Erwerbs-Obstbau (2023) 65:1941–1953
https://doi.org/10.1007/s10341-022-00794-4

ORIGINAL ARTICLE / ORIGINALBEITRAG

Physical and Biochemical Changes Induced by Strigolactones on Calcareous Environments in Grapevine

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Received: 1 July 2022 / Accepted: 14 November 2022 / Published online: 4 January 2023

Abstract

Abiotic stresses are the most common stress factors that plants encounter. Nutrient uptake problems caused by high lime content and high pH values seen in most soils are also among the abiotic stress factors. Eliminating this stress factor is not possible and approaches that will increase the plant's resistance are of great importance. Thus it is extremely important to find alternatives that are natural, easy to use, practicable and harmless to human health. Hormones are effective in plant stress physiology and play an active role in stress tolerance. One of the substances that are introduced as new generation hormones are strigolactones (SL). It has been determined that SL undertake important functions in stress metabolism. This research aimed to provide resistance to lime stress with SL applications on the 'Hasandede' grape variety grafted to '1103 P' rootstock in pot culture conditions in a greenhouse. Different concentrations of calcium oxide (CaO) (0%, 10% and 25%) were applied to the root area of the plants and SL were applied (0 µM, 1 µM, 3 µM and 5 µM) by pouring to the root regions. Samples were taken at 2, 12, 24, 48, and 96 h later after the SL applications. Physical (degree of damage, shoot length, average number of leaves per shoot) and biochemical (membrane injury index, chlorophyll, proline, soluble protein and lipid peroxidation) were examined on the samples. In biochemical features, the highest membrane damage (31.41%) and the lowest chlorophyll content (20.64 SPAD) were determined in the plants at the highest lime dose without SL application. Lipid peroxidation (1.40 nM/g) was five times higher in SL control plants than in SL treatment plants (0.28 nM/g). The data obtained from physical and biochemical analyses show that SL applications have the potential to be used in reducing the damage caused by calcareous environments in grapevine.

Keywords Abiotic stress · Grape · Plant hormones · Protein · Proline

Abbreviations

IAA	Indole acetic acid
MDA	Malondialdehyde
MII	Membrane Injury Index
PEG	Polyethylene glycol
PVP	Polyvinylpyrrolidone
ROS	Reactive oxygen species
SL	Strigolactones
SPAD	The Soil Plant Analysis Development

Introduction

It is known that the stress factors to which living things are exposed are increasing day by day. Some may avoid this stress environment, some develop different characteristics to adapt to stress, and some cannot tolerate this environment and lose their vitality (Punetha et al. 2022) Since plants, an integral part of the ecosystem, cannot change their places, they grow and develop by giving variable responses to stress factors depending on their genetic adaptations (Wolters and Jurgens 2009; Golldack et al. 2011; He et al. 2018; Paes de Melo et al. 2022; Saharan et al. 2022).

Stress in plants occurs in two ways, biotic and abiotic. Abiotic stress is stress caused by complex environmental conditions such as drought, salinity, strong and low light, ultraviolet light, high and low temperature, freezing, heavy metals, and insufficient oxygen. Whatever its origin, the stress environment affects the performance and survival of plants (Dos Santos et al. 2022; Sharma et al. 2022).

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Abiotic stresses threaten the future of agricultural production by reducing the yield of agricultural production by approximately 50% (Mahajan and Tuteja 2005). It is often not possible to eliminate the said stress factor. Although there is recycling in the case of resistance, especially in mild damage to the plant, the stress event generally weakens the plant and causes chronic disease or irreversible damage when the plant's capacity is reached (Mittler 2017; Tognetti et al. 2017; Honglin et al. 2019).

The pH of the soil in which the plants are located and the calcareousness have an important share among the factors that cause physiological and metabolic changes in plants, negatively affecting growth and development and reducing yield and quality (Turner et al. 2020; Fang et al. 2021; Wang et al. 2022).

Except for the northeastern part of the Turkish soil, it is known that the lime content is generally high due to the geogenetic character of the parent material. The base material of sedimentary origin and insufficient precipitation are determining factors on lime concentration of soils (Goulding 2016; Mordi and Al Dosary 2022).

Low precipitation causes the lime not to be washed away and accumulate in certain soil profile layers. High lime and high pH prevent the uptake of nutrients, causing the plant to be stressed and give some reactions. It is impossible to eliminate this stress caused by lime, especially in the short term. With sulfuric preparations, the pH of the soil is lowered and improved. This situation requires time and is difficult to practice when applying on large lands (Mancino 2003). Approaches that will give plants resistance to stresses are critical.

The responses of plants to stresses appear to be primarily related to intrinsic hormones (Chaves et al. 2003; Christmann et al. 2006; Perez Torres 2008; Evelin et al. 2009). It is known that when plants are exposed to biotic stress, they detect signals from injured cells and activate the salicylic acid signaling pathway, and they show different responses by interacting with other plant hormones. This is a highly complex system, and it has been determined that plants gain tolerance in this way (Pieterse et al. 2009; An and Mou 2011). It is thought that intrinsic hormones play a significant role in the expression of plants as "sensitive" or "tolerant" in response to different stresses.

Until recently, it was thought that plant hormones consisted of five groups: auxin, gibberellin, cytokinin, abscisic acid (ABA), and ethylene. However, it has been determined that some other substances synthesized by plants, such as jasmonates, brassinosteroids, and salicylic acid, have very important vital functions in the plant, just like hormones, and these compounds have been added to the class of plant hormones. Another hormone in these substances is strigolactone (SL), a substance derived from carotenoids and produced in plant roots (Al Babili and Bouwmeester 2015; Jia et al. 2018).

SLs are molecularly composed of a tricyclic lactone ring linked to the unsaturated α,β-furanone moiety via an enol ether bridge. It was first detected in cotton root secretions as strigol and strigyl acetate in 1966 (Cook et al. 1966). Today, at least 19 different SLs have been detected naturally in the root secretions of various plants (Xie and Yoneyama 2010; Kisugi et al. 2013) from mosses (Proust et al. 2011) to green algae (Delaux et al. 2012) and terrestrial plants (Bowman 2013; Brewer et al. 2013; Ha et al. 2014; Sun et al. 2014; Van Zeijl et al. 2015; Pandey et al. 2016; Mishra et al. 2017; Jia et al. 2018; Yoneyama 2019; Yoneyama and Brewer 2021).

SLs were previously thought to be only a germination-promoting agent in some root parasitic plants such as *Striga, Orobanche* and *Phelipanchespecies* (Cook et al. 1966), and no studies were conducted on it for many years. It was later determined that SLs act as a signal in regulating the arbuscular mycorrhizal fungus (AMF)–plant relationship, which plays an important role in the development of plants (Akiyama et al. 2005; Matusova et al. 2005; Foo and Reid 2012; Yoshida et al. 2012). Later, it was determined that SLs also play an important role in suppressing shoot branching (Gomez Roldan et al. 2008; Umehara et al. 2008; Brewer et al. 2009) and shaping the root structure (Ruyter Spira et al. 2011) by preventing side-shoot development. Ruyter Spira et al. (2011), who determined that the primary root lengths of *Arabidopsis thaliana* mutants with low SL levels and insensitive to SLs were shorter than those of wild types, used GR24 (a synthetic analog of strigolactones), the first artificial SL analogue, which is more easily synthesized than SL (Gomez Roldan et al. 2008; Zwanenburg et al. 2009) in their research. It was also stated that an increase in the lengths of the cells was observed after GR24 application and that GR24 application, together with exogenous auxin application, had a stimulating effect on lateral root development.

These versatile functions of SLs have led researchers to identify different functions of SLs and conduct new studies to reveal them. Especially in recent years, it has been revealed that SLs act together with auxins in secondary development, root, and tuber formation (Roumeliotis et al. 2012; Foo 2013; Liu et al. 2013; Shinohara et al. 2013; Dierck et al. 2016). As in other hormones, it has been determined that the SL signaling pathway produces reactive oxygen species (ROS) as a secondary messenger (Bartoli et al. 2013). It has been stated that SL biosynthesis pathways are highly conserved in the plant kingdom due to these critical positions they have assumed (Brewer et al. 2013). In another study, Torres Vera et al. (2014) investigated the effects of SLs on the plant defense mechanism. At the end of their study, they determined that the mutant tomato line

Slccd8 with SL deficiency was more susceptible to the fungal pathogens *Botrytis cinerea* and *Alternaria alternata* than the wild types. There are limited studies in the international literature on the effects of exogenous applications of SLs in terms of stress tolerance. One of them stated that the GR24 application to SL-deficient mutant tomato plants also positively affected the response of the roots to IAA, and they acted as a positive regulator in the plants (Mayzlish Gati et al. 2010). A study conducted in in vitro Arabidopsis mutants (Ha et al. 2014) tried to determine the physiological and molecular effects of SLs on drought stress. As a result of the study, in which different mutants producing both low and high levels of SL were used, it was determined that exogenous SL application to SL-deficient mutants increased tolerance in drought-sensitive phenotypes.

In another study, which includes exogenous applications to determine the effect of SLs on drought stress, the effect of SL and salicylic acid on drought in two drought-sensitive and resistant winter wheat genotypes was tried to be determined. It was determined that plants treated with SL and salicylic acid showed a higher tolerance (Sedaghat et al. 2017). Based on these results, the researchers emphasized that SLs could be used as an alternative to drought-resistant transgenic plants in the future.

Ensuring stress resistance is even more critical, especially in plants with high economic value. One of these plants is the grapevine. In addition to its commercial importance, the grapevine and its product grape are an extremely important fruit in medicine and pharmacy with its important phytochemical content. Therefore, the potential impact of practices that will prevent stress-related losses will be higher. A limited number of studies have been found in the extensive literature research to determine the effect of exogenous SL applications on different stresses in the grapevine. In a study based on the fact that abscisic acid in grapes increases during the ripening period and promotes anthocyanin accumulation and the relationship between ABA and SL, Ferrero et al. (2018) examined the effect of SL application on anthocyanin accumulation in berries. In the study, the expression of genes responsible for anthocyanin biosynthesis, ABA biosynthesis, metabolism, and membrane transport were determined. As a result of the research, it was determined that the accumulation of soluble sugar and the amount of anthocyanin in the berries increased.

Examining the effects of SL applications on drought stress in grapes, Min et al. (2019) applied three different concentrations of rac-GR24 (1 µM, 3 µM, and 5 µM) to 2-year-old grapevine and applied 7% polyethylene glycol (PEG-6000) to simulate drought conditions. As a result of the research, it was determined that plants treated with synthetic GR24 tolerate drought stress with lower electrolyte leakage, stomatal opening and ROS values, and higher relative water content, chlorophyll content, and photosynthesis rate values. These results showed that the GR24 application to foliage could ameliorate the adverse effects of drought.

Ren et al. (2020) studied the CRISPR/Cas9 system in regulating VvCCD7 and VvCCD8 gene expressions in 41B grapevine rootstock in their research on the ability of SLs to inhibit shoot branching in grapevine. They transformed 41B embryogenic cells, and sequence analysis showed success in both genes, VvCCD7 and VvCCD8. After regeneration, 6 41B plantlets were identified as transgenic carrying CCD8-sgRNA. It was stated that shoot branching increased in these mutants compared to wild types.

This research aimed to increase the resistance of grapevine in high lime-containing environments based on the effects of SL on stress. In the comprehensive literature research, no research was found to determine the effect of exogenous SL applications on lime stress in grapevine. The effects of SL applications on some physical and biochemical properties of 'Hasandede' cultivar grafted on '1103 P' grown in environments containing different levels of lime were investigated in this study.

Physical (degree of damage, shoot length, the average number of leaves per shoot) and biochemical (membrane damage, chlorophyll, proline, soluble protein, and lipid peroxidation) analyses were made.

Materials and Methods

'Hasandede' variety grafted on '1103 P' (*Vitis berlandieri* × *Vitis rupestris*) American grapevine rootstock was used as plant material. Plant materials were obtained from the Middle Black Sea Transition Zone Agricultural Research Institute (Tokat/TURKEY).

'1103 P': This is a strong rootstock and tends to delay the maturation of the grafted variety. Based on 17% active lime. Drought resistance is high. It is widely used as a rootstock.

'Hasandede': The variety, which is among the white wine grape varieties, has thin-skinned, round and medium-sized berries. It is known that the variety with plump clusters has been cultivated in Kırıkkale, Ankara, Çankırı, Çorum and Yozgat provinces in Turkey for a long time.

This research was carried out in the Yozgat Bozok University Faculty of Agriculture Grafted Grapevine Sapling Production Unit (2020). Cuttings of '1103 P' rootstock and 'Hasandede' variety were taken from a 10-year-old vineyard. Cuttings were stored at cold room (temperature: 8–10 °C and humidity: 70–80%) until grafting period. Before grafting, fungicide soaking and thermotherapy processes were performed, respectively. Cutting buds of rootstock (except the bottom bud) were shaved off. Grafting was made with omega grafting machines in the second week of March (2020). The grafted cuttings were paraf-

Fig. 1 Plants in greenhouse conditions

finized, and the grafted cutting was ensured by placing them in the poplar sawdust environment in the room with a temperature of 25 °C and a humidity of 80–85% for 3 weeks. Grafted cuttings were planted in 2-L pots containing 1:1 perlite/peat in the third week of April to ensure rooting and shoot development and were taken to the production greenhouse. At this stage, both root and shoot development were achieved. Applications started in the second week of June. Throughout this process, the plants were irrigated with Hoagland solution (No:2, basal salt mixture) twice a week (Hoagland and Arnon 1950) (Fig. 1).

During the applications, firstly CaO (Merck, Darmstadt, Germany) (10% and 25%) was applied in the plant root zone in one go (Fig. 2). In order to examine the effect of SL (Chiralix, A Symeres Company, Nijmegen, Netherlands) on lime stress, SL applications were made after CaO application (Fig. 3). These applications were carried out using the SL analog GR24. SL in the form of GR24 dissolved in 3% acetone and the concentrations of 1, 3, and 5 µM (3% only acetone in control) were applied to the root zone of the plant on the 2nd, 4th, 6th, 8th, and 10th days after the CaO application, five times in total.

From the 10th day of the end of the SL application, the last application time was evaluated as the 0th hour, and samples were taken from the plants at the 2nd, 12th, 24th, 48th, and 96th hours. Chlorophyll, shoot length, the number of leaves per shoot, and degree of damage were determined while the leaves were on the plant; the degree of membrane damage were performed immediately after the leaves were taken, and the samples were placed in a deep freezer for further analyses.

Fig. 2 Calcium oxide applications to grapevine cuttings

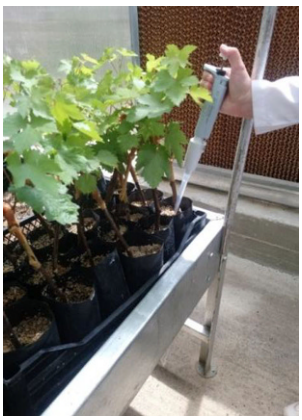

Fig. 3 Strigolactone applications to grapevine cuttings

Degree of Damage

In determining the degree of damage, a grouping was made based on the damage responses on the scale used by the International Plant Genetic Resources Institute (IPGRI) (Campbell 1997). In this scale, the plants that did not show any damage were given a value of 0, and then a ranking was made, extending to the 4th degree with the increase in the damage status as stated below. Accordingly, the degree of damage to plants was determined as;

- 0—Plants without chlorosis (yellowing): Plants with dark green leaves without any chlorosis
- 1—Plants with mild chlorosis: Plants with light green parts between the veins
- 2—Plants with moderate chlorosis: Plants with yellow leaves with main green veins
- 3—Plants with high chlorosis: Plants with yellowing leaves, less than 10% of whom have necrosis
- 4—Plants with intense chlorosis: Plants with yellowing leaves, more than 10% of which have necrosis

Fig. 4 Measurement of shoot length

Shoot Length

The shoot length of the plants in cm with the help of a ruler (Fig. 4).

Average Number of Leaves per Shoot

The average number of leaves per shoot in each replication was determined as pieces.

Membrane Injury Index (MII)

MII was calculated by measuring the electrolyte emitted from the cell (Fan and Blake 1994). Discs of leaves (17-mm diameter) were taken from the third leaves of the shoots belonging to each repetition, and their electrical conductivity (EC) was measured after being kept in 20 mL deionized water for 5 h. Same discs were kept at 100 °C for 10 min and afterwards EC value of solution was measured again. MII in leaf cells was determined in terms of percentage (%) by using below given formula.

The formulation of MII on leaf cells:

$$MII = 1 - [1 - (T1/T2)/1 - (C1/C2)]x100 \quad (1)$$

- T1: EC value of leaf (treated with SL) before autoclave; T2: EC value of leaf (treated with SL) after autoclave; C1: EC value of leaf (control) before autoclave; C2: EC value of leaf (control) after autoclave

Chlorophyll

Chlorophyll analyses were carried out with a Chlorophyll-meter (SPAD-502 Plus, Konika Minolta Sensing, Inc., Tokyo, Japan).

Proline

The amount of proline in the samples was determined according to the method of Bates et al. (1973). Calculations are given in µM/g.

Soluble Protein

The leaf samples taken were homogenized with 4 mL of 50-mM K-phosphate buffer solution (pH = 7.0) containing 2 mM Na-EDTA and 1% polyvinylpyrrolidone (PVP), the homogenates were centrifuged at 4 °C for 10 min at 10,000 cycles/min. Obtained supernatants were used for protein analysis (Ozden et al. 2009). Protein content was determined according to the method of Bradford (1976), and results are given in mg/g.

Lipid Peroxidation

The degree of lipid peroxidation was determined by measuring the level of malondialdehyde (MDA), the end product of lipid peroxidation (Madhava Rao and Sresty 2000). MDA concentration was determined in nM/g by calculating the molar extinction coefficient (ε: 155 mM^{-1} cm^{-1}).

Statistical Analysis

The research was carried out with three replications and 10 plants (10 pots) in each replication. The data obtained at the end of the experiment were evaluated in the SPSS 20 statistical program according to the randomized blocks experimental design, and the differences between the averages were determined according to Duncan's multiple range test ($p \leq 0.05$).

Results and Discussion

The effects of SL applications on degree of damage, shoot length, and average number of leaves per shoot are presented in Table 1. It is seen that there are statistical differences between CaO doses, SL applications, and sampling times on all physical parameters ($p \leq 0.05$).

Table 1 The effects on physical characteristics of strigolactone (SL) applications

CaO (%)	SL (μM)	Time (h)	Degree of damage (scale)	Shoot length (cm)	ANLPS (piece)
0	0	2	0.67 bc[a]	29.16 a–e	5.33 ab
		12	0.33 bc	30.46 a–d	4.00 a–c
		24	0.33 bc	34.95 a	4.00 a–c
		48	0.33 bc	30.73 a–d	3.67 a–c
		96	0.33 bc	27.38 a–f	4.33 a–c
	1	2	1.00 bc	26.08 a–f	4.00 a–c
		12	0.33 bc	27.28 a–f	4.67 a–c
		24	0.67 bc	24.90 b–f	3.67 a–c
		48	0.33 bc	23.56 d–f	4.00 a–c
		96	0.33 bc	34.20 ab	4.67 a–c
	3	2	0.33 bc	22.40 d–f	4.00 a–c
		12	0.67 bc	27.72 a–f	5.00 a–c
		24	0.67 bc	33.52 a–c	3.67 a–c
		48	0.67 bc	28.72 a–f	4.33 a–c
		96	1.33 a–c	25.56 b–f	4.00 a–c
	5	2	1.00 bc	27.56 a–f	3.67 a–c
		12	0.33 bc	24.40 c–f	5.33 ab
		24	0.67 bc	28.01 a–f	5.67 a
		48	0.33 bc	28.04 a–f	3.33 a–c
		96	1.00 bc	24.34 c–f	4.00 a–c
10	0	2	1.67 ab	28.36 a–f	5.00 a–c
		12	0.67 bc	35.01 a	4.33 a–c
		24	1.33 a–c	30.20 a–d	3.33 a–c
		48	0.67 bc	25.60 b–f	4.67 a–c
		96	0.33 bc	28.40 a–f	5.00 a–c
	1	2	0.67 bc	28.96 a-f	4.33 a–c
		12	0.00 c	27.20 a–f	3.00 bc
		24	1.00 bc	23.20 d–f	4.33 a–c
		48	0.33 bc	22.80 d–f	4.33 a–c
		96	1.00 bc	25.80 a–f	4.67 a–c
	3	2	0.67 bc	26.00 a–f	5.00 a–c
		12	1.00 bc	25.76 a–f	3.00 bc
		24	0.67 bc	24.16 c–f	5.33 ab
		48	0.67 bc	24.56 c–f	5.00 a–c
		96	1.00 bc	25.36 b–f	3.00 bc
	5	2	1.00 bc	27.20 a–f	3.33 a–c
		12	0.00 c	26.64 a–f	4.00 a–c
		24	1.00 bc	27.24 a–f	5.33 ab
		48	0.33 bc	23.60 d–f	3.00 bc
		96	1.33 a–c	27.20 a–f	4.33 a–c

Table 1 (Continued)

CaO (%)	SL (μM)	Time (h)	Degree of damage (scale)	Shoot length (cm)	ANLPS (piece)
25	0	2	1.67 ab	23.80 d–f	3.67 a–c
		12	1.00 bc	24.38 c–f	4.00 a–c
		24	1.33 a–c	24.98 b–f	3.00 bc
		48	2.33 a	24.80 c–f	3.67 a–c
		96	1.33 a–c	19.60 f	4.00 a–c
	1	2	1.00 bc	25.04 b–f	4.00 a–c
		12	0.67 bc	24.24 c–f	3.67 a–c
		24	1.00 bc	20.60 ef	3.00 bc
		48	1.00 bc	23.08 d–f	4.00 a–c
		96	0.67 bc	22.64 d–f	2.67 c
	3	2	0.33 bc	24.32 c–f	5.00 a–c
		12	1.33 a–c	24.98 b–f	4.00 a–c
		24	1.00 bc	24.64 c–f	5.00 a–c
		48	0.67 bc	26.38 a–f	4.67 a–c
		96	1.00 bc	25.40 b–f	3.67 a–c
	5	2	0.33 bc	28.32 a–f	3.67 a–c
		12	1.33 a–c	24.42 c–f	4.67 a–c
		24	1.00 bc	27.52 a–f	5.00 a–c
		48	0.33 bc	29.10 ae	4.33 a–c
		96	0.67 bc	25.58 b–f	3.67 a–c

CaO Calcium oxide, *ANLPS* Average number of leaves per shoot
[a]There is a difference between the means with different letters in the same column ($p < 0.05$)

Degree of damage: Significant differences were detected between lime doses, SL applications, and sampling times in terms of degree of damage, which is expressed by giving values between 0 and 4 on a scale. However, it is noteworthy that most of the numerical data are in the same class (Table 1). Numerically, the highest damage (2.33) was observed in the highest lime dose (25%) in plants not treated with SL and taken after 48 h. In Tagliavini and Rombolà's (2001), it was stated that chlorosis of leaves was observed in grapevine rootstocks in calcareous and alkaline soils. The losses caused by drying out in plants due to chlorosis are associated with the inhibition of root growth due to high soil bicarbonate levels and the slowing photosynthesis rate in parallel with the decrease in leaf chlorophyll content (Bavaresco et al. 2003). Our research shows that among the data obtained in terms of damage, there are plants with dark green leaves and damage on a scale of 0.00, where no damage was observed. Remarkably, all of these plants are in the SL applied plants, and it is also seen that they are in a 10% lime environment. No damage was detected in these plants, taken at the 12th hour by applying 1 μM and 5 μM SL, respectively.

Shoot length: Another feature examined physically is the length of the shoots. As a result of the statistical analysis made for the interpretation of the results, it is seen that many numerical values are in the same class in this feature, as in the degree of damage. The least shoot elongation (19.60 cm) was measured in plants with the highest dose of lime, 25% lime content, in which SL was not applied, and the examinations were terminated at the 96th hour. High lime is known to inhibit plant growth.

In a study (Bergmann 1992) conducted on vine rootstocks grown in vitro on this subject, one-bud green cuttings taken from the sixth node of grapevine rootstocks in the first week of June containing different types and doses of lime (0, 10, 20, 30, 40, 50, $CaCl_2$ and CaO) were placed in Knudson-C nutrient medium. For 2 months, growth conditions were investigated at 24 °C, 16/8 h of light/dark conditions. As a result of the research, it was stated that the plants were adversely affected by the lime added to the nutrient medium, and the shoot length values decreased with the increase in the amount of lime in the medium. Although there is no study examining the effect of SLs on shoot growth in calcareous environments, it is known that it has the feature of promoting plant growth based on its general effects on stress. In a study, the effects of SL applications on photosynthetic activity and some physiological characteristics of rapeseed (*Brassica napus* L.) under salt stress were investigated. It was stated that plant growth and photosynthesis values increased in SL applied group (Ma et al. 2017). Similarly, Wani et al. (2022) stated that growth, photosynthesis and glandular trichome attributes regulated positively in *Artemisia annua.*

Average number of leaves per shoot: In terms of new leaf formation capacity, which is also a criterion of shoot nutrition and development, as in the shoot length, the lowest values (2.67 units) were measured at the highest lime dose, the last sampling time, and the lowest dose of SL (1 µM). Although it is noteworthy that this value is lower than the plants in the control group (not treated with SL), it is also seen that the highest number of leaves (5.67) was formed in the plants that did not contain lime, but in which the highest dose of SL was applied and the sampling was made at the 24th hour. This result is significant because SL also showed its effect in stress-free environments. It is understood from the examination of the table that the number of leaves obtained numerically here is, on average, two times more than the number of leaves obtained in the group of plants that form the least leaves. The research conducted in this area stated that the leaf number values decreased in the face of increasing lime doses in grapevine rootstocks grown in vitro. As a result of the research in question, it was stated that 41 B rootstocks could withstand high levels of lime, 420 A and Rupestris du Lot rootstocks could only show moderate resistance Riparia Gloire rootstock had the lowest resistance to lime (Bergmann 1992).

In the general evaluation of the data obtained in terms of physical properties in the research, it is noteworthy that most of the data are in the same class, although there are statistical differences between them. This is thought to be a result of the fact that SL doses have not been administered in a broader range. The limited number of studies that could be taken as a reference at the research stage, the fact that samples were taken at certain times, and the large number of analyses that had to be done in a very short time after sample collection caused the dose range to be limited. It is thought that the differences will be reflected statistically if the dose is studied with much wider lower and upper limits. However, it is thought that the numerical data are also effective in revealing the potential of SL on physical properties.

The results obtained in terms of the effects of SL application and sampling times on some biochemical properties in calcareous environments are presented in Table 2.

It was determined that there were statistical differences between CaO doses, SL applications, and sampling times on all biochemical properties examined ($p \leq 0.05$). It is possible to evaluate the stress state of the environmental conditions in which the plant is located by measuring the integrity and durability of the cells. Therefore, one of the most commonly investigated parameters in studies in stress physiology is the measurement of damage to cell membranes. In this method, which is based on the principle of measuring the electrolyte released from plant cells, the robustness of the cell is associated with the low amount of leakage. High leakage is a sign that membrane integrity is beginning to be damaged. Our research shows that the lowest numerical value (8.23%) in terms of this feature is realized in the first sampling period of the plants that contain 10% lime, and at the same time, the highest SL dose of 5 µM is applied (Table 2).

The cells showing the highest membrane damage in numerical terms (31.41%) were in the leaves of the plants in the group that were grown at the highest lime dose but were not applied SL (plants sampled at 48th hour), it is important in terms of showing the effect of SL. It is also remarkable that damage occurred approximately 3.8 times more in these environments where SL was not applied than the lowest damage (Table 2). It has also been supported by many studies that ROS cause membrane damage in plants under stress (Shalata and Tal 1998; Dinis et al. 2017).

Our study shows that membrane damage was high in plants without SL, which shows that stress is alleviated. A reference to SL applications in drought stress in grapevine was reached in the resource survey conducted during the period when this research was started, and it was stated that membrane damage, that is, ion leakage values, occurred at lower levels in vine plants under drought stress, in which exogenous SL (GR24) was applied (Min et al. 2019).

Chlorophyll content: As it is known, it is the chlorophyll pigment that gives the green color to the plants, which provides photosynthesis and the production of oxygen. It is known that the chlorophyll content in the leaves decreases in most biotic and abiotic stress environments in all plants, from diseases and pests to nutrient deficiencies, although it varies according to the plant species. This symptom is the most visible damage caused by stress. Increasing ROS in the stress environment causes damage to chlorophyll and many other areas and triggers its disintegration. Yellowing between leaf veins and a decrease in biomass, which occur in the stress environment caused by lime, are typical symptoms of lime chlorosis (Bavaresco and Poni 2003). In this study, the effect of SL application on the chlorophyll contents of the leaves of grapevine plants in calcareous environments was investigated, and their contents were determined as SPAD by chlorophyll meter. It is seen that the lowest numerical value (20.64) was determined in the highest lime dose and in the leaves of the plants that were not applied SL, measured at the 96th hour (Table 2). Although it is in the same class as the values in many other application groups statistically, the highest numerically chlorophyll content (30.87) was detected in the 2nd hour leaves containing 10% lime and applied 1 µM SL. In a study conducted in a similar area, the effect of SL application in arid conditions on chlorophyll reduction caused by drought was investigated (Min et al. 2019). In this study, chlorophyll contents were determined spectrophotometrically, not as SPAD, unlike this study. In acetone:ethanol (1:1) mixture,

Table 2 The effects on biochemical characteristics of strigolactone (SL) applications

CaO (%)	SL (µM)	Time (h)	MII (%)	Chlorophyll (SPAD)	Proline (µM/g)	Soluble protein (mg/g)	Lipid peroxidation (nM/g)
0	0	2	12.55 j–p[a]	28.06 a–f	0.02 pr	2.51 b–g[a]	0.47 g–r
		12	14.82 h–p	29.01 a–d	0.07 d–n	2.31 d–l	0.38 m–r
		24	16.28 f–o	27.43 a–g	0.06 f–r	2.37 d–l	0.34 o–r
		48	14.38 i–p	23.97 f–n	0.08 c–k	2.30 d–l	0.35 m–r
		96	16.96 e–n	22.73 h–n	0.07 d–n	2.55 b–f	0.54 f–n
	1	2	13.80 i–p	20.88 mn	0.09 b–i	2.38 d–k	0.49 g–p
		12	14.67 h–p	25.93 d–k	0.08 c–k	2.23 e–m	0.46 g–r
		24	12.97 j–p	26.01 d–k	0.03 n–r	2.33 d–l	0.55 f–m
		48	12.84 j–p	24.67 e–n	0.07 d–n	2.34 d–l	0.40 l–r
		96	9.45 o–p	22.89 h–n	0.04 i–r	2.29 d–m	0.45 g–r
	3	2	13.91 i–p	28.08 a–f	0.04 i–r	2.41 c–j	0.30 pr
		12	13.26 i–p	27.33 a–g	0.04 i–r	2.29 d–m	0.32 o–r
		24	13.82 i–p	23.05 h–n	0.04 i–r	2.06 k–n	0.39 m–r
		48	11.33 n–p	26.07 c–k	0.05 h–r	2.07 k–n	0.35 m–r
		96	10.70 n–p	23.42 g-n	0.04 i–r	2.29 d–m	0.42 h–r
	5	2	11.24 n–p	28.37 a–e	0.04 i–r	2.59 a–e	0.51 g–o
		12	11.63 m–p	27.23 a–g	0.03 n–r	2.32 d–l	0.48 g–r
		24	14.17 i–p	26.91 a–h	0.05 h–r	2.46 c–h	0.43 h–r
		48	11.62 m–p	22.76 h–n	0.06 f–r	2.62 a–d	0.35 m–r
		96	8.85 p	24.47 e–n	0.04 i–r	2.45 c–h	0.42 i–r
10	0	2	13.70 i–p	30.63 ab	0.03 n–r	2.36 d–l	0.72 f
		12	10.73 n–p	28.07 a–f	0.04 i–r	2.30 d–l	0.42 i–r
		24	12.58 j–p	27.85 a–f	0.04 i–r	2.36 d–l	0.59 f–k
		48	11.34 n–p	25.23 d–l	0.02 pr	2.29 d–m	0.54 f–n
		96	10.93 n–p	22.23 j–n	0.05 h–r	1.12 rs	0.55 f–m
	1	2	12.09 l–p	30.87 a	0.02 pr	2.08 j–n	0.45 g–r
		12	11.01 n–p	28.99 a–d	0.03 n–r	2.43 c–i	0.35 m–r
		24	12.14 k–p	26.73 b–i	0.04 i–r	1.94 no	0.40 l–r
		48	12.95 j–p	27.92 a–f	0.02 h–r	2.62 a–d	0.32 o–r
		96	13.46 i–p	21.53 k–n	0.03 n–r	2.72 a–c	0.28 r
	3	2	12.07 l–p	30.16 a–c	0.02 pr	2.30 d–l	0.31 o–r
		12	12.21 k–p	26.12 c–k	0.04 i–r	2.53 b–g	0.48 g–p
		24	10.03 n–p	25.46 d–k	0.03 n–r	2.29 d–m	0.46 g–r
		48	10.49 n–p	24.03 f–n	0.02 pr	2.32 d–l	0.58 f–k
		96	10.40 n–p	25.00 d–m	0.04 i–r	2.29 d–m	0.47 g–r
	5	2	8.23 p	28.08 a–f	0.01 r	2.89 a	0.50 g–o
		12	10.23 n–p	28.62 a–e	0.03 n–r	2.77 ab	0.49 g–p
		24	11.52 m–p	30.38 ab	0.02 pr	1.74 op	0.41 k–r
		48	10.45 n–p	26.12 c–j	0.04 i–r	2.37 d–l	0.48 g–p
		96	9.68 o–p	27.83 a–f	0.05 h–r	1.96 m–o	0.49 g–p

Table 2 (Continued)

CaO (%)	SL (µM)	Time (h)	MII (%)	Chlorophyll (SPAD)	Proline (µM/g)	Soluble protein (mg/g)	Lipid peroxidation (nM/g)
25	0	2	23.32 b–e	21.53 k–n	0.09 b–i	1.32 r	1.15 bc
		12	22.91 b–f	21.05 l–n	0.09 b–i	1.10 rs	1.40 a
		24	25.27 bc	21.57 k–n	0.13 a–c	1.07 rs	1.40 a
		48	31.41 a	22.71 i–n	0.10 b–f	1.04 rs	1.10 b–d
		96	29.10 ab	20.64 n	0.14 ab	0.95 s	1.25 ab
	1	2	19.05 c–k	21.57 k–n	0.07 d–n	2.08 j–n	1.07 c–e
		12	19.41 c–j	21.93 j–n	0.08 c–k	2.16 h–n	0.94 de
		24	21.72 c–g	22.40 i–n	0.11 a–e	2.04 l–n	0.90 e
		48	23.85 b–d	21.19 l–n	0.07 d–n	1.30 r	0.96 de
		96	21.30 c–h	21.68 k–n	0.09 b–i	1.62 p	1.18 bc
	3	2	19.94 c–i	24.80 e–n	0.11 a–e	2.12 i–n	0.72 f
		12	24.55 b–d	24.52 e–n	0.15 a	2.20 f–n	0.60 f–i
		24	21.26 c–h	24.85 d–m	0.12 a–d	2.13 h–n	0.64 fg
		48	21.32 c–h	25.70 d–k	0.11 a–e	2.17 g–n	0.72 f
		96	23.58 b–e	22.87 h–n	0.12 a–d	2.07 k–n	0.56 f–l
	5	2	16.16 g–o	25.22 d–l	0.13 a–c	2.20 f–n	0.58 f–k
		12	18.46 d–m	20.90 mn	0.12 a–c	2.17 g–n	0.62 f–i
		24	15.25 g–p	23.88 f–n	0.14 ab	2.07 k–n	0.62 f–i
		48	18.60 c–l	24.95 d–m	0.10 b–f	2.10 i–n	0.47 g–r
		96	12.43 k–p	23.42 g–n	0.12 a–d	2.12 i–n	0.62 f–i

CaO Calcium oxide, *MII* Membrane Injury Index, *SPAD* The Soil Plant Analysis Development
[a]There is a difference between the means with different letters in the same column ($p < 0.05$)

it was stated that the chlorophyll values, which were determined by turning the leaves completely white and reading the obtained supernatant part at different wavelengths in the spectrophotometer, decreased significantly in arid conditions compared to non-arid conditions. In the study, in which it was stated that the decrease in chlorophyll continued as the drought period increased, it was emphasized that this decrease was more pronounced in the groups without SL compared to the ones applied. While the total chlorophyll values from the 2nd hour samples, which is one of the sampling times, towards the 72nd hour samples, decrease by 47.94% in arid environments where SL is not applied; it was emphasized that this decrease was realized as 41.43%, 30.98%, and 18.79%, respectively, in arid environments where 1, 3, and 5 µM SL were applied. Therefore, it was reported that the lowest rate of decrease was at the highest SL dose. At the end of the research, it was pointed out that GR24 significantly alleviated the chlorophyll reduction caused by drought (Min et al. 2019). In a recent study to determine the effects of SL applications on salt stress in rice, Ling et al. (2020) stated that the amount of chlorophyll they determined as SPAD was significantly lower in plants under salinity stress than the control and emphasized that chlorophyll content was higher in all SL applied groups. From here, the role of SLs in preventing damage to chlorophyll, which is the key point in the photosynthesis capacity of the plant, has been revealed. Examining the effects of SL applications on drought stress in grapevine, Min et al. (2019) applied three different concentrations of rac-GR24 (1 µM, 3 µM, and 5 µM) to 2-year-old grapevine and applied 7% polyethylene glycol (PEG-6000) to simulate drought conditions. GR24 was administered for 7 days with an interval of 24 h. Leaf samples were taken at 2nd, 12th, 24th, 72nd, 96th, and 120th hours after PEG application. As a result of the research, it was determined that plants treated with synthetic GR24 tolerated drought stress with lower electrolyte leakage, stomatal opening and ROS values, and higher relative water content, chlorophyll content, photosynthesis rate values. These results showed that the application of GR24 to leaves can ameliorate the adverse effects of drought (Min et al. 2019).

Proline content: One of the most frequently examined parameters in studies carried out to determine the effects of different stress sources on plants is the changes in the amount of proline. Proline is accumulated in plants as an osmoprotectant, that is, as an osmotic protector, to gain tolerance to stress. The increase in proline indicates a stress situation in the environment on the one hand, and the plant's performance in terms of tolerance to this stress, on the other hand. Accumulation of free proline is observed in many plants in response to a wide variety of biotic and abiotic stresses. In Table 2, it is noteworthy that the proline content is high in plants grown in an environment containing only 25% lime, statistically, without an examination in terms

of SL and sampling time. When the lime environment in question is examined within itself; in plants sampled at 24th and 96th hours without SL applied; in plants sampled at 24th hour and applied 1 µM SL; remarkably, in all sampling periods of the plants applied 3 µM SL and all other sampling periods except the 48th hour of the plants applied 5 µM SL, it was found that the proline contents were statistically higher than the plants in the other group.

Soluble protein content: It is known that under stress, ROS also cause damage to proteins, and the damage can be reduced to the extent that the plant tolerates it. In terms of soluble protein, it is seen that all plants in a 25% lime environment have a low content statistically. Although it varies according to the sampling time, it was determined that the protein contents were higher in the plants treated with 5 µM SL in a lime-free environment and plants treated with 1 µM and 5 µM SL in an environment containing 10% lime.

Lipid peroxidation: Lipid peroxidation, defined as the oxidative breakdown of unsaturated fats in cell membranes, shows the sensitivity of plants to stress and the severity of oxidative damage. In the event of stress, damage occurs in lipid components, and the resulting damage is determined by measuring the amount of malondialdehyde, the end product of peroxidation. It is known that the lipid components of plant organelles are also damaged under stress. Here, the highest level of oxidation in all plants grown without SL application at 25% lime dose and in all plants sampled except the 2nd and 48th hours shows the effectiveness of SL. Notably, the damage (1.40 nM/g) in the plant samples taken at the 12th and 24th hours was five times more than the SL-treated plants (0.28 nM/g), which showed the least damage in this regard.

Conclusion

Grapevine is a plant with a long economic life, and its cultivation spreads over broad areas in the world. Achieving high quality and productivity in the grapevine is only possible in an environment where stress components are minimized. However, vineyards are usually established on arid soils with high lime content, unsuitable for many other cultivars. In the vines grown in soils with high lime content, Fe uptake is affected very negatively, and as a result, chlorosis is observed in the leaves. Advanced conditions have severe consequences as they will prevent many physiological activities of the plant. The varieties of the *Vitis vinifera* species used are resistant to lime, but due to the need to use the American grape rootstock in modern viticulture, they have to be grafted on rootstocks that are less sensitive to lime.

This study was carried out to investigate the effect of SLs on many other stress factors in the grapevine in an environment containing high lime.

Physical (degree of damage, shoot length, average number of leaves per shoot) and biochemical (membrane injury index, chlorophyll, proline, soluble protein and lipid peroxidation) analyses were carried out on the samples. In biochemical features, the highest membrane damage and the lowest chlorophyll content were determined in the plants were not applied SL at the highest lime dose. Lipid peroxidation was in SL-control plant five times more than the SL-treated plants. The data obtained from physical and biochemical analyses show that SL applications have to potential to be used in reducing the damage caused by calcareous environments in grapevine.

The results from our research generally show that SLs have emerged as a compound with great potential for use in the prevention or mitigation of lime damage in the grapevine. It also shows supportive effects on plant growth in environments with no stress. Therefore, in practice, pre-applications with SL in environments with high lime content in viticulture may offer a solution in this sense.

Although it has been determined that SLs play a role in the emergence of responses to different plant stresses such as salinity, drought, and low temperature in studies carried out in different plants to date, in order to understand most of the mechanisms fully, comprehensive studies should be continued by examining the interactions with other plant hormones. Although important information has been gained in understanding SL hormonal interaction at various levels of regulation, this needs to be addressed at both the cellular and molecular levels.

Acknowledgements The authors would like to thank Yozgat Bozok University Project Coordination Application and Research Center for financial support (Award number: 6601a-FBE/21-444).

Funding This work was financially supported by the Yozgat Bozok University Project Coordination Application and Research Center (Award number: 6601a-FBE/21-444).

Author Contribution Emine Sema CETIN contributed to this work in the experimental design and setup, lab processing of samples, data analysis, manuscript writing and discussion. Birol KOÇ contributed to lab processing of samples, data interpretation, manuscript writing and discussion. Authors read and approved the final manuscript.

Declarations

Conflict of interest E.S. Çetin and B. Koç declare that they have no competing interests.

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