ORIGINAL ARTICLE

The impact of strigolactone GR24 on Capparis spinosa L. callus production and phenolic compound content

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Abstract
The effect of strigolactones on plants, which has been recently described as a new group of plant hormones, has not been fully characterized. Capparis spinosa L. callus formation using synthetic strigolactone GR24 (0.1 and 0.2 μM) alone or combined with 1-naphthalene acetic acid (NAA) (10.74 μM) and 6-benzylaminopurine (BAP) (4.44 μM) and its effect on phenolic compounds production were evaluated. Compared to the other media, the media with 10.74 μM NAA + 4.44 μM BAP + 0.1 μM GR24 or 10.74 μM NAA + 4.44 μM BAP gave the highest callus formation. The highest rutin, quercetin and chlorogenic acid content were found in a medium with 10.74 μM NAA + 4.44 μM BAP + 0.1 μM GR24. Aromatic compounds in caper calluses were grouped as sulfur compounds (66.97–87.53%), aldehydes (4.88–7.90%), ketones (0.34–19.3%), hydrocarbons and derivatives (0.56–5.8%), alcohols (1.62–6.08%), others (0.61–2.37%) and their amounts varied at various hormone applications. When 0.2 μM GR24 was applied solitarily, the total sulfur compound in callus samples was 87.53% and the dominant compound was found to be methyl isothiocyanate. These results suggested that GR24 may be effective in the accumulation of chlorogenic acid, rutin and quercetin phenolics in caper callus culture.

Key Message
Our study is the first to evaluate the effect of GR24, alone or in combination with auxin and cytokinins on callus formation and phenolic substance content in capers. It has been observed that the 10.74 μMNAA + 4.44 μM BAP + 0.1 μM GR24 combination may be effective in the production of some phenolic compounds in caper callus cultures.

Keywords Capparis spinosa L. · Callus · Strigolactone · GR24 · Secondary metabolites

Introduction
Capers are tropical/subtropical plants from the Capparaceae family, with more than 350 varieties and can grow naturally in all continents, including Mediterranean countries. Capers as perennials and shrubs have 250 species in the world (Musallam et al. 2012), including two species (Capparis spinosa L. and Capparis ovata Desf.) and six different varieties C. spinosa var. spinosa, C. spinosa var. inermis Turra., C. spinosa var. aegyptia (Lam) Boiss, C. ovata var. palaestina Zoh., C. ovata var. herbacea (wild) Zoh., and C. ovata var. canescens (Coss.) Heywood present in Turkey (Davis 1982).

Alkaloids (Capparispine), flavonoids, lipids, polyphenols, terpenes, indoles, and aliphatic glucosinolates are found in various parts of C. spinosa (Arena et al. 2008; Rajesh et al. 2009; Wang et al. 2007) are used in the treatment of different diseases such as rheumatism, hypertension and diabetes. Sher and Alyemeni (2010) reported that C. spinosa is a safe plant and there are no studies in the literature showing any toxic effect.

About 8000 plant phenolics exist in nature and approximately half of them are flavonoid in both free state and glycosides (Harborne and Herbert 1993). Phenolic compounds and flavonoids have antioxidant and anticarcinogenic properties (Ghasemzadeh and Ghasemzadeh 2011), and can be extracted directly from plant organs. However, this method involves large scale cultivation and expensive isolation and purification processes. Meanwhile, the complexity of the
biosynthesis mechanisms of these compounds makes them very expensive to produce synthetically. Tissue culture techniques such as organ, cell suspension and callus cultures in vitro are alternative methods used to produce plant secondary metabolites (Kalidass et al. 2010; El-Nabarawy et al. 2015; Coskun et al. 2019).

The type and concentration of plant growth regulator is one of the important parameters for successful production of secondary metabolites in tissue culture. There have been many studies showing the effect of growth regulators as BAP, 2,4-D and NAA on callus formation and phenolic compound content (Tyagi et al. 2010; Kumari et al. 2015; Duran et al. 2019). Although the carotenoid-derived plant hormones strigolactones are known to regulate plant growth and development (Hu et al. 2019; Yoneyama and Brewer 2021), especially in interaction with other plant hormones such as auxin and cytokinin (Wang et al. 2007; Koltai 2015), there are very few studies evaluating their effect on in vitro growth and phenolic compound content (Wu et al. 2017).

Several studies have reported that GR24, a synthetic strigolactone analog, acts synergistically with auxins to regulate seed germination in Arabidopsis (Toh et al. 2012). Also, drought resistance and salt tolerance (Ha et al. 2014; Kapulian and Koltai 2014), as well as its effect on the organization of cortical microtubules in hypocotyl cells (Krasilenko et al. 2021). In addition, its effects on tuber formation and stolon architecture in potato (Roumeliotis et al. 2012), stress tolerance mechanism in lupin (Omoarelojie et al. 2020) and rice (Ling et al. 2020), have been noted.

This is the first study evaluating the effect of various strigolactone concentrations on callus formation and phenolic content in caper plant. In this context, it was aimed to assess the effect of synthetic strigolactone GR24, used in various concentrations together with BAP and NAA, on callus formation and fresh weight, and also to investigate the amount of phenolic and aromatic compounds such as rutin and quercetin in the calli formed.

Materials and methods

Plant material and establishment of callus culture

Caper (Capparis spinosa L.) seedlings were used in this study, which was conducted in Süleyman Demirel University Biology Department Plant Biotechnology Laboratory between 2020 and 2021. They were planted in pots containing 1/3 sand-peat mixture and growth under 16 h/day 8 h night photoperiod, 135 μmol/m²/s PAR light intensity, 23–25 °C temperature and 51–54% humidity (measured with Peak Tech 3695) conditions.

Caper young leaves, 1.5 to 2.5 cm in size, were used as explants. These were cut from the stem and washed with tap water, then soaked in 70% ethanol for 10 s. Afterwards, they were rinsed 3–4 times with sterile distilled water, 1% sodium hypochlorite (NaOCl) containing 1–2 drops of Tween-20 for 10 min, and surface sterilization was completed by rinsing 3–4 times with sterile distilled water.

Explant pieces of 0.5–1 cm were inoculated onto MS (Murashige and Skoog 1962; Sigma-M9274) medium with 3% (w/v) sucrose, 0.7% (w/v) agar and containing NAA, BAP and various concentrations of strigolactone GR24. Previous studies on capers stated that the NAA and BAP ratio has significant effects on callus formation (Kumari et al. 2015). For this reason, 4 distinct media were established as follows:

1. NAA (10.74 μM) + BAP (4.44 μM)- M1
2. NAA (10.74 μM) + BAP (4.44 μM) + GR24 (0.1 μM)- M2
3. NAA (10.74 μM) + BAP (4.44 μM) + GR24 (0.2 μM)- M3
4. GR24 (0.2 μM)- M4

The pH of the culture medium was adjusted to 5.8 prior to autoclaving for 20 min. Media were distributed into 9 cm diameter sterile Petri dishes with about 20 ml each. An average of 10–15 explants were planted in a Petri dish, sealed with Parafilm tape and incubated for 4–5 weeks at 22 ± 1 °C under dark conditions. Explants were then subcultured for 10 days in medium with 10.74 μM NAA, 4.44 μM BAP and 30 g 99% L-rhamnose.

For each hormone combination, the number of explants producing callus was recorded as per the formula:

\[ \text{Callus induction frequency(\%)} = \left( \frac{\text{(Number of explant produced callus)}}{\text{(Total number of explants)}} \right) \times 100 \]

The fresh weight of each callus was recorded prior to storage in Eppendorf tubes at −18 °C until examination of the accumulation of the phenolic compounds.

Determination of phenolics and aromatics

Sample analyses were performed at the Innovative Technologies Application and Research Center in Suleyman Demirel University. Callus samples (1000 mg) were weighed and homogenized with 10 mL methanol in a homogenizer (IKA T 25 Ultra-Turrax®, Staufen, Germany). The mixture obtained was filtered with a 0.45-μm filter (Minisart®, Sartorius Stedim Biotech, France) and then evaporated to dryness in an evaporator (Heidolph Hei-VAP G1, Schwabach, Germany) at 40 °C. The dry extract was then dissolved in 1 mL methanol and 20 μL was transferred into the HPLC apparatus. The HPLC system was equipped with a LC—10ADvp pump, SIL—10AD vp auto-sampler and
CTO—10Avp column oven (Shimadzu, Kyoto, Japan). Agilent eclipse XDB-C18 (250 × 4.60 mm, 5 μm) column and a mobile phase consisting of methanol and acetic acid (3% v/v) in water. The flow rate was 0.8 mL/min and the injection volume was 20 μL. Column temperature was set to 30 °C. Diode array detector (DAD) worked at λmax = 278 nm, and chromatograms were obtained at various wavelengths according to absorption maxima of the analyzed compounds. The standards used were rutin trihydrate (Fluka 78095), quercetin dihydrate (Sigma Q0125), chlorogenic acid (Sigma C3878) and kaempferol (Sigma K0133).

For aromatics, the system was known as fused silica SPME fiber assembly Carboxen/Polydimethylsiloxane (CAR/PDMS) (Sigma-Aldrich®) with a column of Restek Rx-5Sil MS (30 m × 0.25 mm i.d., 0.25-μm film thickness) (Restek Corporation, Bellefonte, PA). The flow rate of helium as a carrier gas was 1.61 mL/min. The injector temperature was set to 250 °C for splitless injection. After 2 min at 40 °C, the system reached 250 °C with 4 ºC increments per minute and waited for 5 min at 250 °C. Mass spectra were taken at 70 eV. The sample stood for 30 min with fiber, for 15 min without fiber at 60 °C, and desorbed at 250 °C. Identification of components with mass spectra data according to mass library was used NIST and WILEY reference standard was used. Relative percentage amounts of the separated aromatic substances were calculated from the total ion chromatograms displayed by the computarized integrator (Shimadzu, Kyoto, Japan).

Statistical analysis

Pattern of Randomized block design was used for the trials and were conducted at least three times. The Oneway-ANOVA of the SPSS 23.0 package program was used for the variance analysis of data, and the Duncan Multiple Comparison Test was used for the comparison of means. Graphs for all experimental data were constructed to determine whether the mean values between the different treatment concentrations held a significant difference.

Results and discussion

Callus induction and fresh weight

The effects of strigolactones on plants are not yet fully defined and it is unknown whether the observed effects are universal across species. At 0.2 μM, GR24 used alone in medium M4 significantly reduced both the formation frequency and fresh weight of callus (P < 0.05), while combined with NAA + BAP (M3 medium) it significantly reduced the frequency of callus formation but had no significant effect on fresh weight. On the other hand, at 0.1 μM, GR24 combined with NAA + BAP (medium M2) did not reduce callus fresh weight or induction frequency compared to medium M1 (Fig. 1). Mlodana (2012) found that strigolactone-deficient and insensitive mutants of wild-type A. thaliana Col-O were also successful in forming callus on media containing various amounts of 2,4-D + kinetin (2 + 2 mg/L or 0.5 + 0.05 mg/L), and when these calluses were transferred onto media containing 0.1 μM GR24 and auxin or cytokinin, the amount of callus biomass increased in some of the mutants. Grobbelaar et al. (2014) demonstrated that the strigolactones GR24 and Nijmegen-1 (0.1 μM) generally had a minimal effect on the growth of Salvia frutescens nodal explants. However, when combined with 1 mg/L NAA, they promoted biomass production but had no significant effect on fresh weight. Similar results were also shown by Zulfiqar et al. (2020) with Helianthus annuus L., where 0.01 mg/L GR24 was optimum for callus growth. In all media the callus were generally friable and green to yellowish (Supplementary Fig. 1).

Production of phenolic and aromatic substances

As main active compounds, flavonoids play a notable role in a variety of pharmacological activities, including antiallergic, anti-inflammatory and antioxidant effects (Trombetta et al. 2005; Panico et al. 2005). Germano et al. (2002), Matthaus and Özcan (2005) and Tlili et al. (2009) reported that the caper plant is a rich plant source of the flavonoids rutin (rutocide) and quercetin, while different parts of the plants contain phytosterols, tocopherols, carotenoids and glucosinolates. No previous study has been found concerning the effect of GR24 on the amount of phenolic compounds in C. spinosa callus. In this study, the total flavonoids in the M2 (P < 0.05) medium increased by 19% when compared to M1. Goda et al. (2017) found that the total flavonoid content in C.
Spinosa callus from the 2,4-D medium was 0.85 mg/100 g. It has also been stated in many studies that rutin was the main flavonoid in the aerial parts (Zhou et al. 2011; Argentieri et al. 2012). In our study, rutin was the dominant flavonoid in leaf calluses obtained from all media except M4, and its content in medium M2, of 16.9 μg/g dry weight (DW), increased approximately by 1.5 times when compared to M1 medium (P < 0.05). While GR24 alone significantly reduced the rutin content, the low concentration of GR24 used with NAA and BAP positively affected the amount of rutin (Fig. 2). Grobbelaar et al. (2014) reported that a combination of NAA and Nijmegen-1 positively influenced the accumulation of amino acids, flavonoids (sutherlandins) and terpenoids (sutherlandsides) in Sutherlandia frutescens. Tlili et al. (2010) found a rutin content of 1.352 mg/100 g and 693.14 mg/100 g in caper leaves and flowers bud collected in Tunisia. Mohabali et al. (2018) also showed that high levels of rutin and quercetin in leaves of caper, rutin was 16.93 and quercetin was 908.93 μg/g fresh weight (FW), and in fruit, 1019.52 rutin and 97.86 μg/g FW quercetin.

Palacio et al. (2012) found the amount of quercetin in callus of Larrea divaricata leaves treated with 2 mg/L 2.4 D and 1 mg/L BAP to be approximately 10 μg/g. In our study, quercetin was almost the same amount (5.1–5.4 μg/g dry weight, DW) except for M4 where quercetin was zero (Fig. 2). This suggests that NAA and BAP are effective hormones in the accumulation of quercetin, since GR24 alone negatively affected routine and quercetin production while when combined with NAA and BAP it was suitable for metabolite production. Many in vitro studies recommended to add BAP to the culture medium to increase the production of various secondary metabolites in plants. For example, Udomsuk et al. (2009) reported that BAP had a positive effect on the amounts of some secondary metabolites in addition to the total isoflavonoids extracted, and Shah et al. (1976) showed that kinetin improved polyphenol groups such as quercitin and isomers by interfering with the synthesis of nucleic acids that can affect polyphenol production.

Kaempferol content varied between 4.8 and 3.3 μg/g DW among media tested (Fig. 2). Tlili et al. (2017) detected 3.63% (μg/g DW) kaempferol in caper leaf extracts, but Haifa et al. (2016) did not find kaempferol in C. spinosa leaves from Tunisia.

The total amount of phenolic compounds increased by 48.8% compared to M1 medium which served as the standard, and the highest amount was found to be 72.79 μg/g DW in M2 medium, with 0.1 μM G24 (P < 0.05). With GR24 at 0.2 μM, phenolic compound content was much lower, whether alone or combined with NAA and BAP, compared to the M1 medium (Fig. 3).

Conversely, this was not the case for the content of chlorogenic acid, which was highest on medium M2 with 46.4 μg/g DW, and also caught our attention as the highest among the analyzed phenolics. GR24 used alone also significantly increased the amount of chlorogenic acid compared to medium M1 (Fig. 3). Interestingly, Rad et al. (2021) detected 0.680 mg/g DW chlorogenic acid in caper leaves. There are studies analyzing the effects of auxin and cytokinin on the amount of chlorogenic acid in in vitro cultures of some plants. Thus, Erkoyuncu and Yorgancılar (2021) found that leaf calluses of Echinacea purpura L. cultured on 1 mg/L 2,4- D + 2 mg/L BAP contained 0.23 mg g chlorogenic acid, while Szopa et al. (2020) determined a chlorogenic acid content of 20 mg/100 g DW in Schisandra rubriflora microshoot.
extracts, and Siahposuh et al. (2011) reported that kinetin stimulates chlorogenic acid production positively in *V. persica* callus, and replacement of 2,4-D with NAA does not change chlorogenic acid production.

In our study, caffeic acid was not detected in calluses in any medium, including the M1 medium (data not shown). According to Oudah et al. (2019) the amount of caffeic acid in caper leaves was 73.542 μg/ml, but Rezzan et al. (2013) did not find any caffeic acid in the caper leaves collected from Gaziantep (Turkey).

Antognoni et al. (2008) reported that α-tocopherol production in calli of *Amaranthus caudatus* and *Chenopodium* species was approximately 40 times lower than the tocopherol content in the leaves and other plant organs. In some cases, this is due to the lack of specialized cell structures (St. Pierre et al. 1999; Pasqua et al. 2003). In our study, the highest amount of α-tocopherol was found in the M1 medium, and it decreased significantly in all media with GR24. In callus cultures of *C. spinosa*, α-tocopherol accumulation was approximately 1000 to 5000 times lower than in leaves (20.19 ± 31.71 mg/100 g), regardless of the culture medium (Tili et al. 2009).

In this study, the content of aromatic compounds of calluses generally examined were sulfur compounds, aldehydes, ketones, hydrocarbons and derivatives, alcohols, and others (Table 1). In the M4 medium, the total sulfur compound was 87.53% and the dominant compound was methyl isothiocyanate (556-61-6). The pungent aroma of capers is usually caused by the very sharp methyl isothiocyanate released after an enzymatic reaction with a mustard oil glycoside known as glucocaparin (methyl glucosinolate) (Sozzi et al. 2012). El-Ghorab et al. (2007) and Bakr and El Bishbishy (2016) stated that the predominant essential oil in the caper plant collected from the flora was methyl isothiocyanate at 20.0% and 24.66%, respectively. In our study, this rate was found to be higher in all media in caper calluses, clearly showing that callus culture is a good method for methyl isocyanate production. Zhang (2004) documented the cancer-preventive activity of a significant number of isothiocyanates, most of which occur in plants, especially in cruciferous vegetables. Moreover, glucosinolates via their hydrolysis products are among the most powerful antibiotic substances known from higher plants (Louda and Mole 1991), with an established correlation between the content of glucosinolates (isothiocyanates) and disease resistance (Esteve 2020). Here, M4 medium increased the total aldehyde content from 6.09 to 7.90%.

M2 medium increased ketone and hydrocarbon compounds by 10 and 14 folds, respectively, compared to medium M1, demonstrating that the combination of GR24 with the other two plant growth regulators had a positive

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**Table 1** Effect of various strigolactone GR24 concentrations on the aromatic compounds of caper calluses

| Aromatic compounds | Media     | M1   | M2   | M3   | M4   |
|--------------------|-----------|------|------|------|------|
| Sulphur compounds (%) |           | 83.58| 66.97| 83.27| 87.53|
| Aldehydes (%)      |           | 6.09 | 4.88 | 6.45 | 7.90 |
| Ketones (%)        |           | 1.32 | 19.3 | 6.55 | 0.34 |
| Hydrocarbon and derivatives (%) | | 0.56 | 5.8  | 0.83 | 0.62 |
| Alcohols (%)       |           | 6.08 | 1.62 | 1.86 | 3.00 |
| Others (%)         |           | 2.37 | 1.43 | 1.04 | 0.61 |
effect and this effect was inversely proportional to the GR24 concentration. The dominant ketone was acetoin (513-86-0), and n-hexan (110-54-3) the main hydrocarbon and derivatives. The amount of alcohol and other aromatics was reduced in all media with GR24 compared to M1 medium. This article is the first to show the effect of GR24 on the amount of essential oil in C. spinosa callus. Romeo et al. (2007) recorded 8.42% sulfur compounds, 12.8% hydrocarbon and derivatives and 7.48% alcohol in Eolian capers. Bidabadi and Sharifi (2021) stated that strigolactones (10 µM GR24) increased the essential oil content and yield in Dracocephalum kotschyi under drought stress. They also reported that increasing levels of GR24 application positively influenced essential oil content and yield in S. nemorosa where the lowest NaCl concentration (100 mM) added to 0.3 µM GR24, resulted in the highest essential oil content and yield (Sharifi and Bidabadi 2020).

Phenolic and flavonoid compounds are produced by the phenylpropanoid pathway. The types, concentrations and combinations of plant growth regulators are a simple but effective tool for the regulation of different branches of secondary metabolism in plant tissue cultures, and many studies showed the regulatory effect of NAA and BAP on the phenylpropanoid pathway (Luczkiwicz et al. 2014; Ramabulana et al. 2021). However, strigolactones had rarely been studied in this respect (Grobbelaar et al. 2014). In this study, it is shown that especially a combination of NAA and BAP with 0.1 µM GR24 increases the accumulation of some compounds by regulating this pathway together.

In conclusion, GR24 had no significant positive effect on callus induction and callus fresh weight. Even 0.2 µM GR24 alone had a negative effect on these parameters. However, the combination of NAA, BAP and 0.1 µM GR24 positively influenced the accumulation of chlorogenic acid, rutin and quercetin. It was also determined that GR24 used at lower concentrations was more effective, but further studies on this are still required.

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Data availability All data generated or analyzed during this study are included in this article.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Consent for publication The authors declare consent for publication.

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