



Review Article

Roles of Fungal Endophytes and Viruses in Mediating Drought Stress Tolerance in Plants

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Abstract

Various biotic and abiotic stresses can hamper crop productivity and thus pose threats to global food security. Sustainable agricultural production demands for the use of safer and eco-friendly tools and inputs in farm production. In addition to plant growth-promoting bacteria and mycorrhizal fungi, endophytic fungi can also help plant mitigate or reduce the effect of stresses. Another less well-known is the use of viruses that provide benefit to plants facing growth challenges due to stress. Studies suggest that fungal endophyte and virus could be important candidate and economically and ecologically sustainable means for protecting plants from stress condition. To exploit their benefits, a thorough understanding of the interaction of host-beneficial microbes obtained by scientifically sound experiments with robust statistical analysis is crucial. Another important aspect is to gather available information in a consolidated form that may provide the framework for future investigation, which is currently lacking. In this review, at first, we presented the impacts of drought in crop production worldwide. Then, we attempted to present briefly the various physiological, biochemical and molecular strategies that plant uses to cope with drought stresses. Major part of this review has been reserved to discuss the recent literatures regarding the roles of fungal endophyte and beneficial viruses in mitigating the impact of drought on plants in order to gain more insight into the microbe mediated plant abiotic stress tolerance. In addition, we summarised the mechanism of fungus and virus mediated drought tolerance in plants. At the end, we discussed about the research gap and highlighted points which need prime emphasis in harnessing the beneficial effects of microbes in sustainable agriculture. This review would be helpful for the researcher who work on this field to develop future research plans to better understand the nature plant-microbe interactions and application of beneficial microorganisms in eco-friendly crop cultivation. © 2020 Friends Science Publishers

Keywords: Beneficial virus; Fungal endophyte; Plant growth; Plant-microbe interaction; Water stress

Introduction

Water unavailability, which prevails due to drought, salinity or freezing, is a major limitation for plant growth and development (Lesk *et al.* 2016). The coming decades are likely to experience more frequent episodes of severe drought due to the worsening global climate with potentially devastating impact on agriculture (IPCC 2014). This will pose further challenges to feed a growing world population. Given its threat to agriculture, plant physiology under drought stress has been extensively studied. This has significantly improved our understanding of the responses of plant to water limitation. Plants employ a complex of interconnected physiological, physical and molecular mechanisms to respond to drought stress (Chaves *et al.*

2003; Farooq *et al.* 2009; Kaur and Asthir 2017; Kumar *et al.* 2018; Deepak *et al.* 2019; Jangra *et al.* 2019). Plant stress research also takes into account an important part of plant biology—the plant-microbe interaction, but its impact in modulating plant tolerance to stress.

Our correct understanding is that plants are not independent entities with respect to their ecological and physiological function. In nature, plants afford a unique ecological niche for plethora of microorganisms for example, archaea, bacteria, fungi, virus, protozoa *etc.* A diverse kind of relationship exists between plant and these microbes including but not limited to mutualism and antagonism. The most well documented example is the mycorrhizae-plant mutualism, where both entities are helped by each other. In nature, plants also harbour

endophytic fungi and viruses. These can be mutualists, or pathogens of the host plant depending on the host, microbe and ecological factors. Available studies suggest that fungal endophytes are present in all terrestrial plants. It is reported that, endophytes provide nutritional benefit to plants as well as confer many other benefits such as protection from biotic and abiotic stresses (see recent reviews by Rodriguez *et al.* 2009; Busby *et al.* 2016; Lugtenberg *et al.* 2016; Dastogeer and Wylie 2017; Aamir *et al.* 2020; Kaur 2020).

Plants also harbour an uncountable number of viruses that are rarely common in many other host types. Depending on the type of virus, host and environment, the interaction between virus and plant could range from mutualistic to pathogenic (Roossinck 2011). Since the discovery of the first virus in 1898 (Beijerinck 1898), most of the plant viruses documented to date are isolated and studied as pathogens that incite diseases in crop plants (Zaitlin and Palukaitis 2000). However, in the natural environment, viruses are present in good number in many symptomatic or asymptomatic plants, but not all viruses cause disease, and some virus are beneficial (Roossinck 2010). The world of beneficial viruses is unknown in most cases, but they have been reported from a wide range of hosts including plants, bacteria, fungi and other eukaryotic microbes, insects and humans and other animals. Beneficial effects of some plant viruses are evident, and they exhibit context dependent mutualism and confer fitness benefit to host under abiotic stress. For example, improved drought stress tolerance was recorded in some cultivated and wild crops like beet, tomato, rice, watermelon and nicotiana when treated with virus (Xu *et al.* 2008; Dastogeer *et al.* 2018). The underlying mechanism for this noteworthy observation is unknown it was found that virus infection increased the water content, water retention and the level salicylic acid and some osmoprotectants and antioxidants making the plant more tolerant to water-limiting condition (Xu *et al.* 2008). When the roles of microbial symbionts of plants are studied, most research has concentrated either on direct, pair-wise interactions of the plant and an endophyte or three-way interactions including insects. However, a very interesting linkage of a different kind subsists among plant, endophytes and viruses. In one case, it has been found that a virus in a *Curvularia* fungus remains as an obligate symbiont to form a tripartite interaction that helps plants to grow in soils with higher temperature in Yellowstone National Park (Márquez *et al.* 2007).

In nature, plants are subjected to a mixture of biotic and environmental stresses at the same time, therefore it is plausible that the stress signalling mechanisms could share some common pathways and their consequences may overlap considerably in favour of plants to survive under complex ecological settings. Reports suggest that plants ability to respond to water limitation could be improved by symbiotic fungal endophytes (Hubbard *et al.* 2014; Ghaffari *et al.* 2019; Sadeghi *et al.* 2020) and viruses (Xu *et al.* 2008), individually or in group. In this review, we aimed to

discuss the recent literature available on endophyte and virus-mediated drought tolerance in plants. We anticipate this will be helpful for the researcher working in this field to design and plan their research for further advancement in understanding plant-microbe interaction and plant stress tolerance.

Impact of drought on crop production worldwide

Crop plants are exposed to several abiotic stresses such as water limitation, unfavourable temperature, high salinity or chemotoxicity all of which cause huge losses in crop production worldwide (Zipper *et al.* 2016; Leng and Hall 2019). Among them drought is considered to be the most devastating which decreases crop productivity more than any other stress factor (Lambers *et al.* 2008; Schlenker and Lobell 2010; Mazdiyasi and AghaKouchak 2015; Leng and Hall 2019). The agriculture sector is highly vulnerable to drought, as it depends directly on water availability (Liu and Hwang 2015; Meng *et al.* 2016; Parker *et al.* 2019). An agricultural drought is characterised by a period with dry soils due to lack of precipitation, intense but less frequent rain events, gaps between factual and projected evapotranspiration, water deficits in soil, decreased groundwater or reservoir level all of which lead to reduced plant growth and crop production (Mannocchi *et al.* 2004; Dalezios *et al.* 2017). Despite our better ability to forecast the onset of drought and to modify its impact drought is still the single most crucial threat disrupting world crop production. The magnitude of drought induced damage is unpredictable as it is modulated by various factors such as, the pattern of rainfall, water holding capacity of the soil, and water losses through evapotranspiration, water demand and supply, type and resilience of crop, management practices in the farm among others (Demirevska *et al.* 2009; Farooq *et al.* 2014).

Severe droughts have caused substantial decline in crop yields through negative impacts on plant growth, physiology, and reproduction. A meta-analysis of the data from 1980 to 2015 reported a global reduction of yield up to 21 and 40% in wheat and maize crop, respectively due to drought (Daryanto *et al.* 2016). By using deterministic approaches previous studies analysed the impact of drought on crop production in Australia (Madadgar *et al.* 2017), China (Yu *et al.* 2014), Czech (Hlavinka *et al.* 2009), Moldova (Potopová *et al.* 2016), South Africa (Araujo *et al.* 2016), United States (Troy *et al.* 2015; Zipper *et al.* 2016), and worldwide (Lesk *et al.* 2016; Matiu *et al.* 2017). A global yield loss analysis due to drought in the year 1983 to 2009 showed that the averages of drought-induced yield losses per drought event was 8% for wheat, 7% for maize and soy, and 3% for rice; which correspond to 0.29, 0.24, 0.15, and 0.13 t ha⁻¹, respectively (Kim *et al.* 2019). The global loss of cereal has been reported to 4.9–5.2% for the period of 1964–2007 using the superposed epoch analysis (Lesk *et al.* 2016). Under drought conditions wheat crop is the most vulnerable crop in

USA and Canada, maize in India and rice is most affected in Vietnam and Thailand (Leng and Hall 2019).

The devastating losses of crop production due to droughts are generally witnessed in developing countries, and the most vulnerable regions to drought are situated in Sub-Saharan Africa and some parts of Asia. African countries face drought every year in some places or other. It was estimated that losses due to drought in 2014–2017 was on average USD \$372 billion (Ngumbi 2019) in the African continent. In South Africa, an El Niño drought which began in 2018 and continued to 2020 has been expected to cause a huge loss in crop yield by 20% of the major crops such as wheat, apple, grape and pear (Roelf 2018). A minimum of 23 million hectares in Asia (20% of the total rice area) are prone droughts of varying degrees which is one of the most critical factors causing reduced and unstable farm production (Pandey and Bhandari 2009). Pakistan experienced droughts recurrently every four in 10 years (Anjum *et al.* 2012). The drought in 1998–2002 resulted loss of rain-fed crop yields by 60–80%, irrigated crop yields by 15–20% (FAO/WFP 2002; Sarwar 2008). There have been La Nina events during the years 2000–2010 which resulted in extreme heat and low rainfall in Pakistan. It has been predicted that temperatures will increase on average by 2–3°C by 2045–65, especially in parts of South Asia including Pakistan (IPCC 2014). In Bangladesh annually about 2.7 million hectares of crop land affected by droughts (Tanner *et al.* 2007) and nearly 83% of the Kharif and Rabi crop lands are exposed to different magnitudes of droughts as shown by Climate Change Cell of Bangladesh which has been reported by Alamgir *et al.* (2019). China experienced the worst drought in 2010–2011 that impacted eight provinces in the northern part of the country. Around 20% of the farmland and 35% of the entire wheat crop were damaged due to that drought in the affected china provinces (Krishnan 2011). Maize and soybean are most affected by drought in China a yield reduction of 6.4 and 9.2% respectively (Liu and Shi 2019).

As a result of availability or resources to lessen the effect and adopting the measures, the impact of drought has a propensity to be less extreme on crop production in developed nations. However, crop damages could be high enough despite all kinds of intervention. A recent case in the USA in 2012 when a severe drought affected 80% of cropped land and decreased yields of corn by 27.5% and of soybean by 10% with massive financial losses (USDA 2013). The 2010 droughts in Russia caused reduction in wheat harvest by 32.7% severely diminishing the worldwide wheat supply (Sternberg 2011). The Mediterranean region is also vulnerable to climate change and drought cause affects crop production in these regions (IPCC 2014; EEA 2016). For example, Spain has faced episodes of drought in the recent times, which are in the most severe form in Europe causing an estimated agricultural loss of EUR 3600 million (González-Hidalgo *et al.* 2018; Peña-Gallardo *et al.* 2019).

It is projected that climate change in the coming decades will alter average temperature and rainfall values and will increase the unpredictability of precipitation events which may lead to even more severe and frequent droughts with a raise from 1 to 30% in extreme drought prone regions by 2100 (IPCC 2014; Webber *et al.* 2018; Tibebe *et al.* 2019; Lee *et al.* 2019; Spinoni *et al.* 2020).

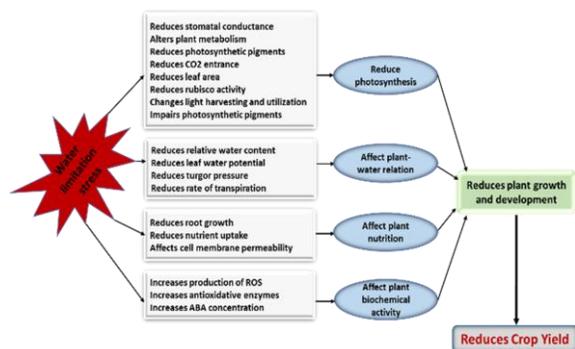
Effects of water stress and plant response mechanisms

Water limitation at any stage of the growth of crops can be detrimental. But the extent of adverse effects is dependent on the magnitude of stress and crop growth stage as well as other environmental factors. Numerous studies have been performed to discern the impacts of water stress on plants and several reviews are available (Farooq *et al.* 2009; Silva *et al.* 2013; Fathi and Tari 2016; Dastogeer and Wylie 2017; Hussain *et al.* 2018) that well explained these effects how plant responds to stress at the morphological, genetical, biochemical, and molecular levels (Fig. 1). Plants need a vast quantity of water and nutrient for their survival and development. Plant draws water and most nutrient from the soil, so a reduction in soil moisture exerts detrimental effects on plant healthy growth. Scarcity in soil water leads to changes in the physical condition, which in turn negatively impact plant physiological and biochemical processes (Silva *et al.* 2009; Deepak *et al.* 2019). Lack of water also reduces nutrient uptake even in the soil with enough nutrient, due the decreased mobility and absorbance of individual nutrients. It causes reduced mineral diffusion from the soil matrix to the roots.

Morphologically, some plants are more sensitive to drought than others. The seed germination and seedling vigour of some plants are affected more severely under scarce water condition. For example, in a laboratory experiment *Glycine max* has been shown to be less affected by simulated drought as compared to *Macrotyloma uniflorum* and *Vigna mungo* (Pantola *et al.* 2017). Also, subsequent development of plants is significantly affected by drought. Limited water may cause a decrease in plant height, leaf size, and root and shoot biomass of plants (Farooq *et al.* 2009; Zheng *et al.* 2016). Water stress also has negative impacts on crop yield (Table 1) and yield parameters which were reported for many plants such as cotton, maize, peanut, sugarcane, sunflower and wheat (Pettigrew 2004; Vasantha *et al.* 2005; Barnabás *et al.* 2008; Furlan *et al.* 2012). The reductions in plant growth and yield are associated with drought-induced alterations at the physiological, metabolic and molecular levels. For example, water scarcity causes a reduction in the photosynthesis and alters gaseous exchange plants. The effects on photosynthesis are associated with reduced leaf area and reduced photosynthesis rate in unit leaf area (Wahid *et al.* 2005). Other possible mechanisms could be the direct effect on plant metabolic activities or by restricting the CO₂ access through the leaf (Apel and Hirt 2004), discrepancy in light

Table 1: Percent yield losses in some important crops caused by drought stress.

| Crop name | Yield losses (%) | References |
|-------------|------------------|--|
| Rice | 53–92 | Lafitte <i>et al.</i> (2007) |
| Wheat | 57 | Balla <i>et al.</i> (2011) |
| Maize | 63–87 | Kamara <i>et al.</i> (2003) |
| Chickpea | 45–69 | Nayyar <i>et al.</i> (2006) |
| Soybean | 46–71 | Samarah <i>et al.</i> (2006) |
| Sunflower | 60 | Mazahery-Laghab <i>et al.</i> (2003) |
| Lentil | 24–70 | Shrestha <i>et al.</i> (2006); Allahmoradi <i>et al.</i> (2013) |
| Faba bean | 68 | Ghassemi-Golezani and Hosseinzadeh-Mahootchy 2009 |
| Mung bean | 26–57 | Ranawake <i>et al.</i> (2011); Ahmad <i>et al.</i> (2015) |
| Common bean | 40–60 | Martínez <i>et al.</i> (2007); Rosales-Serna <i>et al.</i> (2004); Ghanbari <i>et al.</i> (2013) |

**Fig. 1:** Schematic diagram showing how drought causes negative impacts on plant growth and yield

harvesting and utilization (Foyer and Noctor 2000), reduced Rubisco activity (Bota *et al.* 2004), changes of pigments of photosynthesis (Anjum *et al.* 2003) and impairment of photosynthetic apparatus (Fu and Huang 2001).

Water unavailability at the vicinity of plant roots causes significant reduction in relative water content and water potential of the leaf, turgor pressure, as well as the rate of transpiration (Nayyar and Gupta 2006; Campos *et al.* 2011) which have negative impacts on plant-water relation. Plants grown under low soil moisture showed reduced growth of roots and lower amount of nutrient uptake (Subramanian *et al.* 2006; Asrar and Elhindi 2011; Suriyagoda *et al.* 2014). Plants have decreased absorption of some cations (K^+ , Ca^{2+} , and Mg^{2+}) due to the disparity in active transport and permeability of cell membrane under stress (Hu and Schmidhalter 2005; Farooq *et al.* 2009). Also, water stress inhibits some enzymes activities and thus affects plant nutrient assimilation (Ashraf and Iram 2005). Higher accumulation of reactive oxygen species (ROS) in plant under stress is common and is associated with insufficient CO_2 fixation and increased photorespiration (Carvalho 2008; Gill and Tuteja 2010).

Several studies identified several genes that are associated with plant response to water deficit stress. For example, Benny *et al.* (2019) used RNA-seq analysis of different plant species subjected to drought and identified 27 genes that were differentially expressed due to stress. The down-regulated genes were related to cell wall and membrane structure formation and fatty acid biosynthesis

whereas the up-regulated were related to osmotic stress, abscisic-activated signalling pathway and hydrogen peroxide treatment stress. The important transcription factor (TF) families such as MYB, WRKY, bZIPs are involved in plant stress responses (Qin *et al.* 2011). Drought-induced modulation of ABA level modulates expression certain genes including dehydrin genes and glycine-rich protein gene. The expression of the gene miR398 was upregulated in drought stressed peanut while certain other genes downregulated significantly. Several other genes or transcription factors (TFs) have also been reported including but not limited to AP2/ERF, bZIP, HD-ZIP, bHLH, MYB, NF-Y, EAR, NAC, and ZPT2 were differentially expressed under water stress (Bhargava and Sawant 2013). Over the past decades, various works have been carried out to reveal the mechanism of plant responses under drought at the physiological, biochemical, molecular and genomics levels. Plant behaviour under stress is complicated since it depends on space and time, the integration of stress effects and responses at all underlying levels of organization. All these mechanisms could be grouped under, morphological: drought escaping (changing life cycle), or avoidance (alterations in nutrient and water uptake) or, abandonment (removing parts of plant *e.g.* leaf); or physiological: drought tolerance (maintain better osmotic balance and preserve tissue turgidity or resistance (metabolic changes) (Chaves *et al.* 2003; Nadeem *et al.* 2019).

Fungal endophyte and plant abiotic stress tolerance

Endophytes are the organisms that inhabit in the plant without apparently causing any damage to the host at any time in their life cycle (Schulz and Boyle 2005). The presence of fungal endophytes traced in the fossil records proposes that fungal endophyte may have evolved during the terrestrialization of land plants (Rodriguez and Redman 1997; Krings *et al.* 2012). The endophytic fungi have been isolated from various types of plants including conifers, grasses, marine algae, lichens, mosses, ferns and pteridophytes (Li *et al.* 2007; Melo *et al.* 2014; Eo and Park 2019; Gao *et al.* 2019). Majority of the fungal endophytes form mutualism with hosts. Some of them can be pathogenic to plant based on the growth stage and defence of the plant and environmental factors (Schulz and Boyle 2005).

Certain fungal endophytes provide nutritional benefits to plants. Many others provide significant adaptation and fitness benefits to plants (Rodriguez *et al.* 2009; Dastogeer *et al.* 2018; Aamir *et al.* 2020). Researches have shown endophytic fungi in both below ground and above ground plant tissues can shield their host plant from drought stress (Sherameti *et al.* 2008; Sun *et al.* 2010; Hubbard *et al.* 2014; Husaini *et al.* 2012; Sadeghi *et al.* 2020). For Example, *Neotyphodium coenophialum* enhance the drought tolerance in tall fescue (*Lolium arundinaceum*) and perennial ryegrass and perhaps it is the most widely documented feature of endophyte mediated abiotic-stress tolerance plants (Bouton *et al.* 1993; Malinowski *et al.* 1997b). In one of our study we experimentally shown that several non-grass endophytes isolated from wild *Nicotiana* plants when re-inoculated increased the drought tolerance of *N. benthamiana* both *in vitro* and glasshouse condition (Dastogeer *et al.* 2017b). Subsequently, we have found these endophytes mediated plant drought tolerance is associated with changes in stress-related metabolites, changes in antioxidants, osmolytes and altered expression in stress-related genes (Dastogeer *et al.* 2017a; Dastogeer *et al.* 2018). Kane (2011) reported that *Neotyphodium lolii* can provide drought stress tolerance to native perennial ryegrass collections formerly obtained from Mediterranean regions. In one study, a consortium of fungal endophytes was assessed for their effect on the growth, eco-physiological and reproductive success of wheat under heat and drought stress. The findings indicated that the endophytes improved the ability of wheat plant to tolerate drought and heat. Interestingly, seeds produced from drought-stressed wheat infected by the endophyte in the following generation had decreased water use efficiency compared to those produced by drought-affected plants with no endophyte infection. However, regarding vigour endophyte-free stressed parents' germinated seeds more rapidly than those produced by endophyte colonised plants (Hubbard *et al.* 2014). In an effort to explain the mechanism endophyte mediated drought tolerance in plants, scientists have documented several observations. Similar to mycorrhizal fungi, non-mycorrhizal fungal endophytes employ various strategies including modulating, changing or modifying plant physiology, biochemicals and metabolites (see review by Dastogeer and Wylie 2017). Table 2 lists some of the available literature that presents fungal endophyte mediated plant stress tolerance. Endophyte-mediated plant responses to drought may be associated with (a) increase or decrease in plant growth (b) enhanced photosynthesis (c) osmotic balance, (d) increased gaseous exchange and water-use efficiency and (e) enhanced antioxidant activities (f) altered expression of drought related genes. For example, a number of fungal endophytic have been reported to produce biomolecules and metabolic substances (Rasmussen *et al.* 2008; Nagabhyru *et al.* 2013) that help the plant stand in the water limiting environment. Some physiological alterations such altered water potential, increased osmotic balance and augmented growth and

development in tall fescue as a result of *N. coenophialum* infection have also been observed (Elmi and West 1995).

However, it is important to note that that endophyte colonization in plant does not always benefit plant in abiotic stress condition rather their association could be detrimental for plants in some cases (Cheplick 2004). In a review, Cheplick (2007) outlined the effect of endophytes on stress tolerance and mentioned some studies that found a neutral role of endophytes on host drought tolerance. For instance, inoculation of fine fescue with *Neotyphodium* originally isolated from dissimilar host gave variable results in that some genotype decreased biomass, other were neutral while some showed positive influence (Zaurov *et al.* 2001). Also, some strains improved plant aluminium tolerance; others were showed no or negative tolerance compared to endophyte-free counterpart indicating genotype specificity of interactions. By a meta-analysis, Dastogeer (2018) showed fungal endophytes influenced on plant performance in a context dependent manner. The degree of endophytic effects is higher in plants grown in drought than those in normal watering condition. The fate of interactions is dependent on the identity of the plant host and fungal symbionts.

Plant virus and abiotic stress tolerance in plant

Viruses are considered to be the most abundant biological beings on the planet (Suttle 2007). Every living being can be infected by at least one and normally several viruses and most organisms are infected by a diverse and unknown group of viruses. Plants afford enormous number of viruses that are not very common in many other host kingdoms. These viruses use host machinery and resources for their replication and transmission, so it is embedded in our belief that virus infections must always be harmful to their host (Xu *et al.* 2008). Indeed, most of plant viruses documented to date are identified and studied as pathogens that incite diseases in crop plants (Zaitlin and Palukaitis 2000). The first virus identified was tobacco mosaic virus (Beijerinck 1898) and there are over 1000 classified plant viral pathogens (Gergerich and Dolja 2006). Viruses are rarely considered outside of their role as pathogens. In the natural non-agricultural environment, RNA viruses are present in good number in many of the studied symptomatic or asymptomatic plants, but their ecological roles have not been known to the most part (Xu *et al.* 2008). Depending on the nature of virus, host and the environment the interaction between virus and plant could range from mutualistic to pathogenic (Roossinck 2011).

The world of beneficial viruses is unknown in most cases, but they have been found in a wide range of hosts including plants, bacteria, fungi and other eukaryotic microbes, insects and humans and other animals. Beneficial effects of some plant viruses are evident, and they exhibit conditional mutualism and confer abiotic stress tolerance to plants. When *Nicotiana benthamiana* plants were infected with viruses with varying host range such as, cucumber mosaic

Table 2: Endophyte mediated plant drought stress tolerance.

| Endophyte | Plant | Reference | Major effects/Mechanism(s) in brief |
|--|--|---|---|
| <i>Acremonium strictum</i> | <i>Atractylodes lancea</i> | Yang et al. (2014) | Decrease tiller number and length, decrease total fresh weight, shoot and root fresh weight and increase root/shoot ratio, decrease SOD and POD, increase malondialdehyde (MDA) and CAT accumulation, increase proline, soluble sugar and soluble protein under mild stress. Reduce levels of stress damage markers, stress-adaptation metabolites. |
| <i>Acremonium sclerotigenum</i> , <i>Triticum aestivum</i> (Wheat) | | Llorens et al. (2019) | |
| <i>S. implicatum</i> | | | |
| <i>Acrocalymma vagum</i> , <i>Glycyrrhiza uralensis</i> | | He et al. (2019) | Increase AMF fungi, soil organic matter, available phosphorus (P), leaf number, soluble protein, SOD activity, total root length, root branch, and glycyrrhizic acid content. |
| <i>Paraboeremia putaminum</i> , <i>Fusarium acuminatum</i> | | | |
| <i>Acrocalymma vagum</i> | <i>Ormosia hosiei</i> | Liu and Wei (2019) | Increase fresh root weight, root volume, root surface area, root fork, and root tip number. Inoculated seedlings changed from herringbone branching to dichotomous branching. Mitochondria and other organelles in root cells of inoculated seedlings remained largely undamaged under water stress. ABA and IAA content and IAA/ABA ratio of inoculated seedlings were significantly higher, whereas the content of GA, GA/ABA, zeatin riboside (ZR)/ABA, and ZR/IAA in inoculated seedlings were lower. |
| <i>Alternaria</i> spp. | <i>Astragalus</i> spp. <i>Oxytropis</i> spp. | Klypina et al. (2017) | Endophyte did not influence photosynthetic gas exchange and leaf pigment concentrations. |
| <i>Alternaria alternata</i> | <i>Triticum aestivum</i> (Wheat) | Qiang et al. (2019) | Endophyte secretes indole acetic acid (IAA) by both the tryptophan-dependent and independent manner. Endophyte alter antioxidant enzyme activities, level of soluble sugars and proline, increase photosynthesis, C and N accumulation, plant dry biomass. Higher antioxidant capacity both in vivo and in vitro. (Z)-N-(4-hydroxystyryl) formamide (NFA), an analogue of coumarin was responsible for antioxidant activity. |
| <i>Aspergillus fumigatus</i> | <i>Oryza sativa</i> | Qin et al. (2019) | Increase tiller number, leaf number, and the root: shoot ratio and photosynthetic pigment and decrease shoot height and leaf area. Increase |
| <i>Balansia hemmingsiana</i> | <i>Panicum rigidulum</i> | Ren and Clay (2009) | Increase leaf relative water content and stomatal conductance, stimulated root growth. A strain increase germination percentage. Early flowering. |
| <i>Beauveria bassiana</i> | <i>Quercus rubra</i> , <i>Zea mays</i> | Ferus et al. (2019); Kuzhuppillymyal-Prabhakarankutty et al. (2020) | Increase root: shoot ratio, proline content, protein content, and (MDA) content |
| <i>Chaetomium globosum</i> | <i>Triticum aestivum</i> (Wheat) | Cong et al. (2015) | Changes in sugars, sugar alcohols, amino acids and other metabolites; increase root dry mass and relative water content (RWC) |
| <i>Cladosporium cladosporioides</i> , Unknown ascomycota | <i>Nicotiana benthamiana</i> | Dastogeer et al. (2017a) | Increases plant biomass, RWC, soluble sugar, soluble protein, proline content, CAT, POD, and PPO and decrease production H ₂ O ₂ , EC. Upregulation of drought associated genes. |
| <i>Cladosporium oxysporum</i> , <i>H. scoparium</i> , <i>Glycyrrhiza</i> | | Li et al. (2019) | For <i>H. scoparium</i> , fungi improved the root biomass and length based on fungi. |
| <i>Embellisia chlamydospore</i> , <i>uralensis</i> , <i>Zea mays</i> | | | <i>Paraphoma</i> spp. and <i>C. oxysporum</i> had positive effects always. For <i>G. uralensis</i> and <i>Z. mays</i> , endophyte enhanced the root of plants under MD condition and was dependent on the plant–fungus species |
| <i>Paraphoma</i> spp., | | | |
| <i>Epichloe amarillans</i> | <i>Agrostis hyemalis</i> | Davitt et al. (2011) | Increase inflorescence number and seed mass. |
| <i>E. bromicola</i> | <i>Leymus chinensis</i> | Wu et al. (2016) | Increase root biomass and WUE (water use efficiency). |
| | | Ren et al. (2014) | Increase total biomass. |
| <i>E. coenophiala</i> (some reported as <i>Neotyphodium coenophialum</i> or <i>Acremonium coenophialum</i>) | <i>Festuca arundinacea</i> | Assuero et al. (2006) | Increase dry mass. |
| | | Assuero et al. (2000) | Decrease dry weight and tiller number. |
| | | Elmi and West (1995) | Increase tiller survival and leaf elongation rates. |
| | | Hosseini et al. (2016) | Increase plant available water (PAW). |
| | | Hill et al. (1996) | Increase leaf water potential and turgor pressure. |
| | | West et al. (1993) | Enhance tiller density and survival. |
| | | White et al. (1992) | No evidence for endophyte-mediated drought tolerance |
| <i>E. elymi</i> | <i>Elymus virginicus</i> | Rudgers and Swafford (2009) | Increase tillers number and root biomass |
| <i>E. festucae</i> var. <i>lolii</i> (some reported as <i>N. lolii</i>) | <i>Lolium perenne</i> | Amalric et al. (1999) | Increase number of suckers, water potential, stomatal conductance, transpiration rate, net photosynthetic rate, and photorespiratory electron: transport rate. |
| | | Briggs et al. (2013) | Decrease shoot's fresh weight. |
| | | Cheplick et al. (2000) | Decrease tiller production. |
| | | Cheplick (2004) | Decrease tillers, leaf area and total mass. |
| | | Gibert et al. (2012) | Decrease biomass production. |
| | | He et al. (2017) | Increase shoot's drymass. |
| | | Kane (2011) | Increase tiller number, greater tiller lengths, total dry mass and green shoot mass. |
| | | Malinowski et al. (2005) | Increase tiller survival |
| | | Ren et al. (2006) | Increase plant biomass, soluble sugar, tiller number and chlorophyll. |
| <i>E. festucae</i> | <i>Festuca eskia</i> | Gibert and Hazard (2011) | Increase seedling survival. |
| | <i>Festuca rubra</i> | Vazquez-de-Aldana et al. (2013) | Changes in root/shoot ratio |
| | <i>Achnatherum robustum</i> (Bunchgrass) | Hamilton and Bauerle (2012) | Increase CAT, APA (Ascorbate Peroxidase Activity), and GR (Glutathione Reductase) |
| | <i>Achnatherum sibiricum</i> | Han et al. (2011) | No effect on total biomass and chlorophyll content, increase photochemical efficiency (Fv/ Fm) and carotenoid content, reduce malondialdehyde (MDA) and no effect on superoxide dismutase (SOD) and catalase (CAT) |
| | | Ren et al. (2011) | Increase photosynthetic rate. |
| | <i>Elymus dahuricus</i> | Zhang and Nan (2007) | Increase tiller number, plant height chlorophyll content, biomass, SOD, POD, RWC, CAT, APX, Proline and decrease H ₂ O ₂ . |
| | | Zhang and Nan (2010) | Increase biomass, plant height and tiller numbers, SOD, POD, CAT and APX, proline chlorophyll content and decrease H ₂ O ₂ . |
| | <i>Festuca latior</i> (Meadow fescue) | Malinowski et al. (1997a) | Decrease shoot and root drymass. |
| | <i>Hordelymus europaeus</i> | Oberhofer et al. (2014) | Increase plant biomass and tiller production. |
| | <i>Lolium perenne</i> (Ryegrass) | Hahn et al. (2008) | Decrease Osmotic potential, herbage yield and proline content, Increase RWC. |
| | | He et al. (2017) | Increase shoot's drymass. |
| | | Hesse et al. (2003) | Increase vegetative tiller, total dry mass, shoot mass, root mass and root/shoot ratio in dry cultivar |
| | | Hesse et al. (2005) | Decrease vegetative tiller and drymass. |

Table 2: Continue

Table 2: Continued

| | | | |
|--|--|--|--|
| | | Hesse <i>et al.</i> (2005) | Decrease vegetative tiller and drymass. |
| | | Oliveira <i>et al.</i> (1997) | Increase water potential. |
| | | Gundel <i>et al.</i> (2006) | Increase seed germination. |
| <i>Epichloë sinica</i> | <i>Lolium multiflorum</i> | Bu <i>et al.</i> (2019) | Enhance seed germination, Decrease ROS. |
| <i>Exophiala pisciphila</i> | <i>Sorghum bicolor</i> (sorghum) | Zhang and Nan (2010) | Increase seed germination. |
| <i>Exophiala</i> spp. | <i>Cucumis sativus</i> | Khan <i>et al.</i> (2011) | Altered levels of stress-responsive ABA, Increase levels of SA and bioactive Gas, GA3 and GA4. |
| <i>Fusarium</i> spp. | <i>Solanum lycopersicum</i> (Tomato) | Azad and Kaminskyj (2016) | Increase shoot and root biomass, Fv/Fm. |
| <i>Neotyphodium</i> (rather than <i>Epichloë</i>) | <i>Poa alsodes</i> (Grove bluegrass) | Kannadan and Rudgers (2008) | Increase total biomass, shoot and root biomass, Root/soot ratio, decrease RWC. |
| <i>N. occultans</i> | <i>Lolium multiflorum</i> | Miranda <i>et al.</i> (2011) | Increase tillering. |
| <i>N. starrii</i> | <i>Festuca arizonica</i> Vasey | Morse <i>et al.</i> (2002) | Increase net photosynthesis, leaf conductance, leaf are ratio, total biomass, shoo and root biomass, water potential. |
| <i>N. uncinatum</i> | <i>Meadow Fescue</i> | Malinowski <i>et al.</i> (1997b) | Decrease tiller weight and water potential |
| <i>Penicillium brevicompactum</i> , | <i>Lactuca sativa</i> (Lettuce) | Molina-Montenegro <i>et al.</i> (2016) | Increase total biomass, shoot biomass and proline content, decrease root biomass and Peroxidation of lipids (TBARS). |
| <i>P. chrysogenum</i> , | | | |
| <i>P. minioluteum</i> | <i>Chenopodium quinoa</i> | González-Teuber <i>et al.</i> (2018) | Improve root formation. |
| <i>P. resedanum</i> | <i>Capsicum annuum</i> | Khan <i>et al.</i> (2013) | Increase chlorophyll content, shoot length, POD, CAT, GR, polyphenol, SA and Decrease EC, MDA. |
| | <i>Hordeum vulgare</i> (Barley) | Ghahooli <i>et al.</i> (2013) | Increase shoot and biomass. |
| | <i>Capsicum annuum</i> | Khan <i>et al.</i> (2015) | Increase chlorophyll content, soot mass, shoot length, and SA and Decrease ABA. |
| <i>Phialophora</i> sp. | <i>Festuca latior</i> (Meadow fescue) | Malinowski <i>et al.</i> (1997a) | Increase chlorophyll content, GSH, SA and Decrease leaf area, CAT, ABA, JA. |
| <i>Phoma glomerata</i> | <i>Oryza sativa</i> (Rice) | Waqas <i>et al.</i> (2012) | Increase chlorophyll content, GSH and SA and Decrease leaf area, CAT, ABA and JA. |
| <i>Phoma</i> spp. | <i>Helianthus annuus</i> | Seema <i>et al.</i> (2019) | Enhance the extent of usage of organic compounds by the plants available in the soil, Increase ammonium in soil. |
| <i>Piriformospora indica</i> | <i>Arabidopsis</i> | Sherameti <i>et al.</i> (2008) | Increase chlorophyll content, Fv/Fm and fresh weight |
| | <i>Eleusine coracana</i> (Finger millet) | Tyagi <i>et al.</i> (2017) | Increase chlorophyll, RWC and proline content. |
| | <i>Triticum aestivum</i> (Wheat) | Hosseini <i>et al.</i> (2017) | Adjusts plant metabolites and proteome, redistributes resources in the host, maintains aquaporin water channels, modulates proteins involved in autophagy. |
| | <i>Zea mays</i> | Xu <i>et al.</i> (2017) | Increase shoot and root growth CAT, superoxide dismutases proline and upregulate drought-related genes DREB2A, CBL1, ANAC072, and RD29A. Decrease malondialdehyde (MDA) |
| | <i>Hordeum vulgare</i> | Ghaffari <i>et al.</i> (2019) | Reprograms metabolites and proteomes |
| <i>Sarocladium implicatum</i> | <i>Brachiaria</i> spp. | Odokonyero <i>et al.</i> (2016) | Increase RWC; decrease shoot and root biomass |
| <i>Trichoderma hamatum</i> | <i>Theobroma cacao</i> (cacao) | Bae <i>et al.</i> (2009) | Increase total biomass, shoot and root biomass, decrease ASP, Glu, GABA. |
| <i>T. atroviride</i> | <i>Zea mays</i> (Maize) | Guler <i>et al.</i> (2016) | Increase total Chlorophyll, carotenoid, Fv/Fm, RWC, shoot and root fresh weight, shoot and root length, SOD, CAT, APX and GR activity and decrease H ₂ O ₂ MDA, |
| <i>T. harzianum</i> | <i>Oryza sativa</i> (Rice) | Pandey <i>et al.</i> (2016) | Increase chlorophyll, total dry matter and SOD and decrease MDA and proline. |
| | <i>Solanum lycopersicum</i> (Tomato) | Mastouri <i>et al.</i> (2012) | Increase chlorophyll, seed germination, shoot and root dry matter. |
| | <i>Triticum aestivum</i> (Wheat) | Donoso <i>et al.</i> (2008) | Increase biomass dry weight. |
| <i>Talaromyces omanensis</i> | <i>Solanum lycopersicum</i> (Tomato) | Halo <i>et al.</i> (2020) | Improve reproductive characteristics, chlorophyll fluorescence, increase phloem and cortex width, reduce pith autolysis, increase shoot dry weight, root length, the number of flowers, fruit weight and GA3 level. |
| Uncultured <i>Cladosporium</i> , <i>P. glabrum</i> , <i>P. brevicompactum</i> , <i>Lophiostoma corticola</i> , Uncultured <i>Metarhizium</i> | <i>Hordeum vulgare</i> (Barley) | Murphy <i>et al.</i> (2015) | Increase number of tillers, shoot dry weight, decrease root dry weight. |
| <i>Penicillium citrinum</i> , <i>Aurobassium pullants</i> and <i>Dothideomycetes</i> spp., individually and in combination | <i>Citrus reticulata</i> | Sadeghi <i>et al.</i> (2020) | Increase activities of APX, SOD, GR and levels of ASA and GSH), decrease activities of CAT, monodehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR), enhanced ratios of reduced ascorbate/dehydroascorbic acid (Asa/DHA) and reduced glutathione/oxidized glutathione (GSH/GSSG). |
| Unknown ascomycetous fungi | <i>Triticum aestivum</i> (wheat) | Hubbard <i>et al.</i> (2014) | Increase seed germination. |

virus (CMV) having very wide host range (Palukaitis *et al.* 1992; Roossinck 2001); or *Tobacco mosaic virus* (TMV) and *Tobacco rattle virus* (TRV) both with intermediate host ranges; or brome mosaic virus (BMV), a virus that has a very narrow host range (Lane 1981), they survive longer after under water limiting environments (Xu *et al.* 2008). Again, rice and tobacco plants exhibited better tolerance in the drought when inoculated with BMV and TMV, respectively. Improved drought stress tolerance was also recorded in few other cultivated and wild crops like beet, cucumber, *Chenopodium aranticolor*, pepper, squash, *Solanum habrochaites* (a wild relative of tomato), tomato and watermelon as a result of inoculation with CMV (Table 3, Xu *et al.* 2008). Furthermore, beets inoculated with CMV

were found tolerated cold treatments, but all uninfected plants died (Xu *et al.* 2008). The underlying mechanism for this observation is unknown for the most part. However, the phenomenon of plant increased drought tolerance could be explained by the effect of virus on plant morpho-physiological changes. Many cases virus infection causes plant shorter (Hull 2013) with low water requirement thereby can survive during severe drought environment. Viral infection can alter tissues water content and cause the production and movement of metabolic compounds (Hull 2013) helping plant more tolerant to drought. In their study Xu *et al.* (2008) found that CMV augmented the water content and water retention in infected plants which are indicative of decreased of stomatal opening and reduced

Table 3: Virus mediated plant drought tolerance

| Virus | Plant | Mechanisms | References |
|---|--|---|--------------------------------|
| cucumber mosaic virus (CMV) | <i>Nicotiana benthamiana</i> | Increase in several osmoprotectants and antioxidants | Xu <i>et al.</i> (2008) |
| <i>Tobacco mosaic virus</i> | <i>Nicotiana benthamiana</i> | Increase in several osmoprotectants and antioxidants | Xu <i>et al.</i> (2008) |
| <i>Tobacco rattle virus</i> (TRV) | <i>Nicotiana benthamiana</i> | Increase in several osmoprotectants and antioxidants | Xu <i>et al.</i> (2008) |
| cucumber mosaic virus (CMV) | beet, cucumber, <i>Chenopodium amaranticolor</i> , pepper, squash, <i>Solanum habrochaites</i> , tomato and watermelon | Increase in several osmoprotectants and antioxidants | Xu <i>et al.</i> (2008) |
| Yellow tailflower mild mottle virus (YTMMV) | <i>Nicotiana benthamiana</i> | increases in plant biomass, RWC, osmolytes, and antioxidant enzymes. Upregulation of drought-related genes in plants. | Dastogeer <i>et al.</i> (2018) |

transpiration level in virus affected plants (Lindsey and Gudauskas 1975; Keller *et al.* 1989). By metabolite profiling study Xu and associates (Xu *et al.* 2008) found high-level salicylic acid and some osmoprotectants and antioxidants in virus-infected plants causing increased plant adaptation to stress (Singh and Usha 2003). Moreover, TMV infection radically increased ABA levels in *Nicotiana* plants (Whenham *et al.* 1986) which is often regarded as plant adaptation strategy to stress environment, but it is not clear whether this is a usual response of plant to virus infection.

Plant viruses can be grouped into two groups viz. acute or persistent virus based their nature of interaction with host (Roossinck 2010). Majority of the acute viruses cause disease and are well researched because persistent virus does not produce any apparent symptoms on the host information on this type of viruses is very scanty. Persistent plant viruses belong to the families *Endornaviridae*, *Chrysoviridae*, *Partitiviridae* and *Totiviridae* and contain dsRNA in their genomes (King *et al.* 2012). They have also been reported from some cultivated plants like alfalfa, avocado, beets, cherry, common bean, fava bean, melon, pepper, rice, and tomato, among others. No harmful effects have been documented for persistent viruses except for *Vicia faba endornavirus* which has been reported to be related with male sterility. Persistent plant viruses are very common and have been reported in many important crop species, but information on what role they play in the host is mostly unknown. The reason might be the absence of an inoculation method and the problem of producing virus-free lines of the infected plants. Since the persistent virus cannot move between cells rather they spread during cell replication; as a result, the classical virus-inoculation methods like mechanical or graft inoculations are not effective for their transmission (Valverde and Navas-Castillo 2013).

Modern technologies in the recent days and the development of metagenomics reveal the virus richness in many diverse environments and propose that producing disease is not the usual lifestyle of viruses and that many are probably benevolent, and some are clearly beneficial. More and more research works are needed towards a revealing the fundamental mechanisms of plant-virus interaction and enhanced plant tolerance to stress will provide the potential for agricultural applications and also intuition to the key role of viruses in the adaptation and evolution of their hosts. This

is particularly important in the recent era of global climate change when drought is becoming one of the chief limiting factors for crop production worldwide (Wollenweber *et al.* 2005).

Three-Way interaction of endophyte-virus-plant and plant abiotic stress tolerance

There is an exciting three-way interaction exists among plant, endophytes and viruses. However, viruses of endophytic fungi have not been studied very well as animal or plant viruses, and therefore our current knowledge of viruses of endophytes is indeed limited. However, many fungal viruses have been identified since the first mycovirus was discovered by Hollings (1962). Majority of them possess double-stranded RNA (dsRNA) genomes, but species with ssRNA and dsDNA genomes also reported. Most mycoviruses belong to families *Totiviridae* and *Partitiviridae* and few to the family *Hypoviridae* (Ghabrial 1998). In nature, however, it's quite probable that the occurrence of viruses is very frequent in endophytes along with in other fungi. Even though a large number of endophyte viruses possibly thrive in nature, our understanding of them is just at the beginning stage. From the limited examples currently available, they are perhaps not very distinct from the mycoviruses present in other fungi. The review paper of Bao and Roossinck (2013) gives us an excellent and exhaustive account on the endophyte viruses their putative roles where the argued that viruses have been detected from all different kinds of fungal endophytes and their species richness is probably high in endophytes. In particular, the occurrence of RNA viruses is reasonably common with fungal endophytes of grasses, and in several species the prevalence and abundance of virus are quite high (Herrero *et al.* 2009).

Oh and Hillman (1995) isolated and described a virus from the fungal endophyte *Atkinsonella hypoxylon*. Later the virus was named as *Atkinsonella hypoxylon virus* (AhV) which is the type species of *Betapartiti virus* genus under *Partitiviridae* family (Oh and Hillman 1995). A virus named *Curvularia thermal tolerance virus* (CThTV) was detected in *C. protuberata*, an endophyte of panic grass growing in geothermic soils. The virus possesses two dsRNA segments of about 2.2 and 1.8 kbp. The association of this virus in endophyte was reported to confer the benefit

to plant growing at high temperatures 65°C (Márquez *et al.* 2007). Although CThTV is the only well-characterised virus from the genus, viruses are relatively common in *Curvularia*. In a study two dsRNA elements of 3.4 and 4.5 kbp (Herrero *et al.* 2009) were described in an isolate of *C. inaequalis* from *Ammophila arenaria* (Marram grass). In another study, Feldman and associates (2012) surveyed to detect viruses from fungal endophytes from the plants Tallgrass Prairie National Preserve in Oklahoma and they were able to report 25 sets of viral sequences from 20 fungal strains checked from the ragweed and dodder pairs. They identified four sets of dsRNA from *Curvularia* spp. which belong to endornaviruses, chrysovirus, and CThTV-like viruses (Feldman *et al.* 2012). dsRNA elements have also been reported from some very common plant-associated fungi including *Drechslera*, *Stemphylium* and *Alternaria*. Seven putative mycoviruses including endorna-, toti-, chryso-, hypo-, and partitivirus were found in *A. alternata* strain from tallgrass prairie in Oklahoma. Again, one putative chrysovirus dsRNAs in *Stemphylium solani* and *A. alternata*, one partitivirus like sequence were also identified in *Cladosporium* (Feldman *et al.* 2012). Study Report claims that the endophytic fungus *Fusarium culmorum* enhance the salt stress tolerance of its host plant, coastal dunegrass (Rodriguez *et al.* 2008). Later, more than one virus like sequence has been found in the salt-adapted *F. culmorum*, but the roles remain unknown. Besides, two dsRNA elements of 3 and 4.4 kbp were reported in other isolates of *F. culmorum* (Herrero *et al.* 2009). Among different kind of fungal endophytes, the dark septate endophytes have been least studied and characterised and our knowledge is very limited about mycoviruses association with them. Certain viral agents were found in *Phialophora* spp., some of them have dsRNA segments similar to that of *P. graminicola*, however, serological similarity have not been detected (Buck *et al.* 1997). Herrero *et al.* (2009) reported a 2.6 kbp dsRNA in *G. graminis* fungal endophytes collected perennial grass *Holcus lanatus*. The interaction among endophyte, viruses and their host plants are parallel to plant-endophyte interactions. Most of the viruses that have been identified from fungi have limited host ranges and cause no apparent symptoms unlike those infect plant or animal hosts (Ghabrial 1998). Only a small number of mycoviruses have been reported to affect their hosts, causing hypovirulence, disease (Deng *et al.* 2007) or being beneficial. The most noticeable benefit that endophytic virus confers to plant is that the presence of virus in the endophyte increase the abiotic stress tolerance in plant. For example, a virus-infected endophyte was reported to increase heat tolerance to tomato plants (Márquez *et al.* 2007).

Bao and Roossinck (2013) suggested from their survey that the presence of dsRNAs in fungi could be as high as 100% and there are even variations among fungal populations of the same species. However, Average virus incidence in endophyte populations is 10%, and they are

probably not host specific (Feldman *et al.* 2012) and out of which only a handful of endophyte viruses have been detected and their putative roles have been explored in symbiotic systems. Many factors can be attributed that may affect the occurrence of virus in endophytes in a plant host, including the rate of vertical transmission (through spores), horizontal transmission, fungus-virus interaction, and environmental conditions (Bao and Roossinck 2013). It is also urged that the some viruses could be readily lost in the culture which is the reason for very low result in the survey. Although it is very difficult to trace any beneficial or harmful effect that mycoviruses may confer upon the host, it is assumed that they have some effects that are very subtle and challenging to demonstrate experimentally with lower sample number (Diepeningen *et al.* 2006). Till date, only a very few attributes have been evaluated in most experiment, for example growth parameter, reproduction ability, pathogenic effects, or heat resistance. However, viruses could be a vital genetic element for fungi and plant hosts, especially under inhospitable environments, where viruses can confer supportive genetic information through epigenesis.

The mechanism by which the endophyte virus has developed to defend the fungus from the deadly costs of heat, salt and water stress is not understood well. Further research is needed to display how the viral factors might influence the genetic and phenetic expression profiles of the endophyte host that benefit stress adaptation in plants (Bao and Roossinck 2013). The knowledge of endophyte viruses and their potential functions will be useful for sustainable agriculture particularly in the context of climate changes in the global arena. With greater knowledge of endophyte viruses, it will be important to ponder on some pertinent questions in order to apply an endophyte in the sustainable agricultural system. For example (1) Are there any roles of virus(es) in enabling the endophyte to offer habitat-adapted benefits to host? (2) Is presence or absence of virus in endophyte alter its relationship with plant host from mutualistic to antagonistic? (3) Is there any threat that these viruses could be parasitic on plants by evolution? (4) Could there be any synthesis of unexpected or expected by-products in the plant-endophyte, or plant-endophyte-virus interactions? (5) How easier and stable it will be to deliver endophyte and/or its virus in the farming system (Bao and Roossinck 2013)? Current research trend envision that more mutualistic endophyte viruses will be reported and their functions will be investigated in the future.

Mechanisms of endophyte and virus-mediated plant drought tolerance

It is now well-documented that some fungal endophytes provide fitness benefit to plants under drought conditions. There are few excellent reviews on the mechanisms of how fungal endophytes mediate drought tolerance in the plant (Singh *et al.* 2011; Dastogeer and Wylie 2017)

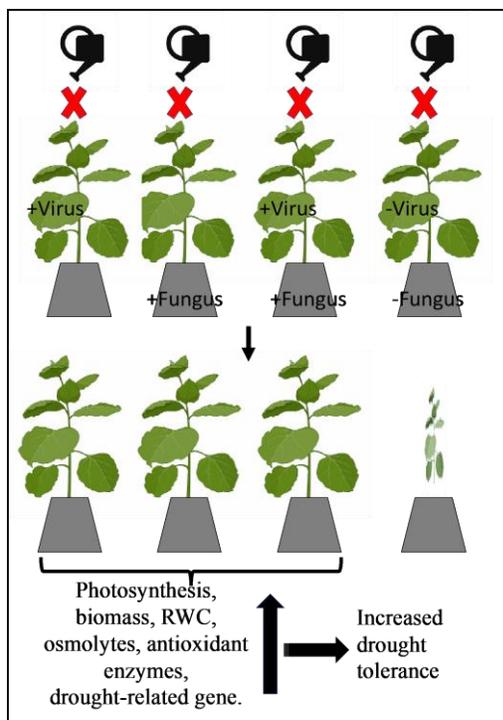


Fig. 2: Schematic representation of fungi and virus mediated drought tolerance in plants

therefore; the current review will not discuss this at length. Endophyte employ complex mechanisms that involve various metabolites and metabolic pathways to improve plant stress tolerance (Fig. 2). Although, many investigations found the role endophytic fungi to confer water limitation tolerance in host, the underlying mechanism(s) are poorly understood. Available literatures suggest that fungal endophytes improve plant drought tolerance through- (a) increase in plant growth and development (Khan *et al.* 2012, 2014; Azad and Kaminskyj 2016; Dastogeer *et al.* 2017a, b; Dastogeer *et al.* 2018) (b) improvement of osmotic balance (Sun *et al.* 2010; Azad and Kaminskyj 2016) (c) increase in gaseous exchange and water-use efficiency (Bayat *et al.* 2009; Nagabhyru *et al.* 2013; Cong *et al.* 2015) and (d) improvement in plant defence against oxidative damage to reduce, alleviate and mitigate the harmful effects of drought in fungal inoculated plants balance (Sun *et al.* 2010; Azad and Kaminskyj 2016).

From the limited studies available so far, it is unclear how virus infection improves plant drought tolerance. But, commonly, virus infection causes a reduction in plant growth and plant become dwarf (Hull 2013) thus reduces the water requirement and give plant more advantage under low water condition. Other physiological changes, for example, reduced water content and changes in metabolites are also associated with plant virus infection (Hull 2013). The drought tolerance in the plant due to infection of CMV (cucumber mosaic virus) and YTMV (Yellowtail flower

mild motile virus) also correlated with the leaf water content of the plant (Xu *et al.* 2008; Dastogeer *et al.* 2018). Higher water retention in virus-infected plants could be linked to the reduction of stomatal opening and reduced transpiration rate (Hall and Loomis 1972; Lindsey and Gudauskas 1975; Keller *et al.* 1989). The virus-infected plant usually shows higher levels sugars such as glucose, fructose and sucrose, which may act as osmoprotectant under stress as compared to non-infected plants (Fig. 2). An in-depth analysis of metabolites profiling will provide a better understanding in this regard. Certain osmolytes and antioxidant enzymes and salicylic acid showed higher accumulation in virus-infected plants under drought (Xu *et al.* 2008; Dastogeer *et al.* 2018). Role of salicylic acid in improving plant tolerance to abiotic stress is known (Singh and Usha 2003). Alteration in metabolite accumulation under stress is considered as one of the vital survival mechanisms of the plant. Metabolic compounds play a role in osmotic adjustment, membranes stability, and protect cellular organelles damage due to stress (Hare *et al.* 1998). Higher accumulation of these protective compounds in virus-infected plants makes the plant more acclimatized for further stress. Changes in gene expressions associated with the virus-mediated plant drought tolerance reflect the physiological changes as described above. Biotic and abiotic stress share some common mechanisms in the plant (Xiong and Yang 2003; Chini *et al.* 2004; Dastogeer *et al.* 2018).

Future perspective and challenges

Although there has been continuous advancement, there are still many challenges which need to be addressed to identify and successfully apply microorganisms. For example, screening a large number of fungal endophytes that are isolated from various plants for their roles as plant drought-tolerant is very time consuming and the results obtained are dependent on the screening methods used. Dastogeer *et al.* (2017b) suggested a simple and rapid screening method, however, in this method; there is no description of the use of mix inoculum which is currently getting more attention by the researcher. One possible modification of this method of the filter paper trial would be to use fungal culture filtrate/mycelial suspension instead of agar block to inoculate fungi so mix inocula could also be added. Further, the response of early-stage seedling may not be the response of the adult plant. So, the experimenter needs to design trial, including the plant at a different time of life cycle.

A pertinent question regarding the application of microbes in the field would be how stable these effects across variable biotic and abiotic conditions are. Also, since most of the studies on plant-endophyte interactions have been conducted under in vitro system or under glasshouse trial which although essential to know the effects primarily and to narrow down the problems targeted. However, these controlled trials do not necessarily reflect the outcome under field condition, which is highly variable due to the

involvement of many known and unknown factors. So, it is important to carry out field-based trials in addition to finding new promising microbial isolates. Again, different inoculation methods give variable results. For example, seed and foliar inoculation is more effective compared to soil and root inoculation methods. The reason could be the presence of resident microbial diversity in the soil is overall more, which may create a competitive environment for the inoculated strains. Although various trials have been performed using endophytes (fungi and/or bacteria) as biocontrol of plant diseases, there is a lack of field-trial information on endophyte mediated plant drought tolerance. Unless sufficient information is available and the outcomes are known, the inclusion of the microbial strains in the integrated package for abiotic stress management is not advisable. Another promising area is the inoculation of beneficial microbes in the consortium. In some cases, especially in case of beneficial bacteria, the application of microbial consortia gave better results compared to individual strains. Efforts have also been made to improve fungi efficacy through genetic engineering but with low success rate. Current genome editing technology such as CRISPR technology might be an important tool in manipulating the genetics of endophytes.

The implementation of endophytes or beneficial viruses into plant stress management program will require a thorough understanding of the mechanisms and the ecology of plant-microbe interactions. Although several studies suggested morphological, physiological and molecular mechanisms, more in-depth studies are needed, which include different beneficial strains with different plant species. The level of gene(s) expression in plants as well as in microbe(s) by using proteomics would be a crucial step to discern the mechanisms. It would allow differential expression of genes under different conditions, detection of microbe- and host gene expression simultaneously, and the identification of new RNA species. Also, the metabolomic approach, in addition to genomic and transcriptomic approach, would give an improved knowledge of the plant-microbe interaction under drought stress (Kaul *et al.* 2016; Levy *et al.* 2018). It essential to develop models that reveal the genetic and metabolic potential, as well as the organisms' ecology and evolution, the complex plant-microbe interactions in order understand their respective roles and utilize this efficiently and sustainably in crop production under stress.

Unravelling the mechanisms of endophyte and virus-mediated enhanced abiotic stress in the plant provides insight into the significant role of microbes in the ecology and evolution of the hosts. In the crop field, a delay in the appearance of stress related symptoms of even for a short time can be crucial. Hence, a better understanding of the mechanistic aspect has the potential implications in agriculture, which are of significant concern during climate change, since the impact of the drought is becoming more severe in crop cultivation

worldwide (Wollenweber *et al.* 2005).

Conclusion

One of the approaches to address the drought problem in crop production is the application of stress-tolerant microbes that may enhance plant growth under stress condition. Various studies demonstrated beneficial effects of the endophytic fungi on plant growth and adaptability to drought stress. This review accumulated the available literature that investigated the fungal endophyte or viruses help plants tolerate to drought stress. Our current understanding of fungal mediated stress tolerance is improving, but virus-mediated stress tolerance is lagging behind, which warrant further studies. The mechanisms suggested from the current literatures provide an incomplete picture of more elaborate, complex and intriguing mechanisms underlying fungus or virus-mediated drought tolerance. The present review shows that in addition to other microbes, some viruses could also play a vital role as an ecological engineer to tackle stress related anomalies in nature. Another important aspect in this area is that majority of the investigations have been performed either in *in vitro* or in a greenhouse or growth chamber and very few under real field conditions. Therefore, to facilitate the widespread and resilient use of beneficial microbes, research should also give trial under field conditions and make farmers aware of microbe-mediated plant stress tolerance. In addition to use of single strain inoculum, application of inoculum consortium with same species or other species or other groups of microbes such as fungi-virus, fungi-bacteria or other possible combination is advocated because in nature microbes' lives in association with various community members.

Author Contributions

KMGD conceived the idea, did literature reviews and wrote the first draft. All other authors (AC, MSAS and MAA) revised the manuscript substantially and modified the tables and figure.

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