

Cultivars to face climate change effects on crops and weeds: a review

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Abstract Climate change is caused by the release of greenhouse gases in the atmosphere. Climate change will impact many activities, but its effects on agricultural production could be acute. Estimates of annual damages in agriculture due to temperature increase or extended periods of drought will be more costly than damages in other activities. Yield losses are caused both by direct effects of climate change on crops and by indirect effects such as increased inputs in crop production for weed control. One possible solution to counteract the effects of climate change is to seek crop cultivars that are adapted to highly variable, extreme climatic conditions and pest changes. Here we review the effects of climate change on crop cultivars and weeds. Biomass increase will augment marketable yield by 8–70 % for C3 cereals, by 20–144 % for cash and vegetable crops, and by 6–35 % for flowers. Such positive effects could however be reduced by decreasing water and nutrient availability. Rising temperature will decrease yields of

temperature-sensitive crops such as maize, soybean, wheat, and cotton or specialty crops such as almonds, grapes, berries, citrus, or stone fruits. Rice, which is expected to yield better under increased CO₂, will suffer serious yield losses under high temperatures. Drought stress should decrease the production of tomato, soybean, maize, and cotton. Nevertheless, reviews on C4 photosynthesis response to water stress in interaction with CO₂ concentration reveal that elevated CO₂ concentration lessens the deleterious effect of drought on plant productivity. C3 weeds respond more strongly than C4 types to CO₂ increases through biomass and leaf area increases. The positive response of C3 crops to elevated CO₂ may make C4 weeds less competitive for C3 crops, whereas C3 weeds in C4 or C3 crops could become a problem, particularly in tropical regions. Temperature increases will mainly affect the distribution of weeds, particularly C4 type, by expanding their geographical range. This will enhance further yield losses and will affect weed management systems negatively. In addition, the expansion of invasive weed species such as itchgrass, cogongrass, and witchweed facilitated by temperature increases will increase the cost for their control. Under water or nutrient shortage scenarios, an r-strategist with characteristics in the order S-C-R, such as Palmer amaranth, large crabgrass, johnsongrass, and spurge, will most probably prevail. Selection of cultivars that secure high yields under climate change but also by competing weeds is of major importance. Traits related with (a) increased root/shoot ratio, (b) vernalization periods, (c) maturity, (d) regulation of node formation and/or internode distance, (e) harvest index variations, and (f) allelopathy merit further investigation. The cumulative effects of selecting a suitable stress tolerator-competitor cultivar will be reflected in reductions of environmental pollution, lower production costs, and sustainable food production.

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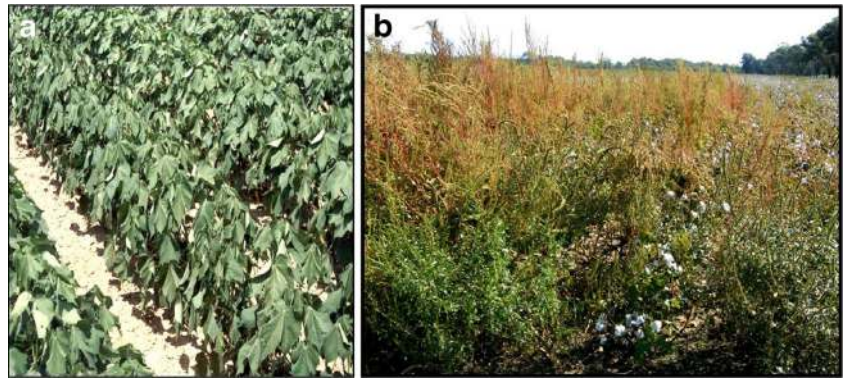
1 Introduction

Climate change refers to long-term changes in the state of the climate (IPCC 2014). These changes are identifiable, i.e., the mean or the variability of climate change components such as the increase of temperature or elevated atmospheric CO₂ levels can be assessed by the application of appropriate analytical and statistical methods (IPCC 2014). The release of greenhouse gases (carbon dioxide, methane, nitrous oxide) due to various anthropogenic activities is very likely to be one of the major causes of recent climatic change (Glover et al. 2008). Plausible climate change scenarios include higher atmospheric CO₂ concentrations, higher temperatures, and changes in precipitation (Adams et al. 1998; Trenberth et al. 2007).

Climate change will impact many aspects of the human and natural world (IPCC 2007), but its effects on agricultural production could be of particular significance (Cline 1992). According to Cline (1992), estimates of annual damages in agriculture due to temperature increase, for example, will be more costly to the US economy compared to those in other sectors and activities such as forestry, electricity, water availability or water pollution, air pollution, human mortality and morbidity, leisure activities, migration, human amenities, and urban infrastructure. The multifaceted climate alterations necessitate the adaptation of crop plants to tolerate increased heat, extended drought periods (Fig. 1a) (Gala Bijl and Fisher 2011), or increased flooding in tropical places. Additionally, the expected changes in the distribution, abundance, and severity of pests and weeds (Bazzaz and Carlson 1984; Ziska and Runion 2007; Ziska 2014a, b) will affect cropping systems and pest control methods (Anonymous 2008). Although climate changes compel agriculture to be adequately productive (Tokatlidis 2013), its effects on agricultural production can be positive in some agricultural systems and regions and negative in others (Gregory et al. 2005; Obirih-Opareh and Adwoa Onumah 2014).

To counteract the effects of climate change, various adaptation strategies have been suggested. These, according to IPCC (2014), are the processes of adjustment to actual or expected climatic changes and its effects. In agricultural production systems, adaptations seek to lessen or avoid damages caused by climate changes or exploit beneficial opportunities (IPCC 2001; Adger et al. 2002). Farmers, throughout history, responded to changes in the environment by adopting new crop cultivars and by adjusting their cultural practices (Gala Bijl and Fisher 2011). At the farm level, these adaptations include alterations in planting and harvest dates, changes in cropping sequence, better management of water for irrigation, optimized use of fertilizers, and adoption of various tillage

Fig. 1 A water-stressed cotton field (a) (with permission from D. M. Oosterhuis) and heavily infested cotton field by Palmer amaranth (b) (with permission from J. K. Norsworthy)



practices (Adams et al. 1998). In addition, studies in Australia showed that crop responses to climate change are strongly cultivar-dependent (Wang et al. 1992). Asfaw and Lipper (2011) predicted that the farmers' primary response to climate change would be to seek and crop cultivars that are most adapted to highly variable, extreme climatic conditions and pest changes brought forth by global warming.

Weed interference, in addition to climate change, enhances the risk for further crop yield losses. Despite the advanced technological achievements for weed control, crop yields are suffering great losses due to weed competition (Fig. 1b). Overall, weeds caused the greatest potential loss (34 %), with animal pests and diseases being, usually, less important (losses of 18 and 16 % respectively) (Oerke 2006). Competitiveness, adaptation, and stress tolerance are the characteristics by which weed species secure their survival in a variety of environmental conditions. Competitiveness, within the context of this paper, pertains to the ability of an organism (weed species in this case) to perform better in acquiring resources in relation to another organism (crop plants) within the same habitat. Adaptation is a change or a process of change by which an organism becomes better suited to a "new" environment, whereas tolerance is the ability of an organism to survive and reproduce under adverse environmental conditions. Weediness, which comprises traits that secure the survival and dispersal of weeds, even under severe environmental conditions, can be described through various morphological, phenological, or physiological characteristics. One of the main components of integrated weed management strategies for farmers is to grow crops able to offset the competitive ability of weeds. The utility of crops with weed-suppressive ability particularly in low input agricultural systems, or in situations when chemical weed control is not possible, can be proven valuable (Gibson et al. 2003; Benaragama et al. 2014). However, selection for weed-suppressive cultivars is difficult because this trait is a manifestation of the joint activity of many genes, controlling many traits. As reports have shown, a combination of characteristics, instead of a single trait, interacts for enhanced weed-suppressive ability (Andrews et al. 2015). These traits are related to (a) crop morphological

performance at early stages (i.e., rapid emergence, rapid root and shoot growth, early groundcover, early biomass accumulation, rapid leaf area development), (b) crop growth characteristics (i.e., height, growth habit, tillering ability, leaf width, maturity date), (c) crop physiological performance (i.e., ability for efficient water and nutrient uptake), and (d) potential allelopathic properties (Korres and Froud-Williams 2002; Korres 2005; Mason and Spaner 2006).

Climate change, in combination with an increasing world population, is predicted to escalate the global need for farmland, a resource that is already in high demand (Barrow et al. 2008) and dwindling rapidly. The adoption of stress-tolerant cultivars that can withstand adverse climatic changes and produce high yields is an effective strategy against the unprecedented risks of climate change on crop productivity (Ciais et al. 2005) and the increasing demand for higher food production (Larson 2013) particularly in low-input farming systems that are common in marginal areas (Darwin and Kennedy 2000). Furthermore, stress-tolerant cultivars that exhibit attributes of increased suppressive ability against weeds would secure yield production even more either directly by dominating over weeds or indirectly by reducing crop management inputs (Korres and Froud-Williams 2002). To our knowledge, information that enables the evaluation of the relative strengths and weaknesses of both crops and weeds under various climate change scenarios is negligible. This paper aims to cover this gap and to discuss the benefits of selecting stress-tolerant cultivar as a tool for integrated weed control under various climate change scenarios.

2 Effects of climate change on crops

2.1 Effects of elevated CO₂

2.1.1 Effects of elevated CO₂ on crop physiological characteristics

Increasing levels of atmospheric CO₂ due to various anthropogenic activities will directly influence photosynthesis,

transpiration, and respiration, the main processes by which elevated CO₂ can be sensed directly by the plants and ecosystems (Drake et al. 1997). C3 and C4 plant types exhibit different responses to CO₂ enrichment. The current amount of CO₂ in the atmosphere is inadequate to saturate the ribulose-1,5-biphosphate (RuBisCO) enzyme that drives photosynthesis in C3 plants (Taiz and Zeiger 1991; Chijioke et al. 2011). Therefore, future increases in CO₂ concentrations up to 57 % by 2050 (Hulme 1996), or even at higher levels (600–800 ppm) (Schmidhuber and Tubiello 2007), will most probably favor C3 plant types (Table 1). In contrast, C4 type plants are likely to respond less to elevated CO₂ levels as they possess an innate concentrating mechanism that increases CO₂ level at the site of RuBisCO to 2000 ppm. Hence, predicted increases in atmospheric CO₂ concentrations, from a current ambient level of about 370 ppm, are less relevant to the photosynthetic capacity of C4 plants which, most probably, will respond only marginally (Poorter and Navas 2003). The association of photosynthesis rate and intercellular CO₂ concentration was compared in soybean (C3) and maize (C4). Photosynthesis in soybean was stimulated by 39 % under elevated CO₂ concentration but not in maize (Leakey et al. 2009).

2.1.2 Effects of elevated CO₂ on crop yields

Carbon dioxide is fundamental for plant production, and increases of atmospheric CO₂ concentrations have the potential to enhance the productivity of agroecosystems (Table 1) (Adams et al. 1998). Elevated CO₂ is expected to increase plant yield through root mass and leaf area increases (Table 1) and to

alter plant chemical composition, hence the rate of nutrient cycling in soil (Campbell et al. 1997). Increases in marketable yield of cereals, particularly those that exhibit C3 photosynthetic pathway, range between 8 and 70 %; those of row, cash, and vegetable crops between 20 and 144 %; and those of flowers between 6 and 35 % (Table 2). The quality of agricultural products may be altered also by elevated CO₂. Nitrogen content, for example, in some non-nitrogen fixing plants grown at elevated CO₂, was found reduced (Ainsworth and Long 2005; Erbs et al. 2010). These changes could affect the nutritional value, taste, and storage quality of some fruits and vegetables (Chijioke et al. 2011; Vermeulen et al. 2012).

2.2 Effects of temperature increases

2.2.1 Effects of temperature increases on crop physiological characteristics

Temperature increases result in altered phenology of leaf development, flowering, harvest and fruit production, decreased vernalization period, and in asynchrony between flowering and pollinators (Baldocchi and Wong 2008). In addition, increased temperatures result in higher respirations rates, shorter seed formation periods, and lesser biomass production, hence lower yields (Stone and Nicolas 1995; Adams et al. 1998). Key stages of crop development, seasonal temperature incidents, day-night temperature fluctuations, and geographical scale are the major parameters that should be taken under consideration when the effects of temperature on crop yields are evaluated. Only few days of extreme temperatures at the

Table 1 Response of C3 and C4 weeds and crops to doubled atmospheric CO₂ levels in relation to biomass and leaf area production for both crop plants and weed species with C3 and C4 photosynthetic pathway

C3 species	Biomass	Leaf area	C4 species	Biomass	Leaf area
Range of response (× growth at ambient CO ₂ concentrations)					
<i>Abutilon theophrastii</i>	1–1.52	0.87–1.17	<i>Amaranthus retroflexus</i>	0.9–1.41	0.94–1.25
<i>Bromus mollis</i>	1.37	1.04	<i>Andropogon virginicus</i>	0.8–1.17	0.88–1.29
<i>Bromus tectorum</i>	1.54	1.46	<i>Cyperus rotundus</i>	1.02	0.92
<i>Cassia obtusifolia</i>	1.4–1.6	1.1–1.34	<i>Digitaria ciliaris</i>	1.06–1.6	1.04–1.66
<i>Chenopodium album</i>	1–1.6	1.22	<i>Echinochloa crus-galli</i>	0.95–1.6	0.98–1.77
<i>Datura stramonium</i>	1.7–2.72	1.46	<i>Eleusine indica</i>	1.02–1.2	0.95–1.77
<i>Elytrigia repens</i>	1.64	1.3	<i>Paspalum plicatum</i>	1.08	1.02
<i>Phalaris aquatic</i>	1.43	1.31	<i>Rottboellia cochinchinensis</i>	1.21	1.13
<i>Plantago lanceolata</i>	1–1.33	1.33	<i>Setaria faberii</i>	0.93–1.35	1–1.4
<i>Rumex crispus</i>	1.18	0.96	<i>Sorghum halepense</i>	0.56–1.1	0.99–1.3
Range of response (% increase)					
<i>Triticum aestivum</i>	17–31		<i>Zea mays</i>	3.7–9	
<i>Hordeum vulgare</i>	30		<i>Sorghum bicolor</i>	9	
<i>Glycine max</i>	39				
<i>Gossypium hirsutum</i>	84				
<i>Ipomoea batatas</i>	59–111				

Adopted from Chandrasena (2009), Patterson (1985), and Streck (2005)

Table 2 Effects of doubling CO₂ concentration on marketable yield of major cereal, row, cash, vegetable crops, and flowers

Crop	Marketable yield (% increase)
Maize ^a	3.7–29
Sorghum ^a	6
Wheat ^a	8–35
Barley ^a	70
Rice ^a	25
Soybean ^b	22–45
Tobacco ^b	42
Potato ^b	51
Tomato ^b	20–26
Lettuce ^b	35–44
Cucumber ^b	30
Sunflower ^b	144
Chrysanthemum ^c	6
Cyclamen ^c	35
Rose ^c	8–27

Adopted from Streck (2005). Values shown in this table were obtained by the compilation and analysis of the results of more than 770 reports about the effects of CO₂ enrichment on the economic yield of 24 agricultural crops and 14 other species

^a Cereals, crops

^b Row, cash, and vegetables

^c Flowers

flowering stage can drastically reduce yield in many crops (Wheeler et al. 2000). Pre- and post-anthesis heat incidents at 35 °C led to significant yield loss of barley, wheat, and triticale (Zheng et al. 2002; Porter and Semenov 2005; Ugarte et al. 2007). Increases in spring temperatures have been shown to induce earlier spring flowering (Pope et al. 2013) and reductions in pollen germination, flowering, and ovule size with subsequent fruit yield declines due to smaller, deformed, and fewer fruit production in perennial crops (Pope 2012; DeCeault and Polito 2008). Each crop species exhibits an optimal temperature for vegetative growth with growth decreasing as temperatures diverge from this optimum. Similarly, there is a range of temperatures within which a plant will set seeds and outside of

which the plant will not be able to reproduce. Maize, for instance, will fail to reproduce at temperatures above 32 °C and soybean above 38 °C (Fig. 2). Consequently, the trend in India toward more production of wheat, rice, and barley, and less production of maize and millets, is likely to accelerate, whereas in the USA, production might shift away from maize into soybean (C3) for forage (Parry 1990). High temperatures (above 35 °C) in combination with high humidity and low wind speed caused a 4 °C increase in rice panicle temperatures, resulting in floret sterility (Tian et al. 2010).

2.2.2 Effects of temperature increases on crop yield

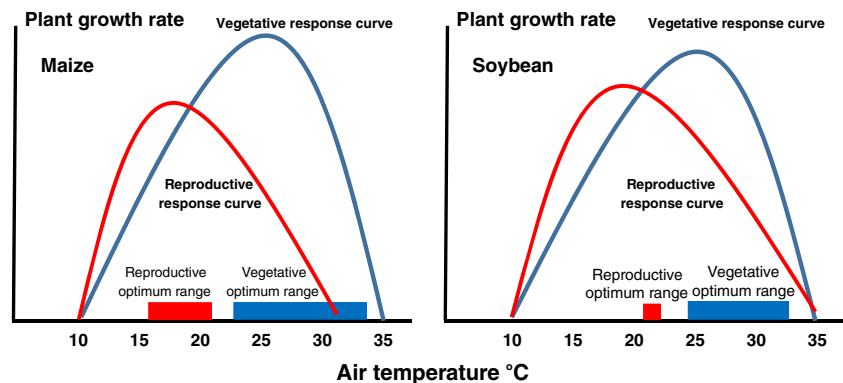
Crop yields particularly those of temperature-sensitive crops such as maize, soybean, wheat, and cotton (Schlenker and Roberts 2009) or specialty crops such as almonds, grapes, berries, citrus, or stone fruits (Lobell and Field 2011; Lobell et al. 2006) will be decreased with temperature increases at the regional and local scales (Lobell et al. 2006). Night temperature increases resulted in rice and wheat grain yield losses (Lobell et al. 2005; Peng et al. 2004; Mohammed and Tarpley 2009). Thus, even a C3 crop like rice which is expected to yield better under increased CO₂ will suffer serious yield losses under high temperature. Since the majority of global rice is grown in tropical and semitropical regions, it is likely that higher temperatures would negatively affect its production in these areas due to an increase in floret sterility that would subsequently decrease yields (Prasad et al. 2006a, b). The detrimental effect of high temperature on rice yield will be exacerbated by increased CO₂ in the atmosphere.

2.3 Effects of water deficit

2.3.1 Effects of water deficit on crop physiological characteristics

Physiological responses of plants to drought stress are complex and vary with plant species and the degree or time of the exposure to drought (Bodner et al. 2015; Evans et al. 1991). Under drought conditions, photosynthesis inhibition occurs

Fig. 2 Vegetative and reproductive response of maize and soybean to temperature increases (based on Karl et al. 2009)



because of stomata closure and reductions in the CO_2/O_2 ratio in leaves (Griffin et al. 2004).

2.3.2 Effects of water deficit on crop yield

Significant crop yield reductions occur under drought stress through dry weight accumulation reductions in all plant organs and shorter plant life cycles (Blum 1996). Pace et al. (1999) recorded significantly fewer nodes, lower dry weights of stems, and reduction in height and leaf area between water-stressed and well-watered cotton plants (Table 3). In addition, water deficit at flowering may limit the viability of pollen, the receptivity of its stigma, and seed development (Blum 1996). Reduced yields, especially in rain-fed cropping systems, is the norm under drought conditions (Kramer 1983), the severity of which may increase due to changing world climatic trends (Le Houerou 1996). One possible scenario is that the irrigated wetland rice (13 Mha of cultivated land) in Asia may experience physical water scarcity by 2025, while the irrigated dry-season rice (22 Mha of cultivated land) may suffer economic water scarcity (human, institutional, and financial capital limit access to water even though water in nature is available locally to meet human demands) (Tuong and Bouman 2003). Deleterious effects of water deficit on crops such as tomato (Ragab et al. 2007), soybean (Sakthivelu et al. 2008; Hamayun et al. 2010), maize (Khodarahmpour 2011), and many others are well known.

2.4 Interactive effects of climate change components on the physiology of crop plants and yield

In previous sections, the effects of climate change components on crop plants were examined individually although environmental changes occur concurrently (Albert et al. 2011) with management practices (Tubiello and Ewert 2002). For instance, crop yield response to elevated CO_2 levels is relatively greater in rain-fed than in irrigated crops, due to a combination

Table 3 Plant height, stem and leaf dry weight, leaf area, and node number in drought-stressed and well-watered control cotton plants at the end of the drought (49 days after planting)

Plant part	Treatment	
	Drought ^a	Control
Plant height	20.0	27.9
Stem dry weight (g)	1.13	1.39
Leaf dry weight (g)	1.41	2.16
Leaf area (cm ²)	56	153
Node number	7.8	9.4

The drought treatment was imposed by withholding water for 13 days

^a Means in a row are significantly different at the 0.05 probability level (based on Pace et al. 1999)

of increased water-use efficiency (WUE) (Table 4) and root water uptake capacity (Tubiello and Ewert 2002). In addition, the projected increases in atmospheric CO_2 concentration will increase crop growth and consequently nitrogen uptake by the crop, thus potentially will increase the need for fertilizer applications if production is to be maximized (Olesen and Bindi 2002). Elevated CO_2 resulted in a sustained larger N pool in aboveground biomass of grasses during a 5-year study on long-term enhancement of N availability under CO_2 concentration increases, suggesting that more N was taken up each year from the soil under elevated CO_2 (Dijkstra et al. 2008). Also, increased soil moisture under elevated CO_2 supported higher rates of N mineralization, thereby reducing N constraints on plant growth. More of the mineralized N ended up in the aboveground biomass of needle-and-thread [*Hesperostipa comata* (Trin. & Rupr.) Barkworth] (C3) than in blue grama [*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths] (C4) under elevated CO_2 (Dijkstra et al. 2008). Therefore, it is possible that C3 species exhibit a higher plant N acquisition and utilization under elevated CO_2 concentrations. Ghannoum (2009) reviewed the C4 photosynthesis response to water stress in interaction with CO_2 concentration and reported that elevated CO_2 concentration lessens the deleterious effect of drought on plant productivity. This is due to reduced stomatal conductance, CO_2 assimilation rate, and intercellular CO_2 levels (Ghannoum 2009; Ripley et al. 2007); therefore, saturating CO_2 concentration keeps the photosynthetic capacity unchanged and limits reductions in plant productivity.

3 Effects of climate change on weeds

Compared with crops, weeds have more variable characteristics as they have not been subjected to the same degree of selection for specific favorable traits (e.g., lack of seed

Table 4 Seasonal water use efficiency (g DM/kg water) under various water regimes and ambient and double CO_2 concentrations in various crop species

	Ambient CO_2	Double CO_2	Ratio
Sorghum	3.08	4.13	1.34
Wheat (well watered)	5.1	6.3	1.23
Wheat (water shortage)	6.2	8.9	1.43
Wheat	2.62	3.45	1.31
Wheat (well watered)	1.58	2.14	1.35 ^a
Wheat (water shortage)	1.27	1.86	1.46 ^a
Faba beans	4.91	7.82	1.59
Water hyacinth	1.4	2.6	1.85

Adopted from Morison (1993)

^a Grain only

dormancy, uniform growth, high yields). Hence, weeds tend to exhibit greater potential capability to adapt to stress than crop plants. The high genetic diversity among weedy plants allows them to achieve a greater competitive fitness against crops as a consequence of climate change (Dukes and Mooney 1999). The major categories under which climate change will affect weed populations include species abundance and richness, geographic range, and phenology (Anonymous 2013; Curtis and Wang 1998).

3.1 Effects of elevated CO₂

3.1.1 Direct effects of elevated CO₂ on weeds

There is an acknowledged consensus regarding the direct impact of increased CO₂ on plant physiology (Ziska 2004). Many weeds respond positively to elevated CO₂ due to decreased stomatal conductance (Bunce 1998) and subsequent improvements in water-use efficiency (Patterson et al. 1999; Ziska and Runion 2006). C3 plant types are likely to respond more strongly than C4 plant types to CO₂ increases (Southworth et al. 2002; Ziska 2004) (Fig. 3) through biomass and leaf area increases (Walthall et al. 2012). Nonetheless, results from various studies indicate significant and wide variations in response to elevated CO₂ due to interactions with temperature, light, water, and nutrients. CO₂ enrichment enhanced the growth and biomass production of annual fescue [*Vulpia myuros* (L.) C.C. Gmel.] (C3 type), Santa Maria feverfew weed (*Parthenium hysterophorus* L.) (C3/C4 intermediate type), and green amaranth (*Amaranthus viridis* L.) (C4 type) (Scott et al. 2014; Naidu and Paroha 2008). Other direct effects of elevated CO₂ are the production of excess pollen in ragweed (*Ambrosia artemisiifolia* L.) (Wayne et al. 2002) and

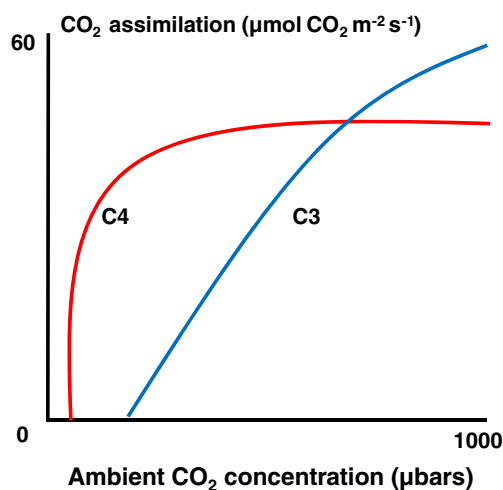


Fig. 3 Response of CO₂ assimilation in C3 vs. C4 plants to increases in CO₂ concentration (based on Taiz and Zeiger 1991)

the accelerated maturity rate in wild oat (*Avena fatua* L.) (Anonymous 2008).

3.1.2 Indirect effects of elevated CO₂ on weeds

Weed reproductive capacity will most probably be enhanced by increased CO₂ (Patterson et al. 1999; Ziska and Runion 2006). In case of the green amaranth, a 274 % increase in flower production under elevated CO₂ (550 ± 30 ppm) in controlled environmental conditions was reported by Naidu and Paroha (2008). Reproductive capacity is linked to resource capture (DeFelice et al. 1988; Benvenuti and Steffani 1994; Bello et al. 1995) which is related to increased biomass and leaf area (Korres 2005). Therefore, increases in biomass with elevated CO₂ levels will enhance weed reproductive output as these two traits are positively correlated (Korres and Froud-Williams 2002; Korres and Norsworthy 2015). Hence, increases in reproductive output will result in increases of weed abundance. Disruptions of soil and native plant populations for urban or rural development, emissions that increase atmospheric CO₂ concentrations, and nitrogen deposition to the ground surface which enhance weed growth (Johnson and Council 2013), and roadside activities which lead to the spread of weeds (Korres et al. 2015) will further enhance weed abundance. In addition, Ziska et al. (2004) observed that elevated CO₂ concentrations increased root biomass of Canada thistle (C3 plant type), suggesting that perennial weeds might be more difficult to control at these higher CO₂ levels.

3.1.3 Effects of elevated CO₂ on crop-weed interference

Some of the world's most troublesome weed species are C4 types and are found in C3 crops (Edwards and Huber 1981). The positive response of C3 crops to increased CO₂ may make such weeds less competitive (Table 5). In contrast, C3 weeds in C4 or C3 crops, particularly in tropical regions, could become a problem (Table 5), although the final outcome will depend on other climate change components (Morison 1989). Despite the fact that many weed species exhibiting a C4 photosynthetic pathway show less response to atmospheric CO₂ relative to C3 crops, in most agronomic situations, a mix of both C3 and C4 weeds occurs. As stated earlier, increases in CO₂ concentrations will enhance C3 weed growth particularly for those species that reproduce by vegetative means (Ziska and George 2004; Ziska 2003). Consequently, the abundance of perennial weeds such as common couch [*Elytrigia repens* (L.) Desv. Ex. Nevski], heartshape pickerelweed [*Monocharia vaginalis* (Burm. F.) Presl], cosmopolitan bulrush [*Scirpus maritimus* L.], hedge bindweed [*Calystegia sepium* (L.) R. Br.], Canada thistle [*Cirsium arvense* (L.) Scop], perennial sowthistle [*Sonchus arvensis* L.], and horsenettle [*Solanum carolinense* L.], most of them found in rice or soybean

Table 5 Response of crop and weed species grown under competition as a function of high CO₂ concentration

C4 weed vs. C3 crops	High CO ₂ favors	Environment
<i>Sorghum halepense</i> vs. <i>Festuca pratensis</i>	Crop	Greenhouse
<i>Sorghum halepense</i> vs. <i>Glycine max</i>	Crop	Growth chamber
<i>Amaranthus retroflexus</i> vs. <i>Glycine max</i>	Crop	Field
<i>Echinochloa glabrescens</i> vs. <i>Oryza sativa</i>	Crop	Greenhouse
<i>Paspalum dilatatum</i> vs. various grasses	Crop	Growth chamber
Various grasses vs. <i>Medicago sativa</i>	Crop	Field
C3 weed vs. C3 crops		
<i>Chenopodium album</i> vs. <i>Beta vulgaris</i>	Crop	Growth chamber
<i>Taraxacum officinale</i> vs. <i>Medicago sativa</i>	Weed	Field
<i>Plantago lanceolata</i> vs. pasture	Weed	Growth chamber
<i>Taraxacum</i> and <i>Plantago</i> vs. pasture	Weed	Field
<i>Cirsium arvensis</i> vs. <i>Glycine max</i>	Weed	Field
<i>Chenopodium album</i> vs. <i>Glycine max</i>	Weed	Field
C4 weed vs. C4 crop		
<i>Amaranthus retroflexus</i> vs. <i>Sorghum bicolor</i>	Weed	Field
C3 weeds vs. C4 crops		
<i>Xanthium strumarium</i> vs. <i>Sorghum bicolor</i>	Weed	Greenhouse
<i>Abutilon theophrasti</i> vs. <i>Sorghum bicolor</i>	Weed	Field

Based on Brunce and Ziska (2000) and Walthall et al. (2012)

cropping systems, may increase, since elevated CO₂ stimulates greater rhizome and tuber growth (Chandrasena 2009).

3.2 Effects of temperature

3.2.1 Effects of temperature on weed physiological characteristics

Soil temperature is the primary determinant of seed germination and survival particularly when soil freezes (Zimdahl 2007). Various responses to temperature fluctuations have been reported for seed germination of weed species. Common chickweed (*Stellaria media* L.) survives well in cold climates (King 1966), whereas some of the most troublesome weeds in soybean, maize, and cotton respond to temperature gradients to varying degrees (Ehleringer 1983). Barnyardgrass (*Echinochloa* spp.) is a weed of warm regions that requires high temperatures for dry matter production and growth (Maun and Bennett 1986). Similarly, prickly sida (*Sida spinosa* L.) needs high temperatures for its development (Anonymous 2001). The spatial distribution of johnsongrass [*Sorghum halepense* (L.) Pers.] in colder climates is restricted by its rhizome intolerance to temperatures below -3 °C (Warwick and Black 1983). Similarly, morning glories are frost intolerant (Halvorson and Guertin 2003; Zia-Ul-Haq et al. 2012), but their germination occurs over a wide range of temperatures (15–35 °C) (Cole and Coats 1973—cited in Halvorson and Guertin 2003) with optimum germination temperature at 24 °C (Crowley and Buchanan 1980—cited in

Halvorson and Guertin 2003). In addition, Ziska and Bunce (2007) reported 88 % increase in biomass and 68 % increase in leaf area of itchgrass [*Rottboellia cochinchinensis* (Lour.) W.D. Clayton] in response to a 3 °C increase in temperature.

3.2.2 Effects of temperature on weed distribution

The geographical range of many weed species is largely determined by temperature and it has long been recognized that temperature determines successful colonization of new environments by weedy species (Woodward and Williams 1987). Warming will affect the growth, reproduction, and distribution of weeds. Increased temperatures could, for example, alter the latitudinal distinction between Midwest and Midsouth regions within the USA, altering the weed geographical limitations. The greater soybean and maize losses experienced in the Midsouth are associated with a number of very aggressive weed species of tropical or subtropical environments such as prickly sida and johnsongrass (Osunsami 2009; Riar et al. 2013). Obviously, increased temperatures will facilitate the spread of these species into other areas of the Midwest with subsequent effects on soybean and maize production (Walthall et al. 2012). Temperature increases are likely to be particularly important in affecting the relative plant growth of C3 and C4 plants, potentially favoring C4 weeds (Dukes and Mooney 1999), such as smutgrass (*Sporobolus indicus* L. R. Br.). This again could provide suitable conditions for more robust growth of some species, which are currently limited by low temperatures, whereas the distribution of some tropical and

subtropical C4 species could shift northwards (Ziska and Runion 2006; Chandrasena 2009), thus exposing temperate-zone agriculture to previously unknown aggressive colonizers.

In addition, Ziska and Bunce (2007) stated that an expansion of invasive weed species such as itchgrass, cogongrass [*Imperata cylindrical* (L.) P. Beauv.], and witchweed [*Striga asiatica* (L.) Kuntze] will be facilitated by temperature increases. They also reported an increase in biomass and leaf area of itchgrass by 88 and 68 %, respectively, in response to a 3 °C increase. On the contrary, additional warming could restrict the southern range of other cooler climate invasive weeds such as wild proso millet (*Panicum miliaceum* L.) or Canada thistle (Ziska and Runion 2007).

3.3 Effects of water deficit

3.3.1 Effects of drought on weed physiological responses

Under more frequent and severe drought stress events due to climate change, the competitive balance would shift in favor of deep-rooted plants (Stratonovitch et al. 2012). Early emerging species, such as the shallow-rooted Sandberg's bluegrass (*Poa sandbergii* Vasey), which uses the resources that are available in the upper soil profile early in the growing season and during periods of light precipitation, will be suppressed (Daudenmire 1970 cited in Sheley et al. 1996).

In addition, dry soil conditions prolong the longevity of weed seeds due to unfavorable conditions for seed predators (Storrie and Cook 2007) and unfavorable conditions for germination. Weed seeds such as black bindweed (*Polygonum cilinode* Michx.) can last up to 7 years in the soil under dry conditions (Storrie and Cook 2007). A summary of the potential impacts of drought stress on some of the most important Australian weeds are shown in Table 6 where a trend of establishment in higher latitudes is expected (Anonymous 2008).

3.3.2 Weed adaptation strategies under water deficit and other unfavorable conditions

As reported by Wiese and Vandiver (1970), species with the greatest growth under high soil moisture conditions will be the most adversely affected by the combination of competition and water shortage. On the contrary, the more competitive species under semidrought conditions are likely to be those that produce little growth in moist soils. Based on the competitive exclusion principle, the species that uses a resource more efficiently will eventually, either wholly or partially, displace the other species. This opportunistic behavior characterizes the r-strategists, those with short life cycle and high energy investments into reproduction and dispersability, as opposed to K-strategists (Sheley et al. 1996; Hardin 1960). Grime (1979) extended the r- and K-classification strategies into stress tolerators (S), competitors (C), ruderals (R), or combinations of the above strategies. Under high stress intensity that can limit plant growth, as in the case of water or nutrient shortage, stress tolerators (S) can perform adequately. Based on the ability of adjacent organisms to exploit the same resource, competitors (C) will perform best, whereas ruderals (R) can withstand physical damages. Most weeds of annual agricultural systems exhibit ruderal-competitive characteristics, whereas most weeds of rangeland and forest ecosystems exhibit stress tolerance-competitive characteristics. Typically, succession is evolved from ruderal to competitive and finally to stress tolerator species (Korres 2005). Hence, under water or nutrient shortage scenarios, an r-strategist with characteristics in the order S-C-R will most probably prevail. In a recent weed survey (Korres et al. 2015), the preference of Palmer amaranth, large crabgrass (*Digitaria sanguinalis* L. Scop.), johnsongrass, and spurges (*Euphorbia* spp.) for disturbed habitats was reported. In the same survey, giant ragweed (*Ambrosia trifida* L.), yellow nutsedge (*Cyperus esculentus* L.), barnyardgrass, and hemp sesbania [*Sesbania herbacea* (Mill.) McVaugh] exhibited a strong preference for moist habitats. Obviously, the former group of weeds is assured of a greater probability for survival under water or nutrient stress conditions in comparison to the latter.

Table 6 Potential effects of drought on Australian agricultural weeds

Weed	Impact
Blackberry (<i>Rubus fruticosus</i> L.)	Expected to retreat to higher altitudes due to its sensitivity to higher temperatures and drought
Chilean needle grass [<i>Nassella neesiana</i> (Trin. & Rupr.) Barkworth]	Expected to increase its range because its increased invasiveness ability (long-lived, seed dispersed by wind and water) and drought tolerance
Gorse (<i>Ulex europaeus</i> L.)	Establishment into high-rainfall zones due to its sensitivity to drought
Lantana (<i>Lantana camara</i> L.)	Establishment into high-rainfall zones

Adopted from Anonymous (2008)

3.4 Interactive effects of climate change components on weed performance and consequences on weed-crop competition

The influence of climate change on simple competitive outcomes will be difficult to predict based simply on a single model, as interactions between the various climate change scenarios are likely to concur and will affect the outcome of the crop-weed competition (Alberto et al. 1996). The growth of a tropical weed is strongly stimulated by relatively small changes in air temperature (Patterson et al. 1984), but the potential synergistic effects of rising CO₂ on these weeds relative to tropical crops are unknown. It is believed that increased CO₂ and temperature can negatively impact plant growth. Scott et al. (2014), for example, reported that increases in both parameters negatively impacted plant growth rates in grassland ecosystems. The effects of elevated CO₂ levels on crops and weeds will alter the weed-crop competitive interactions, sometimes for the benefit of the crop and sometimes for the weeds. Consequently, the control of weeds will also likely be affected by these changes (Patterson 1995; Coakley et al. 1999). Reduction in transpiration and changes in leaf anatomy and leaf surface characteristics, or greater root to shoot ratio caused by elevated CO₂, could also affect herbicide uptake, thus reducing herbicide efficiency (Patterson et al. 1999; Olesen and Bindi 2002; Poorter and Navas 2003; Dukes et al. 2009). This was confirmed by various studies in which increased CO₂ concentration has affected the efficacy of glyphosate on both C3 and C4 weed photosynthetic types (Ziska et al. 1999, 2004; Manea et al. 2011) (Table 7). This response to carbon dioxide in combination with the evolution of glyphosate resistance by many weed species (Heap 2015) will affect weed control schemes significantly. Controlling weeds currently costs the USA, more than \$11 billion a year, with the majority spent on herbicides; hence, both herbicide use and costs are likely to increase as temperatures and carbon dioxide levels rise (Karl et al. 2009).

Additionally, little attention has been focused on the interactions between nutrient availability or drought with rising

CO₂, on weed-crop competition. According to Newton et al. (1996), the proportion of weed biomass increased with elevated CO₂ equally in wet and dry treatments in pasture mixture. In another study, reduced weed competition was observed when tomato (C3 crop) and redroot pigweed (C4 weed) were grown under well-watered conditions, but when drought and high CO₂ occurred synchronously, redroot pigweed performed better (Valerio et al. 2011). Under extreme nutrient limitations, stimulation of biomass with additional CO₂ may be minimal. However, under moderate nutrient limitations, more indicative of agroecosystems, the increase in biomass may be reduced but still occurs (Seneweera et al. 1994). Under a competitive environment between rice (C3 crop type) and barnyardgrass (C4 weed type), the proportion of rice biomass increased relative to barnyardgrass with a 200-ppm increase in atmospheric CO₂, but only when soil nitrogen was adequate. If nitrogen was limited in an enriched CO₂ environment, the competitive ability of rice relative to barnyardgrass was reduced, possibly due to reductions in tiller formation (Zhu et al. 2008). Elevated CO₂ can mitigate some of the adverse effects of increased temperature and drought and also regulate the adaptive mechanism of black knapweed (*Centaurea nigra* L.) (Qaderi et al. 2013). The effects of drought are likely to vary widely among crops and weeds. In maize, drought has been found to both decrease interference from naturally occurring weed flora dominated by foxtail species (*Setaria* spp.) (McGiffen et al. 1997), and increase the competitive ability of johnsongrass (Leguizamon et al. 2011). Drought and high temperatures favor the competitive ability of C4 weeds over C3 crops (Fuhrer 2003), an advantage which will most probably diminish or possibly be reversed under increased CO₂ concentrations (Bazzaz and Carlson 1984; Carter and Peterson 1983).

Spatial-based effects of temperature increases and prolonged drought periods on weeds have also been anticipated. More particularly, long drought periods interspersed with occasional very wet years will enhance weed invasion because established vegetation, both native and crops, will be weakened, leaving some areas open to invasion (Chandrasena

Table 7 Effects of increased CO₂ concentration on glyphosate efficacy for various weed species with different photosynthetic pathways

Common name	Latin name	P/S pathway	Efficacy change
Canada thistle	<i>Cirsium arvense</i> (L.) Scop	C3	Reduced
Dallisgrass	<i>Paspalum dilatatum</i> Poir.	C4	Reduced
Lambsquarters	<i>Chenopodium album</i> L.	C3	Reduced
Lovegrass	<i>Eragrostis curvula</i> (Schrad.) Nees	C4	Reduced
Quackgrass	<i>Elytrigia repens</i> (L.) Gould	C3	Reduced
Redroot pigweed	<i>Amaranthus retroflexus</i> L.	C4	None
Rhodes grass	<i>Chloris gayana</i> Kunth	C4	Reduced
Smut grass	<i>Sporobolus indicus</i> (L.) R. Br.	C4	None

Adopted from Ziska (2014a, b)

P/S pathway photosynthetic pathway

2009). In general, wetter and milder winters are likely to increase the survival of some winter annual weeds, whereas warmer summers and longer growing seasons may permit thermophile summer annuals to grow in regions further north (Peters et al. 2014). Alterations in temperature and nutrients supply can reduce photosynthetic rate of Palmer amaranth. The combination of temperature between 36 and 46 °C with resource supply constraints may restrict the potential distribution range of Palmer amaranth (Ehleringer 1983; Ward et al. 2013).

4 Cultivar selection against weeds and traits that confer competitiveness

Crop ability to suppress weeds can be considered in two ways, namely (a) the ability to tolerate weed competition which can be measured by the ability of the crop to maintain high yields under weedy conditions and (b) the ability of the crop to suppress the growth of weeds, usually determined by comparing different biological characteristics in mixtures with that in pure stands, known as weed suppression ability or competitive ability (Callaway 1992; Korres and Froud-Williams 2004; Andrews et al. 2015). However, there is a confusion between cultivar tolerance to weed competition and cultivar weed-suppressive ability (Olesen et al. 2004). Furthermore, crop tolerance to weed competition varies widely over seasons and locations (Cousens and Mokhtari 1998; Olesen et al. 2004). Thus, weed suppression criterion has been emphasized here for the selection of suitable cultivars against weeds under various climate change scenarios.

4.1 Cultivar phenotypic characteristics and weed suppression

Unlike breeding for diseases and pest resistance, little research has been done on breeding crop cultivars which are more competitive to weeds. Certain crop cultivars are known to be better competitors with weeds than others (Callaway 1992). For example, white bean (*Phaseolus vulgaris* L.) cultivars differ in their ability to compete with weeds (Malik et al. 1993). Certain tomato cultivars (*Lycopersicon esculentum* L.) have considerable tolerance to dodder (*Cuscuta* spp.), a severe parasitic weed in many parts of the world (Goldwasser et al. 2001). Cultivars of small grain cereals with certain characteristics such as short stature, earlier maturity, better winter hardiness, or early season growth have shown differential competitive abilities when grown in mixtures compared to monocultures (Juskiw et al. 2000). As stated by various authors, breeding crop cultivars with an enhanced ability to suppress weeds would be a sustainable contribution to improved weed management in many crops (Didon and Bostrom 2003; Lemerle

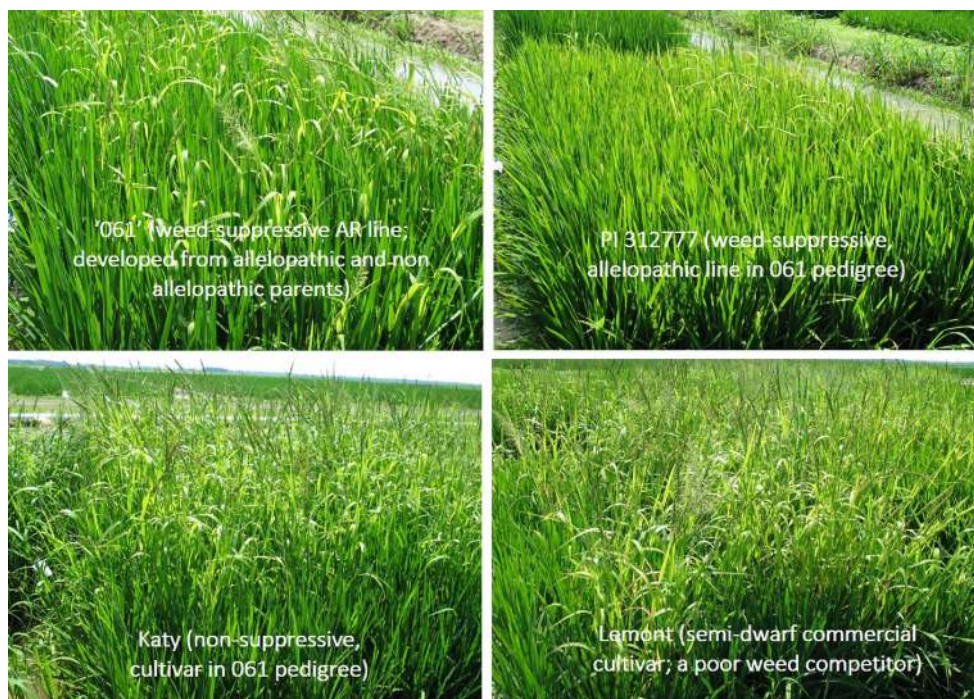
et al. 2001; Paolini et al. 1998; Vollmann et al. 2010). Therefore, cultivar selection with traits that enhance its ability to suppress weeds such as these mentioned above could be explored under various climate change scenarios. Additionally, the belowground traits such as root length density, root elongation rate, total root length, and root spatial distribution are important factors for attributing competition effect (Gealy et al. 2013a; Fargione and Tilman 2006; Stevanato et al. 2011). The greater ability to extract water from dry soil may affect or even determine the competitive ability of a cultivar (Song et al. 2010). Reports have shown that under weed competition, the root/shoot ratio of the crop and weeds was reduced (Kasperbauer and Karlen 1994; Thomas and Allison 1975; Stone et al. 1998), particularly of the less competitive species, although soil water content was not a limiting factor (Thomas and Allison 1975; Rajcan and Swanton 2001). However, as stated by Rajcan and Swanton (2001), competition for water should be viewed as an outcome of the interaction between both soil-plant-atmosphere and the crop-weed systems, rather than simply as a shortage of available water.

4.2 Implications for allelopathic properties

Weed suppression can vary with management factors such as planting method, seeding density, flood depth, and nitrogen fertilization, whereas in some cases, activated charcoal has reduced the inhibition of weeds in soils, implicating allelopathic activity as a possible contributing factor (Kong et al. 2008, 2011). Rondo, for example, a rice cultivar grown in a commercial organic rice production operation in Texas, USA, that combines a high yield potential and a weed suppression ability, is considered as a potential cultivar with allelopathic properties (Gealy and Yan 2012). Bertholdsson (2010) bred spring wheat for improved allelopathic potential by conventional breeding. The material used originated from a cross between a Swedish cultivar with low allelopathic activity and a Tunisian cultivar with high allelopathic activity.

Therefore, research efforts have focused on combining allelopathic activity with other weed-suppressive traits in small grains such as rice (Fig. 4). Breeders in Asia showed that allelopathic traits in rice can be quantitatively inherited (Chen et al. 2008) and weed-suppressive cultivars have now been developed in that region (Kong et al. 2011; Ma et al. 2006; Pheng et al. 2009a, b). Similar progress has been reported in the USA (Gealy et al. 2013b). Breeding efforts with other small grains in Europe, using a dual screening approach of seedling bioassays for allelopathic potential coupled with field evaluations for general weed suppression, have resulted in germplasm with improved weed suppression or tolerance (Bertholdsson 2005, 2007, 2010). It has been reported that early season crop biomass and allelopathic potential were key traits for improved weed suppression by the crop

Fig. 4 Rice weed suppression plots at Stuttgart, Arkansas, USA, in which the superior competitiveness of cultivars STG06L-35-061 and PI312777 compared with Katy and Lemont is shown. A “light” infestation of barnyardgrass can be observed in the former compared to later plots. No herbicide was used to control grass weeds (with permission from D. R. Gealy, USDA-ARS)



(Bertholdsson 2011; Bertholdsson et al. 2012). Worthington and Reberg-Horton (2013) have reviewed important breeding issues for small grains associated with optimization of weed-competitive ability and allelopathic traits. Rice traits such as rapid seedling growth, leaf area, and tiller production and high yield potential have improved weed suppression and minimized crop yield loss (Gealy and Moldenhauer 2012; Gealy and Yan 2012; Gibson et al. 2003; Pérez de Vida et al. 2006). Zhao et al. (2006) successfully selected cultivars for weed-suppressive traits such as yield, early vigor, and height under weed-free conditions to identify weed-competitive cultivars.

5 Traits for developing an ideotype S-C cultivar

The use of tolerant cultivars to a wide range of climatic fluctuations as adaptive tool is widely spread (Matthews et al. 1994). In Australia, for example, the use of late-maturing cultivars secures high yield outcomes that could be otherwise affected by inconsistent climatic conditions (Connor and Wang 1993). A similar strategy, at the crop level, is used in Canada and China, where the diversification of crops counteracts the climatic fluctuations (Hulme et al. 1992; Cohen et al. 1992).

5.1 Cultivars with deep root system

Adapting a cultivar with a deep root system, particularly in areas which experience prolonged dry periods, can be a useful

tool (Bodner et al. 2015). Newly introduced wheat cultivars can better exploit water and nutrients (Korres et al. 2008) mainly due to their greater ability to maintain water uptake and consequently to survive longer in dry soils (Song et al. 2009). Sorghum, for example, seems an attractive option for dry lands where crops frequently encounter drought stress compared to maize. Sorghum has deep root system, high root density, cuticle and epicuticular deposition in leaves, and efficient stomata function under water stress (Assefa et al. 2010; Starggenborg et al. 2008; Schittenhelm and Schroetter 2014). Traits related to competitiveness for water and nutrients that could affect the weed-suppressive ability of the crop include root density, root length, water uptake rate, and root surface area (Aarssen 1989; Callaway 1992; Mohler 2001). In the long term, breeding drought-tolerant cultivars might be advantageous for weed suppression as well as a means to cope with climatic changes in areas with prolonged summer dry periods (Bodner et al. 2015). Acquiring and utilizing water and nutrients more adequately compared to weeds due to their extensive root system, for example, will enable crop cultivars to maintain growth even under drought conditions. Cultivars with high early vigor and earlier maturity can be used as an effective adaptation strategy for areas with semiarid continental climates in temperate zones where more frequent generative droughts are forecasted (Gouache et al. 2012; Bodner et al. 2015). Genetic manipulation using molecular breeding has resulted in commercialization of drought-resistant crops such as the maize-DroughtGrade™ (Monsanto, St. Louis, USA) that is already used extensively in the USA (Waltz

2014). Differences in resistance to drought are known to exist within genotypes of plant species (Grzesiak et al. 2012), e.g., in wheat (Winter et al. 1988; Paknejad et al. 2007), rapeseed (Richards and Thurling 1978), oat (Larsson and Gorny 1988), and triticale (Royo et al. 2000; Grzesiak et al. 2012). Nevertheless, drought tolerance does not necessarily provide competitive advantages to the crop. As reported by Cerqueira et al. (2013), two drought-tolerant upland rice cultivars were affected by the competition of shrubby false buttonweed (*Spermacoce verticillata* L.) regardless of water conditions (presence and absence). In addition, as reported by Chauhan and Abugho (2013), rain-fed rice plants under weed competition with spiny amaranth (*Amaranthus spinosus* L.) and Chinese sprangletop [*Leptochloa chinensis* (L.) Nees] (C4 types) did not survive under limited water conditions. On the contrary, both weed species survived and produced a significant number of tillers and leaves.

5.2 Harvest index and dry mater components

To promote adaptation to high temperatures, plant breeders have suggested phenotypic traits related to heat tolerance during flowering, high harvest index, small leaves, and reduced leaf area per unit of ground area (Walthall et al. 2012). Differences between winter wheat cultivars in harvest index at high temperatures imply that heat-tolerant cultivars maintain higher grain development, compared to more temperature-sensitive cultivars (Wardlaw and Moncur 1995). Lower harvest indices are an indication of injudicious investment of assimilates, a result of favoring biomass production over commercial yield (Hay and Walker 1992). Therefore, genotypes with high harvest indices are expected to be weak competitors because of the relative fewer resources allocated for stem and leaf expansion (Kawano and Jennings 1983), traits that confer competitiveness. Mann (1980) stated that it might be possible to obtain improvements in harvest index and therefore yield, suggesting further reductions in straw length and maintenance of aboveground biomass. Korres (2000) investigating winter wheat cultivar characteristics for increased competitive ability found a negative relationship between the number of leaf area per square meter and infertile tillers per square meter. Questions that merit further thought are related to the manipulation of leaf area and infertile tiller production. If the production of infertile tillers could be manipulated, would this result in leaf area investments? Would increases in leaf area, hence interception of photosynthetic active radiation, in response to increased day length as the crop enters reproductive development cause higher yield production and enhance competitive ability? Would leaf area duration be affected and what would be the consequences for grain yield?

However, specific leaf area, a characteristic which is positively correlated with relative growth rate, is usually reduced

by elevated CO₂ thereby counteracting the positive response of photosynthesis (Bruhn et al. 2001).

5.3 Late-maturing cultivars

Late-maturing soybean cultivars (group IV) depressed weed seed production and seed weight of both pitted morning glory (*Ipomoea lacunosa* L.) and hemp sesbania [*Sesbania exaltata* (Raf.) Rydb. ex A.W. Hill] presumably through increased crop competitiveness (Bennet and Shaw 2000) due to their ability to maintain vegetative growth longer (Nordby et al. 2002). Nevertheless, Rosenzweig and Tubiello (2007) suggested that under warmer climates, crops would tend to mature faster, resulting in less time available for carbohydrate accumulation and grain production. Responses to specific adaptation strategies for given cropping systems can still vary considerably, as a function of location and climate change scenario. Adapting longer maturing cultivars in a winter cereal production system requires enough precipitation over an extended growing season to sustain grain filling. If both warmer and drier conditions prevail, such an adaptation strategy is not applicable. On the contrary, the adaptation of fast growing species (i.e., those with high sink strength, hence positive response of photosynthesis) has the advantage of better competition for resources, thus faster adaptation to a changed climate.

5.4 Nutrient uptake and utilization

Nutrient utilization, mainly nitrogen, is an important factor for cultivar selection as an adaptive strategy but also as a crop competitiveness tool under various climate change scenarios. There is a general agreement that crop cultivars, particularly of cereals, can differ in their responsiveness to nitrogen (Gent and Kiyomoto 1998; Duan et al. 2007; Benin et al. 2012) possibly due to greater sink capacity, hence better nitrogen utilization or more extensive root systems (Lupton et al. 1974; Foulkes et al. 1994). Crop biomass is a component of two processes namely the amount of accumulated intercepted radiation and radiation use efficiency (Monteith 1977; Gallagher and Biscoe 1978). Foulkes et al. (1994) stated that maximum growth depends on the acquisition of sufficient nitrogen to form a canopy of sufficient size to intercept the majority of the incident radiation when adequate moisture to balance evaporation from the canopy is provided. One of the main traits conferring resistance to drought in winter wheat is the flowering date (Foulkes et al. 1997). More particularly, cultivars with early flowering are less prone to drought effects due to shorter life cycle they exhibit. Susceptible cultivars to dry conditions, especially toward the end of the growing season, uptake and utilize lower nitrogen.

Hence, cultivars with efficient N uptake and utilization that exhibit drought resistance characteristics can be used for weed suppression and also as adaptive tools in less fertile or dry soils.

5.5 Heat tolerance—improvements and expectations

Improvements of heat-stress-tolerant germplasm lines have resulted in the development of the Hoveyzehe rice cultivar from Khuzestan delta in south Iran which attains spikelet fertility at average day temperatures of 45 °C (Jennings et al. 1979). Despite the impressive achievements by plant breeding programs, efforts to generate heat-tolerant crops have not been very successful. This is mainly because abiotic stress tolerance in plants is quantitatively inherited, and it is found to be controlled by multiple genes/quantitative trait loci (Blum et al. 1988). Advances in agricultural biotechnology have been

successful in developing heat tolerance transgenically under controlled conditions (Grover et al. 2013).

5.6 A synthesis

Breeding objectives should be reorientated toward a selection of traditional × modern crop characteristics that will result in increased weed-suppressive ability (Dingkuhn et al. 2010), an ability to thrive in harsh environments and high yielding potential (Jones et al. 1997; Johnson et al. 1998). Hybrids of *Oryza glaberrima* × *Oryza sativa* share common parental characteristics such as weed competitiveness, ability to grow under stressful conditions without jeopardizing their yield (Jones et al. 1997; Johnson et al. 1998).

Priority should be focused on crop traits suitable for climate change scenarios for several reasons. This is true considering the detrimental effects of increased temperature

Table 8 Response of crop plants and weeds under elevated CO₂, increased temperature, and prolonged drought periods

Climate change component		Plant response	Result	CO ₂ ^a	Temperature	Drought
Crop plants	Root mass	Root/shoot ratio		+		
	Leaf area	Interception of PAR		+		
	Leaf development	Leaf area			–	
	Flowering	Vegetative stage			–	
	Harvesting	Yield			–	–
	Fruit production	Yield			–	
	Vernalization	Vegetative stage			–	
	Stomata conductance	Rate of photosynthesis			–	–
	Stomata closure	WUE			+	+
	CO ₂ /O ₂	Rate of photosynthesis				–
	Respiration rate	Biomass production			+	
	Seed formation period	Yield			–	
	Biomass production	Yield		+	–	–
	Node number	Biomass, height				–
	Weeds	Stomata closure	WUE		+	
Maturity rate		Vegetative stage		+		
Root biomass		Root/shoot ratio		+		
Distribution					+	
Vernalization		Vegetative stage			–	
Biomass					+	
Seed germination ^b		Distribution			+	
Rhizomes ^b		Distribution			+	
Seed longevity						+

+ and – signs indicate a positive and negative effect, respectively

PAR photosynthetically active radiation

^a Elevated CO₂ favors, in most cases, C3 plant types

^b Seed germination and rhizome production, for most weed species, are affected negatively by low temperatures as it is mentioned in the text. Therefore, it is assumed that under relatively elevated temperatures, they will be affected positively

or extended drought periods on crop yields, for example, in combination with the enhanced plasticity and adaptation ability the weed species respond to various environment changes. If an appropriate trait for climate change adaptation favors the weed-suppressive ability of the crop plant, then its selection should be prioritized. Table 8, in an attempt to facilitate the selection process, summarizes the major responses of both crop plants and weeds under various scenarios of climate change.

As mentioned earlier, increased temperatures will reduce vernalization (i.e., the promotion of flowering in response to a prolonged exposure to low temperatures) requirements for both crops and weeds, particularly grasses. This in turn will shorten the vegetative period due to early reproductive induction (Chauvel et al. 2002), at the vegetative points, of the apex (Chouard 1960; Chauvel et al. 2002) which will result in biomass reductions and, in case of the crop, consequent yield reductions. As it was stated previously, increases in biomass production or its components, e.g., leaf area, tillers, stem weight, etc., are positively related to increased competitiveness for both crop plants and weeds as in the case of cereals, particularly winter wheat, and blackgrass [*Alopecurus myosuroides* Huds.] (Chauvel et al. 2002). Therefore, crop plants that maintain their vernalization periods, under abiotic stresses, unaffected will preserve appropriate vegetative periods for acceptable biomass production and yield but will also retain their suppressive ability against weeds.

In summary:

- The development of tolerant cultivars to drought with increased root/shoot ratio will result in enhanced water and nutrient uptake, unaffected growth rates and biomass production, hence improved weed-suppressing ability.
- Traits related with the maturity of cultivars is another option that merits further consideration for developing cultivars tolerant to drought and enhanced suppressive ability against weeds.
- Traits associated with the regulation of node formation and/or internode distance, particularly under drought stress conditions, can be used for developing high yielding and competitive cultivars against weeds.
- Traits or plant attributes related with harvest index variations such as those of infertile tillers and leaf area as mentioned above merit further investigation since they can influence both yield production through increased utilization of resources (i.e., PAR) and weed-suppressive ability (e.g., shading).
- Cultivars that exhibit allelopathic attributes should be prioritized in breeding programs.
- Cultivars that retain appropriate vernalization periods under increased temperatures, hence preserving the normal duration of vegetative growth stages, can reserve high

yield production but also to exhibit suppressive ability against weeds.

6 Conclusions

Climate change is predicted to affect agricultural production in many ways. Climate change is likely to affect the growth of both crops and weeds, sometimes benefiting the crop sometimes the weeds. Crop yield in many areas will decrease due to increased temperatures or extended drought periods, whereas weed competition, despite the technological advances, will increase further crop yield reductions. A dual adaptive approach is needed not only to counteract the negative effects of climate change but also to enhance crop competitiveness against weeds. As it has been shown in this paper, cultivar selection serves this adaptive approach adequately. Cultivars with C3 photosynthetic pathway are more suitable for adaptation to elevated CO₂ but also to compete with weeds, particularly those with C4 photosynthetic pathway. In addition, cultivars with mechanisms to resist drought through increases in root/shoot ratio will gain a significant advantage under dry conditions in marginal areas. The potential of these cultivars for weed suppression will more likely enhance, due to their ability to acquire water and nutrients effectively. However, increased temperatures, accompanied by extended drought periods, favor the selection of cultivars with longer maturity period which have also proven to be highly competitive by maintaining longer vegetative growth. Cultivars with allelopathic abilities should be used in integrated weed management systems since they have shown great potential for high yield production but also increased weed-suppressing ability. This paper investigates the complex interactions between crops and weeds under various climate change scenarios aiming to facilitate decision-making processes toward sustainable crop production systems. Developing cultivars to tolerate climate changes such as drought, temperature increases, or nutrient shortage can reduce fertilizer and irrigation inputs considerably. The incorporation of cultivars with enhanced weed suppression ability into the system can reduce herbicide inputs substantially (Callaway 1992; Gealy et al. 2003, 2014; Korres et al. 2008; Travlos 2012). This is even more demanding considering the increase of weed herbicide resistance evolution (Heap 2015). The cumulative effects from selecting a suitable S-C cultivar will be reflected in the reductions of environmental pollution, lower production costs, and sustainable food production. It is therefore imperative to expand research efforts to investigate how crop-weed interference under various abiotic stresses and cropping systems influences cultivar performance and subsequent yield outcome. This information could be incorporated into breeding programs for improving performance of cultivars under abiotic (climate change) and biotic (weed competition) stresses without compromising final yield.

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