

Article

Rootstock-Dependent Responses of Monastrell Grape Ripening and Phenolic Traits to Moderate Cluster-Zone Warming Under Semi-Arid Vineyard Conditions

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Highlights

1. Moderate warming increased berry weight and advanced ripening in Monastrell.
2. 140Ru showed larger losses in phenolics and must colour than 110R.
3. Rootstock choice can reduce quality losses under warmer ripening conditions.
4. Monitoring berry heat exposure can improve harvest decisions in warm vineyards.

Abstract

We evaluated moderate cluster-zone warming in field-grown Monastrell grafted onto 110R and 140Ru over two seasons (2020–2021) in a semi-arid vineyard in south-eastern Spain. From pea-size to harvest, an open warming system increased cluster-zone air temperature by 1.15 °C on average. Warming increased cluster-zone mean and maximum temperatures, but berry temperature responses depended on year and rootstock because berry–air temperature differences and also time above thresholds changed. Berry weight increased in harvest in both years, and technological ripening advanced, with higher total soluble solids and maturity index, especially during ripening. Acid composition responded differently between rootstocks: under warming, 140Ru maintained higher malic acid and lower tartaric acid than 110R, resulting in a lower tartaric/malic ratio. Phenolic and colour responses were clearest at mid-ripening. Warming reduced must total phenolic index (TPI), skin-related phenolics, anthocyanins, and must colour more strongly in 140Ru, while 110R retained a more stable phenolic and colour profile. Exposure–response analyses showed that time in the 25–35 °C range and berry thermal time were more closely related to technological and phenolic variation than time above 35 °C. These results suggest that, under the warming conditions imposed in this study, 110R offered a better compromise than 140Ru between ripening advancement and the preservation of phenolic and colour-related traits.

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Keywords: heat exposure; berry–air thermal decoupling; berry temperature; maturity index; anthocyanins; tannins

1. Introduction

Climate change is unequivocal and is already altering temperature regimes and evaporative demand in many agricultural regions. The IPCC Sixth Assessment cycles highlight sustained warming since the mid-19th century and project further increases in mean temperature during the 21st century, with important regional consequences for water availability and extreme events [1]. Rising temperatures pose significant threats to viticulture, a sector highly sensitive to climate change. Mediterranean viticulture is particularly vulnerable because grape ripening frequently occurs under hot, dry conditions, and additional warming is expected to intensify heat loads and atmospheric demand, especially in semi-arid areas such as south-eastern Spain.

Temperature is a key driver of grapevine phenology and berry development. Warmer conditions can advance developmental stages, shift ripening towards hotter periods of the season, and modify the balance between sugar accumulation and organic acid degradation [2,3]. A common consequence in warm seasons is an increase in soluble solids accompanied by lower titratable acidity, mainly due to enhanced malic acid degradation. This increases the maturity index (TSS/TA) and contributes to wines with higher alcohol, lower acidity, and reduced colour intensity, potentially complicating harvest decisions when technological and sensory targets diverge [4–6]. Temperature also influences the accumulation of secondary metabolites, including anthocyanins and tannins, which are critical for red-wine colour and mouthfeel. Elevated berry temperatures around and after veraison can reduce anthocyanin accumulation and/or promote anthocyanin degradation, and may alter phenolic trajectories relative to sugar accumulation, contributing to a partial decoupling between technological and phenolic maturity [7–9].

These challenges underscore the need for adaptive strategies to safeguard wine quality and regional identity. Potential approaches include the adoption of cultivars better suited to future climatic conditions. There is substantial inter- and intra-cultivar variation in traits such as phenology and drought tolerance, offering opportunities to better match grapevine performance to new climate scenarios [10]. Monastrell (also known as Mourvèdre or Mataro), for example, is a late-ripening, black-skinned cultivar native to south-eastern Spain. Well adapted to high temperatures and frequent drought, it exhibits physiological characteristics associated with tolerance to moderate water stress [11]. Nevertheless, being adapted to warm and dry conditions does not necessarily mean that Monastrell berries are insensitive to further temperature increases, especially for compositional traits closely linked to fruit-zone microclimate. In this context, rootstock choice may further influence the magnitude and direction of these responses, as rootstocks modulate vine water uptake, hydraulic conductance, stomatal regulation, vigour and nutrient status, which can, in turn, affect berry growth and composition under stressful environmental conditions [12]. These effects are particularly relevant because rootstock genotype can affect both primary and secondary berry metabolism, including phenolic accumulation and other quality-related traits [13,14]. Thus, the rootstock–scion combination appears to be highly relevant for assessing climate resilience in warm viticultural areas [11,14,15]. In south-eastern Spain, Monastrell is commonly grafted onto drought-tolerant rootstocks such as 110R and 140Ru [11]. Recent studies conducted under well-irrigated conditions have shown contrasting rootstock responses to moderate warming: 110R maintained higher stomatal conductance and transpiration, whereas 140Ru exhibited a more conservative behaviour. In addition, warming treatment delayed veraison and early ripening in 110R but not in 140Ru [16]. Collectively, these findings support the hypothesis that rootstock genotype can influence how warming affects ripening trajectories in warm, semi-arid environments [11,12].

This study examined how a realistic, moderate increase in cluster-zone temperature (mean +1.15 °C, representing local fruit-zone warming rather than a specific IPCC scenario), applied from pea-size to harvest using an open-field warming system, affects Monastrell berry growth, technological maturity, organic acid composition, and phenolic traits, and whether these responses differ between 110R and 140Ru. We also related compositional changes to berry thermal exposure and berry–air temperature differences in order to interpret year-to-year variability under semi-arid field conditions. These findings contribute to better understanding of grapevine adaptability and may help inform future viticultural strategies in semi-arid regions facing progressive warming.

2. Materials and Methods

2.1. Site, Plant Material, and Vineyard Management

The trial was conducted during the 2020 and 2021 growing seasons in an experimental vineyard located in Cehegín (Murcia, south-eastern Spain; 38°6′38.13″ N, 1°40′50.41″ W; 432 m a.s.l.) on a 0.10 ha plot of young *Vitis vinifera* L. cv. Monastrell vines. Vines were 3–4 years old during the experiment, grafted onto 110R and 140Ru rootstocks, planted at 2.8 × 1.0 m (3571 vines ha^{−1}) and trained to a bilateral cordon system. The site has a semi-arid Mediterranean climate, with hot and dry summers and low annual rainfall. During the study years, annual rainfall was 281 mm in 2020 and 386 mm in 2021, while mean annual air temperature was similar between years (18.0 and 18.1 °C, respectively). The main phenological periods considered were budburst–fruit set, fruit set–veraison, veraison–harvest, post-harvest and dormancy. During the veraison–harvest period, mean air temperature was 23.5 °C in 2020 and 24.1 °C in 2021, with very low rainfall in both seasons (6 and 3 mm, respectively). Winter pruning retained six two-bud spurs per vine, and non-productive shoots were removed in May. Irrigation was applied from April to October using the same seasonal water amount for all rootstock × scion combinations (mean 204 mm year^{−1}), scheduled according to ETc estimates. Additional irrigation and fertigation details are provided by Navarro et al. [16].

2.2. Experimental Design and Warming Treatment

The experiment followed a factorial design with two factors: temperature treatment (high temperature [HT] and control temperature [C]) and rootstock (140Ru and 110R), arranged in four blocks (Figure S1). Each block contained the four temperature × rootstock combinations, with six vines per combination, and the same plot structure was used in all blocks. The two outer vines of each plot were excluded to avoid border effects, and measurements were performed on the central vines according to the sampling scheme described in each methodological section. Control plants were positioned within each block, close to the corresponding HT plants and arranged similarly, but without the heating system. Vines were spaced 1.0 m within rows and 2.8 m between rows. The nearest control vine was 0.5 m from the edge of the HT structure, but this border vine was not used for measurements; therefore, the first measured control vine was 1.5 m from the structure edge. The perpendicular distance between adjacent rows was 2.8 m.

An open warming system was installed each season from pea-size until harvest to increase the cluster-zone temperature in the HT treatment. The system consisted of modular transparent cellular polycarbonate panels placed on both sides of the vine row from ground level to cluster height (Figure 1). The panels were assembled in continuous sections, positioned at a fixed distance from the vine row, and stabilized using anchors and vertical supports. Material properties and installation details are described by Navarro et al. [16].



Figure 1. Experimental vineyard with Monastrell vines and the open warming system used in the high temperature (HT) treatment. (A,B) Transparent cellular polycarbonate panels (8 mm; 65 × 210 cm) installed on both sides of the row from ground level to cluster height, set at 70° and positioned 50 cm from the vine row. HT structures were installed from pea-size stage to harvest each year. Control vines were managed identically but without panels (left side in (B)). (C) Cluster-zone microclimate station equipped with a shielded air temperature/relative humidity sensor. (D) TMC6-HD temperature probe positioned within a representative bunch to record berry surface temperature.

2.3. Microclimatic and Berry Temperature Measurements

Temperature and relative humidity in the cluster zone were recorded using data loggers installed in three of the four blocks for each treatment (Figure S1), providing three microclimate replicates per treatment ($n = 3$). Only air temperature was used for the thermal analyses presented in this study. Air temperature sensors (HOBO U12-013 dataloggers; Onset Computer Corporation, Bourne, MA, USA) were placed at cluster height within the fruit zone and protected from direct solar radiation, and temperature was recorded at 10 min intervals.

Berry temperature was monitored using one TMC6 HD probe (Onset Computer Corporation, Bourne, MA, USA) placed inside a representative cluster in each monitored plot (Figures 1D and S1). To reduce variability due to cluster exposure, all monitored clusters were selected with the same orientation and a similar position within the vine and canopy, so that berry temperature measurements provided a standardized estimate of berry temperature under comparable cluster-zone conditions. Berry temperature data were analyzed from 21 June onwards, after probe contact had stabilized.

From the 10 min records of cluster-zone air temperature (T_{air}) and berry temperature (T_{berry}), daily T_{max} (highest value recorded each day) and T_{mean} (mean of all daily records)

were calculated for both variables. Berry–air temperature difference was calculated as $\Delta T = T_{\text{berry}} - T_{\text{air}}$. Thermal exposure was quantified as cumulative hours within the 25–35 °C range and above 35 °C by summing the corresponding 10 min intervals over each period. Berry growing degree-days (GDD; base 10 °C) were calculated from berry T_{mean} as $\Sigma(T_{\text{mean}} - 10)$ for days when T_{mean} exceeded 10 °C.

2.4. Berry Sampling and Chemical Analyses

Monastrell berries were sampled at three common dates per season, corresponding to end of veraison, mid-ripening, and harvest at the experimental vineyard level: 8 August 2020, 1 September 2020, and 23 September 2020 in 2020, and 10 August 2021, 9 September 2021, and 30 September 2021 in 2021. In this sampling scheme, mid-ripening corresponded to 24 and 30 days after the end of veraison in 2020 and 2021, respectively. The same sampling dates were used for all rootstocks and temperature treatments within each season. Therefore, samples were compared at common calendar dates representing the ripening sequence, rather than at identical technological maturity for each treatment. For berry growth and quality analyses, two vines per block were sampled for each treatment combination. The two outer vines of each plot were excluded to avoid border effects. This resulted in eight sampled vines per treatment combination (two vines $\times$ four blocks; $n = 8$).

For each replicate, 500–600 g of berries were randomly collected from multiple clusters per vine, weighed, counted, and stored at -2 °C until analysis. A subset of 10 representative berries per replicate was stored at -80 °C for further skin and seed phenolic analyses. Dry matter was determined on a berry subsample by oven-drying at 60 °C to constant weight and expressed as % dry matter and dry matter per berry (g berry^{-1}). The remaining berries were gently crushed while avoiding seed breakage and centrifuged, and the obtained must (grape juice fraction) was clarified and analyzed for pH, total soluble solids (TSS), titratable acidity (TA), tartaric and malic acids, solutes per berry, and maturity index ($\text{MI} = \text{TSS}/\text{TA}$). Malic and tartaric acids were quantified by ion chromatography with suppressed conductivity detection on a Dionex ICS-3000 ion chromatography system equipped with an IonPac AS11 column (Dionex Corporation, Sunnyvale, CA, USA), with KOH as the eluent, using diluted and filtered samples ($0.45 \mu\text{m}$) and external calibration.

Total phenolic index (TPI) and extractable anthocyanins were determined following the methods described by Saint-Cricq et al. [17] and Ribéreau-Gayon et al. [18], and total tannins (catechin equivalents, mg g^{-1} berry fresh weight) were determined by methyl cellulose precipitation [19]. Must yield (%) was calculated as the juice mass recovered after crushing and centrifugation relative to the initial fresh berry mass. After centrifugation, colour intensity (CI) was calculated as $A_{420} + A_{520} + A_{620}$, hue as A_{420}/A_{520} , and CIELab coordinates (L^* , a^* , and b^*) were measured in clarified must using a Konica Minolta CR-400 colorimeter (Konica Minolta Sensing, Inc., Osaka, Japan) following the calibration procedure of the manufacturer.

2.5. Phenolic and Anthocyanin Extraction

The standard phenotyping protocol proposed by Rustioni et al. [20] was adopted for eno-carpological evaluation. Ten berries per replicate (stored at -80 °C) were dissected to separate skins, pulp, and seeds. These berries were considered a subsample within each vine replicate and not independent biological replicates. Skins were weighed, seeds were counted and weighed, and pulp mass was calculated by difference. Tissue proportions (%) were expressed relative to whole berry fresh weight, and the skin/pulp ratio was calculated as skin mass divided by pulp mass.

Skins and seeds were extracted for 24 h in 20 mL of ethanol:water:HCl (70:29:1). After filtration, total phenolic compounds were quantified spectrophotometrically using the Folin–Ciocalteu assay and expressed as catechin equivalents. Total anthocyanins in skin extracts were determined from absorbance at 540 nm and expressed as malvidin-3-O-glucoside equivalents. Total phenolics and anthocyanin concentrations obtained were normalized to tissue mass and expressed as mg g⁻¹ fresh weight of skin or seed by accounting for extraction volume and tissue mass.

2.6. Statistical Analysis

Data were analyzed separately for each year. For each sampling date, the effects of rootstock, temperature treatment, and their interaction were assessed by two-way ANOVA. When the rootstock × temperature interaction was significant, mean separation among the four treatment combinations was performed using Duncan's multiple range test. When the interaction was not significant, significant main effects were interpreted from the two-way ANOVA. All analyses were performed using Statgraphics Plus 5.1. Linear and non-linear regressions were fitted using SigmaPlot 11.0. Exposure–response analyses were performed using mean values calculated for each year, sampling date, rootstock, and temperature treatment combination, with the thermal exposure metrics (hours at 25–35 °C, hours > 35 °C, or berry GDD, base 10 °C) as covariates and year and/or rootstock as fixed factors. Factor × covariate interactions were tested to compare slopes. When interactions were not significant, a common slope was applied and group differences were evaluated through adjusted means/intercepts. These analyses were used to describe associations between berry thermal exposure and ripening or phenolic variables across sampling dates. Relationships between skin/pulp ratio and phenolic variables at harvest were assessed by Pearson correlation using replicate-level data. Statistical significance was set at $p \leq 0.05$.

3. Results

3.1. Environmental Conditions and Temperature Treatment

Mean temperature in the cluster zone increased under HT at all stages in both years and rootstocks (Table 1), with highly significant differences of approximately 1 °C and no clear divergence between 140Ru and 110R. By contrast, berry surface temperature (hereafter, berry temperature), however, followed a different pattern from cluster-zone air temperature (Table 1), indicating that air warming did not translate linearly into berry warming. This was particularly evident in 110R at mid-ripening in 2020, when HT increased cluster-zone air temperature by +1.38 °C but mean berry temperature was 0.25 °C lower than in control. This decoupling between air and berry temperature was reflected in ΔT ($T_{\text{berry}} - T_{\text{air}}$), which tended to be more negative under HT (Table S1), with clearer effects in 2020 and a more limited response in 2021. Table 1 shows the mean temperature context (cluster-zone air and berry) for both rootstocks and treatments. In 2020, HT effects were limited and included lower mean berry temperature in 110R at the end of veraison and mid-ripening, whereas at harvest HT increased mean berry temperature in 140Ru (+0.39 °C) but not in 110R. In 2021, mean berry temperature was increased by HT at the end of veraison in both rootstocks, at mid-ripening in 110R, and at harvest in 140Ru.

Table 1. Mean and maximum cluster-zone air temperature and mean and maximum berry temperature under high temperature (HT) and control (C) treatments at the end of veraison, mid-ripening, and harvest in 2020 and 2021 for 'Monastrell' grafted onto 110R and 140Ru. Values are period means derived from continuous 10 min records. $\Delta T_{\text{HT-C}}$ indicates the difference between HT and control for each stage and rootstock.

Mean Cluster-Zone Air Temperature							
2020				2021			
		End-Veraison	Mid-Ripening	Harvest	End-Veraison	Mid-Ripening	Harvest
140Ru	C	25.11	25.30	21.26	24.76	25.75	21.36
	HT	26.18	26.63	22.53	25.89	26.61	22.23
	ΔT_{HT-C}	1.07 (***)	1.33 (***)	1.27 (***)	1.13 (***)	0.86 (***)	0.87 (***)
110R	C	25.00	25.19	21.94	24.65	25.69	21.29
	HT	26.19	26.57	22.43	25.93	26.69	22.25
	ΔT_{HT-C}	1.19 (***)	1.38 (***)	1.34 (***)	1.28 (***)	1.00 (***)	0.96 (***)
Mean berry temperature							
2020				2021			
		End-veraison	Mid-ripening	Harvest	End-veraison	Mid-ripening	Harvest
140Ru	C	24.57	25.48	21.83	24.54	26.12	21.79
	HT	24.53	25.70	22.22	25.41	26.28	22.10
	ΔT_{HT-C}	−0.04 (ns)	0.22 (ns)	0.39 (***)	0.87 (***)	0.16 (ns)	0.31 (*)
110R	C	24.97	25.80	21.94	24.56	25.80	21.42
	HT	24.83	25.55	21.86	25.67	26.11	21.87
	ΔT_{HT-C}	−0.14 (***)	−0.25 (*)	−0.08 (ns)	1.11 (***)	0.31 (**)	0.45 (ns)
Maximum cluster-zone air temperature							
2020				2021			
		End-veraison	Mid-ripening	Harvest	End-veraison	Mid-ripening	Harvest
140Ru	C	35.70	37.18	31.52	35.50	36.63	31.21
	HT	37.91	40.13	34.66	37.88	38.87	33.80
	ΔT_{HT-C}	2.21 (***)	2.95 (***)	3.14 (ns)	2.38 (***)	2.24 (***)	2.59 (***)
110R	C	35.48	36.91	30.97	35.32	36.42	30.95
	HT	37.64	39.89	34.41	37.62	38.72	33.24
	ΔT_{HT-C}	2.16 (***)	2.98 (***)	3.44 (***)	2.30 (ns)	2.30 (***)	2.29 (ns)
Maximum berry temperature							
2020				2021			
		End-veraison	Mid-ripening	Harvest	End-veraison	Mid-ripening	Harvest
140Ru	C	35.80	38.73	34.48	35.70	39.16	34.24
	HT	35.03	39.14	35.32	37.63	40.41	35.79
	ΔT_{HT-C}	−0.77 (ns)	0.41 (***)	0.84 (ns)	1.93 (***)	1.25 (ns)	1.55 (ns)
110R	C	36.07	39.95	35.60	35.64	37.94	32.55
	HT	36.00	39.15	34.73	37.59	38.89	34.13
	ΔT_{HT-C}	−0.07 (ns)	−0.50 (ns)	−0.87 (ns)	1.95 (***)	0.95 (ns)	1.58 (***)

Values are means of three microclimate replicates per treatment ($n = 3$). ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively.

HT increased daily maximum cluster-zone temperature by approximately 2–3 °C (Table 1). In 2020, maximum cluster-zone temperature under HT exceeded control at mid-ripening and harvest by 3.1 °C, whereas in 2021 values were lower (2.3 °C). In 2021, the HT–C difference was significant at all stages in 140Ru and at mid-ripening in 110R. With regard to maximum berry temperature, no differences were detected between treatments in 2020, except for the values recorded at mid-ripening for 140Ru (Table 1). However, in

2021, the maximum berry temperature reached by HT at the end of veraison was significantly higher and close to 2 °C, and this increase was maintained later without significant differences at mid-ripening and significant differences in 110R at harvest.

The cumulative hours of berry temperatures on the 25–35 °C range and above 35 °C were calculated (Table 2). HT treatment did not significantly affect the cumulative hours of berry temperature within the 25–35 °C range in either year, but increased cumulative hours above 35 °C in 2021 across stages, with positive and significant HT–C differences at the end of veraison for 140Ru, and for 110R across all stages. The effect of HT treatment on berry thermal exposure was mainly associated with changes in residence time in high temperature (>35 °C) in 2021 rather than with large shifts in mean berry temperature.

Table 2. Cumulative hours of berry temperature in 25–35 °C and >35 °C at end-veraison, mid-ripening, and harvest (2020–2021) for ‘Monastrell’ grafted onto 110R and 140Ru under control and HT. Based on berry temperature records from 21 June onwards.

		2020			2021		
		End-Veraison	Mid-Ripening	Harvest	End-Veraison	Mid-Ripening	Harvest
25–35 °C							
140Ru	C	562	753	910	508	725	811
	HT	603	788	942	494	717	803
	ΔT_{HT-C}	41 (ns)	35 (ns)	32 (ns)	−14 (ns)	−6 (ns)	−1 (ns)
110R	C	551	731	875	512	757	851
	HT	585	770	914	495	729	817
	ΔT_{HT-C}	34 (ns)	39 (ns)	39 (ns)	−17 (ns)	−28 (ns)	−34 (ns)
>35 °C							
140Ru	C	120	218	246	174	303	326
	HT	92	199	233	229	354	381
	ΔT_{HT-C}	−28 (ns)	−19 (ns)	−13 (ns)	55 (*)	51 (ns)	55 (ns)
110R	C	154	268	307	170	272	284
	HT	123	228	262	239	356	377
	ΔT_{HT-C}	−31 (ns)	−40 (ns)	−45 (ns)	69 (*)	84 (*)	93 (*)

Values are means of three microclimate replicates per treatment ($n = 3$).ns and indicate non-significant and significant differences at $p \leq 0.05$, respectively.

Year-to-year differences between treatments are summarized in Table S2 and Figures S2–S4. In 2020, GDD did not differ between control and HT at any stage for either rootstock; however, in 2021, GDD was higher under HT, reaching significance at mid-ripening and harvest in 140Ru. The time series and scatterplots in the Supplementary Section show the same year contrast: HT and control were very similar through most of 2020, whereas in 2021, HT was often more warmer than control during ripening, mainly during warmer periods; the HT–control series shows mostly negative values in 2020 and more sustained positive values in 2021, especially from end-veraison to mid-ripening. Thus, the imposed warming produced a consistent increase in cluster-zone air temperature, whereas berry thermal exposure varied mainly with season and, to a lesser extent, rootstock.

3.2. Berry Growth and Morphological Traits

Berry weight was influenced by temperature treatment and, to a lesser extent, by rootstock (Figure 2). At the end of veraison, HT increased berry weight in vines grafted onto 110R in both years, whereas in 140Ru the effect was slightly negative in 2020 and negligible in 2021. However, the rootstock differences observed earlier in ripening were not maintained at harvest. During ripening, HT generally promoted berry mass increase,

and at harvest, berries from HT treatments were significantly heavier than control berries in both rootstocks and years (Figure 2).

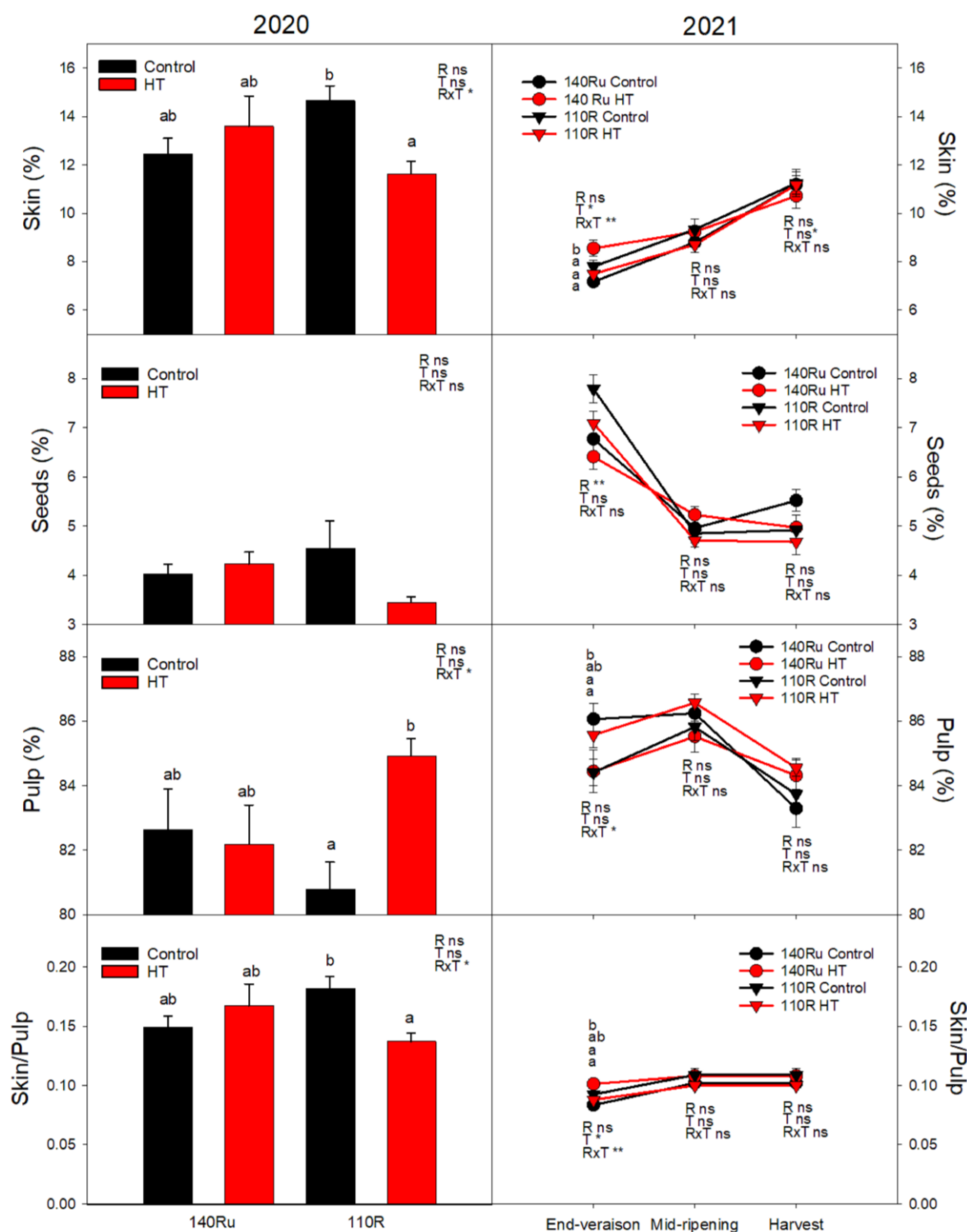


Figure 2. Berry weight, dry matter, and must yield (%) across ripening (2020–2021) in 110R and 140Ru under control and HT. R, T and R × T indicate the significance of rootstock, temperature treatment and their interaction, respectively, according to two-way ANOVA. ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively. Different letters indicate significant differences according to Duncan's multiple range test at the 95% confidence level.

Dry matter accumulation showed year- and rootstock-dependent responses (Figure 2). In 2021, HT increased dry matter, particularly in 110R, whereas in 2020, the percentage of dry matter tended to decrease under HT in both rootstocks during ripening, but not at harvest.

The contribution of skin, pulp, and seeds to total berry weight was also analyzed (Figure 3). In 2020 (harvest), HT reduced the skin percentage and increased the pulp percentage in 110R, resulting in a lower skin/pulp ratio. In 2021, HT effects on tissue allocation were generally small and reached significance only at the end of veraison, when HT tended to increase the skin percentage and reduce the pulp percentage, leading to a higher skin/pulp ratio at this stage. These results indicate that HT promoted berry mass increase in a relatively consistent way, whereas changes in dry matter accumulation and tissue allocation depended more on year, rootstock, and ripening stage.

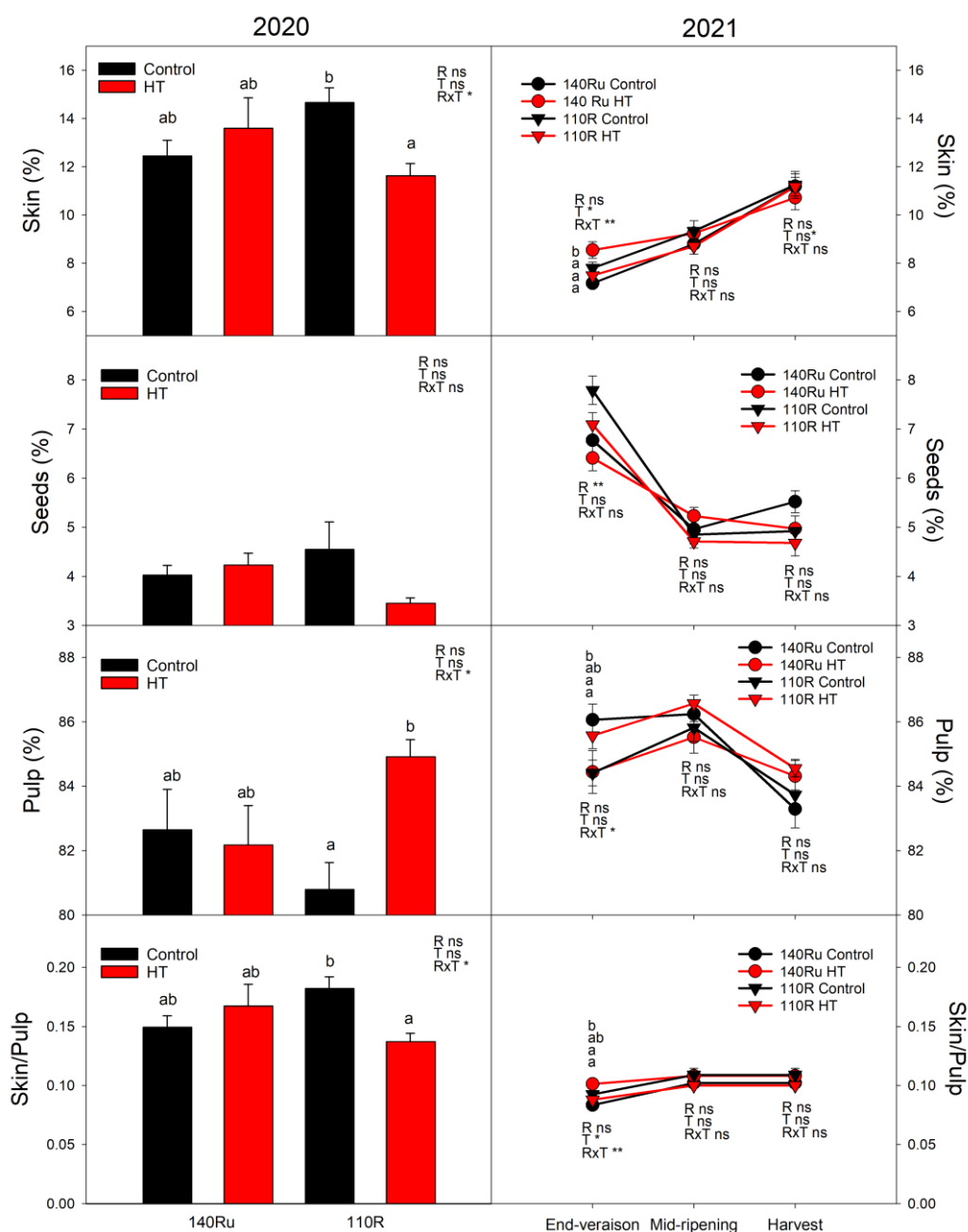


Figure 3. Skin, seed, and pulp proportions and skin/pulp ratio in 2020–2021 (harvest in 2020; ripening in 2021) for 110R and 140Ru under control and HT. R, T and R × T indicate the significance of

rootstock, temperature treatment and their interaction, respectively, according to two-way ANOVA. ns, *, and ** indicate non-significant and significant differences at $p \leq 0.05$, and 0.01, respectively. Different letters indicate significant differences according to Duncan's multiple range test at the 95% confidence level.

3.3. Technological Ripening

3.3.1. Titratable Acidity and Organic Acids

Titratable acidity decreased during ripening in both years and across all treatments (Figure 4), but its dynamics were modulated by rootstock and temperature treatments. In 2020, HT caused an increase in TA in 140Ru at the end of veraison, mainly associated with higher malic acid. This effect was not sustained, and TA was lower under HT at harvest in both rootstocks. In 2021, HT effects on acidity were more rootstock-dependent, decreasing malic acid in 110R at the end of veraison but increasing it in 140Ru at harvest.

Malic acid showed greater variability than tartaric acid (Figure 4) and was the main contributor to treatment differences in TA. Berries from 140Ru generally exhibited higher malic acid concentrations during ripening in both years. At the end of veraison, HT accelerated malic acid decline in 110R in 2021, whereas its effect in 140Ru was stage-dependent, with higher malic acid at harvest in 2021. By contrast, tartaric acid remained relatively stable across treatments and years, while showing modest changes over the course of ripening. In both years, at harvest, tartaric acid increased under HT in 140Ru, whereas it decreased under HT in 110R.

The tartaric/malic ratio increased as ripening progressed, and values were higher in 110R than in 140Ru across sampling dates. At harvest, HT further increased this ratio in 110R in both years. In 140Ru, the harvest response varied by season: the ratio was unaffected by HT in 2020, but it decreased under HT in 2021. These results show that HT affected the acid balance in a rootstock-dependent way, with 110R showing a clearer increase in the tartaric/malic ratio at harvest than 140Ru.

3.3.2. Sugar Concentration and Maturity Index Dynamics

Total soluble solids (TSS) increased progressively during ripening in both years (Figure 5). In 2020, HT had minimal effect on TSS at mid-ripening and harvest, whereas in 2021, the effect of HT was more evident, with significant increases during ripening in berries grafted onto 110R and in both rootstocks at harvest. Total solute accumulation per berry, calculated based on berry weight and must soluble solids, helped to separate the concentration effects from changes in berry weight (Figure 5). In 2020, HT increased total solutes per berry at mid-ripening despite no change in TSS, indicating that enhanced berry growth increased the amount of solutes per berry without necessarily elevating soluble solids concentration. At harvest in 2020, a similar trend was observed, but treatment differences were not significant, likely due to a larger variability at this stage. In 2021, HT increased solutes per berry in both rootstocks during ripening, with the effect being more pronounced in 110R at mid-ripening.

The technological maturity index (MI), calculated as the ratio of total soluble solids to titratable acidity, increased progressively during ripening in both years (Figure 5). This trend reflects the combined effect of sugar accumulation and acid degradation as berries mature. At the end of veraison, a significant rootstock $\times$ temperature interaction was detected in both years: in 2020, HT reduced MI in 140Ru but not in 110R, whereas in 2021, HT increased MI in 110R but not in 140Ru. These interactions diminished as ripening progressed and were no longer evident at harvest. In 2020, MI rose sharply from veraison to harvest, with 110R showing higher values than 140Ru, indicating a faster progression toward technological maturity. HT significantly increased MI at the end of ripening in 2020, so grapes from vines under HT had higher MI at harvest in both rootstocks. In 2021, MI

also increased throughout ripening, but the effect of HT was more evident in stages previous to the harvest. HT elevated MI in both rootstocks. These data indicate that HT advanced technological ripening mainly through higher solute accumulation and changes in acidity, although the response differed between years and rootstocks.

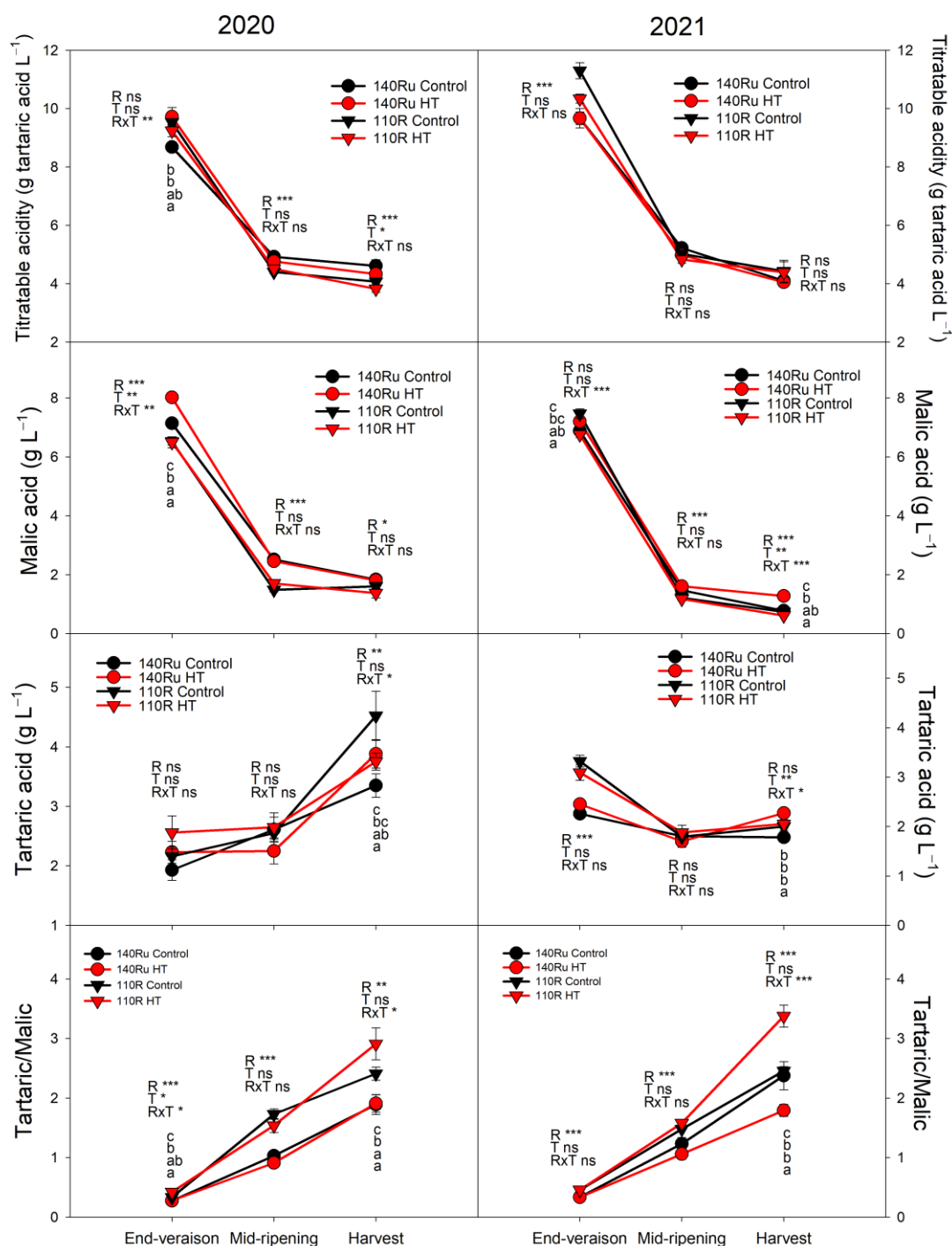


Figure 4. Titratable acidity (TA), malic and tartaric acids, and tartaric/malic ratio during ripening (2020–2021) in 110R and 140Ru under control and HT treatments. R, T and R × T indicate the significance of rootstock, temperature treatment and their interaction, respectively, according to two-way ANOVA. ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively. Different letters indicate significant differences according to Duncan's multiple range test at the 95% confidence level.

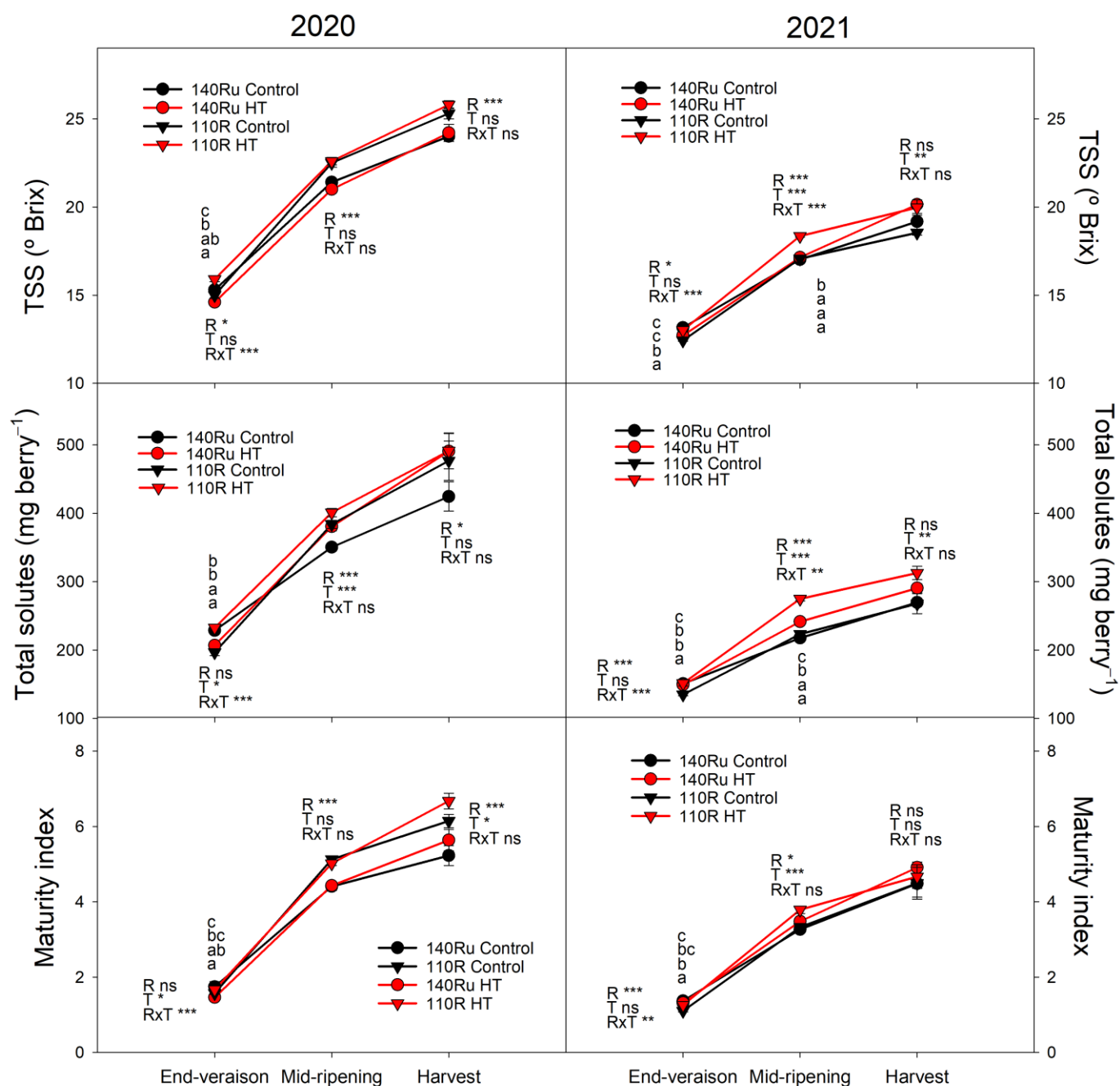


Figure 5. Total soluble solids (TSS), solutes per berry, and maturity index during ripening (2020–2021) in 110R and 140Ru under control and HT treatments. R, T and R × T indicate the significance of rootstock, temperature treatment and their interaction, respectively, according to two-way ANOVA. ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively. Different letters indicate significant differences according to Duncan's multiple range test at the 95% confidence level.

3.3.3. Thermal Exposure Effects on Technological Ripening

Across seasons, the relationships between thermal exposure and technological ripening are shown in Figure 6. As hours at 25–35 °C accumulated, both TSS and MI tended to rise, indicating faster technological ripening as sugars accumulated. By contrast, responses to time >35 °C were non-linear: TSS did not increase with the elevation of time >35 °C, whereas TA declined as high temperature exposure increased, and MI showed a

peak-shaped response, with an initial increase under moderate warmth followed by decreases at higher heat loads. No significant differences in rootstocks were found in the response of these parameters to heat loads.

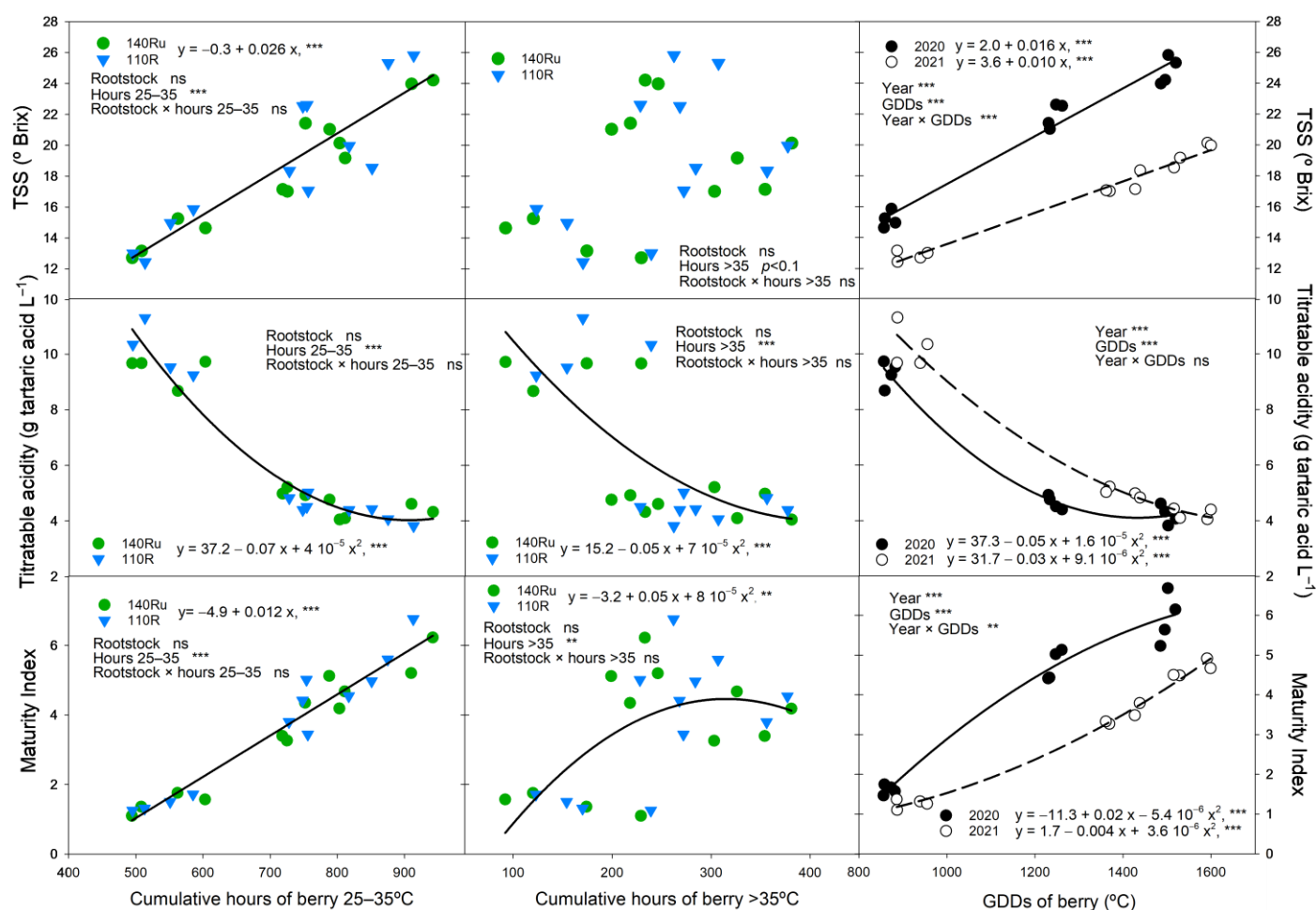


Figure 6. Relationships between berry thermal exposure and technological ripening in 'Monastrell' grafted onto 110R and 140Ru. Columns plot technological variables against cumulative hours with berry temperature in the 25–35 °C range, cumulative hours >35 °C, and berry growing degree-days (GDDs, base 10 °C). Rows show TSS, titratable acidity, and maturity index. Lines and equations represent the fitted linear or non-linear models shown in the corresponding panels. For GDD, separate trend lines are shown for 2020 and 2021 when applicable. Significance terms shown in each panel indicate the factors tested in the ANCOVA/regression analysis: rootstock or year, the thermal exposure variable, and their interaction. ns, **, and *** indicate non-significant and significant differences at $p \leq 0.01$, and 0.001, respectively.

Berry GDDs showed strong relationships with technological parameters, being positively related to TSS and MI, and negatively related to TA in both years. The effect of the technological parameters differed in both years, showing that for a given GDD, berries had lower TA and higher TSS and MI in 2020 than in 2021. Across these relationships, rootstock main effects and rootstock $\times$ exposure interactions were generally small and not significant. These relationships indicate that technological ripening was mainly associated with berry thermal exposure, while rootstock effects were less evident in the exposure–response analysis.

3.4. Phenolic and Colour Ripening

3.4.1. Must Phenolic Index and Tissue Phenolics

Total phenolic content index (TPI) in Monastrell changed with temperature, rootstock, and year, and the response differed between ripening stages (Figure 7). In 2020, HT significantly reduced TPI at harvest, and in 2021, TPI showed a strong decrease from the end of veraison to mid-ripening, and more stable values from mid-ripening to harvest. In both years, HT significantly decreased the TPI values at mid-ripening only in grapes from 140Ru.

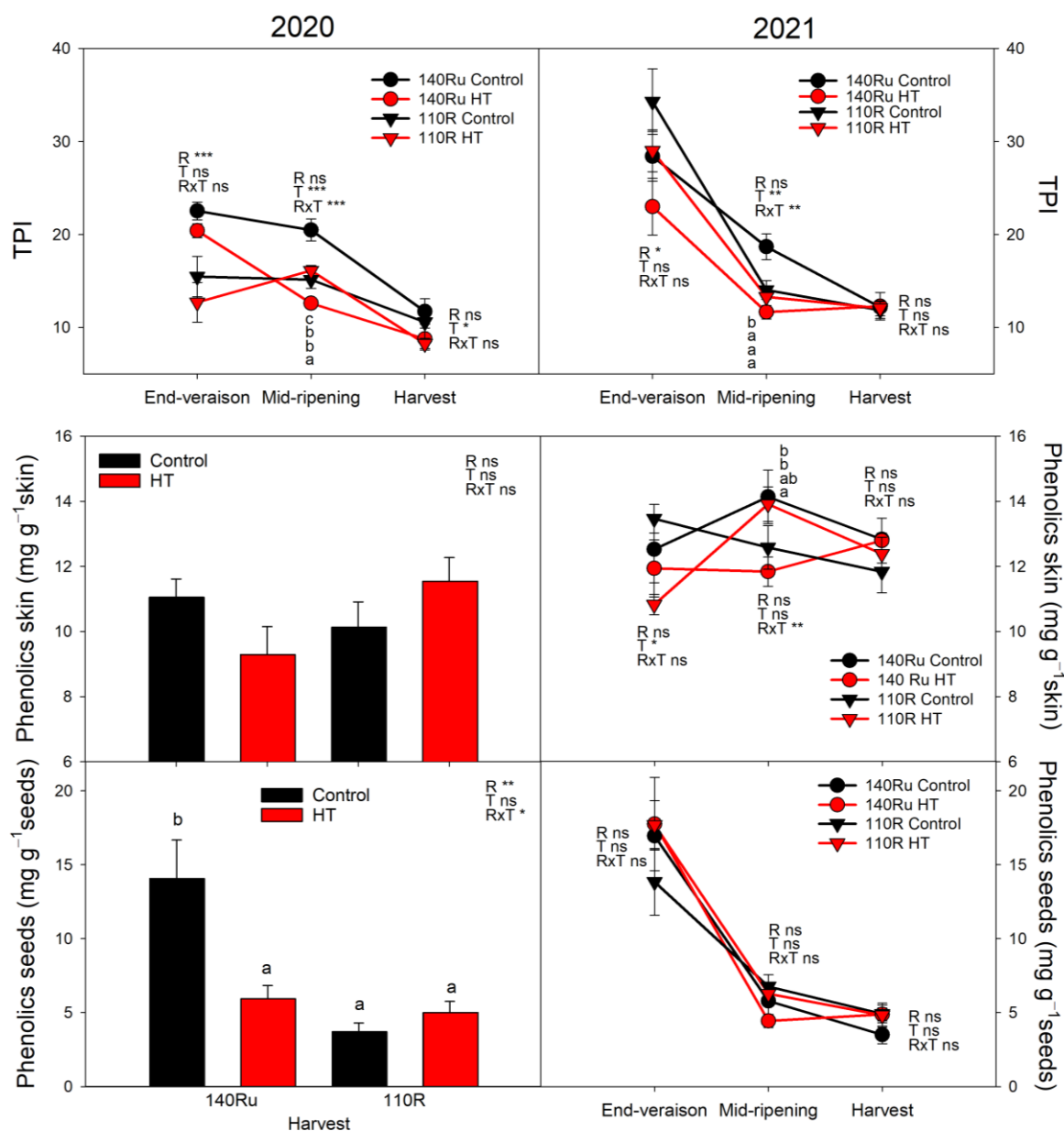


Figure 7. Must total phenolic index (TPI) during ripening (2020–2021), and total phenolics in skins and seeds measured at harvest in 2020 and across ripening in 2021 for ‘Monastrell’ grafted onto 110R and 140Ru under control and HT treatments. R, T and R × T indicate the significance of rootstock, temperature treatment and their interaction, respectively, according to two-way ANOVA. ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively. When the R × T interaction was significant,

different letters indicate significant differences according to Duncan's multiple range test at the 95% confidence level.

The distribution of phenolics between berry tissues (skins and seeds) revealed distinct patterns (Figure 7). In 2021, HT reduced skin phenolics in 110R at the end of veraison and caused a marked decline in skin phenolics from the end of veraison to mid-ripening in 140Ru. However, no significant differences in skin phenolics were observed between treatments at harvest in that year or in 2020. Seed phenolics at harvest in 2020 were markedly higher in 140Ru control than in all other treatments, and HT reduced seed phenolics only in 140Ru. These results indicate that the phenolic response to HT was stronger in 140Ru than in 110R and was more evident at mid-ripening than at harvest.

3.4.2. Anthocyanin and Tannin Concentrations

Anthocyanins in Monastrell berries increased from veraison to harvest, but the magnitude and dynamics varied between seasons (Figure 8). In 2020, anthocyanin concentration peaked at mid-ripening and declined toward harvest. At mid-ripening, berries from 140Ru strongly decreased total and extractable anthocyanins under HT conditions. Additionally, at harvest, anthocyanin levels tended to be lower under HT in both rootstocks, with significance detected only for total anthocyanins. In 2021, anthocyanin levels increased progressively during ripening, and HT had minimal impact on the final concentration. No significant effects of the temperature were found in 2021 in the anthocyanin concentrations in the skin.

Tannin responses to HT showed a different temporal pattern than anthocyanins, but similarly depended on season and ripening stage (Figure 8). In 2020, berries from 140Ru had higher tannin levels at veraison, but HT reduced tannin content in 110R. During ripening, HT significantly decreased tannin concentrations in 140Ru, whereas no comparable decrease was observed in 110R. In 2021, HT reduced tannins in both rootstocks at the end of veraison and in 140Ru at mid-ripening, but differences were not significant at harvest. These data show that anthocyanin and tannin responses to HT were mainly transient and stage-dependent, with the clearest reductions occurring before harvest and being more marked in 140Ru.

The relationship between skin/pulp ratio and phenolic variables at harvest was also assessed (Table S3). In 2020, positive correlations were observed only in 140Ru control, where higher skin/pulp ratio was associated with higher must TPI, total anthocyanins and extractable anthocyanins. In 2021, positive correlations were mainly observed in 140Ru HT for must TPI and extractable anthocyanins, whereas total anthocyanins were not related to skin/pulp ratio. No significant relationships were observed in 110R in either year.

3.4.3. Thermal Exposure Relationships for Phenolics

Phenolic traits showed different associations with temperature ranges and between years (Figure 9). For cumulative hours in the 25–35 °C range, must TPI decreased, total anthocyanins followed a non-linear relationship (with a maximum at 750–800 h), and total tannins decreased. These associations were stronger for cumulative exposure in the 25–35 °C range than with time above 35 °C. For cumulative hours >35 °C, no clear trend was observed for must TPI, whereas total anthocyanins showed an apparent positive association and total tannins decreased.

Phenolic variables showed different relationships with GDDs in 2020 and 2021 (Figure 9). When plotted against berry GDDs, in 2020, total anthocyanins reached an apparent maximum at mid-to-late ripening (1250 GDD) and then declined, whereas in 2021 they showed a more linear positive relationship across the sampled GDD range. TPI and total tannins also showed contrasting patterns in 2020 and 2021, being negatively associated

with GDD in both cases. The relationships with GDD differed between years: for comparable berry GDD values, TPI and total tannins were lower in 2020 than in 2021 (Figure 9). This indicates that berry thermal time alone did not fully explain phenolic variation, as the distribution of heat exposure differed between years.

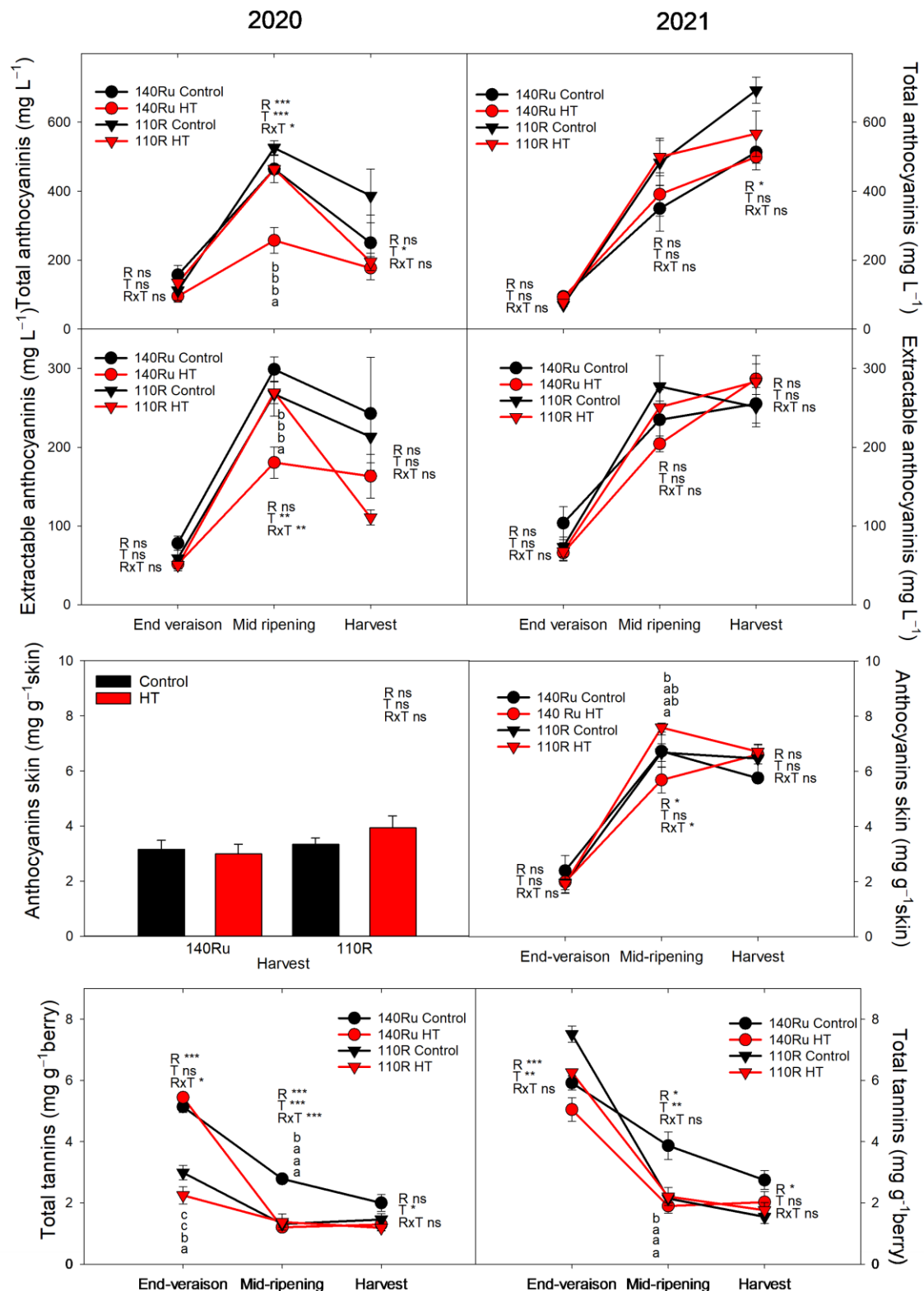


Figure 8. Extractable and total anthocyanins and total tannins during ripening (2020–2021), plus skin anthocyanins (harvest 2020; ripening 2021) in 110R and 140Ru under control and HT. R, T and

R × T indicate the significance of rootstock, temperature treatment and their interaction, respectively, according to two-way ANOVA. ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively. Different letters indicate significant differences according to Duncan's multiple range test at the 95% confidence level.

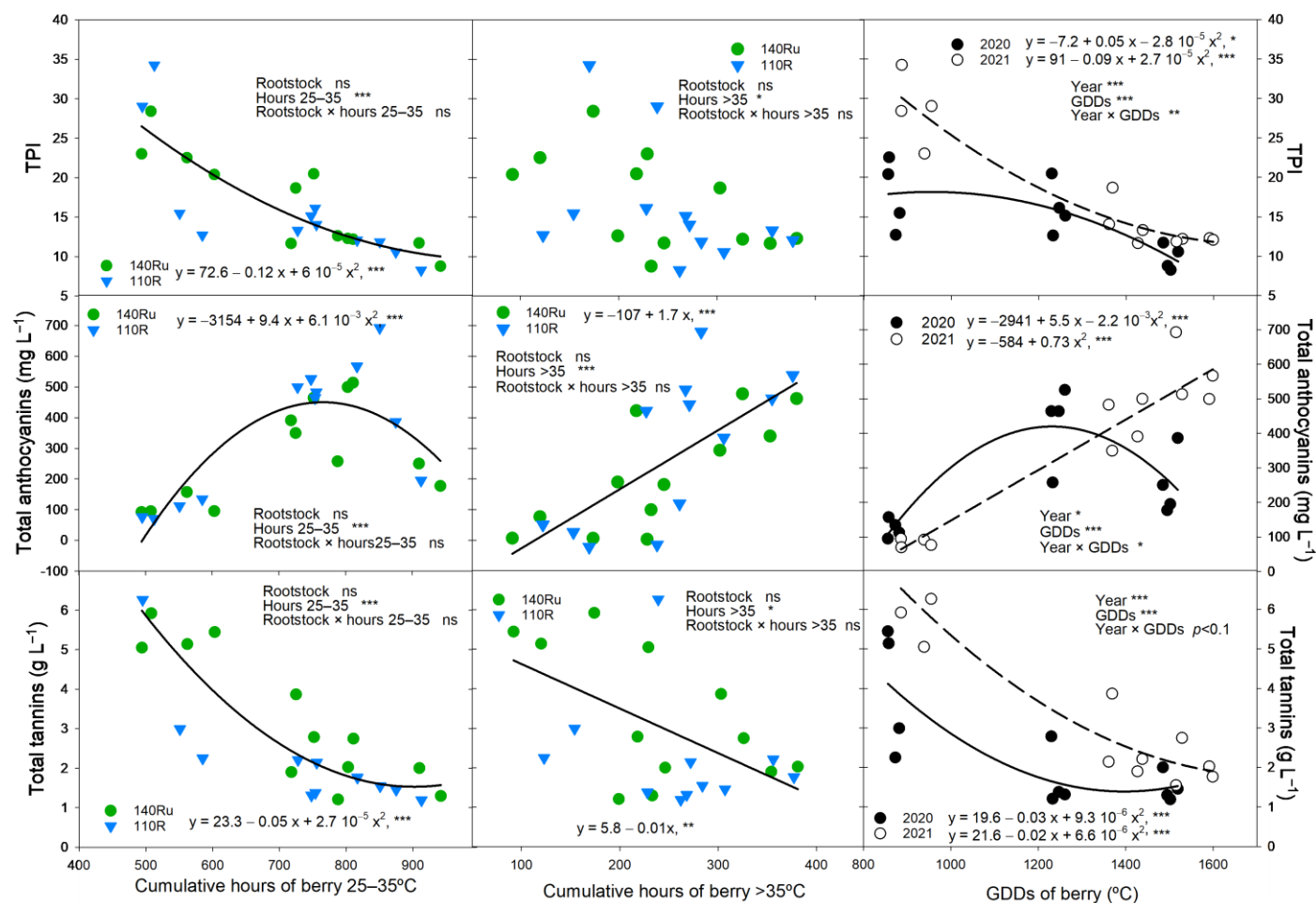


Figure 9. Relationships between berry thermal exposure and phenolic metrics in Monastrell grafted onto 140Ru and 110R. Columns plot phenolic variables against cumulative hours with berry temperature in the 25–35 °C range, >35 °C, and berry growing degree-days (GDD, base 10 °C). Rows show must TPI, total anthocyanins, and total tannins. Lines and equations represent the fitted linear or non-linear models shown in the corresponding panels. For GDD, filled symbols and a solid line represent 2020, while open symbols and a dashed line represent 2021. Significance terms shown in each panel indicate the factors tested in the ANCOVA/regression analysis: rootstock or year, the thermal exposure variable, and their interaction. ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively.

3.4.4. Must Colour and CIELab Coordinates

Colour intensity (CI) increased progressively from the end of veraison to harvest in both years, with values that were generally higher in 2020 than in 2021 (Table 3). In 2020, HT reduced CI at mid-ripening in 140Ru, indicating that elevated temperature negatively affected pigment synthesis at this stage.

CIELab parameters helped describe the chromatic evolution during ripening (Table 3). Lightness (L^*) decreased during ripening, reflecting must darkening as anthocyanins accumulated. However, in 2020, HT increased L^* in 140Ru at mid-ripening, resulting in

lighter musts. Redness (a^*) decreased with maturation in 2020, whereas in 2021, a^* increased until mid-ripening and then stabilized or slightly declined at harvest. HT generally reduced a^* values across years, suggesting a shift toward less vivid coloration. Yellowness (b^*) decreased from veraison to harvest in both years, reflecting a transition toward bluish-red hues. HT increased b^* at mid-ripening in 140Ru in 2020, but decreased b^* across stages in 2021. These colour changes were in line with the anthocyanin response, indicating that the strongest effect of HT on must colour occurred at mid-ripening, particularly in 140Ru.

Table 3. Evolution of the Colour Index (CI) and CIELab parameters (L^* , a^* , and b^*) measured during the maturation period of 2020 and 2021 for each rootstock and temperature treatment.

CI				L*			a*			b*			
2020													
		End- Verai- son	Mid- Ripen- ing	Harvest	End- Verai- son	Mid- Ripen- ing	Harvest	End- Verai- son	Mid- Ripen- ing	Harvest	End- Verai- son	Mid- Ripen- ing	Harvest
Rootstock (R)													
140Ru		1.93	2.80	3.46	39.0	34.0	30.9	36.4	25.5	23.6	29.8	16.8	13.3
110R		2.05	3.54	4.78	40.5	31.8	27.9	30.8	26.8	20.5	29.8	16.6	10.1
		ns	***	***	ns	*	***	***	ns	***	ns	ns	***
Temperature (T)													
Con- trol		2.01	3.38	4.18	39.4	30.7	29.1	34.0	28.1	22.1	29.5	16.4	11.8
HT		1.97	2.96	4.05	40.1	35.1	29.7	33.3	24.3	22.0	30.0	16.9	11.6
		ns	*	ns	ns	***	ns	ns	***	ns	ns	ns	ns
R × T													
140Ru	Control	2.00	3.32 b	3.39	37.9	30.4 a	30.9	37.2	28.8 c	24.2	28.7 a	16.9	14.2 c
140Ru	HT	1.86	2.29 a	3.52	40.2	37.6 c	31.0	35.6	22.2 a	23.0	30.8 c	16.7	12.4 bc
110R	Control	2.03	3.43 b	4.98	41.0	31.0 b	27.4	30.7	27.3 bc	20.0	30.3 bc	16.0	9.5 a
110R	HT	2.07	3.64 b	4.58	40.1	32.5 bc	28.4	30.9	26.3 b	21.0	29.2 b	17.1	10.7 b
		ns	**	ns	ns	*	ns	ns	**	ns	**	ns	*
2021													
		End- Verai- son	Mid- Ripen- ing	Harvest	End- Verai- son	Mid- Ripen- ing	Harvest	End- Verai- son	Mid- Ripen- ing	Harvest	End- Verai- son	Mid- Ripen- ing	Harvest
Rootstock (R)													
140Ru		1.16	2.16	3.92	46.5	34.3	27.2	23.8	26.0	24.2	32.4	22.4	14.4
110R		1.35	2.17	3.96	44.9	33.3	26.4	25.5	29.4	24.4	33.4	21.8	13.1
		***	ns	ns	***	*	ns	*	***	ns	ns	ns	**
Temperature (T)													
Con- trol		1.33	2.14	3.90	44.9	33.7	27.5	26.3	28.8	25.9	33.7	22.9	15.0
HT		1.18	2.19	3.98	46.5	33.8	26.2	23.0	26.5	22.7	32.2	21.3	12.6
		***	ns	ns	**	ns	*	***	***	***	*	**	***
R × T													
140Ru	Control	1.20	2.10	4.13	46.0	33.7 ab	27.6	24.8	27.3	26.0	33.5	23.4	15.6
140Ru	HT	1.12	2.22	3.71	47.0	34.9 b	26.8	22.8	24.6	22.5	31.3	21.5	13.2
110R	Control	1.46	2.18	3.67	43.8	33.8 ab	27.3	27.9	30.4	25.8	33.9	22.5	14.3
110R	HT	1.24	2.15	4.25	45.9	32.8 a	25.6	23.1	28.4	22.9	33.0	21.2	11.9
		ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns

R, T and R $\times$ T indicate the effects of rootstock, temperature treatment and their interaction, respectively, according to two-way ANOVA. Values shown under Rootstock (R) and Temperature (T) correspond to main-effect means. Values shown under R $\times$ T correspond to the four treatment combinations. ns, *, **, and *** indicate non-significant and significant differences at $p \leq 0.05$, 0.01, and 0.001, respectively. When the R $\times$ T interaction was significant, different letters indicate significant differences among treatment combinations according to Duncan's multiple range test at $p \leq 0.05$.

4. Discussion

Temperature strongly influences berry development and composition, with responses varying according to rootstock and season. In the present study, a mean +1.15 °C cluster-zone warming affected Monastrell berry temperature, ripening, and composition, with clear differences between 110R and 140Ru. The warming system was designed as an open-field treatment, with transparent polycarbonate panels placed from ground level to cluster height and below most of the canopy, without enclosing the whole vegetation. However, as in other field warming systems [7,21,22], it may also have modified local radiation, airflow, humidity/VPD, and boundary-layer conditions around the bunches. Therefore, the HT treatment is interpreted here as a moderate cluster-zone warming treatment with associated microclimatic effects, rather than as an isolated air temperature treatment. These responses are interpreted here in relation to berry thermal exposure and rootstock-related differences across years and ripening stages.

4.1. Rootstock-Modulated Berry–Air Thermal Coupling Under Moderate Warming

The HT treatment increased cluster-zone air temperature across stages and years (Table 1), but berry temperature did not follow this linearly, indicating that the treatment altered the effective heat load experienced by the fruit. In 2020, mean berry temperature changed a little under HT (Table 1), and in some cases, such as 110R at mid-ripening, it was slightly lower under HT than under control. Figures S2 and S3 suggest that berry heating was slightly reduced during the hottest periods. This may reflect the strong dependence of berry temperature on convective cooling at the berry surface, whereby small changes in the boundary-layer thickness can enhance heat dissipation and partly offset increases in air temperature [23]. In 2021, HT produced a clearer increase in berry temperature especially around the post-veraison period, with a stronger accumulation of hours above 35 °C in 110R than in 140Ru (Table 2). This pattern suggests that rootstock influenced berry heat load not because air warming differed between rootstocks, but because the berry microenvironment responded differently. In interpreting these berry temperature patterns, it should be noted that berry temperature was monitored in representative clusters selected with the same orientation and a similar canopy position. These records therefore provide a standardized estimate for comparable cluster positions, but they do not capture the full within-plot heterogeneity between exposed and shaded berries or among clusters with different exposures. The observed variation in berry heat load is relevant because key quality-related traits, especially colour and phenolic composition, are more sensitive to short heat events and time above thresholds than to small changes in mean air temperature [8,24,25]. Consequently, the same warming may have little impact in 2020 but a larger impact in 2021, particularly in 110R, which accumulated more hours above 35 °C. These exposure metrics are therefore used to interpret changes in ripening and phenolic development in the following sections.

To explain why a similar increase in mean air temperature resulted in different exposure above thresholds across years and rootstocks, two complementary mechanisms may be considered. First, rootstocks may differ in canopy water use, indirectly modifying the cluster microenvironment and influencing how air warming is translated into berry heat load. In a parallel physiological study conducted on the same experimental vineyard,

110R showed greater stomatal plasticity under HT (higher g_s and E), whereas 140Ru behaved more conservatively [16]. Such differences in canopy water use under warming could indirectly affect conditions around the clusters (e.g., air renewal and boundary-layer conditions on surrounding clusters) and thus how closely berry temperature deviates from air temperature during hot periods. Even subtle changes in the local cluster environment can modify berry heating despite similar imposed air warming [23]. Therefore, the larger HT-induced increase in hours above 35 °C observed in 110R in 2021 may reflect rootstock-dependent differences in how the same air warming leads to berry temperature extremes, as also suggested by the contrasting HT–control patterns observed between 2020 and 2021 (Figures S3 and S4; Table 2). Second, HT increased berry weight in both years and rootstocks. Larger berries may buffer temperature fluctuations, although this effect is likely to weaken when heat events become more frequent or intense, as observed in 2021, when time above thresholds increased [24,25]. In addition, the HT-related increase in berry weight may have enhanced transpiration per berry, depending on changes in cuticular conductance during ripening [26], thereby promoting evaporative cooling and partly limiting berry temperature at some phenological periods.

4.2. Berry Growth Under Moderate Warming: Rootstock Dependent Responses

Before interpreting these stage-dependent responses, it should be noted that all treatments were sampled on common calendar dates within each season, rather than at identical technological maturity. The terms “end of veraison”, “mid-ripening”, and “harvest” therefore refer to common sampling points along the ripening sequence at the experimental vineyard level. Consequently, some treatment differences may reflect both direct effects on berry traits and HT-induced differences in ripening progress.

HT promoted berry mass increase across seasons, indicating that berry growth was not strongly constrained by the imposed warming. However, larger berries may affect must phenolic concentration when berry mass increase changes the relative contribution of skins and pulp tissues, an aspect further considered in relation to the harvest correlations between skin/pulp ratio and phenolic variables. Previous controlled-environment and field-warming studies have shown that moderate increases in berry or canopy temperature (approximately 1–3 °C), under adequate water supply, can enhance berry growth without necessarily shortening the ripening period, whereas warmer conditions may restrict growth depending on the cultivar and developmental stage [27,28]. Since cultivars differ in their optimal temperature range for berry growth, the timing and magnitude of warming relative to the ripening stage may partly explain the rootstock-dependent responses observed here [29]. Under an adequate water supply, moderate warming was associated with larger berries even when mean berry temperature increased only slightly or inconsistently across stages, suggesting that canopy-level processes (such as carbon supply and berry import) contributed more strongly than direct heating at the fruit surface [22,27].

Temperature-driven increases in berry transpiration can steepen the fruit–stem water-potential gradient and facilitate solute import, consistent with berry mass increase under warm, dry atmospheric conditions [30]. In the present trial, berry mass increase occurred even when changes in mean berry temperature were relatively small and stage-dependent (Table 1). This suggests that the increase in berry weight was not simply related to changes in mean berry temperature and may also have been associated with changes in canopy source–sink balance under moderate warming [22,27]. This interpretation is consistent with the results obtained in a parallel physiological study conducted in the same experimental vineyard, where HT increased gas exchange and transpiration mainly in 110R [16]. Under non-limiting water conditions, this may have contributed to

sustaining carbon supply to the berries and may explain the earlier and stronger berry-growth response observed in 110R.

Although berry mass increase in the present study was mainly driven by HT, the rootstock- and year-dependent changes in tissue allocation agree with reports showing that rootstocks can modify berry weight and other yield components in a cultivar-dependent manner [31]. In our study, these differences were not expressed only as changes in whole-berry weight, but also as changes in tissue allocation. In 2020, HT reduced skin percentage and increased pulp percentage in 110R, resulting in a lower skin/pulp ratio (Figure 3), whereas in 2021 this response was not maintained. Such changes may influence technological and phenolic traits through dilution/concentration effects, although the quantitative relationship between skin/pulp ratio and phenolic concentration was not consistent across years, treatments, and rootstocks (Table S3), as discussed below. Dry matter accumulation showed a similar interannual contrast, with patterns in 2020 mainly reflecting dilution during ripening, whereas in 2021 dry matter per berry tended to increase towards harvest under HT (Figure 2). This highlights that the balance between berry growth, tissue allocation, and dry matter accumulation differed between years.

4.3. Rootstock-Dependent Shifts in Sugar–Acid Balance Under Moderate Warming

Under HT, TSS increased during ripening in 110R, and in 2021 at harvest in both rootstocks, whereas effects were smaller in 2020. Similar responses to warming around veraison have been previously reported with higher TSS and potential alcohol, and moderate temperatures can favour photosynthesis and sugar import [5,32–35]. In the physiological study conducted in parallel, HT increased canopy gas exchange mainly in 110R (higher g_s and E , together with higher A ; [16]), which may explain the stronger sugar response observed in this rootstock. Nevertheless, berry sugar concentration can also vary through berry weight (dilution or concentration), so TSS alone can be misleading [36,37]. In the present study, HT increased berry weight (Figure 2) and also elevated solutes per berry, especially in 2021 and more markedly in 110R (Figure 5), supporting enhanced sugar import rather than a simple concentration effect. Under semi-arid conditions, warmer and drier air may favour solute supply to the fruit by increasing bunch transpiration [30,38]. Consistent with this interpretation, 110R maintained a higher stomatal aperture under HT [16], which may have helped sustain assimilate supply and contributed to the higher TSS and MI observed in 110R under similar thermal exposure (Figures 5 and 6).

At harvest, the tartaric/malic ratio under HT differed clearly between rootstocks (Figure 4), increasing in 110R but showing a weaker or opposite response in 140Ru depending on the season. Acid responses are strongly dependent on the ripening stage, since warmer conditions before veraison may favour malate accumulation, whereas warming at veraison and during ripening accelerates malate degradation [39,40]. By contrast, tartaric acid usually changes less during ripening, and treatment effects are more often related to dilution/concentration processes and genotype-specific behaviour than to major metabolic shifts [32,40].

The tartaric/malic ratio measured at harvest integrates several post-veraison processes; consequently, even small rootstock differences in the timing of heat events relative to the malate-sensitive post-veraison window may lead to contrasting harvest ratios under similar mean warming conditions [40]. Under HT, 110R may have experienced greater overlap between heat exposure and the period when malate decline responds more strongly to temperature, favouring a stronger malate loss and thus a higher tartaric/malic ratio at harvest. In contrast, the delayed veraison and ripening onset observed in 140Ru in the physiological study [16] may have reduced this overlap, favouring higher malate retention and lower or less responsive tartaric/malic ratio at harvest.

Having shown that HT effects on the tartaric/malic ratio depend on when heat peaks occur relative to ripening and differ by rootstock, we examined how technological maturity responded to moderate (25–35 °C) versus high (>35 °C) berry temperature exposure (Figure 6). TSS and MI increased with berry growing degree-days (GDD) and with cumulative hours in the 25–35 °C band, whereas these responses levelled off or became non-linear as time above 35 °C increased. This suggests that time spent in the moderate range favoured sugar accumulation during ripening, whereas additional exposure above 35 °C produced limited further increases in TSS and MI. These results agree with reported temperature ranges for canopy photosynthesis and for processes linked to sugar import into the berry [27]. In contrast, TA declined with berry GDD and with time in the 25–35 °C range, and continued to decrease as exposure above 35 °C increased. This matches field reports from warmer, drier conditions and the strong post-veraison temperature sensitivity of malate loss described previously. Relationships based on berry GDD also differed between seasons: for similar berry GDD values, 2020 showed higher TSS and MI but lower TA than 2021 (Figure 6), indicating that thermal time alone did not fully determine ripening outcomes.

Taken together, these results highlight a clearer decoupling between sugar and acid responses. Time above 35 °C was associated with continued acidity loss with little change in TSS, indicating that increases in MI under warmer conditions can come partly from an accelerated malate loss rather than from substantial gains in sugars. Similar partial decoupling has been reported under elevated temperature, with timing and thermal regime around ripening affecting how sugars and acids respond [5,39,40]. In the present study, the magnitude and timing of the MI responses varied with both season and rootstock, indicating earlier technological maturity driven by combined, but not always proportional, changes in sugars and acids (Figures 4 and 5). Comparable responses have been reported in other warming and whole-plant experiments, where increasing heat exposure produced relatively modest sugar gains but stronger acidity losses [5,27,40].

Rootstock differences also helped link thermal exposure to vine physiological behaviour. Such rootstock-dependent differences in ripening indices are in agreement with studies in other grapevine cultivars showing that rootstocks can modify TSS and titratable acidity, although the direction and magnitude of these effects depend on the scion cultivar and growing conditions [41]. Under HT, 110R showed a larger increase in MI and higher solutes per berry than 140Ru, in line with the higher g_s and E reported for this rootstock in the parallel physiological study [16]. This response may have helped maintain carbon supply to the berries during warm periods. In 140Ru, HT also increased technological ripening, but acids differed from 110R (higher malic acid, lower tartaric acid, and a lower tartaric/malic ratio). From a practical perspective, 110R achieved higher MI under warming through combined sugar accumulation and acidity loss, whereas 140Ru tended to develop a less favourable acid composition, which may hinder the desired sugar–acid balance when preserving freshness is a priority.

4.4. Rootstock-Dependent Sensitivity of Phenolic Ripening to Heat Exposure

The most significant alterations related to heat in phenolics were observed during mid-ripening rather than at harvest (Figures 7 and 8). In 140Ru, the reduction in must TPI during mid-ripening under HT was primarily associated with changes in skin phenols, rather than a generalized decline across all tissues. This observation aligns with the role of skins as the primary interface with the microclimate of the bunch, while seed phenolics tend to respond differently and are less directly influenced by skin temperature [42–44]. The decrease in TPI during mid-ripening under HT in 140Ru (also observed in total and extractable anthocyanins, skin phenolics, and total tannins) is unlikely to be solely attributable to a higher heat load on the berries, as berry temperature summaries did not

consistently indicate higher extremes in 140Ru compared to 110R at comparable developmental stages (Tables 1 and 2). Contributing factors may include warm episodes after veraison, which can diminish net skin phenolic accumulation and extractability, and increased sensitivity of 140Ru. Furthermore, changes in berry morphology may influence phenolic indices in must when phenolics do not increase proportionally with juice volume [24,25,44,45]. However, the harvest correlations between skin/pulp ratio and phenolic variables showed that this relationship was not consistent across years, temperature treatments, or rootstocks (Table S3). Positive relationships were mainly detected in 140Ru, but they differed between control and HT conditions and were not observed for all phenolic variables. Therefore, changes in skin/pulp ratio may contribute to phenolic variation in specific cases, but they do not provide a general explanation for the phenolic reductions observed under warming. Other factors, including changes in phenolic accumulation, extractability, and rootstock-dependent sensitivity to heat, should also be considered. This interpretation is consistent with previous work showing that rootstock genotype can influence berry and wine phenolic composition, including anthocyanins and tannins, through effects on scion nutritional status and secondary metabolism [46]. In this context, tissue traits related to the rootstock, such as thicker grape epidermis in 140Ru compared to 110R [13], may also influence the magnitude of these responses. Must colour followed the pattern of the anthocyanin response, with the most pronounced effects of heat stress observed at mid-ripening, especially in 140Ru, characterized by reduced colour intensity and a shift towards lighter (higher L^*) and less red (lower a^*) musts (Table 3). Must TPI as negatively associated with longer time in the 25–35 °C range and with increasing GDD suggest that sustained warm conditions, rather than exposure above 35 °C, may be linked to lower phenolic index in must (Figure 9). Toward the upper end of the 25–35 °C range, the phenylpropanoid/flavonoid pathway may become constrained, thereby reducing net flavonoid pools [8,47]. Total anthocyanins showed a non-linear response to time in the 25–35 °C range: Anthocyanins typically increase after veraison, may level off, and can decline near harvest. Warm post-veraison conditions may reduce net accumulation through both reduced biosynthesis and/or increased losses [8,25,48,49]. The apparent positive relationship between total anthocyanins and cumulative hours >35 °C should therefore be interpreted cautiously because hours >35 °C also increase as the season advances and can covary with the ripening stage. This interpretation is supported by vineyard studies showing that sustained high berry temperatures can reduce the anthocyanin pool [24,25].

Year effects became particularly evident when total anthocyanins were related to GDD (Figure 9). In 2020, anthocyanins reached a maximum at mid-to-late ripening and subsequently declined, whereas in 2021 they increased more linearly with GDD. Cumulative exposure helps explain this contrast: 2020 accumulated more hours within the 25–35 °C range at each sampling stage, whereas 2021 accumulated more hours above 35 °C throughout ripening. These findings demonstrate that GDD alone may not adequately describe how heat is distributed between moderate (25–35 °C) and hotter conditions (>35 °C), nor when these occur relative to post-veraison, which can affect anthocyanin accumulation. Anthocyanin responses to temperature can differ between seasons and depend on when warming occurs during ripening, with early post-veraison often being a sensitive period [24,50,51]. In the present study, the post-peak decline in 2020 may reflect greater losses later in ripening, whereas the more linear 2021 pattern suggests that any temperature-related limitation on net accumulation occurred outside the sampled period, consistent with the strong interannual variability reported in field heating studies [24,44,52].

Total tannins decreased with increasing cumulative thermal exposure (Figure 9). This likely reflects ripening progression, since proanthocyanidins accumulate mainly before veraison and the extractable pool declines as berries enlarge and tissues mature [25,45].

When related to GDD, tannin concentrations were lower in 2020 than in 2021 at comparable GDD values, confirming a marked year effect similar to that reported in other multi-year studies [44,53].

5. Conclusions

This study used an open-field warming system to impose a mean +1.15 °C increase in cluster-zone temperature during ripening and to evaluate its effects on Monastrell berry development and quality under semi-arid Mediterranean conditions. Mean air temperature alone did not fully explain the observed responses, since berry thermal exposure and berry–air temperature differences varied between years and helped explain differences in berry composition.

HT tended to accelerate technological ripening, whereas phenolic and colour traits responded more strongly at specific stages, especially around mid-ripening. These results indicate that moderate warming can reduce the synchrony between technological maturity and phenolic and colour development, thereby complicating harvest decisions based primarily on sugars and acids.

Rootstock choice also appears particularly relevant under these conditions. Under the moderate cluster-zone warming applied in this study, 110R showed a more stable response than 140Ru across the two evaluated seasons, combining increases in MI and solutes per berry with comparatively better phenolic and colour outcomes. However, this response should be interpreted within the thermal range and interannual variability observed here. Thus, 110R should be considered a promising rootstock option for Monastrell under moderate warming conditions. By contrast, 140Ru showed a greater risk of an unfavourable sugar–acid balance and weaker colour/phenolic expression under the warmer conditions observed in this study. These findings also indicate that adaptation strategies for Monastrell vineyards under moderate warming should consider both rootstock choice and berry-scale thermal exposure.

Future work should extend the experiment across additional seasons and vine ages, and include wine-scale analyses to better connect berry compositional changes with sensory outcomes under practical winemaking conditions.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/horticulturae12080913/s1>; Figure S1: Experimental design of the experiment with four blocks. Each block consisted of two lines (one of the plants grafted on 110R and the other plants grafted on 140Ru) with 12 plants each. Six plants were inside the HT structures described in Figure 1, and the other six were control plants, without HT structures. Only the four central plants were included in the measurements; Figure S2: Seasonal dynamics of the daily mean and maximum berry temperatures under control (solid line) and high temperature (dotted line) treatments, in 110R (blue) and 140Ru (green) rootstock, in the 2020 and 2021 seasons. Vertical dotted lines indicate the end of the veraison stage, mid-ripening, and harvest; Figure S3: Comparison of berry temperature in control and HT treatments for 110R (blue) and 140Ru (green) rootstocks across 2020 and 2021 seasons. The reference lines are $y = x$. Each point is the average of three independent replicates. Data were recorded at 10 min intervals; Figure S4: Differential effect of HT vs control (HT–control) on daily mean berry temperature across the 2020 and 2021 seasons for 110R (blue) and 140Ru (green). Daily means were calculated from synchronized 10 min records. Vertical dotted lines indicate the end of the veraison stage, mid-ripening, and harvest; Table S1: Summary of ΔT ($T_{\text{berry}} - T_{\text{air}}$) for Monastrell berries grafted onto 110R and 140Ru during 2020–2021. Values represent mean seasonal tendencies derived from 10 min berry (T_{berry}) and cluster area (T_{air}) temperature records. $\Delta T_{\text{HT}} - \Delta T_{\text{C}}$ represents the difference in ΔT between the HT and control treatment; Table S2: Accumulated degree-days (base 10 °C) and their differences between HT and C treatments ($\Delta T_{\text{HT-C}}$) at the end of veraison, mid-ripening, and harvest in 2020 and 2021 for Monastrell grafted onto 110R and

140Ru under control (C) and high temperature (HT) treatments; Table S3: Linear correlations between skin/pulp ratio and phenolic variables at harvest in Monastrell berries grafted onto 140Ru and 110R under control (C) and high temperature (HT) treatments in 2020 and 2021.

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Abbreviations

The following abbreviations are used in this manuscript:

HT	High temperature
C	Control
T _{air}	Cluster-zone air temperature
T _{berry}	Berry temperature
ΔT_{HT-C}	Difference in temperature between HT and C
GDD	Berry growing degree-days
TSS	Total soluble solids
TA	Titrateable acidity
MI	Maturity index
TPI	Total phenolic index
CI	Colour intensity

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