Gene Expression in Coffee

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Abstract Coffee is cultivated in more than 70 countries of the intertropical belt where it has important economic, social and environmental impacts. As for many other crops, the development of molecular biology technics allowed to launch research projects for coffee analyzing gene expression. In the 90s decade, the first expression studies were performed by Northern-blot or PCR, and focused on genes coding enzymes of the main compounds (e.g., storage proteins, sugars, complex polysaccharides, caffeine and chlorogenic acids) found in green beans. Few years after, the development of 454 pyrosequencing technics generated expressed sequence tags (ESTs) obviously from beans but also from other organs (e.g., leaves and roots) of the two main cultivated coffee species, *Coffea arabica* and *C. canephora*. Together with the use of real-time quantitative PCR, these ESTs significantly raised the number of coffee gene expression studies leading to the identification of (1) key genes of biochemical pathways, (2) candidate genes involved in biotic and abiotic stresses as well as (3) molecular markers essential to assess the genetic diversity of the *Coffea* genus, for example. The development of more recent Illumina sequencing technology now allows large-scale transcriptome analysis in coffee plants and opens the way to analyze the effects on gene expression of complex biological processes like genotype and environment interactions, heterosis and gene regulation in polypoid context like in *C. arabica*. The aim of the present review is to make an extensive list of coffee genes studied and also to perform an inventory of large-scale sequencing (RNAseq) projects already done or on-going.

1 Introduction: Once Upon a Time – The Story of Gene Expression in Coffee Plants

Despite the economic importance of coffee in international market, the knowledge about coffee molecular biology, and particularly regarding gene cloning and expression, can be considered as relatively recent. The first coffee genes described in the literature correspond to the complementary DNA (cDNA) sequences of α-galactosidase (Zhu and Goldstein 1994) and metallothionein I-like protein (Moisyadi and Stiles 1995), the first being a *Short Communication* in *Gene* and the second, a *Plant Gene Register* in *Plant Physiology*. Both articles only reported the cloning of these cDNAs without analyzing the expression of corresponding genes in coffee tissues.

This was the situation when I just arrived in Nestlé-Tours Research and Development Centre to initiate a project aiming to identify genes involved in coffee cup quality. Based on all the researches describing the importance of storage proteins (particularly in cereals) in the quality of final products, our interest was logically focused first to characterize these proteins in coffee fruits. Then in 1999, we reported

the first article describing the expression of *csp1* (*coffee storage protein*) gene coding the 11S proteins accumulated during bean development (Rogers et al. 1999a). At that time, gene expression studies were always performed by Northern blot experiments requiring both high quantities of total RNAs and the preliminary cloning of studied genes in order to synthetize their corresponding radio-labelled DNA probes. This situation persisted until the beginning of the 2000s, and in 2004, there were only 1,570 nucleotide sequences and 115 proteins from coffee deposited in GenBank/EMBL databases.

Few years after, with the development of high-throughput sequencing techniques, the first coffee EST ("expressed sequence tag") sequencing projects were realized, and in 2016 there were 35,153; 25,574; and 25,574 unigenes available in public databases for *Coffea arabica*, *Coffea canephora*, and *Coffea eugenioides*, respectively. Then, the development of real-time quantitative PCR (RT-qPCR) technology significantly accelerated the number of coffee gene expression studies. The access to these ESTs also permitted to set up a 15 K microarray ("PUCECAFE") DNA chip which was used to perform the first large-scale expression analyses aiming to understand transcription networks in flowers, mature beans, and leaves of *C. canephora*, *C. eugenioides*, and *C. arabica* (Privat et al. 2011). The same chip was also used to analyze the leaf expression of homeologous genes in response to changing temperature between *C. arabica* and its two ancestral parents, *C. canephora* and *C. eugenioides* (Bardil et al. 2011).

Soon after came the next-generation Illumina RNA sequencing (RNAseq) method enabling to perform expression analyses of thousands of genes by in silico approaches. The first article using such techniques was published by Combes et al. (2013) who studied the transcriptome in leaves of *C. arabica* submitted to warm and cold conditions suitable to *C. canephora* and *C. eugenioides*, respectively. Since this work, numerous other RNAseq studies were published, and many others are actually ongoing. Using all these data, it is now possible to generate reference transcriptomes which should help us to identify candidate genes (CGs) correlated with agronomic and quality traits in coffee.

2 Coffee Gene Expression

2.1 Reference Genes for qPCR Experiments

Since the development of EST sequencing projects (for reviews, see Lashermes et al. 2008; de Kochko et al. 2010, 2017; and Tran et al. 2016), RT-qPCR experiments, using either SYBR Green fluorochrome or specific TaqMan probes, are nowadays used in routine to study coffee gene expression. In order to quantify the expression levels, these experiments require the use of endogenous reference genes (as internal controls) which must be previously validated for particular tissues (Bustin 2002; Bustin et al. 2009). In that sense, several articles were published to identify the best reference genes to be used in different coffee tissues and growth conditions.

The first were published in 2009 showing that *GAPDH* (coding the glyceraldehyde 3-phosphate dehydrogenase) and *UBQ10* (coding ubiquitin) were stable reference genes for normalization of qPCR experiments in different tissues of *C. arabica*, particularly in leaves and roots under drought stress (Barsalobres-Cavallari et al. 2009; Cruz et al. 2009). These two genes are also the most suitable for data normalization when analyzing multiple or single stresses in leaves of *C. arabica* and *C. canephora* (Goulao et al. 2012). In another study, Fernandes-Brum et al. (2017a) showed that the most stable reference genes were AP47 (coding the clathrin adaptor protein medium subunit), *UBQ*, (ubiquitin 60S), *RPL39* (ribosomal protein L39), and *EF1α* (elongation factor 1-alpha) in all tissues of *C. arabica*, while *GAPDH* and *UBQ*, together with *ADH2* (class III alcohol dehydrogenase) and *ACT* (β-actin), were the most stable for all tissues of *C. canephora*.

When analyzing the caffeine biosynthetic pathway, Sreedharan et al. (2018) showed that *GAPDH* and *UBQ* were the reference genes presenting the lowest variability in leaves and developing endosperm of *C. canephora* between control samples and treatments with salicylic acid (SA), methyl jasmonate (MeJA), light exposure, and PEG, which permitted the quantification of xanthosine methyltransferase (NMT) coding genes. In fact, *UBQ* was commonly used as a reference gene to normalize expression studies during bean development (Salmona et al. 2008; Joët et al. 2009, 2010, 2014; Cotta et al. 2014; Dussert et al. 2018) as well as in other coffee tissues, such as leaves and flower buds (Marraccini et al. 2011, 2012; Vieira et al. 2013; Mofatto et al. 2016). Even though several studies reported that *RPL39* was not the most accurate reference (Cruz et al. 2009; de Carvalho et al. 2013), this gene was also used as a reference to compare expression profiles of several genes in developing beans and also in different organs such as leaves, stems, branches, roots, and flowers (Lepelley et al. 2007, 2012a, b; Pré et al. 2008; Privat et al. 2008; Simkin et al. 2006, 2008; Bottcher et al. 2011).

On the other hand, *GAPDH* and *UBQ* appeared to be the less stable reference genes for transcript normalization in *C. arabica* hypocotyls inoculated with *Colletotrichum kahawae* (causing the coffee berry disease (CBD)), for which the use of *IDE* (coding insulin degrading enzyme) and *β-Tub9* (coding *β*-tubulin) (Figueiredo et al. 2013) as references is recommended. In another study, de Carvalho et al. (2013) showed that *GAPDH* together with *MDH* (coding malate dehydrogenase) and *EF1α* can be used as reference genes in leaves and roots of *C. arabica* subjected to N-starvation and heat stress, while *UBQ10* was the most suitable reference for salt stress treatments. Using RefFinder, a web-based tool integrating geNorm, NormFinder, and BestKeeper programs (Xie et al. 2012), Martins et al. (2017) showed that *MDH* (malate dehydrogenase) presented the highest mRNA stability to study leaf gene expression in both *C. arabica* and *C. canephora* species subjected to single or multiple abiotic stresses such as elevated temperature and CO_2 concentration ($[CO_2]$). In another work, Freitas et al. (2017) showed that the *24S* (ribosomal protein 24S) and *PP2A* (protein phosphatase 2A) genes were the most suitable references to study expression in embryogenic and non-embryogenic calli, embryogenic cell suspensions, and somatic embryos at different developmental stages in *C. arabica*.

2.2 Gene Expression in Coffee Species

At the time of writing this review (I apologize if I forgot mentioning some studies), the number of genes for which expression studies have been carried out individually was around 700. Most of these studies were performed by RT-qPCR using specific primer pairs designed against coffee ESTs generated by sequencing projects. In a chronological order, the first project was the Nestlé and Cornell initiative which generated around 63,000 ESTs from six cDNA libraries from fruits and leaves (at different developmental stages) of *C. canephora* clones of the Indonesian Coffee and Cocoa Research Institute (ICCRI) (Lin et al. 2005). Next was the IRD project which led more than 10,400 ESTs also from fruits and leaves of *C. canephora* (Poncet et al. 2006). Finally, the "Brazilian Coffee Genome" Project (BCGP), coordinated by the UNICAMP [University of Campinas] and the Embrapa [Empresa Brasileira de Pesquisa Agropecuária]), produced more than 200,000 ESTs (Vieira et al. 2006; Mondego et al. 2011) from *C. arabica* (≈187,000), from *C. canephora* (≈15,500), and also from *C. racemosa* (≈10,500). In order to identify the maximum of genes, this project used 43 cDNA libraries; most of them were built from transcripts extracted from fruits and leaves at different developmental stages but also from different plant organs (flowers, roots) and tissues (calli, cell suspensions, etc.) subjected to various biotic (e.g., roots infected with nematodes, stems infected with *Xylella* spp., leaves infected with miner *Leucoptera coffeella* and rust fungus *Hemileia vastatrix*) and abiotic (e.g., suspension cells treated with NaCl and chemicals such as acibenzolar-S-methyl and brassinosteroids) stresses.

As reported in Tables 1, 2, and 3, most of these expression studies were performed in *C. arabica* ($n \approx 550$ genes) and *C. canephora* ($n \approx 100$ genes), with a repartition reflecting quite well the importance of *C. arabica* (59%) and *C. canephora* (41%) species in the worldwide coffee production (ICO 2020). These expression studies were more limited in other coffee species such as in *C. racemosa* ($n = 25$), *C. eugenioides* ($n = 18$), and *C. liberica* ($n = 5$). For 70 genes, expression analyses were performed on both *C. arabica* and *C. canephora* species. However, a limited number of studies (described in Sect. 2.3) analyzed gene expression simultaneously in *C. arabica*, *C. canephora*, and *C. eugenioides* using specific primers and qPCR for each homeolog in each species. Several articles also reported in silico gene expression profiles which were not confirmed by RT-qPCR (Table 4).

2.3 Coffee Gene Expression in C. arabica: A Tricky Case

Before discussing gene expression in coffee, it is important to remember that *C. arabica* ($2n = 4\times = 44$) is an allotetraploid coffee species derived from a natural hybridization event between the two diploid ($2n = 2\times = 22$) species *C. canephora* and *C. eugenioides* (Lashermes et al. 1999) which occurred approximately

Table 1 List of coffee genes studied at the transcriptional level

Function	Gene name	Gene numbers	Expression	Tissues	Species	References
Bean development						
11S storage protein	CaCSP1	Y16976	N	BD	Ca	Marraccini et al. (1999)
	CaCSP1	Cc03_g05570	Q	BD/VT	Ca/Cc	Simkin et al. (2006); Dussert et al. (2018)
	CaCSP1	Cc03_g05570	sQ	BD/VT	Ca	De Castro and Marraccini (2006)
Aspartic proteinase	CaAP2	JU319520	Q	BD	Ca	Abreu et al. (2012)
Cysteine proteinase	CcCP1	JF950589	Q	BD/ BG/VT	Ca/Cc	Abreu et al. (2012); Lepelley et al. (2012a)
	CcCP4	JF950590/ JF950591	Q	BD/ BG/VT	Ca/Cc	Abreu et al. (2012); Lepelley et al. (2012a)
	CaCP23	JU319517	Q	BD/ BG/VT	Ca/Cc	Abreu et al. (2012)
Cysteine proteinase inhibitor	CcCPI1	JF950585	Q	BD/ BG/VT	Cc	Lepelley et al. (2012a)
	CcCPI2	JF950586	Q	BD/ BG/VT	Cc	Lepelley et al. (2012a)
	CcCPI3	JF950587	Q	BD/ BG/VT	Cc	Lepelley et al. (2012a)
	CcCPI4	JF950588	Q	BD/ BG/VT	Cc	Lepelley et al. (2012a)
Expansin	CaEXPA1	GQ434001	N	BD/VT	Ca	Budzinski et al. (2010)
	CaEXPA2	GQ434002	N	BD/VT	Ca	Budzinski et al. (2010)
	CaEXPA3	GQ434003	N	BD/VT	Ca	Budzinski et al. (2010)
Pectin methylesterase	CaPME4	JN863081	N	BD/VT	Ca	Cação et al. (2012)
Late embryogenic abundant proteins	CcLEA1	DQ333961	sQ	BD/VT	Ca/Cc	Hinniger et al. (2006)
Eukaryotic initiation factor 1	CaSUI1	AJ519839	N	VT	Ca	Gaborit et al. (2003)
	CaSUI1	AJ519839	sQ	VT	Ca	De Castro and Marraccini (2006)
Isocitrate lyase	ICL	XM_027208879	sQ	Bd	Ca	Selmar et al. (2006)
	ICL	XM_027208879	sQ	Bd	Ca	Bytof et al. (2007)
	ICL	XM_027208879	sQ	Bd	Ca	Kramer et al. (2010)

Catalase	CAT3	Cc10_g00580	Q	GS/Bd	Ca	Santos et al. (2013)
Peroxidase	PER3	Cc05_g04990	Q	GS/Bd	Ca	Santos et al. (2013)
Isoflavone reductase-like protein	CaIRL	FJ972200	N	R/L/ BD	Ca	Brandalise et al. (2009)
Prolyl oligopeptidase	CaPOP	JN572042/ JN572043/ JN572044	N/Q	BD/L	Ca	Singh et al. (2011)
Sugars/polysaccharides						
Endo-β-mannanase	ManA	AJ293305	N	GS	Ca	Marraccini et al. (2001)
	ManB	AJ278996	N	GS	Ca	Marraccini et al. (2001)
Mannan synthase	CcManS1	EU568115/ Cc06_g04240	Q	BD	Ca/Cc	Pré et al. (2008); Joët et al. (2014); Dussert et al. (2018)
	CcManS2	EU716311	Q	BD	Cc	Pré et al. (2008); Joët et al. (2014)
Galactomannan galactosyltransferase	CaGMGT1	EU568117	Q	BD	Ca/Cc	Pré et al. (2008); Joët et al. (2014)
	CcGMGT2	EU716313	Q	BD	Cc	Pré et al. (2008); Joët et al. (2014)
Glycosyltransferase	CcXT1	EU760961	Q	BD	Cc	Pré et al. (2008); Joët et al. (2014)
	CcGT1	EU716312	Q	BD	Cc	Pré et al. (2008); Joët et al. (2014)
α-Galactosidase	CaGAL1	AJ877911	N/Q	BD	Ca	Marraccini et al. (2005); Joët et al. (2014)
	CcGAL1	AJ877912	N/Q	BD	Ca	Marraccini et al. (2005); Joët et al. (2014)
β-Galactosidase	CaβGal	HQ283330	sQ	BD	Ca	Figueiredo et al. (2011)
Sucrose synthase 1	CaSUS1	AM087674	N/Q	BD/VT	Ca	Geromel et al. (2006, 2008b); Joët et al. (2014)
	CrSUS1	AM087674	N/Q	BD	Cr	Geromel et al. (2008a)
	SS2	DQ834312	Q	BD/L	Ca/Cc	Privat et al. (2008)
Sucrose synthase 2	CaSUS2	AM087675	N	BD/VT	Ca	Geromel et al. (2006, 2008b)
	CrSUS2	AM087675	N	BD	Cr	Geromel et al. (2008a)
	SS1	DQ826510	Q	BD/L	Ca/Cc	Privat et al. (2008)

(continued)

Table 1 (continued)

Function	Gene name	Gene numbers	Expression	Tissues	Species	References
Invertase	CcINV1	DQ834314	Q	BD/L	Ca/Cc	Privat et al. (2008)
	CcINV2	DQ834315	Q	BD/L	Ca/Cc	Privat et al. (2008)
	CcINV3	DQ834316	Q	BD/L	Ca/Cc	Privat et al. (2008)
	CcINV4	DQ842235	Q	BD/L	Ca/Cc	Privat et al. (2008)
Invertase inhibitor	CcInvI1	DQ834317	Q	L	Cc	Privat et al. (2008)
	CcInvI2	DQ834318	Q	L	Cc	Privat et al. (2008)
	CcInvI3	DQ834319	Q	L	Cc	Privat et al. (2008)
	CcInvI4	DQ834320	Q	L	Cc	Privat et al. (2008)
Sucrose phosphate synthase	CcSPS1	DQ834321	Q	L	Cc	Privat et al. (2008)
	CcSPS2	DQ842234	Q	L	Cc	Privat et al. (2008)
Sucrose phosphatase	CcSP1	DQ834313	Q	L	Cc	Privat et al. (2008)
1-Aminocyclopropane-1-carboxylate oxidase (ACO)	CaACO	KC686714	N	BD/VT	Ca	Pereira et al. (2005)
Polyols						
Mannose-6-phosphate reductase	CaM6PR	GT648734	Q	L	Ca	Freire et al. (2013)
	CcM6PR	GT648734	N/Q	L	Cc	Marraccini et al. (2012)
	CaM6PR	GW488867	N/Q	L	Cc	de Carvalho et al. (2014)
	CcM6PR	GT649509	N/Q	L	Cc	de Carvalho et al. (2014)
Phosphomannose isomerase	CaPMI	GT709210	N/Q	L	Cc	de Carvalho et al. (2014)
	CcPMI	DV688525	N/Q	L	Cc	de Carvalho et al. (2014)
Mannitol dehydrogenase	CaMTD	GW445924	N/Q	L	Cc	de Carvalho et al. (2014)
	CcMTD	GT652950	N/Q	L	Cc	de Carvalho et al. (2014)
Galactinol synthase	CaGolS1	GQ497218	N	L/VT	Ca	dos Santos et al. (2011)
	CaGolS2	GQ497220/ Cc03_g00450	N/Q	BD/L/ VT	Ca	dos Santos et al. (2011); Ivamoto et al. (2017a)
	CaGolS3	GQ497219/ Cc02_g35350	N/Q	BD/L/ VT	Ca	dos Santos et al. (2011); Ivamoto et al. (2017a)
	CaGolS4	Cc11_g15250	Q	BD/L	Ca	Ivamoto et al. (2017a)
	CcGolS1	GQ497218	N/Q	L	Cc	dos Santos et al. (2015)

Raffinose synthase	CaRS1	Cc05_g15530	Q	BD/L	Ca	Ivamoto et al. (2017a)
Isoprenoid (MVA) biosynthesis						
3-Hydroxy-3-methyglutaryl-CoA reductase	CaHMGR1	HQ540670	N	BD/L/F	Ca	Tiski et al. (2011)
	CaHMGR1	HQ540671	N	BD/L/F	Ca	Tiski et al. (2011)
Cytochrome P450s						
Triterpene biosynthesis	CaCYP72A15	Cc05_g08890	Q	L	Ca	Ivamoto et al. (2017b)
Jasmonic acid catabolism	CaCYP94B1	Cc01_g18610	Q	L	Ca	Ivamoto et al. (2017b)
Monoterpenoid biosynthesis	CaCYP76C4	Cc02_g36410	Q	L	Ca	Ivamoto et al. (2017b)
Lipoxygenase pathway	CaCYP74A1	Cc10_g03570	Q	L	Ca	Ivamoto et al. (2017b)
Homoterpene biosynthesis	CaCYP82C2	Cc04_g10600	Q	L	Ca	Ivamoto et al. (2017b)
Ent-kaurene oxidase	CaCYP701A3	Cc10_g03710	Q	L	Ca	Ivamoto et al. (2017b)
Monoterpenes hydroxylation	CaCYP71A25	Cc04_g11300	Q	L	Ca	Ivamoto et al. (2017b)
PAL pathway						
Phenylalanine ammonia lyase	CcPAL1	AAN32866	Q	BD/VT	Cc	Lepelley et al. (2012b)
	CcPAL2	AEO94540	Q	BD/VT	Cc	Lepelley et al. (2012b)
	CcPAL3	EO94541	Q	BD/VT	Cc	Lepelley et al. (2012b)
Chlorogenic acid synthesis						
Hydroxycinnamoyl-CoA quinate hydroxycinnamoyl transferase	CcHQT	EF153931	Q	BD/VT	Cc	Lepelley et al. (2007, 2012b)
Hydroxycinnamoyl-CoA shikimate/ quinate hydroxycinnamoyl transferase	CcHCT	EF137954	Q	BD/VT	Cc	Lepelley et al. (2007)
p-Coumarate 3-hydroxylase	CcC3H1	EF153932	Q	BD/VT	Cc	Lepelley et al. (2007)
Caffeoyl-CoA 3-O methyltransferase	CcCCoAOMT1	EF153933	Q	BD/VT	Cc	Lepelley et al. (2007)
Carotenoid biosynthetic pathway						
Phytoene synthase	CcPSY	DQ157164	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
Phytoene desaturase	CcPDS	DQ357179	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
z-Carotene desaturase	CcZDS	DQ357180	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
Plastid terminal oxidase	CcPTOX	DQ233245	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)

(continued)

Table 1 (continued)

Function	Gene name	Gene numbers	Expression	Tissues	Species	References
Lycopene e-cyclase	CcLCY-E	DQ357178	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
b-Carotene hydroxylase	CaCRTR-B	DQ157169	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
Zeaxanthin epoxidase	CcZEP	DQ357177	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
Violaxanthin de-epoxidase	CaVDE	DQ234768	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
Carotenoid cleavage dioxygenase 1	CaCCD1	DQ157170	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
Fibrillin family	CcFIB1	DQ157168	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
9-Cis-epoxycarotenoid dioxygenase	CaNCED3	DQ157167	Q	BD/VT	Ca/Cc	Simkin et al. (2008, 2010)
	CcNCED3	DQ157167	Q	R/L	Cc	Costa et al. (2015); Thioune et al. (2017)
Trigonelline						
Trigonelline synthase	CTgS1	AB054842	sQ	BD/L/F	Ca	Mizuno et al. (2014)
	CTgS2	AB054843	sQ	BD/L/F	Ca	Mizuno et al. (2014)
Lipids						
Oleosin	CaOLE-1	AY928084/ Cc02_g04750	sQ	BD/VT	Ca/Cc	Simkin et al. (2006); Dussert et al. (2018)
	CcOLE-2	AY841272	sQ	BD/VT	Ca/Cc	Simkin et al. (2006); Dussert et al. (2018)
	CcOLE-3	AY841273	sQ	BD/VT	Ca/Cc	Simkin et al. (2006); Dussert et al. (2018)
	CcOLE-4	AY841274	sQ	BD/VT	Ca/Cc	Simkin et al. (2006); Dussert et al. (2018)
	CcOLE-5	AY841275	sQ	BD/VT	Ca/Cc	Simkin et al. (2006); Dussert et al. (2018)
Steroleosin	CcSTO-1	AY841276	Q	BD/VT	Ca/Cc	Simkin et al. (2006); Dussert et al. (2018)
Non-specific lipid transfer protein (nsLTP)	CaLTP1*	HG008739	Q	BD/PB	Ca	Cotta et al. (2014); Mofatto et al. (2016)
	CaLTP2*	HG008740	Q	BD/PB	Ca	Cotta et al. (2014); Mofatto et al. (2016)
	CaLTP3*	HG008741	Q	BD/PB	Ca	Cotta et al. (2014); Mofatto et al. (2016)
	CcLTP3	HG323822	Q	BD	Cc	Cotta et al. (2014)
Linoleate 13S-lipoxygenase 3-1, chloroplastic	LOX3	Cc00_g30760	Q	L	Ca/Cc	Scotti-Campos et al. (2019)
Linoleate 9S-lipoxygenase 5	LOX5A	Cc02_g33320	Q	L	Ca/Cc	Scotti-Campos et al. (2019)

Linoleate 9S-lipoxygenase 5, chloroplastic	LOX5B	Cc03_g03580	Q	L	Ca/Cc	Scotti-Campos et al. (2019)
ω-3 fatty acid desaturase, chloroplastic	FAD3	Cc02_g06400	Q	L	Ca/Cc	Scotti-Campos et al. (2019)
Cell protection and TAFs						
Dehydrin	CcDH1	DQ323987/ DQ323988	sQ/Q	BD/L	Cc	Hinniger et al. (2006); Thioune et al. (2017)
	CcDH2	DQ323989	sQ/Q	BD	Cc	Hinniger et al. (2006)
	CcDH3	DQ333960	sQ/Q	BD	Cc	Hinniger et al. (2006)
	CaDH3	DQ333961	sQ/Q	Bd	Ca	Kramer et al. (2010)
	CaDH1	JP709195/ JP709196	sQ/Q	R/L/CS	Ca	Santos and Mazzafera (2012)
	CaDH2	DQ323989	sQ/Q	R/L	Ca	Santos and Mazzafera (2012)
	CaDH3	DQ333960/ JP709199	sQ/Q	R/L/CS	Ca	Santos and Mazzafera (2012)
Metallothionein-like protein 1	CaMT21	Cc06_g02650	Q	L	Ca	Barbosa et al. (2017)
Metallothionein I	CaMT1	CF588839	Q	L	Ca/Cc/ Cd	Fortunato et al. (2010)
Glutathione reductase	CaGRed	GT020496	Q	L	Ca/Cc/ Cd	Fortunato et al. (2010)
Dehydroascorbate reductase	CaDHAR	GT731606	Q	L	Ca/Cc/ Cd	Fortunato et al. (2010)
Chitinase class III	Cachi3-1	CF588617	Q	L	Ca/Cc/ Cd	Fortunato et al. (2010)
Chitinase class III	Cachi3-2	CF589150	Q	L	Ca/Cc/ Cd	Fortunato et al. (2010)
Chitinase class IV	Cachi4-1	CF588708	Q	L	Ca/Cc/ Cd	Fortunato et al. (2010)
Class III peroxidase	CaPRX	JN705803	Q	VT	Ca/Cc	Severino et al. (2012)

(continued)

Table 1 (continued)

Function	Gene name	Gene numbers	Expression	Tissues	Species	References
Endoplasmic reticulum heat-shock protein 90	CcHSP90	KU049664	Q	L	Cc	Thioune et al. (2017)
MYB transcription factor	CcMb102	KT698109	Q	L	Cc	Thioune et al. (2017)
Arabidopsis transcription factor ABF2	CcABF2	KU049665	Q	L	Cc	Thioune et al. (2017)
Arabidopsis NON-YELLOW COLORING gene	CcNYE1	KU049666	Q	L	Cc	Thioune et al. (2017)
Arabidopsis thaliana ACTIVATING FACTOR 1	CcATAF1	KU049666	Q	L	Cc	Thioune et al. (2017)
Dehydration-responsive-element-binding protein 1D	CcDREB1D	Cc02_g03430	Q	L	Cc	Marraccini et al. (2012); Vieira et al. (2013); Thioune et al. (2017)
	CaDREB1D	Cc02_g03430	Q	L/R	Ca/Cc	Alves et al. (2017, 2018)
Photosynthesis						
Rubisco small subunit	CaRBCS1	AJ419826	N	L	Ca	Marraccini et al. (2003)
	CcRBCS1*	FR728242	Q	L	Ca/Cc/Ce	Marraccini et al. (2011)
Chlorophyll a-/b-binding protein CP24	CaCP24	GT010356	Q	L	Ca/Cc/Cd	Batista-Santos et al. (2011)
Chlorophyll a-/b-binding 22 kDa protein	CaCP22	HQ130481	Q	L	Ca/Cc/Cd	Batista-Santos et al. (2011)
Photosystem II 10 kDa polypeptide precursor	CaPII10a	CF588865	Q	L	Ca/Cc/Cd	Batista-Santos et al. (2011)
Cytochrome f	CaCytf (petA)	GW469919	Q	L	Ca/Cc/Cd	Batista-Santos et al. (2011)
Photosystem I subunit	CaPI (psaB)	EF044213	Q	L	Ca/Cc/Cd	Batista-Santos et al. (2011)

Caffeine						
3,7-Dimethylxanthine N-methyltransferase	CaMTL1	AB039725	sQ	R/St/L	Ca	Ogawa et al. (2001); Kumar and Giridhar (2015); Kumar et al. (2017)
	CaMTL2	AB048792	sQ	R/St/L	Ca	Ogawa et al. (2001); Kumar and Giridhar (2015); Kumar et al. (2017)
	CaMTL3	AB048793	sQ	R/St/L	Ca	Ogawa et al. (2001); Kumar and Giridhar (2015); Kumar et al. (2017)
7-Methylxanthine N-methyltransferase	CaMXMT1	AB048794	sQ	R/St/L	Ca	Ogawa et al. (2001); Kumar and Giridhar (2015); Kumar et al. (2017)
3,7-Dimethylxanthine N-methyltransferase	CaMTL1	AB039725	sQ	L/BD	Ca	Uefuji et al. (2003)
	CaXMT1	AB048793	sQ	L/BD	Ca	Uefuji et al. (2003)
7-Methylxanthine N-methyltransferase	CaMXMT1	AB048794	sQ	L/BD	Ca	Uefuji et al. (2003)
	CaMXMT2	AB084126	sQ	L/BD	Ca	Uefuji et al. (2003)
3,7-Dimethylxanthine N-methyltransferase	CaDXMT1	AB084125	sQ	L/BD	Ca	Uefuji et al. (2003)
7-Methylxanthine N-methyltransferase	CCS1 (CtCS6)	AB086414	sQ	BD/VT	Ca	Mizuno et al. (2003a, b); Koshiro et al. (2006)
3,7-Dimethylxanthine N-methyltransferase	CtCS7	AB086415	sQ	BD/VT	Ca	Mizuno et al. (2003a, b); Koshiro et al. (2006)
7-Methylxanthine N-methyltransferase	CTS2	AB054841	N/sQ	BD/VT	Ca	Mizuno et al. (2003a, b); Koshiro et al. (2006)
7-Methylxanthosine	CmXRS1	AB034699	sQ	BD/VT	Ca	Mizuno et al. (2003a, b); Koshiro et al. (2006)
Methionine synthase	MS	AF220054	sQ	BD/VT	Ca	Mizuno et al. (2003a, b); Koshiro et al. (2006)
Xanthosine methyltransferase	CcXMT1	JX978509	Q	BD/L	Ca/Cc	Perrois et al. (2015)
7-Methylxanthine N-methyltransferase	CcMXMT1	JX978507	Q	BD/L	Ca/Cc	Perrois et al. (2015)
3,7-Dimethylxanthine N-methyltransferase	CcDXMT	JX978506	Q	BD/L	Ca/Cc	Perrois et al. (2015)

(continued)

Table 1 (continued)

Function	Gene name	Gene numbers	Expression	Tissues	Species	References
Xanthosine methyltransferase	CaXMT1	JX978514	Q	BD/L	Ca/Cc	Perrois et al. (2015)
	CaXMT2	JX978515	Q	BD/L	Ca/Cc	Perrois et al. (2015)
7-Methylxanthine N-methyltransferase	CaMXMT1	JX978511	Q	BD/L	Ca/Cc	Perrois et al. (2015)
	CaMXMT2	JX978512	Q	BD/L	Ca/Cc	Perrois et al. (2015)
3,7-Dimethylxanthine N-methyltransferase	CaDXMT2	KJ577792	Q	BD/L	Ca/Cc	Perrois et al. (2015)
7-Methylxanthosine synthase	CmXRS1	AB034699	sQ/Q	BD	Ca	Maluf et al. (2009)
Theobromine synthase	CTS2	AB054841	sQ/Q	BD	Ca	Maluf et al. (2009)
Caffeine synthase	CCS1	AB086414	sQ/Q	BD	Ca	Maluf et al. (2009)
Flowering						
AGAMOUS	CaC03	GU332281	Q	F/R/L	Ca	de Oliveira et al. (2010)
APETALA3	CaC12	GU332287	Q	F/R/L	Ca	de Oliveira et al. (2010)
SEPALLATA3	CaC14	GU265820	Q	F/R/L	Ca	de Oliveira et al. (2010)
FLOWERING LOCUS C	CaFLC	HQ845334	Q	F/R/B/L	Ca	Barreto et al. (2012); Vieira et al. (2019)
FRIGIDA-like	CaFRL4	HQ845335	Q	F/R/B/L	Ca	Barreto et al. (2018)
	CcFRL-1*	Cc01_g15840	Q	F/L/BD/SE	Ca	Vieira et al. (2019)
	CcFRL-2*	Cc03_g03790	Q	F/L/BD/SE	Ca	Vieira et al. (2019)
	CcFRL-3*	Cc04_g05540	Q	F/L/BD/SE	Ca	Vieira et al. (2019)
	CcFRL-4*	Cc05_g14640	Q	F/L/BD/SE	Ca	Vieira et al. (2019)
	CcFRL-5*	Cc00_g14390	Q	F/L/BD/SE	Ca	Vieira et al. (2019)

Somatic embryogenesis (SE)						
BABY BOOM-like gene	BBM1	Cc09_g04020	Q	SE(DS)	Ca/Cc	Nic-Can et al. (2013); Silva et al. (2015); Torres et al. (2015); Pinto et al. (2019)
AP2/ERF-like transcription factor	CaERF-like	AY522505	Q	SE(DS)	Ca/Cc	Nic-Can et al. (2013); Silva et al. (2015); Torres et al. (2015); Pinto et al. (2019)
LEAFY COTYLEDON1	CcLEC1	Cc09_g00330	sQ/Q	SE(DS)	Cc	Nic-Can et al. (2013)
WUSCHEL-RELATED HOMEOBOX4	CcWOX4	Cc10_g04700	sQ/Q	SE(DS)	Cc	Nic-Can et al. (2013)
Somatic embryogenesis receptor-like kinase 1	SERK1	Cc10_g06160	Q	SE (DS)/ CS/R/L	Ca/Cc	Silva et al. (2014); Torres et al. (2015); Pérez-Pascual et al. (2018)
Cyclin-dependent kinase type A	CaCDKA	AJ496622	sQ	SE	Ca	Valadez-González et al. (2007)
Auxin response factor (ARF)	CcARF5	Cc10_g01900	Q	SE(DS)	Cc	Quintana-Escobar et al. (2019)
	CcARF6	Cc09_g08740	Q	SE(DS)	Cc	Quintana-Escobar et al. (2019)
	CcARF9	Cc08_g16330	Q	SE(DS)	Cc	Quintana-Escobar et al. (2019)
	CcARF18	Cc06_g03950	Q	SE(DS)	Cc	Quintana-Escobar et al. (2019)
Auxin/indole-3-acetic acid regulator	CcAux/IAA7	Cc03_g04670	Q	SE(DS)	Cc	Quintana-Escobar et al. (2019)
	CcAux/IAA12	Cc01_g17790	Q	SE(DS)	Cc	Quintana-Escobar et al. (2019)
Gretchen Hagen 3 protein	CaGH3.9	Cc01_g20620	Q	SE(DS)	Cc	Pinto et al. (2019)
	CaGH3.13	Cc05_g05640	Q	SE(DS)	Cc	Pinto et al. (2019)
	CaGH3.15	Cc05_g12940	Q	SE(DS)	Cc	Pinto et al. (2019)
	CaGH3.16	Cc07_g06610	Q	SE(DS)	Cc	Pinto et al. (2019)
Water transport						
Aquaporin	CaPIP2;1	LM654169	sQ/Q	R/L	Ca	dos Santos and Mazzafera (2013); Miniussi et al. (2015)
	CaPIP2;2	LM654170	sQ/Q	R/L	Ca	dos Santos and Mazzafera (2013); Miniussi et al. (2015)
	CaPIP1;1	LM654171	Q	R/L	Ca	Miniussi et al. (2015)

(continued)

Table 1 (continued)

Function	Gene name	Gene numbers	Expression	Tissues	Species	References
	CaPIP1;2	LM654172	sQ/Q	R/L	Ca	dos Santos and Mazzafera (2013); Miniussi et al. (2015)
	CaTIP4;1	LM654173	Q	R/L	Ca	Miniussi et al. (2015)
	CaTIP2;1	LM654174	Q	R/L	Ca	Miniussi et al. (2015)
	CaTIP1;1	LM654175	Q	R/L	Ca	Miniussi et al. (2015)
	CaTIP1;2	LM654176	sQ/Q	R/L	Ca	dos Santos and Mazzafera (2013); Miniussi et al. (2015)
	CaTIP1;3	LM654177	Q	R/L	Ca	Miniussi et al. (2015)
Phytate and ferritin biosynthesis						
Myo-inositol 1-phosphate synthase	CaMIPS1	GU108583	Q	BD	Ca	Nobile et al. (2010)
Phosphatidyl inostitol kinase 1	CaIPK1	EZ421795	Q	BD	Ca	Nobile et al. (2010)
Phosphatidyl inostitol kinase 2	CaIPK2	EZ421796	Q	BD	Ca	Nobile et al. (2010)
Ferritin	CaFER1	GQ913984	Q	BD	Ca	Nobile et al. (2010); Bottcher et al. (2011)
	CaFER2	GU001880	Q	BD	Ca	Nobile et al. (2010); Bottcher et al. (2011)
	CaFER3	EZ421798	Q	BD	Ca	Nobile et al. (2010)
Self-incompatibility RNases						
Putative S-RNase (AR1a allele)	Ca1a	FN547919	sQ	P/S/L	Ca/Cc	Asquini et al. (2011)
Putative S-RNase (CA1a allele)	Cc1a	FN547910	sQ	P/S/L	Ca/Cc	Asquini et al. (2011)
Putative S-RNase (CA1b allele)	Cc1b	FN547911	sQ	P/S/L	Ca/Cc	Asquini et al. (2011)
Putative S-RNase (CA1c allele)	Cc1c	FN547912	sQ	P/S/L	Ca/Cc	Asquini et al. (2011)
Putative S-RNase (CA1d allele)	Cc1d	FN547913	sQ	P/S/L	Ca/Cc	Asquini et al. (2011)
Biotic stress (CLR)						
Protein unknown function	CaR111	CF589193	Q	L	Ca	Ganesh et al. (2006)
Non-race-specific disease resistance	CaNDR1	CO773976	Q	L	Ca	Ganesh et al. (2006); Couttolenc-Brenis et al. (2020)
WRKY transcription factor	CaWRKY1	CO773974	Q	L	Ca	Ganesh et al. (2006)
	CaWRKY1a*	DQ335599	Q	L	Ca/Cc/Ce	Petitot et al. (2008)
	CaWRKY1b*	DQ335598	Q	L	Ca/Cc/Ce	Petitot et al. (2008)

R gene nucleotide-binding site leucine-rich repeat	CaNBS-LRR	GT030058	Q	L	Ca	Diola et al. (2013); Couttolenc-Brenis et al. (2020)
Biotic stress (CLM)						
Class III chitinase PR-8	CaPR8	CK484623	MA	L/VT	Ca	Mondego et al. (2005)
Probable microsomal signal peptidase complex SPC25	CaSPC25	CK484624	MA	YL/GB	Ca	Mondego et al. (2005)
Photosystem I	CaPSAH	CK484626	MA	L/F/GB	Ca	Mondego et al. (2005)
Putative calcium exchanger	CaCAX9	CK484625	MA	L/GB	Ca	Mondego et al. (2005)
BEL1-related homeotic protein 29	CaBEL	CK484627	MA	F/BD	Ca	Mondego et al. (2005)
Biotic stress (CBD)						
Receptor-like kinase	RLK	CF589181**	Q	H	Ca	Figueiredo et al. (2013)
Pathogenesis-related protein 10	PR10	CF589103**	Q	H	Ca	Figueiredo et al. (2013)
Abiotic stress						
Gene responding to dehydration stress	CcRD22	nd	Q	L	Cc	Menezes-Silva et al. (2017)
	CcRD29B	nd	Q	L	Cc	Menezes-Silva et al. (2017)
	CcRAB18	nd	Q	L	Cc	Menezes-Silva et al. (2017)
Putative cytosolic ascorbate peroxidase (cAPX)	APXc	JQ013438	Q	L	Ca/Cc	Ramalho et al. (2018b)
Membrane-bound ascorbate peroxidase (mAPX)	APXm	Q013439	Q	L	Ca/Cc	Ramalho et al. (2018b)
Stromatic ascorbate peroxidase (sAPX)	APXt+s	JQ013441	Q	L	Ca/Cc	Ramalho et al. (2018b)
Putative class III peroxidase (POX4)	PX4	JQ013435	Q	L	Ca/Cc	Ramalho et al. (2018b)
Violaxanthin de-epoxidase	VDE2	DQ234768	Q	L	Ca/Cc	Ramalho et al. (2018b)
Ascorbate peroxidase	APX	Q42564***	Q	R	Ca	Bazzo et al. (2013)
Superoxide dismutase	SOD	O81235***	Q	R	Ca	Bazzo et al. (2013)
Catalase	CAT	Q42547***	Q	R	Ca	Bazzo et al. (2013)
Citrate synthase	CS	Q9SJH7***	Q	R	Ca	Bazzo et al. (2013)

(continued)

Table 1 (continued)

Function	Gene name	Gene numbers	Expression	Tissues	Species	References
Malate dehydrogenase	MDH	Q9ZP06***	Q	R	Ca	Bazzo et al. (2013)
Germin-like protein	GLP	Q9LEA7***	Q	R	Ca	Bazzo et al. (2013)
Mg transporter	MGT1	Q9S9N4***	Q	R	Ca	Bazzo et al. (2013)
Phospholipase C1	PLC1	Cc02g06510	Q	CS	Ca	González-Mendoza et al. (2020)
Phospholipase C2	PLC2	Cc06g01320	Q	CS	Ca	González-Mendoza et al. (2020)
Phospholipase C3	PLC3	Cc02g06530	Q	CS	Ca	González-Mendoza et al. (2020)
Phospholipase C4	PLC4	Cc01g14270	Q	CS	Ca	González-Mendoza et al. (2020)
N-transport and metabolism						
Nitrate and ammonium transporters	CaAMTa	GW473095/ Cc03_g06810	sQ/Q	R	Ca	dos Santos et al. (2017, 2019)
	CaAMTb	GW483639/ Cc01_g14140	sQ/Q	R	Ca	dos Santos et al. (2017, 2019)
	CaAMTc	GT683246/ Cc07_g19360	sQ/Q	R	Ca	dos Santos et al. (2017, 2019)
	CaNRTa	GW479551/ Cc02_g36020	sQ/Q	R	Ca	dos Santos et al. (2017, 2019)
	CaNRTb	GW442751/ Cc06_g08580	sQ/Q	R	Ca	dos Santos et al. (2017, 2019)
	CaNRTc	GT693501/ Cc04_g15770	sQ/Q	R	Ca	dos Santos et al. (2017, 2019)
Cytosolic glutamine synthetase	CaGS1	GW485208/ Cc07_g13290	Q	L	Ca	Baba et al. (2020)
Plastid glutamine synthetase	CaGS2	GR998899/ Cc07_g13290	Q	L	Ca	Baba et al. (2020)
Nitrate reductase	CaNR	GT687366/ Cc00_g12040	Q	L	Ca	Baba et al. (2020)
Asparagine synthetase	CaAS	GW450683/ Cc01_g14420	Q	L	Ca	Baba et al. (2020)

Circadian clock						
Zeitlupe protein family	ZTL	Cc06_g13030	Q	L	Ca/Ce/Cc	Bertrand et al. (2015)
ZTL protein (proline-rich protein 5)	PRR5	Cc02_g00820	Q	L	Ca/Ce/Cc	Bertrand et al. (2015)
Timing of CAB expression 1	TOC1	Cc04_g14990	Q	L	Ca/Ce/Cc	Bertrand et al. (2015); Breitler et al. (2020)
Circadian clock regulator – late elongated hypocotyl	CcLHY	Cc02_g39990	Q	L	Ca/Ce/Cc	Bertrand et al. (2015); Toniutti et al. (2019b); Breitler et al. (2020)
Circadian clock regulator – Gigantea	CcGIGANTEA	Cc10_g15270	Q	L	Ca/Ce/Cc	Bertrand et al. (2015); Toniutti et al. (2019b); Breitler et al. (2020)
Circadian clock regulator – Gigantea	CcLUX-ARRYTHMO	Cc06_g20160	Q	L	Ca	Toniutti et al. (2019b); Breitler et al. (2020)
Starch degradation	CcGWD1	Cc11_g15490	Q	L	Ca	Toniutti et al. (2019b); Breitler et al. (2020)
Chlorophyll biosynthesis	CcPOR1A	Cc05_g12370	Q	L	Ca	Toniutti et al. (2019b); Breitler et al. (2020)
Chlorophyll biosynthesis	CcPOR1B	Cc05_g06850	Q	L	Ca	Toniutti et al. (2019b)
Starch degradation	CcISA3	Cc10_g06640	Q	L	Ca	Toniutti et al. (2019b)

The genes mentioned in this list were described in articles describing expression studies of a limited ($n < 10$) number of genes. Coffee species: *Ca*, *Coffea arabica*; *Cc*, *C. canephora*; *Cd*, *C. dewevrei*; *Ce*, *C. eugenioides*; *Cr*, *C. racemosa*. Gene numbers: the numbers correspond to GenBank accession numbers (https://www.ncbi.nlm.nih.gov) and to the gene names of *C. canephora* reference genome (http://coffee-genome.org/) or to the SOL Genomics Network (**: https://solgenomics.net/). Expression techniques used: *N* Northern blot, *Q* real-time quantitative PCR (RT-qPCR), *sQ* semiquantitative RT-PCR. Tissues: *BD* bean under development (different stages), *Bd* bean under drying process, *CS* cell suspension, *F* flowers, *GB* green beans, *GS* germinating seeds, *H* hypocotyl, *L* leaves, *P* pistil, *PB* plagiotropic buds, *R* roots, *S* stamen, *St* stem, *SE* somatic embryogenesis, *SE(DS)* somatic embryogenesis (at different stages), *VT* various tissues, *YF* young flowers. Expression studies performed for more genes or in the frame of RNAseq projects are described in Tables 2 and 3, respectively. (*): expression analysis *CaCe* and *CaCc* homeologs in *C. arabica* cv. Catuaí. (***): in the absence of nucleic accession numbers, UNIPROT codes are given (https://www.uniprot.org/). *CLM* coffee leaf miner, *CLR* coffee leaf rust, *CBB*, coffee berry borer

Table 2 List of coffee genes studied at the transcriptional level

Topic	*N*	Techniques	Tissues	Species	References
Coffee fruit development	111	Q	BD	Ca	Salmona et al. (2008)
	137	Q	BD	Ca	Joët et al. (2009, 2012)
	26	Q	BD	Ca	Joët et al. (2014)
	28	sQ	BD	Ca	Gaspari-Pezzopane et al. (2012)
	10	Q	BD	Ca	Ságio et al. (2014)
Genetic resources	10	Q	B/L	Ce	Yuyama et al. (2016)
Flowering (MADS box)	18	Q	F	Ca	de Oliveira et al. (2014)
Somatic embryogenesis	17	Q	L	Cc	Pérez-Pascual et al. (2018)
	19	Q	SE (DS)	Ca	de Oliveira et al. (2019)
DREB-like genes	31	Q	L/R	Ca/Cc	Torres et al. (2019)
Abiotic stress (drought)	49	N(8)/Q(41)	L	Cc	Marraccini et al. (2012)
	35	Q	L	Cc	Vieira et al. (2013)
	48	Q	L	Ca	Nguyen Dinh et al. (2016)[a]
Abiotic stress (cold)	19	Q	L	Cc	Dong et al. (2019b)
Abiotic stress (heat stress/ high CO2)	12	Q	L	Cc	Martins et al. (2016)
Abiotic stress (T°C)	23	Q	BD	Ca	Joët et al. (2014)
Biotic stress (CLM)	23	Q	L	Ca/Cr	Cardoso et al. (2014)
Biotic stress (CBD)	14	Q	H	Ca	Diniz et al. (2017)
Biotic stress (CLR/NEM/ JA)	18	Q	L	Ca	Ramiro et al. (2010)
	21	Q	L	Ca	Diola et al. (2013)
Photosynthesis	8	Q	L	Ca	Avila et al. (2020)

The genes mentioned in this list were described in articles reporting expression studies of a number of genes ≥8. The legend is identical to that of Table 1. The reader needs to access to the articles to know what genes were studied

[a]RT-qPCR study performed to analyze tRNA splicing and gene expression of chloroplast genes

10,000–50,000 years ago (Cenci et al. 2012). Consequently, the transcriptome of *C. arabica* is a mixture of transcripts expressed from homeologous genes harbored by its two sub-genomes, respectively, namely, *CaCc* (also referred as C^a) for *C. canephora* sub-genome and *CaCe* (also referred as E^a) for *C. eugenioides* sub-genome.

In the first attempt to analyze gene expression contributions of each sub-genome in *C. arabica*, Vidal et al. (2010) used qPCR coupled with allele-specific combination TaqMAMA-based method (Li et al. 2004) and developed a pipeline to find SNP (single nucleotide polymorphism) haplotypes of *CaCc* and *CaCe* homeologs in the ESTs of the BCGP. Of the 2069 contigs studied, these authors observed a biased expression for 22% of them, with 10% overexpressing *CaCc* homeologs and 12% overexpressing *CaCe* homeologs, therefore showing that the two sub-genomes do

Table 3 List of high-throughput expression studies

	Species	Tissues	n° EST*/ uni.	cDNA lib.	RNA tech.	NCBI	N	Expression	References
Genetic resources									
	Cc	BD/L	±50000*/ 13,175	5	454	DV663352-DV713545	No	No	Lin et al. (2005)
	Cc	BD/L	5814/4606	2	454	EE191792-EE200565	No	No	Poncet et al. (2006)
	Ca	BD/L/ F/VT	32961*/ 10,799	3	454	nd	No	No	Montoya et al. (2007)
	Ca/Cc/ Ce	L	2092	1	454	DQ655733-DQ655790	No	No	Aggarwal et al. (2007)
	Ca/Cc/ Cr	VT	214964*/ 32,155	43	454	GT640310-GT640366 GT669291-GT734396 GW427076-GW492625 GT645618-GT658452	No	No	Vieira et al. (2006); Mondego et al. (2011)
	Ce	L/F	36,935	2	Illumina	SRP052722	10	Q	Yuyama et al. (2016)
	Ca	L/F/BD	65,364	7	Illumina	PRJNA339585	4	Q	Ivamoto et al. (2017a)
	Ca/Ce	L	56,216	5	Illumina	nd	No	No	Combes et al. (2013)
	Ca	R	34,654	9	Illumina	ERP017352	12	Q	dos Santos et al. (2019)
	Ca	BG	14,005	3	Illumina	PRJNA305756	7	Q	da Silva et al. (2019)
	Ce/Cc	L	14,206	17	Illumina	PRJEB7565	No	No	Combes et al. (2015)
	Ca/Cc/ Ce	L	nd	4	Illumina	PRJEB5543	No	No	Lashermes et al. (2016)
	Ca/Cc/ Ce	L	15,522	12	Microarray	GSE24682	No	No	Bardil et al. (2011)

(continued)

Table 3 (continued)

	Species	Tissues	n° EST*/ uni.	cDNA lib.	RNA tech.	NCBI	N	Expression	References
	Ca/Cc/ Ce	L	15,522	12	Microarray	GSE24754-GSE24682	111	Q	Privat et al. (2011)
	Ca	BD	15,522	1	Microarray	GSE107949	6	Q	Dussert et al. (2018)
	Cc	R	25,574	8	Illumina	nd	3	Q	Costa (2014); Costa et al. (2015)
Somatic embryogenesis									
	Cc	SE(DS)	nd	12	Illumina	GSE128888	6	Q	Quintana-Escobar et al. (2019)
Biotic stress									
Coffee berry borer (CBB)	Ca/Cl	B	6048/5952	2	454	nd	5	Q	Idárraga et al. (2012)
Coffee leaf rust (CLR)	Ca	L	527	2	SSH/454	CF588584-CF589197	10	sQ	Fernandez et al. (2004)
	Ca	L	13,951	1	454	nd	No	No	Fernandez et al. (2012)
	Ca	L	43,159	10	Illumina	PRJNA353233-353185-353182	13	Q	Florez et al. (2017)
	Ca	L	4,895	23	Illumina	PRJNA448416	No	No	Echeverría-Beirute et al. (2019)
Coffee leaf miner (CLM)	Ca	L	±1500*	6	SSH/ macroarray	CK484622-CK484627 CV998038-CV998046 CV998048-CV99050 CX068758-CX068760	5	N	Mondego et al. (2005)
	Ca	L	±22000*	6	Microarray	nd	18	Q	Cardoso et al. (2014)

Abiotic stress									
SAR chemical inducer	Ca	L/R	1587/138	2	454	AM232089-AM232226	8	Q	De Nardi et al. (2006)
Drought	Ca	PB	41,512	4	454	PRJNA282394	38	Q	Mofatto et al. (2016)
Salt	Ca	L	19,581	2	Illumina	nd	No	No	Haile and Kang (2018)
Cold	Cc	L/BD	nd	7	Illumina	PRJNA561881	38 (L)	Q	Dong et al. (2019a)
Others									
Circadian clock	Ca	L	nd	3	Illumina	nd	7	Q	Toniutti et al. (2019b)
Self-incompatibility RNases	15 species	L/F/BD/R/P	61	15 species	454	JN035305-JN035366	3	sQ	Nowak et al. (2011)

The legend is identical to that described for Table 1. *SAR* systemic acquired resistance induced by benzo(1,2,3)thiadiazole-7-carbothioic acid-S-methyl ester (BTH). Coffee species: *Cl Coffea liberica*. Tissues: *PB* plagiotropic buds. The number of DNA sequences generated for each project corresponds to ESTs (*) or unigenes/contigs. The sequencing techniques (RNA tech.) used were 454-pyrosequencing or Illumina for RNAseq or SSH (suppression subtractive hybridization) and microarray. More information about RNAseq projects already achieved or still ongoing are available at https://www.ncbi.nlm.nih.gov/bioproject using the (NCBI) numbers. *N* for each project, the number of genes for which expression was analyzed by N (Northern blot), Q (RT-qPCR), or sQ (semiquantitative RT-PCR), is indicated. *nd* information not given or found. *no* gene expression studies not performed

Table 4 Expression studies performed in silico (without checking gene expression by RT-qPCR)

Topic	Genes	References
Genetic resources	Several genes	Mondego et al. (2011)
	Several genes	Combes et al. (2012)
Abiotic stress	Several genes expressed under drought	Vinecky et al. (2012)
	Several genes expressed under drought	Marraccini et al. (2012)*
	Drought memory genes	de Freitas Guedes et al. (2018)
Biotic stress	NBS-LRR and others	Alvarenga et al. (2010)
	Genes of SA, JA, and ET pathway	Diniz et al. (2017)
Bean development	LEA and other genes (bean and other tissues)	Dussert et al. (2018)**
Flowering development	MADS box	de Oliveira et al. (2010)
Photosynthesis	Photosynthetic genes	Bang and Huyen (2015)
Caffeine transport (purine permease)	Purine permeases	Kakegawa et al. (2019)
Diterpene biosynthesis	Several genes	Sant'Ana et al. (2018)

(*) and (**): studies also cited in Tables 2 and 3, respectively

not contribute equally to the transcriptome of *C. arabica*. By analyzing gene ontology (GO), these authors also proposed that the *CaCe* sub-genome expressed genes of proteins involved in basal biological processes (such as those related to photosynthesis, carbohydrate metabolic processes, aerobic respiration, and phosphorylation). On the other hand, the *CaCc* sub-genome contributed to adjust Arabica expression (e.g., to biotic and abiotic stresses) through the expression of genes of regulatory proteins such as those related to hormone stimuli (mainly auxin), GTP signal transduction, translation, and ribosome biogenesis proteasome activity.

The 15 K "PUCECAFE" microarray (Privat et al. 2011) was also used to perform genome-wide expression study in order to analyze the effects of warm and cold temperatures on leaf gene expression of *C. arabica* and those of its two ancestral parents (*C. canephora* and *C. eugenioides*) (Bardil et al. 2011). Even though this global gene expression analysis did not allow determining the relative contributions of homeologs to the *C. arabica* leaf transcriptome, it revealed the existence of transcription profile divergences between the allopolyploid and its parental species that were greatly affected by growth temperature. Two other "in silico" analyses that studied the effects of warm vs. cold temperature in *C. arabica* were performed. The first one used SNP ratio quantification to monitor the relative expression of 13 homeologous gene pairs in five organs (cotyledons, young leaves, leaves, stems, and roots) in addition of warm/cold temperatures (Combes et al. 2012). No case of gene silencing or organ-specific silencing was detected, but 10 out of 13 sampled genes showed biased expression: 4 genes toward *CaCe*, 4 genes toward *CaCc*, and 2 genes toward *CaCe* or *CaCc* depending on the organ considered. In the second study, the effects of warm/cold temperatures on *C. arabica* leaf

transcriptome were analyzed by RNA sequencing (Combes et al. 2013). The relative homeologous gene expression, assessed in 9,959 and 10,628 pairs of homeologs in warm and cold growing conditions, respectively, revealed that 65% of these genes had an equivalent expression level, while the rest (35%) showed biased homeologous expression. Although the warm and cold conditions were suitable for *C. canephora* or *C. eugenioides* parental species, respectively, neither sub-genome appeared preferentially expressed to compose the final transcriptome of *C. arabica*.

Because *CaCc* and *CaCe* sub-genomes of *C. arabica* have low sequence divergence (with an average difference for genes of only 1.3%) (Cenci et al. 2012), we can conclude that all the studies analyzing gene expression in *C. arabica* by "wet lab" approaches (e.g., Northern blot experiments for the most ancient and even RT-qPCR using primer pairs probably designed in highly conserved cDNA regions) quantify the transcripts expressed by both *CaCc* and *CaCe* sub-genomes.

However, few studies succeed in discriminating specifically the expression of *CaCc* and *CaCe* homeologs in *C. arabica*. All of them (described below) used the presence of SNPs or the small insertions and deletions (INDELs), for example, present in the 3′ and 5′ untranslated regions (UTRs), to design *CaCc* and *CaCe* primer pairs which permitted to identify homeologous differential expression (HDE) by qPCR. The first one concerned the expression of the *CaWRKY1a* (*CaCc*) and *CaWRKY1b* (*CaCe*) genes in *C. arabica* (Petitot et al. 2008, 2013) coding transcription factors known to be associated with plant defense responses to biotic and abiotic stresses (reviewed in Ülker and Somssich 2004; Eulgem 2006). In this species, both homeologs were concomitantly expressed in leaves and roots under all treatments (salicylic acid and infection by leaf rust [*H. vastatrix*] and root-knot nematode (RKN) *Meloidogyne exigua*), suggesting that they undergo the same transcriptional control.

A different situation was observed in *C. arabica* for the *RBCS1* gene with the predominant expression of the homeolog *CaCe* (over the *CaCc* homeolog) in the leaves of non-introgressed ("pure") cultivars such as Typica, Bourbon, and Catuaí (Marraccini et al. 2011), suggesting that specific suppression of *RBCS1 CaCc* expression occurred during the evolutionary processes that generated the *C. arabica* species. This situation fits with the concept of genome dominance (or genome expression dominance) for which the total expression of homeologs of a given gene in an allopolyploid is statistically the same as only one of the parents (Grover et al. 2012). However, *RBCS1 CaCe* and *CaCc* homeologs were co-expressed (with the same order of magnitude) in the leaves of *C. arabica* Timor hybrid HT832/2 used to create the IAPAR59; Tupi and Obabã cultivars of *C. arabica*, for example; as well as in Icatú which comes from a cross between *C. canephora* and *C. arabica* Bourbon. For all these "introgressed" Arabica cultivars, *CaCc* expression was always higher than *CaCe*. The existence of a bias in favor of *CaCc* homeologs suggests that one (or several) genetic factor of *C. canephora* species was introgressed in *C. arabica* together with the HdT (hybrid of Timor, a spontaneous hybrid between *C. arabica and C. canephora*) genes conferring resistance to leaf rust and activated (or unrepressed) the *CaCc* sub-genome.

In a work analyzing the effects of abiotic stress on the expression of genes of the mannitol biosynthesis pathway, de Carvalho et al. (2014) reported that the *CaCc* homeologs of *CaM6PR* (coding mannose-6-phosphate reductase), *CaPMI* (coding phosphomannose isomerase), and *CaMTD* (coding the NAD+-dependent mannitol dehydrogenase, oxidizing mannitol to produce mannose) were also highly expressed in leaves of *C. arabica* IAPAR59 subjected to drought, high salinity, and heat-shock stress.

HDE was also observed when analyzing expression of *nsLTP* (encoding non-specific lipid transfer proteins) genes in the separated tissue of developing beans (Cotta et al. 2014). More precisely, transcripts of *CaLTP3* (*CaCc*) homeolog were detected at different stages of pericarp development, while *CaLTP1/2* (*CaCe*) homeologs were weakly expressed in this tissue. However, both *CaLTP* homeologs were highly expressed during the first stages of endosperm development. In another study, we also reported the high expression of *CaCc* and *CaCe* homeologs of *CaLTP* genes in the plagiotropic buds of the drought-tolerant cultivar "IAPAR59" subjected to water limitation but not in those of the drought-susceptible cultivar "Rubi" (Mofatto et al. 2016). This could be related to the thicker cuticle observed on the abaxial leaf surface in IAPAR59 compared to Rubi.

In a more recent study, Vieira et al. (2019) analyzed the expression of five *FRI GIDA-like* (*FRL*) genes in flowers, beans, and somatic embryos of *C. arabica*. As previously reported (Combes et al. 2013), gene silencing was not detected for *CaFRL* genes, both *CaCc* and *CaCe* homeologs being expressed in all tissues analyzed. However, HDE was observed, for example, during early stages of flower development with a bias toward the expression of *CaCc* homeolog of *CaFRL2*, while a bias toward a *CaCc* homeolog *CaFRL4* was noticed in the latter stages of endosperm development. However, for this latter gene, a bias toward the overexpression of *CaCe* homeolog was observed in somatic embryos. This homeostasis of gene expression observed in the allopolyploid *C. arabica* could explain why this species had a greater phenotypic plasticity compared to its *C. canephora* parent (Bardil et al. 2011; Bertrand et al. 2015).

3 Gene Expression in Coffee Tissues

3.1 Beans

Several thousands of bean cDNAs were generated in the frame of the first coffee EST sequencing projects. For example, the Nestlé and Cornell project used three fruit libraries of *C. canephora* realized at early (whole cherries, 18–22 WAP), middle (endosperm and perisperm, 30 WAP [weeks after pollination]), and late (endosperm and perisperm, 42–46 WAP) stages of fruit development, leading to 9,843; 10,077; and 9,096 ESTs, respectively (Lin et al. 2005). On the other hand, the IRD and C ENICAFE sequencing projects also generated, respectively, more than 5,800 ESTs from *C. canephora* and 9,500 ESTs from *C. arabica* but without mentioning the fruit

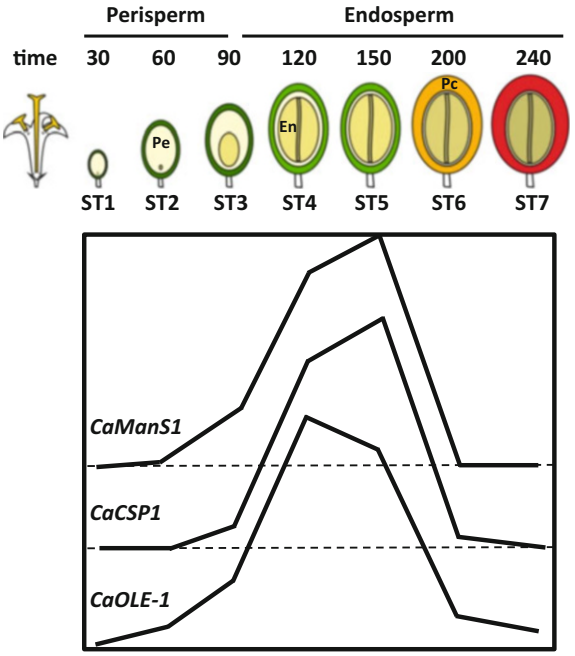

Fig. 1 Schematic representation of the seven developmental stages and tissue changes occurring during fruit development of *C. arabica*. The time is indicated in days after flowering (DAF). Tissues: *Pe* perisperm, *En* endosperm, *Pc* pericarp. RT-qPCR gene expression profiles of *CaCSP1*, *CaOLE-1*, and *CaManS1* (coding for 11S globulin, oleosin, and mannan synthase, respectively) are chosen to illustrate accumulation of storage proteins, triacylglycerols, and cell wall polysaccharides. Adapted from Dussert et al. (2018)

developmental stage (Poncet et al. 2006; Montoya et al. 2007), while the BCGP project produced 14,779 ESTs from 2 fruit libraries (FR1 and FR2) of *C. arabica* and 15,162 from 2 libraries (FR4 and FV2) of *C. racemosa* (Vieira et al. 2006; Mondego et al. 2011).

Regarding the 700 genes reported in Tables 1, 2, and 3, most expression studies were performed in developing coffee beans in which it is not a surprise if we consider that the analysis of its transcriptome is absolutely required to understand the basis of genetic and environmental variations in coffee quality. The time between anthesis and full ripening varies between *C. arabica* (from 6 to 8 months) and *C. canephora* (from 9 to 11 months), and it is usually referred to as days (or weeks) after anthesis (DAA), flowering (DAF), or pollination (DAP) (De Castro and Marraccini 2006). The different stages of developing coffee cherries are mainly defined on its size and also in accordance to the changes of exocarp (pulp) color occurring during the latest maturation steps (Pezzopane et al. 2003; Morais et al. 2008; Gaspari-Pezzopane et al. 2012; Vieira et al. 2019).

Considering the bean and its own tissues, it is now very well known that some important changes occur during its development. Soon after fecundation and up to mid-development (e.g., 90–120 DAF for *C. arabica*), the bean is mainly constituted of perisperm (maternal) which is thereafter progressively replaced by the endosperm which hardens as it ripens during the maturation phase (Fig. 1). For a practical point of view, most of the gene expression studies performed during bean development (referred to as BD in Tables 1, 2, and 3) analyzed the bean as a whole without extracting RNA from separated perisperm and endosperm issues. If it is true to

consider that perisperm represents the main tissue in the earliest stages of development (up to 90 DAF), this is no more the case after, when it is reduced to the fine silver skin membrane surrounding the bean. Several works analyzed expression in separated perisperm and endosperm tissues like those studying expansins and HMGRs (human 3-hydroxy-3-methyglutaryl-CoA reductase) (Budzinski et al. 2010) or enzymes of the mevalonic acid (MVA) pathway involved in the biosynthesis of cafestol and kahweol diterpenes (Tiski et al. 2011).

In 2008, Salmona et al. performed a transcriptomic approach combining targeted cDNA arrays, containing 266 selected candidate gene sequences and RT-qPCR on a large subset of 111 genes to decipher the transcriptional networks during the *C. arabica* bean development. This study was the first dividing coffee bean development in seven stages (ST1 0–60 DAF, small fruit with aqueous perisperm; ST2 60–90 DAF, perisperm surrounding a very small liquid endosperm; ST3 90–120 DAF, aqueous endosperm growing and replacing the perisperm; ST4 120–150 DAF, soft milky endosperm; ST5 150–210 DAF, hard white endosperm with green pericarp; ST6 210–240 DAF, ripening cherries with pericarp turning to yellow; ST7 $>$ 240 DAF, mature cherries with red pericarp) (Fig. 1). Few years later, the same research group completed this study by combining gene expression and metabolite profiles (analyzed by high-performance liquid chromatography) in order to identify the key metabolic pathways of coffee bean development (Joët et al. 2009, 2010, 2012).

Regarding sucrose metabolism, Geromel et al. (2006, 2008b) reported high expression of *CaSUS1*, coding the sucrose synthase isoform 1, at the earlier stages of endosperm development (ST4), and high expression of *CaSUS2* (sucrose synthase isoform 2) at the later stages of endosperm development (ST6–7) but also in the perisperm at 205 DAF (Joët et al. 2009). Even restricted at a fine membrane surrounding the endosperm, the high *SUS2* expression detected at that time in the perisperm could contribute to the peak of sucrose detected at the latest development stages in both pericarp and endosperm tissues (Rogers et al. 1999b).

Together with other studies, the genes involved in the most important biochemical pathways were now studied like those involved in sucrose (Geromel et al. 2006, 2008b; Privat et al. 2008; Joët et al. 2014), raffinose (dos Santos et al. 2011, 2015; Ivamoto et al. 2017a) metabolism, polysaccharide synthesis such as galactomannans (Marraccini et al. 2005; Pré et al. 2008; Joët et al. 2014; Dussert et al. 2018), lipid synthesis and transport (Simkin et al. 2006; Cotta et al. 2014; Dussert et al. 2018), caffeine (Ogawa et al. 2001; Uefuji et al. 2003; Mizuno et al. 2003a, b; Koshiro et al. 2006; Perrois et al. 2015; Maluf et al. 2009; Kumar and Giridhar 2015; Kumar et al. 2017), chlorogenic acids (CGAs) (Lepelley et al. 2007, 2012b), carotenoids (Simkin et al. 2010), trigonellines (Mizuno et al. 2014), storage proteins (Marraccini et al. 1999; Simkin et al. 2006; Dussert et al. 2018), and dehydrins and LEAs (Hinniger et al. 2006) (Table 1). Altogether, these studies revealed the existence of several phases during coffee bean development. The first one (perisperm-specific) is characterized by the synthesis of CGA occurring early in the perisperm and accumulation of chitinases, as also confirmed by 2D gel electrophoresis and protein sequencing (De Castro and Marraccini 2006; Alves et al. 2016). More recently, Ivamoto et al.

(2017a) performed the first large-scale transcriptome analysis of *C. arabica* beans during initial (from 30 to 150 DAF) developmental stages, showing the predominant expression of genes of catalytic protein, kinases, cytochrome P450, and binding site domains in the perisperm, for example. The second phase (between ST3 and ST6) is characterized by the activation of cell wall polysaccharide (mainly galactomannans and arabinogalactans) biosynthetic machinery and the synthesis of storage proteins (Marraccini et al. 1999; Pré et al. 2008; Joët et al. 2014; Dussert et al. 2018) (Fig. 1). The third phase concerns the metabolic rerouting of CGA characterized by the *HCT1* expression peak during the latest stages of seed development and the synthesis, storage, and exports of fatty acids requiring oleosins and LTPs (lipid transfer proteins). Finally, the last (endosperm-specific) stage is characterized by the sucrose synthesis and accumulation and dehydration of beans. These steps were recently confirmed by the recent long-read sequencing full-length (LRS) coffee bean transcriptome (Cheng et al. 2018). In that case, the last steps of coffee bean development were characterized by the drastic drop of chitinase transcripts and the great upregulation of genes coding late embryogenesis abundant (LEA) proteins, heat-shock proteins (HSPs), and ROS (reactive oxygen species) scavenging (e.g., superoxide dismutases, catalases, glutathione reductases, glutaredoxins, and glutathione peroxidases) and antioxidant (e.g., dehydroascorbate reductases, glutathione reductases, monodehydroascorbate reductases, and thioredoxins) enzymes, for example (Dussert et al. 2018).

The regulation of gene expression during coffee bean development should implicate specific transcription factors (TFs). In a recent study, Dong et al. (2019a) identified 63 *NAC-like* genes in the reference genome of *C. canephora*, coding TFs well-known to play important functions in plant development and stress regulations (Puranik et al. 2012). After FPKM (Fragments Per Kilobase of transcript per Million mapped reads) treatment of RNAseq data generated at different stages of fruit development, these authors identified 54 *CcNAC* genes with DEG (differentially expressed gene) profiles during the bean development which were verified by qPCR for 10 of them. This led to classify the *CcNAC* genes with continuous upregulated expression as positive regulator of bean development, while those showing downregulated expression were considered as negatively correlated with bean development.

In addition to the gene expression studies performed during coffee bean development, several works also analyzed gene expression in beans during drying (Bytof et al. 2007; Kramer et al. 2010; Santos et al. 2013; Selmar et al. 2006) and germination (da Silva et al. 2019; Lepelley et al. 2012a; Marraccini et al. 2001; Santos et al. 2013) processes.

3.2 Leaves

In the frame of the Nestlé/Cornell (Lin et al. 2005) and IRD (Poncet et al. 2006) sequencing projects, 8,942 and 4,606 ESTs were generated from *C. canephora*

leaves, respectively, while 12,024 ESTs were also sequenced from *C. arabica* leaves by CENICAFE (Montoya et al. 2007). On the other hand, the BCGP produced 26,931 ESTs from 4 leaf libraries (LV4, LV5, young leaves from orthotropic branches, and LV8, LV9, mature leaves from plagiotropic branches) of *C. arabica*, as well as 5,567 ESTs of *C. arabica* leaves infected with leaf miner and leaf rust (RM1 library), and 13,111 ESTs from 2 leaf libraries (SH1 and SH3) of *C. canephora* plants grown under water deficit (Vieira et al. 2006; Mondego et al. 2011; Vinecky et al. 2012). In this project, leaf ESTs were also generated in the SS1 (960 ESTs), SH2 (7,368 ESTs), and AR1-LP1 (5,664 ESTs) cDNA libraries from tissue pools of *C. arabica* plantlets well-watered, drought-stressed, and treated with arachidonic acid, respectively. Since these studies, numerous projects aiming to study the effects of biotic and abiotic stresses in leaves by RNAseq were performed (see Sects. 4 and 5).

In coffee, leaves are important organs not only as source organs performing photosynthesis and sugar biosynthesis (Campa et al. 2004) but also because they synthesize many other biochemical compounds such as caffeine (Frischknecht et al. 1986; Ashihara et al. 1996; Zheng and Ashihara 2004; Ashihara 2006), chlorogenic acids (CGAs) (Ky et al. 2001; Bertrand et al. 2003; Campa et al. 2017), and trigonelline (Zheng et al. 2004; Zheng and Ashihara 2004) which are further exported to beans and involved in the final cup quality (Leroy et al. 2006).

From the data of Tables 1, 2, and 3, leaf expression studies were reported for more than 400 genes. The first published concerned the three methyltransferases of the caffeine pathway encoded by the XMT (xanthosine N-methyltransferase), MXMT (7-methylxanthine-N-methyltransferase or theobromine synthase), and DXMT (3,7-dimethylxanthine-N-methyltranferase or caffeine synthase) genes (Ogawa et al. 2001; Uefuji et al. 2003; Mizuno et al. 2003a, b). These studies, initially performed by semiquantitative PCR, were further completed by RT-qPCR to better specify the expression of *CaXMT1*, *CaMXMT1*, and *CaDXMT2* genes (belonging to the *C. canephora* sub-genome) and *CaXMT2*, *CaMXMT2*, and *CaDXMT1* (belonging to the *C. eugenioides* sub-genome) in young and mature leaves of *C. arabica* and *C. canephora* (Perrois et al. 2015).

Numerous other studies also detailed the leaf expression profiles of genes of photosynthesis (Marraccini et al. 2003, 2011), sugar metabolism (Privat et al. 2008), and the biosynthetic pathways of carotenoids (Simkin et al. 2008), trigonelline (Mizuno et al. 2014), CGAs (Lepelley et al. 2007, 2012b), and diterpenes (Ivamoto et al. 2017b), for example.

3.3 Roots

More than 12,000 root ESTs were produced in the frame of the BCGP from 4 libraries (RT3, roots; NS1, root infected by nematodes; RT5, roots treated with acibenzolar-S-methyl – a systemic acquired resistance [SAR] inducer; and RT8, roots stressed with aluminum) of *C. arabica* (Vieira et al. 2006; Mondego et al.

2011). In 2006, 1,587 ESTs were produced from embryonic roots of two *C. arabica* cultivars (De Nardi et al. 2006). Among them, 1,506 sequences were used to set up a cDNA microarray which led to the identification of 139 genes differentially expressed in response to induced SAR. In the frame of PhD thesis of T.S. Costa (2014), 25,574 cDNA sequences were generated from roots of drought-susceptible and drought-tolerant clones of *C. canephora* Conilon submitted to water limitation. Even though these data were not deposited in public databases, this study permitted to identify several genes with upregulated expression under drought (see Sect. 5.1). In a more recent RNAseq study, dos Santos et al. (2019) obtained 34,654 assembled contigs from N-starved roots of *C. arabica* and identified three *AMT* (coding specific transporters of ammonium) and three *NRT* (coding nitrate transporters) for which in silico gene expression profiles (dos Santos et al. 2017) were validated by RT-qPCR (dos Santos et al. 2019). Expression profiles in roots were also reported for genes of sugar (Geromel et al. 2006) and caffeine (Ogawa et al. 2001) biosynthetic pathways.

3.4 Flowers

Compared to fruits, leaves, and roots, the studies analyzing gene expression in flowers are very limited. In terms of genetic resources, the BCGP generated 23,036 ESTs from 3 cDNA libraries (FB1, FB2, and FB4) of flowers in different developmental stages and 14,779 ESTs from 2 libraries (FR1 and FR2) corresponding to a mixture of transcripts extracted from flower buds and fruits at different developmental stages (Vieira et al. 2006; Mondego et al. 2011). The CE NICAFE research group also reported the production of 8,707 EST sequences from flowers of *C. arabica* (cv. Caturra), but these data were neither released in public databases. In a recent RNAseq study, Ivamoto et al. (2017a) identified several genes that were exclusively expressed in flowers such as those coding a FASCICLIN-like arabinogalactan protein precursor (FLA3, a protein with InterPro FAS1 Domain IPR000782) and a pectin esterase inhibitor (InterPro Domain IPR006501).

The studies of Asquini et al. (2011) and Nowak et al. (2011), aiming to characterize S-RNase genes and to analyze their expression in pistils (at pre- and post-anthesis stages) and stamens of *C. arabica* and *C. canephora* flowers, were also worth noting.

Other studies characterized the genes of *C. arabica* coding MADS-box TFs (involved in the floral organ identity) and also checked the expression of *FLOWERING LOCUS C* (*FLC*), *AGAMOUS*, *APETALA3*, and *SEPALLATA3* (de Oliveira et al. 2010, 2014). In a more recent study, Vieira et al. (2019) analyzed the expression of five *FRIGIDA-like* (*FRL*) genes, coding key proteins that regulate flowering by activating FLC (Wang et al. 2006). In that case, these authors used the qPCR TaqMAMA-based method (Li et al. 2004) to identify the expression of *CaCc* and *CaCe* homeologs of *FRL* genes in *C. arabica* flowers at different development stages (see also Sects. 2.3 and 3.5). Altogether, these results should help us to understand the genetic determinisms controlling the gametophytic self-

incompatibility system of *C. canephora* (Berthaud 1980; Lashermes et al. 1996; Moraes et al. 2018) and coffee male sterility (Mazzafera et al. 1990; Toniutti et al. 2019a).

3.5 Somatic Embryogenesis

In coffee, the somatic embryogenesis (SE) is important particularly to propagate elite clones of *C. canephora* and F1 hybrids of *C. arabica* that could not be spread by seeds (Etienne et al. 2018; Bertrand et al. 2019; Georget et al. 2019). This is the reason why several laboratories are working to identify the genes controlling the main phases and key developmental switches of coffee SE. This also explains the important number (12) of cDNA libraries from suspension cells, calli (primary, embryogenic, and non-embryogenic), and embryos performed in the frame of the BCGP, which generated more than 65,000 ESTs (Vieira et al. 2006; Mondego et al. 2011).

Among these genes, it was reported that the expression of *CcLEC1* (LEAFY C OTYLEDON 1, a key regulator for embryogenesis) and *CcBBM1* (BABY BOOM 1, a AP2/ERF TF associated with cell proliferation) was only observed after SE induction in *C. canephora*, whereas *CcWOX4* (WUSCHEL-RELATED HOMEO BOX4, a plant regulator of embryogenic patterning and stem cell maintenance) expression decreased during embryo maturation (Nic-Can et al. 2013). The expression of *BBM* and *SERK1* (somatic embryogenesis receptor-like kinase 1, a positive regulator of SE activating the YUCCA [flavin-containing monooxygenase]-dependent auxin biosynthesis) genes could also constitute a good parameter for evaluating the development and quality of *C. arabica* (Silva et al. 2014, 2015; Torres et al. 2015) and *C. canephora* (Pérez-Pascual et al. 2018) embryogenic cell suspensions. The fact that expression of *FLC* and *FRL* (especially that of *CaFRL-3*, *CaFRL-4*, and *CaFRL-5*) genes, initially reported as regulators of flowering development, was also observed in both zygotic and somatic embryos of *C. arabica* (Vieira et al. 2019) clearly indicates that both embryogenesis processes share common developmental pathways.

In order to better understand the transcriptomic changes occurring during SE process, Quintana-Escobar et al. (2019) recently performed the first RNAseq study analyzing different stages of SE induction in *C. canephora*. Among the genes differentially expressed, these authors identified eight *ARF* (auxin response factors) as well as seven Aux/IAA (auxin/indole-3-acetic acid regulators) and confirmed that *CcARF18* and *CcARF5* genes were highly expressed after 21 days of the SE induction. In another recent study, Pinto et al. (2019) characterized 17 *GH3* genes from *C. canephora* (encoding the Gretchen Hagen 3 already reported to be key proteins controlling somatic embryogenesis induction through auxin) and analyzed their expression profiles in cells with contrasting embryogenic potential in *C. arabica*, showing that *CaGH3.15* was correlated with *CaBBM*, a *C. arabica* ortholog of a major somatic embryogenesis regulator (Silva et al. 2015). Altogether,

these genes could be useful as markers to follow the SE stage converting somatic to embryogenic cells.

4 Coffee Gene Expression in Response to Biotic Stress

Recent modeling studies have delivered warnings on the threat of climate change (CC) by increasing attacks by pests and pathogens (Avelino et al. 2004, 2015; Ghini et al. 2008, 2011, 2015; Jaramillo et al. 2011; Kutywayo et al. 2013; Magrach and Ghazoul 2015). For both *C. canephora* and *C. arabica*, the main pests and diseases are (1) the leaf rust caused by the fungus *H. vastatrix*, (2) the leaf miner *Leucoptera coffeella* (Guérin-Mèneville), (3) the root attacks caused by nematodes, (4) the fruit damages caused by the borer *Hypothenemus hampei*, and (5) the coffee berry disease (CBD) caused by the hemibiotrophic fungus *Colletotrichum kahawae* which is a major constraint of *C. arabica* coffee production in Africa (van der Vossen and Walyaro 2009).

Regarding the coffee genetic diversity, most of *C. canephora* are resistant to coffee leaf rust (CLR), while "pure" (non-introgressed) *C. arabica* are susceptible. However, Catimor and Sarchimor cultivars of *C. arabica* introgressed with the HdT are considered as totally or partially resistant to CLR (Eskes and Leroy 2004). Natural resistances to coffee berry borer (CBB) and coffee leaf miner (CLM) are rather limited in both *C. canephora* and *C. arabica* species. However, natural resistance to the CLM can be found in several wild coffee diploid species, such as in *C. racemosa* (Guerreiro-Filho et al. 1999; Guerreiro-Filho 2006), and has been introgressed into *C. arabica* to generate new cultivars (e.g., Siriema) resistant to CLR (Matiello et al. 2015). Regarding nematodes, a large genetic diversity exists particularly in diploid species (e.g., *C. canephora*, *C. liberica*, and *C. congensis*) but less in *C. arabica*, regarding the variation in resistance particularly to the root-knot *Meloidogyne* spp. from high susceptibility to near immunity as it is the case of the clone 14 of *C. canephora* Conilon (Lima et al. 2014, 2015). Information about genetic resistance to coffee berry borer (CBB) is very limited for both *C. arabica* and *C. canephora* species. However, Romero and Cortina (2004, 2007) reported a reduction of CBB growth rate when *H. hampei* is fed with *C. liberica* fruits. In another study, Sera et al. (2010) showed that *C. kapakata*, *Psilanthus bengalensis*, *C. eugenioides*, as well as genotypes introgressed with *C. eugenioides* were CBB resistant. In that case, the CBB^R of *C. eugenioides* and *C. kapakata* was observed at the pericarp level (but not in the bean), while *P. bengalensis* presented CBB^R in both tissues. In addition to be CLR^R, some *C. arabica* coming from HdT, but also the F1 hybrid cultivar Ruiru 11, were also reported as CBD^R (Omondi et al. 2004, Walyaro 1983; Van der Vossen 1985). This genetic diversity observed in the *Coffea* genus regarding these different abiotic stresses could be used to identify the genes controlling these resistances and to initiate new breeding programs aiming to create new hybrids better resistant to pests and diseases.

On the other hand, the BCGP produced more than 5,000 ESTs of *C. arabica* from RM1 (leaves infected with CLM and CLR) and NS1 (roots infected with nematodes) (Vieira et al. 2006; Mondego et al. 2011. In a recent study, genes coding for the LOX (lipoxygenase), AOS (allene oxide synthase), AOC (allene oxide cyclase), and OPR (12-oxo-phytodienoic acid reductase) enzymes involved in the production of jasmonic acid (JA), one of the key plant hormones involved in plant defense against insect pests, were identified in *C. canephora* by bioinformatic approaches (Bharathi and Sreenath 2017) but without confirming gene expression of this pathway in infested coffee plants.

4.1 Coffee Leaf Rust (CLR)

In 2004, Fernandez et al. used suppression subtractive hybridization (SSH) method and semiquantitative RT-PCR to identify *C. arabica* L. genes involved in the specific hypersensitive reaction (HR) upon infection by *H. vastatrix*. Among the genes showing HR upregulation were those coding for receptor kinases, AP2 domain and WRKY TFs, cytochromes P450, heat-shock 70 proteins, several glucosyltransferases, and NDR1, for example. Other studies showed that SA and MeJA treatments markedly upregulated the expression of *CaNDR1* (coding a non-race-specific disease resistance protein well-known to be involved in resistance signalization pathway in *Arabidopsis thaliana*) and *CaWRKY1* genes, suggesting a key role of their corresponding proteins in the molecular resistance responses of coffee to *H. vastatrix* (Ganesh et al. 2006; Cacas et al. 2011; Petitot et al. 2008, 2013). This was confirmed by Ramiro et al. (2010) who showed that in addition to *CaWRKY1*, expression of *CaWRKY3*, *CaWRKY17*, *CaWRKY19/20/21*, and *CaWRKY22* genes was also highly upregulated upon CLR. Although a significant correlation was also observed between *WRKY* expression profiles after MeJA and rust treatments, expression of coffee genes involved in JA biosynthesis, including allene oxide synthase (*CaAOS*) and lipoxygenase (*Ca9-LOX* and *Ca13-LOX*), did not support the involvement of JA in the early coffee resistance responses to CLR.

The first valuable EST dataset from *C. arabica* CIFC 147/1 (CLR resistant) infected by leaf rust was produced by Fernandez et al. (2012) who identified 205,089 ESTs and 13,951 contigs from coffee together with 57,332 ESTs and 6,763 contigs from *H. vastatrix*. Among the most abundant coffee genes expressed in rust-infected leaves were those coding for several pathogenesis-related (thaumatin-like) proteins and enzymes of carbohydrate, amino acid, and lipid transport/metabolism. Florez et al. (2017) also used the *C. arabica* cultivars Caturra (CLR susceptible) and HdT CIFC 832/1 (CLR resistant) to generate 43,159 contigs which were assembled using as a reference the genome of *C. canephora* (Denoeud et al. 2014). Among DEG profiles identified by RT-qPCR were genes coding for a putative disease resistance protein RGA1, putative disease resistance response (dirigent-like protein) family protein, and Premnaspiridione oxygenase with higher expression at early stage of rust infection in the resistant cultivar plant than in the

susceptible genotype. In addition, expression of several TFs (putative basic helix-loop-helix bHLH DNA-binding superfamily protein and ethylene-responsive transcription factor 1B) was detected earlier in HdT than in Caturra, suggesting that they may be involved in the defense mechanisms of the CLR^R cultivar. In a more recent study, Echeverría-Beirute et al. (2019) performed RNAseq approach to study the effects of CLR and fruit thinning in leaves of susceptible cultivars red Catuaí (Caturra x Mundo Novo) and F1 hybrid H3 (Caturra x Ethiopian 531) of *C. arabica*. Using regression and prediction statistical models, these authors identified 460 DEGs between the inbred and the F1 hybrid. Among them, the expression of *PR* (*pathogenesis-related*) genes was upregulated in Catuaí, while those coding proteins involved in homoeostasis increased in the F1 hybrid. Even though these results were not confirmed by RT-qPCR, they validate the hypothesis of lower impact of CLR in F1 hybrids (Echeverria-Beirute et al. 2018) due to their physiological status, which itself depends on their genetic background, plant vigor, agronomic conditions, and environmental factors (Toniutti et al. 2017, 2019b).

4.2 Coffee Leaf Miner (CLM)

Although the defense mechanisms to leaf miner are not well understood, previous genetic analyses suggested that this resistance was dominant and controlled by a limited number of genes (Guerreiro-Filho et al. 1999). The first attempt to identify these genes was performed by SSH method coupled with the screening of DNA macroarrays to study gene expression in the leaves of the CLM-susceptible (CLM^S: red Catuaí) and CLM-resistant cultivar (CLM^R corresponding to a backcross of [*C. racemosa* x *C. arabica* x *C. arabica*]) infested by *L. coffeella* (Mondego et al. 2005). From the 1,500 ESTs spotted on the array, upregulated expression upon CLM infestation was observed for several ESTs coding proteins previously reported to be related to plant defense and biotic stress and similar to the phospholipase D, the lipoxygenase LOX3, the late embryogenesis abundant protein 1 (LEA1), the acid phosphatase vegetative storage protein (VSP), and the lipid transfer protein/trypsin inhibitor/seed storage domain, for example. For *CaPR8* (class III chitinase), *CaSPC25* (signal peptidase complex subunit), *CaPSAH* (photosystem I), *CaCAX9* (a putative calcium exchanger), and *CaBEL* (BEL1-related homeotic protein 29) genes, their upregulated expression upon CLM infestation suggested that they play a key role in coffee defense mechanisms against *L. coffeella*.

In a more recent study, Cardoso et al. (2014) used a 135 K microarray (NimbleGen) based on the 33,000 genes identified in the frame of the BCGP, to identify DEG genes in CLM^S and CLM^R cultivars of *C. arabica* at three stages (T0, non-infected/control; T1, egg hatching, and T2, egg eclosion) of interaction with *L. coffeella*. Even though previous studies reported that caffeine has no effect on leaf miner survival rates (Guerreiro-Filho and Mazzafera 2000; Magalhães et al. 2010), high upregulated expression of a putative *caffeine synthase* gene was reported at both T0 and T2 in CLM^R leaves compared to CLM^S ones. In the same study,

expression profiles of genes involved in plant response pathways to herbivory attacks (e.g., linoleic acid cycle, phenylpropanoid synthesis, and apoptosis), as well as JA (e.g., coding lipoxygenase and enoyl-CoA hydratase) and flavonoids (e.g., coding chalcone synthase and flavanone 3-hydroxylase-like) biosynthesis, were also upregulated in CLM^R plants even in the absence (at T0) of leaf miner infestation, indicating that defense was already built up in these plants prior to infection, as a priming mechanism.

4.3 Nematodes (NEM)

Despite the important damages caused by nematodes, there are a limited number of studies analyzing the coffee gene responses to these pathogens. When studying *WRKY* genes coding transcription factors regulating plant responses to biotic stresses, Ramiro et al. (2010) reported that expression of *CaWRKY6*, *CaWRKY11*, *CaWRKY12*, *CaWRKY13/14*, *CaWRKY15*, and *CaWRKY17* genes was upregulated in roots of *C. arabica* cv. IAPAR59 infected by the RKN *Meloidogyne exigua*. In another work, Severino et al. (2012) reported upregulated expression of *CaPRX* (encoding a putative class III peroxidase) in roots inoculated with RKN *M. paranaensis* but with significant difference between susceptible (*C. arabica* cv. Catuaí) and resistant (*C. canephora* cv. Robusta) plants. The nematode-resistant (NEM^R) clone 14 of *C. canephora* Conilon (Lima et al. 2014, 2015) was also used to investigate gene expression in roots at regular days after infestation (4, 8, 12, 20, 32, and 45 DAI) by the root-knot *M. paranaensis* (Lima 2015). The RNAseq data (not yet publicly available) showed higher expression levels of several *PR* (pathogenesis-related) genes, such as those coding class III chitinase and NBS-LRR proteins, in infected roots of NEM^R clone 14 than in those of NEM^S clone 22. In addition, the peak of *NBS-LRR* transcripts was detected at 8 and 20 DAI for the clones 14 and 22, respectively, suggesting earlier expression of this gene in NEM^R than in NEM^S coffee clones (Valeriano et al. 2019). RT-qPCR experiments also showed that expression of *CcCPI1* (coding a cysteine proteinase inhibitor) was higher in roots of clone 14 than in those of 22, with or without nematode infestation, suggesting that the this protein, also highly expressed in coffee beans under development and germination (Lepelley et al. 2012a), could also play a key role in controlling nematode development. In that sense, CPIs have already been reported to inhibit proteinases in the digestive tracts, therefore reducing the destructive effects of herbivorous insects (Benchabane et al. 2010; Schluter et al. 2010), and to increase tolerance to nematodes as well as to fungal and bacterial pathogens in transgenic plants (Urwin et al. 2003; Martinez et al. 2005).

4.4 Coffee Berry Borer (CBB)

Considering that *C. arabica* fruits are more susceptible to CBB than those of *C. liberica*, Idárraga et al. (2012) constructed cDNA libraries from fruits for these two species infested with *H. hampei* and generated 3,634 singletons and 1,454 contigs. In silico analyses revealed that infested *C. arabica* berries displayed a higher number of DEG genes coding proteins involved in general stress responses, while genes coding proteins involved in insect defense were overexpressed in *C. liberica*. For some of these genes, expression profiles in infested cherries were checked by RT-qPCR. Interestingly, expression levels of genes coding a hevein-like protein, an isoprene synthase, a SA carboxyl methyltransferase, and a patatin-like protein appeared much more upregulated in *C. liberica* than in *C. arabica*. The upregulation of these genes was already reported in other plants in response to insect herbivory and JA treatments (Kiba et al. 2003; Reymond et al. 2000; Falco et al. 2001), suggesting that they could be involved in the partial resistance to CBB in *C. liberica*.

4.5 Coffee Berry Disease (CBD)

Cytological and biochemical studies revealed that coffee resistance to *C. kahawae* is characterized by restricted fungal growth associated with several host responses, such as hypersensitive-like cell death (HR), callose deposition, accumulation of phenolic compounds, lignification of host cell walls, and increased activity of oxidative and peroxidase enzymes (Silva et al. 2006; Gichuru 1997, 2007; Loureiro et al. 2012).

The first study analyzing gene expression in response to *C. kahawae* was performed by Figueiredo et al. (2013) in hypocotyls of *C. arabica* cultivars Catimor 88 (HdT derivative CBD^R) and Caturra CIFC 19/1 (CBD^S). These authors showed that expression levels of *RLK* (coding a receptor-like kinase) and *PR10* (coding a pathogenesis-related protein 10) genes were higher in Catimor than in CBD-infected Caturra. Interestingly, upregulated expression of these two genes was also reported during coffee infection with *H. vastatrix* (Fernandez et al. 2004). In order to understand the molecular mechanisms involved in coffee resistance to *C. kahawae*, Diniz et al. (2017) evaluate the expression of genes involved in SA, JA, and ethylene (ET) pathways in the same cultivars. From the 14 genes studied by RT-qPCR, these authors showed the involvement of JA and ET phytohormones rather than SA in this pathosystem. Regarding the ET pathway, the strong activation of *ERF1* gene (coding for ET receptor) at the beginning of the necrotrophic phase suggests the involvement of ethylene in tissue senescence.

4.6 Gene Expression in Response to Other Pests and Diseases

Of the two commercially cultivated coffee species, *C. arabica* and *C. canephora* are considered as susceptible and resistant, respectively, to the insect pest *Xylotrechus quadripes* known as coffee white stem borer (CWSB). Using SSH approach, Bharathi et al. (2017) identified 265 unigenes overexpressed in *C. canephora* bark tissues upon CWSB larval infestation, many of them coding putative pectin-degrading enzymes like a pectate lyase (*Cc07_g00190*[1]), three polygalacturonases (*Cc03_g15700*, *Cc03_g15740*, and *Cc03_g15840*), and a pectinacetylesterase (*Cc08_g04630*). By RT-qPCR, these authors also showed that the expression of *Cc07_g00190* was strongly induced at 72 h after CWSB infestation. The possible role of this pectinolytic enzyme in the production of oligogalacturonides was proposed, which could act as elicitors involved in defense responses of *C. canephora* to CWSB (Bharathi and Sreenath 2017).

5 Coffee Gene Expression in Response to Abiotic Stress

Several models predicted that CC will have strong negative impacts on both *C. canephora* and *C. arabica* species at environmental, economic, and social levels (Assad et al. 2004; Bunn et al. 2015a, b; Ovalle-Rivera et al. 2015; Davis et al. 2012, 2019; Moat et al. 2017, 2019). Drought and high air temperatures are undoubtedly the major threats to coffee production, forecasted by potential climate changes (IPCC 2013). Drought is a limiting factor that affects flowering and yield of coffee (DaMatta and Ramalho 2006), as well as bean development and biochemical composition and consequently the final cup quality (Silva et al. 2005; Vinecky et al. 2017). Increased [CO_2] in air is also a key factor for coffee plant acclimation to high temperature; strengthening the photosynthetic pathway, metabolism, and antioxidant protection; and modifying gene transcription and mineral balance (Ramalho et al. 2013; Martins et al. 2014, 2016; Ghini et al. 2015; Rodrigues et al. 2016). In this context, understanding the genetic determinism of coffee's adaptation to abiotic stress has become essential for creating new varieties (Cheserek and Gichimu 2012).

5.1 Drought

The first study analyzing the effects of drought stress was performed by Simkin et al. (2008), who reported the gene expression profiles of the carotenoid biosynthesis pathway in leaf, branch, and flower tissues of *C. arabica* subjected to water

[1]Gene names found in the Coffee Genome Hub (http://coffee-genome.org/)

withdrawal. In this work, it was shown that the transcript levels of *PTOX*, *CRTR-B*, *NCED3*, *CCD1*, and *FIB1* increased under drought, suggesting that drought favored the synthesis of xanthophylls implicated in the adaptation of plastids to changing environmental conditions by preventing photooxidative damage of the photosynthetic apparatus. On the other hand, drought was reported to decrease the *RBCS1* gene expression in both *C. arabica* and *C. canephora* species (Marraccini et al. 2011, 2012). However, this reduction was not accompanied by a decrease of RBCS1 protein in the leaves of *C. canephora* under water withdrawal. In the same work, it was also shown that the transcriptional contribution of each *RBCS1* homeolog may be affected by drought in *C. arabica* cultivars (Marraccini et al. 2011). In *C. canephora*, and whatever the clone studied, drought was also shown to downregulate the leaf expression of many genes related to photosynthesis such as *CcCAB1* (coding chlorophyll a-/b-binding proteins), *CcCA1* (coding for the carbonic anhydrase supplying CO_2 for Rubisco), as well as expression of *CcPSBO*, *CcPSBP*, and *CcPSBQ* genes coding proteins of the PSII oxygen-evolving complex (Marraccini et al. 2012; Vieira et al. 2013).

On the other hand, drought stress significantly upregulated the expression of genes coding proteins involved in maintenance, reinforcement, and protection during the dehydration-rehydration process such as dehydrins and glycin-rich and heat-shock proteins in *C. canephora* (Marraccini et al. 2012; Vieira et al. 2013) and *C. arabica* (Santos and Mazzafera 2012; Mofatto et al. 2016). Drought stress was also shown to increase expression of some *PIP* (plasma membrane intrinsic proteins) genes in the leaves and roots of different coffee species, suggesting the involvement of these aquaporins in controlling the water status in coffee plants (dos Santos and Mazzafera 2013; Miniussi et al. 2015).

In coffee, like in many other plants, drought stress was also reported to affect the metabolic pathways involved in the synthesis of many solutes such as sugars of the raffinose family oligosaccharides (RFOs) (e.g., trehalose, raffinose, and stachyose), already described to be involved in osmoprotection against abiotic stresses in plants (Kerepesi and Galiba 2000). The upregulated expression of *CaGolS2* and *CaGolS3* genes coding galactinol synthases explained the increase of raffinose and stachyose contents also observed in leaves of *C. arabica* cv. IAPAR59 plants submitted to severe water deficit (dos Santos et al. 2011). In *C. canephora* Conilon, water limitation also increased *CcGolS1* gene expression in leaves of the drought-tolerant (D^T) clone 14 but decreased the expression of the same gene in leaves of the drought-susceptible (D^S) clone 109A (dos Santos et al. 2015). Drought was also shown to upregulate the expression of *M6PR* gene coding the mannose-6-phosphate reductase in leaves of both *C. canephora* (Marraccini et al. 2012) and *C. arabica* (Freire et al. 2013). In *C. arabica* cv. IAPAR59, the increased expression of *CaPMI* (mannitol synthesis) and decreased *CaMTD* (controlling mannitol degradation) expression under drought were correlated with high mannitol levels detected in leaves under drought conditions (de Carvalho et al. 2014).

Drought also increased the expression of regulatory genes *CcRD29*, *CcRD26*, and *CcDREB1D* coding a RD29-like protein, a NAC-RD26-like TF, and an AP2/ERF DREB-like TF, respectively, in D^T (14, 73, and 120) and D^S (22) clones of

C. canephora Conilon (Marraccini et al. 2012; Vieira et al. 2013). Even though these studies highlighted the existence of different mechanisms among the D^T clones of *C. canephora* regarding water deficit, they also showed that *CcDREB1D* expression was always higher in leaves of D^T clones (particularly in clone 14) than in those of D^S clone 22 under water withdrawal (Fig. 2). Upregulated expression of the *CcDREB1D* was also reported in leaves of *C. canephora* and *C. arabica* subjected to low relative humidity (Thioune et al. 2017; Alves et al. 2018). A study of *CcDREB1D* promoter regions in the D^T clone 14 and D^S clone 22 revealed the existence of several haplotypes diverging by several SNPs and insertions/deletions (Alves et al. 2017). A functional analysis of these promoters in transgenic plants of *C. arabica* var. Caturra showed that haplotype HP16 (found in the D^T clone 14) was able to drive the expression of the *uidA* reporter gene under water deficit in leaf mesophyll and guard cells more strongly and earlier than the HP15 (present in both clones) and HP17 (only present in D^S clone 22) haplotypes (Alves et al. 2017). In a more recent work aiming to study the expression of *DREB*-like genes regarding various abiotic stresses (Torres et al. 2019), drought (mimicked by water limitation) was shown to upregulate expression of *CcDREB1B*, *CcRAP2.4*, *CcERF027*, *CcDREB1D*, and *CcTINY* mainly in leaves of *C. canephora* D^T clones, while drought (mimicked by low humidity) upregulated the expression of *CaERF053*, *CaRAP2.4*, *CaERF017*, *CaERF027*, *CaDREB1D*, and *CaDREB2A.1* in leaves of *C. arabica*. On the other hand, expression of *CcDREB2F*, *CcERF016*, and *CcRAP2.4* genes was greatly upregulated under drought specifically in the roots of D^S clone 22 (Fig. 2), which could help this clone to compensate its low efficiency in controlling stomatal closure and high reduction of net CO_2 assimilation (*A*) observed upon drought acclimation (Marraccini et al. 2012).

M.G. Cotta (2017) also analyzed the expression profiles of genes coding the PYR/PYL/RCAR-SnRK2-PP2C proteins known to be involved in the first steps of ABA perception and signal transduction in plants (Klingler et al. 2010), in leaves, and in roots of D^T (14, 73, and 120) and D^S (22) clones of *C. canephora* subjected to drought. In leaves, drought downregulated the expression of *CcPYR1*, *CcPYL2*, and *CcPYL4* genes (coding ABA receptors) and upregulated the expression of *CcAHG2* and *CcHAB* (coding PP2C phosphatases functioning as negative regulators of ABA pathway) in D^T clones. However, expression of *SnRK2* genes (coding protein kinases functioning as positive regulators of this pathway) was poorly affected by drought conditions. On the other hand, drought upregulated the expression of *PP2C* (e.g., *CcABI1*, *CcABI2*, *CcAHG3*) and *SnRK2* (e.g., *SnRK2.2*, *SnRK2.6*, and *SnRK2.7*) genes mainly in roots of *C. canephora* D^T clone 120. *CcPYL8b* was the gene most expressed in drought-stressed roots, particularly in D^T clones 73 and 120, while expression of *CaPYL8a* was upregulated by drought mainly in leaves of *C. arabica* D^T accession (Santos et al. 2019).

In *C. canephora*, Menezes-Silva et al. (2017) reported that coffee plants exposed to multiple drought events tended to display a higher expression of the *RD29B* and *RD22* genes which could be involved in acclimation to repeated drought events. Recently, de Freitas Guedes et al. (2018) performed an RNAseq study to analyze the effects of multiple drought stress on gene expression in leaves of the D^T clone

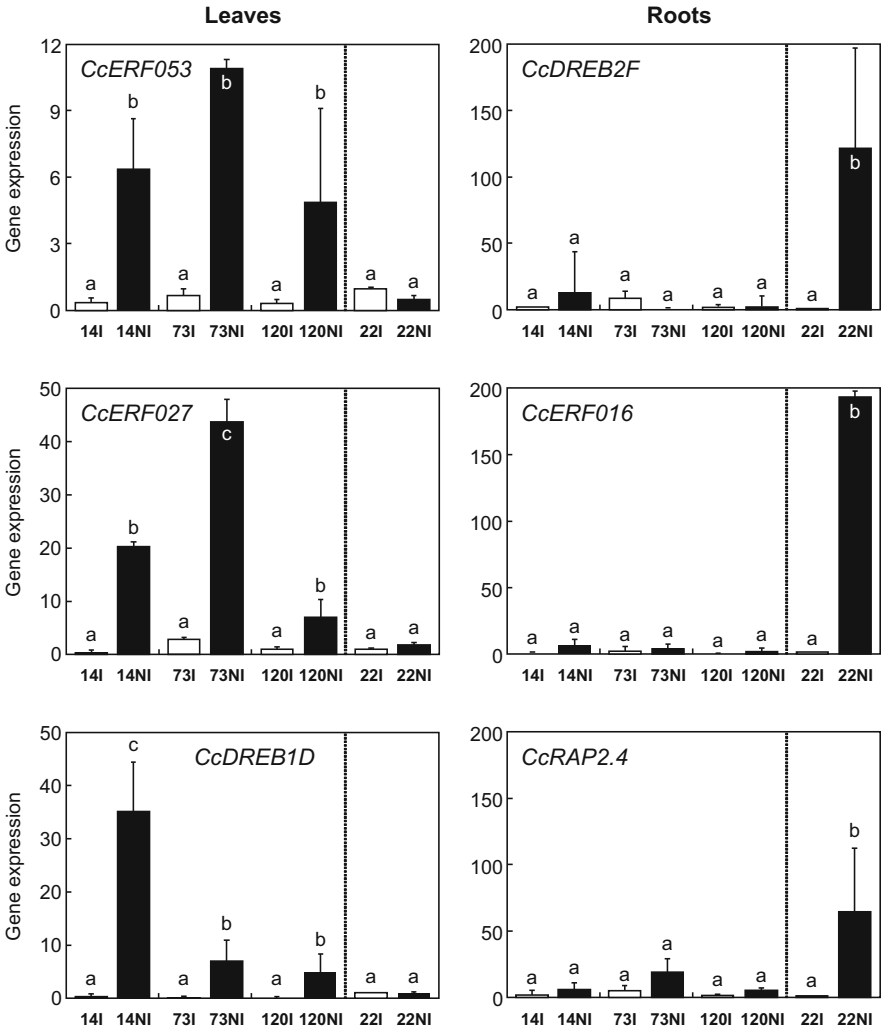

Fig. 2 Gene expression profiles of *DREB*-like genes in leaves and roots of D^T (14, 73, and 120) and D^S (22) clones of *C. canephora* Conilon subjected (*NI* not irrigated, black isobars) or not (*I* irrigated, white isobars) to water limitation. The D^T and D^S clones are separated by a vertically dotted line. Gene names are indicated in the histograms. Expression values corresponding to the mean of three biological and technical replications (±SD) are expressed in fold change relative to the expression level of the sample 22I as the reference sample (relative expression = 1). Transcript abundances were normalized using the expression of the *CcUBQ10* (Barsalobres-Cavallari et al. 2009) as the endogenous control. Treatments sharing the same letter are not significantly different. Data adapted from Torres et al. (2019)

120 and D^S clone 109 of *C. canephora*. Among the 22,764 genes generated, these authors identified 49 genes in the D^T clone (e.g., coding a MYB-like proteins or for defense-related proteins containing LRR and kinase domains), which could be involved in stress "memory."

As previously mentioned, Costa (2014) analyzed the expression profiles of several genes in roots of D^S and D^T clones of *C. canephora* Conilon submitted to water limitation. Among the identified DEGs, it is worth noting that upregulated expression was specifically observed under drought in roots of the D^T clone 14 for the *CcMJE1* (coding a protein involved in MeJA metabolism), *CcNCED3* (encoding a rate-limiting protein involved in the synthesis of abscisic acid), *CcPAP1* (coding a putative protein containing the acid phosphatase domain TIGR01675 characterizing vegetative storage proteins (VSPs)), *CcPRX1* (coding for a putative peroxidase), and *CcclXIP* (coding a chitinase-like xylanase inhibitor protein), as well as *CcM6PR*, *CcGOLS3b*, and *CcLTP4* (involved in RFOs and lipid biosynthesis pathways) genes. More recently, Vasconcelos et al. (2011) reported that the protein expressed from the *CaclXIP* cDNA (originally identified as a class III chitinase encoding gene from *C. arabica*) functioned as a chitinase-like xylanase inhibitor protein (clXIP) of fungal xylanases. Altogether, these responses suggest the existence of cross talk between abiotic and biotic pathways in roots of D^T clone 14 which could explain its drought tolerance and resistance to several species of RKN of *Meloidogyne* spp. (see Sect. 4.3).

It is also worth noting that expression of many genes cited in this section (e.g., coding dehydrins, enzymes of carotenoid and RFO pathways, and other proteins involved in stabilization of membranes and proteins) was also studied during the last stages of coffee bean development (Hinniger et al. 2006; Simkin et al. 2010; Ivamoto et al. 2017a; Dussert et al. 2018), characterized by the intense dehydration of endosperm (De Castro and Marraccini 2006; Eira et al. 2006).

5.2 High Temperature

The study of Bardil et al. (2011) was the first to analyze the effects of low (LT, day 26°C/night 22°C) and high (HT, day 30°C/night 26°C) temperature on homeologous genes expressed in leaves of *C. arabica* and in those of its two ancestral parents, *C. canephora* and *C. eugenioides*. Among the 15 K unigenes analyzed, around 50% appeared differentially expressed (with 25% upregulated) at low temperature between *C. arabica*, *C. canephora*, and *C. eugenioides*. Similar proportions were found at high temperature when comparing the transcriptome of *C. arabica* vs. *C. eugenioides* and *C. canephora* vs. *C. eugenioides*. However, only 8.9% of transcriptome divergence was observed when comparing *C. arabica* vs. *C. canephora*. In terms of expression patterns observed in *C. arabica*, the number of genes with "*C. canephora*-like dominance" increased from 8–14% under LT (in the Java and T18141 cultivars) to 21–26% under HT conditions. In that case, it was worth noting that transcription profiles of T18141 (a cultivar recently introgressed with *C. canephora* genome) were more similar to that of *C. canephora* than that of the "pure" (non-introgressed recently) Java cultivar. Altogether, these results indicate that *C. arabica* mainly expressed genes from its *CaCc* sub-genome under hot temperatures.

In another work, Bertrand et al. (2015) analyzed gene expression profiles in leaves of *C. arabica*, *C. eugenioides*, and *C. canephora* (cv. Nemaya) exposed to four thermal regimes (TRs: 18–14, 23–19, 28–24, and 33–29°C). Under hot temperatures, upregulated expression in *C. arabica* was observed for several genes like *Cc10_g00570* coding a catalase (CAT3) (when compared to *C. canephora*) and *Cc06_g11950* coding a photosystem II subunit X (when compared to *C. eugenioides*). On the other hand, expression profiles of *Cc05_g04680* coding a L-ascorbate oxidase homolog and those of photosynthetic genes coding light-harvesting complex (LHCII: *Cc04_g16410*) and chlorophyll a–b-binding protein (CAB: *Cc10_g00140*, *Cc05_g12720*, *Cc09_g09020*, *Cc05_g09650*, and *Cc09_g09030*), or for respiration-like genes *Cc10_g00410*, *Cc02_g25840*, and *Cc07_g00550* (coding a chloroplast glyceraldehyde-3-phosphate dehydrogenase, a chloroplast ribose-phosphate pyrophosphokinase, and a Rubisco methyltransferase, respectively), were strongly downregulated in *C. arabica* compared with its two parents.

In leaves of *C. arabica*, heat-shock conditions also upregulated the expression of *CaGolS1*, *CaGolS2*, *CaGolS3*, *CaPMI*, *CaMTD*, and *CaERF014* and downregulated expression of *CaM6PR* (dos Santos et al. 2011; de Carvalho et al. 2014; Torres et al. 2019). The interactions of high temperature and high [CO_2] on expression profiles of gene coding protective and antioxidant proteins were also studied by Martins et al. (2016) and Scotti-Campos et al. (2019) (see Sect. 5.4 below).

5.3 Cold Stress

The first studies to analyze the effects of cold stress on coffee gene expression were realized by Fortunato et al. (2010) and Batista-Santos et al. (2011) who subjected several cultivars and hybrids of *C. canephora*, *C. arabica*, and *C. dewevrei* to gradual cold treatments. These authors showed that upregulation of *CaGRed* and *CaDHAR* genes (coding a glutathione reductase (GR) and dehydroascorbate reductase, respectively) and of *CaCP22*, *CaPI*, and *CaCytf* (coding proteins involved in PSII, PSI, and Cytb6/f complex, respectively) could explain the ability of Icatu (*C. arabica* × *C. canephora*) cultivar to better support cold stress by reinforcing its antioxidative capabilities and maintaining efficient thylakoid functioning.

In their analysis of gene expression profiles in leaves of *C. arabica*, *C. eugenioides*, and *C. canephora* (cv. Nemaya) exposed to different thermal regimes, Bertrand et al. (2015) also reported upregulated expression profiles under cold stress in *C. arabica* for *Cc07_g15610* gene coding a L-ascorbate oxidase, for genes involved in respiration (e.g., *Cc02_g08980*, *Cc00_g15710*, and *Cc02_g06960* coding a phosphoenolpyruvate carboxylase kinase, a ribulose bisphosphate carboxylase small chain, and a sedoheptulose-1,7-bisphosphatase, respectively), and also for genes of photosynthesis (e.g., *Cc02_g28520*, *Cc05_g15930*, *Cc07_g10820*, and *Cc06_g19130* coding a ferredoxin-nitrite reductase, a photosystem II 10 kDa

polypeptide, a ferredoxin-NADP reductase, and a ferredoxin-dependent glutamate synthase, respectively). On the other hand, overexpression of *Cc05_g10250*, *Cc00_g35890*, and *Cc05_g10310* genes (coding polyphenol oxidases) was seen in *C. canephora* under low temperatures. For the *LHY* (late elongated hypocotyl, *Cc02_g39990*) gene involved in circadian cycle, RT-qPCR experiments confirmed in silico data, showing the highest expression under low than high temperatures particularly in leaves of *C. canephora*.

More recently, two studies investigated the effects of cold stress on the leaf gene expression in *C. canephora*. In the first one, Dong et al. (2019a) performed gene expression analyses in leaves of *C. canephora* plants subjected to cold stress (C1 (7 days at day 13°C/night 8°C) followed by C2 (3 days at day 4°C/night 4°C)) but also in fruits at different stages of development. For the 38 *CcNAC* genes analyzed by qPCR in cold-stressed leaves, expression was (1) upregulated upon C1 and C2 treatments for 4 genes, (2) downregulated upon C1 (but not C2) for 10 genes, (3) upregulated upon C2 (but not C1) for 7 genes, and (4) downregulated upon both cold treatments for 17 genes. In the second work, the same authors characterized 49 *CcWRKY* genes from the reference genome of *C. canephora* and analyzed their expression profiles by qPCR for 45 of them in cold-stressed leaves as reported in the previous study (Dong et al. 2019b). This led to identify 14 *CcWRKY* genes with expression induced during the cold acclimation stage (upon C1 and C2 treatments), 17 genes upregulated by cold treatment (C2 but not C1), and 12 downregulated by both cold stress treatments. Among the 14,513 putative target genes of *CcWRKY* identified in *C. canephora* by a genome-wide analysis, 235 were categorized into response to the cold process, including carbohydrate metabolic, lipid metabolic, and photosynthesis process-related genes. Like in many other plants, these observations clearly highlight the vital regulatory role played by WRKY TFs in various developmental and physiological processes (such as seed development) but also in a range of abiotic stress (like cold, heat, drought, as well as salinity) and biotic stress (Rushton et al. 2010).

In a more recent work, Ramalho et al. (2018a) analyzed the impacts of single and combined exposure to drought and cold stress in *C. arabica* cv. Icatu, *C. canephora* cv. Apoatã, and the hybrid *C. arabica* cv. Obatã. At the physiological level, the Icatu cultivar showed a lower impact upon exposure to cold and drought stress, characterized by a reduced lipoperoxidation under stress interaction, for example. At the molecular level, simultaneous exposure of Icatu to both stresses increases the expression of genes coding ascorbate peroxidase (APX) involved in H_2O_2 removal (e.g., *APXc* [cytosolic] and *APXt+s* [stromatic]) and consequently total APX enzymatic activity. To a lesser extent, this situation was also observed in *C. canephora*, while Obatã was the less responsive genotype considering the studied genes.

5.4 CO_2 Concentration

The research group of J.C. Ramalho (Lisbon University, Portugal) published several articles studying the effects of elevated [CO_2] on coffee. They demonstrated that elevated [CO_2] mitigated the impact of heat on coffee physiology (Rodrigues et al. 2016) and also contributed to preserve the bean quality (Ramalho et al. 2018b). In a study aiming to analyze the interactions of elevated [CO_2] and high temperature on protective response mechanisms in coffee, Martins et al. (2016) showed that the maintenance (or increase) of the pools of several protective molecules (e.g., neoxanthin, lutein, carotenes, α-tocopherol, heat-shock proteins HSP70, and raffinose), activities of antioxidant enzymes (e.g., superoxide dismutase, APX, GR, and catalase [CAT]), and the upregulated expression of *ELIP* (coding chloroplast early light-induced protein) and *Chap20* (coding chloroplast 20 kDa chaperonin) genes were correlated with heat tolerance (up to day 37°C/night 30°C) at 380 and 700 μL CO_2 L^{-1} for both *C. arabica* L. cvs. Icatu and IPR108 and *C. canephora* cv. Conilon clone 153. These authors also showed that upregulated expression of genes related to protective (*ELIPS*, *HSP70*, *Chap20*, and *Chap60*) and antioxidant (*CAT*, *APXc*, *APXt+s*) proteins was largely driven by temperature, while enhanced [CO_2] promoted a greater upregulation of these genes mainly in *C. canephora* CL153 and *C. arabica* Icatu. In the more recent study analyzing the expression of genes related to lipid metabolism under elevated [CO_2], heat, and their interaction, Scotti-Campos et al. (2019) showed that the strong remodeling (unsaturation degree) of membrane lipids observed during the heat shock (from day 37°C/night 30°C to day 42°C/night 34°C) of plants grown under high [CO_2], coordinated with *FAD3* (coding for fatty acid desaturase) downregulation in *C. arabica* and upregulation of lipoxygenase-coding genes *LOX5A* (in CL153 and Icatu) and *LOX5B* (in Icatu), could contribute to long-term acclimation of coffee chloroplast membranes to climate changes.

5.5 Salt Stress

In leaves of *C. arabica* cv. IAPAR59, upregulated expression of galactinol synthase genes *CaGolS2* and *CaGolS3* was observed after irrigation with 150 mM NaCl (dos Santos et al. 2011). In the same cultivar, salt stress upregulated the expression of *CaM6PR* and *CaPMI* genes and markedly downregulated that of *CaMTD* (de Carvalho et al. 2014). In parallel, leaf mannitol contents increased gradually to reach a peak after 12 days of salt stress imposition. However, this content was lower than in leaves of plants under water deprivation, indicating that coffee plants have different responses to drought and salinity.

The effects of salt stress in leaves were recently studied by RNAseq in leaves of *C. arabica* seedlings irrigated with normal water (control, ECw [electrical conductivity] = 0.2 $dS.m^{-1}$) or with deep sea water (salt treatment, ECw = 2.3 $dS.m^{-1}$) (Haile and Kang 2018). From the 19,581 genes aligned on the reference genome of

C. canephora, in silico analyses identified 611 genes presenting significant DEG profiles between the control and salt treatment. Among the most expressed upregulated genes were *Cc00_g13890*, *Cc04_g05080*, and *Cc08_g11060*, coding for WRKY TFs; *Cc06_g01240* coding a putative trihelix TF GT-3a already reported in controlling the developmental process and response to abiotic and biotic stress (Park et al. 2004; Wang et al. 2016); and *Cc10_g04710* coding the putative ethylene-responsive (ERF011) TF. On the other hand, salt stress also downregulated the expression of *Cc05_g16570* (coding a putative MYB family transcription factor APL), *Cc02_g17440* and *Cc07_g03240* (both coding putative bHLH TFs), and *Cc02_g10740* and *Cc06_g21410* (coding putative transcription elongation factor SPT of RNA polymerase II). However, the DEG expression profiles of these TF-encoding genes were not verified in vivo by qPCR experiments.

5.6 Wounding

WRKY and *NDR* genes were previously reported as playing key roles in the molecular resistance responses of coffee to *H. vastatrix* (see Sects. 2.3 and 4.1). In the first study, Ganesh et al. (2006) reported upregulated expression of *CaNDR1*, *CaWRKY1* (see Sect. 4.1), and *CaR111* (coding a putative protein of unknown function) genes in leaves of *C. arabica* wounded by performing transversal cuts with scissors. Few years after, Petitot et al. (2008, 2013) showed that expression of both *CaWRKY1a* (*CaCc*) and *CaWRKY1b* (*CaCe*) homeologs was upregulated in wounded leaves of *C. arabica* (see Sect. 7). In parallel, wounding also markedly upregulated expression of *CaWRKY1a* and *CaWRKY1b* genes in leaves of *C. canephora* and *C. eugenioides*, respectively, confirming that both genes were functional. In addition to *CaWRKY1*, Ramiro et al. (2010) also showed that *CaWRKY19/20/21* genes, as well as *CaWRKY15* and *CaWRKY17*, were also highly induced by wounding. In another work, Brandalise et al. (2009) showed that expression of *CaIRL*, coding an isoflavone reductase-like protein, was induced in leaves of *C. arabica* submitted to a mechanical injury, leading to further study the promoter of this gene (see Sect. 8).

6 Gene Expression in F1 Hybrids of *C. arabica*

In the context, the creation of new coffee varieties better adapted to biotic and abiotic stresses to low levels of inputs and to CC is now one of the challenges of several coffee research institutes (van der Vossen et al. 2015; Bertrand et al. 2019).

In *C. arabica*, it is possible to create and select in a relatively short time (e.g., around 8 years against 25 years for conventional breeding programs) new F1 hybrid varieties with increased production (e.g., under agroforestry) and also improved aromatic quality without increasing fertilizer quantities (Bertrand et al. 2006, 2011), by crossing pure commercial line varieties with phylogenetically distant plants

Table 5 List of experiments (and related RNAseq analyses) planned in the frame of the BREED CAFS project (see www.breedcafs.eu)

Trial number	Place	Condition	Experiment
1	Univ. of Lisbon	Phytotron	Drought/[CO_2]
2	Univ. of Lisbon	Phytotron	Heterosis/[CO_2]
3	Cirad	Phytotron	Nitrogen/light/[CO_2]
4	Cirad	Phytotron	Heterosis/T°C
5	Univ. of Copenhagen	Greenhouse	Heterosis/shade
6	Cirad	Greenhouse	Heterosis/N-depletion
7	Cirad	Phytotron	Shade/nitrogen/T°C/rust
8	Cirad	Greenhouse	Drought/heterosis
9	Cirad	Greenhouse	Circadian clock
10	Cirad	Greenhouse	Heterosis/circadian clock
11	Cirad	Phytotron	Grafting/T°C
12	Cirad	Rhizoscope	Grafting/nitrogen
13	Costa Rica	Field	Grafting/elevation/shade
14	Nicaragua	Nicaragua	Heterosis/shade
15	Nicaragua	Nicaragua	25 best cultivars
16	Nicaragua	Nursery	Heterosis/T°C
17	Vietnam	Field	Drought/AFS
18	Salvador	Field	F1 hybrids/parents
19	Nicaragua	Field	Maternal effect
20	Nicaragua	Nursery	Genomic selection

corresponding to wild individuals from Ethiopia and Sudan, for example (Van der Vossen et al. 2015). The objective of the H2020 BREEDCAFS[2] (BREEDing Coffee for Agroforestry Systems) project, supported by the EU (2017–2021), is to identify robust markers (allelic, molecular, epigenetic) that could be used as early predictors to speed up future *C. arabica* breeding programs aiming to create new F1 hybrids with increased resistance and greater resilience to climate change in agroforestry systems (Bertrand et al. 2019). This project intends to compare the leaf transcriptomic profiles in F1 hybrids and cultivated varieties (and/or hybrids to their two parents) upon different abiotic stresses either performed in phytotrons and greenhouses (e.g., in order to test the effects of temperature, light, drought, CO_2, and N_2) or in field trials (or in networks of "demoplots" in farms). The numerous RNAseq studies planned to be perform within the framework of this project (Table 5) should also help us to better understand why the pure line varieties are less adapted to environmental constraints than F1 hybrids. For example, Toniutti et al. (2019b) showed that hybrid vigor (heterosis) could be explained by the modification of leaf expression profiles of several genes involved in the circadian clock (e.g., *LHY* and *GIGANTEA*), the chlorophyll synthesis (e.g., *POR1A* and

[2] www.breedcafs.eu.

POR1B), and starch degradation (e.g., *CcGWD1* and *CcISA3*) in leaves of the *C. arabica* F1 hybrid GPFA124 compared to those of the inbred Caturra line. In the same work, upregulated expression of chloroplast genes in the *C. arabica* GPFA124 was also reported (see Sect. 7).

7 Expression of Chloroplast Genes

The chloroplast genome of *C. arabica* consists of 155,189 base pairs encoding 130 genes with 18 intron-containing genes (Samson et al. 2007). In a pioneer work, Dinh et al. (2016) analyzed the effects of drought, cold, or combined drought and heat stresses on intron splicing and expression patterns of 48 chloroplast genes from *C. arabica*. By RT-qPCR, these authors showed that the transcript levels of chloroplast mRNAs were globally decreased in seedlings submitted to drought or cold treatments. For example, expression of *rbcL* (coding the large subunit of Rubisco) and *psaA* and *psaB* (coding photosystem I proteins) was significantly reduced in *C. arabica* under cold stress conditions but not under drought. Regarding intron-containing genes, it was also shown that the splicing efficiencies of *trnG*, *trnK*, and *trnA* genes increased upon drought, combined drought and heat, or cold stress treatments, while these efficiencies decreased for *trnL* under these stresses. On the other hand, the splicing efficiencies of mRNA genes *rps16*, *atpF*, *petB*, and *rpl2* were decreased upon drought but increased upon cold stress treatment.

Overexpression of *CaPsbB* gene (coding the photosystem II CP47 chlorophyll apoproteins) was also reported, either by in silico (Vieira et al. 2006; Mondego et al. 2011; Vinecky et al. 2012) or by in vivo (Mofatto et al. 2016) analyses, in leaves of drought-stressed coffee plants but also in those infected by *H. vastatrix* (Fernandez et al. 2012).

In addition to the circadian genes (see Sect. 6), Toniutti et al. (2019b) also reported increased photosynthetic electron transport efficiency in the *C. arabica* hybrid GPFA124 probably explained by higher expression of chloroplast genes *CaPsbA* and *CaPsbD* (coding the D1 and D2 proteins of PSII, respectively); *CaPetA*, *CaPetD*, and *CaPetB* (coding proteins of the cytB6/f complex); and *CaPsaA*, *CaPsaB*, and *CaPsaJ* (coding proteins of PSI), in this hybrid compared to the *C. arabica* cv. Caturra.

8 Coffee Promoters

The expression studies previously detailed also led to the identification of coffee promoters (De Almeida et al. 2008). For several of them, they were functionally characterized using the *uidA* (coding the *β*-glucuronidase) as the reporter gene by transgenic approaches either in *Nicotiana tabacum* or in *Coffea* sp. The first promoter was cloned from the *CaCSP1* gene of *C. arabica* coding for the 11S seed

storage protein and was shown to function as a bean (endosperm)-specific promoter in transgenic tobacco plants (Marraccini et al. 1999). A similar result was also observed for the shorter and medium promoter fragments of the *CaLTP* gene coding non-specific lipid transfer proteins (Cotta et al. 2014). Leaf-specific expression was also reported for *CaRBCS1* and *CcMXMT1* coffee promoters in transgenic tobacco (Marraccini et al. 2003; Satyanarayana et al. 2005). The *SERK1* (somatic embryogenesis receptor-like kinase 1) promoter from *C. canephora* was also shown to drive the *uidA* expression in different embryo structures such as globular, heart, torpedo, and cotyledonal embryos present at 60 days after embryogenic induction (Jiménez-Guillen et al. 2018). Regarding abiotic stress, Brandalise et al. (2009) showed that the promoter of *CaIRL* was induced by wounded leaves of *N. tabacum*. In 2016, Nobres et al. analyzed the promoter function of the *CaHB12* from *C. arabica*, a gene coding member of the homeodomain-leucine zipper I subfamily (HD-Zip) and conferring greater tolerance to drought stress when overexpressed in *Arabidopsis* (Alves-Ferreira et al. 2012). The study of transgenic *A. thaliana* plants bearing *pCaHB12*::*GUS* constructs showed that this promoter was expressed in leaves during drought and in roots after polyethylene glycol or mannitol treatments. On the other hand, the different haplotypes of the *CcDREB1D* promoter from *C. canephora* were shown to be upregulated by different abiotic stresses in the leaves of *C. arabica* (see Sect. 5.1) and *N. tabacum* transgenic plants (Alves et al. 2017, 2018; de Aquino et al. 2018). Regarding biotic stress, Petitot et al. (2013) analyzed the promoter activities of *CaWRKY1a* (named pW1a) and *CaWRKY1b* (named pW1b) homeologous genes, previously identified to be induced by CLR infestation in the *C. arabica* leaves (see Sects. 2.3, 4.1, and 5.6), in transient assays of *N. benthamiana* leaves, and in stable transgenic plants of *C. arabica*. These authors also showed increased activities of both promoters in leaves of tobacco treated with SA or in those of coffee infected with CLR, as well as increased activities of pW1a upon wounding. The other coffee promoters already described in the literature but without being tested in transgenic plants are cited in Table 6.

9 Coffee Small RNA (sRNA)

Using small (20 ± 26 nt) homologous sequences, small RNAs (sRNA) are known to play important roles by silencing pathways at the transcriptional or translational levels. Plant sRNAs are classified as (1) microRNAs (miRNAs) which are derived from self-complementary hairpin structures and (2) small interfering RNAs (siRNAs) which are derived from double-stranded RNA (dsRNA) or hairpin precursors (Borges and Martienssen 2015). The core mechanism of sRNA production requires the endonuclease activity of DICER-LIKE 1 (DCL1) and ARGONAUTE (AGO) proteins as effectors of silencing, while siRNA biogenesis involves action of RNA-dependent RNA polymerase (RDR), Pol IV, and Pol V. With the release of the *C. canephora* genome (Denoeud et al. 2014), sRNAs were now identified.

Table 6 List of coffee promoters already described in the literature

Gene	Function	Tissue specificity	Validation	References
CaCSP1	11S storage protein	Endosperm	*Nt*	Marraccini et al. (1999)
		Nd	nd	Acuña et al. (1999)
CaRBCS1	Rubisco small subunit	Leaf	*Nt*	Marraccini et al. (2003)
CaSUI1	Translation initiation factor SUI1	Nd	nd	Gaborit et al. (2003)
CcMXMT1	*N*-methyltransferase	Leaf	*Nt*	Satyanarayana et al. (2005)
CcOLE-1	Oleosin	Nd	nd	Simkin et al. (2006)
CcDH2a	Dehydrin	Nd	nd	Hinniger et al. (2006)
CaIRL	Isoflavone reductase-like protein	Leaf (wounding)	*Nt*	Brandalise et al. (2009)
CaWRKY1	Transcription factor	Leaf (wounding, CLR, SA)	*Nb/Ca*	Petitot et al. (2013)
CaLTP	Non-specific lipid transfer proteins	Endosperm	*Nt*	Cotta et al. (2014)
CaHB12	Homeodomain-leucine zipper I subfamily	Leaf, root (drought, PEG, mannitol)	*At*	Nobres et al. (2016)
CcDREB1D	Dehydration-responsive element-binding TF	Leaf	*Ca*	Alves et al. (2017, 2018)
		Leaf (dehydration, HS, cold)	*Nt*	de Aquino et al. (2018)
CcSERK1	Somatic embryogenesis receptor-like kinase 1	SE(DS)	*Cc*	Jiménez-Guillen et al. (2018)

CLR coffee leaf rust, *SE(DS)* somatic embryogenesis (at different stages), *HS* heat shock. The gene names, with their function and tissue-specific expression, are indicated. The transgenic plants used to validate the promoters are also indicated (*At*, *Arabidopsis thaliana*; *Ca*, *Coffea arabica*; *Cc*, *Coffea canephora*; *Nb*, *Nicotiana benthamiana*; *Nt*, *Nicotiana tabacum*). *nd* not determined

One of the first attempts to study coffee miRNAs was performed by Nellikunnumal and Chandrashekar (2012) who identified 18 miRNAs, belonging to 12 families, from *C. canephora* ESTs by computational approaches. By RT-PCR, these authors showed that expression was detected for seven families (viz., mir156, mir169, mir172, mir319, mir393, mir395, and mir396) in *C. canephora* leaves. By the same computational approach, Rebijith et al. (2013), Loss-Morais et al. (2014), and Devi et al. (2016) also identified miRNAs in *C. arabica* and *C. canephora*, showing that the majority of their potential targets corresponded to mRNA coding proteins involved in transcriptional regulation and signal transduction pathways. In another study, Akter et al. (2014) identified a potential miRNA (named mir393) from *C. arabica* ESTs and also showed that this sequence had as potential targets several genes coding transcription factors (e.g., bHLH7 and WRKY TFs) or proteins

involved in auxin signaling pathway and plant defense responses (e.g., auxin signaling F-box 2 and auxin transporter protein 1). Using a specific pipeline to search for miRNA homologs on expressed sequence tag (EST) and genome survey sequence (GSS) coffee databases, Chaves et al. (2015) identified 36 microRNAs and a total of 616 and 362 potential target genes for *C. arabica* and *C. canephora*, respectively. Using a stem-loop RT-PCR assay, these authors also detected a higher amount of miRNAs (miRNAs 171, 172, 390, and 167) in leaves of *C. arabica* than in those of *C. canephora*, suggesting a possible role of sRNA in regulating *C. arabica* transcriptome.

Fernandes-Brum et al. (2017b) identified 11 AGO proteins, nine DCL-like proteins, eight RDR proteins, and 48 other proteins implicated in the sRNA pathways. These authors also identified (1) 235 miRNA precursors producing 317 mature miRNAs belonging to 113 MIR families and (2) 2239 putative *C. canephora* miRNA targets in different pathways. In another study, Bibi et al. (2017) also identified potential miRNAs potentially targeting 150 genes coding transcription factors but also proteins involved in multiple biological and metabolic processes, hypothetical proteins, signal transduction, transporters, growth and development, stress-related processes, structural constituents, and disease-related processes, for example.

In the study analyzing coffee memory to multiple drought exposures, de Freitas Guedes et al. (2018) also reported upregulated expression of mir398 and mir408 by the drought cycles in *C. canephora*. In addition to drought, these genes were also reported to be regulated in other plants by ABA, heat, UV, and also biotic stress events (Zhu et al. 2011; Khraiwesh et al. 2012; Guan et al. 2013). Interestingly, transgenic chickpea plants overexpressing mir408 were shown to be tolerant to several stresses including drought (Hajyzadeh et al. 2015; Ma et al. 2015). In the recent study, dos Santos et al. (2019) analyzed the transcriptome in N-starved roots of *C. arabica* and also identified 86 microRNA families targeting 253 genes. RT-qPCR assays showed that expression profiles of mir169, mir171, mir167, mir393, and mir858 were upregulated in roots after N-starvation, while mircar1 was downregulated after prolonged N-restriction. Altogether, these results highlight the role that might play sRNA in modulating the expression of genes involved in the adaptive responses of coffee plants to environmental factors.

10 Conclusions

Like many other crops, gene identification and characterization are of fundamental biological interest in coffee to understand the transcription networks involved in important agronomic traits and further to identify SNPs that can serve as markers of specific phenotypes to better drive future breeding programs. In that way, the high number of large-scale expression analyses, together with the recent access to long-read sequencing of transcripts (Cheng et al. 2017), to reference transcriptomes (Yuyama et al. 2016; Cheng et al. 2018), and to reference genomes of

C. canephora (Denoeud et al. 2014) and *C. arabica* (de Kochko et al. 2015, 2017; Gaitan et al. 2015; Morgante et al. 2015; Yepes et al. 2016), now opens the way to identify SNPs associated with bean biochemical compound content (Tran et al. 2018) and adaptation to environmental factors (de Aquino et al. 2019) and to initiate marker-assisted selection (Alkimim et al. 2017) and genome-wide association studies (Andrade 2018; Sant'Ana et al. (2018); Carneiro et al. 2019). Together with the help of CRISPR/Cas9 technology (Breitler et al. 2018), it is now possible to greatly shorten the time required to create new coffee varieties with improved agronomic traits under CC.

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