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REVIEW

Regulation of cuticular wax biosynthesis in plants under abiotic stress

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Abstract
Cuticular waxes are the covering of the outer layer of the plant, consist of hydrocarbon appears like whitish film or bloom in plant organs. They play a vital role like a safeguard from different stress condition in the plant. Since environmental factors are active regulators of cuticular wax biosynthesis, composition, quantity, and deposition, it is evident that cuticular wax is associated with plant stress responses. The diversity of cuticular wax compositions is a proof of the wealth of genes associated in plant wax production. Moreover, a number of wax genes were distinguished in plant/crops at abiotic stress conditions but, regulation of control of those wax genes has not been studied very well in major crop plants at abiotic conditions. A very few transcriptions factors were identified to regulate the expression level of wax genes of cuticular wax biosynthesis at abiotic stress condition. However, further study is needed to identify more candidate transcriptional regulation factors to cuticular wax production in different crop plants in diverse abiotic environments. Therefore, regulation of cuticular wax production under diverse abiotic stresses and the role of transcription factors into the plant cuticular wax accumulation will be helpful to engineer crop plants and improve transgenic crops for stress tolerance. In this review, we focused on a new perspective on transcriptional factors to regulate functional genes of cuticular wax biosynthesis in plants at abiotic stresses.

Keywords Transcriptional factors · Transpiration · Water stress · Membrane damages · Plant-water relations · Stress tolerance

Introduction

Abiotic stresses adversely affect plant's life cycle and productivity (Ahuja et al. 2017). Plants have developed diverse physiological, morphological, and genetic mechanisms to mitigate abiotic stresses condition (Hasanuzzaman et al. 2012, 2013; Chen et al. 2017; Shao et al. 2008; Shepherd and Griffiths 2006; Shaheenuzzamn et al. 2019). The cuticular wax deposition is one of the major adaptive morphological mechanisms in abiotic conditions (Lee and Suh 2015). Cuticular waxes control non-stomatal water loss, scatters ultraviolet (UV) radiation, gaseous exchange, pathogen, insect, fungi, and atmospheric impurities like ozone, carbon dioxide, acid rain, biotic and abiotic stresses (Bernard and Joubès 2013; Nawrath et al. 2013). Cuticular waxes are a complex mixture consisting mostly of very long-chain fatty acids (VLCFAs; > 20 carbons in length) and their derivatives (Tafolla-Arellano et al. 2018). Cuticular waxes biosynthesis depends on the diverse stress conditions such as drought, temperature, cold/ frost stress, UV irradiation, humidity, heavy metal stress, pathogen, plant–insect interaction, and water stress, etc. The genetic factors also control cuticular wax biosynthesis and composition. Recently, numerous cuticular wax genes in the model plant (*Arabidopsis*) as well as crops such as rapeseed, potato, tomato, rice, maize, barley, wheat, broccoli, sesame, tobacco, cucumber and cabbage were reported (Racovita et al. 2016; Shaheenuzzamn et al. 2019). Wax-deficient mutant's analysis, such as *glossy* (*gl*), *bloomless* (*bm*), and *eceriferum* (*cer*), were helped to identify a huge number of genes in response to

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the biosynthesis of cuticular waxes, transport and regulation (Lee and Suh 2015).

Transcriptional factors are the most important factors during plant adaptation to abiotic stresses condition (Tafolla-Arellano et al. 2018). TFs interact with target gene promoters and regulate stress genes networks to control physiological responses in plants (Yamaguchi-Shinozaki and Shinozaki 2006). TFs also regulated cuticular waxes biosynthesis, transport, and deposition, which have a wide range of experimental evidence (Li-Beisson et al. 2013). Major TFs families are APETALA2/ethylene-responsive family (AP2/ERF), myeloblastosis (MYB) families, homeodomain-leucine zipper class IV (HD-Zip-IV) family, WRKY and NAC (Borisjuk et al. 2014; Lee and Suh 2015; Tafolla-Arellano et al. 2018). These TFs altered cuticular wax deposition and composition in overexpression functions, and increased tolerance of transgenic plants (Bi et al. 2016). Among them, the MYB TF families have four major subfamilies named as 1R-MYB, R2R3- MYB, 3R-MYB (R1R2R3-MYB) and 4R-MYB. These MYB TFs involved regulating diverse mechanisms at stresses condition such as development, differentiation, and metabolism (Ambawat et al. 2013; Baldoni et al. 2015). Among them, R2R3-MYB TFs were reported to regulate wax biosynthesis in plants (Bi et al. 2016; Xue et al. 2017). Moreover, several family's TFs identified to regulate waxes biosynthesis in *Arabidopsis* (Lee and Suh 2015). Some transcriptional factors also have identified in crop plants such as rice, maize, tomato, barley, soybean, *Camelina*, wheat and sorghum (Wang et al. 2012; Zhou et al. 2014; Bi et al. 2016; Borisjuk et al. 2014; Buxdorf et al. 2014; Xu et al. 2016; Bao et al. 2017). It is reported that overexpression of transcriptional factors altered cuticular waxes depositions, cuticle structure, and permeability and enhanced tolerance in transgenic plants (Seo and Park 2011; Qin et al. 2011). Several extensive studies have reported cuticular wax composition, biosynthesis, wax morphology, biochemistry, structure, and transport (Xue et al. 2017). However, there have not enough information to identify transcription factors to regulate plant cuticular wax production during abiotic stresses. In this present review, we focused on the regulation of cuticular waxes biosynthesis in plants under abiotic stress and the role transcription factors on the plant cuticular wax accumulation.

Regulation of cuticular waxes biosynthesis under abiotic stresses

Biosynthesis, wax accumulations, and waxes morphology alter at environmental factors, especially abiotic factors that are an actively regulated method (Fig. 1). In this section, we focused on major abiotic stresses such as drought,

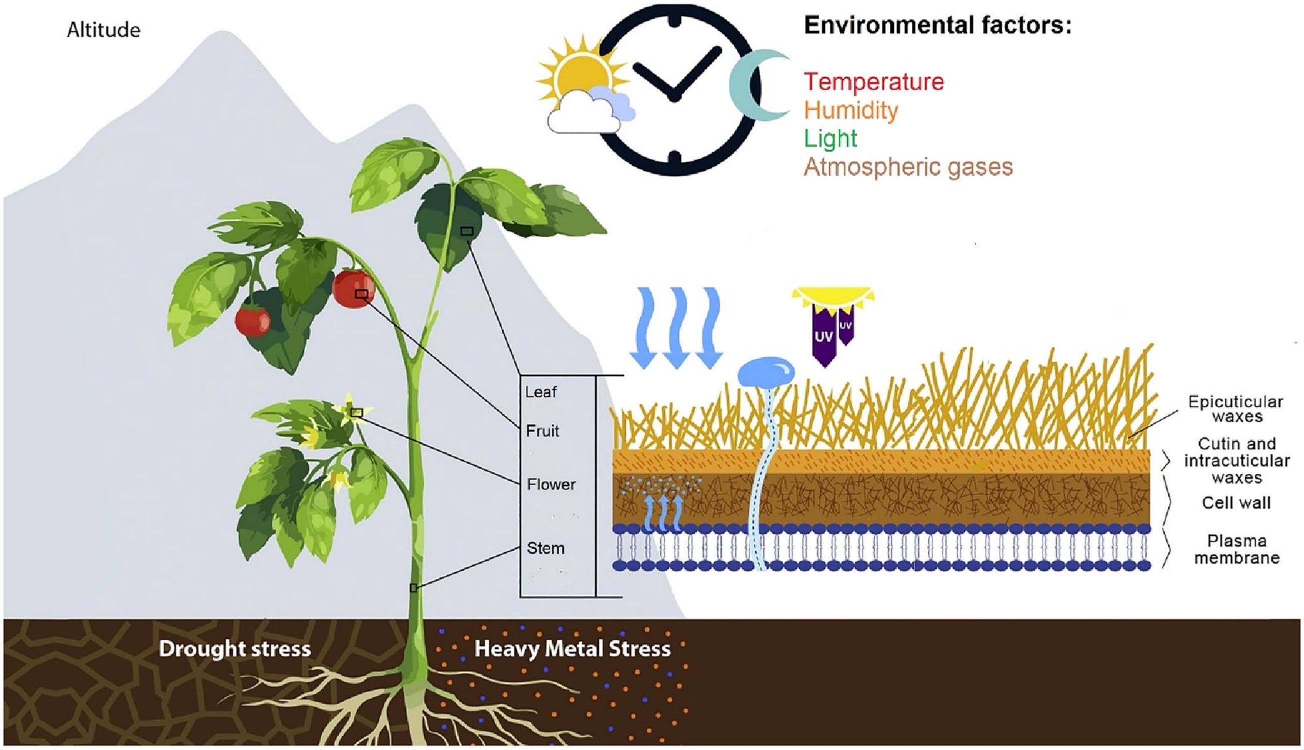


Fig. 1 Environmental conditions influence cuticular wax biosynthesis (Adapted from Tafolla-Arellano et al. 2018; with permission from Elsevier)

temperature, cold/frost, UV-radiation, humidity, water deficit, and salinity stresses, which are involved in regulating cuticular wax production, which are discussed in the next sections.

Drought

Many studies reported that abiotic stresses increased the amount and content of cuticular waxes in the model plant, *Arabidopsis* (Xue et al. 2017), as well as some other crops such as rapeseed (Pu et al. 2013; Tassone et al. 2016), *Cemelina sativa* (Razeq et al. 2014; Tomasi et al. 2017), potato (Szafranek and Synak 2006), eggplant (Halinski et al. 2012), tomato (Wang et al. 2011; Smirnova et al. 2013; Isaacson et al. 2009; Kosma et al. 2010; Halinski et al. 2015), wheat (Zhang et al. 2013, 2015; Wang et al. 2015a; Recovita et al. 2016), barley (von Wettstein-Knowles 1971; Avato et al. 1982), rice (Mao et al. 2012; Wang et al. 2017), maize (Javelle et al. 2010), broccoli (Lee et al. 2015), sesame (Kim et al. 2007), tobacco (Cameron et al. 2006), cucumber (Wang et al. 2015b) and cabbage (Laila et al. 2017). In those of the studies reported that cuticular waxes amount and composition increased 2.5-fold in leaves at drought stress conditions (Xue et al. 2017). The cuticular waxes deposition increased up to 90% at drought conditions in sorghum (Saneoka and Ogata 1987). The consequence of drought in wheat is correlated to cuticular wax deposition. The overall cuticular waxes amount and contents increased equally in all compound classes, including primary alcohols in leaf blade (Wang et al. 2015b). In another study, the cuticular waxes composition in wheat was increased by 2.2- to 2.6-fold within 4 h of 20% PEG 6000 treatment (Wang et al. 2015b). The amount cuticular wax increased with the increase of alkanes with chain lengths of C29 and C31 showed amplitude after drought (Li et al. 2020). Several studies found that cuticular waxes accumulation and yield in crops depended on high drought tolerance (Guo et al. 2016). So, there is a considerable correlation among cuticular wax accumulation, yield and water use efficiency (WUE) in crops at drought stress such as sorghum (Jordan et al. 1984), barley (Febrero et al. 1998), rice (Zhu and Xiong 2013), and wheat (Richards et al. 1986). In a wheat study as related to cuticular wax reported that the glaucous genotypes have higher grain yield than non-glaucous one in the standard and modest drought condition (Johnson et al.1983). Moreover, in a study of wheat found that wheat grain yield is completely relay on cuticular wax, especially under drought (Monneveux et al. 2004; Zhang et al. 2013). In barley, similar positive correlation was observed among grain yield and the amount of cuticular wax under drought stress environment (González and Ayerbe 2010). The drought-tolerance and yield were higher in crops having more cuticular wax than those with less wax or non-waxy crops (Zhou et al. 2013; Guo et al. 2016).

The amount of cuticular wax load increases approximately 75% compared with non-treated plant by increasing alkane constituent (93%) dramatically in leaves in *Arabidopsis* at water-deficit stress conditions (no irrigation). Alkane synthesis which is major component of the plant cuticular wax is a key indicator during water stress conditions (Kosma et al. 2009). Kosma et al. (2009) reported that cuticular wax deposition increased in water-deficit stress in many plants such as sesame (*Sesamum indicum*), soybean (*Glycine max*), tobacco (*Nicotiana glauca*), and rose (*Rosa* × *hybrida*). In another reported that cuticular wax deposition correlated with water loss rates in leaf at water stress condition, and increased by 32% to 80% per unit area, due to increasing primarily 29–98% alkanes (Kosma et al. 2009). It is also found that cuticular waxes increased over 150% in the leaves of tree tobacco to expose multiple drying events at water deficit conditions (Cameron et al. 2006). It was found similar results in higher plants, including dicotyledonous and grass species at water deficit stress (Kosma et al. 2009).

Salinity stress

Salinity stress (NaCl) induced in *Arabidopsis* plants found that the amount of leaf cuticular wax increased significantly in per unit area. This NaCl stress (150 mM) influenced to increase cuticular wax accumulation per unit area about 80% because of wax alkanes deposition increased primarily in *Arabidopsis* (Kosma et al. 2009). It is reported in plant that cuticular wax amounts and compositions decreased appreciably at 40 mM NaCl in *Grewia tenax* (Forssk.) leaves due to hydrophobic nature of leaf surface, and wax load was very low amount which was not influenced by NaCl at 160 mM in tamarind. This reduction did not show any changes in leaf wettability and wax morphology (Hunsche et al. 2010). Moreover, the effect of salinity had very limited or no effect on cuticular wax biosynthesis (Fricke et al. 2006) or increased only a small amount (Delarosaibarra and Maiti 1995). Further reported that wax crystal and amount of cuticular wax was not altered in rice and *P. tenuiflora* exposed to $NaHCO_3$ stress (Yang et al. 2015). So, more studies are needed on the effect of salinity stress on cuticular wax production in the crop plants.

Temperature stress

The temperature has a major influence on the cuticular waxes production in plants. Several studies reported that temperature influenced cuticular wax thickness in plants such as barley, *Brassica* species, and carnation plants (Shepherd and Griffiths 2006). It was reported that cuticular waxes production is relatively higher at low temperatures (15 °C) compared with high temperature (25 °C) in controlled environments (Kartini and Azminah 2012). The amount and compositions of cuticular waxes increased significantly at cold conditions (4 °C), where alkanes and secondary alcohols mostly increased in *Arabidopsis* (Ni et al. 2014a) and *Thellungiella salsuginea* (He et al. 2019). The glaucous plants of *B. oleracea* produced more unsaturated fatty acid and products of the reductive pathways (fatty acid, aldehyde, primary alcohol, ester) at lower light and higher temperature levels and more decarbonylation products (alkanes, secondary alcohol, ketones) at higher light and lower temperature levels (Baker 1974). But alkane biosynthesis increased in the pathways of decarbonylation at high temperatures. Another study reported that cuticular wax chain lengths (C_{27}, C_{29}, and C_{35}) in *Miscanthus sinensis* leaves as well as chain length (C_{31}) in *Pleioblastus chino* leaves were completely correlated with increasing period temperature (Zhang et al. 2004). In further reported that biosynthesis longer chain hydrocarbons were significantly dependent on mean annual temperature in *Austrocedrus chilensis* plants (Bush and McInerney 2013). However, the temperature effect on cuticular waxes chain length distributions are complex (Dodd and Poveda 2003). So, the temperature effect on cuticular wax long-chain n-alkane needs to investigate in crop plants in natural conditions (Duan and He 2011). The cuticular wax accumulation showed differences in plants in the warm climate (Gao et al. 2015), and cuticular wax compositions were also altered due to climate change within plant species (Frei et al. 2014). Moreover, biosynthesis and cuticular waxes deposition depend on mean temperature, the mean annual temperature, and the aridity index (Guo et al. 2015). These reports indicate that temperature has a vital role in cuticular wax properties in plants.

Cold stress

Cold or frost stress is a serious hazard to the sustainable cultivation of crop production, and have a great impact in cuticular wax depositions. Cold stress severities vary widely in a different place, and effect on plant growth and development including less germination, chlorosis, short seedlings, and necrosis, reduce leaf expansion, and wilting. Cold stress also rigorously obstructs the development of plants. Shepherd and Griffths (2006) reported that cuticular wax deposition reduced up to 29% in maize plants at the stage of four-leaf due to exposure to 7 days cold stress. Increases cuticular wax accumulation and alkane synthesis associated with low frost tolerance abilities in willow, *Salix* species. Cold stress effects on cuticular wax biosynthesis, deposition, wax morphology, and wax genes have studied well in the model plant, but very limited studies are found, especially in crop plants. It is needed further study to the effect of cold/frost stress on cuticular wax biosynthesis and accumulation in crops. It will help to select cold stress crops (Yu et al. 2014).

UV radiation stress

Cuticular wax is a major factor to defend crop plants from extreme ultraviolet (UV) radiation. Several studies reported that changes in cuticular wax production and gas exchange depend on high UV-B radiation in plants (Ni et al. 2014b). It is established that the accumulation of cuticular wax increased 20–28% in bean (*Phaseolus vulgaris* L.), barley (*Hordeum vulgare* L.) and cucumber (*Cucumis sativus* L.) through using UV-B light (Xue et al. 2017). It is reported that in vitro grown carnation plants increased gas exchange rate due to coarse cuticular wax (Majada et al. 2001), and cuticular waxes accumulations have an effect on the rate of gas exchange in the leaf surface of canola (*Brassica napus*) (Qaderi and Reid 2005; Ni et al. 2014b), pea (Gonzalez et al. 1996), cotton (Kakani et al. 2003) and mulberry (Yu et al. 2015). The amounts of primary alcohols and alkanes increased approximately two-fold by exposing an intermediate dose of UV-B in the cotyledons per unit area in cucumber (Fukuda et al. 2008). The amount of alkanes increased 20% as compared to non-irradiated controls, but there was no effect significantly on the amount of primary alcohols to use UV-B radiation in cotyledon per unit area (Steinmüller and Tevini 1985). It is proved that UV-B irradiations have a great influence on cuticular wax production and deposition. So, it is needed to find out the regulation mechanism of cuticular wax accumulation under high UV-B radiation to find out the relationship of gas exchange rate and plant performance.

Humidity stress

Soil and air humidity take part in an important task in plant development and morphology. Environmental humidity index changes have a considerable effect on cuticular wax amounts and contents, morphology, and deposition patterns. Cuticular waxes accumulation increased in *E. gunni*, *B. oleracea*, and *T. majus* by dropping relative humidity from 100 to 35% or from 98% to 20–30% (Shephered and Griffiths 2006). In other studies, cuticular waxes amounts and crystal density decreased with notably increased in leaf surface wettability at 98% RH, and increased total amounts of cuticular waxes with significantly reduced in leaf surface wettability at 20–30% RH in *Eucalyptus gunnii*, *B. oleracea* and *Tropaeolum majus* (Koch et al. 2006). Wax crystal morphology and compositions changed during cultivation at 98% RH in *Brassica*, however wax chemical compositions and crystals morphology remain unchanged in *Tropaeolum* and *Eucalyptus* (Koch et al. 2006), but another study showed that the cuticular wax component classes changed in *Brassica oleracea*, in where ketones and primary alcohols increased but secondary alcohols and aldehydes reduced at the highest relative humidity (98%) (Koch et al. 2006). But a further study reported that the relative amounts of ketones (6%) decreased, but aldehydes (4%) increased while 40% RH to 98% RH air humidity increased (Baker 1974). Farther reported in spring wheat seedlings that cuticular waxes deposition significantly increased with 28% total waxes, including primary alcohols (26%) under low humid condition (10–20% RH) as compared with high humidity (90–95% RH) (Wang et al. 2016).

Transcriptional regulation of cuticular wax biosynthesis in different plants

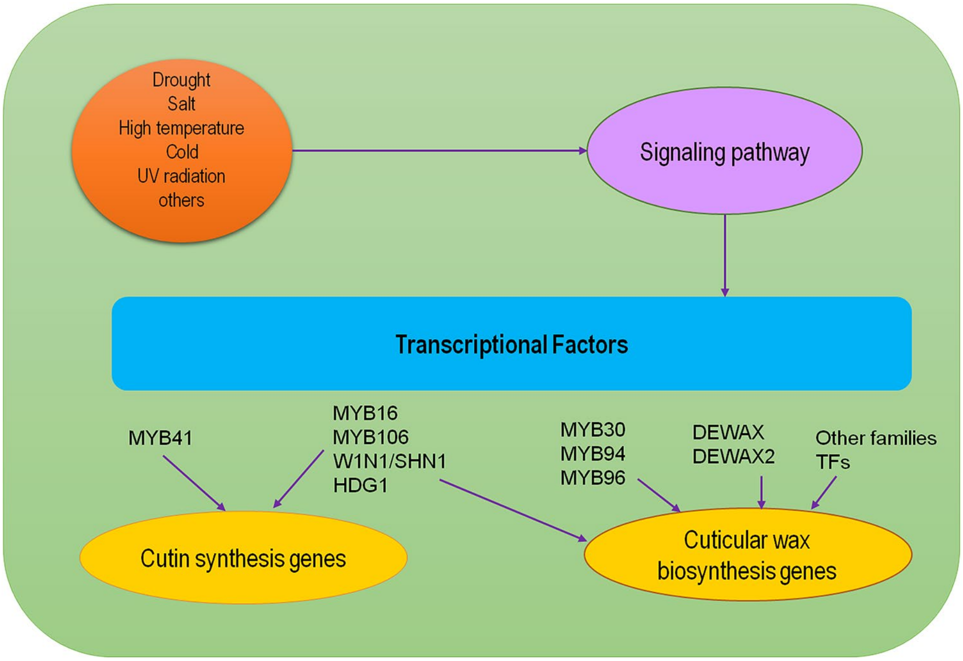
Regulation of cuticular wax biosynthesis in model plant

Transcriptional factors are known as the key regulatory factors for cuticular wax production in *Arabidopsis* (Lee and Suh 2015; Yu et al. 2017), which have been listed (Table 1; Fig. 2). WIN1/ SHN1 (WAX INDUCER1/SHINE1) is the first reported TF of an AP2-EREBP family, which upregulated cuticular waxes biosynthesis genes, *CER1*, *CER2,* and *KCS*. Overexpression of *AtWIN1* caused 4.5-fold increase in cuticular wax production in transgenic *Arabidopsis* than wild plants (Broun et al. 2004). In another study, it was found that WIN1/SHN1 is homologue AtSHN2 and AtSHN3 which belongs to AP2/EREBP TF family. An *Arabidopsis thaliana* mutant *shine* (*shn*) showed brilliant and shiny green leaf surface with six-fold increase in total cuticular wax deposition (mainly ninefold increased of alkanes) with compared to wild-type plants, and overexpression of three *SHN* clade genes SHN1/WIN1, SHN2 and SHN3 reported similar as to the original *shn* mutant (Aharoni et al. 2004). Further research about WIN1/SHN1 TFs found that it regulated directly in the expression level of *CYP86A7*, *CYP86A4*, *GPAT4*, *LACS2,* and *HTH-like* genes of cutin and that ultimately controlled wax accumulation (Kannangara et al. 2007). In MYB30 TF study found that this TF was a positive transcriptional regulator, which regulated the expression level of wax genes *FDH*, *KCS1*, *KCS2*, *KCR1*, *ECR*, *PAS2/HCD*, *LTPG1*, *CER2*, and *CER3* genes to engage in the biosynthesis of cuticular waxes (VLCFA) due to pathogen attack (Raffaele et al. 2008). MYB96 is an *A. thaliana* abscisic acid (ABA)–responsive R2R3-type MYB TF and transcriptional activator of cuticular wax promotes to drought resistance. MYB96 regulates the transcription of these genes which were related to VLCFA like *KCS1, KCS2, KCS6*, and also *KCR1*, also the *CER1, WBC11, WSD1*, and *LTP3* genes after 6 h induced by MYB96, respectively. As a result, wax biosynthesis and deposition increased by 6 h induced of MYB96 in the transgenic *Arabidopsis* leaves and offered to drought stress (Seo et al. 2011). Another study of MYB94 reported that it regulated the expression level of the *KCS1*, *KCS2*, *KCS6*, *CER3,* and *KCR1* genes directly to involve in wax production at drought stress (Lee and Suh 2014). AtMYB96 TF overexpressed in the oil seed crop *Camelina* found that deposition of cuticular wax amount and wax crystal increased significantly in transgenic *Camelina* compared with control and enhanced drought tolerance by

Table 1 Transcriptional regulations of cuticular wax biosynthesis in the model plant *A. thaliana*

Protein family	Gene	Gene locus	References
AP2-EREBP-type	WIN1/SHINE1	At1g15360	Broun et al. (2004); Aharoni et al. (2004); Kannangara et al. (2007)
	SHINE2	At5g11190	Aharoni et al. (2004)
	SHINE3	At5g25390	Aharoni et al. (2004)
R2R3—type MYB	MYB30	At3g28910	Raffaele et al. (2008)
	MYB96	At5g62470	Seo et al. (2011)
	MYB94	At3g47600	Lee and Suh (2014)
	MYB96	At5g62470	Lee et al. (2014)
	MYB16	At5g15310	Oshima et al. (2013)
	MYB106	At3g01140	Oshima et al. (2013)
	MYB94, MYB96	At3g47600, At5g62470	Lee et al. (2016)
AP2/DREB-type	RAP2.4	At1g78080	Yang et al. (2020)
WW Domain protein	CFL1	At2g3351	Wu et al. (2011)
Class IV HD- ZIP	HDG1	At3g61150	Wu et al. (2011)
AP2- ERF- type	DEWAX	At5g61590	Go et al. (2014)
	DEWAX2	At5g07580	Kim et al. (2018)
	WRINKLED4 (WRI4)	At1g79700	Park et al. (2016)
bHLH TFs	CFLAP1 and CFLAP2	At2g33510	Li et al. (2016)

Fig. 2 Transcriptional regulation of functional genes involved in cuticular wax biosynthesis under abiotic stress



up-regulating cuticular wax biosynthesis genes of *CsKCS2, CsKCS6, CsKCR1, CsECR, CsCER1, CsCER3, CsMAH1, CsCER4,* and *CsWSD1*(Lee et al. 2014). Another two MYB TFs showed that MYB16 and MYB106 TFs engaged to cuticle formation, but MYB106 TF regulated positively to the WIN1/SHN1 expression and wax biosynthetic genes (Oshima et al. 2013). Functional expression of MYB 94 and MYB 96 found that cuticular wax load reduced approximately 44 and 52% in the myb94, myb96 and myb94 myb96 plants leaves compared with wild type plant observed under well-watered and drought stress condition. The expression levels of *KCS1, KCS2/DAISY, KCS6, KCR1, CER2, CER1, CER3* and *WSD1* at drought stress condition and *KCS1, KCS2/DAISY, KCS6, KCR1, CER1, CER3* and *WSD1* at well-watered condition depend on both MYB94 and MYB96 (Lee et al. 2016). It is found in MYB96 TF study that *LTP3*, a lipid-transfer protein, which was regulated by AtMYB96, and increased tolerance in the plant at drought stress condition (Guo et al. 2013). In another study reported that MYB94 TF is strongly correlated with the MYB96 TF, which is regulated to the expression level of the *WSD1*, *FAR3*, *CER2*, *ECR,* and *KCS2/DAISY* genes to involve wax production in drought condition (Dubos et al. 2010). Further reported that the KCS2/DAISY is the target gene of two TFs, MYB96 and MYB94, and influenced directly in wax production at drought conditions (Lee and Suh 2014). WW domain protein family transcription factor CFL1 and homeodomain-leucine zipper (HD-ZIP) family transcription factor HDG1 showed responsible to cuticle formation, and also regulated negatively of *HDG1* gene and positively of *FDH* gene (Wu et al. 2011). Only a few transcription factors are known to be negatively regulated wax production at the daily light/dark phase. DEWAX is AP2/ERF-type TF, which down-regulated expression level of wax genes *CER1*, *FAR6*, *ACLA2*, *LACS2*, and *ECR* genes at day and light phage (Go et al. 2014). Another report found that DEWAX2 encodes an AP2/ERF-type TF, which reduced wax productions about 15 and 26% in the stems and rosette leaves as compared with WT, respectively. Transcriptome and quantitative RT-PCR analysis of DEWAX2 showed that it down-regulated the expression level of cuticular wax genes of *CER1*, *LACS1*, *LACS2*, *KCS12* and *ACLA2* in overexpression line as comparison with the WT (Kim et al. 2018). In another study reported that WRI4 encodes an AP2/ERF TF, which is expressed mainly in stem epidermis and involved to activate wax production in *Arabidopsis* stems at salt stress. Overexpression showed that this TF regulated expression level positively in wax genes, *KCR1*, *LACS1*, *PAS2*, *WSD1* and *ECR,* and as well as down-regulated fatty acid biosynthetic genes, such as *PKP1*, *PKP2*, *PDHE1a*, *BCCP2*, and *ENR* (Park et al. 2016). Two bHLH TFs CFLAP1and CFLAP2 related to *AtCFL1* protein, which regulated the expression level of fatty acids, cutin and wax biosynthesis genes, and decreased cuticular wax crystal loading. qRT-PCR result confirmed the up-regulation of wax genes of *FDH*, *BDG,* and *DEWAX* genes and down-regulation *KCS8* gene (Li et al. 2016). RAP2.4 is an AP2/DREB-type TF which activated and up-regulated *KCS2* and *CER1* genes, resulting to increase cuticular wax load in *Arabidopsis* leaves under drought condition (Yang et al. 2020).

From the above discussion, it is evident that some transcription factors are regulated positively, and some are regulated negatively to produce cuticular wax in *Arabidopsis* in different abiotic conditions. It is needed to understand completely about the regulation of transcriptional factors controlled cuticular wax production in the plant at different abiotic conditions.

Regulation of cuticular wax biosynthesis in the crop plants

The regulation of wax production is comparatively not as much focused on plants as compared to the model plant. Some TFs are involved in regulating wax biosynthesis in abiotic stress conditions in crop plants (Table 2). In rice, WR1 (OsWR1) is homologue of AtWIN1/AtSHN1, regulated wax production by up-regulating of *OsLACS1* and *OsFAE1* genes, respectively (Wang et al. 2012). Another study found that OsWR2 is homologue AtWIN1/AtSHN1 TF, which regulated the wax productions and cutin monomers during rice development, and up-regulated the expression level more than 3.5 times of the very long chain fatty acid synthesis genes *CER6*/ *CUT1*, *FDH2*, *FAE*, and *LACS1* in panicles and *CER1*, *CER2*, and *MAH1* genes in leaves (Zhou et al. 2014). OsWRKY89 TF increased wax deposition in leaf surface in the OsWRKY89 overexpression lines but decreased wax production in the OsWRKY89 RNAi lines, and played a significant role at drought stress condition in rice. However, overexpression of OsWRKY89 was not found to regulate any cuticular wax biosynthesis genes (Wang et al. 2007). In maize, GL3 is a MYB TF, which reduced levels of aldehyde, and regulated the expression level of the cuticular wax biosynthesis gene of *CER3* (Liu et al. 2012). Another study found that OCL1 TF belongs to HD-ZIP family, which controlled cuticle development by up-regulating expression level of *ZmLTPII.12*, *ZmFAR1,* and *ZmWBCIIa* genes (Javelle et al. 2010). In tomato, CD2 (CUTIN DEFICIENT2) TF belongs to HD-ZIP family and homologue to *Arabidopsis* ANTHOCYANINLESS2 (ANL2), which regulated cutin production in drought condition (Isaacson et al. 2009). Another study found in tomato that SlSHINE3 TF reduced the total amount of cutin monomer up to 40% in the cuticle of fruit in the RNAi line as compared with wild type, and wax productions significantly increased in the MG cuticles of fruit in the RNAi line. SlSHINE3 TF down-regulated the expression level significantly including three cytochrome P450s (*SlCYP77A1*, *SlCYP86A68* and *SlCYP86A69*), two putative acyltransferases (*SlDCR* and *SlGPAT6*), two GSDL-motif lipases (*SlGDSLa* and *SlGDSLb/SlGDSL1*), an oxidoreductase (*SlHTH*) and one long-chain acyl-CoA synthetase (*SlLACS2*) (Shi et al. 2013). In *Eutrema salsugineum*, EsWAX1 TF is homologue to

Table 2 Transcriptional regulation of cuticular wax biosynthesis in plants

Species	Organ	Protein family	Gene abbreviation	Reference
Rice	Leaf	*Arabidopsis* WIN1/SHN1 homolog	OsWR1	Wang et al. (2012)
	Leaf	*Arabidopsis* WIN1/SHN1 homolog	OsWR2	Zhou et al. (2014)
	Leaf	WRKY transcription factor	OsWRKY89	Wang et al. (2007)
Maize	Seedling leaf	MYB transcription factor	GL3	Avato et al. (1987); Liu et al. (2012)
	Seedling leaf	Homeo domain-leucine zipper IV transcription factor	OCL1	Javelle et al. (2010)
Tomato	Leaf, fruit	Class IV HD-ZIP	CD2	Isaacson et al. (2009); Nadakuduti et al. (2012)
	Fruit	MADS-box transcription factor	RIN	Kosma et al. (2010)
	Fruit	non-MADS-box transcription factor	NOR	Kosma et al. (2010)
	Fruit	AtSHN transcription factor	SlSHINE3	Shi et al. (2013)
Eutrema salsugineum	Leaf	Arabidopsis MYB96 homolog	EsWAX1	Zhu et al. (2014)
M. truncatula	Leaf	AP2 domain-containing putative transcription factor	WXP1 and WXP2	Zhang et al. (2005), Zhang et al. (2007)
B. napus	Leaf	GRAS proteins	BnLAS	Yang et al. (2011)
Camelina	leaf	R2R3-MYB	CsMYB96	Kim et al. (2019)
Wheat	Leaf	R2R3-MYB TF	TaMYB31	Zhao et al. (2018)
	Leaf	MYB	TaMYB31 and TaMYB74	Bi et al. (2016)
Durum wheat	Leaf	AP2/ERF family TF	TdSHN1	Djemal and Khoudi (2016)
Sorghum	Leaf	ERF transcription factor	SbWINL1	Bao et al. (2017)
Apple	Leaf, stem	AP2/EREBP transcription factor	MdSHINE2	Zhang et al. (2019a)
	Leaf	R2R3-MYB transcription factor	MdMYB30	Zhang et al. (2019b)
	Leaf	AP2/SHEN family	McWRI1	Hao et al. (2017)

AtMYB96, which regulated the expression level of several wax genes *AtKCS1*, *AtCER1,* and *AtKCR1* in drought condition (Zhu et al. 2014). WXP1 and WXP2 belong to AP2/ERF-type TFs in *M. truncatula,* and BnLAS is a GRAS protein in *B. napus*, which regulated wax production genes in drought condition and increased tolerance in transgenic *Arabidopsis*, *Madicago sativa* and *Camelina sativa* (Bi et al. 2016). In *Camelina sativa* found that the ectopic expression of AtMYB96 TF up-regulated expression level significantly of cuticular wax biosynthesis genes *CsKCS2*, *CsKCS6*, *CsKCR1-1*, *CsKCR1-2*, *CsECR* and *CsMAH1* (Lee et al. 2014). In wheat, TaMYB31 belongs to R2R3-MYB transcription factor family, which up-regulated expression level of cuticular wax related genes *WIN1/SHN1*, *CYP96A15*, *FAR3*, and *CER1-L1* under drought condition (Zhao et al. 2018). Another study found that two transcriptional factors TaMYB31 and TaMYB74 are homologues to AtMYB96 and AtMYB41 TFs, which regulated expression level of *ATT1* and *KCS1* genes at drought stress condition (Bi et al. 2016). A further study reported that TaMYB74 TF regulated cutin and cuticular waxes biosynthesis under drought conditions (Bi et al. 2016). In durum wheat, TdSHN1 is an AP2/ERF member from durum wheat, is homologous to AtWIN1/AtSHN1 which was found in transgenic tobacco plant than wild type plant led to increase cuticular wax biosynthesis by up-regulating NtCER1 at environment stress condition (Djemal and Khoudi 2016). In soybean, GmSHN1 and GmSHN9 TFs belong to P2/ERF family, which regulated eight genes to involve in fatty acid production, including *AtKCS1*, *AtKCS2*, *AtCER6/CUT1*, *AtKCS10/FDH*, *AtKCR1*, *AtPAS2*, *AtCER10*, and *AtCER2* in the transgenic plant at abiotic condition (Xu et al. 2016). In Sorghum, SbWINL1 regulated significantly in the expression level of cuticular wax synthesis genes of *CER1, CER2, WAX2,* and *KCS1* (Bao et al. 2017). MdSHINE2 is an AP2/EREBP TF from apple and homolog to AtSHINE2, which is expressed in numerous apple tissues at diverse levels. Overexpressing MdSHINE2 in *Arabidopsis* altered wax crystal and morphology and composition of wax in leaves and stems (Zhang et al. 2019a). The TF MdMYB30 belongs to R2R3-MYB transcription factor family from apple up-regulated *MdKCS1*gene which ultimately increased cuticular wax production and altered wax composition (Zhang et al. 2019b). McWRI1 is a TF from apple which belongs to AP2/SHEN families transcription factor found the changes of wax composition and structure by up-regulating and promoting wax genes expression of *McKCS*, *McLACs* and *McWAX* in very-long-chain fatty acid biosynthesis pathway resulting alkanes deposition and wax structure alteration in fruit surface (Hao et al. 2017).

Those reports provide evidence that Transcription factors act as positive or negative regulators in wax production at abiotic stresses condition in different crop plants. It is needed to find out more transcription factors to regulate the functional gene of cuticular wax production at various abiotic conditions in different crop plants.

Conclusion

Cuticular waxes protect plants from abiotic stresses, play the role of growth, development, and adaptations of plants. Cuticular wax biosynthesis and deposition depend on different abiotic factors. Among them, we have reported in this review only some major abiotic factors such as drought, temperature, cold/frost, UV-radiation, humidity, water, and salinity stresses. Genetic factors are also responsible for wax production in abiotic conditions. Some cuticular wax genes in different crop plants have been identified, but regulation of those functional wax-genes is not clearly understood in crop plants at various abiotic stress conditions. Some transcriptional factors of cuticular wax biosynthesis have been identified in the crop plants at abiotic stresses. Transcriptional factors are very important to plant stress mechanisms which are imperative to understand their functions in wax productions provide new approaches to engineer stress tolerance crop plants. Cuticular wax not only improves crop stress tolerance but also increases the productivity of crop plants. It needs to study further about transcription factors of cuticular wax biosynthesis in major crop plants at abiotic conditions. Thus, this review may provide valuable clues and genetic information for future crop breeding.

Authors' contributions MS and ZW outlined the review. MS, SS, KS, HW, TL. PA and MH collected the literature and wrote the manuscript draft. M.H. edited the manuscript and prepared the figures. All authors approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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