



Review Article

# Plant and seed germination responses to global change, with a focus on CO<sub>2</sub>: A review

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## Abstract

Earth atmospheric CO<sub>2</sub> concentration has risen by over 35% since 1750 and is presently increasing by about 2 parts per million (ppm) every year. Due to contributions from human activity, CO<sub>2</sub> is projected to keep rising in the predictable future and to double sometime during this century if fossil fuels burning remains. As a result, air temperature is projected to rise from 2 to 5 °C by 2100. Following this rise in CO<sub>2</sub>, some ecosystems will face challenges in the next few decades as plants will live in warmer temperatures, higher evaporating demand and widespread changes in drought lengths and severity. To yield healthy crops and forests in changing climate surroundings, it is vital to define whether elevated CO<sub>2</sub> disturbs seed germination and plant formation, but even more, the physiological traits conferring drought tolerance. Here, we review the current understanding on the role that CO<sub>2</sub> plays on plant growth and seed germination, as well as its impact during the exposure of abiotic stresses like drought and salinity.

## Keywords

global change, climate change, seed germination, plants, CO<sub>2</sub>

## Introduction

### Global warming causes and consequences

Over the years, the impact of global climate change significantly altered the properties of our environment. The variation of these properties is especially found in agricultural related sectors and it is threatened by the negative consequences of climate change (Onyekachi et al. 2019). Earth atmospheric CO<sub>2</sub> concentration has risen by over 35% since 1750 and is presently increasing by about 2 parts per million (ppm) every year (Domec et al. 2017). Climate change magnifies the amount of carbon dioxide and other greenhouse gases in the air. Moreover, it increases the temperature of the environment in abnormal ways (Rosenzweig et al. 2014). The driving forces of global warming includes anthropogenic causes and natural events. The climate of the earth has transformed several times in the past with origins linked to nature, such as the difference in the solar radiation produced by the sun, volcanic eruptions and the difference in the solar radiation on Earth because of the Milankovitch cycle (Riebeek 2010). The Milankovitch cycle is a long standing phase that happens every 10,000 years, this cycle starting natural global warming and cooling by three factors: the eccentricity, the obliquity and the precession. The eccentricity is the change in the elliptical shape of the Earth's orbit, while the obliquity is the alteration in the declination angle of the Earth and the precession is defined as the wobble of the Earth's axis (Al-Ghussain 2016).

The sun irradiation has been measured by NASA since 1978 and the readings display a very minor drop in the level of energy produced by the sun over this period of time (Change 2018). Estimations were made to define the consequence of the variation of solar radiation and the results identified that the change in the solar radiation might be accountable for 10% or less of the 20<sup>th</sup> century warming. Furthermore, if the warming is initiated by the rise in solar activity, the whole layers of atmosphere are theoretically to be warmed as well; instead, scientists detected a cooling pattern in the upper layers of the atmosphere and a warming pattern in the lower layers of the atmosphere (Lockwood 2010). Volcanic eruptions have a substantial impact on the temperature of the Earth; their eruptions convey ash and gases into the upper atmosphere. Amongst these gases, sulphuric gases particularly, contribute in the creation of clouds, triggering the reduction of the global temperature for 3 years. Furthermore, volcanoes release large quantities of carbon dioxide and water vapour, which play a role in the global warming; yet, the amount of carbon dioxide and water vapour produced by the volcanoes is very minor in comparison to human emissions (Man et al. 2014). Volcanoes produce an annual average between 130-230 million tonnes of carbon dioxide, whereas anthropogenic sources cause annual emissions of 100 times more than volcanoes (26 billion tonnes of carbon dioxide) (Reibeek 2005).

Natural events are still contributors, but with small and slow impact on the climate compared with human activity influences. Scientists established climate models, based on data from satellites and from ground stations to reform temperature models over the past 150 years to identify that anthropogenic activities have the main impact on the climate. The imitations of the model were able to match the global temperature remarks by seeing only

the solar natural patchiness and the volcanic releases for the period between 1750 and 1950, but after 1950, the global temperature trends cannot be explained without bearing in mind the greenhouse gases produced by humans (Reibeek 2005, Al-Ghussain 2016).

After the Industrial Revolution took place, the temperature on the Earth's surface began to increase. Experts at Goddard Institute for Space Studies (GISS) stated that since 1880, the Earth's surface average temperature has risen by about 0.8 degrees Celsius. The Japan Meteorological Agency, NASA, NOAA and the Met Office Hadley Centre in United Kingdom documented the annual temperature variances from 1880 to 2014; all the data show the same trend of peaks and valleys with different values (Hansen et al. 2010). Earth's average surface temperature will keep rising as the human race continues environmentally harmful activities, particularly burning fossil fuels. According to three CO<sub>2</sub> emissions scenarios, scientists forecast that the average surface temperature will increase by 2-5 degrees Celsius by the end of the 21<sup>st</sup> century (Riebeek 2010). Animals, crops and plants require precise conditions to survive and develop, such as the proper ambient temperature and sufficient amount of water and the increase in the global temperature will disrupt the growth and the breed of these organisms. Furthermore, the rise in the global temperature will result in the spread of dangerous weather outcomes like floods, heat waves, droughts and hurricanes. This will raise the number of human and material losses. In addition, as the climate gets warmer, the snow and the ice meltdown, triggering sea levels to increase and also the transformation of sunlight reflecting surfaces (like snow and glaciers surfaces) to sunlight absorbing surfaces will result in more energy being locked in the Earth's atmosphere (Riebeek 2010, Al-Ghussain 2016). The intensity and the geographic pattern of precipitation have considerably transformed in the past 40 years where dry areas have become drier and wet regions have become wetter; nevertheless, the overall precipitation rate of the world has marginally changed. Global warming is accountable for these changes where the rise in the atmospheric temperature amplified the capability of the atmosphere to hold moisture. As the moisture levels in the atmosphere increases, the ability of producing heavier precipitation will increase; though, these precipitations events become shorter and less recurrent as it requires more time to replenish the atmosphere with moisture (Easterling et al. 2000).

The occurrence of great floods has increased considerably during the 20<sup>th</sup> century, the dense precipitations over a short period of time contributing to the increase in the floods in different parts of the world. The capability of soil to take in the water in cases of heavy precipitation will be small, which will increase the quantity of run-off water, resulting in floods. Moreover, areas neighbouring water bodies will face floods because of the rise in the water level (Trenberth et al. 2014). Drying trends have been witnessed in the Southern and Northern Hemispheres since the 1950s and the amount of very dry zones across the world have doubled since the 1970s. Climate models cannot describe these trends and extensions without including the effect of global warming, where it is affecting the factors that cause the increase in droughts, like the shift in the precipitations trends from average and light rains to short and heavy precipitations, as well as snow-melt and the rise in the evaporation percentage from vegetation and soil (Davis 1989, Dai 2011).

Heatwaves are another consequence of climate change and they are defined as extended periods of hot weather where such events have substantial impact on human health and where the exposure to high temperature for a long time leads to grave health issues, such as fainting and heatstroke (Al-Ghussain 2016). Heatwaves were once extremely unique in the period between 1951 and 1980 when very hot temperatures impacted only 0.1% of the world, but after 1980, extreme heat events have become more widespread. Heatwaves presently affect nearly 10% of the world and it could distress 17% of the world after one decade if the warming continues (Wang et al. 2015). The climate will shift towards a warmer climate creating more events of extreme weather as the average global temperature increases.

### **Greenhouse gases**

One of the many definitions of Global Warming is the rise in the surface average temperature of the Earth caused by the increase in the levels of greenhouse gases (GHGs), such as ozone, carbon dioxide, water vapour, methane, chlorofluorocarbons (CFCs) and nitrous oxide (Al-Ghussain 2016). The greenhouse effect is the main reason for Earth being a suitable place to live on. Without GHGs, the Earth's surface temperature would be too low and, as a result, no life could be sustained on Earth. Yet, the abnormal increase in the amount of GHGs in the atmosphere has resulted in the catastrophic phenomenon of global warming (Anderson et al. 2016). The atmosphere of the Earth is made up of nitrogen, oxygen and argon primarily and other gases in small amounts, including GHGs and some pollutants. The percentage of the permanent gases (nitrogen, oxygen and argon) is fixed and does not change, while the percentage of the trace gases (carbon dioxide, methane, nitrous oxides and ozone) changes constantly on daily, seasonal and annual bases (Rodriguez 2020). GHGs have the capability to absorb and release infrared radiation because of the inner vibrational modes that their atoms consist of, not like the other main compounds of the atmosphere (Oktyabrskiy 2016).

The solar radiation spectrum is made up of three wavelength ranges; ultraviolet range, visible range and infrared range and each range holds an amount of the solar energy. Infrared waves carry nearly half of the solar energy in the spectrum, the majority of these infrared waves being with high wavelength because of the sun surface temperature (Anderson et al. 2016). When the sun radiation travels through the atmosphere, small amounts of it are captured by the GHGs and reflected towards space due to clouds and aerosols. Ozone absorbs the waves in ultraviolet region, while carbon dioxide and methane absorb the waves in the infrared region. Furthermore, the absorption outcome of water vapour is dispersed through all the wave lengths (Pokorný et al. 2010). When the Earth's surface and terrestrial objects start to become warmer, they radiate short-wave infrared radiation due to their low temperature in comparison with the sun towards the atmosphere, which will be captured by GHGs (Dai 2011).

## The role of plants under global change conditions

Plants are a vital part of the survival of most species. They are used in producing food for human consumption, animal feed or as elements for beautifying streets and lands. For each purpose, specific species are best to be used. Great pressure is being placed on arable lands as the human population continues to grow. This pressure is a result of the constant demand for crops and forage to produce food resources for people. The balance of the ecosystem can easily be damaged if unplanned farm construction is performed. According to the World Food Programme, one in nine people suffer from hunger (Ravallion 2017). In order to contribute to tackling this issue of world hunger, new methods for plant production need to be considered and developed. It is also important to note the significance of plants in resolving some of the environmental problems, such as desertification. Arid and semi-arid environments provide habitat to more than one billion humans and they cover over 40% of the land surface on Earth (Veron et al. 2006). People who live in these areas depend mainly on the efficient use of natural resources. However, it is widely known that these lands are at risk of desertification. Desertification is land degradation in arid, semi-arid and dry sub-humid areas resulting from various factors, such as climate changes and human activities and this poses a serious threat to the environment and human welfare (Veron et al. 2006).

To combat desertification, plants play an ecological role in minimizing its negative consequences. Plant species, especially in arid environments like the UAE, have an array of uses, such as landscaping and forage production, both of which improve soil carbon sequestration. Forages can be defined as fibrous plant materials that are harvested or best utilised from other plants to feed farm animals. There are many species that have the potential to be classified as forage and the most readily available ones are grasses, such as Orchardgrass (*Dactylis*) and legumes, such as alfalfa (*Medicago sativa*) (Capstaff and Miller 2018). Landscape plants are the plants used to enhance the appearance of any type of land. Depending on the climate and available resources, the common species of landscaping plants vary from one country to another. In the UAE, for example, Date palms (*Phoenix dactylifera*) and Arabian Almond (*Prunus arabica*) are often planted (Almejdi et al. 2005). Plant roots function as a medium for removal of atmospheric carbon into the soil in the form of compounds containing carbon, like organic acid, phenolic acid, amino acid etc. Root lysis and root exudates donate noteworthy amounts of carbon left in sub-surface soil. Apart from surface soil, these deposits have the ability for a greater influence to long-term soil carbon sequestration due to relaxed oxidation.

Carbon components impact agriculture by reducing microbial growth, pH and nutrient mobilisation. The particular quantity of sequestration relies on climate, edaphic factors, land-management practices and the total number and quality of plant and microbial levels (Kumar et al. 2006). Studies on carbon allocation via roots will create a new idea that will permit better judgements on the precise use of fertilisation, soil amelioration and crop rotation. These methods deliver valuable tools for addressing many problems in both natural and agricultural soils. Carbon sequestration will positively play a role in decreasing atmospheric CO<sub>2</sub> concentration and will lessen drought, desertification and salinity stress. It will be a feasible approach towards sustainable agriculture. Therefore, sequestered soil

and plant carbon may be used for forestry, agriculture and, ultimately, be a potential option to lessen global change (Kumar et al. 2006).

## Plant growth and the impact of Global Change

Plants constantly face a wide range of environmental stresses which creates a restriction to growth and, therefore, agricultural efficiency. The environmental stresses faced by plants can be classified as abiotic stress and biotic stress.

Examples of abiotic stresses include drought, flood, salinity, extremes in temperature, radiation and heavy metals. Abiotic stress is a leading factor that causes the loss of major crop plants globally. This situation will be more harsh due to increasing desertification of the world's lack of water resources, increasing salinisation of soil and water and environmental pollution (Verma et al. 2013).

Biotic stress, on the other hand, includes attack by numerous living pathogens, such as fungi, bacteria, nematodes, oomycetes, and herbivores. Infections created due to these pathogens are responsible for major yield loss worldwide. As plants are sessile, they cannot escape from these environmental stresses. To combat these threats, plants have developed various mechanisms for becoming adapted to such conditions for survival (Ashraf and Harris 2013). Plants have the ability to feel the outside stress environment, become stimulated and then produce suitable cellular reactions. These cellular reactions work by sending the stimuli from sensors that are positioned on the cell external or cytoplasm to the transcriptional mechanism which is located in the nucleus with the aid of many signal transduction trails (Viljevac et al. 2013). This results in a degree of difference in transcriptional alterations, making the plant tolerant to the stress. The signalling trails play an essential part and act as a joining link between sensing the stress environment and generating an appropriate physiological and biochemical response. As the mechanism of photosynthesis includes various steps, including photosystems and photosynthetic pigments, CO<sub>2</sub> reduction pathways and the electron transport system, any misplacement at any level initiated by a stress may decrease the overall photosynthetic ability of a green plant (Verma et al. 2013).

Various stressful environments have been stated to decrease the contents of photosynthetic pigments. For instance, salt stress can break down chlorophyll. This effect is linked to amplified level of the toxic cation Na<sup>+</sup> (Ashraf and Harris 2013). Even though salt stress decreases the chlorophyll content, the degree of the decrease is dependent on salt tolerance of plant species. It is commonly known that, in salt-tolerant species (like *Juniperus virginiana*), chlorophyll content increases, while it decreases in non-salt-tolerant species (like *Pisum sativum*) under saline conditions (Ashraf and Harris 2013).

Heat is another form of stress that impacts plants and results in membrane disruption, particularly in thylakoid membranes. This thereby prevents the activities done by membrane-linked electron carriers and enzymes, ultimately resulting in a reduced frequency of photosynthesis (Kramer and Boyer 1995). As in salinity stress, drought stress

results in not only considerable damage to photosynthetic pigments, but it also leads to the decline of thylakoid membranes. The root systems can also be greatly impacted by stress factors (Kramer and Boyer 1995).

## **CO<sub>2</sub> enrichment protocols in plant growth assessment**

Over the last 40 years, researchers have utilised enclosed and open-top chambers and, more recently, Free-Air Carbon Enrichment (FACE) facilities that experimentally enrich the amounts of CO<sub>2</sub> in the atmosphere (Domec et al. 2017). Chamber studies could yield an overestimation of the CO<sub>2</sub> elevation effects, while FACE replicates an environment parallel to real field conditions (Ainsworth et al. 2008).

Experimental approaches, like FACE technology, allowed us to examine the interaction effects of land management practices (like nitrogen addition) and environmental conditions (like elevated CO<sub>2</sub>, ozone levels and natural variation in water availability) on plant construction and function. Important field data acquired from those two types of studies were used to authenticate computer models forecasting responses to elevated CO<sub>2</sub> (Reid et al. 2003). These studies allow measurement of bulk comebacks of ecosystems to differences in environmental conditions and resource accessibility. They also determine the situation within which elevated CO<sub>2</sub> and drought interact to impact structural and anatomical changes, providing a mechanistic understanding of the interaction between plants and water (Reid et al. 2003). These mechanisms can then be integrated into forecasting models to estimate crop yields and forest efficiency in water-stressed environments in present and future climate situations and sites with a range in nitrogen availability (Tor-ngern et al. 2015).

## **CO<sub>2</sub> enrichment and plant growth**

Many plant species react differently to CO<sub>2</sub> fertilisation. Though most experiments have looked at the effect of elevated CO<sub>2</sub> on individual species and not at the interactions amongst species, woody species, such as trees and shrubs, are likely to have a more pronounced photosynthetic and productivity response to elevated CO<sub>2</sub> than species in grassland ecosystems (Nowak et al. 2004). Generally and if other resources, such as soil nutrients, are not limiting (Johnson et al. 2016), elevated CO<sub>2</sub> increases the leaf-level photosynthetic rate and nitrogen-use productivity and reduces stomatal conductance substantially in C3 species, but has less of an impact in C4 species (Palmroth et al. 2006, Medlyn et al. 2015). A rise in the availability of CO<sub>2</sub> increases photosynthesis (carboxylation) and decreases the oxygenase activity of Rubisco, hence reducing photorespiration (oxygenation) and thus increasing net assimilation per leaf area (Domec et al. 2017). The C4 and CAM plants developed internal CO<sub>2</sub> concentrating mechanisms, which minimise photorespiration independent of the CO<sub>2</sub>, so their photosynthetic activity is anticipated to be less sensitive to elevated CO<sub>2</sub> (Domec et al. 2017).

A main, unsolved issue in global change biology is to what extent improved plant growth under elevated CO<sub>2</sub> can be constant into the future. Open-air FACE studies generally indicate that elevated CO<sub>2</sub> encouraged higher leaf photosynthetic rates and plant growth rates are sustained over 5–13 years of application (Cole et al. 2010), even though cases of shorter-lived growth stimulations exist (Kim et al. 2015). There are no data on the effect of elevated CO<sub>2</sub> throughout an entire tree lifespan, though Cole et al. (2010) used a reflective approach to show that, over the last 50 years, the progressive increase in CO<sub>2</sub> has improved growth levels of natural stands of *Populus tremuloides* Michx. by over 50% and that this growth stimulation was lower during drought episodes (Reid et al. 2003). Cole et al. (2010) observed that elevated CO<sub>2</sub> raises ring thickness at all moisture levels as a consequence of higher water use effectiveness. The mechanical understanding of the effect of elevated CO<sub>2</sub> on stomatal closure and transpiration is not yet clear (Reid et al. 2003, Domec et al. 2017).

Stomata respond to changes in intercellular CO<sub>2</sub>, but are not thought to directly respond to changes in atmospheric CO<sub>2</sub>. In *Pinus taeda* L. and *Liquidambar styraciflua* L., for example, a short-term manipulation in elevated CO<sub>2</sub> caused no direct response in stomatal conductance (Tor-ngern et al. 2015). The observation of a long-term 21% reduction in stomatal opening was the result of the indirect effect of decreased leaf hydraulic conductance and lower light capture, associated with greater leaf area index (Tor-ngern et al. 2015). Long-term treatments of enriched CO<sub>2</sub> can, therefore, disturb the hydraulic system and the variances in the elevated CO<sub>2</sub> response of plant hydraulic capacity is projected to be linked to the development of contrasting anatomical traits during plant growth (Domec et al. 2017).

The most significant direct effect of elevated CO<sub>2</sub> on plant growth is consequently an increase in carbohydrate availability for growth and amplified water-use effectiveness owing to the concomitant increase in photosynthesis and the decrease in stomatal conductance (King et al. 2001). The improved plant productivity with CO<sub>2</sub> enrichment is fundamentally linked to the greater leaf area produced, which was first observed on wheat and has since been recognised in a large number of species, although these physiological responses to elevated CO<sub>2</sub> depend on the species, soil nutrient and water availability (Gimeno et al. 2016, Domec et al. 2017). Eventually, both increased carbon accessibility and more efficient water use are combined to stimulate cell propagation by promoting cell division and expansion. Cell expansion happens due to an osmotic gradient moving water into the cell, which permanently stretches the plasticised cell wall. An extra of non-structural carbohydrates can be utilised to lower the osmotic potential, resulting in more water entering the cell and the cell expanding more at a given leaf water potential than under lower CO<sub>2</sub> (Gimeno et al. 2016).

For a given quantity of available water, the capability of a specie to make the most of the extra carbon under elevated CO<sub>2</sub> will mainly be a function of its inherent structural and physiological qualities included with anatomical and morphological malleability (Domec et al. 2017). Higher leaf area and, in some cases, leaf mass per area, is likely to be conveyed by the larger cross sectional area of the xylem and larger amounts of coarse and fine roots, therefore possibly not considerably altering the allometric associations amongst the areas

of the absorbing, transporting and transpiring surfaces when water is not restrictive (Poorter et al. 2012, Domec et al. 2017). Nevertheless, the excess carbohydrates invested in cell production cause the regulation of the cell cycle in plants and could be a part of changes in cell anatomy like wider xylem conduit diameter with capability effects on xylem porosity and, consequently, the capacity for water flux (Poorter et al. 2012).

## The Impact of Global Change at the Seed Level

Plant seed germination is a vital phase in the life cycle of plants and the successful establishment of plants fundamentally rest on successful germination (Gorai and Neffati 2007). Usually, seed germination tends to be very irregular over space and time. However, climate has a large effect on seed endurance. For instance, with short winters, seeds may remain partly dormant in spring and need a prolonged time to germinate (Walck et al. 1999). The change in temperature and water supply because of global climate change could prevent, delay or improve regeneration from seeds (Kim and Han 2018).

Despite the considerable number of studies on the effects of climate change on plants, there have been few attempts to investigate its effect on seed germination (Hedhly et al. 2009). Several environmental influences, such as temperature, light, salinity and soil moisture, instantaneously influence seed germination. Amongst several factors, temperature has been measured as the most important factor. The variation in the ideal temperature for seed germination relies on the considered species and, for the majority of species, seed germination is established over a wide range of temperatures. This variation in the optimal temperature and the germination rate between species establishes some adaptive strategies to harsh environmental conditions. It has been presented that temperatures above the thermal optimum frequently aggravate an inhibition of germination and irreversible damage (Gorai et al. 2006).

Furthermore, plant regeneration from seed is fundamentally ruled by germinability and speed of germination. These mechanisms have established significantly less attention in CO<sub>2</sub> research relative to studies of vegetative or reproductive output responses (Kim and Han 2018). Moreover, the limited literature has not been thoroughly reviewed for patterns of responses and potential mechanisms. Marty and BassiriRad (Marty and BassiriRad 2014) presented a meta-analysis summing up the results of studies that have addressed the parental and direct effects of enriched CO<sub>2</sub> on seed germination success and germination percent (Marty and BassiriRad 2014). There is little experimental evidence that enriched CO<sub>2</sub> can have a direct effect on a germinating seed and, like parental responses, this direct impact on germination is quite unpredictable.

A study on historical climate change period (Davis 1989) displayed that woody plants migrate along with climatic zones, but its moving velocity is projected to be 4–200 km per 100 years. Consequently, excluding tree species with a high migration velocity, they will not be able to catch up with the migration of climatic zones and turn out to be at high risk of extinction because of climate change (Davis 1989).

## Germination parameters

Of all the responses that have been observed from climate change, the increased concentration of CO<sub>2</sub> is by far the most understood. Jablonski et al. (Jablonski et al. 2002) presented in a meta-analysis of studies on the impact of elevated CO<sub>2</sub> on seed production, mass and quality of 79 plant species, (Jablonski et al. 2002) that, on average, plants produced more (16%), heavier (+4%) seeds that had lower nitrogen levels (-14%) (Jablonski et al. 2002, Hovenden et al. 2008). Nevertheless, most previous studies examined crop plants, which tend to have seed production that is more responsive to elevated CO<sub>2</sub> than 'wild' plants (Jablonski et al. 2002). Most of the studies of reproduction of wild plants to elevated CO<sub>2</sub> applied to plants that are short-lived under non-nutrient limiting environments. Based on this, (Körner 2003) claimed very little data about the impacts of elevated CO<sub>2</sub> on reproduction of perennial wild plant species growing in unfertilised conditions are available (Körner 2003). Since most plant species fall under this group, much more information is required in this area.

## Seed Morphology

### The impact of elevated CO<sub>2</sub> on seed germination

Plants display changes in their physiology, morphology and ecology in response to environmental stress. With regards to soil CO<sub>2</sub>, negative associations have been found between CO<sub>2</sub> concentration and plant physiological parameters, such as photosynthetic rate, stomatal conductance and transpiration rate (Wu et al. 2014, He et al. 2016). Chlorophyll is affected by elevated soil CO<sub>2</sub> levels (Male et al. 2010). According to studies at the Artificial Soil Gassing and Response Detection site in the UK, the chlorophyll content of pasture and turf grass was considerably reduced in areas with higher soil CO<sub>2</sub> concentrations (50–70%) (Patil et al. 2010). A similar result was obtained at a natural CO<sub>2</sub> spring, though this was as the result of the long-term adaptation of plants to a constantly-retained high soil CO<sub>2</sub> level (Vodnik et al. 2006). It was reported by Vodnik et al. that leaf chlorophyll content was negatively correlated with soil CO<sub>2</sub> concentration (Vodnik et al. 2006). Some plant bioactivities, such as transpiration rate, leaf moisture, stomata conductance and root respiration, have also been stated to be inhibited by elevated soil CO<sub>2</sub> concentrations (Wu et al. 2014, He et al. 2016). Repression of root respiration in response to elevated levels of soil CO<sub>2</sub> could result in a decline in stomata conductance, since lower root activities delay the absorption of water and nutrients from roots, making the plants close their stomata (Morard et al. 2000). Closure of stomata can cause CO<sub>2</sub> shortage inside the leaf and this can further decrease the photosynthetic rate (He et al. 2016).

Persistent decrease in photosynthesis could change plant morphology as well. Plant height and root length were stated to be reduced by 13.7% and 20.2% by high soil CO<sub>2</sub> concentrations (15–65%) (Al-Traboulsi et al. 2013). At a study site near a natural CO<sub>2</sub> spring, it was observed by Vodnik et al. that plant height in areas with a soil CO<sub>2</sub> concentration of 30% was smaller than in areas with a soil CO<sub>2</sub> concentration of 10%

(Vodnik et al. 2006). Other studies at the Artificial Soil Gassing and Response Detection site were that plants turned yellow or brown and even died at a soil CO<sub>2</sub> levels of 75% (He et al. 2016). The collective response of plant physiology and morphology to elevated soil CO<sub>2</sub> levels is a significant decline in plant biomass (Al-Traboulsi et al. 2013, He et al. 2016).

Nevertheless, the responses of plants to high soil CO<sub>2</sub> concentrations differ by plant group. This can result in replacement of one group by another, which leads to a change in plant community (Ali 2012). At the Artificial Soil Gassing and Response Detection site, grasses were the dominant species in areas where the soil CO<sub>2</sub> concentration was around 45%, whereas, in areas of normal soil CO<sub>2</sub> concentrations, there was a better diversity of plant species. This suggests that monocotyledonous species could be more tolerant to higher CO<sub>2</sub> concentrations than dicotyledonous kinds (West et al. 2009). A similar finding was found at a natural CO<sub>2</sub> vent (Ciotoli et al. 2008). On the contrary, Ciotoli et al. (2008) reported that *Polygonatum arenastrum* (dicotyledonous specie) was more abundant at a CO<sub>2</sub> vent (concentrations ranged between 10 and 35%) (Ciotoli et al. 2008). An acid-tolerant grass *Agrostis capillaris* was the dominant plant in the relatively high CO<sub>2</sub> zone in Latera, Italy (He et al. 2016). These conflicting results propose that the sensitivity of plants to elevated soil CO<sub>2</sub> concentrations differs with plant species.

Plants are also impacted by high soil CO<sub>2</sub> concentrations during their germination phase because plants were found to be more sensitive to anaerobic conditions during their early growth. Xue and Ma reported that the germination potential of four species of C4 plants was not impacted up to 8% of CO<sub>2</sub> elevation (Xue and Ma 2014, Xue et al. 2017). However, Al-Traboulsi et al. (2013) documented that half the winter bean crop did not develop when soil CO<sub>2</sub> level was 20% and the 50–70% soil CO<sub>2</sub> level were entirely deadly to the field bean. Even though these two studies investigated the high CO<sub>2</sub> concentrations on plant germination, there are few studies that likened the effects of high CO<sub>2</sub> concentrations on germination of different plant groups and we still need information to specify the effects (Ye et al. 2005, Al-Traboulsi et al. 2013, Wu et al. 2014, He et al. 2016).

### **The impact of heat on seed germination**

A shorter growing season could mainly be harmful during early plant development. Elevated temperatures following fertilisation harmfully impacts grain development (East et al. 1972, Folsom et al. 2014, Begcy et al. 2018). Elevated seed growth and reduced seed size are the most noteworthy consequences of high stress in initial seed development. The process of grain filling, which includes nutrient build-up in emerging and growing grains, is also sensitive to environmental conditions and has marked effects on the final yield and quality. Early seed growth requires a free nuclear stage (syncytial) and is followed by cellularisation of endosperm (ED) nuclei (Begcy et al. 2018). The cellularised ED remains to perform mitotic divisions. The rate and length of nuclear divisions and subsequent mitotic cell divisions are significant factors of sink ability during the grain filling period. Environmental disturbances during the primary phases likely affect later stages of seed development and, as a result, grain size (Folsom et al. 2014). Many regulatory and

metabolic pathways have been linked with abiotic stress-induced seed development (Begcy et al. 2018). Most severe and sustained high heat studies only report treatment impact on seed size and molecular network forms for the generation in which the stress was implemented (Chen et al. 2016, Begcy et al. 2018). The transgenerational impact of high heat is much less categorised. High stress during seed development considerably impacts seed dormancy quality, germination and emergence, as well as seedling formation (Begcy et al. 2018). Elevated temperatures had a robust harmful consequence on seed germination potential and resulted in downgraded seed practicality and deprived germination (Fahad et al. 2017). Reduced germination and seed vigour due to high heat have been linked with reduced thermos-stability of the plasma membrane and membrane fluidity, which delayed activation of calcium signalling, kinases and heat shock elements (Begcy et al. 2018). Hormonal and other chemical treatments can enhance seed germination, establishment and seedling vigour via a process called seed priming. In rice, for example, seed priming is used to reach faster and more even emergence (Hussain et al. 2017). Seed priming has agricultural uses and will likely gain a better reputation as farmers seek better resilience in their production practices in constant unstable weather patterns. A better understanding of seed priming and its ways of activity would consequently be of substantial value. Two major phytohormones, Gibberellin (GA) and ABA play a main role in response to stress and during normal plant development, particularly during seed germination. Endogenous ABA and GA levels negatively and positively control seed germination (White et al. 2000). A comparison of dormant and non-dormant rice cultivars, exhibited that ABA and GA, show dynamic changes in early, late and middle phases of seed development. Moreover, exposure to high stress can result in increased ABA levels, with declining GA biosynthesis (Begcy et al. 2018).

### **Radical emergence**

Seed germination is considered as a crucial phase in the life cycle of plants. Seed germination occurs by sequence of molecular and physiological events which is initiated upon seed imbibition and further lead to the radicle protrusion through the seed external envelopes (testa and endosperm) (Bewley 1997). During seedling growth, food reserve is hydrolysed and mobilised to the site of active growth. Seed germination and growth potential of embryo are predominantly influenced by various abiotic and biotic environmental factors (Kuriakose and Prasad 2008). The abiotic factors, such as temperature, light, salinity, CO<sub>2</sub> and moisture significantly influence seed germination (Baskin 1998, Ainsworth and Long 2005, Chauhan et al. 2006, Chauhan and Johnson 2010). The effects of abiotic stresses on plants is greatly increased by climate change.

Effects of increasing atmospheric carbon dioxide levels and climate change might influence variation in weather conditions and wide range of environmental conditions can be impaired or destroyed. One of the basic abiotic factors that influences seed radicle emergence and healthy plant development is the availability of water and water utilisation efficacy during germination. Adaptation of plants to salinity during germination and early seedling stages is also crucial for radical emergence and the establishment of species in saline environments (Ungar 1995). The seed germination process requires optimum

environment conditions for activation of stored mRNA and proteins (Rajjou et al. 2004). Abiotic stress caused by environmental variations can cause damage at the DNA level and can result in aborted development of the seedling. Global warming and increasing drought conditions is shifting the ideal plant growth environment in many regions of the world.

### **Water stress on impact radical emergence**

The water accessibility and proficiency of water utilisation at the time of germination is one of the basic factors influencing the field emergence rate. In many species, increase in seed water uptake was recorded when grown under enriched atmospheric CO<sub>2</sub> conditions (Baskin and Baskin 1998). As the CO<sub>2</sub> future projection shows an increasing trend, it is extremely important to widen the studies in this area. The protrusion of the radicle through the seed coat is accomplished by cell elongation without any cell division (Sliwinska et al. 2009) and occurs along with water uptake during seed imbibition. Moisture imbibition causes enzyme activation, food storage breakdown and nutrient translocation to meristematic regions, which aids seedling development. The interactions between abscisic acid (ABA), gibberellins (GA) and brassinosteroids (BR) are regulatory processes that determine dormancy and germination. A study on seed priming with Ascorbic acid AsA (0.5, 1.0 and 1.5 mM) Reiahi and Farahbakhsh (2013) found improved seed germination and seedling resistance of sorghum (*Sorghum bicolor*) to drought stress.

### **Elevated CO<sub>2</sub> impact on radical emergence**

The rise in CO<sub>2</sub> concentration in the atmosphere is changing the air temperature and precipitation patterns, creating a challenge to the current agricultural productivity. The field-controlled chamber experiments confirmed the adverse impact of CO<sub>2</sub> in reducing germination and emergence of C3 crops, such as *Arabidopsis thaliana* (Andalo et al. 1996), soybean, pea, sunflower, pumpkin (Ziska and Bunce 1993) and canola (Qaderi and Reid 2005). Under an enriched CO<sub>2</sub> environment, the germination percentage of chick pea reduced by 65–69% compared to 87–90% reduction under ambient conditions, possibly due to significant N-dilution effects (Saha et al. 2015). A major future challenge to the seed industry is to develop cultivars that can maximise the crop production in a changing climate of rising CO<sub>2</sub>.

An increase in atmospheric CO<sub>2</sub> and temperature will certainly exert a profound influence in crop productivity and quality (Wang et al. 2020). Temperature affects germination and the dormancy status of the seed. A favourable temperature is crucial for the complex sequence of chemical changes occurring during seed germination. Metabolic activities, such as enzyme activation, breakdown of food reserves, their translocation to the growing parts and their utilisation in seedling growth and development are dependent on optimum temperatures. Some annuals whose seed breaks the dormancy in response to cold stratification in winter and initiate germination in spring are called summer annuals (Baskin and Baskin 1998). For example, seeds of *Echinochloa crusgalli* dispersed in autumn are cold-stratified during winter. A favourable temperature is crucial for the complex sequence of chemical changes to occur during seed germination.

## Salinity stress impact on radical emergence

Salinity and osmotic stress affect seed germination and seedling development in numerous ways. Increase in salinity leads to a reduction or delay in seed germination of both halophyte and glycophyte seeds (KATEMBE et al. 1998). Although plants in these saline soil experience high levels of abiotic stress associated with high salinity, they have special adaptations for root initiations. *Aegiceras corniculatum* and *Avicennia marina* are two viviparous mangrove species, not significantly affected by salinity and germination and subsequent development of the propagule take place while still attached on the mother tree. Following release of these propagules, the further development of these propagules into seedlings was maximum at a salinity concentration of 3 ppt for *Aegiceras corniculatum* (Clarke and Hannon 1970) and 15 ppt for *Avicennia marina* (Ball 1988). However, for those of *Acanthus ilicifolius*, a non-viviparous species, germination is significantly delayed about 4 days at salinities over 25 ppt (Ye et al. 2005). Seed germination under saline conditions relies heavily on adaptation strategies by certain plants. The salt concentration at the surface of salinised soil changes over time as continuous evaporation of groundwater gradually deposits salt on the soil surface. After the rainfall or snow melting, the salt quickly leaches out from the soil surface and supplies water to seeds. Thus, for the successful establishment of certain plants in saline environments, seeds must remain viable at high salinity and germinate when salinity decreases (Ungar 1978, Ungar 1991, Ungar 1995). For example, the establishment of *Kalidium caspicum* in saline environments, salt must be completely removed at the soil surface which is enabled by the leaching of salt from the soil surface by snow-melt in early spring. A study by Xiong and Zhu in 2002 found that salinity and drought stress result in secondary oxidative stress and generation of free radicals which damage membrane bilayer lipids, proteins and nucleic acids during seed germination (Ball 1988). This becomes crucial when the optimum environment conditions are violated during seed germination.

## Biochemical changes during plant growth

### Effects of CO<sub>2</sub> concentrations at optimal conditions

Hereinafter, 'optimal conditions' represent optimal soil conditions for species-specific initiation of seed germination, which include optimal mineral and organic constituents, moisture content and temperature of the soil surrounding the germinating seed. It is well established that the seed germination differs in ambient and elevated CO<sub>2</sub> (aCO<sub>2</sub> and eCO<sub>2</sub>, respectively) depending on the three-way interactions of plant species, plant type (C3 and C4) and CO<sub>2</sub> such that an increase, decrease or no change in seed germination are reported in different plant species exposed to a range of CO<sub>2</sub> concentrations for different periods of time (Hampton et al. 2013, Domergue et al. 2019). Most of the studies are done at 700 ppm eCO<sub>2</sub>, although other eCO<sub>2</sub> concentrations do appear in different trials. In this review, the range of eCO<sub>2</sub> concentrations and exposure times are included under the umbrella term eCO<sub>2</sub>. Thus, the notion of further interactions (four-way and five-way) are excluded by omitting the eCO<sub>2</sub> in the aforementioned interactions to reduce the complexity in further explanations.

Considerable changes in seed biochemistry happen during germination in response to aCO<sub>2</sub> (Bewley and Black 2014) and eCO<sub>2</sub> (Marty and BassiriRad 2014). It is noteworthy that different plant species show different seed germination potentials even in the ambient CO<sub>2</sub> conditions themselves, let alone the eCO<sub>2</sub>. Biochemical changes occur during the seed germination are not fully decoded yet (Nonogaki 2006). As a result, complex non-uniform changes in seed germination biochemistry in response to aCO<sub>2</sub> and eCO<sub>2</sub> are reported. It is obvious that soil sown seeds are surrounded by a high CO<sub>2</sub> environment created by soil microbial respiration (He et al. 2016). However, no extensive studies have been done, in this context, elaborating different aspects of seed germination and changes in seed biochemistry. Normally, respiration, enzyme and organelle activity and RNA and protein biosynthesis shoot up in germinating seeds (Bettey and Finch-Savage 1996, Bewley and Black 2014). In this review, these variables are considered as the major biochemical changes to occur during seed germination.

Seed carbohydrate reserves are actively consumed at the early stages through respiration to provide energy for the germination process (Ziegler 2017). Sucrose, stachyose and raffinose are the major energy substrates consumed at the initial stages of seed germination (Palmer 1969, East et al. 1972, Kuo et al. 1988). Elevated CO<sub>2</sub> normally increases sucrose, stachyose and raffinose content compared to aCO<sub>2</sub> under optimal conditions (Bellaloui et al. 2017). Increased enzyme activity is directly correlated to the initial energy production reactions (Ali and Elozeiri 2017). According to Ali and Elozeiri (2017), a surge in enzyme activity also denotes seed protein reserves are actively metabolised along with carbohydrates. Increase in seed C/N ratio and subsequent decrease in total seed protein content are predicted in eCO<sub>2</sub> compared to aCO<sub>2</sub>, ultimately affecting embryo growth and seed vigour (Hampton et al. 2013). No studies were found on the change in enzyme activity during seed germination under eCO<sub>2</sub> in our literature search. Thus, it is assumed here that such changes depend on the interactions of eCO<sub>2</sub> with plant type and plant species.

Active mitochondria is a priority requirement for initiation of seed germination and only some plant species had it active even before seed imbibition in aCO<sub>2</sub> (Attucci et al. 1991). In other plant species, the transformation of mitochondria from a quiescent to mature form in the germinating seeds and its subsequent contribution to the energy production seem to be an important event succeeding water imbibition (Ma et al. 2019, Nietzel et al. 2020). This transformation of mitochondria is essential for its protein import functionality during the initial stages of seed germination (Law et al. 2014). No studies relevant to the changes in mitochondrial activity in eCO<sub>2</sub> have been found in our literature search. Here as well, species-specific responses of mitochondria are assumed in relation to seed germination responses. Mitochondrial activation is required for cellular signalling, amino acid synthesis and nitrogen assimilation. Thus, it has been assumed that any changes, effected by eCO<sub>2</sub> on seed germination, have already changed cellular signalling, amino acid synthesis and nitrogen assimilation. Protein synthesis has been reported to commence soon after seed imbibition supported by a transient increase in the stored messenger fraction (MF) in the embryo (Bewley and Black 2014). Stored mRNA's are directed to the polysomes and are translated to protein during seed germination (Sano et al. 2020). As mentioned before,

eCO<sub>2</sub> can change C/N ratio and subsequent *de novo* protein synthesis in germinating seeds compared to aCO<sub>2</sub> (Hampton et al. 2013), suggesting that eCO<sub>2</sub> had a prior effect on mRNA production and subsequent translation.

### Effects of CO<sub>2</sub> concentration and abiotic stress interactions

Abiotic stresses are known to decrease seed germination in aCO<sub>2</sub> (Daszkowska-Golec 2011) and in eCO<sub>2</sub> (Qaderi and Reid 2008) depending on the plant species. Abiotic stresses, like drought, higher than optimal growing temperature (hereinafter referred to as high temperature) and salinity, decrease seed germination in different plant species in aCO<sub>2</sub> (Jisha et al. 2013, Ashraf et al. 2018). Similarly, drought, temperature and eCO<sub>2</sub> interactions have been shown to decrease seed germination (Gamar and Qaderi 2019). Such interactions could also vary further at genotype level in the same plant species (Gamar and Qaderi 2019). We could not find any studies which assessed the effects of salinity and eCO<sub>2</sub> on seed germination. However, climate change and related sea level rise has been shown to increase salinity in coastal areas (Dasgupta et al. 2015). In this context, an indirect connection could be drawn between higher atmospheric CO<sub>2</sub> (major factor in climate change) and salinity. It already known that salinity can decrease seed germination and, in this case, it could explain the recent reduction in seed germination in coastal areas. As detailed before, any change in seed germination pattern could indicate a relative change in seed biochemistry.

Introduction of drought treatments significantly decreased sucrose (up to 50%) and increased stachyose and raffinose content, in both aCO<sub>2</sub> and eCO<sub>2</sub> (Bellaloui et al. 2017). It is noteworthy that the increase in stachyose and raffinose content in eCO<sub>2</sub> was less than that in aCO<sub>2</sub> (Bellaloui et al. 2017). In nature, higher atmospheric CO<sub>2</sub> is often accompanied by higher atmospheric temperature resulting in heatwaves and subsequent drought events (Roy et al. 2016). Thus, in the future, it would be interesting to see the strength of the three-way interaction of eCO<sub>2</sub>, high temperature and drought in different parts of the world (representing external factors affecting the three-way interaction) and how such interactions affect seed germination. To the best of our knowledge, no studies compared the effects of the three-way interactions or respective main effects of temperature and drought in aCO<sub>2</sub> and eCO<sub>2</sub> on enzyme biosynthesis, organelle activity and RNA and protein biosynthesis during seed germination. In this context, it is assumed that the such changes during seed germination might depend on the interactions of the aforementioned abiotic stresses, plant type and plant species with different CO<sub>2</sub> concentrations and exposure times.

### Effects of CO<sub>2</sub> concentrations at optimal conditions

CO<sub>2</sub> enrichment promotes plant growth by increasing photosynthesis (Ainsworth and Long 2005). Although not exclusive, under optimal conditions, most C3 plants grow better than C4 plants in eCO<sub>2</sub> (Ainsworth and Long 2005, Reich et al. 2018). Higher photosynthetic responses are common in short-term eCO<sub>2</sub> exposures (Finn and Brun 1982, Fauset et al. 2019) however, photosynthetic acclimatisation becomes active in long-term exposures and

stalls the eCO<sub>2</sub>-enhanced growth in both C3 and C4 plants (Griffin et al. 2000, Pastore et al. 2019). Improvements in photosynthesis and plant growth in eCO<sub>2</sub> are always correlated to changes in plant biochemistry and, thus, photosynthesis-related biochemical changes are elaborated here. Rubisco, nonstructural carbohydrates and chlorophyll are the major biochemicals which change in response to eCO<sub>2</sub> exposures. Here, changes in the biochemicals in response to eCO<sub>2</sub> levels are presented in comparison to respective aCO<sub>2</sub> levels.

Rubisco is an abundant enzyme present in plant leaves and plays a major role in photosynthesis (Jensen 2000). It is one of the most studied enzymes and is considered as the rate-limiting factor in photosynthesis (Reid et al. 1998). Rubisco content responds inconsistently to higher CO<sub>2</sub> concentrations depending on plant types (Campbell et al. 1988, Vu et al. 1997, Watling et al. 2000). Even between two C3 plants, the response of Rubisco content to eCO<sub>2</sub> varies. In *Arabidopsis thaliana*, Rubisco content decreased for both C3 (Tissue et al. 1993, Vu et al. 1997) and C4 plants (Moore et al. 1998). It seems that the magnitude of the reduction in Rubisco content is the key factor which either increases photosynthesis and plant growth or leads to photosynthetic acclimatisation in response to eCO<sub>2</sub> exposures under optimal growing conditions. In C3, non-structural carbohydrates increased (Moore et al. 1998, Mizokami et al. 2019), whereas leaf nitrogen and chlorophyll content changed inconsistently (Ainsworth et al. 2002, Li et al. 2008). In C4, leaf nitrogen, chlorophyll content (Vodnik et al. 2005) and non-structural carbohydrates (Kakani et al. 2011) remained unaffected initially. However, in the later stages, leaf nitrogen decreased and non-structural carbohydrate increased (Lecain et al. 2003). These inconsistent biochemical responses suggested complex interplays amongst plant types, plant species and intrinsic photosynthetic biochemical factors (which influence each other), ultimately altering photosynthetic biochemical contents in response to eCO<sub>2</sub> exposures.

### Effects of CO<sub>2</sub> concentration and abiotic stress interactions

Combining the effects of drought, high temperature and salinity with CO<sub>2</sub> treatments is the best way to mimic natural conditions that are expected in future climate scenarios to compare their effects on plant photosynthetic performance. We could not find any studies which deal with the combined effects of the aforementioned stresses and eCO<sub>2</sub> (four-way interactions). Similarly, we could only find two studies which explained a three-way interaction of drought, temperature and CO<sub>2</sub> (Ward et al. 1999, Hamerlynck et al. 2000, Yu et al. 2012). According to Yu et al. (2012) introduction of combined stresses of drought and high temperature decreased photosynthesis in aCO<sub>2</sub>; however, it failed to cause any significant decrease in eCO<sub>2</sub>-enhanced photosynthesis in a C3 plant (Yu et al. 2012). In contrast, it has been reported that a brief period of heat stress was enough to decrease photosynthesis in a C3 plant subjected to drought (Hamerlynck et al. 2000). Although studies done in aCO<sub>2</sub> are available, listing the C4 (maize) photosynthetic responses to combined effects of drought and heat stress (Killi et al. 2017), to the best of our knowledge, no studies detailing responses of C4 plants to eCO<sub>2</sub>, drought and high temperature combinations have been found. Similarly, no studies were found on our search for three-way interactions of combined effects of CO<sub>2</sub> x drought x salinity and CO<sub>2</sub> x high

temperature x salinity on both C3 and C4 plants. Thus, eCO<sub>2</sub>-enhanced photosynthesis and respective biochemical changes in presence of drought in a range of eCO<sub>2</sub> concentrations are explained under the umbrella of the two-way interactions of eCO<sub>2</sub> x drought. Drought has been a major factor contributing to photosynthetic efficiency under eCO<sub>2</sub> in C4 and, in absence of drought, is predicted to keep photosynthesis unchanged in eCO<sub>2</sub> compared to aCO<sub>2</sub> (Leakey et al. 2009). In addition, drought seems to affect C4 photosynthesis more than C3 without showing any apparent effects of eCO<sub>2</sub> on plant photosynthesis (Ward et al. 1999, Vanaja et al. 2011). Drought and eCO<sub>2</sub> combinations decreased chlorophyll content and increased sugar content (Li et al. 2013); and decreased Rubisco (Vu et al. 1987) in C3. Similarly, drought and eCO<sub>2</sub> combinations increased non-structural carbohydrates and decreased Rubisco (Vu and Allen Jr 2009) and did not affect chlorophyll content in C4 (Zhang et al. 2021). Overall, abiotic stresses inconsistently affected photosynthesis biochemistry in aCO<sub>2</sub> and eCO<sub>2</sub> treatments depending on the plant type and species. In this context, future studies, mimicking natural conditions, are recommended to obtain a better insight into the plant responses.

### **Root/soil interface**

The drastic increase of abiotic stress factors, induced to nature either naturally or by anthropogenic causes, are limiting the plants from achieving their full genetic growth potential (Tuteja and Sopory 2008). In nature, a variety of distinct abiotic stress factors are known to occur either singly or in combinations, causing harmful effects on plant growth and development. Hence, it is necessary to redefine the agricultural practices and ecology studies with knowledge about the significance of mitigating such harmful effects to increase plant productivity (Govindasamy et al. 2018). The chemical, physical and biological properties of soil very close to the roots (rhizosphere) is different from that of soil in different locations. The soil, very close to or that adhering to the root surface, is particularly defined as root soil interface. This rhizosphere distance may vary in the range of 1-10 mm depending on different factors (Young 1998). It is a very small volume of soil which is capable of impacting and being impacted on by plant roots and is said to be the most active region in terrestrial ecosystems (Gregory 2006). Different types of organisms, which either beneficial or detrimental to plants, are colonised in the rhizosphere. Amongst these, the category of plant-growth-promoting rhizobacteria (PGPR) can contribute to the beneficial effects of plants, such as increased growth and alleviation of biotic stresses, like susceptibility to diseases caused by plant pathogens (Kloepper et al. 2004). Many studies are being conducted to study the effects of rhizosphere organisms in eliciting physical and chemical changes in plants as part of a defensive mechanism against different biotic stresses and these mechanisms are together called the Induced Systemic Resistance (ISR) (Van Loon et al. 1998). However, the study of rhizosphere response to abiotic stress came later and the term Induced Systemic Tolerance (IST) has been proposed which represents the changes in plants which can result in enhanced tolerance to different types of abiotic stress (Yang et al. 2009). The microbial communities in the root soil interface undergo dynamic interactions within themselves and with plant roots to improve plant tolerance to environmental changes (Govindasamy et al. 2018). Endophytic interaction is one amongst this where diverse groups of microbial communities colonie at inter- and

intracellular spaces of plants. The IST can explain different mechanisms employed by the endophytic organisms to impart tolerance against abiotic stresses in plants (Govindasamy et al. 2018). Nadeem et al. (2007) identified a unique approach of biopriming which was found to be enhancing the seed germination efficiency against different types of abiotic stresses and, at the same time, causing little interference with the biological equilibrium of soil compared to chemical additions. Bacteria in association with plants are provided with some special characteristics to nullify the effects of abiotic stress. Hence, seed biopriming with such bacterial colonies is the best tool to manage the stress conditions (Prasad et al. 2016). This positive effects of PGPR are described by various mechanisms. The ethylene production inside the plant will increase during abiotic stress and this is detrimental to overall development of plants (Jackson 1997). 1-aminocyclopropane-1-carboxylate (ACC) deaminase is found in bacteria which helps to dissociate ACC, the precursor of ethylene (Kohler et al. 2008). PGPR are also found to be involved in the synthesis of exopolysaccharides and helps to aggregate and maintain soil structure even during stress conditions (Konnova et al. 2001). Further, these microorganisms also help to improve the uptake of nutrients which are unavailable due to fixation (Munns and Tester 2008). PGPR were also involved in the production of phytohormones (Ansari et al. 2017). Studies are being conducted to identify and characterise the beneficial strains of microorganisms to alleviate abiotic stresses (Ribeiro and Cardoso 2012). Two strains of bacteria *Azotobacter* were found efficient for their multiple plant growth-promoting functions like N<sub>2</sub>-fixing, synthesis of growth-promoting hormones in plants and antimicrobial activity against plant pathogens in tomato plants. These two strains of *Azotobacter chroococcum* exhibited high tolerance against drought and salt stresses (Viscardi et al. 2016).

## Drought stress

Drought stress is one of the most detrimental factors which affects germination and growth of plants. Hence, understanding of plant responses and growth under limited water availability is of paramount importance in plant science. Even though the exact mechanisms of plant drought stress tolerance enhancement by root soil interface remain unclear, possible explanations are being put forth by scientists during different times (Dimkpa et al. 2009). These include production of plant growth hormones, production of essential enzymes, 1-aminocyclopropane-1-carboxylate (ACC) deaminase and that of bacterial biofilm which is an extracellular matrix (Dimkpa et al. 2009). Biofilm is an extracellular layer of sugars and polysaccharides which helps in improving water availability in root medium. Timmusk et al. (2014) suggested a practicable strategy of alleviating drought stress by application of rhizospheric bacteria co-evolved with plant roots in high stress environments over centuries and which has traits that can improve plant fitness. The bacterial priming of wheat seeds had resulted in 78% greater plant biomass and five-fold higher survival under drought conditions (Timmusk et al. 2014). Arbuscular mycorrhizal fungi (AMF) are a type of beneficial microorganism, which are able to colonise roots of ~ 80% terrestrial plants and establish a symbiotic association. Such association helps the host plant to obtain nutrients and water from the soil and, as a reward, the AMF take up to about 20% of photosynthetic products from the plant (Parniske 2008). Many studies have been performed to evaluate the efficacy of AMF in different types of land

plants (Wu et al. 2012). The AMF inoculated plants have shown higher water stress tolerance in citrus (Wu et al. 2013). The activity of AMF in root soil interface is elicited by different mechanisms. AMF can infect the plant root surface at certain points and the external hyphae are extended from the points into the soil and establish a link called the mycorrhizal network (Simard et al. 2012). These hyphae have the main function of uptake and translocation of nutrients and water from soils into the plant roots (Peterson et al. 2004). AMF can also accelerate the uptake of mineral nutrients, especially those having lower mobility in soil like P, Zn and Cu (Smith and Smith 2011). AMF in the plant rhizosphere was also found to be adjusting the Root System Architecture (RSA) which is the spatial arrangement of a root system in the soil, hence the plant can withstand drought stresses (de Dorlodot et al. 2007). However, the RSA changes are highly dependent on the species of fungus and the water-nutrient availability (Matsubara et al. 2006). Another beneficial impact of AMF is Osmotic Adjustment (OA) by the reduction of the osmotic potential as a response to drought stress. Accumulating different solutes (organic and inorganic acting as osmoprotectants) facilitate water uptake and stabilise the plant during drought stress (Gomes et al. 2010).

### **Salinity stress**

In the current global scenario of increased population growth and need for more production of food to meet the hunger of the world, agricultural lands are exploited significantly. As a consequence, increase in the salinity has become a most important abiotic factor limiting the plant growth and yield. More than 50% of cultivated land is predicted to be altered by salinity by the mid-21st century (Panta et al. 2014). Salt stress is not only limited to stunting plant growth alone, but it also has severe impacts on plant physiology modifications (Panta et al. 2014). Thus, an extensive study is required to identify the response of plants against salt stress. Inoculation with AM fungi will increase shoot growth of plants in non-saline soils (Copeman et al. 1996), whereas, in highly salty soils, the AMF in the rhizosphere suppress the growth of root and plant development. This might be because of the suppression of spores and subsequent limiting of root growth (Juniper and Abbott 2006). Many plant species have reduced root length under saline conditions (Li et al. 2016). In a study conducted in maize to find the changes in hydraulic properties under water and salinity stress, it was found that both stresses reduced the permeability of the rhizosphere aggregates and the reduction in salinity stress was more significant than the other (Wang et al. 2020). However, many studies have demonstrated that symbiotic associations between the root and the microbes inhabiting the rhizosphere have positive effects on nutrients uptake, maintaining osmotic balance and enhancing the enzymes activity (He et al. 2007) which eventually alleviate the salinity stress. The competent strains of PGPR have the effect on producing ACC deaminase and, thus, mitigate the salt stress in maize plant by modulating ethylene metabolism (Misra and Chauhan 2020). In another study on maize itself, it was demonstrated that the improvements in root activity and the coarse root system of plants induced with mycorrhiza had higher salt stress tolerance (Sheng et al. 2009). Increase in root/shoot ratio was observed in some woody seedlings grown under salt stress (Fernández-García et al. 2014). However, not many studies on the influence of salt stress at the rhizosphere of woody species have been conducted. In an experiment on

such a species, *Robinia pseudoacacia* showed that seedling biomass decreases according to the reduction of root, stem and leaf biomass with the increase of salinity stress. This was found to be an adaptation of the plant to adjust the water status in the biomass with decreasing uptake by roots (Mao et al. 2016). Guo et al. (2018) found a detrimental effect of rhizosphere at salt stress which showed that the increased metabolic activity of rhizosphere organisms can mobilise heavy metals like cadmium and, subsequently, it can accumulate in the plant tissues. Plant roots and rhizosphere microbes will release exudates that can alter the mobility of soil heavy metals as a result of acidification (Li et al. 2016).

## Impact of elevated CO<sub>2</sub>

A drastic increase in atmospheric CO<sub>2</sub> concentration is a noteworthy issue in the global environmental scenario (Keeling et al. 1989). Studies are being conducted to find the effect of increasing CO<sub>2</sub> to the plant productivity. In almost all studies, it is reported that plant growth is stimulated by CO<sub>2</sub> elevation because of the increased photosynthetic rate, accumulation of more plant biomass and subsequent enhancement in the economic yield of the crop. The increased use of CO<sub>2</sub> in greenhouse cultivation over a long period of years signifies the importance of CO<sub>2</sub> in plant production. Plant responses to CO<sub>2</sub> are the combination of other environmental factors, like light, temperature and water. Other abiotic stresses have been shown to be ameliorated when CO<sub>2</sub> levels are elevated. In some short-term plants, the growing season is found to be reduced with the application of more CO<sub>2</sub> and economic yield for most crops increases by about 33% for a doubling of ambient CO<sub>2</sub> concentration (Rogers et al. 1994). However, there are also some exceptions of the negative effects of this. The subsequent allocation and ultimate fate of this increased photosynthetically-fixed carbon are important determinants of global carbon dynamics (Canadell et al. 1995).

In a study conducted on soybean to find the effect of elevated CO<sub>2</sub>, it was found that the rhizosphere microbial composition has changed and N fixing microbes has increased in the community as a result of this. This is due to the increased demand of N (Wang et al. 2020). Increased CO<sub>2</sub> imparts weak effects on biomass and enzyme activity of plants, but has a significant effect on carbon and nitrogen in the soil microbial biomass. The elevated CO<sub>2</sub> also can nullify the negative effect of drought on the microbial biomass (Xue et al. 2017). Elevated levels of CO<sub>2</sub> cause increase in microbial biomass and the fungal community is more susceptible to change in CO<sub>2</sub> than that of bacterial biomass. It is also evident to note that the gene composition of microbes changes in elevated CO<sub>2</sub> as C, N, P, S and methane recycling genes have increased in the rhizosphere of elevated CO<sub>2</sub> (Wang et al. 2017). Similarly, the composition and richness of species of rhizosphere AMF community can also be changed according to the difference in CO<sub>2</sub> (Asha et al. 2017).

## Summary

The levels of greenhouse gases have substantially increased over the last couple of decades. This increase has altered to balance the atmosphere and its components. An

increase in greenhouse gases, mainly CO<sub>2</sub>, results in global warming and many consequences are witnessed from increased temperature. While some natural events contribute to climate change, human activities are the largest contributor of this continuous change. In plants particularly, various impacts are being documented on the impact of increased heat on both plant growth and seed germination. These impacts vary depending on plant species and heat exposure periods. Similarly, exposure to elevated levels of CO<sub>2</sub> have been shown to improve the growth of particular plants while retarding it in other species. In some cases, the combined effect of elevated heat and CO<sub>2</sub> offsets the negative impacts of high heat on seed germination and plant development.

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