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Concurrent Stresses Are Perceived as New State of Stress by the Plants: Overview of Impact of Abiotic and Biotic Stress Combinations

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Abstract

Crop plants under natural conditions often encounter abiotic and biotic stresses either individually or in combination, single or multiple times in their life cycle. During their concurrence, different stressors interact with each other over the plant interface leading to altered plant responses. Initial stressor can modulate plant physiology and thereby influences plant response towards another stressor. Consequent to the stress interaction, plants encountering concurrent stress show different responses in comparison to the plants exposed to the individual stresses. Additionally, plant defence responses are somewhat skewed towards one stressor during concurrent occurrence of stresses. Such different responses are the cognate 'net effect' of combined stress felt by the plant. The net effect exhibited by plants under combined stress is unique to each stress combination. Thus, in lieu of the combined stress responses, which are different from the individual stress responses, the combined stress has been proposed as a new state of stress. Plant responses towards this new state are not just dictated by either of the individual stresses alone but by more complex interaction. In this chapter, we present an overview of the combined stresses with emphasis on drought and bacterial stressors and discuss the stress interaction effect and net effect.

Keywords

Concurrent stress • Stress interaction • New stress • Unique responses

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1.1 Introduction

Under field conditions, the environmental constraints do not always occur independently but most often occur in conjunction with pathogens, and this is detrimental to survival of crop plants. Extreme weather patterns have led to the periodic incidences of drought and pathogen infections (Desprez-Loustau et al. 2007; Yáñez-López et al. 2012; Elad and Pertot 2014). Conventionally, disease triangle represents drought altered plant-pathogen interaction by influencing either the host defence or the pathogen virulence (Achuo et al. 2006; Amtmann et al. 2008; Goel et al. 2008; Hanso and Drenkhan 2009; Atkinson and Urwin 2012). Severe drought in 2003 stimulated *Diplodia pinea* (causal agent of Sphaeropsis blight) epidemic on conifers in Central Europe, and *Diplodia pinea* emerged as a new pathogen infecting *Pinus nigra* in Estonia (Hanso and Drenkhan 2009). The concurrence of drought and pathogen stress and their interaction over plant interface leads to altered plant physiology and resistance responses (Choi et al. 2013; Dossa et al. 2016; Gupta et al. 2016b; Sinha et al. 2016). Plant responses to concurrent drought stress and pathogen infection vary depending on the severity and duration of each stress, nature of infecting pathogens and plant genotype (Achuo et al. 2006; Xu et al. 2008; Ramegowda et al. 2013; Dossa et al. 2016; Gupta et al. 2016a; Sinha et al. 2016). Previously, few studies involving concurrent stresses on plants showed that stress interactions provoke a set of unique plant responses wherein some of the acclimation strategies are attuned to the constraints involved and are not seen under either of the individual stress (Xu et al. 2008; Atkinson et al. 2013; Prasch and Sonnewald 2013a; Gupta et al. 2016b). Moreover, combined stress also evokes responses which are 'common' to each of the individual stresses (Prasch and Sonnewald 2013a; Gupta et al. 2016b). Some of these responses are 'similar' between combined and individual stress, whereas certain common responses are evoked to a different level under combined stress when compared to individual stress and are termed as 'tailored responses'. Considering the existence of unique, tailored and similar responses under concurrent drought and pathogen stress compared to individual stresses (Suzuki et al. 2014; Gupta et al. 2016b), it is perceivable that combined stressed plants experience a new state of stress. This underlines the fact that the net impact of a concurrent stress and cognate plant response cannot be studied exclusively from single-stress experiments (Atkinson and Urwin 2012; Suzuki et al. 2014). In this chapter, we attempt to describe the delineation between stress interactions and net impact on plants.

1.2 Stress Interaction

1.2.1 Direct Impact of Drought on Pathogen

Drought stress can influence pathogen survival and spread in environment and thus impacts the disease incidence (Hanso and Drenkhan 2009). In case of rhizosphere-dwelling pathogens, the outcome of interaction between drought stress and bacterial pathogen varies depending upon the nature of the pathogen and whether the pathogen thrives in wet or dry soils. For example, drought favours *Streptomyces scabies* (causal agent of common scab in potato) multiplication in the rhizosphere and thereby increases the opportunity for subsequent infection in plants (Goto 1985). Most often, foliar pathogens experience low water availability in phyllosphere as the most important deterrent. Several studies showed that epiphytic microbial populations increase in wet months (the presence of water) but decline during dry periods (Hirano and Upper 1983, 1990). The leaf surface water does not only support pathogen multiplication but can also be conducive for sustaining plethora of microbial pathogens on phyllosphere and thereby increasing the subsequent chances of plant infection. Ercolani (1991) reported increased diversity of microbial pathogens on olive leaf surface during cooler wet months which however declined during the warmest and driest months of the season. Furthermore, Beattie (2011) reported that abundance of surface water favours bacterial invasion into the leaf tissue. Under water stress, many genes involved in pathogenicity and virulence (of bacteria), including genes in the hypersensitive response and pathogenicity alternative sigma factor (HrpL) regulon, were suppressed in *Pseudomonas syringae* pv. *tomato* DC3000 (causal agent of bacterial speck) (Freeman 2009). Thus, by modulating the pathogen multiplication and survival in the environment, drought (outside the plant) has been shown to regulate incidence of plant infection by these pathogens.

1.2.2 Stress Interactions at the Plant Interface

Drought and pathogen stressors can interact with each other at plant interface wherein drought directly impacts the *in planta* pathogen multiplication and spread. Bacterial movement inside the host is regulated by its flagella, which in turn is favoured by water availability in the leaf apoplast. In an instance, spread of *P. syringae* pv. *syringae* (causes brown spot of beans) in bean seedlings has been shown to be promoted by water (Leben et al. 1970). Instances for drought-induced *in planta* multiplication and spread for other pathogens are also available. Lowered water potential in pea leaves leads to reduced sporulation of *Erysiphe pisi* (causal agent of powdery mildew) (Ayres 1977). Drought stress also restricted *in planta* movement of *Tomato spotted wilt virus* (causal agent of tomato spotted wilt) and attenuated disease symptoms in tomato plants (Córdoba et al. 1991). These examples present a scenario of drought-induced tolerance towards pathogen in plants under combined stress by modulating systemic spread of pathogen.

Drought stress can interfere with plant immunity making the plant susceptible or resistant towards pathogen attack (Mohr and Cahill 2003; Koga et al. 2004; Hatmi et al. 2014). Drought stress imparted susceptibility to *Arabidopsis thaliana* cv. Ler against an avirulent bacterial pathogen *P. syringae* pv. *tomato 1065* (Pst1065) (Mohr and Cahill 2003) and to grapevines against *Xylella fastidiosa* (causal agent of bacterial leaf scorch and Pierce's disease) (Choi et al. 2013). Drought stress increased the severity and progression of leaf scorch disease caused by *X. fastidiosa* in *Parthenocissus quinquefolia* vine (McElrone et al. 2001). The acclimation of *Nicotiana benthamiana* to moderate drought stress reduced the growth of *P. syringae* pv. tabaci (causes wildfire disease in tobacco) (Ramegowda et al. 2013). However, in the same study, severe drought stress had been shown to increase the susceptibility of the plants to *P. syringae*. Here, drought stress increased the ABA accumulation and hence interfered with plant defence responses (Ramegowda et al. 2013).

Water availability facilitated bacterial pathogenesis by suppressing the plant vasculature defences during effector-triggered immunity (ETI) in *A. thaliana* (Cook and Stall 1977; Freeman and Beattie 2009) and PAMP-triggered immunity in *N. benthamiana* (Oh and Collmer 2005). Freeman and Beattie (2009) showed that plants promote ETI and cause localized desiccation at the site of pathogen infection consequently restricting pathogen multiplication. Drought stress tolerance in grapevine involved activation of polyamine oxidation contributing to improved immune response and low susceptibility to *Botrytis cinerea* (causes grey mould disease) (Hatmi et al. 2014).

Drought stress also instigates physiological changes in plants which may be favourable to the pathogen. Drought-stressed sorghum plants were more susceptible to *Macrophomina phaseolina* (causal agent of charcoal rot) infection (Edmunds 1964). Reportedly, the sorghum root volatiles diffuse more rapidly through dry soil and favour *M. phaseolina* infection under drought conditions (Kerr 1964). In another instance, increased *M. phaseolina* infection in drought-stressed common bean has been reported (Mayek-Perez et al. 2002). Ijaz et al. (2013) suggested that drought stress led to accumulation of carbohydrates and amino acids (viz. asparagine and proline) which served as nutrient for the *M. phaseolina* instigating *in planta* pathogen growth and multiplication. Similarly, the drought-induced proline accumulation and ROS metabolism invoked susceptibility towards *Diplodia pinea* in Austrian pine (Sherwood et al. 2015).

In spite of the drought-imposed obstacles for *in planta* pathogen multiplication and survival, pathogen interacts with plant and tends to establish itself *in planta* during combined stress. In an attempt to overcome the obstacle posed by low water availability, bacteria actively modify the leaf surface habitat during drought stress. For example, bacteria can increase the wettability of leaves by secreting surfactants (Bunster et al. 1989; Hutchison and Johnstone 1993). The water films created by these biosurfactants hydrate epiphytic bacterial cells and facilitate movement of bacteria to more favourable sites (Lindow and Brandl 2003). Bacteria also modify their local environment by producing extracellular polymeric substances (EPS) which helps them hold on to the leaf surface and prevent desiccation by encapsulating cells in a hygroscopic matrix (Wilson et al. 1965; Takahashi and Doke 1984). Synthesis of alginate, a component of EPS, is stimulated by desiccation stress in *P. syringae* (Singh et al. 1992; Keith and Bender 1999) and contributes to epiphytic fitness of this organism during drought stress (Yu et al. 1999). High cell densities induce the expression of particular genes (Pierson et al. 1998; Bassler 1999) and contribute to epiphytic fitness (Monier and Lindow 2003) via quorum sensing cell to cell signals. *Xanthomonas campestris* (causal agent of wilt) was able to reverse stomatal closure induced by ABA via secretion of virulence factors (Gudesblat et al. 2009). Taken together, all these evidences suggest that drought influence pathogen multiplication and survival both outside and inside its host. Although at the same time, pathogen has also adopted combat mechanisms and establishes itself in the plant under combined stress conditions.

Further, studies also show that pathogen influences host plant physiology and water relations to predispose it to drought stress. The vascular wilt pathogens cause desiccation state in host plant which leads to reduced photosynthesis and reduced flow of photo assimilates to the roots and eventually causes reduced root growth. As a result, the host plant is more susceptible to the drought stress. *X. fastidiosa*, a xylem-limited bacterial pathogen, induces drought stress in alfalfa (Daugherty et al. 2010). These pathogens colonize and block xylem vessels and reduce their hydraulic conductivity, thereby aggravating the drought stress conditions in plants (Yadeta and Thomma 2013). Tomato plants infected with *Verticillium dahliae* (causal agent of Verticillium wilt) showed decreased leaf water potential (Ayres 1978).

A. thaliana plants infected with *V. longisporum* were tolerant to drought stress. *V. longisporum* induces the expression of vascular-related NAC domain (*VND7*) gene in these plants and triggered de novo xylem formation which leads to enhanced water storage capacity under drought stress conditions (Reusche et al. 2012). *P. syringae* infection in host plant could interfere with plant-water relation by causing water-soaking and the resultant desiccation of the infection site (Beattie 2011), and such case leads to more drought stress experienced by plants.

Both drought stress and foliar bacterial pathogen infection influence ABA levels and stomatal closure in plants. ABA treatment leads to susceptibility of *A. thaliana* towards avirulent bacterium *P. syringae* pv. *tomato* 1065 (Pst1065) infection where the susceptibility increased in a concentration-dependent manner (Mohr and Cahill 2003). Similarly, application of HopAM1 a type III effector of *P. syringae* increases the multiplication and virulence of *P. syringae* under drought stress (Goel et al. 2008). HopAM1 also enhanced ABA-mediated stomatal closure under drought stress (Goel et al. 2008). Pathogen effectors released inside the plant cell cause increased ABA accumulation and stomatal closure and decreased leaf transpiration rate, which altogether improved drought tolerance in combined stressed plants. For instance, application of purified HrpN-a protein produced by *Erwinia amylovora* (causal agent of fire blight) alleviated drought symptoms in *A. thaliana* (Dong et al. 2005). The increased ABA levels in response to the HrpN treatment enhanced the expression of several ABA-signalling regulatory genes as well as the drought-inducible gene *rd29B* (response to dehydration B), the gene product of which mediates ABA-induced responses (Dong et al. 2005). Root colonization with rhizobacteria, *P. chlororaphis* O6 also induced stomatal closure, reduced water loss by transpiration and increased drought tolerance in *A. thaliana* plants (Cho et al. 2008).

In conclusion, the two stressors when co-occurring influence the plant resistance as a result of stress interaction. Thus, in order to study plant-pathogen interaction, the actual scenarios must be accounted, and such understanding cannot be extrapolated from single-stress studies.

1.3 Net Effect of Combined Stresses

From the earlier discussions, it appears that combined stress is perceived as two interacting stressors by the plants where one could see the reminiscence of two individual stresses. However, looking at the existence of a set of unique responses and net impact, it can be settled that combined stress in plants is perceived as a new state of stress. The simultaneous occurrence of more than one stress influences plants as result of stress interaction and direct net impact of occurring stresses together (Daugherty et al. 2010; Atkinson et al. 2013; Ramegowda et al. 2013; Rasmussen et al. 2013; Bostock et al. 2014; Kissoudis et al. 2014; Prasch and Sonnewald 2013a, 2015; Gupta et al. 2016b). The net impact depends on the specific combination of stresses where the concurrence of two stressors can guard or further disrupt plant processes, and both the stresses, when occurring concurrently, most often act in unison to hamper plant growth and development (positive drought-pathogen interaction) (Fig. 1.1). As a result, the combined stresses can cause severe reduction in crop yield when compared with the losses incurred by individual stresses (Siddiqui 1980; Bhatti and Kraft 1992; McElrone et al. 2001; Janda et al. 2008; Prasch and Sonnewald 2013a; Fig. 1.1). Edmunds (1964) observed that concurrent drought stress and *Macrophomina phaseoli* infection caused more damage compared to individual stressed sorghum plants.

The set of net impact resulting from stress interactions in turn depends on common physiological effect or common traits influenced by the two constituent stressors (of concurrent stress) impacting on plant, and the outcome is more devastating than either of the individual stress. Individual drought stress and *X. fastidiosa* infection both lead to low water potential in leaf and influence reduction in stomatal conductance and xylem dysfunction. As a result of such synergism, *X. fastidiosa*, in combination with drought stress, increases the severity and progression of leaf scorch in *Parthenocissus quinquefolia* causing severe reduction in total biomass as compared to individual stresses (Fig. 1.1; McElrone et al. 2001, 2003). Drought stress invokes stomata closure in the plants (Wilkinson and Davies 2002), while on the other hand, *P. syringae* infection signals stomata opening (Melotto et al. 2008). When *Vicia faba* and *A. thaliana* were subjected to a combination *P. syringae* and water deficit, stomatal closure was more pronounced (Ou et al. 2014). In such case of antagonistic stress interaction, responses to abiotic stresses were found to override the responses to biotic stresses (Ou et al. 2014). Recent studies also suggest that the net impact could be the reminiscent of the stress interaction or due to direct impact of combined stress. In the following section, we attempt to delineate and assess the net impact of combined stresses.

1.4 Assessment of Net Impact of Combined Stress

As stated earlier, combined stressed plants experience net impact as a results of one of the following.

(a) Interaction of each stressor with plant
(b) Interaction between two stressor inside the plant
(c) Interaction of one stressor with plant influencing other stressor

In order to tag a combined stressed plant under natural field conditions, dissection of the component contributing towards net impact is important which so far is not understood. Further, for crop protection and improvement, systematic identification of contributory factors (through interaction) to combined drought and pathogen stress is needed. Foremost prerequisite for such studies is the identification of a common agronomically important parameter targeted by both the stressors. For example, yield reduction is seen in case of individual drought and charcoal rot infection in sorghum (Edmunds 1964). The alteration in the identified parameter can be used to answer how the two stressors are interacting with each other and with plant. During such studies, net impact of combined stress can be instanced in one of the following equations:

(i) $CS = D > P$
(ii) $CS = P > D$
(iii) $CS = D + P$ (additive/positive interaction)
(iv) $CS = D - P$
(v) $CS = P - D$
(vi) $CS \neq D$ or P or $D + P$ or $D - p$ or $P - D$

Here, D, P and CS denote net impact imparted by individual drought and pathogen stresses and their combination, respectively.

In case (i) drought could be said as the 'dominant' stressor, influencing the net impact of the combined stressed plants. The dominant stressor, here, refers to the stress which can modulate the plant processes and decides the plant interaction with subsequent stressor, and also the net impact of the combined stress plants is largely similar to the net impact of dominant stressed plants. In this case, drought can reduce pathogen growth, or it can interfere with plant resistance and impact yield loss (parameter considered here as net impact). For example, drought stress instigated activation of polyamine oxidation and improved immune response which lead to subsequent resistance in grapevine to *Botrytis cinerea* (Hatmi et al. 2014). Likewise, in case (ii) pathogen can be considered as dominant stressor where it can reduce drought effect while interfering with plant-water relations and curb yield loss, e.g. *Erwinia amylovora* alleviated drought symptoms in *A. thaliana* (Dong et al. 2005). In case (iii) the net impact (total loss in yield) is equivalent to the additive losses incurred by individual drought and pathogen stresses and results

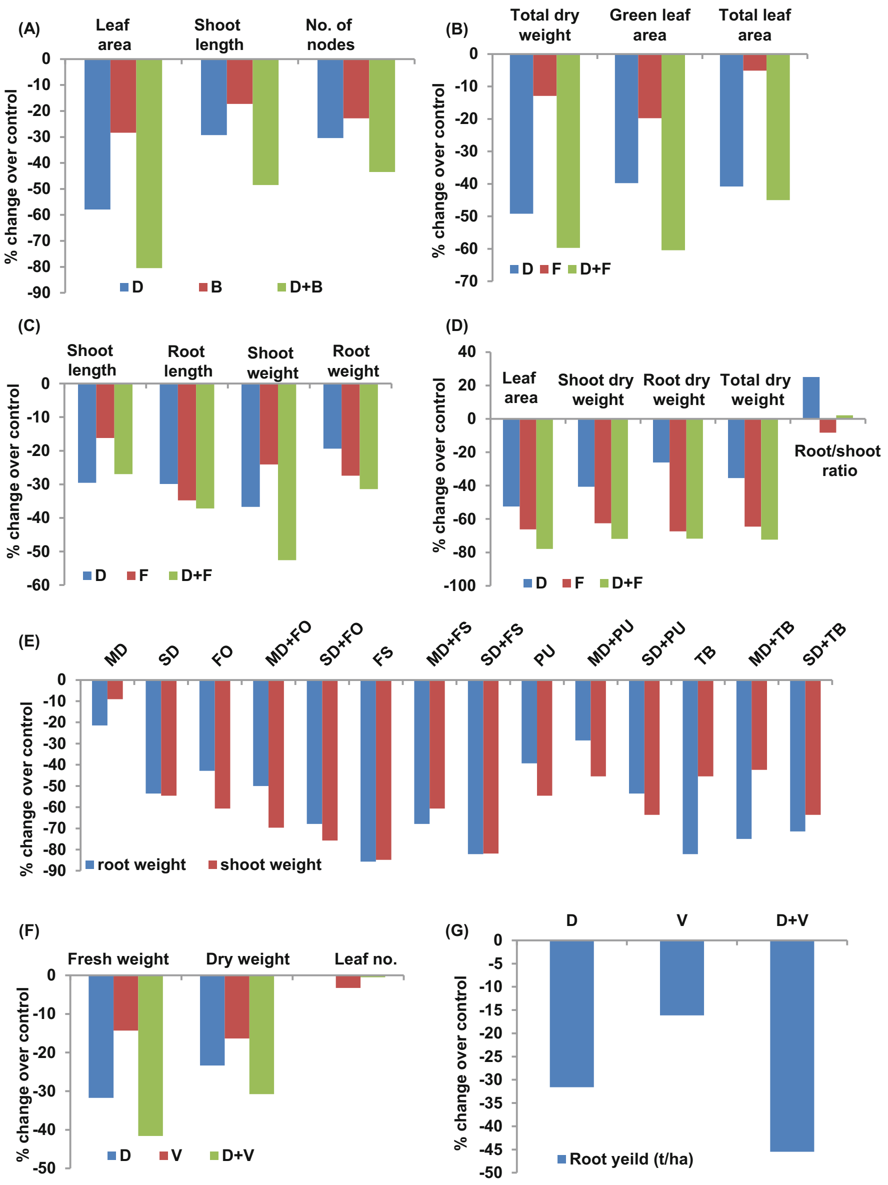

Fig. 1.1 Effects of concurrent drought and pathogen stress on plants. Graphs showing effect of concurrent stresses on yield contributing traits. Drought and bacterial stress (*Xylella fastidiosa*) effect on *Parthenocissus quinquefolia* (McElrone et al. 2001) (**a**), drought and fungal stressor (*Puccinia helianthi*, causes rust) effect on *Helianthus annuus* (Siddiqui 1980) (**b**), drought and fungal (*Drechslera tritici-repentis*) stressor effect on *Triticum aestivum* (Janda et al. 2008) (**c**), drought and fungal (*Macrophomina phaseolina*) stressor effect on *Phaseolus vulgaris* (Mayek-Perez et al. 2002) (**d**), drought and fungal (*Fusarium oxysporum*, FO; *Fusarium solani*,

from positive interaction between drought and pathogen. The example of drought and wilt pathogen interaction can be cited where both these stressors enhance each other's effect in combined stressed plants. In cases (iv) and (v), the net impact, e.g. on yield loss, is equivalent to the subtractive losses (to those incurred by individual stresses) and results mainly because of the antagonistic interaction between two stressors. This instance for this case is presented in Fig. 1.1, where the total biomass under combined stress was the difference of total biomass seen under individual *Pythium ultimum* infection and mild drought stress in *Cicer arietinum* (Bhatti and Kraft 1992). In all these cases (i–v), mainly the stress interaction culminates in net impact which is reminiscent of the individual stresses. In such case, combined stress effect or net impact can be deduced by studying individual stress effect, and shared responses can be exploited for studying stress interaction. However, still another scenario appears where combined stressed plants exhibit a stress effect without stress interaction, e.g. (vi) in this case, the net impact is not equivalent to either of the individual stresses or their positive or negative interaction but is different.

All these situations can be delineated by making use of different stress levels, different pathogen (virulent and avirulent) and different plant genotypes (differing in their resistance responses). By screening different genotypes (exploiting common parameter for stress interaction), one can dissect components of combined stress impact. Recently, a study by Dossa et al. (2016) analysed ten rice genotypes which differed in bacterial blight (BB) resistance (having *R* genes) or drought tolerance (comprising drought quantitative trait loci) or a cross of both BB resistance and susceptible genotype. They imposed different drought stress levels (mild and moderate) and different *Xanthomonas oryzae* pv. oryzae strains (Xoo) (causal agent of rice blight) (virulent PXO99 and avirulent PXO145) under simultaneous stress. Rice genotype IRBB7 (*R* gene, Xa7) showed less Xoo spread and reduced Xoo multiplication under drought stress compared to the well-watered control with PXO145. In contrast, in genotypes with a different BB R gene and/or drought QTLs [IRBB4 (Xa4), IR87705:6.9.B (Xa4 + qDYT2.2), IR87707:445.B.B.B (Xa4 +qDYT2.2 + qDYT4.1) and IR87707:446.B.B.B (Xa4 +qDYT2.2 + qDYT4.1)], Xoo multiplication and spread *in planta* were higher with drought stress. Janda et al. (2008) studied the interaction between drought and fungal stress on wheat. They included three different levels of drought (0, 5, 15 and 20% of PEG) followed by inoculation with *Drechslera tritici*-repentis (DTR, causal agent of tan spot disease

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Fig. 1.1 (continued) FS; *Pythium ultimum*, PU; *Thielaviopsis basicola*, TB) stressors effect on *Cicer arietinum* (Bhatti and Kraft 1992) (**e**), drought and viral (*Turnip mosaic virus*) stressor effect on *Arabidopsis thaliana* (Prasch and Somnewald 2013) (**f**) and drought and viral (*beet yellows virus*) stressor on *Beta vulgaris* biomass (Clover et al. 1999) (**g**). The values were extracted from research papers, and % change in yield parameter was calculated over control samples. Negative values in graph denoted reduction in biomass over control treatments. *D* drought, *B* bacteria, *D*+*B* combined drought and bacterial stress, *F* fungus, *D*+*F* combined drought and fungal stress, *V* virus, *D*+*V* combined drought and viral stress, *MD* mild drought stress, *SD* severe drought stress, *FO Fusarium oxysporum*, *FS Fusarium solani, PU Pythium ultimum, TB Thielaviopsis basicola* in wheat) at two different time (6 and 72 h after the PEG treatment) in different wheat genotypes with two DTR resistant (M-3 and Mv Magvas) and two sensitive (Bezostaya 1 and Glenlea) varieties. While 15% PEG reduced the level of infection in sensitive Bezostaya variety, 20% PEG treatment lowered the tolerance level of M-3.

Both these studies indicated drought as the dominant stressor, where it might have affected the plant resistance in influencing the *in planta* pathogen multiplication. On similar lines, Prasch and Somnewald attempted to study the natural genetic variation of combined biotic and drought stress response, by studying the expression profile of common genes (between individual and combined stress) in natural accessions of Arabidopsis (Prasch and Sonnewald 2013b).

1.5 Combined Stress as a New State of Stress: Reminiscent and Different from Either of the Individual Stresses

Certain physiological responses are modulated in a plant under combined stress which is either unique or common (tailored or similar with individual stressed plants). For instance, concurrent viral and drought-stressed plants accumulated proline at a level different from individual drought stress or viral infection (Xu et al. 2008). Moreover, these combined stressed plants did not accumulate sucrose which was induced upon individual virus infection. Ascorbic acid content in drought-stressed plants declined by 37.5% and was undetectable in virus-infected plants. However, concurrent stressed plants did not show any change in ascorbic acid levels as compared to control plants. Likewise, more anthocyanins were accumulated in concurrent stressed plants over individual stressed plants. The above-mentioned instance explains existence of common responses between individual and combined stresses which are tailored to suit the plant defences under combined stress.

The extent of common (tailored or similar) and unique responses between combined and individual stresses depends on the nature of pathogens that infect drought-stressed plants. Transcriptome studies in *A. thaliana* exposed to concurrent drought stress and *P. syringae* infection revealed that 31% of the differentially expressed transcripts were unique to concurrent dual stresses and were lacking under individual stress treatments and 22% were common with either of the individual stress (Gupta et al. 2016b). However, under *X. fastidiosa* and drought stress interaction, 56% of differentially regulated genes were shared with either of the individual stresses (Choi et al. 2013). Gupta et al. (2016b) studied transcriptome profile of *A. thaliana* and compared time of occurrence of pathogen during concurrent drought and *P. syringae* infection. Comparison of differentially expressed genes across individual and combined stress drought and *P. syringae* infection revealed 505 genes unique to drought followed by pathogen stress and 885 unique genes under pathogen followed by drought combined stress (Gupta et al. 2016b). The existence of common genes between individual and combined stresses indicates that plants economize their defence resources while using existing stress-responsive molecular machinery for upcoming new or additional stresses.

Thus, although the biotic and abiotic stress response pathways share common responses, the net effect of concurrent abiotic and biotic stress interaction on plants cannot be predicted from the individual stressed plants (Suzuki et al. 2014). Reports indicates that these common responses can also be tailored in terms of the magnitude or fold change which cannot be extrapolated from individual stress response (Atkinson and Urwin 2012; Prasch and Sonnewald 2015; Rasmussen et al. 2013) (Fig. 1.1). Based on these evidences, we propose that the concurrent stress combinations are perceived by plants as a 'new stress' leading to a reprogramming of the defence responses while compared to plants under individual stress. In addition to these different responses, combined stressed plants also maintain a state reminiscent of individual stresses.

1.6 Conclusions and Future Perspective

Frequent incidences of combined drought and pathogen stress result in inevitable losses in crop yields. The limited understanding on the plant responses towards combined stress highlights the importance of nature of infecting pathogen, time of occurrence of each stress, intensity of the stress, plant age and genotype of the plant. The two constituent stressors of combined stress can interact with each other outside or inside the plant and influence plant resistance and physiology. Each stressor can interact with plant genotype and modulate physiology and resistance response towards subsequent stressor. In these cases, the net impact on plant can be predicted from independent stress studies. Alternatively, the combined stress can directly be perceived as a different stress, and the resultant net impact is not reminiscent of either of the individual stresses. In such case, the net impact on the plant is difficult to comprehend from individual stress studies and warrant an explicit study to dissect the combined stress responses. In this purview, studying the plant genetic architecture with reference to combined stress is a viable approach. Incorporating different levels of stress, time and plant genotype in future studies helps to dissect the constituents of combined stress responses, while at the same time, the need for identification of a parameter to screen combined stressed plants is of utmost importance. Altogether, the gained knowledge can be better translated to assess the utilization and environmental risks of different genotypes under combined stress. The increased understanding of plant responses and genetic architecture under combined stress further opens up avenues for breeding programmes for improvement of cultivars.

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