreak and at berry set reduced fine root production compared with defoliation applied later in the season, a response consistent with the seasonal changes in source–sink relationships described by Hale and Weaver (1962). Similarly, the timing of shoot hedging, a widely used vineyard practice in which shoots extending beyond the upper catch wires are removed, can influence vegetative growth, lateral shoot development, and cluster architecture (Reynolds & Wardle, 1989; Vasconcelos & Castagnoli, 2000; Molitor *et al*., 2015; Logan *et al*., 2021). Although previous work found limited effects of application timing on lateral shoot development (Logan *et al*., 2021), fine root growth may respond differently, as fine root production is strongly influenced by vine phenology and seasonal source–sink relationships (Hale & Weaver, 1962; Hunter & Roux, 1992; Bates *et al.*, 2002; Comas *et al*., 2005).

Conventional shoot hedging removes the shoot apex, disrupting apical dominance and stimulating lateral shoot emergence and vegetative regrowth (Mason *et al*., 2014). Alternative shoot tip management practices, including shoot wrapping and shoot tucking, have been proposed to control canopy growth while retaining shoot tissue. Unlike conventional hedging, which removes shoot apices, shoot wrapping and shoot tucking reposition shoots within the canopy without removing shoot tissue (France *et al*., 2018; Logan *et al*., 2021). Our previous study of aboveground responses in the same experimental vineyard showed that early wrapping reduced fruit-zone lateral shoot counts by 41 %, 23 %, and 56 % in 2017, 2018, and 2019, respectively, and mean lateral shoot length by 41–50 % across those years. Tucking effects were less consistent: fruit-zone lateral shoot counts were reduced by 15 % under late application in 2018 and by 33 % under early application in 2019 relative to the corresponding hedging controls (Logan *et al*., 2021). These differences in canopy architecture and vegetative development suggest that shoot wrapping and shoot tucking may modify whole-vine source–sink relationships differently from conventional hedging, thereby influencing the amount and timing of carbon allocated to fine root growth and development. To facilitate interpretation of the belowground responses evaluated in this study, a summary of the principal aboveground responses previously reported for the same experimental vineyard and shoot tip management practices (Logan *et al*., 2021) is provided in Table S1.

Hormonal regulation may provide another link between shoot tip management and root responses. Apical dominance involves interactions among auxin, cytokinins, and sugar availability (Gallavotti, 2013; Cao *et al*., 2023). In grapevine, downward shoot orientation increased IAA concentrations in apical internodes and reduced shoot hydraulic conductivity (Lovisolo *et al*., 2002), suggesting that retaining and repositioning the apex may influence hormonal regulation differently from removing it. These effects could modify canopy development and potentially shoot–root signalling, providing a complementary hypothesis for belowground responses.

Despite evidence that canopy management can influence root growth and development, little information is available regarding how shoot tip management practices affect grapevine fine root dynamics. Furthermore, the extent to which root responses vary with the timing of shoot tip management remains poorly understood.

Therefore, this study aimed to determine how shoot tip management practices (shoot hedging, shoot tucking, and shoot wrapping) and application timing influence fine root production, the distribution of roots among age classes, the vertical distribution of fine roots, and fine root lifespan in *Vitis vinifera* L. cv. Cabernet franc grafted onto 3309C rootstock. We hypothesised that shoot wrapping and shoot tucking would alter fine root dynamics relative to conventional hedging because these practices modify canopy architecture and vegetative development. Specifically, we expected shoot wrapping to induce larger changes in fine root production, the distribution of roots among age classes, and the vertical distribution of fine

roots than shoot tucking because previous work demonstrated greater reductions in lateral shoot emergence and vegetative regrowth under shoot wrapping than under shoot tucking (Logan *et al*., 2021). We further hypothesised that early application would have greater effects on fine root dynamics than late application because earlier canopy modification would allow more time for changes in canopy development and source–sink relationships to influence root growth.

MATERIALS AND METHODS

1. Climate data

Climate data were obtained from the Cornell University Network for Environment and Weather Applications (NEWA) Lansing station except for September and October 2019. Data for these two months were not available at the Lansing station, and instead data were obtained from the Romulus station (42°42'00.0" N, 76°45'00.0" W) as that region is climatically similar to the Lansing station (newa.cornell.edu). Rainfall and growing degree days (base threshold of 10 °C) were calculated from precipitation and temperature data obtained from 1 April to 31 October.

2. Experimental set-up

From 2016 to 2019, this study was conducted on nine rows of *Vitis vinifera* L. cv. Cabernet franc cl. 1 grafted onto 3309C rootstock, planted in 2008, in a 0.25 ha research vineyard at 124 m elevation on a 58 % west-facing slope in Lansing, NY (42°34'15" N, 76°35'39" W). After the experiment was established, it was determined that one of the nine rows was Cabernet franc cl. 4 (rather than cl. 1). While the cl. 4 row did not differ visually from the cl. 1 rows, the row was included as a random effect in the statistical model to account for this difference.

The vineyard had a vine × row spacing of 1.8 × 2.8 metres and was planted on a Hudson-Cayuga silt loam soil type. Each row contained six panels of four vines each for a total of 24 vines. Two experimental units, each consisting of three panels of four vines per panel for a total of 12 vines per experimental unit, were established in each row. The interior two panels of each experimental unit (eight vines) were designated as treatment data collection panels. Row middles were originally planted with fescue species but, by the start of the experiment, were filled with a range of grass and broadleaf species. Also, row middles were maintained with periodic mowing; under-vine herbicide strips were maintained with glyphosate applications twice per season.

During dormancy, vines were cane-pruned to 40 nodes per vine and shoot-thinned to 30 shoots per vine in 2017 and 2018, and 28 shoots per vine in 2016 and 2019. Vines were trained to a two-tier flatbow system in which canes were laid down bilaterally on two fruiting wires, with four canes per vine and trained to vertical shoot positioning (VSP). The experiment followed a randomised split-plot design with three spatial blocks, each comprising three adjacent vineyard rows, to account for spatial heterogeneity. Within each block, the three shoot tip management practices: hedging (control), shoot tucking, and shoot wrapping (Figure 1) were randomly assigned to whole rows, which served as main plots. Early and late application timings were then randomly assigned to the two experimental units within each row, which served as subplots. Early treatments were applied when shoots extended approximately 30 cm above the top catch wire, and late treatments when shoots extended approximately 90 cm above it. Each management practice × timing combination was represented once per block, giving three replicates. Early treatments were applied from mid-June to early July, and late treatments from early to mid-July, with both timings preceding veraison. The exact application dates for each study year are provided in Table S2. The treatment combinations were as follows: for early applications of techniques: control (CE), shoot tucking (STE), shoot wrapping (SWE); and for late applications of techniques: control (CL), shoot tucking (STL), shoot wrapping (SWL).

3. Root observations and measurements

On 9 November 2016, two 93 cm long and 6 cm in diameter minirhizotron root observation tubes were installed at a 30° to vertical per experimental unit. The top thirty cm of the tubes were above the surface, giving an observation depth of 55 cm. The tubes were placed about 50 cm in the row north of the vine and 25 cm west of the vine's trunk. Tubes were plugged with PVC at the bottoms to prevent water infiltration and taped with black electrical tape to avoid light penetration, then capped with black plastic caps and white covers to prevent overheating (Bauerle *et al.,* 2008). Because 2016 served as the establishment year for the minirhizotron, fine root observations began in spring 2017.

Root images were taken approximately every two weeks with a BTC MiniRhizotron Digital Image Capture camera system (Bartz Technology, Carpinteria, CA, USA), beginning at budbreak and continuing through the growing season. Images were collected approximately once a month during the dormant period from December to March. The images were taken on the upper surface of the tube as described previously (Bauerle *et al.,* 2008). Root images were analysed with WinrhizoTron MF software (Regents Inc., Quebec, Canada) for fine root number, distribution, diameter (threshold of ≤ 2 mm), age, survival rates, and date of first appearance and disappearance/death. Each tube had 45 viewing windows (15 × 18 mm) for a total viewing area of 0.0125 m^2.

Fine root birth was estimated by calculating the date midway between the previous observation and the date when the fine root was first observed. Fine root death and disappearance were also estimated with a similar protocol (Bauerle *et al.,* 2008). Timing of when fine roots were produced, disappeared, or died was recorded; new fine root growth was determined to be white in colour, while dead fine roots were identified to be black and shrivelled in appearance (Comas *et al.,* 2000). To determine the standing crop for the growing season, the difference between total fine root production and total fine root disappearance and mortality was quantified over time from 2017 to 2019 (Bauerle *et al.,* 2008).

From 2017 to 2019, from bud break to harvest, aboveground phenological stages were recorded using the Eichhorn-Lorenz phenological stage system (Lorenz *et al.,* 1995) whenever root images were collected. The imaging sessions performed at the following phenological stages were selected for this analysis: ecodormancy (EC), bloom (BL), veraison (V), harvest (H), and leaf fall (LF). The corresponding calendar dates for each phenological stage in each study year are provided in Table S2.

4. Data analysis

Fine root production and root standing crop were studied over time by observing roots at key phenological stages and analysed with negative binomial mixed models to control for overdispersion in the root count over time. One minirhizotron tube was excluded because root counts exceeded five standard deviations from the mean and inspection revealed air gaps and substantial root intrusion from other plants. A second tube was excluded because an imaging software malfunction resulted in missing images. Fine root tip age was calculated as the time elapsed between its first appearance in the minirhizotron images and the observation date. Mean root tip age was analysed using linear mixed-effects models following a log (x + 1) transformation of mean age in days. Fixed effects were assessed using analysis of variance (ANOVA). Fine root tip age data were grouped into the following age classes: 0–28 days, 29–60 days, 61–179 days, and 180+ days based on the distribution of the data. To assess mean root tip age, the groups were divided into 1–60 days, 61–179 days, and 180+ days, as the original 1–28-day and 29–60-day groups did not follow a normal distribution after averaging the ages of individual fine root tips. Also, the vertical fine root distribution data were grouped into the following distribution classes: shallow (0–18 cm), middle (18–36 cm), and deep (36–55 cm), according to Centinari *et al.* (2016). The proportions of roots within each age class and soil depth class were analysed using linear mixed-effects models after logit transformation. Age class and soil depth class were included as categorical explanatory variables in their respective models; the response was a numerical proportion rather than an ordered categorical outcome.

For the mixed-effects analyses, a two-way factorial model was used, with technique and timing of application as fixed factors, including their interaction (technique × timing). Additional fixed effects included phenology, year, fine root age classes, and soil depth sections. Models of root age and root distribution included random intercepts for half-row–replicate combinations and tube identity. The tube random intercept accounted for non-independence among repeated

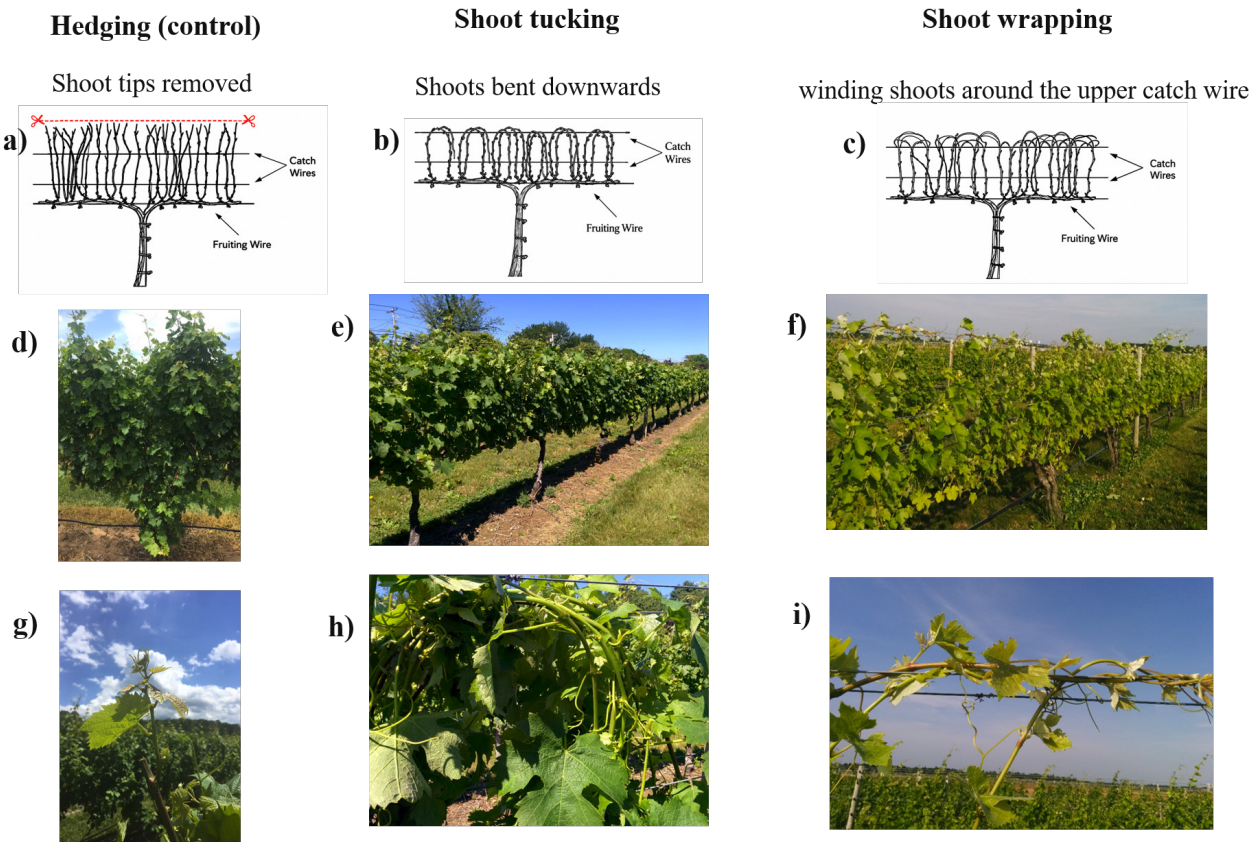


FIGURE 1. Shoot tip management practices applied to *Vitis vinifera* L. cv. Cabernet franc cl. 1 grafted onto 3309C rootstock: shoot hedging (control; a, d, g), shoot tucking (b, e, h), and shoot wrapping (c, f, i).

Schematics illustrate shoot placement (a–c), photographs show canopy appearance (d–f), and close-up photographs show a cut shoot following hedging (g) and retained shoot positioning after tucking (h) and wrapping (i). Hedging removed the shoot apices. Shoot tucking involved bending shoots downwards and placing them between the catch wires, whereas shoot wrapping involved winding shoots around the upper catch wire, while retaining leaf area.

observations within the same minirhizotron tube across phenological stages and years, whereas temporal fixed effects described variation in the mean response. For root production, mortality and standing crop, models containing both random intercepts failed to converge; these analyses therefore retained only the half-row–replicate random intercept, with each half-row representing an experimental unit. Differences in mean values between treatments were determined using Tukey's adjusted pairwise comparison. The marginal means and standard errors were then converted to root tips per square metre viewing window. The lme4 (Bates *et al.,* 2015) and lmerTest (Kuznetsova *et al.,* 2017) packages in R (R Core Team, 2024) were used to fit the models. Negative binomial mixed-effects models were fitted using glmmTMB (Brooks *et al.,* 2017).

Root lifespan data were analysed with Cox proportional hazards regression, comparing the control against shoot tuck and against shoot wrap, allowing the influence of all other covariates to be held constant, to determine the 'hazard' of an individual covariate (Cox, 1972). The 'hazard' of a covariate refers to the risk of mortality of a root at a given time, which is modelled as the product of a baseline hazard function and the effects of k covariates (Allison, 1995; Bauerle *et al.,* 2008). The tested covariates included soil layer (as determined by location on the tube), root diameter, hedging technique, and timing of application.

The hazard ratios were also calculated. These ratios are individual ratios of hazards between two levels of a covariate, for example, control technique versus shoot tuck, and early timing versus late timing.

The vegetative and reproductive datasets from the above ground components of this experiment (Logan *et al.,*2021), together with the belowground data obtained in the present study, were analysed using Pearson's correlation coefficients. Correlation analyses were performed separately for each shoot tip management practice, pooling observations across years (2017–2019) and application timings to explore overall associations between aboveground and belowground traits. Pooling was motivated by the limited effects of phenological timing of treatment application and year, which had limited impacts on aboveground and belowground traits. These correlation analyses were exploratory and were not adjusted for year or application timing; the reported *P*-values were not corrected for multiple comparisons. Correlation matrices were generated using the *corrplot* package in R (Wei & Simko, 2024). Figures were generated using MATLAB (The MathWorks, Inc., 2024) and R (R Core Team, 2024) statistical software.

RESULTS

1. Weather conditions

The 2017–2019 growing seasons had variable amounts of rainfall and growing degree days (GDDs) (Figure 1). The wettest year in this study was 2017, with high precipitation of 811 nm in total from April to July, while the driest was 2019, with a total of 572 mm. The greatest accumulation of GDDs was in 2018, with an accumulation of 1762 °C, compared to 1677 °C in 2017 and 1513 °C in 2019 (Figure 2).

2. Fine root age structure

The distribution of fine root age varied among shoot tip management practices and phenological stages (Figure 3) for the pooled 2018–2019 dataset. The 2017 dataset was excluded from this analysis because minirhizotron observations began late in the season, preventing older root cohorts from being represented. Across treatments, most fine roots were classified within the 61–179-day age class and ≥ 180-day age classes, whereas fine roots younger than the 60-day age class represented a smaller proportion of the total fine root population. The distribution of fine root age changed seasonally across all treatments, with a greater proportion of younger fine root tips occurring during budbreak and bloom (Figures 3b and 3c), while older fine root tips predominated during ecodormancy and harvest (Figures 3a and 3e).

Within this seasonal pattern, shoot tip management practices affected the distribution of fine root age at specific phenological stages. At ecodormancy (Figure 3a), SW increased the frequency of fine root tips in the 61–179-day age class compared with Control and ST. At budbreak (Figure 3b), SW produced a greater frequency of fine root tips in the ≥ 180-day age class than the other treatments. During bloom (Figure 3c), treatment differences were limited to the 61–179-day age class, whereas no significant differences among shoot tip management practices were observed at veraison or harvest (Figures 3d and 3e).

No significant interactions between shoot tip management practice and application timing were detected, indicating that timing effects were independent of shoot tip management; therefore, timing effects are presented separately (Figure 4). Overall, application timing exerted limited influence on fine root age structure. Significant differences were detected only at budbreak in 2018 (Figure 4a) and bloom in 2018 and 2019 (Figures 4c and 4d). However, these responses were restricted to specific root age classes and differed across years, suggesting no consistent effect of early versus late application timing in fine root age.

3. Vertical fine root distribution

Fine root distribution along the soil profile was not affected by year; therefore, the data were pooled across years for analysis (Figure 5). Across all treatments, most fine root production occurred in the shallow soil layer (0–18 cm), although shoot tip management practices altered the distribution of fine roots among soil depths (Figure 5a). SW shifted fine root distribution toward the deep soil layer (36–55 cm) relative to ST, particularly at budbreak, bloom, and harvest (Figure 5b). Conversely, SW allocated a smaller proportion of fine roots in the shallow soil layer compared with C and ST treatments during these phenological stages. In contrast, the depth distribution of fine roots in ST vines remained similar to that of the C throughout the growing season.

Overall, SW consistently stimulated a greater proportion of fine roots in deeper soil layers, whereas ST had little effect on root distribution relative to C. Descriptive statistics, including coefficients of variation for the depth distribution of fine roots across soil layers, are provided in Table S4.

4. Fine root production

Fine root production varied among phenological stages, years, and shoot tip management practices (Figure 6). Across all treatments, root production followed a seasonal pattern, increasing from budbreak to bloom and veraison before declining toward harvest and ecodormancy.

No significant differences among shoot tip management practices were detected in 2017, regardless of application timing (Figures 6a and 6d). Differences among treatments were observed in 2018 and, to a lesser extent, in 2019. Under the early application, SW produced more fine roots than ST treatments at budbreak, bloom, and veraison in 2018 (Figure 6b), and maintained greater root production at veraison in 2019 (Figure 6c).

Responses under the late application differed from those observed under the early application. In 2018, the C and ST treatments generally produced more fine roots than SW at budbreak, bloom, and veraison (Figure 6e), whereas no consistent differences among treatments were observed in 2019 (Figure 6f).

Overall, treatment effects on fine root production depended on application timing, year, and seasonal environmental conditions (Figure 2). However, the most pronounced treatment response occurred in SW vines following the early application, particularly during periods of active root growth. Descriptive statistics, including coefficients of variation for fine root production across phenological stages, application timings, and years, are provided in Table S5.

5. Fine root lifespan

Root lifespan was evaluated using Cox proportional hazards regression (Tables S6 and S7). Neither shoot tip management practices nor application timing significantly affected the hazard of fine root mortality (Table S6). In contrast, significant effects were detected for year of root birth, soil depth, and phenological stage. Fine roots located in the deepest soil layer (36–55 cm) exhibited a lower mortality risk than those in the shallow soil layer (0–18 cm), and hazard ratios indicated that absorptive fine roots (< 0.5 mm diameter) had a greater mortality risk than transport fine roots (0.5–2 mm diameter) (Table S7).

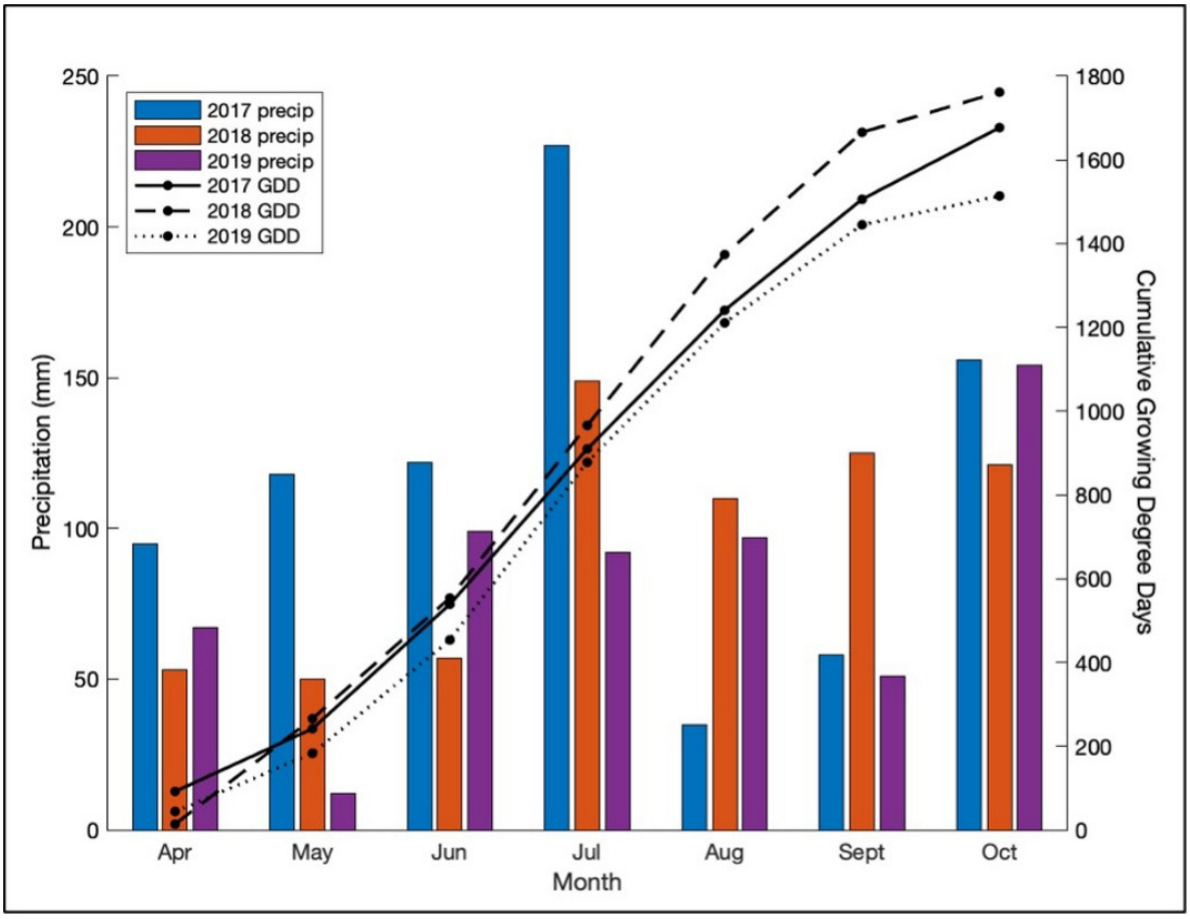


FIGURE 2. Growing degree day accumulation (GDD base 10 °C) calculated from daily minimum and maximum temperatures from 1 April to 31 Oct. and precipitation (mm) for the experimental site from 2017 to 2019.

Data were obtained from Network for Environment and Weather Applications (NEWA) stations at Lansing, NY, except for Sept. and Oct. 2019, which were obtained from the NEWA station at Romulus (Thirsty Owl).

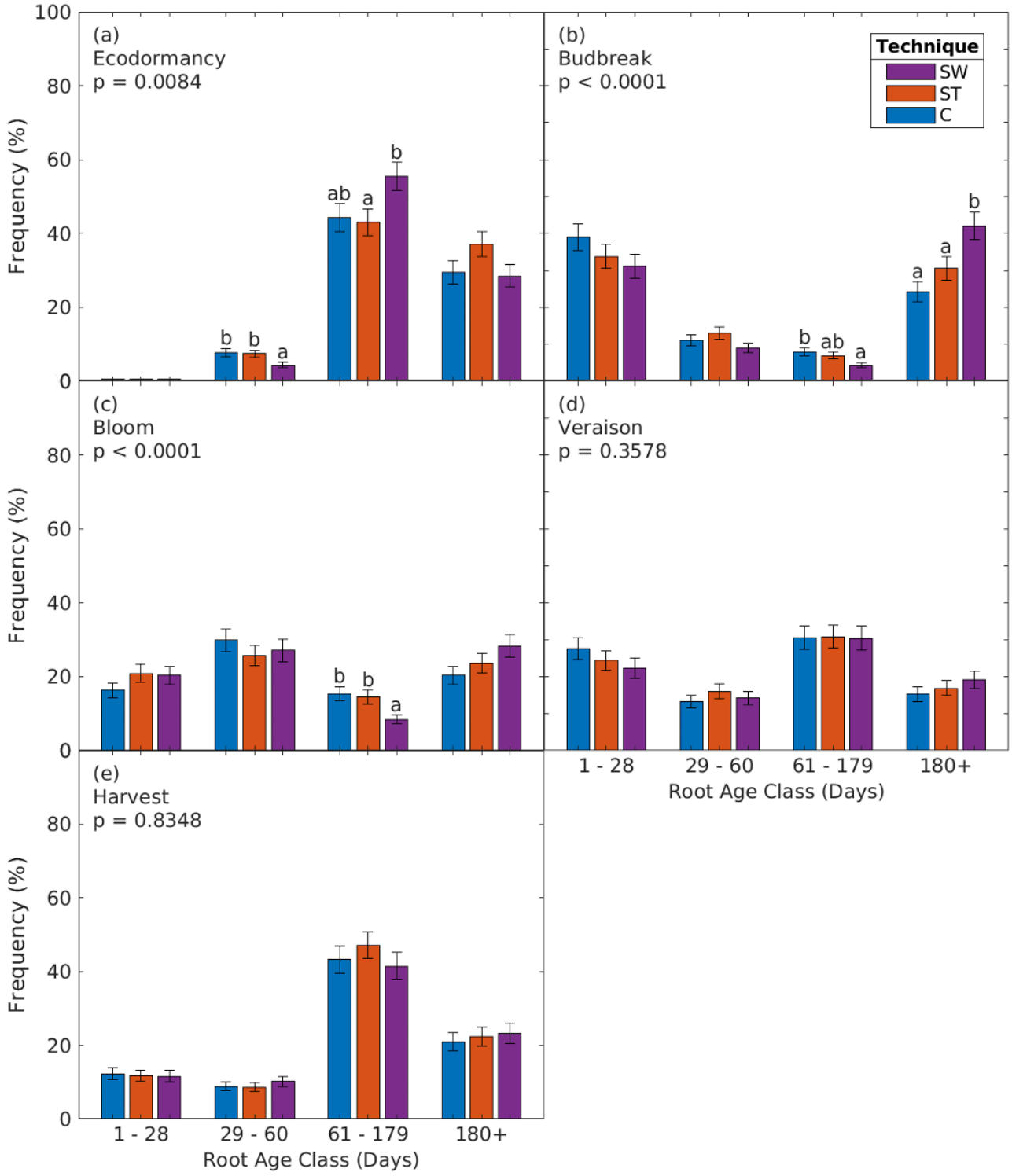


FIGURE 3. Fine root age structure (relative frequency of root tips in each age class, expressed as a percentage), at ecodormancy (a), budbreak (b), bloom (c), veraison (d), and harvest (e), in response to shoot tip modification techniques (Control = C, Shoot Tuck = ST, and Shoot Wrap = SW) applied early and late (shoots at 30 and 90 cm above the top catch wire, respectively) to Cabernet franc vines in Lansing, NY.

Estimated marginal means summarise observations across 2018–2019 and both application timings. Data from 2017 were excluded because observations began later in that season and root tips were ≤ 150 days old. Bars represent model-derived estimated marginal means back-transformed to the percentage scale; error bars indicate ±1 standard error. Different letters indicate significant differences among management practices within an age class at a given phenological stage ($P < 0.05$). *P*-values shown in each panel refer to the technique × age-class interaction.

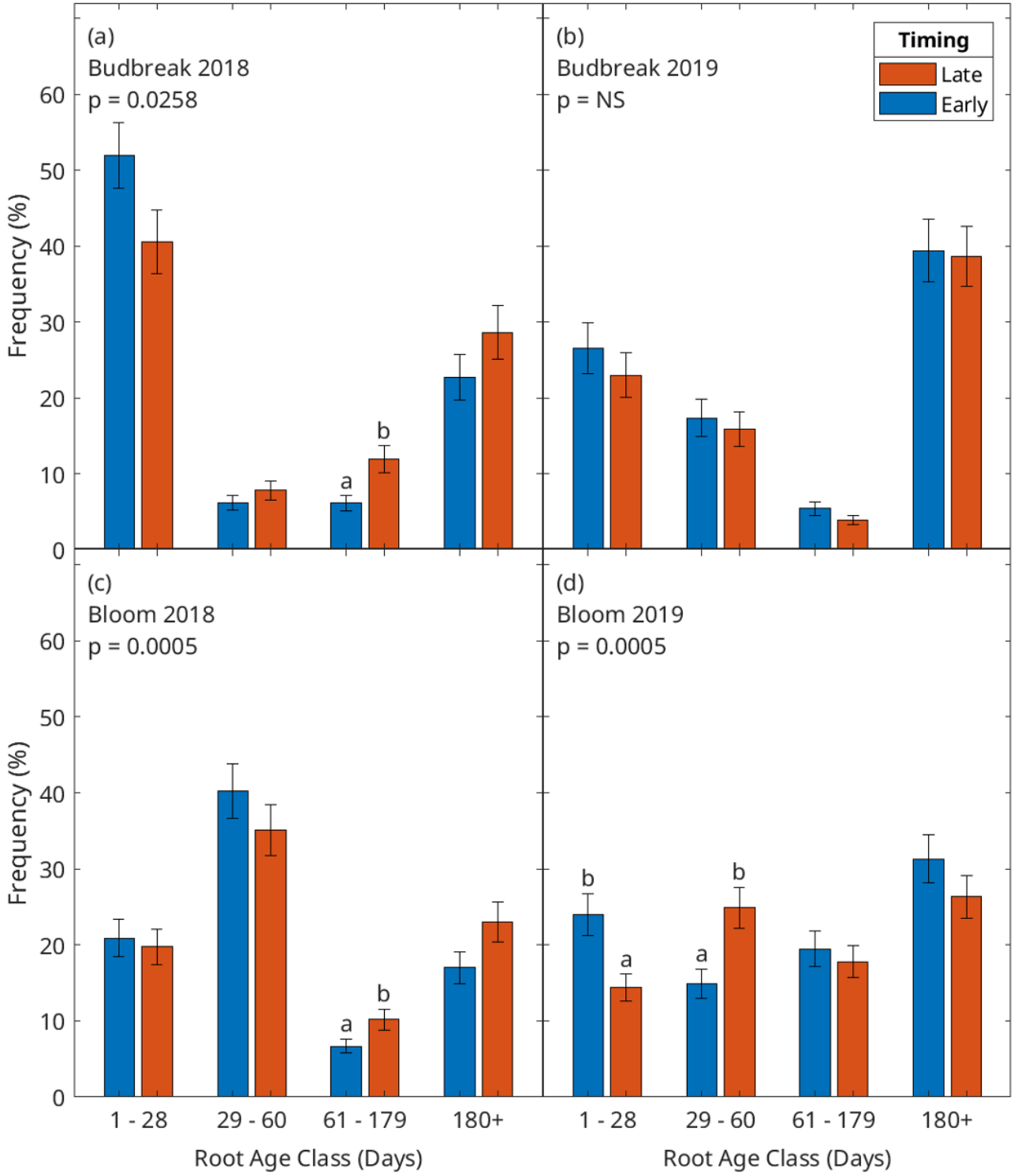


FIGURE 4. Fine root age structure (relative frequency of root tips in each age class, expressed as a percentage), at budbreak in 2018 (a) and 2019 (b), and bloom in 2018 (c) and 2019 (d), in response to application timing: Early and Late (shoots at 30 and 90 cm above the top catch wire, respectively) to Cabernet franc vines in Lansing, NY.

Bars represent model-derived estimated marginal means back-transformed to the percentage scale; error bars indicate ±1 standard error. Different letters indicate significant differences between application timings within an age class, year and phenological stage ($P < 0.05$). *P*-values are shown for each year and phenological stage; NS indicates a non-significant result. Analyses of the individual fine root age classes (Figures S1–S4) revealed only limited and inconsistent treatment effects. Differences in the 1–60-day age class were generally small (3–5 days) despite statistical significance at selected phenological stages (Figures S1 and S2). Differences in the 61–179-day age class were detected only at budbreak in 2018 (Figure S3), while differences in the ≥ 180-day age class occurred primarily at harvest in 2018 and at budbreak and bloom in 2019 (Figure S4). These responses varied among years and phenological stages. Descriptive statistics, including coefficients of variation for fine root age classes, are provided in Table S3.

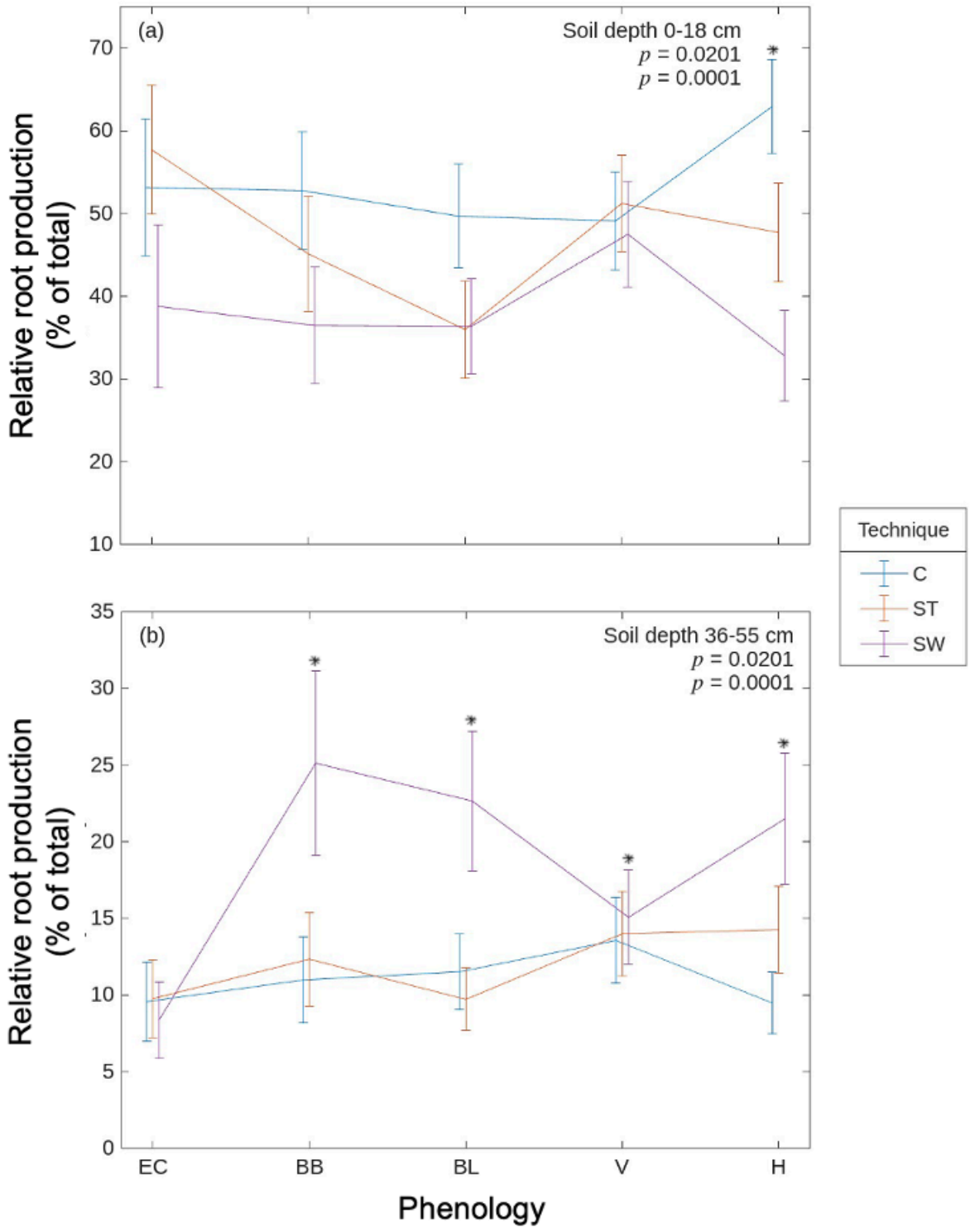


FIGURE 5. Vertical root distribution of newly produced fine root tips in the shallow (0–18 cm) soil layer (a) and the deep (36–55 cm) soil layer (b), expressed as a percentage of total root tips produced per minirhizotron tube from ecodormancy to harvest in response to shoot tip management practices (Control = C, Shoot Tuck = ST, and Shoot Wrap = SW) applied early and late (shoots at 30 and 90 cm above the top catch wire, respectively) to Cabernet franc vines in Lansing, NY.

Estimated marginal means summarise observations across 2017–2019 and both application timings. Values represent model-derived estimated marginal means back-transformed to the percentage scale; error bars indicate ±1 standard error. Asterisks indicate significant differences among management practices within a phenological stage and soil depth layer, based on Tukey-adjusted pairwise comparison ($P < 0.05$). Phenological stages were as follows: EC: Ecodormancy, BB: Budbreak, BL: Bloom, V: Veraison, H: Harvest. The displayed *P*-values refer to the technique × phenology × depth ($P = 0.0201$) and technique × soil depth interaction ($P = 0.0001$) for both Figures 5a and 5b.

6. Relationship between aboveground and belowground traits

Pearson correlation analysis revealed treatment-specific relationships between aboveground and belowground traits in the Control (Figure 7a), Shoot Tuck (ST; Figure 7b), and Shoot Wrap (SW; Figure 7c) treatments. Across all shoot tip management practices, fine root tips (root tips × 100 m^{-2}) produced at harvest (HB) were consistently and positively correlated with reproductive traits, including berry number (BN), berry weight (BW), cluster compactness (CC), and cluster number (CN). Conversely, veraison standing crop (VSC) was generally negatively correlated with these reproductive traits. Fruit-zone lateral shoot counts (FZC) were positively correlated with root standing crop at veraison (VSC) in ST, whereas total lateral growth (LG) was negatively correlated with average root tip diameter (AD) in C (Figure 7).

DISCUSSION

Shoot tip management practices affected grapevine fine root dynamics, but the degree and consistency of these responses depended on the treatments, application timing, and year. SW modified fine root age structure and depth distribution, but its effects on fine root production depended on application timing and year. Early SW increased production relative to ST at several phenological stages in 2018, whereas late SW generally produced fewer roots than C and ST in the same year (Figures 6b and 6e). In contrast, ST responses were more similar to those of C than SW across most fine root traits. Fine root lifespan was largely unaffected by the treatments, suggesting that these practices primarily influenced fine root production and spatial distribution rather than fine root longevity. While application timing contributed to some of the observed responses, its effects were less consistent among years than those associated with shoot tip management practices. Together with the previously reported differences in canopy architecture and vegetative development from the same experimental vineyard (Logan *et al*., 2021) These findings support the concept that aboveground and belowground traits are physiologically coordinated.

The contrasting belowground responses observed among shoot tip management practices, particularly in fine root production (Figure 6), fine root age structure (Figures 3 and 4), and vertical distribution of fine roots (Figure 5), may reflect differences in how these practices reshape canopy architecture and vegetative growth (Logan *et al*., 2021). Despite both SW and ST retaining shoot tissue compared with C, previous work in the same experimental vineyard showed that these practices modify canopy architecture in distinct ways (Logan *et al*., 2021; Table S1). Specifically, SW consistently reduced lateral shoot emergence, vegetative regrowth and cluster compactness relative to both C and ST, while maintaining the primary shoot intact. In contrast, ST generally resulted in aboveground responses more similar to C treatment, particularly with lateral shoot development and overall vine growth (Logan *et al*., 2021). The reductions in lateral shoot emergence observed under SW have also been reported by France *et al*. (2018), suggesting that this response is consistent across vineyard conditions rather than being unique to the present study.

Because vegetative growth and cluster development represent major carbon sinks during the growing season (Comas *et al*., 2005), the reduction in vegetative regrowth associated with SW may have altered whole-vine source–sink relationships and carbon allocation between aboveground

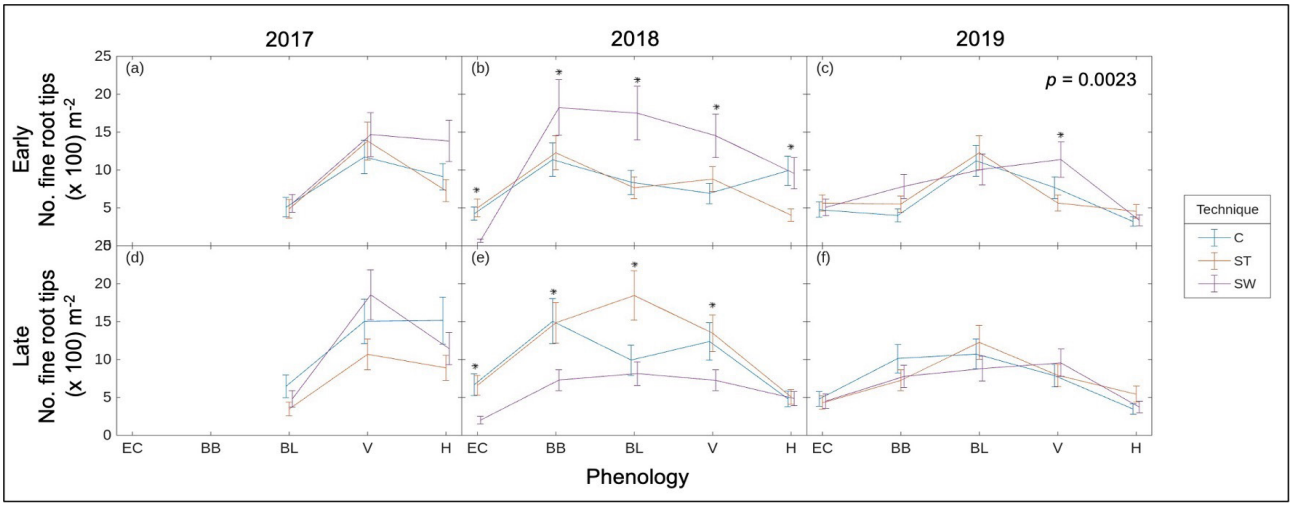


FIGURE 6. Model derived estimated marginal mean counts ± standard errors of fine root tips born at each phenological stage, expressed per m^2 of minirhizotron viewing area, in response to shoot tip modification techniques (Control = C, Shoot Tuck = ST, and Shoot Wrap = SW) applied early (a, b, and c) and late (d, e, and f) in the season to Cabernet franc vines in Lansing, NY, in 2017 (a and d), 2018 (b and e), and 2019 (c and f) respectively.

Early and late were when shoots were at 30 and 90 cm above the top catch wire, respectively. Asterisks indicate significant differences among techniques within each timing and phenology–year combination (Tukey-adjusted pairwise comparisons, $P < 0.05$). Phenological stages were as follows: EC: Ecodormancy, BB: Budbreak, BL: Bloom, V: Veraison, H: Harvest. The displayed *P*-value ($P = 0.0023$) refers to the overall technique × timing × phenology-year interactions across panels (a–f).

and belowground organs. Although carbon partitioning was not measured in this study, this mechanism provides a plausible physiological explanation linking the aboveground responses previously reported by Logan *et al*. (2021) with the contrasting belowground responses observed in the present study. Differences in fruit demand could also contribute to the observed root responses. However, Logan *et al*. (2021) reported inconsistent treatment effects on yield and substantial crop losses to birds and disease. Although dormant pruning weights did not differ among treatments, repeated shoot removal from hedging treatments limited their reliability as indicators of vine size. Consequently, the yield-to-pruning-weight ratio would not consistently distinguish treatment effects on vine balance, limiting our ability to assess the contribution of fruit sink demand to fine root responses.

Hormonal regulation and source–sink relationships may work together to explain the contrasting responses to hedging, ST, and SW. Removing the apex versus retaining and repositioning it may alter lateral shoot development through interactions among auxin, cytokinins and sugar availability (Gallavotti, 2013; Cao *et al*., 2023). In pea, sugar availability and cytokinin signalling interact during bud release after apex removal (Cao *et al*., 2023), supporting the possibility that carbon availability and hormonal regulation jointly influence lateral shoot development. Thus, the reduced lateral development reported under SW (Logan *et al*., 2021) could involve altered apical control as well as changes in assimilate competition. Effects on shoot–root signalling provide a further possible link to root development but were not tested here. Because neither hormone dynamics nor carbon partitioning was measured, their contributions to the observed belowground responses remain hypothetical.

Fine root production was strongly regulated by seasonal phenology and varied with shoot tip management practices, application timing, and year. Across treatments, fine root production followed the seasonal pattern previously described for grapevines, generally peaking between budbreak and veraison before declining towards harvest and ecodormancy (McArtney & Ferree, 1999; Comas *et al*., 2005). However, the magnitude of treatment effects differed among years, indicating that the influence of shoot tip management on belowground growth was dependent on the growing season (Figure 2). Our hypothesis that early application would have greater effects on fine root dynamics received only partial support. Early SW increased fine root production relative to ST at several phenological stages in 2018, whereas late SW generally produced fewer roots than C and ST during the same year (Figures 6b and 6e). Treatment differences were absent in 2017 and more limited in 2019. Thus, a longer period following canopy modification alone cannot explain the observed responses. A reduction in lateral shoot growth does not necessarily lead to a proportional

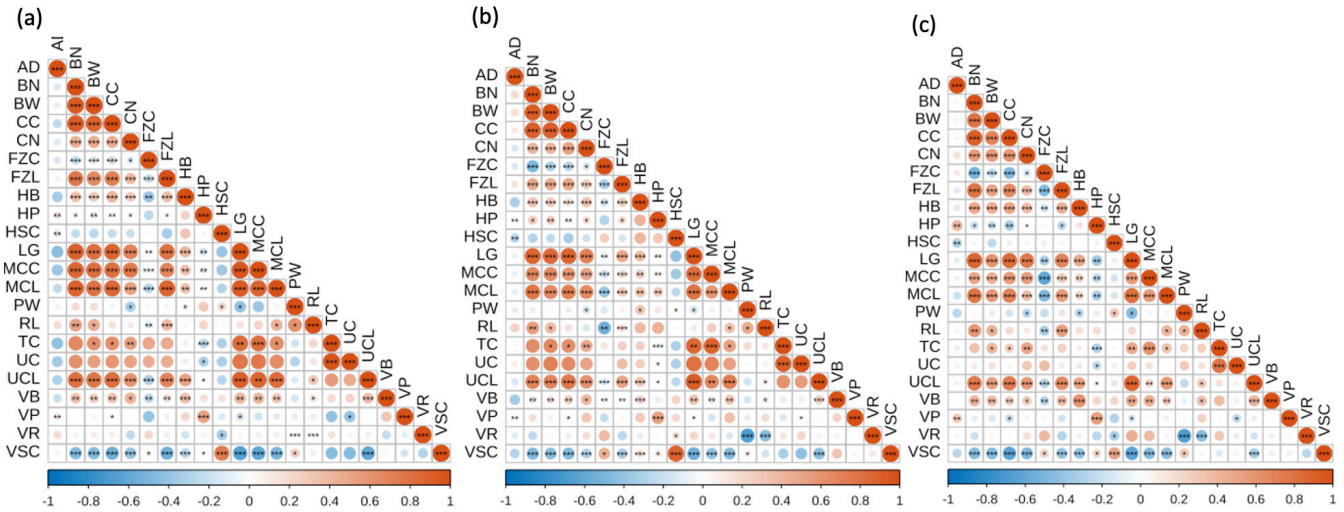


FIGURE 7. Pearson correlation plots showing relationships between above-ground and below-ground parameters collected between veraison (EL-36) and harvest (EL-38) in 2017 to 2019, in response to shoot tip modification techniques Control, Shoot Tuck, and Shoot Wrap (a, b, and c, respectively) on cv. Cabernet franc vines in Lansing, NY.

Correlations were calculated separately for each management practice using observations pooled across 2017–2019 and both application timings. These exploratory correlations were not adjusted for year or application timing. Colour indicates correlation direction (red, positive; blue, negative), while colour intensity and circle size indicate its strength. Asterisks denote significance at $P < 0.05$ (*), 0.01 (**), and 0.001 (***). The reproductive and root variables abbreviations and units were: BW = berry weight (g per berry), CC = cluster compactness (number of berries per cm rachis), BN = berry number per cluster, RL = rachis length (cm), CN = cluster number per vine, PW = pruning weights per vine (kg), VR = veraison rating (rating of veraison progression with 1 = green, 5 = fully red and soft), AD = average root tip diameter (mm), VB and HB = number of fine root tips produced at veraison and harvest, respectively (root tips × 100 m^{-2}), VP and HP = percent of root tips produced at soil depth range of 36–55 cm at veraison and harvest, respectively, and VSC and HSC = standing crop at veraison and harvest, respectively (running cumulative dead – annual live root tip production/m^2) over observation sessions. The vegetative variable abbreviations and units were: FZC and FZL = fruit zone lateral counts per vine and mean length per shoot, respectively (fruit zone = 30 cm from the fruit zone wires), LG = total lateral growth (lateral lengths x total lateral counts), MCC and MCL = middle canopy counts per vine and mean length per shoot (middle canopy = 30 cm above fruit zone), and UC, UCL = upper canopy counts per vine and mean length per shoot (upper canopy = 30 cm above middle canopy).

increase in root production, because carbohydrates may also support fruit development, maintenance and reserve storage (Comas *et al*., 2005). Consequently, similar aboveground responses could be accompanied by different root responses depending on vine phenology and seasonal growing conditions, although the contributions of these factors were not resolved in this study. Similar interactions between vine phenology, seasonal variability, and fine root growth have been reported in grapevines and other perennial species (Hale & Weaver, 1962; Comas *et al*., 2005; Eissenstat & Yanai, 1997; Lynch, 1995; Radville *et al*., 2016). These year-to-year differences in fine root production may also help explain the observed differences in fine root age structure (Figures 3 and 4).

In addition to affecting fine root production, shoot tip management practices also influenced fine root age structure (Figures 3 and 4). The proportion of older root cohorts was greater under SW at specific phenological stages, particularly during ecodormancy and budbreak (Figures 3a and 3b). In contrast, differences in the mean age of roots within individual age classes were limited and inconsistent (Figures S1–S4), suggesting that shoot tip management practices influenced fine root age structure by altering the proportion of roots within different age classes rather than changing the mean age of roots within each age class.

The greater proportion of older fine root cohorts observed under SW, particularly during ecodormancy and budbreak (Figures 3a and 3b), likely reflects cumulative responses from the preceding growing season rather than immediate responses to treatment application. The reduced lateral shoot emergence previously reported under SW (Logan *et al*., 2021) may have altered late-season carbon allocation, thereby shifting fine root production and turnover before dormancy. This interpretation is supported by seasonal patterns of fine root production (Figure 6), suggesting that treatment differences in fine root age structure emerged late in the growing season and persisted into winter. Consequently, these responses may reflect changes in late-season fine root production, greater persistence of previously produced roots, and reduced root turnover during winter. Because carbohydrate dynamics and non-structural carbohydrate accumulation were not directly measured, this interpretation remains hypothetical. The absence of similar responses in all years further suggests that seasonal environmental conditions influenced the magnitude of these legacy effects.

One of the most consistent responses observed in this study was the greater proportion of fine roots located in the deeper soil layer (36–55 cm) under SW compared with the C and ST treatments (Figure 5b). Unlike fine root production, which varied among years, the effects of SW on fine root depth distribution remained relatively consistent across phenological stages, suggesting that shoot tip management practices, particularly SW, influenced not only the amount of new root growth but also their spatial distribution within the soil profile. Changes in carbohydrate availability alone do not explain the greater proportion of fine roots at depth. Root distribution may also depend on depth-specific soil conditions, including water and nutrient availability, but their contributions to the observed treatment responses were not assessed. The observed shift in root distribution could improve access to deeper water and nutrient resources, particularly in perennial species growing under variable seasonal conditions (Comas *et al*., 2013; Lynch, 1995). However, because carbon allocation, root hydraulics, and soil moisture dynamics were not directly measured, the mechanisms driving this distribution and its potential functional benefits remain unconfirmed.

The correlation patterns (Figures 7a–7c) suggest exploratory associations between aboveground and belowground traits within each shoot tip management practice. However, these correlations cannot establish causal relationships. Although timing and year effects were limited for many traits, the pooled correlations may partly reflect interannual variation or differences between application timings. The number of trait combinations examined and repeated sampling of the same experimental unit also warrant caution when interpreting statistical significance. Furthermore, minirhizotron observations were limited to the upper 0.55 m of the soil profile and may not fully capture fine root dynamics occurring at greater depths. Future studies integrating measurements of canopy carbon assimilation, non-structural carbohydrate reserves, hormonal regulation, root physiological function, and ^{13}C-based carbon tracing would provide a more mechanistic understanding of how shoot tip management practices influence fine root dynamics.

These findings suggest that growers should consider belowground responses when selecting canopy management practices, although their variability among years and application timings limits general recommendations. Practical adoption of wrapping or tucking also depends on labour requirements and whether they replace existing mechanised operations. Under the economic assumptions used by Logan *et al*. (2021), application times of approximately 30 seconds per vine gave costs comparable to two mechanical hedging passes, while 60 seconds per vine approached the combined costs of hedging and mechanical leaf removal. Any additional labour required to release retained shoots from wires during dormant pruning remains unquantified. Growers should therefore evaluate these practices on a small scale, considering canopy benefits, labour availability and local operating costs before wider adoption.

CONCLUSIONS

Although shoot tip management practices are widely used to regulate canopy architecture, their effects on grapevine fine root dynamics have remained largely unexplored. Our findings demonstrate that modifying canopy development through shoot tip management also influences belowground development, with shoot wrapping producing the most consistent responses among the evaluated treatments. These results highlight the importance of adopting a whole-vine perspective when evaluating viticultural practices. Future research should clarify how carbon allocation, hormonal regulation, and shoot–root signalling contribute to these

belowground responses. Such studies will improve our understanding of the coordination between aboveground and belowground development and inform vineyard management strategies that enhance vine resilience under increasingly variable environmental conditions.

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DATA AVAILABILITY

The data analysed during the current study are available from the corresponding author upon reasonable request.

AUTHOR CONTRIBUTION

Hereby, all authors declare that they have contributed to the development of this field trial and that they are all in agreement with the manuscript.

CONFLICT OF INTEREST STATES

There is no conflict to declare.

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