Chapter 6
Impacts of Climate Alterations on the Biosynthesis of Defensive Natural Products

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Abstract Climate change fluctuations, specifically CO_2 concentration, temperature, rainfall patterns, droughts, and soil salinity, are increasing due to anthropogenic activities. These variations are identified as major constraints to plant survival and therefore limit plant growth and productivity. Photosynthesis inhibition, excessive ROS (reactive oxygen species) production, biomass reduction, increased pathogen infestation, and ultimately lower yields are the major limiting attributes that have attracted a lot of attention from researchers worldwide. Since climate change predictions indicate that ecological damage will be more frequent and severe in the upcoming futuristic scenarios, the question of fulfilling the food requirement of the ever-growing population becomes imperative. Plants are sensitive to the effects of climate change. Alterations in photosynthesis and carbon assimilation mechanisms are attributed to reduced productivity. To cope with these stresses, secondary metabolite production elicits defensive responses in plants. These natural by-products are synthesized from primary metabolites and protect against various abiotic and biotic stresses. Synthesis and accumulation of secondary metabolites differ among plant species growing in different environmental conditions. Phenolics, flavonoids, alkaloids, terpenoids, tannins, glucosinolates, and so on are a useful array of natural products that increase plant resistance against various stresses. Although these are synthesized in minimal concentrations, they display a crucial role in the scavenging of ROS molecules.

Keywords Abiotic stress · Climate change · Photosynthesis · Reactive oxygen species · Secondary metabolites · Yield

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6.1 Introduction

Anthropogenic activities including the burning of fossil fuels, urbanization, and a rise in the concentration of greenhouse gases (GHGs) are the major factors responsible for global climate change (Dutta et al. 2020). Elevated concentration of GHGs in the atmosphere since the industrial revolution has increased the concentration of CO_2 from 280 ppm to >410 ppm and is expected to rise further to 730–1000 ppm by 2100 (IPCC 2014). Recently, IPCC (2021) revealed that this enhancement in atmospheric GHGs further raises the global temperature approximately by 0.84–1.10 °C, and consequently disturbing the rainfall patterns and prevailing drought conditions in arid regions of the world (IPCC 2014). Such variability in climate is influencing crop production with each successive year and somewhere evokes an uncertainty in terms of food production (Reddy and Hodges 2000). It is predicted that agricultural outputs will be declined (10–20%) by the end of 2080 in developing countries (Thompson and Cohen 2012). Consequently, the subject of achieving food security worldwide becomes a daunting task with an ever-growing population (Barnett 2011; Funk and Brown 2009; Rice and Garcia 2011). In the current scenario, about 1 billion people are food-deprived, 150 million children are chronically undernourished, 50 million children are acutely malnourished with a higher mortality rate, and another 38 million children are overweight (Misselhorn et al. 2012; Fanzo 2018). The situation in India is similar to the global scenario: whether the increasing population and demand for food supply will continue to rise with climate change. Temperature increases of 1–2 °C have a negative influence on the productivity of major cereal crops, which in turn affects the nutritional status of the population (Easterling et al. 2007; Rao et al. 2016).

Climate change unavoidably disturbs plants by hampering the physiological and biochemical processes such as altered photosynthesis, plant–water interactions, and CO_2 assimilations, which severely affects their growth and yield (Fig. 6.1) (Anjum et al. 2011). These variations induced oxidative stress in plants via increased generation of reactive oxygen species (ROS), leading to lipid peroxidation, DNA damage, and inactivation of important enzymes (Akula and Ravishankar 2011). In addition to this, overproduction of ROS also inhibits CO_2 fixation in chloroplasts, as they are the primary source of ROS generation (Asada 2006). In response to such constraints, plants have acquired alternative strategies such as increased antioxidative response, phytohormones, osmotic adjustment, and enhanced production of secondary metabolites (Yadav et al. 2021; Jogawat et al. 2021; Zandalinas et al. 2022). Secondary metabolites play a vital role in plant defense against herbivory, insect attack, and environmental stress (Chomel et al. 2016). Several biotic and abiotic stresses act as an elicitor for the stimulation of secondary metabolites (Radman et al. 2003; Ghorbanpour et al. 2014). Their synthesis and accumulation differ among plant species grown under different environmental conditions (Radušienė et al. 2012). Shikimate pathway, acetate–malonate pathway, and side reactions involving glycolysis and TCA cycle are different metabolic routes through which biosynthesis of secondary metabolites takes place in plants (Geilfus 2019;

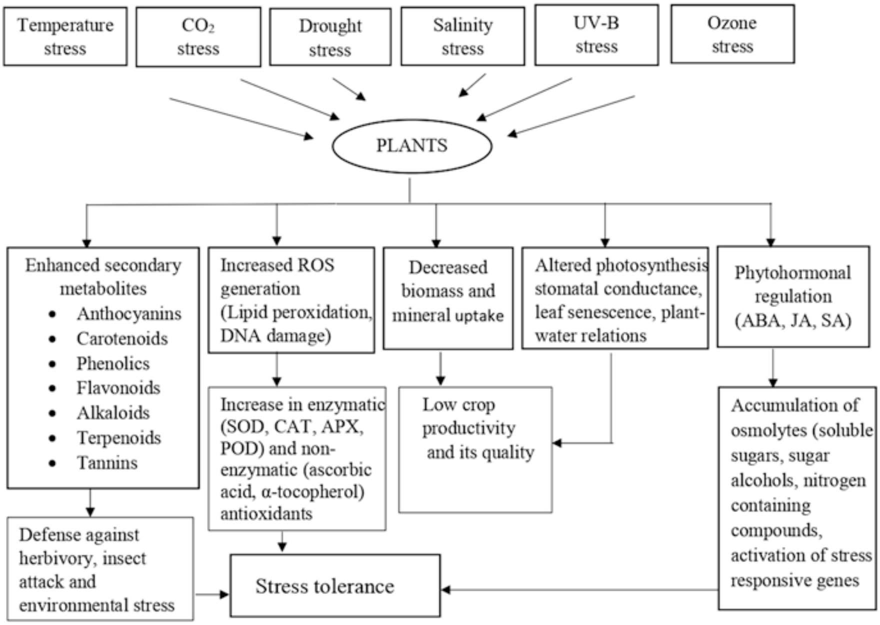

Fig. 6.1 Effect of different abiotic stress responses in plants due to climate change

Nabavi et al. 2020). Phenolics, flavonoids, and terpenes synthesized in very low concentrations facilitate antioxidative defense mechanisms, thus increasing their acclimatization to oxidative stress in plants (Edreva et al. 2008). Phytohormones, particularly ABA and jasmonic acid (JA), are positively correlated with the production of secondary metabolites, as they work in a synergistic manner. For example, ABA and JA were responsible for the increase in phenolics and flavonoid contents in *Castanea sativa* (Camisón et al. 2019). This could protect the plants against increased oxidative stress through the activation of NAC transcription factors (Choudhary et al. 2021).

6.2 Elevated CO_2 and Temperature Stress

Increased anthropogenic activities have accelerated the level of CO_2 concentrations in the atmosphere. At the time of pre-industrialization, the CO_2 levels were 280 ppm initially, but with increasing trends, it has been reported to be nearly 410 ppm (September 2019) (IPCC 2019). In view of this, a two-fold increase in CO_2 concentration has been expected (IPCC 2013). These elevated levels of CO_2 not only causes global warming but also reduces ecosystem productivity. According to NOAA (2020), the surface temperature of land and oceans is 0.98 °C warmer than the twentieth-century average (13.9 °C). Kimball (2016) found that increasing CO_2

concentration by 200 ppm will increase canopy temperature (ET) by 0.7 °C. Increased ET becomes a problem, particularly for developing countries, as it has reduced crop productivity and grain yield (Chaturvedi et al. 2017; Wang et al. 2017). CO_2 levels play a significant role in plant metabolic processes. Short-term exposure to elevated CO_2 (~400 ppm) reported enhanced photosynthesis, biomass, and decreased oxidative stress. Various plants, such as *Solanum lycopersicum* L., *Stevia rebaudiana* L., and *Parthenium hysterophorus* L., have demonstrated the beneficial impact of elevated CO_2 (Hussin et al. 2017; Bajwa et al. 2019; Pan et al. 2020). However, prolonged exposure to higher CO_2 levels (~800 ppm), promoted negative effects on plant growth, i.e., reduced photosynthesis, and altered biomass that ultimately affected crop yield and its quality (Wang et al. 2013). For instance, decreased photosynthesis and fruit yield has been observed under high CO_2 concentrations in strawberry (Balasooriya et al. 2018). This significant reduction is due to the low availability of RuBisCO content and nitrogen concentration (Gamage et al. 2018; Rosa et al. 2019). Many crops, including *Lactuca sativa* and *Spinacia oleracea*, had lower nutritional quality (Mg, N, Fe, Zn, and S) under increased CO_2 concentrations (Giri et al. 2016; Dong et al. 2018).

Variable environmental factors influence secondary metabolite biosynthesis in plants. Phenolics such as flavonoids, condensed tannins, and alkaloids in response to elevated CO_2 concentration have significantly modulated secondary metabolism in plants (Levine et al. 2008; Jia et al. 2014). CO_2 enrichment in the atmosphere increases the susceptibility of plants to insect attack by boosting photosynthesis and higher production of carbohydrates (Ainsworth and Rogers 2007; Bernacchi et al. 2007). To avoid insect damage, plants allocate the primary metabolites to secondary metabolites grown under high CO_2 levels. In woody plants, phenolic compounds and terpenoids provide defense against herbivory at higher CO_2 concentrations (Feeny 1976; Rhoades and Cates 1976). Robinson et al. (2012) reported increased total phenolics (19%), flavonoids (27%), and tannins (22%) in plants grown under elevated CO_2. On the other hand, flavonoids such as quercetin, fisetin, and kaempferol were enhanced in the leaves and rhizomes of ginger, hence exhibiting higher antioxidative defense responses (Ghasemzadeh et al. 2010). Similarly, soybean plants mediate anti-herbivory by increasing the ratios of quercetin and kaempferol while decreasing the genistein concentration (Piubelli et al. 2005). Higher phenylalanine ammonia-lyase (PAL) enzyme activity is linked with the upregulation of secondary metabolites in elevated CO_2. For example, a significant increase in phenolics and flavonoid concentration was observed in *Eleais guneensis* L. due to increased PAL enzyme activity (Ibrahim and Jaafar 2012). Similarly, *Triticum aestivum* L. exhibited higher PAL activity along with an accumulation of phenolic compounds (Mishra et al. 2013). Generally, warming conditions are associated with phenolic contents in leaves and increased terpenoid concentrations in foliage (Peñuelas and Staudt 2010; Zvereva and Kozlov 2006). However, under elevated CO_2, phenolic concentrations were increased in the foliage while decreased in woody tissues (Zvereva and Kozlov 2006). On the other hand, terpenoid concentration was significantly lowered as CO_2 concentration increased in conifers. Similarly, the emission of phenolics and flavonoid content was significantly intensified by elevated temperature in *Zingiber officinale* L. (Ghasemzadeh et al. 2011). Several plant species, such as *Thymus hyemalis* L., *Thymus vulgaris* L., *Valeriana jatamansi* L., and *Camellia sinensis* L., have been reported with an increased concentration of secondary metabolites in plants (Biel et al. 2005; Vurro et al. 2009; Li et al. 2017; Kaundal et al. 2018). Sobuj et al. (2018) observed the differential response of flavonoid concentration in male and female plants. Under elevated CO_2 conditions, female plants had a significantly higher concentration of flavonoids as compared to male plants. The anti-carcinogenic and anti-inflammatory activities of glucoraphanin and sulforaphane have been linked to increased hydrolysis of glucosinolates (GSs) in response to elevated CO_2 (Table 6.1) (Almuhayawi et al. 2020). Jasmonic acid (JA) plays an integral role in plant defense mechanisms through the elicitation of different secondary metabolites such as alkaloids, flavonoids, phenylpropanoids, and terpenoids (Tamogami et al. 1997). For example, higher ascorbic acid and carotenoid content have been observed in *Origanum majorana* L. (Złotek 2017). Similarly, various plants have been reported to produce differential secondary metabolites being elicited by JA (Thakur et al. 2019).

Temperature stress also affects plant ontology and metabolic processes, i.e., physiological and biochemical changes such as chlorophyll pigment breakdown, leaf senescence, membrane damage, and protein denaturation (Waraich et al. 2012). Other effects of higher temperature (heat stress) can be identified by decreased quantum efficiency of Photosystem II (PSII), stomatal conductance, CO_2 fixation, altered secondary metabolites, and ROS generation (Hasanuzzaman et al. 2013; Verma and Shukla 2015). However, low temperature is responsible for disturbing the plant–water interactions and metabolic activities, ultimately hampering the plant growth and productivity (Chinnusamy et al. 2007). Plant growing under low temperature synthesizes cryoprotective substances such as soluble sugars (trehalose, raffinose, stachyose, and saccharose), sugar alcohols (inositol, ribitol, and sorbitol), and nitrogen-containing compounds (glycine betaine, proline) to maximize cold stress tolerance (Janská et al. 2010). In *Arnica montana*, enhanced ratios of quercetin–kaempferol have been reported under low temperature (Albert et al. 2009). Increased artemisinin content has been observed after exposure of *Artemisia annua* to cold stress (Yin et al. 2008; Vashisth et al. 2018).

Variations in temperature influence the biosynthesis and accumulation of alkaloids in plants. For instance, in *Papaver somniferum* L., the accumulation of morphinane, benzylisoquinoline, and phthalisoquinoline becomes restricted at low temperature (Bernáth and Tetenyi 1979). Contrary to this, the concentration of isoflavonoids (genistein, genistin, and daidzein) is significantly enhanced in the roots of *Glycine max* L. at low temperature (Janas et al. 2002). Similarly, several studies have been reported with increased alkaloid contents in plants incubated at a higher temperature. For example, *Lupinus angustifolius* has been reported with higher alkaloids concentration when grown under elevated temperature (Jansen et al. 2009). In *Catharanthus roseus* L., increased concentrations of catharanthine, vindoline, and vinblastine were observed at a higher temperature, while incubation at low temperature resulted in a two- to four-fold reduction of catharanthine and vindoline contents (Dutta et al. 2007). These findings suggest that higher temperature

Table 6.1 Impact of CO_2 and temperature stress on different secondary metabolites in plants

Stress	Dose	Plants	Endogenous response of secondary metabolites	References
CO_2	(400–1000 ppm)	*Triticum aestivum* L.	Flavonoid contents (homoorientin and rhamnoside) increased by 28–64%; a significant increase in tyrosine and trans-caffeic acid	Levine et al. (2008)
	(350–700 μmol mol^{-1})		Significant reduction in total phenolic acids (21.4%), condensed tannins (22.2%), and indole alkaloids (48.1%)	Jia et al. (2014)
	(700 ppm)		Increased PAL activity by 39.2% along with a significant increase in total phenolics by 11.7%	Mishra et al. (2013)
	(400–800 μmol mol^{-1})	*Zingiber officinale* L.	Elevated flavonoids contents (kaempferol, fisetin, and naringenin) in leaves by 44.9% and rhizomes by 86.3%; phenolic compounds (gallic acid, vanillic acid, and ferulic acid) increased in leaves by 112.2% and rhizomes by 109.2%	Ghasemzadeh et al. (2010)
	(400–1200 μmol mol^{-1})	*Eleais guineensis* L.	Enhanced total flavonoids by 132%; total phenolics by 91%	Ibrahim and Jaafar (2012)
	(550 μmol mol^{-1})	*Valeriana jatamansi*	Elevated essential oil content by 17.7%; sesquiterpenes by 17.2%	Kaundal et al. (2018)
	(800 μmol mol^{-1})	*Camellia sinensis* L.	Upregulated expression of catechins and theanine biosynthetic genes while caffeine synthetic genes were downregulated	Li et al. (2017)
	(400 μmol m^{-2} s^{-1})	*Brassica oleracea* L.	Slight increase in myrosinase activity accounts for the effective production of sulforaphene	Almuhayawi et al. (2020)

(continued)

Table 6.1 (continued)

Stress	Dose	Plants	Endogenous response of secondary metabolites	References
Temperature	(7.5–12.5 °C)	*Arnica montana* L.	Ratios of quercetin–kaempferol were significantly enhanced	Albert et al. (2009)
	(4 °C)	*Artemisia annua* L.	Artemisinin content significantly elevated by 27.16%	Vashisth et al. (2018)
	(10 °C)	*Glycine max* L.	Increased concentration of isoflavonoids consisting of daidzein (200%), genistein (240%), and genistin (310%)	Janas et al. (2002)
	(15.5 °C)	*Lupinus angustifolius* L.	Estimated increase in alkaloid contents by 0.11%	Jansen et al. (2008)
	(4 °C)	*Catharanthus roseus* L.	Significant reductions in catharanthine content by two-fold along with two- to four-fold reduction in vindoline content	Dutta et al. (2007)
	(20 °C)	*Chamomilla recutita* L.	Increased concentrations of α-bisabolol were detected	Fahlén et al. (1997)
	(40 °C)	*Pinus ponderosa* L.	Significant increase in sesquiterpenes (α-bergamotene, α-farnesene, β-caryophyllene, and β-farnesene) concentrations	Helmig et al. (2007)
	(6–22 °C)	*Betula pendula* L. *Populus tremula* L.	DMNT (homoterpene) increased consistently; SQTs (β-bourbonene, γ-cadinene) were significantly enhanced	Ibrahim et al. (2010)
	(26.8–31.2 °C)	*Panax quinquefolius* L.	Ginsenoside concentrations in roots significantly increased by 49%	Jochum et al. (2007)

DMNT 4,8-dimethylnona-1,3,7-triene, *PAL* phenylalanineammonia-lyase, *SQTs* sesquiterpenes

enhanced the concentration of alkaloids in plants and low temperature significantly hinders their biosynthetic pathway genes (Dutta et al. 2007). The antioxidative properties of terpenes provide stability to the thylakoid membrane of the chloroplast. In *Chamomilla recutita*, the combination of photoperiod (21-3h) and temperature (20 ± 2 °C) resulted in the highest concentration of α-bisabolol (Fahlén et al. 1997). Temperature dependency is correlated with the yield of terpenoids. For example, pine species have been reported with increased emissions of sesquiterpene compounds (α-bergamotene, α-farnesene, β-caryophyllene, and β-farnesene) at elevated temperature (Table 6.1) (Helmig et al. 2007). Differential response of temperature on volatile organic compounds (VOCs) has been studied in *Betula pendula* and *Populus tremula*, resulting in an exponential increase in DMNT (4,8-dimethyl-nona-1,3,7-triene) concentration (Ibrahim et al. 2010). In the roots of *Panax ginseng* and *Panax quinquefolius*, ginsenoside content was significantly enhanced under elevated temperature, while photosynthesis and biomass were considerably reduced (Yu et al. 2005; Jochum et al. 2007).

6.3 Drought Stress

High temperature and solar radiations are accompanied by water deficit conditions that induce drought (Xu et al. 2010). Among abiotic stressors, drought hampers agricultural productivity by upto 50–70% (Verma and Deepti 2016). It has been estimated that drought affects 40% of the global population and now has been predicted to pose a risk of displacement to 700 million populations by 2030 (WHO 2020). Drought stress severely alters plant growth through photosynthesis inhibition, decreased stomatal conductance, CO_2 assimilation, and leaf senescence (Nezhadahmadi et al. 2013; Wang et al. 2018; Zargar et al. 2017). Plant defense responses, including secondary metabolites production, are triggered by decreased water potential and turgor pressure caused by increased transpiration rate (Ashraf et al. 2018). Drought stress induces ROS production through oxidative stress, resulting in enhanced production of flavonoids and phenolic acids (Larson and Weber 2018). Through transcriptomics, Morales et al. (2017) identified pathways as well as genes involved in drought-tolerant quinoa. Upregulation of drought-tolerant genes such as *GmbZIP44*, *GmbZIP46*, *GmbZIP62*, and *GmbZIP78* has been known to provide tolerance against drought (Xie et al. 2009). In addition, enhanced expression of the *GmbZIP1* gene in wheat has been reported as an excellent resource for overcoming drought stress (Gao et al. 2011). Activation of the PAL gene resulted in enhanced phenolic and flavonoid contents in *Lactuca sativa* L. (Rajabbeigi et al. 2013). Various plants such as *Artemisia*, *Hypericum brasiliense*, *Hypericum perforatum*, and *Trachyspermum ammi* have been reported with increased secondary metabolites such as artemisinin, betulinic, ruetin, hyperforin, and quercitin (Azhar et al. 2011; Zobayed et al. 2007; Verma and Shukla 2015). Similarly, water-deficit conditions (80–85% field capacity) decreased the number of total flavonoids in *Glechoma longituba* (Zhang et al. 2012).

The major enzymes responsible for the biosynthesis of flavonoids include chalcone synthase (CHS), chalcone isomerase (CHI), flavone synthase (FNS), flavanone 3-hydroxylase (F3H), flavonol synthase (FLS), dihydroflavonol 4--reductase (DFR), and anthocyanidin synthase (ANS) (Shih et al. 2008). The antioxidant property of flavonoids lies in the position of hydroxyl groups and carbon modifications such as glycosylation, methylation, and prenylation (Rice-Evans et al. 1997). Flavonoids under drought stress act as an antioxidant and protect plants from severe damage induced under water-deficit conditions (Nichols et al. 2015). For instance, in *Pisum sativum* L., flavonoid concentration was significantly increased by 45% in response to drought stress (Nogués et al. 1998). Similarly, roots of *Scutellaria baicalensis* were reported with elevated concentrations of flavonoids (Yuan et al. 2012). This increased accumulation of flavonoids represents effective detoxification of H_2O_2 molecules induced via drought stress (Hernández et al. 2009). In addition, drought stress also influenced phenolic concentration in plants, which was mediated via alteration in the phenylpropanoid pathway (Table 6.2) (Gharibi et al. 2019; Rezayian et al. 2018; Li et al. 2018). *Salvia dolomitica* and *Salvia officinalis* showed an increase in flavonoids (101%) and phenolics (139%) content under drought conditions (Caser et al. 2018, 2019). Drought stress reduced oil, sesamin, and quercetin concentration, however, a significant increment was noticed in flavonoids and phenolics contents in *Sesamum indicum* L " (Kermani et al. 2019). Biosynthesis of glycine betaine via enhanced expressions of glycine betaine hydrogenase was responsible for the alleviation of drought stress in *C. roseus* (Jaleel et al. 2007). Similarly, the artificial introduction of mannitol in seedlings elevated the concentrations of carbohydrates, proline, thymol, and γ-terpinene (Razavizadeh and Komatsu 2018). Water stress altered essential oil content (geraniol and citral) in *Cymbopogon citratus* L. (Singh-Sangwan et al. 1994). However, moderate drought conditions exhibited a higher concentration of β-thujone and camphor in *Salvia officinalis* (Bettaieb et al. 2009). Additionally, Nowak et al. (2010) reported higher concentrations of monoterpenes (33%) in the same plant. Essential oil contents do not always increase; however, it depends on the plant species and the severity of the stress. Paulsen and Selmar (2016) reported a considerable increase in terpene content, whereas the total amount of terpene was markedly reduced due to biomass reduction.

6.4 Salinity Stress

Salinity stress is one of the major limiting factors in plant growth and development. Due to increased anthropogenic activities and global climate change, it is projected to worsen in the near future (Rengasamy 2010). For instance, salinity stress significantly decreased crop yield by 10–50% in most salt-sensitive plant species (Panta et al. 2014). Globally, salinization has recorded an estimated economic loss of US$ 27.3 billion/year (Qadir et al. 2014). This significant increasing trend in salinity becomes a subject of great concern for national as well as global food security. Keeping this in view, the Indian government has planned to restore 26 million ha of salt-affected lands by 2030 (Kumar and Sharma 2020). Photosynthesis inhibition, ROS production, and reduced germination are some of the negative impacts commonly observed under salt stress. The generation of ROS mediated via salt stress

Table 6.2 Impact of drought stress on different secondary metabolites in plants

Stress	Dose	Plants	Endogenous response of secondary metabolites	References
Drought	Field capacity (60–100%)	*Trachyspermum ammi* L.	Increased total phenolic contents (4.44 mg/g) was estimated	Azhar et al. (2011)
	9–12 days	*Hypericum perforatum* L.	70-fold higher hyperforin concentration; antioxidants increased by 2.5-fold	Zobayed et al. (2007)
	Field capacity (80–85%)	*Glechoma longituba* L.	Significant increase in yield of total flavonoids	Zhang et al. (2012)
	30–70 days	*Scutellaria baicalensis* L.	Increased total flavonoid contents both in roots and leaves; baicalin and baicalein (major active compounds) contents remained unchanged	Yuan et al. (2012)
	7–28 days	*Achillea pachycephala* L.	Phenolic acids and flavones such as chlorogenic acid (7.23 mg/100 g DW) and luteolin (5.1 mg/100 mg DW) were markedly elevated, major flavonoid (apigenin-7-*O*-glucoside) present in abundant concentration (10.41 mg/100 g)	Gharibi et al. (2019)
	PEG (0, 5, 10, 15%)	*Brassica napus* L.	Influence of increased PAL enzyme activity on total phenols, flavonoids, and flavonols concentration accompanied with increased tocopherol content and decreased anthocyanin contents significantly	Rezayian et al. (2018)
	PEG (5–10%)	*Cucumis sativus* L.	Upregulated expression of phenolic compounds (vanillic acid and 4-hydroxycinnamic acid)	Li et al. (2018)
	0–34 days	*Salvia sinaloensis* L.	Altered chemical profiles of BVOC and EO; significant increase in phenolics, flavonoids, and monoterpenes (camphor) while sesquiterpene (Germacrene D) contents decreased significantly	Caser et al. (2018)
		Salvia dolomitica L.	Substantial reduction in total phenols and flavonoid contents; sesquiterpene hydrocarbons (66.32%) were significantly increased; monoterpene hydrocarbons (29.41%) and oxygenated hydrocarbons (2.19%) were considerably reduced	Caser et al. (2019)
	–	*Sesamum indicum* L.	Elevated phenolics (caffeic, *p*-coumaric and ferulic acids) and flavonoids (rutin and apigenin) levels; oil contents, sesamin, and quercetin decreased significantly	Kermani et al. (2019)
	Field capacity (25, 50, 100%)	*Salvia officinalis* L.	Enhanced essential oil constituents (β-thujone, camphor, and 1,8-cineole)	Bettaieb et al. (2009)

BVOC biogenic volatile organic compounds, *EO* essential oils, *PAL* phenylalanineammonia-lyase alters plant metabolic activities such as the disruption of membrane and ion toxicity (Ashraf et al. 2015; Chaudhary and Choudhary 2021). Secondary metabolites can scavenge ROS through the enhanced accumulation of phenolic compounds. Polyphenol concentrations significantly increased in *Cakile maritime* after exposure to different concentrations of NaCl (0, 100, 400 mM), indicating a protective role against salt stress (Ksouri et al. 2007). Similarly, *Cynara cardunculus* were reported to have increased phenolic contents on exposure to moderate levels of NaCl (>75 mM) (Hanen et al. 2008). *Fagopyrum esculentum* L. under variable salt concentrations (10–200 mM) showed a remarkable increase in phenolic contents (isoorientin, rutin, orientin, and vitexin) compared to control (Lim et al. 2012). Exposure to increased salinity levels (0–200 mM) significantly enhanced the total non-flavonoids (30%), total phenolics (135%), and total tannins (72%) content in *Brassica napus* L. (Falcinelli et al. 2017). In contrast, *Brassica oleracea* L. showed a decrease in phenolic compounds (chlorogenic and derivatives of sinapic acid), indicating the accumulation of phenolic acids in a plant-specific manner (Lopez-Berenguer et al. 2009). Similarly, *Salvia macrosiphon* L. has been reported with a remarkable decrease in total phenolics (2.6 times) after exposure to 8 dS ms^{-1} salinity level (Valifard et al. 2017). Furthermore, this lack of correlation, however, depends on the synergistic interactions of different antioxidant molecules (Tarchoune et al. 2012a, b). The effects of different salt concentrations on various plant species are shown in Table 6.3.

Salt stress stimulates the production of tropane alkaloids in *Datura innoxia* L. (Brachet and Cosson 1986). In *C. roseus*, vincristine content was significantly enhanced in response to 150 mM NaCl but gradually declined with increasing salinity levels (Osman et al. 2007). Ali et al. (2008) reported altered ricinine content in *Ricinus communis* L. Similarly, reserpine and vincristine (alkaloids) contents significantly increased in *C. roseus* and *R. tetraphylla*, respectively (Ahl and Omer 2011). *Rosmarinus officinalis* governs increased concentrations of camphor and cineole on account of salt stress, whereas borneol, camphene, nopol, and α-terpineol concentrations were decreased significantly (Tounekti et al. 2011). Furthermore, roots of *Zea mays* L. drastically improved the zealexins levels by five-fold at higher levels of NaCl (500 mM); however, kauralexins contents increased upto two-fold at lower levels (100 mM) (Vaughan et al. 2015). Different concentrations of salt (0–150 mM) significantly enhanced the expression of flavonoid biosynthetic genes (CHS, FS, and PAL) and resulted in increased production of lutein and quercetin in *Solanum nigrum* L. (Ben Abdallah et al. 2016).

6.5 UV-B Stress

Depletion of the ozone layer raises its concern over increased exposure to UV-B radiation on plants and animals. UV-B radiation, which comprises 0.5% of total solar radiation, possesses a significant impact on terrestrial life forms (Rozema et al. 2009; Verdaguer et al. 2012; Correia et al. 2012). Equatorial regions receive

Table 6.3 Impact of salinity stress on different secondary metabolites in plants

Stress	Dose	Plants	Endogenous response of secondary metabolites	References
Salinity	(0, 100, 400 mM)	*Cakile maritima* L.	Significant increase in polyphenol concentration (56%) along with higher MDA contents (1.6–2.6-fold)	Ksouri et al. (2007)
	(25–150 mM)	*Cynara cardunculus* L.	Two-fold increase in polyphenol concentrations at moderate salinity levels, 50-fold higher (IC_{50}) antioxidant activity	Hanen et al. (2008)
	(10–200 mM)	*Fagopyrum esculentum* L.	Two-fold increase in phenolic contents (isoorientin, orientin, rutin, and vitexin) with subsequent increase in antioxidant activity (60%); carotenoids contents elevated upto 40%	Lim et al. (2012)
	(0–200 mM)	*Brassica napus* L.	Total phenolics increased upto 135%, non-flavonoids upto 30%, and total tannins upto 72%; higher DPPH exhibited positive correlation with total phenolic contents	Falcinelli et al. (2017)
	(4–80 mM)	*Brassica oleracea* L.	Enhanced glucosinolate and flavonoid levels; significant decrease in phenolic contents, i.e., chlorogenic acid and sinapic acid (63.8%)	Lopez-Berenguer et al. (2009)
	2.3–6.8 dS m^{-1}	*Salvia macrosiphon* L.	2.6 times decrease in phenolic compounds accompanied with significant increase in antioxidant activity; negative correlation is established	Valifard et al. (2017)
	(100–150 mM)	*Catharanthus roseus* L.	Remarkable increase in alkaloid (vincristine) content (2-peak) attributed to increased levels of arginine	Osman et al. (2007)
	(50–150 mM)	*Solanum nigrum* L.	Quercetin levels increased about 2.6-fold; amount of carotenoids (lutein and β-carotene) was substantially high	Ben Abdallah et al. (2016)

DPPH 2,2-diphenyl-1-piacrylhydrazyl, *MDA* malondialdehyde content

about 12 kJ m^{-2} d^{-1} of solar UV-B radiation (Forster 2011). During the pre-1980s, about 6–14% of increment was detected. However, current scenarios reflect this percentage remaining elevated for the next decades (WMO 2010). UV-B influenced plants by reducing photosynthesis, biomass, deformities in chloroplast structure, and increased ROS generation (Pandey and Chaplot 2007; Yang et al. 2007; Kataria et al. 2014; Yao and Liu 2006; Kakani et al. 2003; Choudhary et al. 2017). Elevated UV-B levels significantly altered the concentrations of secondary metabolites such

Table 6.4 Impact of UV-B stress on different secondary metabolites in plants

Stress	Dose	Plants	Endogenous response of secondary metabolites	References
UV-B radiation	5.4–31 kJ m^{-2} d^{-1}	*Rosamatinus officinalis* L.	Predominant rosmarinic acid and carnosic concentrations followed by naringin and carnosol, while vanillic acid and hispidulin are considerably reduced	Luis et al. (2007)
	5.8–7.2 kJ m^{-2} d^{-1}	*Pisum sativum* L.	Significant increase in quercetin (114%) and kaempferol (72%) contents	Choudhary and Agrawal (2014b)
	5.8–7.2 kJ m^{-2} d^{-1}	*Vigna radiata* L.	Total flavonoids increased significantly by 36% along with maximum induction of PAL activity (105%)	Choudhary and Agrawal (2014a)
		Glycine max L.	Increased PAL activity (45%) correlates with increased kaempferol (83%) and quercetin (95%) contents; higher contents of lignin (60%) and wax (88%)	Choudhary and Agrawal (2016)
	0.43–1.13 W m^{-2}	*Glycyrrhiza uralensis* L.	Stimulated glycyrrhizin concentration in root tissues; melatonin present in roots and leaves	Afreen et al. (2005)
	ambient+1.8 kJ m^{-2} d^{-1}	*Acorus calamus* L.	Increased percentage of aristolene, *p*-cymene, caryophyllene oxide, and carvacrol; reduced contents of β-asarone	Kumari et al. (2009a, b)
	35 μmol s^{-1} m^{-2}	*Fagopyrum tataricum* L.	9.35-fold increase of rutin concentration in leaves with substantial increase in quercetin content; 30–40-fold higher abundance of FtCHI and FtCHS transcripts	Huang et al. (2016)
	8.64–9.50 kJ m^{-2} d^{-1}	*Glycine max* L.	Considerable increase in flavonoids concentration (quercetin, rutin, ferulic acid); no significant difference in phenolic compounds	Mao et al. (2017)
	6.5–12.4 kJ m^{-2} d^{-1}	*Olea europaea* L.	Significant decrease in phenolic contents (seciridoids, oleuropein (54%), and 2″-methoxy oleuropein) increased significantly by 68%; flavonoids (4′-methoxy luteolin) decreased; ouercetin-3-*O*-rutinoside, luteolin-7-*O*-glucoside, luteolin-7,4′-diglucoside, and apigenin 7-*O*-glucoside contents remains unchanged; HCAds and β-hydroxyverbacoside increased significantly by 75%	Dias et al. (2020)
	0.5–2.0 kJ m^{-2} d^{-1}	*Brassica oleracea* L.	Accumulation of kaempferol-3-*O*-disinapoyl-triglucoside-7-*O*-glucoside, kaempferol, and quercetin derivatives significantly decreased	Neugart et al. (2012)
	ambient +9.6 kJ m^{-2} d^{-1}	*Curcuma caesia* L.	Total flavonoid content increased by 62%, anthocyanin content by 44%; reduction in D-camphor, eucalyptol, curcumenol, isocurcumenol compounds; increment in 1,8-cineole, epicurzerenone, and elemene compounds; stimulation of anti-cancerous compounds (caryophllene, furanodiene, curzerene, epicurzerenone, and verrucarol)	Jaiswal et al. (2020)
	54 kJ m^{-2} d^{-1}	*Cuminum cyminum* L.	Increased trends in flavonoid and alkaloid contents with more pronounced effect on expression levels of PAL and DAHPs	Ghasemi et al. (2019)
	2.8 W m^{-2}	*Withania coagulans* L.	Enhanced contents of both withanolide A and withaferin by 3.42- and 1.38-folds; upregulated expression of terpenoid biosynthetic genes (FPPS, SQS, and $CYP_{51}G_1$)	Tripathi et al. (2021)

CHI chalcone isomerase, *CHS* chalcone synthase, $CYP_{51}G_1$ Cytochrome P45051G1, *DAHPs* deoxyriboninoheptulosinate-7-phosphate synthase, *FPPS* farnesyl pyrophosphate synthase, *HCAds* hydroxycinnamic acid, *PAL* phenylalanineammonia-lyase, *SQS* squalene synthase.

as alkaloids, anthocyanins, cyanogenic glycosides, flavonoids, and tannins in plants (Table 6.4) (Hirata et al. 1993; Morales et al. 2010; Gouvea et al. 2012). For instance, in *C. roseus*, the amount of catharanthine and vindoline production was significantly enhanced after supplemental UV-B radiation (Ramani and Jayabaskaran 2008). In another study, increased kaempferol and quercetin contents have been reported in *Populus trichocarpa* (Warren et al. 2003). Similarly, different rice cultivars have been observed with increased C-glycosyl flavones content under high UV-B intensity. Enhanced UV-B radiation leads to a more pronounced effect on flavanols accumulation in *Trifolium repens*, resulting in increased quercetin levels by 200% (Hofmann et al. 2000). These flavanols protect by acting as UV-B filters and further help to scavenge ROS (Agati et al. 2009, 2011).

UV-B-absorbing compounds such as flavonoids and hydroxycinnamic acids (derivatives of phenolic acids) confer protection at elevated UV-B levels (Agati and Tattini 2010; Jansen et al. 2008; Qian et al. 2020). For example, an increased concentration of flavonoids was reported in *Lactuca sativa* and *Gynura bicolor*, which were grown under ambient and high UV-B radiation (García-Macías et al. 2007; Schirrmacher et al. 2004). Accumulation of flavonoids in leaf epidermis confers resistance to the detrimental effects of UV-B radiation. Higher flavonoid contents illustrate increased PAL activity, a key enzyme involved in the phenylpropanoid pathway (Liu et al. 2002). Quercetin and kaempferol levels are certainly beneficial for plants to quench free radicals generated at the initial stage of UV-B exposure (Harborne and Williams 2000). Important crop plants, mainly *Vigna radiata* L., *Pisum sativum* L., and *Glycine max* L., demonstrated enhanced concentrations of quercetin and kaempferol contents induced via elevated UV-B exposure (Choudhary and Agrawal 2014a, b, 2016). In *Fagopyrum tataricum*, UV-B treatment resulted in a dramatic increase in concentrations of rutin (4.82 mg/g) DW and quercetin (0.04 mg/g) DW, respectively (Huang et al. 2016). Similarly, Mao et al. (2017) reported enhanced concentrations of rutin and quertein (flavonoids) in soyabean. Prolonged exposure to UV-B resulted in upregulation of flavonoid synthetic genes, i.e., FLS and F3′H in *Gingko biloba* (Zhao et al. 2020). The highest estimated flavonoid concentration was recorded in *Alternanthera sessilis* (Klein et al. 2018). In *Olea europaea* L. leaves, abundant concentrations of luteolin-7-*O*-glucoside account for the species' high tolerance to UV-B stress (Dias et al. 2020).

UV-B elicitation greatly influences the biosynthesis of phenolic compounds in plants. Increased ROS production initially triggered by UV-B resulted in enhanced phenolic contents that acts direct scavenger of ROS (Solovchenko and Merzlyak 2008). Ambient UV-B doses significantly enhanced flavonoid concentration in root and leaves of *Tropaeolum majus* L. and *Brassica oleracea*, suggesting UV-B as a systemic inducer of phenolic compounds in plants (Schreiner et al. 2009; Neugart et al. 2012). Phenolic compounds under UV-B exposure become elevated in post-harvested fruits and crops, including apples, peaches, onions, and strawberries (Marais et al. 2001; Kataoka and Beppu 2004; Higashio et al. 2004). The upregulation of phenylpropanoid enzymes by UV-B causes an increase in phenolic concentration (Tomás-Barberán and Espín 2001; Treutter 2005). Moderate UV-B exposure increased catharanthine concentration in *C. roseus* (Ramani and Chelliah 2007).

Various plants such as *Acorus calamus*, *Cyambopogon citratus*, *Mentha piperata*, and *Ocimum basilicum* have been reported with important pharmacological compounds, induced via UV-B (Kumari et al. 2009a, b; Dolzhenko et al. 2010; Maffei and Scannerini 2000). Sesquiterpenes such as artemisinin and Germacrene-D concentrations were found to be elevated by 11.6% and 10.5% under UV-B exposure (Kumari and Agrawal 2011; Rai et al. 2011). Another plant, *Glycyrrhiza uralensis*, exhibited a 1.5-fold increase in Glycyrrhizin content on exposure to UV-B dose (0.43 W m^{-2}) (Afreen et al. 2005). One of the major pharmacological important diterpenes, carnosic acid, present in *R. officinalis*, becomes elevated with UV-B dose (31 kJ m^{-2} d^{-1}) (Luis et al. 2007).

Exposure to UV-B radiation induced the production of terpenoids in various medicinal plants such as *Artemisia annua*, *Curcuma caesia*, *Cuminum cyminum* L., and *Vitis vignifera* L. (Li et al. 2021; Jaiswal et al. 2020; Ghasemi et al. 2019; Gil et al. 2012). These terpenoids protect the plant leaves from heat stress induced via UV-B (Liu et al. 2017). Withaferin A and withanolide A contents are increased by 1.38- and 3.42-fold in *Withania coagulans* L. (Tripathi et al. 2021). Thus, it can be concluded that UV-B can be used as a potential elicitor in increasing the contents of pharmacologically important compounds (Tripathi et al. 2021; Takshak and Agrawal 2014, 2015; Choudhary et al. 2021).

6.6 Tropospheric Ozone Stress

Ozone (O_3) is a potent air pollutant and greenhouse gas that may influence vegetation and human health directly or indirectly (DeLang et al. 2021; Wedow et al. 2021). Consumption of fossil fuel increases the concentration of precursor gases such as nitrogen oxide, carbon monoxide, and volatile organic compounds (VOCs), including methane and CO_2 that drive increased O_3 concentrations (Bhatia et al. 2012). Currently, tropospheric O_3 has reached 35–40 ppm globally and is expected to rise further to 70 ppm or more by 2050 (Frei 2015; Sicard et al. 2017; Pfister et al. 2014). Being a strong antioxidant, O_3 incorporates into plant tissues through stomata and induces ROS production that ultimately causes lipid peroxidation, DNA and RNA degradation, and programmed cell death (Mishra and Agrawal 2015; Picchi et al. 2017; Choudhury et al. 2017). Likewise, a variety of responses marked by elevated O_3, i.e., foliar injury, reduced chlorophyll and RuBisCO content, stomatal conductance, photosynthesis inhibition, and alteration in carbon allocation, cause a reduction in biomass, yield, and its quality (Emberson 2020). The activation of the PAL enzyme corresponds to increased production of flavonoids, phenolic acids, and monolignols, which improves the tolerance ability of plants by acting as scavengers against O_3 stress (Iriti and Faoro 2009). Long-term exposure to elevated O_3 concentrations concerning accumulation of phenolic compounds has been extensively studied (Richet et al. 2012). In *Linum usitatissimum* L., various secondary metabolites (flavonoids, anthocyanins, lignin, and wax) were enhanced under elevated O_3 (27.7–59.0 ppb) (Tripathi and Agrawal 2013). This enhancement reflects more utilization of assimilate in the production of secondary metabolites and less availability for reproductive organs that ultimately contribute to less yield (Singh et al. 2014). Fatima et al. (2018) investigated the effects of treatment of higher O_3 concentration (ambient + 30 ppb) on different wheat cultivars. These findings state that higher induction of flavonoids and total phenols subsequently declined reproductive structures and final yield. Differential responses in the accumulation of total phenolic contents in early and late sown cultivars of wheat indicated a correlation with higher ascorbic acid involved in the production of polyphenols (Yadav et al. 2019). Furthermore, various plants such as wheat, caster, groundnut, and cotton elucidate the sensitivity to ozone pollution (Chaudhary et al. 2021; Rathore and Chaudhary 2019; Ghosh et al. 2020a, b; Chaudhary and Rathore 2021a, b).

Weed invasion delineates the struggle of crop plants for their healthy survival under progressive climate change (Clements et al. 2014). It has been reported that weed interference causes an annual yield loss of 34% in some agronomically important crop species (Oerke 2006). The reason behind the aggressiveness of weeds lies in their higher content of phenolics and alkaloids, which alters the nutrient uptake in the soil (Majeed et al. 2012). A recent study was performed on *Chenopodium album* L. and *Triticum aestivum* L. plants to investigate the allelopathic interaction with a concomitant elevation in the concentration of O_3. The study revealed that O_3 raised the concentrations of ferulic acid (FA) and *p*-coumaric acid (CA) in the roots of the former and attributed a negative change in the root length of the latter (Ghosh et al. 2020a, b). Greater tolerance to O_3 stress is determined by increased PAL activity (Di Baccio et al. 2008). Elevated O_3 concentrations significantly increased total phenolic contents and PAL activity in *Vigna radiata* L. (Mishra and Agrawal 2015). Accumulated phenolic compounds triggered by higher O_3 levels during the initial days of exposure were later observed with a slight decrement in *Salvia officinalis* L. This suggested that higher doses of O_3 displayed a priming effect, and later, these plants failed to invest in their response strategy, indicating a slow production of secondary metabolites (Marchica et al. 2021). *Brassica campestris* L., a rich source of glucosinolate (GLS), exhibited an alteration in the amount of indole, aliphatic, and aromatic GLS (Han et al. 2021).

Exposure to higher levels of O_3 also affects isoprene emissions. Isoprene biosynthesis in plants maintains photochemical efficiency and ROS levels induced via excess O_3 (Pollastri et al. 2019; Loreto and Velikova 2001). O_3-induced emission of isoprene has been documented in several studies (Hewitt et al. 2009; Arab et al. 2016). Taking this into account, date palm has a high potential to resist photochemical changes induced by short-term exposure to O_3 (Du et al. 2018). A more realistic Free-air CO_2 enrichment (FACE) study demonstrated that emission of isoprene declined significantly with higher O_3 concentrations, but the number of total monoterpenes stimulated in date palm leaves was attributed to increased emission of aldehyde volatiles (Table 6.5) (Paoletti et al. 2021).

Table 6.5 Impact of tropospheric ozone stress on different secondary metabolites in plants

Stress	Dose	Plants	Endogenous responses of secondary metabolites	References
Ozone	27.7–59.0 ppb	*Linum usitatissimum* L.	Significant increment in flavonoids (32.8%) and anthocyanins (34.4%); increased lignin content (14.1%) and epicuticular wax	Tripathi and Agrawal (2013)
	15–30 ppb	*Zea mays* L.	Higher carotenoid and flavonoids levels; more induction of phenols accompanied with higher PAL activity	Singh et al. (2014)
	30 ppb	*Triticum aestivum* L.	Quercetin and kaempferol content responded differently; phenylpropanoid enzymes (CAD, 4CL) showed enhanced activities	Fatima et al. (2018)
	58.3 ppb	*Triticum aestivum* L. *Chenopodium album* L.	Strong stimulation of flavonols (kaempferol and Quercetin) and total phenolics in roots and leaves	Ghosh et al. (2020a, b)
	68.9 ppb	*Vigna radiata* L.	Total phenols elevated significantly by 34.2% along with increased PAL activity by 37%	Mishra and Agrawal (2015)
	45–90 ppb	*Phoenix dactylifera* L.	Isoprene emission declined significantly at elevated O_3 (−58% and −50%); stimulation of monoterpenes (α-pinene, β-octanal, nonanal, camphor, iso-bornrol)	Paoletti et al. (2021)
	60 ppb	*Brassica campestris* L.	Significant increase in lycopene, total carotenoids, and lutein content; negative correlation between total aromatic GLS and total aliphatic GLS	Han et al. (2021)

CAD cinnamyl alcohol dehydrogenase, *4CL* 4-coumarate CoA ligase, *GLS* glucosinolate synthase, *PAL* phenylalanineammonia-lyase

6.7 Conclusion

Climate change caused by increased anthropogenic activities has significantly altered CO_2 concentrations, temperature fluctuations, water-deficit conditions, salinity stress, UV-B intensity, and tropospheric ozone concentrations on Earth's surface. This is accompanied by a parallel decrease in physiological processes in plants. Elevated CO_2 concentrations induce photosynthetic processes, but plants become more susceptible to insect attack at the same time. To avoid insect damage, plants allocate photo-assimilates to secondary metabolite production. Phenolics and terpenoids decreased as CO_2 concentrations increased; however, these were significantly intensified by elevated temperature. Higher temperature prevails drought conditions and, with a concomitant increase in salt levels, severely impacts plant growth and yield via ROS production and reduced osmotic potential, which mediates biochemical changes. To confer resistance, plants facilitate antioxidative defense mechanisms through enhanced production of phenolics and flavonoids. Similarly, increased UV-B exposure and ozone stress induce morphological, physiological, and biochemical alterations in plants. Despite this, it needs to further investigate the synergistic role of different abiotic stresses responsible for actual synthesis and modulation at the same time. More importantly, scientists mimic the climate change perspectives through experimental studies, which raises concern about achieving food security and nutritional status worldwide.

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