Chapter 12
The Interactive Effects of Drought and Herbivory on Ecophysiology of Trees

Sheel Bansal

12.1 Introduction

The impact of drought or herbivory on tree growth and physiology can range from moderate and recoverable to severe and lethal depending on the intensity of either stressor. When these two stressors occur simultaneously, their combined impact on tree performance is assumed to be synergistic, i.e., greater than expected based on simple additive effects from either stressor alone (Niinemets 2010). This assumption is fueled from repeated observations of massive forest dieback following insect outbreaks during years with extreme drought (Ayres and Lombardero 2000; Mattson and Haack 1987). Drought affects a broad set of physiological processes such as transpiration and photosynthesis, hydraulic conductivity, and carbohydrate utilization, while herbivory elicits a number of carbon- and nitrogen-expensive defense mechanisms (Taiz and Zeiger 2002). Thus, the two stressors complement their negative impacts on tree ecophysiology. However, tree responses to either stressor may trigger physiological adjustments that protect against the effects of the second stressor (Fujita et al. 2006), thereby leading to antagonistic (less than expected) responses to co-occurring drought and herbivory. There are thousands of published studies on the effects of drought or herbivory, yet very few have simultaneously considered their combined impacts on tree performance (Bansal et al. 2013; Trowbridge et al. 2014). Unfortunately, studies on multiple stressors frequently show non-additive effects (i.e., synergistic or antagonistic), and therefore the combined effects cannot be predicted based on results from single-stressor studies. Given that both drought events and biotic stressors (e.g., insect outbreaks) are expected to occur with increased frequency and intensity with climate change (Mitchell et al. 2013), research on the effects from these combined stressors on tree growth and physiology is critical for predicting future forest health and productivity.

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12.2 Drought Alone

The environmental condition known as "drought" can be defined simply as the condition when soil moisture falls below a minimum threshold causing reduced plant growth (Bréda et al. 2006). However, under natural scenarios, "drought" can be episodic or chronic, moderate or severe, and caused by warm temperatures, low precipitation, high vapor pressure deficit, intense solar radiation, salt accumulation, and/or freezing soils (Larcher 2003). Also, the effects of drought on plant ecophysiology are a function of innate adaptive plant traits to conserve water, current plant health and vigor, and competitive interactions to acquire limited soil moisture supply. Consequently, the impacts of drought on growth and physiology are context-dependent on a number of external and internal factors. Nevertheless, the physiological responses of trees to drought have many similarities across species. This topic has been well reviewed, particularly in recent years, because the traditional mechanisms assumed to cause drought-induced tree mortality are being questioned and expanded upon (McDowell et al. 2008; McDowell 2011; Ryan 2011; Sala et al. 2010).

The fast-acting responses of trees to drought occur at the genetic, biochemical, and cellular levels (Fig. 12.1; Osakabe et al. 2014). Soil drying and desiccation of root tissues trigger the expression of drought-induced genes that synthesize various hormones, in particular abscisic acid (ABA; Fig. 12.2; Chaves et al. 2003).

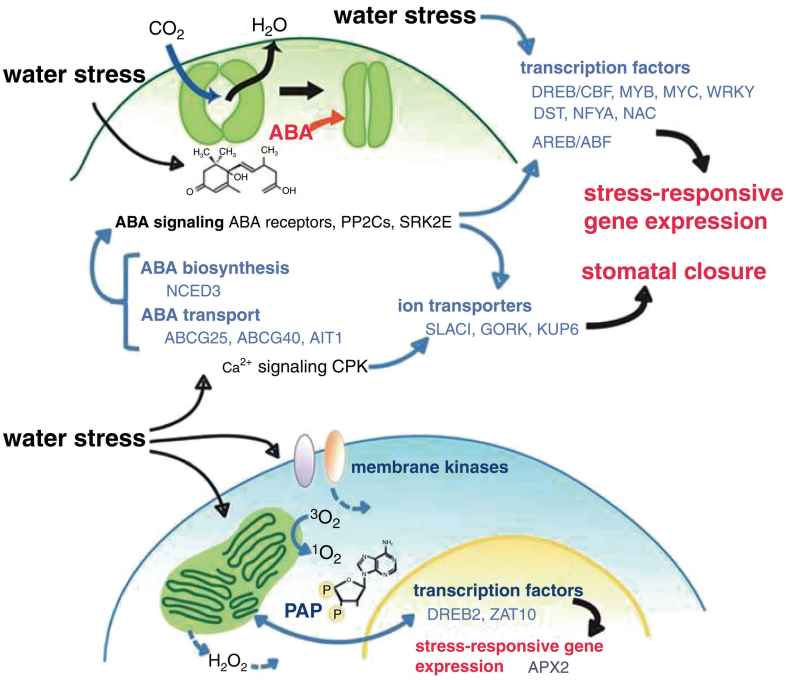

Fig. 12.1 Genetic, biochemical, and hormonal signaling factors in stomatal closure and retrograde signaling during water stress. (Figure from Osakabe et al. 2014)

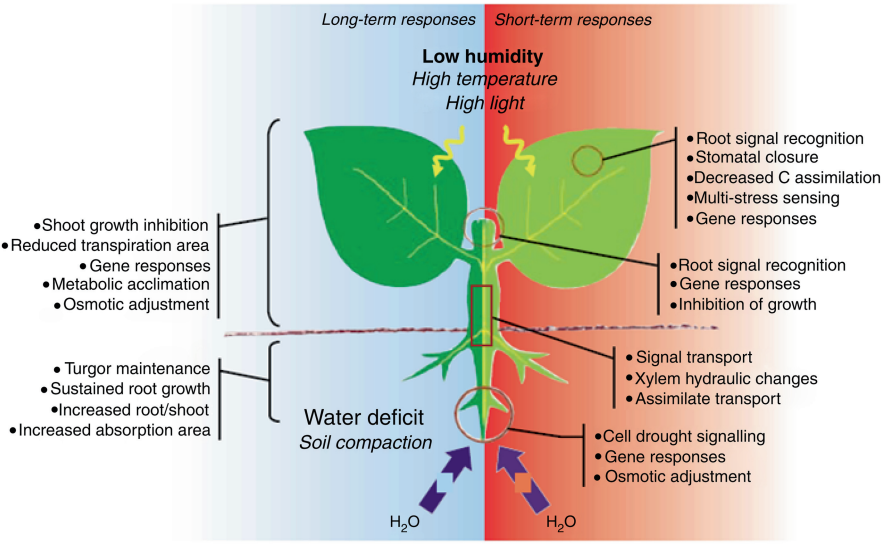

Fig. 12.2 Whole-plant responses to drought stress. *Left*, long-term or acclimation responses; *right*, short-term response. (Figure from Chaves et al. 2003)

ABA is a ubiquitous plant hormone that activates several physiological processes in response to environmental stress. In the case of drought stress, ABA is translocated to leaf tissues from roots, and there it binds to the plasma membrane of stomatal guard cells (Taiz and Zeiger 2002). The result is a flux of ions across the cell membrane, leading to rapid osmotic adjustments, shrinkage, and closure of the stomatal guard cells. ABA-induced stomatal closure is a key physiological mechanism to quickly limit water loss and to increase water-use efficiency, particularly for isohydric species. However, stomatal closure may not be 100% effective at constraining water vapor loss ("leaky stomata"), and water vapor also diffuses through the cuticular membranes that enclose leaf tissues (cuticular transpiration; Burghardt and Riederer 2003; Kerstiens 1996; Schreiber and Riederer 1996). Moreover, stomatal closure comes at significant costs of reduced CO_2 uptake for photosynthesis, thus limiting the production of carbon assimilates that are needed for growth, maintenance, reproduction, and/or the production of defense compounds against herbivores (Kempel et al. 2011).

There are many longer-term morphological adjustments that occur in response to drought stress. At the leaf level, reduced turgor pressure in cells decreases growth rates, in particular the process of cellular elongation (Meier et al. 1992). Reduced elongation is evident in droughted plant leaves as a decrease in the ratio of leaf area to leaf mass (i.e., lower specific leaf area; Abrams et al. 1994). Lower specific leaf area has adaptive value for plants exposed to chronic moisture stress because there is less leaf area for water loss through stomatal or cuticular transpiration (Grace 1990; Bansal et al. 2014). Unfortunately, lower specific leaf area also

reduces leaf area for light interception and CO_2 uptake, which has negative impacts on photosynthetic carbon assimilation rates (Oren et al. 1986).

At the whole-plant level, large-scale redistribution of carbon assimilates can be used to further minimize water loss and to increase soil moisture uptake. Specifically, plants typically undergo an increase in the ratio of root-to-shoot biomass, an increase in rooting depth and root density, and leaf shedding or abscission in response to drought (Larcher 2003). While these changes may be critical for plant survival during periods of extreme drought stress, they also come at a severe cost to carbon uptake and assimilation.

If drought conditions persist, even extreme physiological and morphological adaptive responses may not adequately prevent dysfunction of basic processes necessary for survival (Sevanto et al. 2014). If water loss continues via cuticular transpiration, even after water uptake by roots has diminished, tension builds up on the transpiration stream in the xylem (i.e., more negative xylem water pressure), particularly for trees because of their high transpirational areas and long distances to transport water (Taiz and Zeiger 2002). With increasing tension, hydraulic conductance of water to leaves from roots is eventually disrupted by cavitations and embolisms of air bubbles into the xylem stream. These breaks in the water column can quickly lead to 100% loss of hydraulic conductivity, although the extent that plants are vulnerable to cavitations under conditions of negative xylem water pressure differs greatly among plant taxa (Cochard 1992; Maherali et al. 2004; Tyree and Ewers 1991).

Hydraulic failure has been the traditional mechanism assumed to cause mortality in trees exposed to frequent and severe drought events. However, as described above, many of the ecophysiological responses to cope with drought stress reduce carbon assimilation, which have led to the development of a newer "carbon-starvation" hypothesis regarding drought-induced tree mortality (McDowell et al. 2008; Sala et al. 2010). While hydraulic failure is expected to cause tree mortality relatively quickly, carbon starvation is hypothesized to take place over longer periods of time in which plants experience negative carbon balances (i.e., greater carbon use than carbon gain). As trees become depleted in carbohydrates, they are unable to meet metabolic demands for basic functioning, or to biosynthesize carbon-rich defense compounds necessary against biotic agents (Fig. 12.3; Gutbrodt et al. 2011; McDowell 2011). Clearly, these consequences of carbon starvation have direct implications for tree–herbivore relationships.

12.3 Herbivory Alone

Herbivory can be defined as the consumption of plant material, often occurring on living plants, but not always lethal (Ohgushi 2005). However, this simple definition is one of the only ubiquitous generalizations that can be made regarding the impact of herbivory on plant performance. The reason being that the effects of herbivory are context-dependent on a number of factors, including the herbivore func-

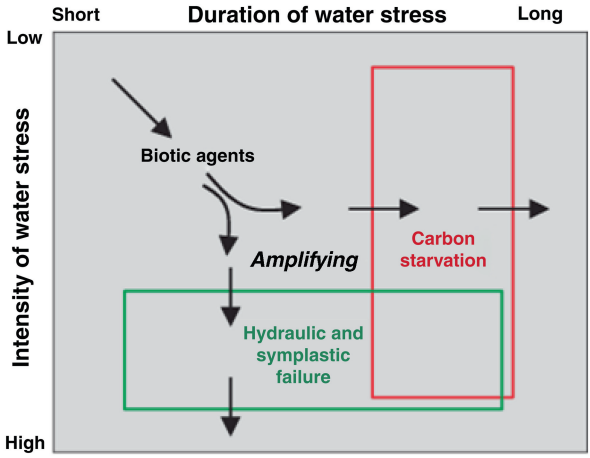

Fig. 12.3 Theoretical relationship, based on the hydraulic framework, between the temporal length of drought (duration), the relative decrease in water availability (intensity), and the three hypothesized mechanisms underlying mortality. Carbon starvation is hypothesized to occur when drought duration is long enough to curtail photosynthesis longer than the equivalent storage of carbon reserves for maintenance of metabolism. Hydraulic failure is hypothesized to occur if drought intensity is sufficient to push a plant past its threshold for irreversible desiccation before carbon starvation occurs. Biotic agents, such as insects and pathogens, can amplify or be amplified by both carbon starvation and hydraulic failure. (Figure from McDowell et al. 2008)

tional group (e.g., insects, mites, mammals), feeding behavior (e.g., defoliators, phloem-feeders, cell-content feeders), and stage of host physiological development (e.g., seed, juvenile, adult; Agrawal 1998; Karban and Myers 1989). In addition, the impacts from herbivory may be confounded by hitchhiker pathogens such as parasites, bacteria, fungi, and viruses that are often introduced during feeding (Hatcher 1995; Trapp and Croteau 2001). Among herbivores, trees are probably most affected by phytophagous insects, and entire forests have been decimated from beetles, moths, weevils, budworms, and caterpillars (Ayres et al. 2014). Herbivore-induced plant responses include the production of secondary metabolites, physical deterrents, compensatory physiology and growth, and tissue abscission (Agrawal 1998; Strauss and Agrawal 1999). Many of these responses come with high carbon costs (Dungan et al. 2007), similar to the impacts from drought stress.

Like drought, plant responses to herbivory begin at the subcellular level (Fig. 12.4; Wu and Baldwin 2009). Wounding of plant tissues from feeding or the injection of foreign compounds from herbivores initiates the release of hormones such as jasmonic acid (JA), elicits defense-related genes, and increases the production and modification of secondary metabolites (Karban and Myers 1989; Kessler and Baldwin 2002). The ultimate goal of these defense compounds is to reduce the preference for the host plant or the performance of the herbivore. Secondary metabolites are generally categorized as terpenoids or phenolics, which are carbon-rich allelochemicals such as flavonoids, tannins, and lignins, or as nitrogen-containing

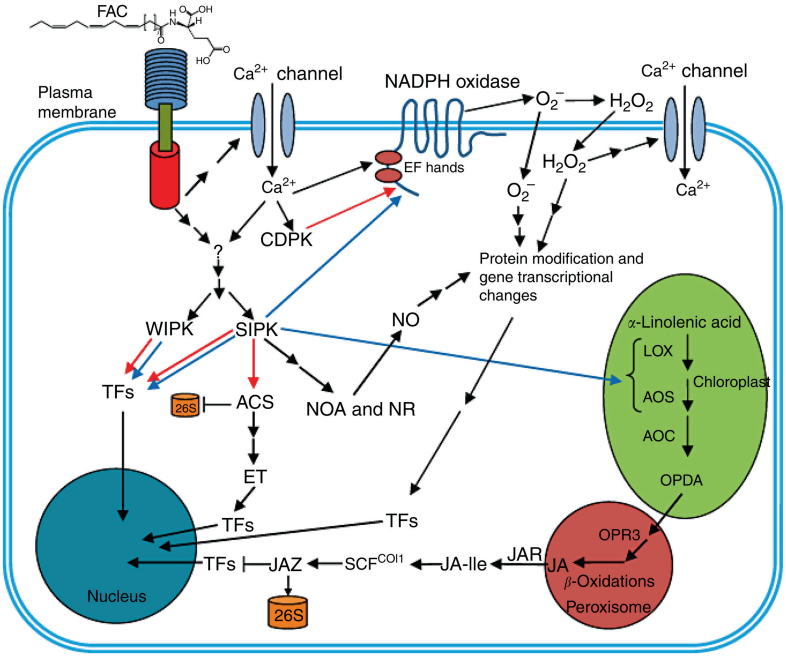

Fig. 12.4 A model summarizing early signaling events in herbivore-attacked plants. After herbivore attack, herbivore elicitors (here FAC??) bind to putative receptors on plasma membranes and activate further responses. Through an unknown mechanism, Ca^{2+} influx is initiated, which depolarizes cell membranes. Increased Ca^{2+} (likely together with a CDPK) greatly enhances NADPH oxidases located in cell membrane and leads to ROS production. MAPKs (at least SIPK and WIPK) are quickly activated; they transcriptionally regulate many genes involved in JA and ethylene biosynthesis, as well as NADPH oxidase and WRKY transcription factors (TFs). SIPK is likely also involved in NO production; both ROS and NO modify amino acids in proteins and induce transcriptional changes of various defense-related genes. A yet to-be-indentified pathway triggers JA biosynthesis. JA is further converted to JA-Ile by JAR; binding of JA-Ile to SCF^{COI1} initiates the degradation of JAZ proteins that negatively regulate JA-responsive genes. Without phosphorylation, ACS is degraded through 26S proteasome pathway; after being phosphorylated by SIPK, it gains higher stability and enhances ethylene biosynthesis. *Red arrows* represent phosphorylation; *blue arrows* represent transcriptional regulation. *AOC* allene oxide cyclase, *AOS* allene oxide synthase, *CDPK* calcium-dependent protein kinase; *FAC* Fatty acid chains; *JAZ* jasmonate ZIM-domain, *LOX* lipoxygenase, *OPDA* 12-oxo-phytodienoic acid, *OPR3* OPDA reductase 3, *NO* nitric oxide, *NOA* NO-associated protein, *NR* nitrate reductase, *ROS* reactive oxygen species, *SCF* Skp, Cullin, F-box, *SIPK* salicylic acid-induced protein kinase, *WIPK* wound-induced protein kinase. (Figure from Wu and Baldwin 2009)

compounds, which include alkaloids, cyanogenic glycoside, and lectins (Taiz and Zeiger 2002). Because these compounds are carbon and nutrient expensive to plants, they are only produced when necessary, especially those that have no apparent function toward growth or development (Langenheim 1990; Poorter and Villar 1997).

Conifer trees utilize volatile monoterpenes as a primary defense against insect herbivory and exude oleoresins following wounding, which constitute large carbon investments into compounds that are not recycled and ultimately lost to the environment (Croteau and Johnson 1985; Trapp and Croteau 2001; Trowbridge et al. 2014).

Plants also undergo defensive, morphological adjustments to protect against herbivory (Hanley et al. 2007). These changes can include the production of external thorns, prickles, spines, and hairs (Myers and Bazely 1991) or an increase in epicuticular waxes, cutins, and suberins (Eigenbrode and Espelie 1995). In addition, plants can cope with herbivory through repair of wounded tissues, abscission of infected tissues, or compensatory regrowth of lost tissues (Neely 1970). Like chemical defenses, morphological changes comes at large carbon investments for the host plant, which increase survivorship but at the cost of reduced growth, reproduction, and carbohydrate storage (Fig. 12.5; Agrawal 2011; Dungan et al. 2007; Orians et al. 2011).

Insect herbivores have additional impacts on plant carbon balance beyond the induction of plant chemical and morphological defense responses. Consumption of leaf tissues by defoliators reduces the amount of leaf area available for photosynthetic carbon assimilation, while phloem-feeders (such as weevils or beetle larvae) directly consume phloem sap sugars as they are transported through the stems from leaves to roots (Karban and Myers 1989). Both of these impacts from herbivory can have tremendous consequences on carbohydrate reserves that are needed for growth, reproduction, and metabolic functions, thus reducing plant vigor and ultimately leading to mortality.

12.4 Drought Combined with Herbivory

When trees experience more than one stressor simultaneously, complimentary impacts on related physiological processes may turn an otherwise recoverable situation into catastrophic dysfunction and mortality. From the above descriptions on the impacts of drought stress or herbivory alone, it is clear that there are several ecophysiological mechanisms that would be negatively impacted if both stressors co-occurred. Herbivory tends to increase carbon demands, while drought stress decreases carbon gain, making it easy to assume that the two stressors combined will have a synergistic, negative effect on plant carbon balance. Thus far, very few studies have empirically tested the interactions of drought and herbivory on plant performance, particularly for trees (Bansal et al. 2013; Trowbridge et al. 2014).

One study that explicitly tested for synergistic, additive, or antagonistic effects from drought combined with herbivory (simulated phloem-feeding weevils in this case) on ecophysiology of *Pinus sylvestris* seedlings found, contrary to expectations, that many traits were affected antagonistically (Fig. 12.6; Bansal et al. 2013). Specifically, gas exchange and growth rates were sharply reduced when both stressors co-occurred, although the total, combined effects were less than expected based on additive effect of either stressor alone. While these findings were unantici-

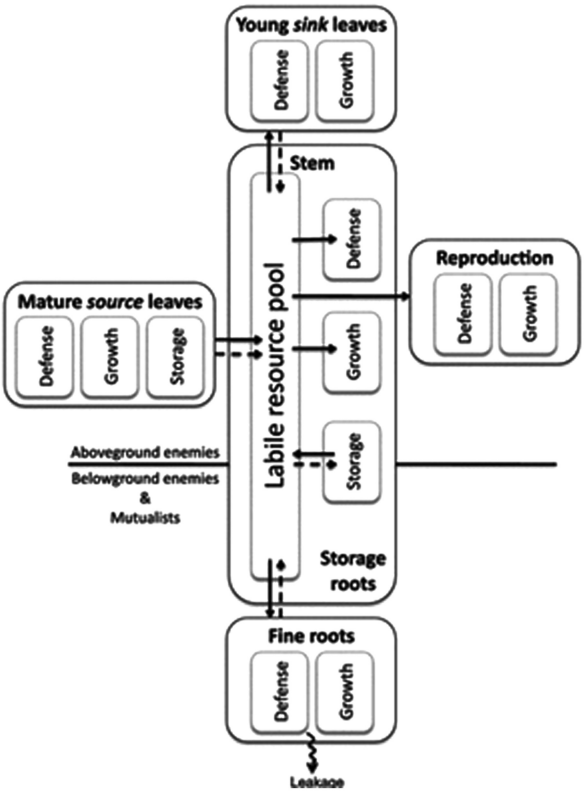

Fig. 12.5 Conceptual model for resource flows in plants. The labile resource pool is derived from newly captured pools of carbon and nutrient pools or from remobilized storage reserves. The labile carbon pool is generated from photosynthesis, primarily by mature source leaves. The labile nutrient pool is obtained from roots. The resulting labile resource pool can then be allocated to support the growth of sink tissues (roots, leaves, or reproductive tissues), to defense traits, and to storage tissues. Herbivore-induced export of resources from leaves or from fine roots (*dashed arrows*) into stems and storage roots functions to sequester resources in tissues inaccessible to the respective herbivores but may incur opportunity costs if resources allocated for storage limit growth and reproduction or ecological costs if other enemies specialize on these storage tissues. (Figure from Orians et al. 2011)

pated, there are a few biological mechanisms that could explain the results. First, exposure to drought stress *or* herbivore wounding may have triggered a series of stress-induced genes and physiological responses that "primed" or protected the trees from the second, co-occurring stressor (Bowler and Fluhr 2000; Fujita et al. 2006; Leshem and Kuiper 1996; Rennenberg et al. 2006). For example, some studies have shown a short-term increase in resin acid concentrations in plants exposed to moderate drought stress (Turtola et al. 2003), which could facilitate wound healing and monoterpene emissions to cope with herbivory. *Pinus taeda* showed an

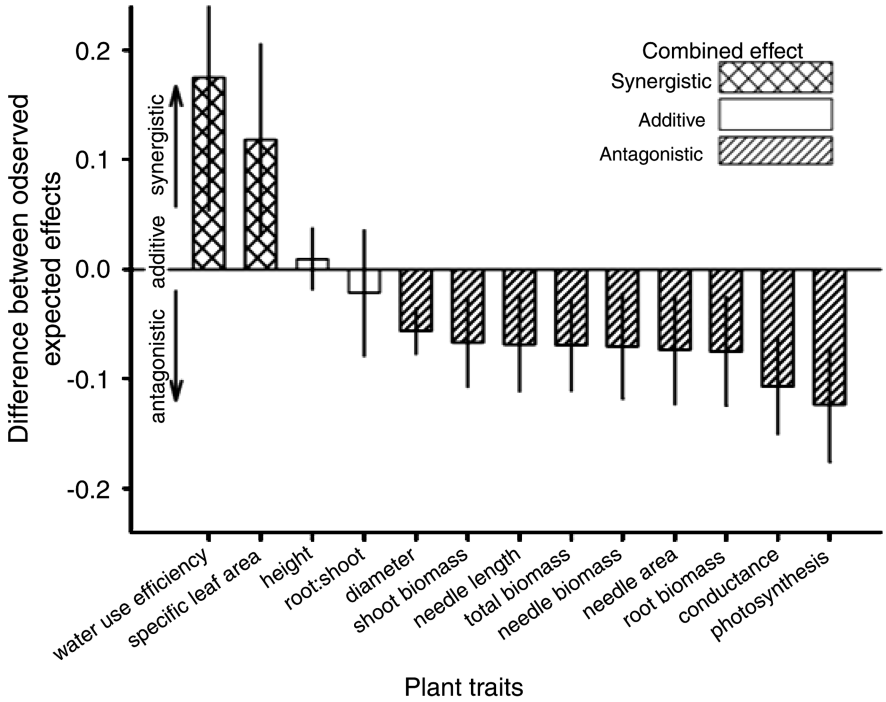

Fig. 12.6 The combined impacts from drought and herbivory on various plant traits were synergist, additive, or antagonistic (greater than, equal to, or less than expected effects, respectively, based on single stressor effect sizes). The *bars* represent the overall effect size difference (mean ±95 % CI) between the observed and expected additive effects from combined drought and herbivory on morphological traits at final harvest and second-year physiological traits of *P. sylvestris* seedlings. The *zero line* represents the expected additive effects from combined stressors. When the means (and their 95 % confidence limits) were greater than or less than the zero line, they were considered synergistic or antagonistic, respectively. (Figure from Bansal et al. 2013)

increase in defense resin synthesis in response to soil moisture stress despite a decrease in growth rates (Lorio and Sommers 1986). This phenomenon of interacting responses to multiple stressors has also been documented for the combined effects of fire and herbivory on *Pinus radiata,* in which tree exposed to fire had increased antiherbivore resin defenses that provided protection against subsequent bark beetle attacks (Lombardero and Ayres 2011).

A second possibility for antagonistic effects from drought and herbivory on tree ecophysiology was that the impact of drought stress overrode the effects of herbivory. A study conducted in situ that monitored monoterpene emissions of *Pinus edulis* found the influence of soil moisture was relatively strong compared to herbivory during the midsummer drought (Trowbridge et al. 2014). However, they also showed how herbivory played a dominant role in affecting plant defenses during periods of the growing season with higher soil water availability, thus dem-

onstrating the importance of stressor severity and temporal variability on the interaction of drought and herbivory.

Even though Bansal et al. (2013) generally found antagonistic effects of drought and herbivory on tree physiology and growth, there were two key functional traits, specific leaf area and water-use efficiency (ratio of carbon gain to water loss), that exhibited relatively strong, synergistic effects from the combined impact of the two stressors (Fig. 12.6). These two traits are particularly important to resource-use efficiency, carbon gain and allocation, and survival (Reich et al. 1997). Droughted seedlings had decreased shoot biomass and needle size, thus reducing water demands disproportionately to water supply. Those morphological adjustments allowed the seedlings to maintain relatively high water saturation for individual needles, which in turn led to an increase in specific leaf area in response to drought. The increase in water-use efficiency of droughted seedlings was driven by stomatal closure in response to decreased soil moisture. Unlike with drought, the mechanisms leading to an increase in specific leaf area and water-use efficiency from herbivory were less clear, as were the mechanisms driving the synergistic effects from both stressors combined. Regardless of the mechanisms involved, the synergistic increase in specific leaf area increased light-capturing area for photosynthetic carbon gain, while the increase in water-use efficiency decreased carbon gain but conserved relatively more water under droughted conditions. Consequently, these two synergistic effects aided in establishing seedlings and coping with multiple stressors.

Intensity-dependent effects from multiple stressors have rarely been explored. In Bansal et al. (2013), stressor intensity played an important role in determining the impact of drought or herbivory alone but also affected how the two stressors interacted. For example, the cumulative effects from the two stressors on height, diameter, and shoot biomass were stronger (synergistic or additive) when both stressors were of moderate intensity, but were antagonistic when either stressor was severe. This suggests that co-occurring stressors at lower intensity could have a disproportionate, negative impact on seedling growth (Mitchell et al. 2013). In contrast, the combined effects of drought and herbivory were stronger on needle length and gas exchange when drought stress was severe, irrespective of herbivore intensity, thus demonstrating how the effects of multiple stressors are also trait-dependent.

12.5 Drought Effects on Herbivores and Plant–Herbivore Interactions

Clearly, drought and herbivory has many overlapping consequences on tree ecophysiology. However, from an ecological perspective, drought also has a direct effect on herbivorous insect populations. In addition, the changes in plant chemistry that occur from drought can affect herbivore feeding preferences, thus altering plant–insect interactions (Gutbrodt et al. 2011; Mattson and Haack 1987).

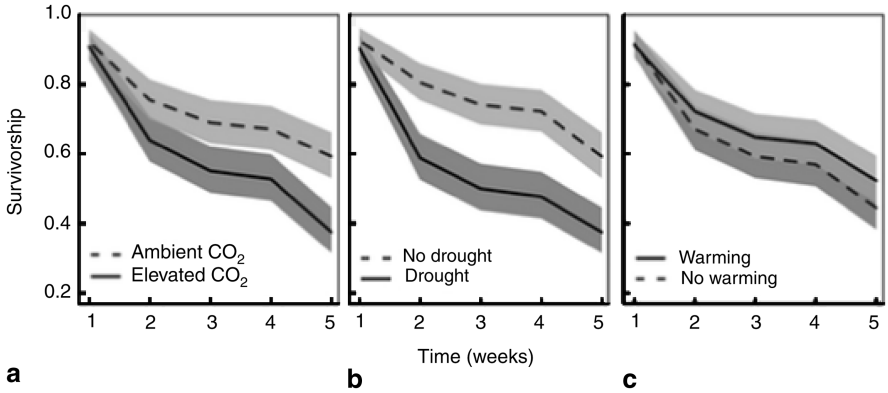

Fig. 12.7 Kaplan–Meier survivorship of *Lochmaea suturalis* larvae over time for plots with elevated treatments ($N=24$ per time point, *solid lines*) and ambient plots ($N=24$ per time point, *broken lines*). *Gray shaded areas* show 95 % confidence intervals of the Kaplan–Meier estimator. Significance of interactions with time: **a** $P=0.057$ and **b** $P<0.0001$. **c** Warming was only significant in a three-way interaction with CO_2 and drought ($P=0.019$). (Figure from Scherber et al. 2013)

Drought can have either negative or positive impacts on herbivore populations, depending on the severity and duration of the drought. Moisture stress typically has negative impacts on the fitness of developing larvae (Fig. 12.7; Scherber et al. 2013). However, drought is frequently associated with warmer temperatures, which accelerates insect metabolism, leading to faster growth, consumption, and developmental rates (Jamieson et al. 2012). Warmer winter temperatures in particular tend to enhance insect overwintering survival (Bale et al. 2002; Bentz et al. 2010), as well as induce earlier emergence and phenological development (Parmesan and Yohe 2003). Consequently, the effects of drought on herbivorous insect populations are not unidirectional and context-dependent.

The direct effects of drought on herbivore populations are confounded by indirect effects of drought on their forage quality, i.e., on host plant ecophysiology (Bauerfeind and Fischer 2013; Koricheva et al. 1998; Rouault et al. 2006). There has been a long-standing "plant stress hypothesis" which states that plants under abiotic stress have lower defensive capabilities and are therefore more suitable as a food source for herbivorous insects (Mattson and Haack 1987; White 1974; White 1984). Temporal correlations between drought events and insect outbreaks support this hypothesis (Hart et al. 2014). Alternatively, the "plant vigor hypothesis" predicts that insects will preferentially feed on faster-growing, healthier plants that have higher nutritional content and lower defense compounds (Price 1991). A suite of meta-analyses, modeling, and manipulative studies have shown that drought stress does not consistently lead to increased or decreased insect consumption, and is often dependent on species, feeding guild, and specialization of the herbivores (Bauerfeind and Fischer 2013; Grinnan et al. 2013; Haynes et al. 2014; Huberty and Denno 2004; Larsson 1989; Rouault et al. 2006). A unique study conducted by Gutbrodt et al. (2011) elegantly demonstrated how the effects of drought stress on plant tissue

moisture content (health) and secondary metabolite concentrations (defense) led to differing feeding preferences for a generalist compared to a specialist herbivore. These changes in feeding behavior that occur on drought-stressed plants will likely impact subsequent insect population dynamics, and further influence plant vigor and chemistry, thus creating a feedback system and further complicating the interaction of drought and herbivory.

12.6 Conclusions

In the environment, the co-occurrence of multiple environmental stressors is the rule rather than the exception (Chapin et al. 1987; Niinemets 2010; Vierling and Kimpel 1992). Global climate change is expected to increase the frequency and intensity of drought events and herbivorous insect outbreaks (Allen et al. 2010; Bale et al. 2002; Vinebrooke et al. 2004; Williams and Jackson 2007), thereby increasing the probability that the two will co-occur in the future. Moreover, expected increases in other stressors, such as extreme heat events and wildfires, could exacerbate conditions beyond a critical threshold of plant tolerance. Consequently, forests worldwide are at increased risk of extreme dieback. For drought and herbivory in particular, their combined, negative impact on tree carbon balance has important implications for forest productivity and carbon sequestration at global scales. Therefore, improving our understanding of the interacting effects of multiple stressors on tree growth and physiology is crucial (but poorly investigated) for managing future forests.

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