Chapter 2
The Impact of Enhanced Atmospheric CO_2 Concentrations on the Responses of Maize and Soybean to Elevated Growth Temperatures

Richard C. Sicher and James A. Bunce

2.1 Introduction

The agricultural industry is uniquely dependent upon climate and a changing climate has the potential to alter crop productivity and affect economic returns to growers. Atmospheric CO_2 levels have risen about 40 % since the advent of the industrial revolution and this is largely due to fossil-fuel combustion and changes in land management (IPCC 2007). Because atmospheric CO_2 absorbs heat from the sun, global mean temperatures, over both land and water, increased to an average of 0.85 °C between 1880 and 2012 (IPCC 2013). Additional increases in the global mean temperature are likely to occur during the current century and this will have consequences for both mechanized and subsistence agriculture. The IPCC (2007) has concluded that global mean temperatures could increase by an additional 4 °C by the end of the current century, if mitigation measures are not enacted. Moreover, a report by Hatfield et al. (2008) predicts that agriculture will face a more variable, future climate with an increased frequency of extreme weather events including, prolonged drought, intense heat waves, and episodes of drenching rains. Above optimal temperatures decrease both the vegetative and reproductive growth of crop plants but this may be partially offset by greater rates of net photosynthesis due to CO_2 enrichment (Baker and Allen 1989; Boote et al. 2005). Several excellent reviews exist that discuss the effects of heat and/or abiotic stress (Vierling 1991; Wahid et al. 2007; Ahuja et al. 2010; Mittler et al. 2011) and of CO_2 enrichment (Kimball et al. 1993; Allen et al. 1996; Sicher and Kim 2011; Barnaby and Ziska 2012) on plants. The current chapter briefly discusses these subjects but principally focuses on how elevated temperatures and increased atmospheric CO_2 concentrations interact to affect the growth and harvestable yields of important crop plants.

R. C. Sicher (✉) · J. A. Bunce
Crop Systems and Global Change Laboratory, Beltsville Agricultural Research Center, Room 342, Building 001, 10300 Baltimore Avenue, Beltsville, MD 20705, USA
e-mail: Richard.Sicher@ars.usda.gov

R. Mahalingam (ed.), *Combined Stresses in Plants,* DOI 10.1007/978-3-319-07899-1_2

Our primary focus will be on soybean and maize but, where inadequate data are available, results for related legumes, tropical grass species, and specific crop plants also will be cited.

2.2 Positive Effects of CO_2 Enrichment on Plants

The carbon for plant growth is derived from CO_2 in the atmosphere and the light-dependent reactions of photosynthesis. The current atmospheric CO_2 concentration, i.e., 396 μmol mol^{-1}, does not saturate rates of photosynthesis for the majority of terrestrial plants that possess the C_3 pathway of photosynthesis (Stitt 1991). Many important agricultural crops, including rice, cotton, potato, wheat, and soybean, possess the C_3 pathway of photosynthesis. Supra-ambient CO_2 concentrations normally increase rates of photosynthesis, photoassimilate accumulation, and growth of most terrestrial plants. The conversion of carbon dioxide into organic products takes place in the chloroplast stroma and is catalyzed by the bifunctional enzyme, Rubisco. The concentration of CO_2 within the chloroplast is estimated to be 10 μM, which is close to the apparent Michaelis constant (K_m) for the CO_2 fixation reaction of Rubisco. Rubisco also functions as an oxygenase, that competitively inhibits the carboxylase activity of the enzyme, and the former reaction initiates the first step in photorespiratory metabolism. Therefore, an increase in atmospheric CO_2 concentration is capable of accelerating the rate of CO_2 fixation in the chloroplast by simultaneously enhancing the carboxylation and inhibiting the oxygenation reactions of Rubisco (Kobza and Edwards 1987). Stitt (1991) has argued that increasing the atmospheric CO_2 concentration from 396 to 700 μmol mol^{-1} should accelerate the net rate of photosynthesis of C_3 plants by 25–75 %.

Other plants, including maize, sorghum, and sugar cane, are dependent upon a second carboxylase enzyme, i.e., phospho(enol) pyruvate carboxylase (PEPCase), to catalyze the initial reactions of photosynthesis. The immediate products of the PEPCase reaction are C_4 acids, which are subsequently decarboxylated in the vicinity of Rubisco (Sage and Kubien 2003). This raises the intracellular CO_2 concentration in a manner that facilitates the carboxylase activity of Rubisco and almost completely inhibits the oxygenase activity. Unlike C_3 plants, photosynthetic rates of plants possessing the C_4 biochemical concentrating mechanism are effectively saturated at ambient atmospheric CO_2 levels. Therefore, rates of CO_2 fixation, whole plant growth rates, and harvestable yields of C_4 plants are not nearly as responsive to rising atmospheric CO_2 concentrations as that of C_3 plants. However, both C_3 and C_4 plants exhibit stomatal closure in response to elevated CO_2 and this has important consequences for plant–water relations (Bunce 2004). Because high concentrations of intracellular CO_2 are maintained, partial stomatal closure due to CO_2 enrichment normally does not inhibit photosynthetic rates of maize and other C_4 plants (Sage 1999). Therefore, growth rates of maize can be positively affected by CO_2 enrichment, in part, because of improved water relations. However, any growth enhancement of C_4 plants due to CO_2 enrichment is usually much smaller than that reported for C_3 plants (Kimball et al. 1993; Hatfield et al. 2011).

2.3 Negative Effects of CO_2 Enrichment on Plants

CO_2 enrichment is broadly beneficial for plant growth, although continuous exposure to elevated CO_2 can have a negative impact on plant development. It has been observed that the C/N ratio is frequently higher in plants grown in elevated than in ambient CO_2 (Baker et al. 1989; Foyer et al. 1994), which suggests that the uptake and assimilation of N, and possibly other nutrients from the soil, is not commensurate with the C gain due to CO_2 enrichment from the atmosphere. In some instances, plants grown in elevated CO_2 can become N deficient, which reduces tissue protein concentrations and decreases photosynthetic capacity (Stitt 1991). There are examples where photosynthetic rates of older leaves in the elevated CO_2 treatment were below that of comparable leaves in the ambient CO_2 treatment and this occurred when gas exchange rates were measured at the respective CO_2 concentrations used for plant growth (Sicher and Kremer 1996).

Increased leaf starch levels are almost always observed in leaves of CO_2-enriched plants and this may partly be due to low leaf N concentrations and to accelerated rates of net CO_2 assimilation (Stitt 1991). Some authors (Sasek et al. 1985) argue that excessive starch levels in the chloroplast can alter the structure of photosynthetic membranes and this physical disruption negatively impacts leaf photosynthetic rates. Leaves of plants grown in CO_2-enriched atmospheres can also become chlorotic, brittle, and malformed (Sasek et al. 1985; Sicher 1998). Low chlorophyll levels in CO_2-enriched tissues have been attributed to nitrogen insufficiency and to the onset of premature senescence (Sicher and Bunce 1998). Premature senescence as a result of CO_2 enrichment has been observed for cereal crops, such as wheat and barley, but this same treatment delays the onset of senescence in soybean (Rogers et al. 2004). Clearly, alterations in the timing of senescence affect the overall yield potential of annual crops. In some plant species, the initial stimulation of photosynthesis in response to CO_2 enrichment may be reversed over time as nitrogen becomes insufficient and chlorosis develops. This process is known as photosynthetic acclimation to CO_2 enrichment and photosynthetic rates can ultimately be below that of control plants grown with ambient CO_2 concentrations.

2.4 Elevated Temperature Effects on Plant Growth

The relationship between plant growth and temperature is complex. The variation between day and night temperatures and also mean annual or seasonal temperatures is an important determinant of plant growth rates. Also, the interaction of temperature with other environmental variables, such as irradiance, water availability, and atmospheric CO_2 levels, affects plant development. The growth of all plants is characterized by a number of critical temperatures that can be determined empirically. For example, all plants possess a minimum, maximum, and optimum temperature for growth (Luo 2011; Table 2.1). The minimum and maximum temperatures are the lowest and highest temperatures, respectively, that will sustain the growth of

Table 2.1 Responses of reproductive yields of major crop species to temperature. The optimum and maximum temperatures for reproductive yield (T_{opt} and T_{max}, respectively) are means of day and night values

Crop	T_{opt}, °C (yield)	T_{max}, °C, (yield)	Yield (T_{opt}) t ha^{-1}	Yield (28 °C), t ha^{-1}	Yield (32 °C), t ha^{-1}	% decrease (28–32 °C)
Rice	25	36	7.6	6.3	2.9	54
Soybean	26–28	39–40	3.4	3.4	3.1	10
Dry bean	22–24	32	2.9	1.4	0	100
Peanut	23–25	40	3.4	3.2	2.6	20
Sorghum	23–25	35	12.2	11.8	7.0	41
Maize	20–25	35	10.9	–	–	–

Temperature data are from Hatfield et al. (2011) and Luo (2011). Yield data are from Dr. V. R. Reddy (personal communication)

a given plant species. Agricultural crops have an optimum temperature for yield and this is normally below that of the temperature optimum for vegetative growth (Muchow et al. 1990; Luo 2011). The explanation for this is that lower temperatures usually extend the growing season, thereby maximizing light interception and enhancing crop yields. Temperatures above the vegetative and reproductive growth optima are deleterious, although plants do possess adaptive mechanisms that facilitate growth and successful reproduction under stress-inducing, elevated growth temperatures.

2.5 Heat Stress Responses of Plants

Exposing plants to high temperatures for the first time, even for a few hours, can cause heat stress, which is a dangerous condition that can result in cell damage or even death (Mittler et al. 2011). Because leaves are thin and have a low heat capacity, cellular injuries can occur within minutes when plants are exposed to acute heat stress (Sharkey 2005). Cellular damage also occurs at moderately high temperatures but only after longer periods of exposure. The heat stress response of plants is complex and involves many components including the following: susceptible proteins become inactivated or denaturated (Zhang et al. 2005), membrane integrity and function is compromised (Howarth 2005); metabolic pathways break down (Wahid et al. 2007); the assembly and elongation of microtubules is disrupted (Smertenko et al. 1997); ion fluxes decrease (Schöffl et al. 1999), toxic compounds and reactive oxygen species (ROS) accumulate and both RNA and protein synthesis become impaired (Schöffl et al. 1999; Howarth 2005). To cope with heat stress, plant cells completely reprogram metabolic networks and synthesize stress-related metabolites, proteins, and lipid constituents (Wahid et al. 2007). Plants that are pretreated with high temperatures normally have an improved ability to withstand

future heat stress episodes and this occurs by a process known as acquired thermotolerance. At the cellular level, acquired heat tolerance requires gene activation and specific changes to the metabolome and transcriptome. Low molecular weight metabolites accumulate that function as compatible solutes in the protection of cellular proteins and membranes (Kaplan et al. 2004). Conversely, processes involved in establishing a basal level of heat tolerance are not upregulated by stress pretreatments (Qin et al. 2008).

One of the most important and most thoroughly studied aspects of thermotolerance is the accumulation of heat shock proteins (HSP) in response to heat stress and related environmental stresses (Wang et al. 2004). Families of HSPs vary by molecular weight, i.e., Hsp60, Hsp70, Hsp90, Hsp100, and small or sHSP, and are synthesized within a few hours of acute heat stress in plants. These proteins function as molecular chaperones and are involved in stabilizing and resolubilizing proteins that have denatured due to heat stress. Specific HSPs can be found in the nucleus, chloroplast, mitochondria, and in other cellular compartments (Kotak et al. 2007). This suggests that HSPs are involved in protecting and sustaining numerous, vital processes throughout the cell.

It is also clear that the oxidative stress is a significant factor in the heat stress response of plants and of other species. Heat stress frequently induces the synthesis of highly reactive molecules including, singlet oxygen, the superoxide radical, hydrogen peroxide, and hydroxyl radicals (Wahid et al. 2007). One consequence of ROS is the peroxidation of membrane lipids, which can lead to membrane leakage and a loss of membrane integrity. Brief exposures to high temperatures also induce a burst of hydrogen peroxide in plant cells that may be derived from NADPH oxidase activity (Neill et al. 2002). It is believed that this burst of hydrogen peroxide is a signal for the induction of several heat stress-related genes. Various antioxidant molecules, including ascorbate and glutathione, can protect against ROS and controlling ROS is a crucial mechanism in minimizing damage due to heat stress.

2.6 Heat Stress Effects on Photosynthesis

There is broad agreement that photosynthetic reactions within the chloroplast are among the most highly sensitive to heat stress in higher plants (Berry and Bjorkman 1980; Sharkey 2005). Both light-driven electron transport reactions in the thylakoid membranes and enzymatic reactions promoting CO_2 fixation in the stroma are thought to be thermolabile (Weis and Berry 1988; Havaux and Gruszecki 1993). Various lines of evidence suggest that the oxidizing side of photosystem-II was impaired by heat stress (Havaux and Gruszecki 1993; Heckathorn et al. 1998). However, the reduction of plastoquinone by photosystem-II is relatively thermotolerant and cyclic electron flow involving photosystem-I actually increased with heat stress (Bukhov et al. 1999; Schrader et al. 2004). The above adjustments decrease linear electron flow and reduce rates of CO_2 fixation.

2.7 Effects of CO_2 Enrichment and Heat Stress on Photosynthesis

Soybean, which possesses C_3 photosynthesis, generally has a substantial, long-term increase in leaf photosynthesis when grown at elevated CO_2 (Sicher and Bunce 1998; Bunce 2014; Fig. 2.1a). Under field conditions, soybean exhibits little (Bernacchi et al. 2005) or no downregulation of photosynthesis at elevated CO_2 when measured at high light, except when the plants are under water stress (Sicher and Bunce 1998). This contrasts with the often substantial downregulation of photosynthesis observed at elevated CO_2 in this species when grown in controlled environment chambers (Sicher et al. 1995; Sims et al. 1998). However, during long-term growth experiments, single-leaf photosynthetic rates were not increased by CO_2 enrichment when measured at limiting light levels (Rogers et al. 2006; Bunce 2014). This finding suggested that long-term exposure to elevated CO_2 decreased the quantum efficiency of photosynthesis in soybean, similar to that observed for various other species (Bunce and Ziska 1999; Lewis et al. 1999; Takeuchi et al. 2001).

In plants with C_3 photosynthesis, such as soybean, the optimum temperature for photosynthesis increases with the carbon dioxide concentration, primarily because

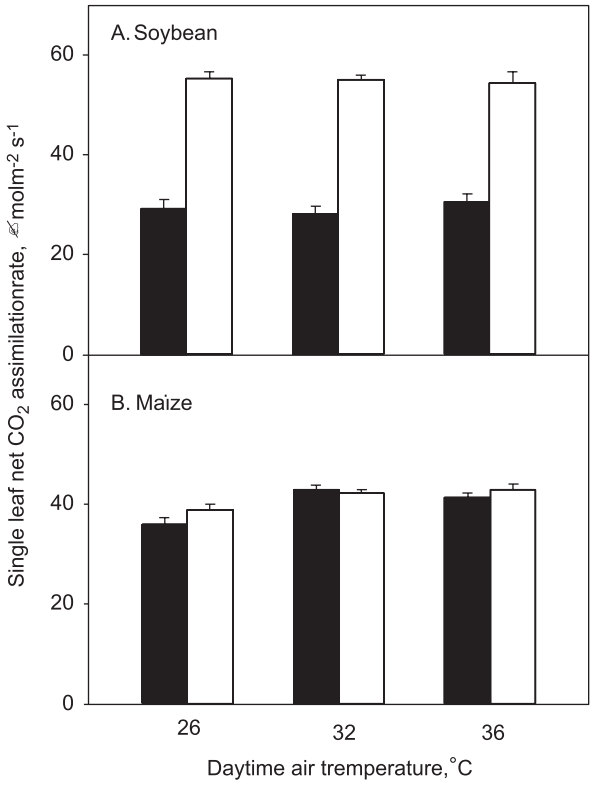

Fig. 2.1 Effects of elevated temperatures and CO_2 enrichment on single-leaf photosynthetic rates of maize and soybean. Plants were grown from seed in naturally sunlit, temperature-controlled enclosures at Beltsville, MD, and foliar photosynthetic rates were determined on sunny days shortly after canopy closure. Data are shown for ambient (*dark fill*) or twice ambient (*no fill*) CO_2 concentrations and are courtesy of Dr. V. R. Reddy

of the suppression of photorespiration and increased carboxylation rates due to CO_2 enrichment discussed above, i.e., due to changes of the V_c/V_o ratio (Long 1991; Kirschbaum 1994). This is true whether photosynthesis is light limited or light saturated. However, elevated temperatures can lower the ratio of the velocity of carboxylase to the velocity of oxygenase (V_c/V_o) (Jordan and Ogren 1984). Although a relative increase in photorespiration is a principal effect of elevated temperatures on photosynthesis, it is clear that other factors are also involved. The temperature at which the optimum rate of photosynthesis occurs largely depends upon the thermal stability of the RuBP-regeneration system, because the Rubisco protein itself is stable to at least 45 °C (Bjorkman et al. 1989; Devos et al. 1998). However, Crafts-Brandner and Salvucci (2000) and Ristic et al. (2009) observed that Rubisco became deactivated after the prolonged exposure of leaf tissue to acute heat stress. Briefly, in the inactivate state, the Rubisco enzyme tightly binds a substrate molecule to the active site, thereby blocking catalytic activity. A second protein, Rubisco activase, facilitates removal of the substrate from the active site and allows Rubisco to become activated and catalytically active. Both in vivo and in vitro evidence suggests that exposing leaf tissue to elevated temperatures can inactivate Rubisco activase. Therefore, one of the principal effects of elevated temperatures on photosynthesis is the conversion of Rubisco from an active to an inactive state. Lowering the Rubisco activation state decreases the carboxylation efficiency of photosynthesis and may lead to the production of excess energy that contributes to photo-oxidative stress (Ort and Baker 2002). However, Wise et al. (2004) and Kubien and Sage (2008) have argued that decreases in Rubisco activation state are a secondary effect caused by a reduction in electron transport rates. According to these authors, the deactivation of Rubisco at elevated temperatures functions naturally to restore the imbalance between electron transport rates and rates of CO_2 fixation.

The stimulation of photosynthesis by elevated CO_2 usually increases strongly and predictably with temperature (Long 1991). However, at excessively high temperatures, the CO_2-dependent stimulation of photosynthesis may be negated by low rates of Rubp-regeneration. When this situation occurs, the stimulation of photosynthesis by elevated CO_2 is highly insensitive to measurement temperatures (Bunce 2007; Ziska 2001; Yamori et al. 2005). Additionally, acclimation of photosynthesis to seasonal changes in temperature can result in the stimulation of photosynthesis by elevated CO_2 being nearly constant at different times of the year despite seasonal variations in temperature. This phenomenon has been attributed to thermal acclimation of the photosynthesis system (e.g., Bunce 1998, 2000; Tesky 1997; Tjoelker et al. 1998).

Above the optimum temperature of photosynthesis, photosynthetic rates may become unstable and decrease continuously with time. There is a critical temperature below which photosynthesis will completely recover after the plants are returned to ambient growth temperatures. However, above this critical temperature, irreversible damage occurs to the photosynthetic machinery of the leaf (Berry and Bjorkman 1980). This makes the assessment of CO_2 effects on responses of photosynthesis to extremely high temperatures difficult. Taub et al. (2000) found that for about 60 %

of the species they examined, cultivating plants in atmospheres containing elevated CO_2 resulted in about a 1 °C increase in the temperature required to damage photosystem II. This could also be due to decreased stomatal conductance during the growth at elevated CO_2 caused by leaves acclimating to warmer temperatures. A similar effect on photosynthetic thermal tolerance due to elevated CO_2 was reported in wheat (Gutierrez et al. 2009), birch, and aspen trees (Darbah et al. 2010). However, no effect of elevated CO_2 on the thermal tolerance of photosynthesis was observed with either creosote bush (Naumberg et al. 2004) or *Phillyrea angustifolium* (Vitale et al. 2008). Soybean photosynthesis has a relatively high temperature optimum (Harley et al. 1985) and photosynthesis was not damaged by exposures to temperatures up to 48 °C at either ambient or elevated CO_2 when plants were grown with a daytime temperature of 28 °C (Bunce, unpublished data). Thus, it is unlikely that soybean photosynthesis suffers from heat damage in any of the locations where it is currently grown.

As stated above, plants with C_4 photosynthetic metabolism, such as maize, generally exhibit little or no stimulation of leaf photosynthesis when grown at elevated CO_2 (Kim et al. 2007, Fig. 2.1b). However, maize plants in the field displayed episodic CO_2-dependent increases in photosynthetic rates during water stress events when stomatal conductance was reduced (Leakey et al. 2006). In maize, photosynthesis can be limited by PEP carboxylase (or C_4 cycle) activity, Rubisco activity, or by Rubp-regeneration capacity. Unlike Rubisco, PEP carboxylase activity is saturated by ambient atmospheric CO_2 concentrations. Therefore, photosynthesis rates of intact maize leaves are only limited by very low subambient CO_2 concentrations. Determining whether Rubisco activity or rates of Rubp-regeneration are limiting for photosynthesis in C_4 species often requires measuring light response curves, in addition to CO_2 response curves (Massad et al. 2007). Crafts-Brandner and Salvucci (2002) observed that photosynthesis rates of corn leaves decreased at temperatures above 38 °C. These authors attributed this to a reduced activation state of Rubisco rather than to either diminished C_4 cycle or electron transport activity (i.e., Rubp-regeneration). Because high intracellular CO_2 concentrations are available to Rubisco, C_4 species, in general, tend to have greater optimum temperatures for photosynthesis than do C_3 species (Pearcy and Ehleringer 1984). This is partly because rates of photorespiration are normally very low in C_4 species. Maize evolved at higher elevations in the tropics, so it is more heat sensitive than many closely related C_4 species. Qu et al. (2014) found that photosynthesis in corn leaves was inhibited by brief exposures to 45 °C and the temperature effect was more acute at elevated than at ambient CO_2 (Fig. 2.2). Hamilton et al. (2008) also found that elevated CO_2 decreased photosynthetic thermal tolerance in maize, as well as in *Amarathus retroflexus,* another C_4 species, although these earlier treatments were based on air temperature rather than leaf temperature.

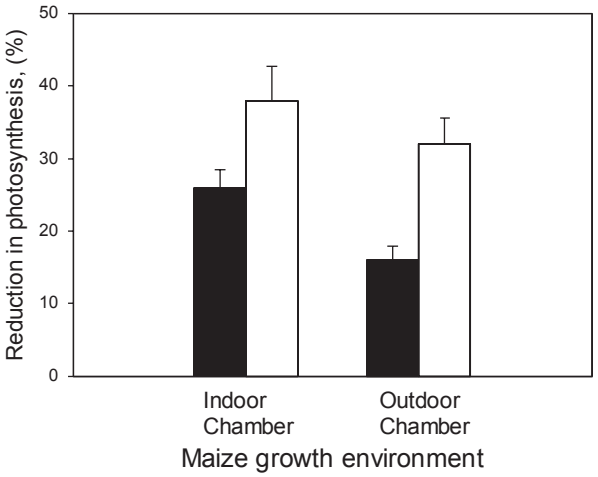

Fig. 2.2 Percentage reductions in single leaf rates of photosynthesis for *Zea mays* L. cv. Silver Queen, after leaf tissue was exposed to 45 °C for 2 h using plants grown in indoor or outdoor chambers. The "ambient" and "elevated" treatments were with 380 mmol mol^{-1} (*dark fill*) and 560 mmol mol^{-1} (*gray fill*) CO_2, respectively. In all cases, stomatal conductance was greater after heat treatment in comparison to the untreated controls. Data are unpublished results from Drs. M. Qu and J. Bunce

2.8 Effects of CO_2 Enrichment and Heat Stress on Leaf Components and Metabolism

Both CO_2 enrichment and supraoptimal temperatures affect a number of metabolic processes in plants including photosynthesis, photorespiration, and dark respiration. Consequently, these two environmental factors independently affect concentrations of primary and secondary metabolites in plant tissues (Kaplan et al. 2004; Prasad et al. 2004). As mentioned briefly above, CO_2 enrichment enhances the accumulation of carbon-containing compounds, such as starch, sucrose and hexoses, and may decrease levels of many nitrogen-containing metabolites, including soluble amino acids, photosynthetic proteins, such as Rubisco, and membrane-associated pigment-protein complexes. These conclusions are true for most C_3 plants, although soybean normally does not exhibit large changes of nitrogen metabolism in response to CO_2 enrichment (Campbell 1990; Sicher et al. 1995; Rogers et al. 2006).

As described above, heat stress affects the plant metabolome and leaf metabolites usually exhibit a greater response to heat stress than those found in other tissues on the plant (Rizhsky et al. 2004). Summarizing changes of plant metabolites due to elevated temperatures is complicated by the fact that two fundamentally different experimental approaches have been used. Some investigators examined metabolite changes in response to an acute heat shock treatment and other studies involved modified growth temperatures over longer period of time. These are two related but different approaches to studying heat stress that can have varying outcomes

(Kaplan et al. 2004). A second problem is that plants are usually adapted to specific cool or warm environments and this can affect the extent of thermal tolerance observed (Yu et al. 2012). Third, acute heat treatments when applied to plants can cause leaf tissues to lose water and become desiccated. This is a complication that can result in indirect treatment effects on foliar metabolite levels.

Although the total dataset is limited, the heat stress metabolome of *Arabidopsis* may be smaller than that for cold or drought stress. Kaplan et al. (2004) reported that 143 and 311 out of 497 real and putative compounds from *Arabidopsis* rosettes were affected by a heat and cold shock, respectively. Rizhsky et al. (2004) observed that 5 of 48 targeted metabolites in *Arabidopsis* rosettes differed from the controls after raising the growth temperature from 22 to 35 °C for 6 h. In the latter experiment, it also was observed that 17 of 48 metabolites were altered by water stress. To our knowledge, similar metabolite analyses from combined stress experiments have not been performed in other species.

Nonstructural Carbohydrates Elevated growth temperatures decreased partitioning to both transitory and storage starch (Geigenberger et al. 1998; Prasad et al. 2004). However, reports of changes of soluble nonstructural carbohydrates in response to elevated temperatures in plants have been variable. Sucrose, glucose, and fructose in leaves of specific crops and forage species frequently remained unchanged or decreased in response to elevated growth temperatures (Chatterton et al. 1987; Liu and Huang 2000; Sicher 2013). However, foliar sucrose levels also increased due to supraoptimal temperatures in reports by other authors (Kaplan et al. 2004; Yu et al. 2012). Sugar alcohols, or polyols, typically increased in soybean leaflets at elevated growth temperatures. Pinitol, which is a methylated derivative of inositiol, is particularly abundant in soybean leaves and it accumulates in response to elevated growth temperatures (Guo and Oosterhuis 1995; Sicher 2013). This result suggested there was a shift in metabolism from sucrose to pinitol synthesis in response to heat stress. Mannitol, myo-inositol, galactinol and raffinose have also been observed to accumulate in response to elevated temperatures (Kaplan et al. 2004; Sicher 2013). The former two compounds are polyols that likely function as osmolytes or compatible solutes that protect proteins and membranes from abiotic stress. Galactinol, raffinose, and myo-inositol also are involved in scavenging ROS (Loewus and Murthy 2000).

Organic Acids Organic acids are normally synthesized from soluble sugars, which are then converted to amino acids by transamination. In the *Arabidopsis* literature, changes of organic acids in response to heat shock were relatively minor. Rizhsky et al. (2004) reported that hydroxysuccinic acid and lactic acid increased with rising treatment temperatures. Hydroxysuccinic acid is another name for malic acid, which, surprisingly, did not respond to heat stress and lactic acid is normally synthesized during anaerobic metabolism. Kaplan et al. (2004) mentioned four organic acids and all increased with heat stress. These were quinic acid, citramalic acid, fumarate, and malate. Quinic acid is a cyclic polyol, citramalic or 2-methylmalic acid is involved in leucine synthesis and the latter two compounds are tricarboxylic acid (TCA) cycle intermediates with multiple cellular functions.

http://www.springer.com/978-3-319-07898-4

Combined Stresses in Plants
Physiological, Molecular, and Biochemical Aspects
Mahalingam, R. (Ed.)
2015, XV, 264 p. 52 illus., 18 illus. in color., Hardcover
ISBN: 978-3-319-07898-4