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REVIEW ARTICLE

The physiological responses of cacao to the environment and the implications for climate change resilience. A review

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Abstract

Cacao (*Theobroma cacao* L.) is a tropical perennial crop which is of great economic importance to the confectionary industry and to the economies of many countries of the humid tropics where it is grown. Some recent studies have suggested that climate change could severely impact cacao production in West Africa. It is essential to incorporate our understanding of the physiology and genetic variation within cacao germplasm when discussing the implications of climate change on cacao productivity and developing strategies for climate resilience in cacao production. Here, we review the current research on the physiological responses of cacao to various climate factors. Our main findings are as follows: (1) water limitation causes significant yield reduction in cacao, but genotypic variation in sensitivity is evident; (2) in the field, cacao experiences higher temperatures than is often reported in the literature; (3) the complexity of the cacao/shade tree interaction can lead to contradictory results; (4) elevated CO_2 may alleviate some negative effects of climate change; (5) implementation of mitigation strategies can help reduce environmental stress; and (6) significant gaps in the research need addressing to accelerate the development of climate resilience. Harnessing the significant genetic variation apparent within cacao germplasm is essential to develop modern varieties capable of high yields in non-optimal conditions. Mitigation strategies will also be essential, but to use shading to best effect shade tree selection is crucial to avoid resource competition. Cacao is often described as being sensitive to climate change, but genetic variation, adaptive responses, appropriate mitigation strategies and interactive climate effects should all be considered when predicting the future of cacao production. Incorporating these physiological responses to various environmental conditions and developing a deeper understanding of the processes underlying these responses will help to accelerate the development of a more resource use efficient tree ensuring sustainable production into the future.

Keywords Cocoa · Ecophysiology · Tropical agriculture · Water deficit · High temperature · Elevated CO_2

Contents

1 Introduction

Cacao (*Theobroma cacao* L.) is an understory tropical tree which has its origins in the Amazon Basin. It is one of the most commercially important perennial tropical crops and is

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grown for its beans which are used in the production of chocolate. Approximately 3.99 million tonnes of cacao were produced in 2015/2016 (ICCO 2017) with an estimated market value of $98.3 billion (Marketsandmarkets 2011). Since 2008, demand for cocoa has grown by approximately 3% year on year (WCF 2014). While demand is predicted to continue increasing, on current trajectories, supply is not expected to continue to meet the growing demand (WCF 2014). There are numerous constraints to supply including significant losses to pests and diseases, aging farms and trees, limited yield potential of planting material and, in some areas, changes in climate.

Cacao is cultivated worldwide in the humid tropics within 20° north and south of the equator; production is concentrated in West Africa, South-East Asia and Latin America. Within West Africa, which accounts for over 70% of global cacao supply, the main producing countries are Côte d'Ivoire, Ghana, Nigeria and Cameroon. In South-East Asia, Indonesia is, by far, the greatest producing country followed by Papua New Guinea, and within Latin America, production is greatest in Brazil, Ecuador and Colombia. Approximately five to six million farmers are involved in cacao production around the world, the majority of which produce on smallholdings (WCF 2014). Cacao farming is mainly a low-input, rain-fed system. Fertiliser application is variable, and use of mechanisation is currently limited to a small number of farms. In West Africa, cacao trees are seed-derived, whereas across South America and South-East Asia, both seed-derived and grafted (clonal) cacao are cultivated. The trees come into bearing after 2–3 years (depending on variety and propagation method) when small flowers are produced on the trunk and branches. Usually less than 5% of flowers form fruits (usually termed 'pods'; juvenile pods are termed 'cherelles'). These hard-walled pods take approximately 5 to 6 months to reach maturity after pollination and typically contain 20–40 seeds which, after fermenting and drying, are sold into the cocoa market (Toxopeus 1985). Figure 1a shows cacao trees growing on a typical farm in Ghana; Fig. 1b shows the flushing behaviour of a young cacao seedling.

The progression of climate change in tropical regions is expected to have an overall negative impact on agriculture. The low-input agricultural systems in West Africa are likely to be among the most vulnerable (Sultan and Gaetani 2016). Current atmospheric CO_2 concentrations are around 400 ppm, and depending on future emission scenarios, it is predicted to increase to between 490 and 1370 ppm by the end of this century (Van Vuuren et al. 2011), leading to changes in global temperatures and precipitation patterns. Average global temperatures are expected to increase by approximately 1.4–4.8 °C, while changes in precipitation are more variable across regions (IPCC 2013). Increases in rainfall in the tropics are predicted in many models, while others predict declining rainfall in the future or no strong trend either way (Biasutti 2013). The number of extreme wet days is predicted to increase in West Africa during June, July and August (Sultan and Gaetani 2016), and dry season length and severity has increased significantly in West African rainforest regions (Malhi and Wright 2004). As cacao production is a low-input farming system, without adaptation practices, productivity may be vulnerable to changing climate conditions.

Recent claims, based on model predictions, have suggested that large parts of cacao-producing regions in West Africa will become unfit for production in the future (Läderach et al. 2013; Schroth et al. 2016). These claims are largely based on predicted temperature increases which are expected to drive greater evaporative demand resulting in increased incidence of water deficit. This research has been very influential


Fig. 1 Cacao smallholding in Ghana (left), developing flush leaves on cacao seedling (right)

in leading the discussion around how cacao can be expected to respond to climate change. However, the major shortcomings of this research are a lack of consideration of the physiological responses of cacao to varying environmental conditions and the potential for the crop to be adapted to sub-optimal conditions. The genetic variation within cacao germplasm in relation to responses to water deficit, high temperature and elevated CO_2 has so far been largely untapped by breeders. We suggest that there is potential to develop improved cacao varieties that can continue to yield well under a range of climate change scenarios through the exploitation of the existing genotypic variation in response to climate and through understanding the physiological processes underlying resilience to environmental stress.

This review details the current state of knowledge on the physiological responses of cacao to individual climate variables and, where available, their interactions and the genetic variation in these responses. A summary of the documented responses of various physiological parameters to these climate variables is shown in Tables 1 and 2. Areas currently lacking research are highlighted, and suggestions are made on possible ways forward in the development of a cacao crop that can be more resilient to future climatic conditions.

2 Water relations

Rainfall is the most important environmental factor influencing cacao yields (Wood 1985). Alvim (1977) stated that an average rainfall of between 1400 and 2000 mm year^{-1} is sufficient to support growth of cacao trees, and less than 1200 mm year^{-1} results in soil water deficits and reduced growth and yield. However, the annual distribution of rainfall is often more important than the total annual amount, and different soil types have different water retention properties which alter the sensitivity of cacao trees to soil water deficits. Prolonged dry periods where rainfall is less than 100 mm month^{-1} for more than 3 months can have substantial negative effects on tree growth and yield. Evapotranspiration rates of 949 mm year^{-1} were measured for 13-year-old cacao and 6-year-old cacao grown under *Gliricida* shade in Indonesia (Falk 2004; Köhler et al. 2009). Evapotranspiration rates of cacao vary between the wet and dry seasons. Radersma and de Ridder (1996) estimated daily evapotranspiration of cacao to range from an average of 1.6 mm day^{-1} during the dry season to 3.2 mm day^{-1} during the wet season. Juvenile cacao is particularly sensitive to changes in soil moisture content and plant water status and will not recover if it is stressed beyond a critical level. For this reason, establishment of cacao seedlings in the field can be a challenge in areas that experience a distinctive dry season. Flooding is also an issue in some lowland cacao-growing regions (Bertolde et al. 2012) and could possibly become more significant in the future as extreme rainfall events may increase in some areas (Sultan and Gaetani 2016).

2.1 Water limitation

Water limitation is currently an issue in many cacao-growing regions. The dry season experienced in parts of West Africa can be challenging. For example, in the establishment of young cacao plants in the field, and in mature trees, the length and severity of the dry season can impact on that season's yield. The environment of the Amazon basin, where cacao evolved, was not usually a water-limited environment, and many of the physiological and morphological features of cacao are not best suited to deal with water limitations. Cacao has large, broad leaves that lose water quickly under high irradiance conditions. It also has a relatively shallow root system with the majority of fine and coarse roots located at the top 0.4–0.8 m of the soil (Moser et al. 2010) and therefore is not adapted for deep water extraction. There is also evidence that the hydraulic system in cacao is adapted for efficient movement of water from roots to leaves rather than protection against soil water limitation. The xylem of cacao stems has a larger diameter than the roots which may increase the sensitivity of cacao to cavitation under drought (Kotowska et al. 2015). In order to deal with soil moisture deficit, plants can adopt a series of mechanisms at various levels (morphology, physiology, biochemistry, cellular and molecular level); they can escape the stress through the completion of the lifecycle before the stress sets in (this system is not feasible in a perennial crop like cacao); they can adapt to the stress through changes in morphology and growth pattern (cacao shows some adaptive traits to soil moisture deficit described below), or they can avoid the stress through changes in physiology to prevent damage at the cellular level.

Prolonged soil water limitation can negatively impact yield, and seasonal variation in cropping patterns is often largely determined by the timing of rainfall and dry periods. In Ghana, maintenance of the top 0.30 m of soil at field capacity through supplementary irrigation increased pod production by 40% during a severe dry season and reduced the incidence of cherelle wilt (a fruit-thinning process in cacao) (Hutcheon et al. 1973). Model simulations of cacao productivity identified annual radiation and dry season precipitation as accounting for 70% of the variation in bean yield in cacao (Zuidema et al. 2005). However, the relationship between rainfall and yield is complex and is dependent on the stage of pod development at which the stress occurs (Ali 1969). Rainfall has been reported to be beneficial to yield in the initial stages of pod development but becomes less influential in the later stages and can even have a negative effect as pods reach maturity, as damp conditions can lead to an increase in disease incidence (Bridgland 1953 in Fordham 1972). In Nigeria,

Table 1 Summary table of the measured responses of various leaf level parameters to major climate variables. The direction of response is indicated. A dash indicates no measured change in response. A blank cell indicates no available data. Responses to irradiance refer to high light levels where shade is reduced or light levels above saturation are imposed. Where conflicting results have been reported, a link to the reference has been included

	Photosynthesis	Stomatal conductance	Transpiration rate	Intrinsic water use efficiency	Leaf water potential	PSII efficiency (F_{v}/fm)	Leaf number	Leaf area	Greenhouse/controlled environment studies	Field studies (study location)
Water deficit	↓	↓	↓	↕	↓ (Dawn and mid-day)	–	↓	↓	Mohd Razi et al. (1992), de Almeida et al. (2016), Lahive et al. (2018)	Balasimha et al. (1991) (India), Rada et al. (2005) (Venezuela), de Almeida et al. (2016) (Venezuela)
Flooding	↓	↓	↓	↕	↓/– (Dawn)	↓/–	↓	↓	Sena Gomes and Kozlowski (1986), Bertolde et al. (2010, 2012), de Almeida et al. (2016)	
High temperature	↓ (> 34 °C)	↑ (20–30 °C)[1] ↓ (19–27 °C) ↑ (> 27 °C)[2]	↑ (20–30 °C)		↓	↓	↑	↑	Sale (1968), Sena Gomes and Kozlowski (1987)[2], Raja Harun and Hardwick (1988a)[1], Daymond and Hadley (2008)	Balasimha et al. (1991) (India)
Vapour pressure deficit	↓ (> 1.2 kPa)	↓	↑ (1–2.5 kPa)[3] ↓ (> 1.5 kPa)[1]	↓	↑ (Mid-day)				Sena Gomes et al. (1987), Raja Harun and Hardwick (1988a)[1], Baligar et al. (2008)[3]	Balasimha et al. (1991) (India)
Irradiance	↑	↑	↑			↓		↓	Galyuon et al. (1996a, b), Baligar et al. (2005)	Miyaji et al. (1997a) (Brazil)
Carbon dioxide concentration	↑	↓/–	↓	↑			–	↑	Baligar et al. (2005, 2008), Lahive et al. (2018)	

Table 2 Summary table of measured responses of various whole plant and reproductive parameters to the major climate variables. The direction of response is indicated by arrows. A dash symbolises no change in response was measured. A blank cell indicates no available data. (RGR: relative growth rate)

	Aboveground biomass	Root biomass	Root/ shoot	Flowering intensity	Yield (pod or bean DW)	RGR	Cherelle wilt	Pod size	Greenhouse/controlled environment studies	Field studies (study location)
Water deficit	↓/–	↕	↕	↓	↓	↓	↑	↓	Sale (1970), Mohd Razi et al. (1992), dos Santos et al. (2014, 2016), Handley (2016), Lahive et al. (2018)	Hutcheon et al. (1973) (Ghana), Moser et al. (2010) (Indonesia), Schwendenmann et al. (2010) (Indonesia)
Flooding	↓	↓ (Adventitious root formation ↑)	↓			↓			Sena Gomes and Kozlowski (1986), Bertolde et al. (2010, 2012), de Almeida et al. (2016)	
High temperature Vapour pressure deficit			↓	↑			↑	↓	Sale (1969a), Sena Gomes and Kozlowski (1987), Daymond and Hadley (2004, 2008)	Daymond and Hadley (2011) (Brazil)
Irradiance	↓ (Seedlings)	↓ (Seedlings)		↑	↑ Canopy cover up to 47%, ↓ canopy cover > 60%	↓			Galyuon et al. (1996a, b), Baligar et al. (2005)	Bisseleua et al. (2009) (Cameroon), Asare et al. (2018) (Ghana), Andres et al. (2018) (Ghana)
Carbon dioxide concentration	↑	↑	↓		↑	↑		↑	Handley (2016), Lahive et al. (2018), Baligar et al. (2005)	

rainfall was positively related to bean weight in the first 4 months of pod development but in the later stages had little or no effect (Toxopeus and Wessel 1970), while a study in Indonesia demonstrated that withholding rainfall during the initial stages of pod development caused a reduction in yield that was not recovered when rainfall was reintroduced during later development (Schwendenmann et al. 2010). Moser et al. (2010) reported a 10% reduction in bean yields in response to soil moisture deficit imposed over 13 months via a rain shelter. Interestingly, in the first harvest following relief from water deficit, bean dry weight was more than 50% lower in trees which had experienced water deficit in the months before, suggesting that the timing of water limitation is an important factor in determining yield response to water deficit. In cacao, pod development typically takes 5 to 6 months and for the first 8 weeks after pollination, pod growth is very slow. Rapid cell division and rapid expansion occur during 8 to 18 weeks after pollination (Chairun Nisa Haris 1988). In cacao, the mechanism by which water deficit impacts on early pod development is not well understood. Fruit development, in general, occurs through a process of cell division and cell enlargement. In plants, total cell number generally has a greater influence than cell size on the constituent organ size (Dante et al. 2014). Fewer cell divisions result in less cells available for subsequent cell enlargement. In tomato and peach, final fruit size is regulated by the number of cell divisions which occur before cell enlargement takes place. The number of cell divisions a cell undergoes is controlled by telomere length which is influenced by factors such as external growth conditions (Fishman et al. 2002). Cell enlargement is also influenced by external factors such as water availability as it is turgor pressure which provides the physical force required for cell expansion. In cereals, water deficit during early seed development is linked to reduced seed size by reducing the number of endosperm cells and amyloplasts formed (Saini and Westgate 2000). Cacao seeds have a high lipid content, and a major metabolic activity in developing seeds is the conversion of sucrose, via glycolysis, to oil and lipids. A decline in carbon uptake during water deficit may limit sugar transport and lipid deposition in the developing seeds, which may explain the observed lower seed weight associated with water deficit (Toxopeus and Wessel 1970; Handley 2016).

Maximal photosynthetic rates in cacao are associated with high midday leaf water potential (Ψ) (Balasimha et al. 1991). At a midday leaf Ψ below − 1.5 MPa, stomatal conductance (g_s) and photosynthetic rate have been observed to decline significantly (Deng et al. 1990a; Mohd Razi et al. 1992). Rada et al. (2005) observed leaf Ψ over the course of a day in water-deficit stressed and non-stressed cacao in the field in Venezuela; leaf Ψ values closely tracked vapour pressure deficit (VPD) during the day. Water potential was highest in the early morning (between − 0.5 and − 1 MPa) when VPD was lowest (ca. 1 kPa) and declined throughout the late morning and afternoon (reaching values close to −2 MPa in stressed plants) as VPD increased, before increasing again in the late afternoon as VPD once again declined. Diurnal patterns of leaf Ψ followed a similar trend in both non-stressed and stress plants with lower values associated with greater degrees of stress (Rada et al. 2005). In response to drought in both field and greenhouse experiments in Venezuela, pre-dawn leaf Ψ decreased significantly relative to controls, but it was declined in midday leaf Ψ that distinguished genotypic variation in water-deficit tolerance (de Almeida et al. 2016). Similarly, Araque et al. (2012) observed genetic differences in midday leaf Ψ during the dry season but not in predawn measurements.

Stomatal regulation is one of the key mechanisms involved in water conservation during periods of water deficit as the stomata are crucial for regulating transpiration rate (E), although stomatal closure can also limit carbon uptake for photosynthesis. However, as a reduction in g_s limits water loss to a greater extent than carbon uptake (Farquhar and Sharkey 1982), intrinsic (A/g_s) and instantaneous (A/E) water use efficiency (iWUE and IWUE, respectively) are often improved in plants grown under water deficit (i.e. more CO_2 is taken up at the leaf surface per unit water transpired). In cacao, such a response has been demonstrated in iWUE and IWUE in both short- (Balasimha 1993; Rada et al. 2005) and long-term measurements (Schwendenmann et al. 2010). However, genotypic variation in the response of IWUE to drought has been observed with increases and decreases reported (Araque et al. 2012; de Almeida et al. 2016; Ávila-Lovera et al. 2016). A decline in WUE during drought may be due to severe stress conditions which negatively impact on photosynthetic efficiency (Apshara et al. 2013; Alban et al. 2016), either through changes in photosynthetic metabolism or the occurrence of oxidative stress.

Reductions in growth and leaf area expansion of cacao have been shown to decline in response to water deficit before declines in photosynthetic or assimilate export rates were observed (Joly and Hahn 1989; Deng et al. 1989, 1990b). In cacao, leaf production occurs by a series of flushes involving rapid growth of the terminal bud and production of typically three to six pairs of leaves. These are initially soft but gradually harden after full leaf expansion (Toxopeus 1985) (Fig. 1b). Leaf flushing in cacao is controlled both endogenously and environmentally. If environmental stresses are not apparent, it is mainly under endogenous control (Taylor and Hadley 1988); however, during periods of water deficit, flushing is suppressed, and once soil moisture is replenished, flushing is observed (Sale 1970; Antwi et al. 1994). Today, commercial production of cacao occurs in regions that periodically experience conditions such as high temperatures, irradiance and high vapour pressure deficit (VPD) and soil moisture deficit, which cacao has not evolved to cope with. Morphological changes during leaf development have been observed in other species in response to environmental stress. For example, in coffee grown under prolonged water deficit, leaf area declined due to increased senescence and the production of fewer and smaller leaves (Meinzer et al. 1992). Cacao shows the potential for adaptive morphology under water-deficit conditions. The leaves produced following a dry period tend to be smaller and have a shorter lifespan (Sale 1970), which may be an adaptive trait that can help to limit transpirational area. Antwi (1994) also observed increased leaf thickness and epicuticular wax content on cacao leaves grown with water deficit. Rapid leaf drop occurs in some genotypes in response to water deficit, and similarly, this may help to sustain plant water status by reducing transpirational surface area (Antwi et al. 1994). In young cacao, reductions in leaf area, leaf, shoot and root dry weight, plant height and stem girth have been reported in response to water deficit (Mohd Razi et al. 1992; Alban et al. 2016; Lahive et al. 2018). However, in mature fruit-bearing trees grown in the field, no significant decrease in net primary productivity (i.e. total leaf, wood and root production) was observed in response to 13 months of water deficit in Indonesia. In cacao grown under agroforestry systems in Brazil, the particularly severe drought during the El Niño-Southern Oscillation (ENSO) event of 2015–16 increased tree mortality and reduced average potential yield by 89%. This suppression of yield was still evident 9 months later after the drought had ended (Gateau-Rey et al. 2018). In tropical tree seedlings, higher levels of non-structural carbohydrates before the onset of water deficit was associated with increased survival of fatal drought (O'Brien et al. 2014). The greater carbohydrate stores in mature cacao trees may account for the difference in tolerance to water deficit compared with seedlings. Larger root systems in older trees also allow greater access to soil moisture, which may be inaccessible to smaller seedlings. Biomass allocation patterns often change in plants exposed to water deficit causing shifts in root/shoot ratios. In cacao, changes to root biomass production under water deficit vary and appear to be genotype specific with both increases and decreases in root growth reported in response to water deficit (Mohd Razi et al. 1992; Moser et al. 2010; dos Santos et al. 2014, 2016). The ability to increase root growth under water deficit may be a beneficial trait for conferring tolerance to soil water deficit, by enabling greater access to and uptake of soil water (dos Santos et al. 2014, 2016). In robusta coffee, root depth was associated with greater tolerance to drought as water limitation could be avoided for longer in varieties with deeper roots (Pinheiro et al. 2005). Cacao has a shallow rooting system that occupies the upper soil layers and likely limits the potential for deep water access during periods of water limitation (Nygren et al. 2013; Kummerow et al. 1982). Root architecture and distribution of the roots in the soil profile is important in determining water and nutrient uptake. The ability of a plant to adjust its root surface area in response to environmental conditions is also very important (Smith and De Smet 2012) and is an area that has not been investigated in cacao. There is some evidence that potassium application can help to mitigate the negative effect of water deficit on cacao seedling growth, and this response appears to be genotype specific (de Almeida and Valle 2007; Djan et al. 2018). In other plant species, potassium is associated with stomatal regulation, cell membrane stability and enhanced root growth which can improve plant tolerance to soil moisture deficit (Wang et al. 2013). There is a need for further study of this interaction on mature trees in the field.

Reproductive development of cacao is thought to be more sensitive to water limitation than vegetative growth (Schwendenmann et al. 2010). Sale (1970) showed that flowering and pod size at maturity were reduced in cacao trees subjected to water deficit compared to trees grown with sufficient water. Similar reductions in flowering were also reported in greenhouse (Machado et al. 1981) and field-grown cacao (Schwendenmann et al. 2010). In Ghana, supplementary irrigation stimulated flowering and pod setting in field-grown cacao (Hutcheon et al. 1973). Adjaloo et al. (2012) reported an increase in flowering intensity during the major rainy season, a decline in the minor rainy season and a further decline in the dry season. In Costa Rica, Young (1983) reported peaks in flowering coinciding with peaks in rainfall. However, in the latter study, a drop-off in flowering was noted during the wettest months which may have been associated with lower irradiance levels and/or cooler temperatures. Thus, plant water status appears to be a key factor regulating flowering in cacao. While flower numbers are rarely limiting in cacao (typically less than 5% of flowers are converted to pods) (Toxopeus 1985), seasonal variation in flower numbers is associated with subsequent cropping (Daymond 2000), probably as flowering intensity of a given variety is indicative of carbohydrate allocation to reproduction. There is very little known about the dynamics of carbon allocation in cacao and how this is influenced by climatic conditions. The limited information available is focused on partitioning between aboveground and belowground organs, with little attention to allocation patterns between vegetative and reproductive organs. Cacao tends to favour allocation of resources towards vegetative over reproductive growth and has a relatively low harvest index. For example, in 10-year-old trees in Vanuatu, cacao fruits accounted for 12% of annual dry matter production (Bastide et al. 2009). Vegetative sinks appear to outcompete reproductive sinks in the current system (Bastide et al. 2009). There is the potential for significant yield improvements through determination of the optimum balance between vegetative and reproductive growth in cacao and the mechanisms regulating this. More research is needed in this area and in determining the influence of environmental factors on allocation patterns and translocation processes to develop a more efficient cacao variety.

2.2 Flooding

Given that more extreme events are predicted with a changing climate, it is reasonable to assume that more flooding events may occur in some cacao-growing areas. Although cacao appears to be more sensitive to water limitation than flooding (de Almeida et al. 2016), it does have a depressive effect on photosynthesis and g_s (Sena Gomes and Kozlowski 1986; de Almeida et al. 2016; da Silva Branco et al. 2017) which, in the long term, leads to a reduction of leaf, stem and root growth, and changes in root/shoot ratio (Sena Gomes and Kozlowski 1986; Bertolde et al. 2010). Reductions in leaf chlorophyll content and damage to PSII have also been observed in flooded plants (Bertolde et al. 2012; da Silva Branco et al. 2017). and genetic variation in these responses is evident (Bertolde et al. 2010). Stem adventitious root production is an adaptive response to flooding in some plant species. Evidence of adventitious root formation was reported after 12 days of flooding in young, pot-grown cacao. Genetic variation was evident in this trait and was associated with higher photosynthetic rates and turgor potential during flooding (de Almeida et al. 2016). An interaction between the level of shading and response to flooding was reported in a study in southern Bahia, Brazil; the decline in photosynthesis and g_s in response to flooding was delayed in shaded conditions compared to unshaded cacao (da Silva Branco et al. 2017). In these studies, seedlings or young plants propagated by rooted cuttings were used. The only study on flooding in mature trees that we are aware of was carried out in Peru during a particularly bad flooding episode in 2012 (Delgado et al. 2016). Survival of flooded trees seemed to be associated with the age of the trees, with fewer young trees surviving flooded conditions. Maintenance of glycolysis and fermentation induction during flooding have also been identified as potential traits conferring flood tolerance and genes associated with these processes have been identified, which could potentially be used in germplasm selection (Bertolde et al. 2014). Lower levels of chlorosis during flooding have been suggested as a potential trait to identify flood tolerance among cacao genotypes (Bertolde et al. 2010).

In summary, precipitation plays a very important role in cacao production during the season and impacts on growth, leaf production, photosynthetic activity and stomatal behaviour. While cacao has been described as particularly sensitive to water deficit, mature trees appear to be less sensitive than seedlings in the field likely due to the greater resource availability of older trees. Reproductive processes also show sensitivity to plant water status, but the pod development processes, which are most sensitive to water deficit, have not been clearly identified. Although to date water deficit is a more pressing issue than flooding in cacao-growing regions, this area could potentially become more relevant if rainfall patterns become more variable in the future.

3 Temperature and vapour pressure deficit

There is limited research available on the physiological responses of cacao to temperature despite de Almeida and Valle (2007) describing cacao growth and development as highly dependent on temperature and Daymond and Hadley (2004) stating that temperature was the main factor determining where cacao can be grown. Table 3 shows the range of minimum and maximum temperatures typically experienced in various cacao-growing countries throughout the year. Minimum monthly temperatures tend to range from 18 to 24 °C, with exceptions in Cameroon where lower minimum temperatures are experienced and in India where minimum temperatures can reach above 26 °C. Maximum monthly temperatures tend to range between 26 and 34 °C with slightly higher maximum temperatures recorded in southern India and Nigeria. The data shown in Table 3 is compiled from weather station data available in CLIMWAT 2.0, a climatic database developed by FAO. The weather data consists of at least 15 years of data during the period 1971–2000 (Muñoz and Grieser 2006). Note that the weather stations are sometimes located distant from cacao farms.

Daily maximum temperatures much higher than the maximum monthly temperature have been reported. For example, daily maximum temperatures between 35 °C and 40 °C and as high as 44 °C have been reported in regions of Ghana (Asare et al. 2017; Abdulai et al. 2018a). The monthly average maximum and minimum temperatures, which are often quoted, do not necessarily reflect absolute extremes of the temperature experienced. The minimum temperature requirements for cacao have been described by Erneholm (1948 in Alvim 1977) as a mean monthly minimum temperature of 15 °C and an absolute minimum of 10 °C. However, cacao has been reported to survive temperatures lower than this (Alvim 1977), although it appears that it is the length of exposure to these lower temperatures that results in damage (Wood 1985). Joly and Hahn (1991) showed that overnight chilling at temperatures between 4.7 °C and 15.8 °C caused a subsequent linear decline in photosynthesis and g_s, but full recovery was seen within 8 days. The base temperature for vegetative growth has been reported to vary between genotypes and range between 18.6 °C and 20.8 °C (Daymond and Hadley 2004). Base temperature for pod development is lower with a base temperature of 9 °C reported for the 'Catongo' variety (Alvim 1977) and a range between 7.5 °C and 12.9 °C reported for pod growth of different cacao genotypes (Daymond and Hadley 2008).

The optimum temperature for photosynthesis in cacao has been reported to be between 31 °C and 33 °C (Balasimha et al. 1991) and 33 °C–35 °C (Yapp 1992). Sena Gomes and Kozlowski (1987) reported a decrease in g_s over the range 18.7 °C to 27.2 °C and an increase at temperatures above this, most likely to enhance cooling at higher temperatures. However, the opposite effect was described by Raja Harun and Hardwick (1988a). In this study, g_s and transpiration (E) increased within the range of 20 °C–30 °C. In field-grown cacao in India, photosynthetic rate declined as mean monthly temperature increased above 34 °C during the dry season (Balasimha et al. 1991). Under controlled environment conditions, the temperature under which leaves develop influences final photosynthetic capacity. Leaves formed in a warm night time temperature regime (27/24 °C (day/night)) achieved maximum photosynthetic rates more than twice that of leaves formed under cooler conditions (27/19 °C) (Yapp 1992). The lower photosynthetic rate was associated with greater accumulation of starch and sucrose in the leaves formed in the cooler temperature regime (Yapp 1992). Vapour pressure deficit between the external atmosphere and the leaf is positively influenced by temperature, especially during the dry season, driving water loss through the leaf surface as temperatures

Table 3 Annual minimum and maximum temperature conditions, based on monthly averages, in various cacao-growing countries. Data was compiled from the CLIMWAT 2.0 database. The temperature range for the mean monthly minimum and maximum temperatures throughout the year is shown

Region	Country	Station name	Location	Altitude (m)	Mean min temp (°C)	Mean max temp (°C)
West Africa	Côte d'Ivoire	Gagnoa	6.13 N, 5.95 W	210	20.5–22.4	28.7–33.9
	Ghana	Sefwi-Bekwai	6.2 N, 2.33 W	172	20.2–22.8	28.2–33.6
	Cameroon	Yaoundé	3.83 N, 11.51 E	760	13.9–20.0	26.2–30.9
	Nigeria	Ilorin	8.48 N, 4.58 E	305	18.7–23.2	28.8–35.9
South/Central America	Brazil	Ilhéus	14.8 S, 39.06 W	60	18.9–23.5	25.8–29.4
	Ecuador	Pichilingue	1.10 S, 79.46 W	73	19.5–21.9	27.4–30.7
	Trinidad & Tobago	Piarco Int. Airport	10.61 N, 61.35 W	15	19.7–22.5	29.2–31.3
Asia	India	Tiruchchirapalli	10.76 N, 78.71 E	88	20.6–26.5	29.3–37.1
	Malaysia	Ipoh	4.56 N, 101.1 E	39	21.8–23.4	31.8–33.8
	Indonesia	Surabaya, Perak	7.21 S, 112.7 E	3	19.1–22.7	31.0–34.2
	Indonesia	Menado	1.53 N, 124.9 E	80	20.6–21.7	31.7–33.9
	Papua New Guinea	Madang	5.21 S, 145.8 E	12	22.9–23.3	29.6–30.2

rise. If predicted temperature increases are not accompanied by greater precipitation, it follows that relative humidity will decline and the vapour pressure deficit between the atmosphere and the leaf will increase. Stomatal conductance and photosynthesis are positively correlated with relative humidity reflecting cacao's evolution in humid environments (Sena Gomes et al. 1987; Raja Harun and Hardwick 1988a). In a field study in Ghana, sap flux density in cocoa grown was positively correlated with VPD and temperature (Abdulai et al. 2018a). Stomatal conductance decreases linearly with increasing VPD, while photosynthesis appears to be less sensitive to changes in VPD, declining at values greater than 1.8 kPa (Raja Harun and Hardwick 1988a; Balasimha et al. 1991; Baligar et al. 2008). However, effective transpiration control does not appear to be present in drier atmospheric conditions. Sena Gomes et al. (1987) reported higher rates of E in low humidity relative to high humidity conditions. Similarly, despite a decline in g_s with increasing VPD, a linear increase in E was observed up to 1.5 kPa before declining (Raja Harun and Hardwick 1988a; Hernandez et al. 1989). In three genotypes of cacao, Baligar et al. (2008) demonstrated a linear increase in E as VPD increased from 1 to 2.5 kPa, while g_s and photosynthesis declined over the same range. Cuticular transpiration may be a significant source of water loss from the leaf under drier atmospheric conditions since stomatal restriction is high in these conditions. However, few attempts have been made to quantify this in cacao, and further research is needed in this area. Inefficient use of water at low humidity could exacerbate stress under hot, dry conditions. Shade trees can help to maintain high humidity levels within the canopy and could help to mitigate against stressful environmental conditions.

Enhanced growth with increasing temperature has been described in cacao. Extension growth in young cacao plants was enhanced at daytime temperatures of 30 °C compared to either 23.3 °C or 26.7 °C (Sale 1969b). The loss of apical dominance at higher temperatures resulted in higher flushing intensity and increased leaf number and leaf area (Sale 1968). Similarly, in seedlings, leaf number, leaf dry weight and plant height increased with temperature between 18.7 °C and 33.3 °C. Leaf area also increased but only up to 30.5 °C (Sena Gomes and Kozlowski 1987). Assimilate partitioning also varies with temperature, with increased partitioning to the leaves at higher temperatures and lower temperatures favouring partitioning to the stems and roots (Sena Gomes and Kozlowski 1987). Genotypic variation in growth response to temperature has also been identified by Daymond and Hadley (2004). In this study, higher temperatures were associated with increased growth as previously described, but the magnitude of response varied among genotypes, indicating the potential to match genotypes to specific growing environments (Daymond and Hadley 2004).

Plant reproductive development, in general, is considered more sensitive to temperature than vegetative development (Bita and Gerats 2013). In cacao, flowering is continuous in regions with minimal seasonal variations in temperature and rainfall, but varies in regions with distinct seasonal changes in temperature (e.g. Bahia, Brazil) (Alvim 1967). In a multi-locational trial of various genotypes across Brazil, Venezuela, Trinidad and Côte d'Ivoire, there was a significant interaction between genotype and season in all four countries, suggesting the existence of genotypic variation in seasonal flowering response (and hence cropping pattern). Also, within this study, a linear response of flowering to increasing temperature was identified in Bahia, Brazil (Daymond and Hadley 2011), an area characterised by a distinct cooler season. In a controlled experiment conducted in Trinidad, daytime temperatures above 26.7 °C led to an increase in flowering intensity, while a night time temperature of 26.7 °C was identified as optimum for enhancement of flowering (Sale 1969a). Pod development is also impacted by temperature conditions. Cacao pods reach maturation earlier at higher temperatures (End et al. 1988; Daymond and Hadley 2008), and pod losses to cherelle wilt also increased (Daymond and Hadley 2008; Hadley et al. 1994). The study of Hadley et al. (1994) demonstrated higher pod respiration rates with an increase in temperature, which may have partly accounted for greater pod losses. Furthermore, since higher temperatures promote leaf and shoot growth, these may outcompete young fruits for assimilates as seen in apples (Quinlan and Preston 1971), which may also contribute towards the greater occurrence of cherelle wilt at higher temperatures. Final pod and bean size also decline with increasing temperature, although this response appears to be genotype specific (End et al. 1988; Daymond and Hadley 2008), as is the variation in fatty acid content in response to temperature (Daymond and Hadley 2008). Saturated fatty acid content and the melting point of cacao butter also increase in beans grown in warmer conditions (End 1990). In soybean, higher growth temperatures were associated with reduced oil content in the seeds (Thomas et al. 2003) and a similar response was observed within several seed oil crops (Canvin 1965). Variation in fatty acid profiles have also been observed in seeds of soybeans grown under different temperature conditions (Canvin 1965).

It is evident that there is a great deal of variation in the temperatures cacao trees are exposed to in the field. Climate change predictions suggest that higher temperatures will be experienced in cacao-growing regions, and it has been suggested that this could be detrimental to productivity in West Africa (Schroth et al. 2016). However, more research is required to identify the true extremes in temperatures and the length of exposure to elevated temperatures that cacao can tolerate without negatively impacting productivity and bean quality. Genetic variation in the response to higher temperatures needs to be clarified along with identification of farm management practices to help protect against elevated temperature damage. Furthermore, a greater understanding of the extent to which VPD will change with increased temperatures is needed since this could further exacerbate temperature stress.

4 Irradiance

As an understory, species in its natural habitat cacao can tolerate a low light environment. Overhead shade, typically provided by companion crops such as plantain, is required for early establishment of seedlings in the field as these are particularly sensitive to high light levels (Alvim 1977; Owusu 1978). Niether et al. (2018) measured light transmission through the canopy of various cacao-growing systems in Alto Beni in Bolivia. Above the canopy, under clear skies, light levels of between 1580 and 2028 μmol m^{-2} s^{-1} were recorded depending on the time of year. Light levels within the canopy (1.3 m aboveground) varied depending on the growing system and pruning activity. In an open sun monoculture of cacao, where trees were grown at a spacing of 4 × 4 m, irradiance ranged from between 985 and 1546 μmol m^{-2} s^{-1} before and after pruning, respectively. Within an agroforestry system, where cacao was combined with woody shade trees and banana or plantain, irradiance levels of between 243 and 1273 μmol m^{-2} s^{-1} were recorded, before and after pruning, respectively. In a successional agroforestry system, where shade tree density is higher, light levels reached between 317 and 949 μmol m^{-2} s^{-1} before and after pruning activity. Baligar et al. (2005) reported that high light levels (1050 μmol m^{-2} s^{-1}) were detrimental to shoot, root and leaf growth of seedlings, and reduced uptake and influx of certain nutrients. In the first 3 months of establishment, high levels of shade are required, since there is little or no self-shading at this stage, but this can be reduced as the seedlings develop (Raja Harun and Kamariah 1983).

As a species tolerant to shade, maximum photosynthetic rate at the leaf level is achieved under relatively low light levels in cacao (Baligar et al. 2008). Saturation irradiances up to 400 μmol m^{-2} s^{-1} have been reported for cacao (Raja Harun and Hardwick 1988b; Baligar et al. 2008), and genetic variation in saturation irradiance has also been identified (Daymond et al. 2011). Light compensation point (the irradiance level at which CO_2 uptake through photosynthesis and release through respiration are equal) has also been shown to vary across eight genotypes between 11.7 and 24.7 μmol m^{-2} s^{-1} (Daymond et al. 2011). Raja Harun and Hardwick (1988b) observed a reduction in photosynthesis in cacao leaves exposed to irradiance levels above about 200 μmol m^{-2} s^{-1} (i.e. below saturating intensity) after 3 h. At irradiances above 500 μmol m^{-2} s^{-1}, the rate of decline was more rapid and the reduction greater. Photosynthetic capacity declined linearly with exposure time and at light intensities between 200 and 800 μmol m^{-2} s^{-1}. However, Balasimha et al. (1991) found that this depressive effect of irradiance was only observed when soil water was limiting. Galyuon et al. (1996a) reported higher photosynthetic rates in certain genotypes grown in full sunlight compared to under shade. The authors suggest that prolonged growth (17 weeks) at full sunlight resulted in acclimation to high irradiance with the production of thicker leaves, higher rates of E and higher stomatal densities. However, efficiency of PSII and electron transport rate declined in these sun leaves (Galyuon et al. 1996b), which suggests that photodamage may have occurred which over time may lead to photoinhibition. Miyaji et al. (1997a, b) also observed higher maximum photosynthetic rates in sun leaves compared to shade leaves in cacao, but the photosynthetic rate declined faster over the lifespan of the sun leaves while shade leaves maintained slower rates of photosynthesis but over longer periods. Similarly, higher respiration rates were recorded in the sun leaves resulting in lower net assimilation rates overall, especially as the relationship between photosynthesis and respiration was not the same throughout the lifespan of the leaf (Miyaji et al. 1997a). Leaf lifespan and turnover is related to carbon balance, photosynthetic carbon gain minus respiratory carbon loss for constructing and maintaining the leaves (Chabot and Hicks 1982). Galyuon et al. (1996a) observed that leaf area and relative growth rate declined at high irradiances, but flushing frequency increased which led to higher total leaf production. The increased flushing, flowering and yield of cacao in high light conditions may be explained by increased carbohydrate production made available through higher assimilation rates, as peaks in free sugar levels in the bark were seen to coincide with peaks in flowering and flushing (Owusu et al. 1978). Resource availability is essential when growing cacao in high light environments. Higher rates of photosynthesis and growth in these conditions can only be maintained if other resources (i.e. nutrients, water) are made available to sustain the increased productivity. Many of the studies described above have focussed on juvenile plants and/or on single leaf photosynthesis. In a mature canopy, self-shading will occur, and so lower leaves will not always reach light saturation, particularly in shaded systems. Thus, it is reasonable to assume that the greater yields often observed with shade removal are due to a greater proportion of the canopy being illuminated and hence higher canopy photosynthesis.

For many years, general practice was to grow cacao under shade of other trees, but there has been a trend towards reducing shade on cacao farms as higher light levels have been associated with increased yields (Ahenkorah et al. 1974). However, yields have also been reported to decline faster in these conditions (Obiri et al. 2007), particularly where no fertiliser is used (Ahenkorah et al. 1974). Canopy cover up to 39% has been shown in increase bean yields at the field level in Ghana compared to cacao grown in full sun, but increasing shade above this level can limit yields (Andres et al. 2018; Asare et al. 2018). While in Cameroon, increasing canopy cover up to 47% enhanced yield but greater than 60% cover caused yield limitations (Bisseleua et al. 2009). Growing cacao without shade will require more intensive management of the crop including increased fertiliser inputs to maintain such a system in the long term. Unshaded conditions will also increase evapotranspiration and could exacerbate soil moisture-deficit stress where access to irrigation is limited. The need for shade may not be required in all cacao-growing regions, and its applicability is dependent on local climate conditions. According to Beer et al. (1997), shade systems are likely to be most effective in hot, dry climates where they can help to create more favourable growing conditions through modification of the microclimate. Acheampong et al. (2013, 2015) reported higher g_s and photosynthetic rates during the dry season in cacao trees grown under heavy shade compared to those grown under lighter shade, but the opposite effect occurred during the wet season. These observations are likely to be due to lower VPD being maintained within the canopy in the heavy shade regime. As g_s is strongly negatively influenced by increased VPD (Sena Gomes et al. 1987; Raja Harun and Hardwick 1988a), the heavy shade helped ameliorate stress during the dry season by reducing VPD within the canopy. Similarly, Miyaji et al. (1997a) showed that leaves lower in the canopy (i.e. more shaded) maintained higher leaf water content (and likely leaf Ψ) than those grown in unshaded conditions. Germplasm which can utilise low light levels more effectively will be essential to achieve high yield under shaded conditions, where shade trees may be used to ameliorate the microenvironment and/ or provide an additional crop through companion planting. Variation among genotypes in responsiveness to light environment has been identified. For example, leaf production, leaf area and stem dry weight varied between genotypes in response to light environment and genotypic differences in assimilate partitioning in response to light have been reported (Acheampong et al. 2013). Genotypic variation in the characteristics of cacao canopies has also been identified (Daymond et al. 2002); therefore, genotypes of cacao that have a more open structure with greater light penetration to the lower layers would be more suited to cultivation under shade. Furthermore, yield in mature cacao grown in Malaysia has been reported to be related to light distribution through the canopy (Yapp and Hadley 1994). This study demonstrated that light penetration through the canopy, rather than light interception, had a greater influence on yield in mature cacao with a closed canopy. This was attributed to a greater proportion of leaves lower in the canopy being exposed to higher irradiance, thereby increasing canopy photosynthesis in trees with a more open structure.

5 Carbon dioxide

Increases in CO_2 are predicted across the globe during this century, which is likely to have significant impacts on agriculture. However, very few studies examining the responses of cacao to elevated CO_2 have been carried out to date. In recent years, detailed photosynthetic and biochemical analysis of another tropical perennial tree crop, coffee, has been carried out (Ramalho et al. 2013; Ghini et al. 2015; Da Matta et al. 2016). CO_2 is essential for photosynthesis and plant growth and at current concentrations limits photosynthetic rates in C_3 plants. Therefore, increases in the amount of CO_2 available for uptake by plants will have considerable effects on photosynthesis and plant growth. Increasing concentrations of atmospheric CO_2 generally impacts on photosynthesis by increasing photosynthetic rate, reducing g_s and E, and therefore, iWUE and IWUE are often improved. The increase in CO_2 concentration from 380 ppm (year 2000 level) to about 550–700 ppm has the potential to increase photosynthetic rates in C_3 plants by an average of about 38% (Long et al. 2004) with trees predicted to show the greatest response (Ainsworth and Long 2005). In cacao, elevated CO_2 concentrations have resulted in increased photosynthetic rates both in instantaneous exposure studies and more long-term growth studies (Baligar et al. 2005, 2008; Lahive et al. 2018). Under elevated CO_2 (700 ppm), vegetative growth was enhanced in seedlings, juvenile trees and mature pod-bearing trees, with increases in root, shoot and leaf dry weights, stem height, leaf area, root/shoot ratio and relative growth rate compared to plants grown at ambient CO_2. However, the growth enhancement appeared to be smaller in older trees compared to young trees or seedlings (Baligar et al. 2005; Lahive 2015; Lahive et al. 2018). Similarly, mango trees grown at 700 ppm accumulated more dry matter and a larger leaf area than those grown at ambient CO_2 (Schaffer et al. 1997). Photosynthesis in coffee does not appear to acclimate to elevated CO_2 in long-term growth studies; after 2-year growth at ca. 600 ppm, a 40% increase in photosynthetic rate was measured which was still apparent 2 years later (Ghini et al. 2015; Rakocevic et al. 2018). Nutrient uptake and nutrient use efficiency for several mineral nutrients including N were improved by growth at elevated CO_2 (Baligar et al. 2005) while no such change in nutrient concentrations was seen in coffee plants grown at elevated CO_2 (Da Matta et al. 2016), and in mango, the concentration of several minerals decreased in leaves grown at elevated CO_2 relative to ambient CO_2 (Schaffer et al. 1997). In general, in C_3 plants, increases in CO_2 concentration cause a decline in g_s (Ainsworth and Rogers 2007) and in some cases a reduction in stomatal density (Woodward 1987). This has implications for iWUE as water loss is reduced through stomatal restriction, and carbon uptake is increased (Brodribb et al. 2009; Cernusak et al. 2011). In a study of iWUE (measured via carbon isotope discrimination in tree rings) in tropical trees in Brazil, Hietz et al. (2005) concluded that iWUE increases in recent decades were due to increases in assimilation rate rather than declines in g_s. In cacao, the response of g_s to elevated CO_2 has varied between studies. Baligar et al. (2008) measured a 65% reduction in g_s as CO_2 concentration increased from 370 to 680 ppm, which resulted in improved iWUE. However, Lahive et al. (2018) did not observe any effect of CO_2 on g_s in juvenile plants of the Amelonado variety grown at 700 ppm CO_2 for several months. The latter study also found that stomatal index increased in leaves which developed in an elevated CO_2 environment, a response contrary to trends among most C_3 species over the last century (Woodward 1987; Lammertsma et al. 2011). Stomatal conductance in coffee appears to remain unchanged in response to elevated CO_2 (Ramalho et al. 2013; Da Matta et al. 2016), but the response varied depending on position within the canopy (Rakocevic et al. 2018). Quantum efficiency was enhanced under elevated CO_2 with a concurrent decrease in light compensation point compared to plants grown under ambient CO_2. This effect was dependent on soil moisture conditions with a greater improvement seen in well-watered plants compared to stressed plants (Lahive et al. 2018). In coffee, quantum efficiency, as well as instantaneous carboxylation efficiency, increased in response to elevated CO_2 but only in leaves in the upper canopy (Rakocevic et al. 2018). Shade-tolerant species tend to have greater relative response to elevated CO_2 in terms of quantum efficiency and light utilisation than shade-intolerant species (Sefcik et al. 2006; Ellsworth et al. 2012), likely due to the greater responsiveness of stomata to lower light levels making more efficient use of available light (Woods and Turner 1971). Soil water status also influenced photosynthetic responses to elevated CO_2 as the reduction in photosynthesis due to water deficit was lessened under elevated CO_2 (Lahive 2015).

To date, only one study has been carried out examining pod development responses to elevated CO_2. Following growth at 700 ppm CO_2 for 2 years under greenhouse conditions, pod dry weight increased due to greater husk dry weight rather than bean weight. This enhancement was only observed in the second year of exposure suggesting that there was a lag between increases in assimilation rate at the leaf level in response to CO_2 and an observed increase in pod characteristics (Lahive 2015; Handley 2016). Changes to biomass partitioning within the fruiting organ has been demonstrated in other tropical perennials. Total fruit weight increased in macadamia and mango grown at elevated CO_2; in macadamia, this was due to greater dry matter accumulation in the husk and kernel, and in mango, partitioning to the flesh of the fruit increased (Schaffer et al. 1999). The effect of elevated CO_2 on bean quality appears to be complicated with varying responses reported on the same trees over the 2 years. Competition for assimilates between vegetative and reproductive sinks may have a role in determining how bean quality is influenced by elevated CO_2 (Handley 2016). The effect of CO_2 on bean fat content appears to be dependent on soil moisture conditions, with higher fat content in beans developed in an elevated CO_2 environment compared to those developed at ambient, but only when sufficient soil water was available (Handley 2016). In coffee, harvestable bean yield was higher in plants grown under elevated CO_2 (Ghini et al. 2015). Similarly in avocado, mango and macadamia fruit retention increased in response to elevated CO_2, and in mango and macadamia, total fruit weight was also increased (Schaffer et al. 1999).

To date, CO_2 research in cacao has been carried out in greenhouses. In other species (generally annual temperate crops), it has been shown that the effect of elevated CO_2 on photosynthesis and yield appears to be greatest in controlled environment–based studies and the magnitude of response is reduced in free air CO_2 enrichment (FACE) systems which are more representative of field conditions (Leakey et al. 2009). There is a need to expand the research in relation to CO_2 responses to get a clearer understanding of how cacao trees can be expected to CO_2 increases predicted in the future. As mentioned previously, there was a lag in the response of pod production to elevated CO_2 in cacao grown in greenhouse conditions (Handley 2016) which indicate that for a perennial crop like cacao, long-term studies are crucial to properly understand the dynamic responses to climate overtime which may be substantial in such a system. For example, a 17-year study of *Citrus aurantium* grown under elevated CO_2 detailed the variation in response over time with the peak enhancement observed following 2 to 4-year exposure and a plateau in enhancement later in the study (Kimball et al. 2007).

6 Interactions between climate variables

It is important to consider not only cacao responses to individual climate variables but also how these variables interact to influence growth and productivity of cacao. In cacao, very limited research has been performed in this area to date. The interactive nature of various climate variables on plant development can be quite significant. For example, respiratory losses are greatest at higher temperatures; however, elevated CO_2 concentrations can help to reduce respiratory losses through higher carboxylation rates (Morison and Lawlor 1999). Meta-analysis has suggested that the response of photosynthesis in C_3 species to elevated CO_2 was greater in plants grown at higher temperatures; however, this did not necessarily translate into a greater response of biomass production in FACE studies (Bishop et al. 2014). Generally speaking, as CO_2 increases, the temperature optimum for light saturated photosynthesis increases, the reduction in maximum quantum yield associated with high temperatures is reduced and light compensation point, which increases at higher temperatures, is reduced (Long 1991). Elevated CO_2 helped to mitigate the negative effect of high temperatures on photosynthesis in coffee. The decline in photosynthesis in response to extreme high temperatures was significantly less severe in plants growing under elevated CO_2 compared to those grown at ambient CO_2 (Rodrigues et al. 2016). Photoinhibition in high-temperature stressed coffee was also lowered in plants grown under elevated CO_2, likely through enhancement of protective and antioxidant mechanisms (Martins et al. 2016). However, such interactions have yet to be quantified in cacao. Similarly, in some cases, stress by water deficit has been ameliorated by growth at elevated CO_2 through various mechanisms including improved iWUE, maintenance of higher plant Ψ through reduced g_s and greater fine root production (Wullschleger et al. 2002). Enhanced iWUE under elevated CO_2 may slow the decline in soil moisture thereby delaying the onset of water-deficit stress. In a meta-analysis of FACE and OTC studies in C_3 plants, soil water was observed to play a significant role in determining the yield response to CO_2, with the greatest relative increase in yield in response to CO_2 seen in drier soil conditions (Bishop et al. 2014). In young Amelonado trees, the negative effect of water deficit on growth and photosynthesis was reduced in those grown under elevated CO_2 compared to ambient CO_2-grown plants (Lahive et al. 2018). The impact of soil moisture deficit in combination with high-temperature stress needs to be studied in cacao as there is concern that water-deficit stress will be further increased by higher temperatures and greater evaporative demand. Improved light utilisation observed in young cacao trees grown under elevated CO_2 (Lahive et al. 2018) could prove beneficial where shaded conditions are used to reduce high-temperature stress. There is also a need to do more long-term studies, so the impact on yield over time can be assessed.

7 Mitigating against climate change

7.1 Crop husbandry

Irrigation is an obvious solution to combat soil water limitation in the field, and the positive effects of supplementary irrigation have been mentioned previously. However, it has not been widely adopted in West Africa due to practical limitations (e.g. the remoteness of smallholder farms from water supplies) and cost restrictions. There is a lack of informative studies on the impacts of irrigation in the field (Carr and Lockwood 2011). In India, 20 L of water per tree per day supplied by drip irrigation was determined as the ideal amount to achieve highest yields during the long dry season (December to May) (Abdul Haris et al. 1999). This treatment increased dry bean yields by 26% over 4 years compared to 10 L per tree per day. Hutcheon et al. (1973) also improved yields through irrigation in Ghana, with the greatest benefit observed during years with a severe dry season. These authors also noted that in conditions where there is a high evaporative demand, which is more likely to occur during dry conditions, the positive effect of irrigation is limited due to strong effect of VPD on g_s (Hutcheon et al. 1973). In Côte d'Ivoire, Jadin and Jacquemart (1978) compared the impact of sprinkler and drip irrigation on yields with a non-irrigated control. While both methods resulted in considerable increases in yield, the largest increases were observed with drip irrigation.

As a potential alternative to irrigation, plastic and organic mulching, in the form of coffee husks, has been shown to have a positive effect on soil moisture levels, leading to improvements in g_s and photosynthesis, and consequently establishment rates in certain genotypes of cacao (Acheampong et al. 2018). Mulching can have numerous beneficial effects including reducing evaporation from the soil thereby helping to conserve soil moisture, reducing soil temperature around the roots and reducing soil erosion (Prosdocimi et al. 2016 and references within). Organic mulches have the added benefit of adding nutrients to the soil through their decomposition. The early yields from cacao grown with coffee mulch were higher than that of trees grown with plastic mulch, with the authors attributing this to the joint effect of water conservation and nutrient addition (Acheampong et al. 2018). Cover crops can also be grown in the understory to perform a similar function to mulching (Baligar and Fageria 2007).

Bae et al. (2009) showed that tolerance to water deficit was significantly improved in cacao seedlings colonised with the endophytic fungus *Trichoderma hamatum*, which appeared to delay the initial response to stress. Root growth increased in plants colonised with the fungus, and the authors suggest that this may have improved water uptake or access to water by the roots of colonised plants and delayed the onset of drought. Cacao forms symbiosis with arbuscular mycorrhizal fungi (AMF) (Laycock 1945) which in other plant species have been shown to improve drought responses. The methods by which AMF enhance drought tolerance are varied including improved water and nutrient (especially P) acquisition and enhanced root growth (Augé 2001). Colonisation of cacao seedlings with native and exogenous AMF enhanced growth (Droh et al. 2016) and a range of species of AMF have been identified associated with cacao (Cuenca and Meneses 1996; Soumaila et al. 2012; Ramírez et al. 2016). The potential to exploit the positive effects of this relationship on cacao farms needs further exploration.

Growing cacao under shade trees may help to alleviate extreme temperature stress and soil water deficit during dry periods. In Bahia, Brazil, within the canopy of heavily shaded, 15-year-old cacao, planted at a density of 3 × 3 m, de Miranda et al. (1994) demonstrated that temperature and relative humidity became uncoupled from outside temperatures. The maximum difference in temperature measured outside and inside the layers of the cacao canopy were approximately 2 (± 0.5) °C. Relative humidity within the canopy increased to a higher level than that recorded outside the canopy (de Miranda et al. 1994). In a more extreme case in Ghana, maximum air temperature differences of up to 7 °C were recorded between full sun and shaded systems. In the shade systems, VPD was also maintained at lower levels compared to the full sun system (Abdulai et al. 2018a). In contrast, a study in Ghana found that maximum air temperatures above the cacao canopy were not affected by shade, and while shade had positive effects on the lowest daily mean, highest minimum and the absolute minimum air temperature, the differences were always less than 1 °C (Asare et al. 2017). In the Bolivian Andes, shade provided by a variety of woody trees and banana reduced soil temperature and consequently lowered soil evaporation leading to higher soil moisture content in the uppermost soil layers compared to a monoculture system. Moreover, shaded cacao was less exposed to high temperatures and evapotranspiration which lowered the water demand of cacao (Niether et al. 2017). Cacao farmers in drier regions of Ghana incorporate more shade species at higher densities on their farms compared to farmers in the wet region (Abdulai et al. 2018b).

Selection of the appropriate shade species is essential to achieve the maximum benefits of shade, and the use of inappropriate shade trees can have a detrimental effect. This was demonstrated in a study in Ghana which showed that shading cacao with *Albizia ferruginea* or *Antiaris toxicaria* resulted in greater levels of mortality compared with non-shaded trees following a prolonged drought, even though the transpiration rate and sap flux density of shaded cacao was lower than that of full sun cacao. The greater mortality was attributed to non-complementary resource use by the shade and cacao trees. Soil moisture content was depleted in the top 0.6 m of the soil profile suggesting that the cacao and shade trees were accessing watering from the same soil layers (Abdulai et al. 2018a). Köhler et al. (2009) demonstrated that increased shading from *Gliricidia* trees significantly increased maximum water use rates of associated cacao trees. Variation in the effect of different shade species on soil moisture content has been observed (Kyereh 2017). *Gliricidia* is often used as a shade tree on cacao farms. The root systems of these trees penetrate deeper than cacao roots therefore reducing competition for water between the two species (Moser et al. 2010). Clearly, the shade trees used need to be chosen careful so that water use is complementary and soil water is exploited regularly over the soil profile. Light penetration also needs to be considered when selecting shade trees. In this respect, more research is required to identify the optimal shade species and their planting density, and as demonstrated by Abdulai et al. (2018b), climatic conditions within a region also need to be considered when recommending shade tree species. Shade trees often grown on cacao farms include fruit trees such as avocado, coconut, cashews and mango, or timber trees such as *Terminalia superba* and *Alstonia boonei* (Abdulai et al. 2018b). A detailed collation of information on shade species for use with cacao is provided by Asare (2005). Recommendations for best shade management practices in cacao have been outlined by Tscharntke et al. (2011).

7.2 Identification of tolerant genotypes

It is likely that traits conferring tolerance to a variety of abiotic stresses may be beneficial across a range of stresses and highlights the importance of testing germplasm under various and interacting environmental conditions. Research has shown that breeding for resilience to multiple environmental stresses at the same time is the most effective way forward (Farrell et al. 2018). Interestingly, during a severe drought in the field in Brazil, cacao clones not selected for drought tolerance, but another beneficial trait (usually high yields or disease resistance) showed greater tolerance than hybrids or common Amelonado types. The authors suggest that this may be due to their selection in high-input, low-shade environments (Gateau-Rey et al. 2018). Breeding in cacao to date has largely focused on yields and pest and disease tolerance, with limited focus on breeding for climate resilience. However, according the Farrell et al. (2018), the cacao accessions currently available are sufficient for effective breeding to be achieved.

While cacao is sensitive to water deficit, there is evidence that some genotypes are more tolerant to water stress episodes. There is potential to exploit this variability to breed for varieties that are more tolerant to the more frequent and/or intense drought episodes that are predicted to occur in many cacao-growing regions. Balasimha and Daniel (1988) devised a screening method based on monitoring leaf Ψ on detached leaves as they dried out. The more tolerant genotypes tended to show a slower decline in leaf Ψ than more sensitive ones. Balasimha et al. (1988) attributed higher levels of drought tolerance in cacao to effective regulation of stomatal opening. However, Balasimha et al. (1991) found no difference in photosynthesis or g_s between genotypes determined as drought tolerant and sensitive but did note that the drought-tolerant genotypes were able to maintain less negative Ψ during the driest months of the year. Although there is no doubt that stomatal regulation is important in minimising water loss, other traits have also been identified which have the potential to act as selection traits. In a study of a range of TSH material in Trinidad, the genotypes most tolerant to water deficit showed little or no change in g_s and E and much earlier declines in g_s were associated with more sensitive genotypes (Antwi et al. 1994), suggesting that g_s alone may not be a suitable screening method. In the same study, the clone TSH 919 was identified as being particularly tolerant to water deficit as it maintained higher leaf Ψ during periods of soil moisture deficit. There were a number of traits that may have contributed to this clone's enhanced tolerance including changes to the pattern of root growth under water deficit (one adventitious root became dominant and developed into a tap root-like structure), basal leaves were shed more quickly in response to the stress compared to less tolerant clones, which allowed the upper leaves to maintain higher leaf Ψ, and leaf rolling towards the abaxial surface occurred which may have helped to reduce water loss by transpiration (Antwi et al. 1994).

Osmotic adjustment may also play a role in conferring soil water-deficit tolerance in some genotypes and appears to be genotype specific (e.g. Rada et al. 2005; Moser et al. 2010; Araque et al. 2012). Osmotic adjustment is an adaptive mechanism which, through the accumulation of solutes within cells, lowers the osmotic potential that attracts water into the cell and helps to maintain turgor. Increases in leaf K and P concentrations were observed in certain cacao genotypes as leaf Ψ fell below − 1.5 MPa, and this was suggested to have a role in osmotic adjustment (de Almeida and Valle 2007). In a study by dos Santos et al. (2014), decreases in N, P, K, Ca and Mg were seen in response to water deficit, and genotypes most sensitive to the stress had the greatest reductions in N, P and K compared to the non-stressed controls. The authors also reported that the ability to maintain levels of Ca and Mg under water deficit contributed to an increase in biomass and leaf area in the stress-tolerant genotypes compared to the well-watered controls (dos Santos et al. 2014). Araque et al. (2012) showed a correlation between osmotic adjustment and tree survival under water-deficit conditions in cultivars of Criollo cacao. Those cultivars that used osmotic adjustment to avoid stress were also highest yielding in dry conditions.

Dos Santos et al. (2014) reported eight variables sufficient to separate water deficit–tolerant and sensitive cacao genotypes. These variables were total leaf area per plant, root dry weight, stem dry weight, leaf dry weight, total dry weight, relative growth rate and Ca and Mg concentrations. While in a later study dos Santos et al. (2016) included the variables root length, root volume, root diameter (of roots < 1 mm) and root diameter (of roots > 1 mm < 2 mm). The authors suggest that the high heritability of a number of these traits has the potential to be used in the selection of cacao genotypes with enhanced water-deficit tolerance (dos Santos et al. 2016). It is worth noting that most of these traits are measures of vigour. These may be useful in the selection of material for improved establishment under dry conditions. However, these traits could potentially accelerate the onset of soil moisture stress as vigorous growth will also place a greater demand on available soil water. Bae et al. (2008) identified correlations between the expression of genes encoding enzymes involved in polyamine biosynthesis and changes in g_s, photosynthesis, PSII efficiency and leaf Ψ. Polyamines play a role in plant responses to various stresses due to their antioxidant properties and their function in stabilising membranes and cell walls (Gill and Tuteja 2010). Increased activity of the antioxidant enzyme guaiacol peroxidase in response to water deficit has also been suggested as an indicator of water-deficit tolerance among cacao genotypes (dos Santos et al. 2014).

There is a need for a clear definition of what is meant by drought tolerance in cacao (and woody perennial crops in general). Probably, a more accurate term to use is resilience to soil water deficit that describes a plant that can recover quickly following a stress period and return to pre-stress performance levels soon after the stress has ended. When viewed from this perspective, plasticity in key stress response traits is important to identify. Plasticity in g_s has been an important trait used to identify drought tolerance in cacao. However, as yield is strongly linked to g_s in a range of crop species (Roche 2015) and is also strongly correlated with maximum photosynthetic rate in cacao (Daymond et al. 2011), research to develop drought resilient cacao needs to look beyond just minimising water loss and towards greater efficiency of water use in photosynthesis and biomass allocation to the beans.

Genetic variation in response to temperature has been shown in cacao in terms of photosynthetic responses, fruit growth and bean quality. Identification of genetic material with greater high-temperature tolerance as well as identification of physiological traits which confer this tolerance could be used in breeding cacao to maintain high productivity and bean quality under higher temperature conditions. However, relatively little work has been done in this area.

8 Gaps in current research

8.1 Detailed understanding of physiological processes in cacao

For such an important crop, there are significant gaps in the current understanding of cacao physiology. The reasons for the relatively low photosynthetic rate of cacao are not fully understood, and how this links to yield and biomass allocation is an important area of physiological research. In coffee, low rates of photosynthesis have been attributed to low stomatal and mesophyll conductance and high hydraulic resistance (DaMatta et al. 2016). Endogenous and environmental control mechanisms of flowering and pod development are poorly understood in cacao. However, studies focused on the various aspects of reproductive physiology in cacao are currently very limited. In addition to this, the cauliflorous nature of cacao results in the relatively unusual development of flowers and pods on the trunk and branches of the tree, some distance for the carbohydrate source of the leaves. The implications of this for carbohydrate storage, remobilisation and transport mechanisms within the tree are significant. Studies examining the mechanisms underlying biomass partitioning between leaves, roots and pods and the influence the environment has on partitioning between the organs are currently lacking. There is a need to study and model the carbohydrate partitioning between various organs and source/sink relations within the plant under stressful environmental conditions. The area of biomass partitioning is particularly important in a crop such as cacao which tends to favour vegetative over reproductive growth, often resulting in high pod losses through cherelle wilt. Historically, crop yield increases have been achieved through the alteration of biomass partitioning rather than changes in photosynthetic rate (Gifford and Evans 1981). An understanding of the mechanisms regulating these relationships within the plant is essential for the development of high yielding cacao under environmental stress. Belowground processes in cacao are an almost untouched area of research, understandable given the difficulty with measuring this in a tree crop. However, advances in imaging technology may help to progress this in the future (Judd et al. 2015 and references within). Research into cacao root systems will be integral in the development of water-deficit resilient germplasm, as improvements in soil water accessibility are an important strategy in this area. Rooting depth was identified as a key trait conferring drought tolerance in coffee (Pinheiro et al. 2005). Root stock effects and the identification of environment-specific root stocks could be utilised to enhance resilience to various environmental conditions. In grapevine, water deficit–tolerant rootstocks have been used to improve yield in conditions where water is limiting. Various mechanisms have been exploited to achieve this through improvements in water uptake and transport, ABA signalling from rootstocks to limit stomatal aperture and hydraulic signalling (Serra et al. 2013 and references within).

There is a need to understand better the upper temperatures at which cacao yields are significantly impacted and to quantify the duration of exposure to high temperature at which an impact occurs. A deeper understanding of how environmental stresses influence various physiological processes needs to be developed both in controlled environment/greenhouse studies and in the field.

8.2 Interactive effects

So far, ecophysiological research in cacao has mainly focused on individual climate variables with limited focus on interactions. While useful, single-factor studies are of limited use when attempting to predict plant responses to multiple interacting environmental variables. Identification of additive and interactive effects of various environmental variables will provide greater certainty in predictions of how cacao will respond to climate change. In other tree species, the amelioration of high temperature and water-deficit stress by elevated CO_2 has been shown. For example, in coffee, tolerance to high temperatures, in relation to photosynthetic rate, PSII efficiency and electron transport rate, was enhanced by growth at elevated CO_2 (Rodrigues et al. 2016). In peach seedlings, elevated CO_2 enhanced iWUE in water stressed compared to well-watered plants (Centritto et al. 2002). However, the extent to which this may occur in cacao is unknown. The interaction between temperature and soil moisture is also of importance as rising temperatures could potentially exacerbate soil moisture through increased evaporation. The use of shade to mitigate against environmental stress has been suggested, but our understanding of the implications of various agroforestry systems on the physiology of cacao needs further development, as well as the identification of appropriate shade tree species, to ensure that these systems are used effectively to mitigate against environmental degradation and plant stress while also maintaining productivity. The influence of soil nutrition on various aspects of cacao physiology has not been discussed here. A detailed review of current research in this area can be found in van Vliet and Giller (2017). Nutrition plays a central role in many of the issues discussed here especially in relation to CO_2 elevation and utilisation of full sun–growing systems. To achieve maximum benefits under these environmental conditions and to understand the interactions between soil nutrition and environmental stress, further research in this area is warranted, especially in field studies.

8.3 Linking physiological responses and their underlying genetic controls

The molecular controls underlying various physiological processes are largely unknown in cacao. Various molecular mechanisms involved in stress response have been identified in other plant species, but in cacao, this area of research is relatively underdeveloped. For example, aquaporin proteins have an important role in regulating plant-water relations. A putative aquaporin-encoding gene was repressed in cacao colonised with the endophytic fungus *T. hamatum*, and this was linked to a delay in the onset of water-deficit stress (Bae et al. 2009). Heat shock proteins are one important mechanism by which tolerance to high temperature is achieved. These proteins are involved in maintaining correct protein folding under stress which is essential for the maintenance of cell membranes (Wang et al. 2004). Mapping populations or genome-wide association studies may be useful strategies in speeding up the identification of specific climate resilience traits and the incorporation of these into future breeding programmes. Farrell et al. (2018) have highlighted the fact that despite calls for one, no program is in place for climate change resilience breeding cacao. Cacao is lagging behind other major crops in the development of varieties capable of withstanding predicted changes in climate and long-term commitment, and coordination by the various partners is required to bring breeding efforts in cacao up to speed with other crops (Farrell et al. 2018).

8.4 Field-based studies on detailed physiological responses

Much of the research described in this review has been carried out in greenhouse conditions. While this is very useful in minimising the influence of non-treatment effects, it is not representative of the complexity of field conditions. It is also difficult to work with sufficient replication of mature trees in these conditions, so much of the information to date is based on seedlings and young trees which are physiologically quite different to mature trees. Therefore, it is essential that resilience traits identified in greenhouse studies are tested in field studies.

9 Conclusion

For such an important crop species, there are critical research gaps in our understanding of cacao ecophysiology. Here, we have provided a review of the current state of the research related to cacao and its response to the environment. As we face climate uncertainty and greater variation in climate conditions, this area of research needs a new lease of life if cacao production is to meet the growing demand for chocolate worldwide. Taking a more holistic view of cacao productivity, by incorporating the various physiological processes underlying variations in yield and quality as well as obtaining a better understanding of how environmental conditions influence these processes, has the potential to speed up the development of higher yielding, more climate-resilient cacao varieties. In order for this to be most effective, it is vital that the cacao physiology and breeding communities work together in a coordinated effort to accelerate progress in this area and to ensure continued productivity thereby maintaining the livelihoods of millions of cacao farmers around the world.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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