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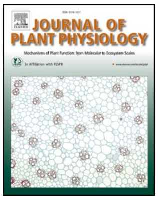

Early-Career Researcher Review

Climate change-associated multifactorial stress combination: A present challenge for our ecosystems

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ABSTRACT

Humans negatively influence Earth ecosystems and biodiversity causing global warming, climate change as well as man-made pollution. Recently, the number of different stress factors have increased, and when impacting simultaneously, the multiple stress conditions cause dramatic declines in plant and ecosystem health. Although much is known about how plants and ecosystems are affected by each individual stress, recent research efforts have diverted into how these biological systems respond to several of these stress conditions applied together. Studies of such "multifactorial stress combination" concept have reported a severe decrease in plant survival and microbiome biodiversity along the increasing number of factors in a consistent directional trend. In addition, these results are in concert with studies about how ecosystems and microbiota are affected by natural conditions imposed by climate change. Therefore, all this evidence should serve as an important warning in order to decrease pollutants, create strategies to deal with global warming, and increase the tolerance of plants to multiple stressful factors in combination. Here we review recent studies focused on the impact of abiotic stresses on plants, agrosystems and different ecosystems including forests and microecosystems. In addition, different strategies to mitigate the impact of climate change in ecosystems are discussed.

1. Introduction

Earth ecosystems are under siege. The constant increase of human population, the deterioration of agricultural land, the accumulation of CO_2 in the atmosphere by the burning of fossil fuels, the gradual increment in the concentration of many human-made contaminants and different pollutants, and the global warming lead to drastic changes in our climate, termed climate change. These conditions would trigger unprecedented heat waves, droughts, fires, and floods across continents as well as losses in Earth's biodiversity (Sage, 2020; Wagner et al., 2021; Zandalinas et al., 2021a; Masson-Delmotte et al., 2021). Such environmental changes would further threaten global food production and security, potentially leading to unrest, hunger, and even a mass extinction event (Sage, 2020; Savary and Willocquet, 2020). Plants growing within many ecosystems are therefore impacted by such array of environmental conditions that negatively affect their reproduction and survival. In addition, many of these environmental stressful factors enhance the susceptibility of plants to attack by different pests and pathogens, as well as modify the performance of many insects, causing a deterioration of forest ecosystems and insect-driven pollination (Cohen and Leach, 2020; De Laender, 2018; Desaint et al., 2020; Hamann et al., 2021). Several combinations of these environmental factors, pollutants, and pathogens will progressively increase their frequency in the coming years (Alizadeh et al., 2020; Mazdiyasni and AghaKouchak, 2015; Rillig et al., 2019; Zandalinas et al., 2021b) (Fig. 1). Therefore, understanding the joint effect on plants of multiple environmental changes is a major scientific challenge. In contrast to the studies typically conducted on plants analyzing the effect of a single stress, scientific community has begun accepting the existence of multiple stress drivers affecting plants in nature (Coolen et al., 2016; Defo et al., 2019; Mooney et al., 1991; Nilsen and Orcutt, 1996; Popkin, 2021; Z. Zhou et al., 2020). Studies focused on unravelling molecular responses of plants subjected to a combination of two different stresses (*i.e.,* high temperatures and drought) started over 20 years ago (Rizhsky et al., 2002, 2004). Since then, many other studies of abiotic/biotic stress combination, combining two or at most three different stresses, have been performed in diverse plant species, revealing that plant responses to a combination of different stressors can be very different from the conditions encountered by plants in the field, where several stresses occur simultaneously (*e.g.,* Balfagón et al., 2022,

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Abbreviations

ABA	abscisic acid
AMF	arbuscular mycorrhizal fungi
GABA	γ-aminobutyric acid
GBF3	G-box binding factor 3
ictB	inorganic carbon transporter B
JA	jasmonic acid
PSII	Photosystem II
SBPase	sedoheptulose1-7 bisphosphate
SUMO3 ligase	small ubiquitin-like modifier ligase
TCA cycle	tricarboxylic acid cycle
TF	transcription factor
UPR	unfolded protein response

2019; Choudhury et al., 2017; Prasch and Sonnewald, 2013; Shaar-Moshe et al., 2019, 2017; Sinha et al., 2022, 2021; Suzuki et al., 2014; Zandalinas et al., 2018, 2017, 2016b, 2020a; Zhang and Sonnewald, 2017). In addition, it was shown that the intensity of each stressful factor involved, the order in which they impact the plant, and the specific plant species could define the result of a stress combination: synergistic, antagonistic, or additive (Mittler and Blumwald, 2010; Zandalinas et al., 2020b; Zandalinas and Mittler, 2022; Zhang and Sonnewald, 2017). However, due to the increase of the intensity of different pollutants (*e.g.,* organic compounds, microplastics, different heavy metals, pesticides, herbicides, or ozone), and the fluctuating weather patterns due to the climate change, the complexity of combinations of stressors impacting plants simultaneously or sequentially in the natural environment rises considerably and, therefore, studies of plant responses to the combination of two- or three-stress factors could not be adequate (Zandalinas et al., 2021a). For this reason, very recently, a new avenue in the research of plant responses to combined stress emerged, termed multifactorial stress combination (Zandalinas et al., 2021a, 2021b; Zandalinas and Mittler, 2022). This new concept of stress combination highlights that although each individual stress could have minor effects on plant growth and survival, the additive influence of multifactorial stress combinations could be detrimental, demonstrating that negative interactions of different stress factors can lead to a decrease in plant yield and agricultural productivity (Zandalinas et al., 2021a, 2021b, 2021a). Furthermore, multifactorial stress combination could affect the plant microbiome that are key for plant development, reproduction and survival (Rillig et al., 2019, 2021; Yang et al., 2021).

Therefore, one of the major effects of climate change is a large decline in plant survival, Earth's biodiversity and global food production (Sage, 2020; Savary and Willocquet, 2020; Wagner et al., 2021; Zandalinas et al., 2021a). In this review, recent studies focused on the impact of different climate change-associated stress factors impacting plants, agrosystems and ecosystems are described.

2. Agrosystems: from the lab to the natural environment

An important goal in plant stress research is to obtain possible targets that can be used in plant breeding programs to enhance tolerance of crops that grow in the natural field. To achieve this goal, identifying stress-regulatory networks activated under different combinations of adverse conditions seems crucial. Translating basic research performed in the lab to crop improvement involves studies of multiple stress combination in plants under controlled conditions in the lab and the subsequent application of such results on crops in field trials.

2.1. Effects of different stress combinations on plants: studies in the lab

In the past several years, different studies have dissected physiological, molecular and metabolic responses of different plant species to stress combination under controlled conditions in the lab (*e.g.,* Bai et al., 2018; Balfagón et al., 2022, 2020, 2019; Iyer et al., 2013; Mahalingam and Bregitzer, 2019; Qaseem et al., 2019; Rasmussen et al., 2013; Rizhsky et al., 2004, 2002; Suzuki et al., 2016; Zandalinas et al., 2016a; Zhou et al., 2017). A key plant process influenced by the combination of different abiotic factors is photosynthesis. Several studies demonstrated that photosynthetic efficiency decreased under different combinations

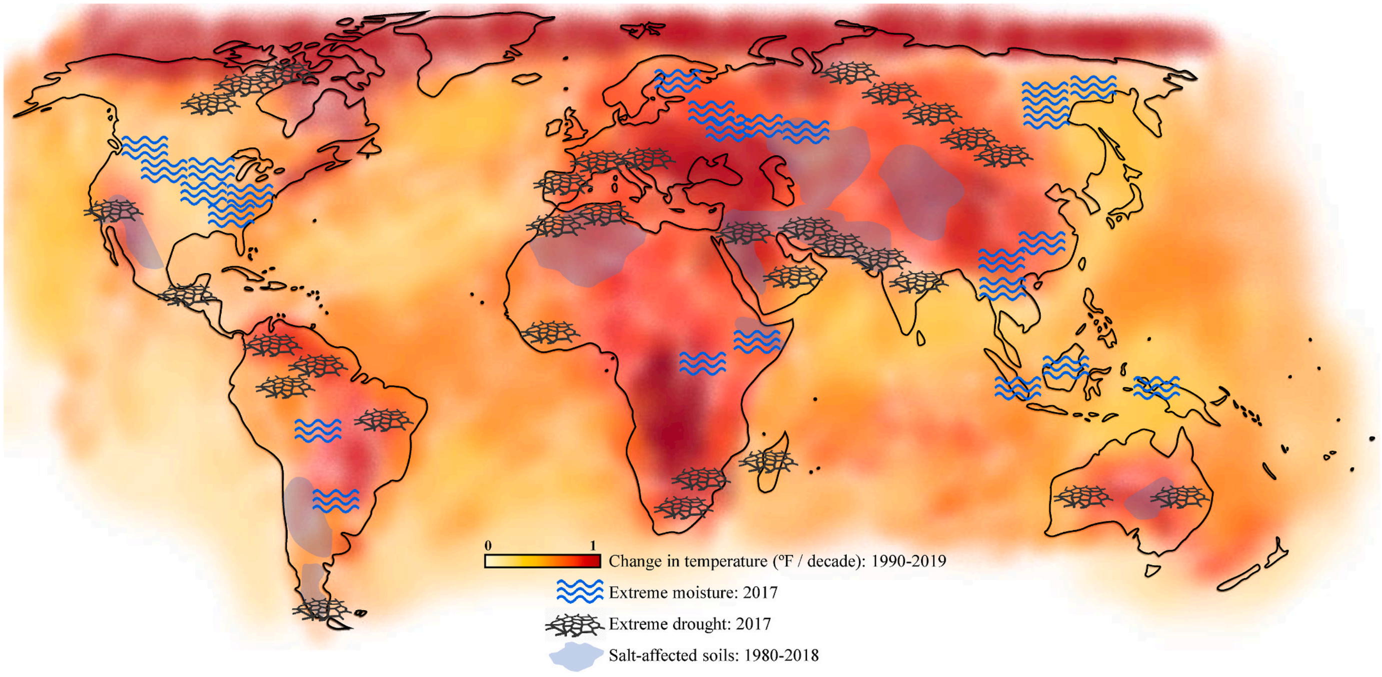

Fig. 1. Climate change affects differently diverse regions around the globe and could include the co-occurrent or sequential impacts of two or more different stresses such as heat waves, flooding, drought and/or salinity. Map was modified from (Rivero et al., 2022) and data was obtained from www.climate.gov, www.noaa.gov (NOAA) and (Hassani et al., 2020).

of salinity, drought, and/or high temperatures (Perdomo et al., 2017; Zandalinas et al., 2016a, 2016b; Zlatev and Lidon, 2012). For example, the combination of heat and drought triggered a marked decrease in photosynthetic activity (higher than the effects of drought or heat applied individually) in tomato (Zhou et al., 2017), tobacco (Rizhsky et al., 2002), Arabidopsis (Rizhsky et al., 2004; Zandalinas et al., 2016a), soybean (Cohen et al., 2021), maize (Hussain et al., 2019), the perennial grass *Leymus chinensis* (Xu and Zhou, 2006), and wheat (Perdomo et al., 2015). Contrary to the synergistic effect of drought and high temperatures when applied in combination, other stress combinations can result in antagonistic effects. For example, during the combination of drought and ozone, or drought and pathogen infection, the effects of drought closing stomata could prevent the entrance of ozone or pathogen to the plant (Gupta et al., 2016). Intriguingly, different combinations of stresses can have a synergistic effect on a particular plant species, such as the combination of high temperatures and salinity on Arabidopsis (Suzuki et al., 2016), and the same combination of stresses can have an antagonistic effect on another plant species, such as tomato plants (Rivero et al., 2014). Therefore, the intensity of the individual factors composing the stress combination, the order in which they are applied, and the particular plant species studied, can define the final effect of a stress combination (Mittler, 2006; Mittler and Blumwald, 2010; Zandalinas et al., 2020b; Zhang and Sonnewald, 2017).

Molecular studies in plants under controlled conditions revealed common transcripts altered in response to single stresses and their combination (Pandey et al., 2015; Rizhsky et al., 2004; Shaar-Moshe et al., 2017, 2019; Zandalinas et al., 2021a, 2021b), indicating that those genes could be implicated in a universal stress response or be part of crosstalk of stress signaling pathways (Prasch and Sonnewald, 2015). For example, in Arabidopsis plants, 29 transcripts, including heat shock proteins (HSPs) or abscisic acid (ABA)- and ethylene-related transcripts were upregulated in response to drought and heat applied individually or in combination (Rizhsky et al., 2004). Another example could be the G-BOX BINDING FACTOR3 (GBF3), that was upregulated during individual and all possible combinations of high temperatures, drought and virus (*Turnip mosaic virus*, TuMV) (Prasch and Sonnewald, 2013), as well as during high temperatures, salt and osmotic stress applied individually or in combination (Sewelam et al., 2014). These studies suggest that GBF3 might participate in broad stress responses in plants. In addition to common responses to stresses applied in isolation or in combination, unique molecular responses to different stress combinations have been previously reported. For example, the expression of more than 770 transcripts were exclusively altered by the combination of drought and high temperatures, while both stresses applied individually did not change their expression (Rizhsky et al., 2004). Other examples of studies that reported transcripts exclusively altered by combined stresses include transcriptomic analysis of drought and O_3 (Iyer et al., 2013), and high light and heat (Balfagón et al., 2019). In addition to molecular studies, metabolomic reprograming has been also reported to occur during abiotic stress combination, rendering unique accumulation patterns of primary and secondary metabolites, and hormones (Zandalinas et al., 2022 and references therein). For example, Arabidopsis plants subjected to a combination of high temperatures and high light showed a specific metabolomic signature that involved significant accumulations of sugars such as maltose, glucose and fructose, reduced content of metabolites related to the tricarboxylic acid (TCA) cycle, and a markedly accumulation of the amino acid γ-aminobutyric acid (GABA) and the hormone jasmonic acid (JA) (Balfagón et al., 2019, 2022).

Despite the importance of the study of plant responses to combinations of two or three stresses under controlled conditions in the lab, future climate situations might involve the concurrent or sequential exposure of plants to multiple stresses (*i.e.,* multifactorial stress combination), including heat combined with other stress factors such as nutrient deficiency, drought, salinity, flooding, high CO_2 and/or several biotic stressors, suggesting that a new approach of studies of stress combination is needed. In this sense, a recent report showed that with the cumulative number and complexity of up to 6 abiotic factors in combination, Arabidopsis survival decreased although the level of each individual stress had an insignificant effect, pointing to a synergistic interaction between multiple low-level stresses (Zandalinas et al., 2021b). In addition, this study showed that the change in transcript expression in response to multifactorial stress combination was unique. Interestingly, several components of the WRKY transcription factor (TF) family were accumulated in response to single stresses and/or some of their simple two-factor combinations but were not activated by more complex combinations of three to six-factor stresses, including WRKY26, 22, 61, 29, 30, 51 and 21 (Fig. 2). Contrastingly, other WRKY TFs such as WRKY2, 7, 3, 12, 14, 44 and 59 were specifically accumulated in response to four- to six-factor stress combinations (Fig. 2; Zandalinas et al., 2021b). In addition, responses to multifactorial stress combinations involved pathways typically associated to stress including the unfolded protein response (UPR), osmoregulation, autophagy, or heat shock factors (HSFs). It was also suggested that the increased expression of unknown transcripts in response to specific combinations of three or four stresses could indicate that some of these pathways could be replaced by yet unidentified pathways (Zandalinas et al., 2021b). Therefore, it could be predicted that a multifactorial stress combination may have an additive effect on plants when growing in the field leading to a remarkable decline in their growth, productivity and survival (Fig. 3). This decrease is predicted to be initially slow, but when more stresses are combined, plant survival rapidly declines even if the level of each single stress is low enough to not have a significant effect on plant growth and survival (the plant multifactorial stress principle; Fig. 3; Zandalinas and Mittler, 2022). Consequently, conclusions of studies of multiple stress combination under controlled condition in the lab are urgently needed to be applied in field research using different plant species in order to achieve crop improvement. Below, studies of stress combination in the field are described.

2.2. Effects of different stress combinations on plants: studies in the field

The study of plants responses to stress combination under controlled lab conditions over the last decades rendered important information about pathways, transcripts and metabolites involved in the acclimation of different plant species to these stressful conditions. However, it is important to test whether such responses are maintained in crops growing in the field. Some reports analyzed plant responses to the combination of two stresses in different field-grown crops. Field trials using maize plants grown under drought, high temperatures and the combination of drought and high temperatures showed a link between grain yield and metabolism, and suggested different metabolites that could be used as markers for breeding programs of tolerant maize plants (Obata et al., 2015). In addition, Nelimor et al. (2020) used different maize landraces growing in the field under drought, heat and their combination to show specific accession adapted to those stresses. These landrace accessions could be studied to find transcripts associated to their tolerance as a resource for enhancing the tolerance of maize varieties to combined stress conditions (Nelimor et al., 2020). Field-grown rice cultivars subjected to drought, heat and their combination displayed distinct metabolic profiles in flowering spikelets, flag leaves, and developing seeds among the different cultivars, and identified possible metabolic candidates for grain quality and yield in response to the combination of drought and high temperatures (Lawas et al., 2019). Another study in different rice cultivars under field conditions showed that the reduction in grain mineral content in response to the combination of elevated CO_2 levels and heat stress was more intense than that in response to elevated CO_2 levels individually applied (Chaturvedi et al., 2017). Studies using different lentil (*Lens culinaris Medikus*) genotypes subjected to drought, heat and their combination revealed that the combined stress negatively affected photosynthetic activity, carbohydrate metabolism and water relations in seeds and leaves, and partial cross tolerance to high temperatures and drought in tolerant plants was

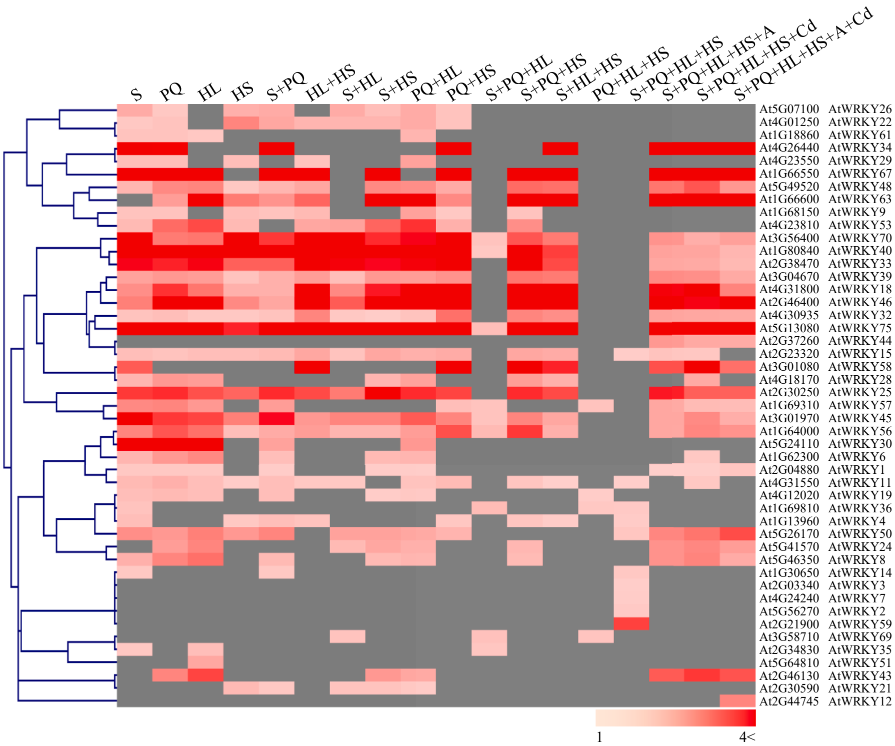

Fig. 2. Effects of multifactorial stress combination on plant transcript expression. Heat map showing the expression of WRKY TFs of *Arabidopsis thaliana* seedlings whose expression is enhanced in response to a multifactorial stress combination of six different stresses (Salt, HS, HL, PQ, Acidity and Cd in different combinations). Data was obtained from Zandalinas et al. (2021b). Abbreviations: A, acidity; Cd, cadmium; HL, high light; HS, heat stress; PQ, paraquat; S, salt.

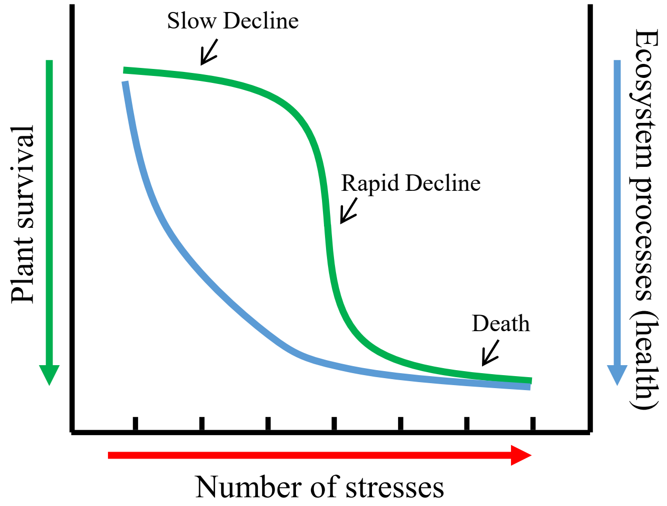

Fig. 3. The synergistic effects of the increasing number of stresses in combination on plant survival and ecosystem processes. In green, the plant multifactorial stress principle: with increased number of stressors impacting plants, plant survival dramatically declines, even if the level of each single stress is low enough to not have a significant effect on plant growth and survival. In blue, the synergistic effects of multiple stress factors on ecosystem processes: with increased number of stressors impacting an ecosystem, ecosystem processes dramatically decline. Graph was adapted from Zandalinas and Mittler (2022). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

observed (Sehgal et al., 2017). Drought and heat combination had also a more pronounced effect compared to that of the individual stresses on membrane damage, PSII function, leaf Rubisco activity, and sucrose and starch concentrations in chickpea (Awasthi et al., 2014). Field studies with soybean (*Glycine max*) showed that a combination of drought and heat counteracted the boost C3 plants received from growing in a CO_2 enriched environment (Gray et al., 2016). These studies from field research imposing different stress combinations to different plant species suggest the likelihood of negative effects of different global change factors in combination on key global commodity crops. Although these examples provided valuable information about how plants respond to stress combination when growing in the field, no information is available about plant responses to more than two stresses applied at the same time in the field. Since large agrosystems such as crop fields, normally present limited biodiversity (only a dominant crop is cultivated), it is feasible that the outcome of multiple stresses impacting plants simultaneously will be negative (synergistic) (Zandalinas and Mittler, 2022), making the study of plant responses to multifactorial stress combination in the field an urgent need.

2.3. Different approaches for plant tolerance to stress

Translating knowledge about plant abiotic stress responses to breading programs are contributing to enhancing global crop yield every year (*e.g.*, Gilliham et al., 2017; Heuer et al., 2017; Richards et al., 2014; Roy et al., 2014). Different genetic engineering avenues for the improvement of crops were previously described (examples in Table 1), and success has already been achieved in several crops to different individual stressful factors growing in the field or under semi-controlled conditions. For example, improving photosynthetic processes through genetic engineering may improve yield in crops growing in the field (Simkin et al., 2019). In this sense, it was shown that overexpressing the C3 photosynthesis cycle enzyme sedoheptulose-1-7 bisphosphatase (SBPase) considerably increased photosynthetic carbon gain and biomass yield in tobacco plants growing in the field under an open-air increase of CO_2 (Rosenthal et al., 2011). In addition, transgenic tomato plants with increased SBPase activity growing under semi-controlled greenhouse conditions displayed better levels of

Table 1
Examples of effective genetic engineering in abiotic stress survival strategies in different crops. Abbreviations: eCO_2, elevated CO_2 levels; HS, heat stress. [a], reported as less stomatal opening in response to light, resulting in a reduction in water loss per CO_2 assimilated under field conditions.

Crop	Stress	Target gene	Improvement	References
Tobacco	eCO_2	SBPase	Increased photosynthetic carbon gain and biomass	Rosenthal et al. (2011)
	Low water availability[a]	PsbS	Prevented excessive water loss	Głowacka et al. (2018)
Tomato	Cold	SBPase	Increased levels of photosynthesis, growth, and chilling tolerance	Ding et al. (2016)
Soybean	eCO_2 + HS	SBPase	Improved seed yield	Köhler et al. (2017)
	Drought	ictB	Increased levels of photosynthesis and biomass production	Hay et al. (2017)
	Drought	MYB14	Improved yield and stress tolerance	Chen et al. (2021)
Wheat	Drought	DREB1	Enhanced stress tolerance	Zhou et al. (2020)
Rice	Drought	NAC5 NAC9 NAC10	Enhanced stress tolerance and grain yield	Jeong et al. (2013), 2010; Redillas et al. (2012)
Cotton	Drought + HS	SIZ1	Increased fiber yield	Mishra et al. (2017)

photosynthesis, growth, and chilling tolerance (Ding et al., 2016). In a study of soybean plants expressing the cyanobacterial SBPase growing in the field under ambient and elevated CO_2 levels, and under ambient and high temperatures, Köhler et al. (2017) showed that elevated temperatures alone led to a diminished seed yield on both wild-type and SBPase over-expressing lines by 19–31%. However, under elevated CO_2 combined with high temperatures, SBPase-overexpressing plants maintained seed yield whereas wild-type plants showed between 11% and 22% reductions on seed yield compared with plants grown under elevated CO_2 alone (Köhler et al., 2017). These results suggest that SBPase may serve as a valuable candidate for genetic engineering to improve yield under different stresses and their combination in several crops. Another example was reported by Hay et al. (2017) using transgenic soybean plants constitutively expressing cyanobacterial *ictB* (inorganic carbon transporter B) gene grown in greenhouse and field conditions. Results showed significant increments in photosynthetic levels and biomass production during a drought mimic study in the transgenic lines with respect to wild-type plants in both greenhouse and field trials (Hay et al., 2017). Additionally, tobacco plants with increased *PsbS* expression showed a 25% decrease in water loss per CO_2 assimilated under field conditions, suggesting that manipulating *PsbS* could be effective in preventing excessive water loss under conditions of insufficient water availability in the field (Głowacka et al., 2018). In addition to genetic engineering related to photosynthesis improvement, manipulation of transcription factors (TFs) and other proteins has been recently demonstrated to provide resistance to different plant species grown in the field against several abiotic stresses. For example, overexpression of the TF *GmMYB14* improved yield and tolerance to drought of soybean by adjusting plant architecture mediated by brassinosteroids (Chen et al., 2021), and overexpression of the soybean TF *GmDREB1* improved tolerance to drought in transgenic wheat growing in the field (Y. Zhou et al., 2020). In addition, the overexpression of the TFs *OsNAC5*, *OsNAC9* and *OsNAC10* enhanced stress tolerance and grain yield in rice under field drought conditions (Jeong et al., 2010, 2013; Redillas et al., 2012). In cotton, an overexpression of the rice SUMO E3 ligase gene *OsSIZ1* enhanced fiber yield in response to the combination of drought and high temperatures as well as under field conditions (Mishra et al., 2017) (Table 1).

In addition to molecular engineering, other stress mitigation strategies have been extensively documented by previous studies. For example, microbiome engineering is a promising biotechnological approach to enhance crop yield and stress tolerance (Arif et al., 2020; Kaul et al., 2021). Many studies reported the beneficial effects of bacterial inoculation on plant physiology in response to different stresses such as osmotic stress, flooding, temperature stress, iron toxicity, nutrient deficiency, salt or drought (reviewed in Dimkpa et al., 2009; Vives-Peris et al., 2020). Seed priming is another agronomic strategy involving the treatment with different natural and synthetic compounds to the seeds before sowing to improve tolerance to different stresses such as drought or heat, and to improve the long-term performance of crops (Jisha et al., 2012; Kumari et al., 2021). These compounds include chemicals that lower water potential such as KNO_3, KCl, K_3PO_4, KH_2PO_4, $MgSO_4$, $CaCl_2$, NaCl and mannitol; nutrients such as potassium, Zn^{2+} and ascorbic acid; phytohormones such as ABA, gibberellic acid and auxin; and other chemicals including butanolide, selenium, choline and chitosan (Jisha et al., 2012). Another successful strategy to enhance plant tolerance to different stresses involves exogenous treatments with bioestimulants. For example, GABA-treated mungbean plants subjected to heat stress produced more pods and seed weight than untreated plants, suggesting a role for GABA in protecting reproductive systems in response to high temperatures (Priya et al., 2019). Exogenously applied proline improved tolerance of different plant species exposed to salt and drought stress (reviewed in Per et al., 2017). Application of silicon has been shown to confer tolerance to different abiotic and biotic stresses by regulating the synthesis and metabolism of secondary metabolites (Ahanger et al., 2020). In addition, other types of naturally-occurring metabolites, such as phytohormones (*e.g.*, methyl jasmonate, ABA, gibberellic acid and salicylic acid), sugars (such as trehalose), and polyamines (*e.g.,* spermidine, spermine and putrescine) have been used in many plant species to improve salt stress tolerance (Kumari et al., 2021; Patel et al., 2020). Another strategy to develop stress-resilient crops is the use of inbred recombinant lines with improved tolerance to different stresses. For example, tomato recombinant inbred lines with better nitrogen use efficiency (NUE) were more tolerant to the combination of high temperatures and salinity (Lopez-Delacalle et al., 2020). Different studies have also identified selected maize inbred lines with improved tolerance to drought and heat stress conditions (Chen et al., 2012) as well as the combination of both stresses (Cairns et al., 2013; Chiuta and Mutengwa, 2020).

Although several studies successfully achieved the tolerance of plants growing in the field to a specific abiotic stress, fewer have addressed how to accomplish tolerance to two stresses acting at the same time, and none has focused on the tolerance of crops to multiple stress combinations when growing in the field. It is, therefore, key to understand the mechanisms of crop responses to multiple simultaneous stresses to develop tolerant crops to climate change-driven conditions.

3. Impact of climate change on ecosystems and biodiversity

Studies of stress combination under controlled conditions in the lab and under field conditions provide important information about how plants and crops respond to situations similar to those climate change may impose on plants. In addition to these studies, knowledge about how climate change-associated stresses impact larger biological organizations including ecosystems is key to adopt specific mitigation and adaptation strategies. It was recently predicted that with increased number of stressors impacting an ecosystem, ecosystem processes will dramatically decline (Fig. 3). Below we describe how climate change is negatively affecting important ecosystems such as forests.

3.1. Forests as an example of ecosystems in danger due to climate change-associated multifactorial stresses

Climate change-associated multifactorial stresses disturb forest dynamics, their structural complexities, and their benefits to society, in addition to increase forest mortality, their vulnerability to insect outbreaks, fires and windthrows (Figs. 3 and 4). Forest vegetation dynamics are deeply affected by changes in global stressors (extreme temperatures, CO_2, and vapor pressure deficit) and disturbances (including land-use change, windstorms, drought, wildfire, and insect outbreaks), forcing forests toward younger, shorter, and lower-biomass ecosystems (McDowell et al., 2020). Severe weather events such as prolonged periods of drought or intense precipitation together with warmer temperatures increase the mortality of trees around the word. As an example, rapid mortality of a dominant forest species, white oak (*Quercus alba*), in forests of lower Midwest of US has been connected to periods of excessive precipitation in a warming climate (Hubbart et al., 2016). In this scenario, increasing extreme wet weather probably contributed to the development of biotic stressors such as fungal-like oomycetes (water molds) or other pathogens that may cause root death and eventually tree death (Hubbart et al., 2016). In Europe, around 0.79% of forests were negatively influenced by natural or man-made mortality every year between 1984 and 2016, resulting in intense changes in forest dynamics with significant consequences for carbon storage and biodiversity preservation (Senf et al., 2018). Interestingly, it was reported that, among trees within forests, the largest trees are affected at twice the rate of smaller trees due to climate change, and abiotic stress gradients of water, temperature, and competition regulate the intensity of the height-mortality relationship, threatening critical ecological, economic, and social benefits (Stovall et al., 2019).

Global warming has also increased the frequency of forest fires, which has globally doubled since 1984. An estimation of the wildfire probability in southern California reported an increase from 36 days per year during 1970–1999 to 58 days per year under moderate greenhouse gas emission scenario, and 71 days per year by 2070–2099 under a high emission scenario, suggesting that expected greenhouse gas emissions will considerably rise the fire danger (Dong et al., 2022). High temperatures increase the evaporation of water in soils, causing drier soils in forest flora (Mansoor et al., 2022). Very recently (2019–2020), a series of mega-fires, termed the 'Black Summer' fires, burnt around 5.8 million ha of the total temperate forest biome in Australia, coinciding with a record period of low rainfall and heat combination (Boer et al., 2020; Canadell et al., 2021). In addition, overlapping stress events including severe drought, heat waves and/or insect outbreaks, together with shifting fire regimes limit post-fire resprouting and recruitment capacity of forests (Nolan et al., 2021) (Fig. 4).

In addition, a study of the vulnerability of European forests to windthrows and insect outbreaks between 1979 and 2018 showed that about 33.4 billion tons of forest biomass could be negatively altered by different stress factors (Forzieri et al., 2021). Around the year 2000, temperatures substantially affected forest tolerance to pest outbreaks, reducing plant defense and making European forests gradually more vulnerable to insect outbreaks. In this sense, rising temperatures could affect plant water status by enhancing the vapor pressure deficit and reducing stomatal aperture, which eventually reduced secondary metabolism, carbon storage, and plant resistance. In agreement to this, recent increments in infestations of bark beetles associated to massive attacks on coniferous forests of different European areas have been observed (Forzieri et al., 2021).

Forests provide many benefits for society and can help alleviate

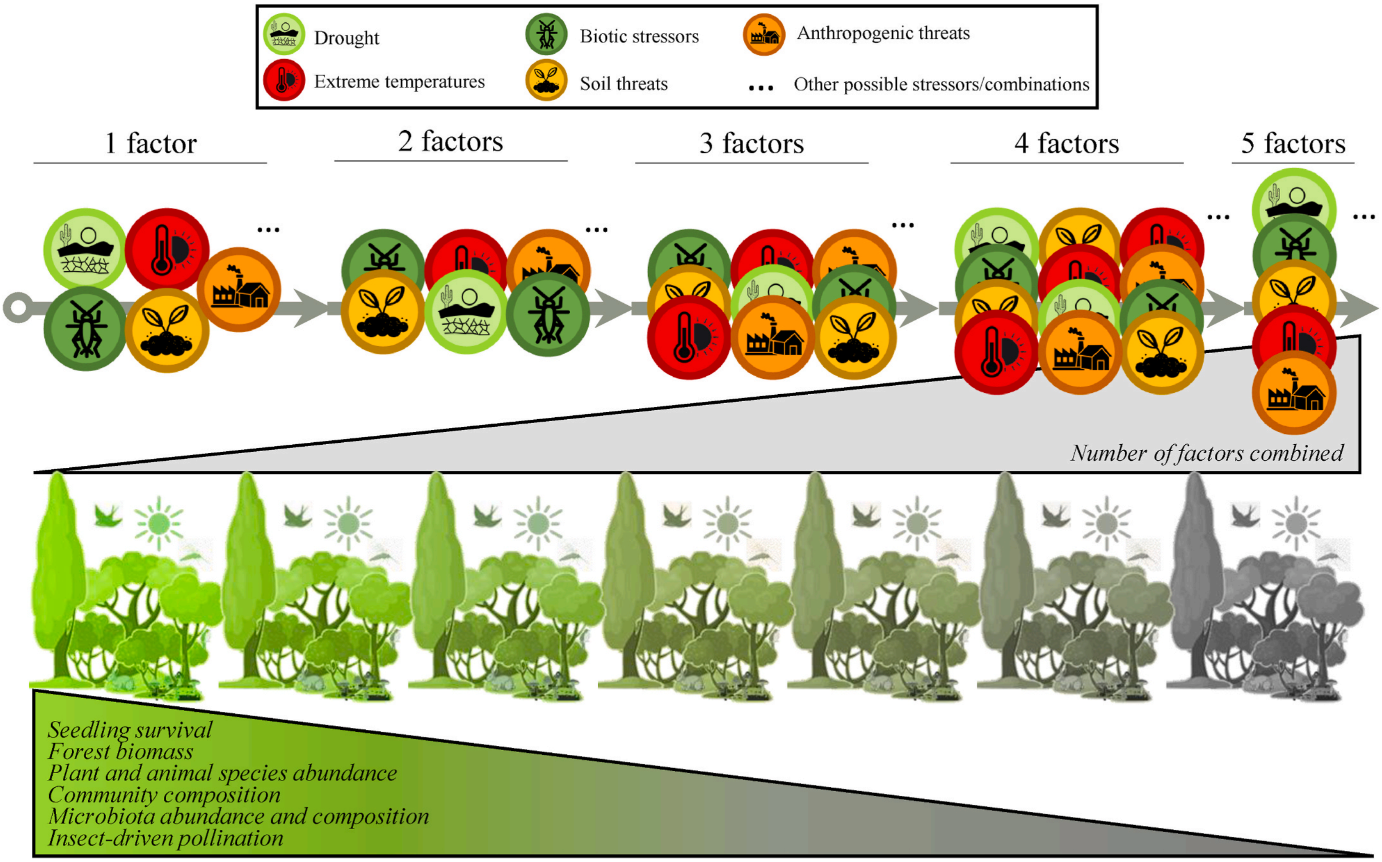

Fig. 4. Global warming, climate change and environmental pollution present plants, animals, microbiota and ecosystems with multiple combinations of different abiotic and biotic stresses that could have a detrimental effect on seedling survival, forest biomass, plant and animal species abundance, community composition, microbiota abundance and composition, and insect-driven pollination.

human-caused climate change. Nevertheless, climate change-associated effects may threaten carbon sinks of forests in the 21st century and biodiversity conservation, altering the ranges of tree species and forest community assemblages, impacting carbon cycle and leading to forest vulnerability to stresses (Anderegg et al., 2020; Forzieri et al., 2021). A meta-analysis showed that the interaction effects normally amplify carbon losses for many climate-sensitive stressors and areas (Anderegg et al., 2020; Seidl et al., 2017). Warmer and drier situations especially lead to drought, fire and insect disturbances, whereas warmer and wetter situations enhance stresses related to pathogens and wind (Seidl et al., 2017). Despite these studies, the combined effect of multiple stresses (*i.e.,* more than 3 stresses) impacting plant communities within their habitat remains unknown in modelling ecosystem alterations. This uncertainty appears because the majority of studies (including those related to plant mortality after fire, or the impacts of fire frequency and intensity on tree mortality), have mainly focused on individual stresses (Nolan et al., 2021). Therefore, quantifying forest vulnerability to abiotic and/or biotic multifactorial stress combination and studying the underlying mechanisms is essential to develop adaptation and mitigation approaches (Forzieri et al., 2021).

3.2. Other ecosystems in danger due to climate change-associated multifactorial stresses

In addition to forests, other important ecosystems are in danger due to the effects of climate change. For example, the Indian River lagoon ecosystem, one of North America's most biodiverse estuaries, has been exposed to many different stresses such as habitat modification, toxic spills, industrial pollution and climate change. As a result, harmful algal blooms, that can cause serious seagrass die-offs and marine, mammal, bird, and fish kills, occurred (Adams et al., 2019). Another ecosystem affected by global change is arid zone ecosystems. Increments in soil temperature and persistent droughts related to the climate change were suggested to impact the transition from seed to established seedling, representing a crucial filter for plant recruitment in arid regions (Lewandrowski et al., 2021). In the subarctic tundra, synergistic effects of insect herbivory and climate change modified plant volatile emissions, altering different ecological interactions (Rieksta et al., 2021). A simulation of different global change factors created different synergistic and antagonistic effects on photosynthetic activity and microarthropod communities in a bryophyte ecosystem, suggesting complex results of interactions between different stresses (Vanbergen et al., 2021).

Losses in biodiversity have also been reported in many other ecosystems. Insect declines are observed worldwide for ground, flying and aquatic lineages, affecting their essential ecosystem services of their respective communities. Climate change, agricultural intensification, habitat alterations, introduction of invasive species, atmospheric nitrification and the effects of droughts and shifting precipitation patterns are some of the factors insects are challenged by (Wagner, 2020; Wagner et al., 2021). In addition, impacts of climate change on marine ecosystems include alterations on primary production, ocean temperature, and species distributions and abundance (Fig. 5). It was recently reported that under a high greenhouse gas emission scenario, total marine animal biomass may be reduced by 15%–30% by 2100 in the North and South Atlantic and Pacific as well as in the Indian Ocean (Bryndum-Buchholz et al., 2019). Especially important is the notable change in seawater acid-base chemistry toward more acidic as a result of increased CO_2 in the ocean due to the enhanced atmospheric CO_2 levels (Doney et al., 2020). Ocean acidification leads to changes in population dynamics and organism physiology as well as altered ecosystems and communities. Simultaneous exposure to high CO_2 and increased temperature results in reduced survival of marine species, and slower growth and development

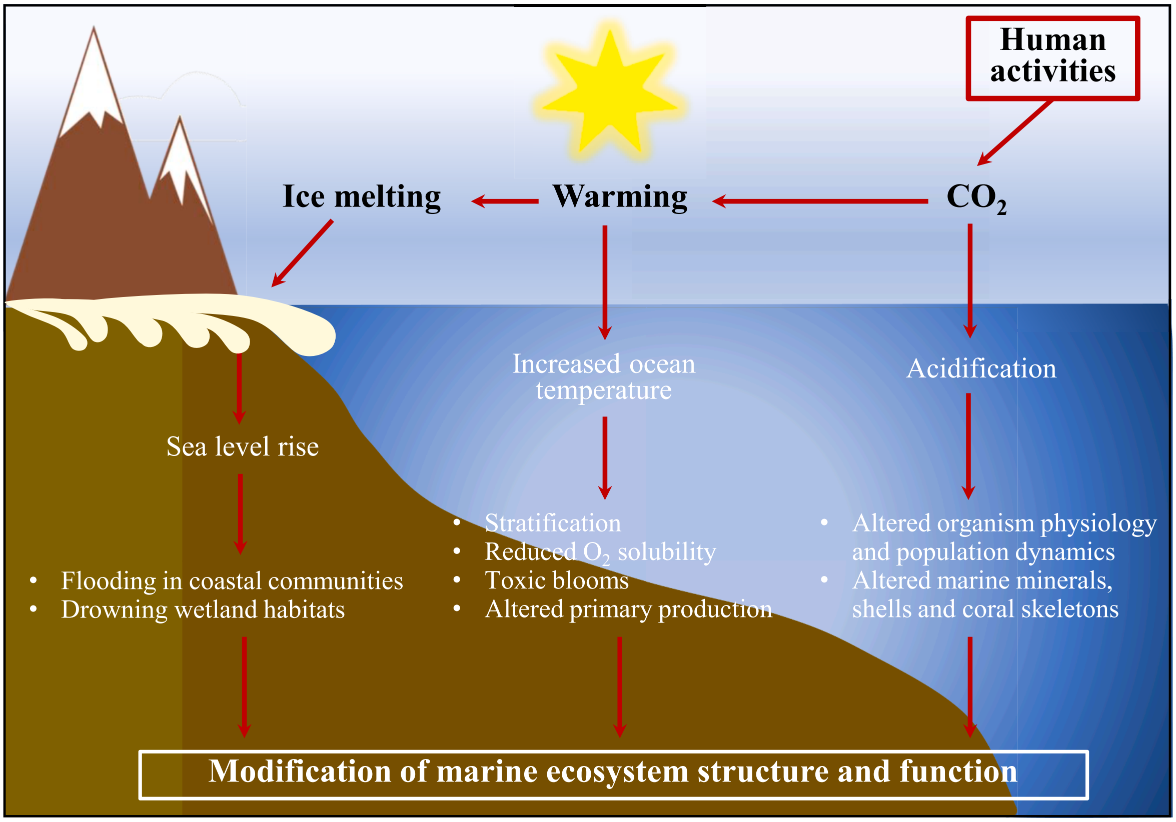

Fig. 5. Global warming and environmental pollution pose a serious threat to marine ecosystems. Increased CO_2 atmospheric levels lead to ocean acidification that, in turn, alters organism physiology and population dynamics as well as marine minerals, shells and coral skeletons. Global warming results in increased ocean temperature, ice melting and, consequently, sea level rise, further altering marine ecosystem structure and function.

(Kroeker et al., 2013). In addition, toxic planktonic cyanobacterial blooms are exacerbated by the synergistic effect of global warming and other climate change-associated drivers such as droughts or extreme rainfall periods (Paerl, 2018). These alterations will significantly modify marine ecosystem structure and function with associated socio-economic impacts on ecosystem services that the ocean provides to society, including aquaculture, fisheries, and shoreline protection (Bryndum-Buchholz et al., 2019) (Fig. 5). Therefore, a wide range of multiple stressors including acidification, warming, and other environmental alterations should be considered in studies of the ecological effects caused by the combination of these factors on marine ecosystems.

4. Impact of climate change on microecosystems

Soils are a major repository of terrestrial biodiversity (including nematodes, collembola, fungi or bacteria), harboring nearly a quarter of all species on Earth, and provide many beneficial functions including waste decomposition, pathogen resistance, nutrient cycling, and climate regulation. The soil microbiome regulates cycling of micronutrients and macronutrients that are key for plant and animal growth and preserve a healthy soil for future generations (Jansson and Hofmockel, 2019). In addition, plants and their associate soil microbiome are important players for understanding ecosystem responses to global climate change. Climate change can directly alter the diversity and structure of microbial communities (*e.g.*, temperature and seasonality) or indirectly (*e.g.,* root exudates, plant composition). Short- and long-term warming primarily enhanced the respiration and growth of soil microorganisms, resulting in CO_2 release and reduction of substrates, and triggering a decline in biomass and microbial activity (Walker et al., 2018). In addition, significant variations in bacterial and fungal communities were reported in forest soils with an annual temperature of more than 20 °C on average, as well as in response to warming across a 9-year study of tall-grass prairie soils (reviewed in Jansson and Hofmockel, 2019). Climate change is predicted to enhance the intensity, incidence, and duration of cyanobacterial blooms in different eutrophic reservoirs, lakes and estuaries, producing hepatotoxins, neurotoxins and dermatoxins, that can affect mammals and birds. For example, toxic cyanobacteria have been found in Lake Erie (USA), Lake Taihu (China), Lake Victoria (Africa), Lake Okeechobee (USA), and the Baltic Sea (reviewed in Jansson and Hofmockel, 2019). Arbuscular mycorrhizal fungi (AMF) are considered key symbiotic microorganisms of many terrestrial plants, and their function and growth depend on the photosynthetic carbon supplied by the host plant. In turn, AMF diversity is associated to plant productivity and thus ecosystem stability and sustainability (Jeffries et al., 2003), and can increase plant water and nutrient uptake, and resistance to different abiotic stresses including drought (Alguacil et al., 2021). However, AMF diversity is generally lower in soils exposed to abiotic stress than in non-disturbed soils, and most of environmental factors such as salinity, pollution, drought, extreme temperatures, CO_2, calcareous and acidity affect different AMF developmental steps including total root colonization, spore germination, sporulation and/or hyphae elongation (Fu et al., 2021; Lenoir et al., 2016). Recently, a study analyzing the effects on soils of different combination of ten global change factors including resource availability, abiotic factors, toxic compounds (inorganic and synthetic organic), and microplastics, showed that the complexity, composition, and overall abundance of soil microbiomes declined along the number of factors in a consistent directional trend (Rillig et al., 2019). These results suggest the need to reconsider current studies of global change focusing on the number and interactions of multiple stressors.

5. Strategies to mitigate the impact of climate change on ecosystems

Although substantial interventions towards more environmentally sustainable practices (including carbon taxes on transportation fuels, low-carbon fuel standards, bike and car sharing programs, and regulation of coal power generation) have been the focus of many countries, decreasing the sources and increasing the sinks of greenhouse gases are the most direct means to alleviate climate change (Bonan and Doney, 2018). Ecosystems are at risk due to climate change, but developing practical restoration, protection, and management of ecosystems, is key to assist climate change mitigation and adaptation strategies (Malhi et al., 2020). For example, reforestation, afforestation, or prevented deforestation create a large carbon sink in its early decades and, in the longer term, store large amounts of carbon (Bonan and Doney, 2018; Leijten et al., 2020; Morecroft et al., 2019). Restored and natural environment can promote water retention and counter flooding as well as adjust rainfall. In addition, protected areas in agricultural land maintain populations of pollinators, predators that regulate pests, and assist seed spreading. Other natural habitats perform key functions in mitigating climate change, including peat bogs, wetlands and rainforests, that can be powerful carbon sinks; or intact wetlands and coral reefs, that can protect coasts against elevation of sea level (Malhi et al., 2020; Roberts et al., 2020). Furthermore, in the deep sea, unfished mesopelagic fish populations support carbon sequestration, and protection of marine ecosystems can promote carbon storage capacity (O'Leary and Roberts, 2018). However, natural ecosystem-based solutions are not sufficient to fight climate change and there is still an urgent need to address the greenhouse gas emissions problem as a necessary approach to mitigate the effects of climate change (Malhi et al., 2020). In this sense, other approaches used to fight climate change include traditional agricultural procedures including intercropping, agroforestry, crop rotation, or organic composting (Sharma et al., 2022). In addition to these traditional practices, modern approaches such as the use of biotechnological methods to increase fertilizer efficiency (Ferrante et al., 2017), the development of climate-resilient crops through genetic engineering, CO_2 biomitigation by enhancing CO_2 absorption of microalgae (Yang et al., 2017), or the use of biofuels instead of fossil fuels (Delangiz et al., 2019) are acquiring more importance for climate change mitigation. Microbial engineering can be an approach to develop crops and microbiota with enhanced tolerance to climate drivers (Sharma et al., 2022). However, due to the complexity of microecosystems, to what extent the microbiome can be manipulated towards a more sustainable agricultural, an eco-friendly environment and fighting climate change, needs to be further investigated.

Different models of atmospheric chemistry and dynamics are the foundation of the science of climate change. However, a deeper understanding of climate involves a strong interdisciplinary perspective because microecosystems, and terrestrial and marine ecosystems, with their biodiversity, do not correspond to fluid dynamics of atmospheric models. Therefore, a comprehensive vision of our ecosystems and our role in defining the environment with the integration of atmospheric research, socioeconomics, ecology and public policies are required to study ecosystem dynamics and shape Earth's future (Bonan, 2016).

6. Conclusions and future perspectives

Scientific community is in concert when predicting the effects of climate change on plants, crops, animals, biodiversity, microbiomes and ecosystems in the near future: further polluting our environment will trigger a dramatic and unexpected deterioration in our Earth's health leading to a planet that cannot support the fast surge in the growth of human population (Bailey-Serres et al., 2019; Challinor et al., 2014; Lobell et al., 2011; Zandalinas et al., 2021a). The potential interactions among all climate-driven stresses and soil pollution together with stronger biotic stress pressures are expected to be synergetic. Although a clear deterioration on ecosystems, soil conditions, plant growth, overall agricultural production and ecosystems could not be observed when a low level of an individual stress is applied, a rapid decline in them can occur when additional factors are introduced (Rillig et al., 2019; Zandalinas et al., 2021b; Zandalinas and Mittler, 2022) (Figs. 3 and 4).

Therefore, the new concept in plant biology of multifactorial stress combination should be addressed when studying plant responses to global change-associated factors and their interactions under controlled conditions in the lab as well as on fields and ecosystems/microsystems. With effective approaches, such as engineering and/or breeding plants for tolerance to multifactorial stress combination, and manipulating plant-microbiome interactions, the global change factors that threaten Earth's ecosystems and biodiversity could be alleviated (Rivero et al., 2022; Sage, 2020; Zsögön et al., 2021).

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Author contributions

LSP, CS-M, AG-C, ML-C, VV-P and SIZ prepared the figures, and wrote and approved the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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