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Closing the Gap in the "ABC" Model in Legumes: A Review

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ABSTRACT

From the ancestral bisexual flower (BC model) with radial symmetry to Fabaceae flower with bilateral symmetry and a keel petal, it is critical to understand ABC model because high seed yield and food safety depend on flower bud development. Thus, we summarize the information of the genetic mechanism that explains the identity of the floral organs for Sophoreae, Phaseoleae, Dalbergieae and Genisteae tribes. Moreover, we examine the role of non-coding RNAs on floral development at Cajaninae subtribe, Dalbergieae and Genisteae tribes.

Key words: ABC model, Fabaceae, Flower development, Legume, Non-coding RNA.

Flowers are reproductive organs organized in whorls, that play an essential role in reproduction and yield (Pawar and Rana 2019; Lyngdoh *et al*. 2018). The genetic study of *Arabidopsis thaliana* and *Antirrhinum majus* mutants led to the proposition of the ABC model of flower development (Alvarez-Buylla *et al*. 2010), which explains the identity of floral whorls being controlled by three classes of genes (A, B and C). Function A only specifies the identity of the sepals; the identity of the petals is controlled by functions A and B; the identity of the stamens is controlled by functions B and C and function C, specifies the identity of the carpels (Soltis *et al*. 2007; Fig 1). Thus, ABC model and its variations apply to a wide range of gymnosperm (Soltis *et al*. 2007) and angiosperm species (Irish, 2017). Amongst them, the Fabaceae comprise an affordable source of protein (Jukanti *et al*. 2017) and minerals for a large proportion of rural populations in the world (Jayalaxmi *et al*. 2016) and under a context of climate change and a need for food security, their contribution is recognized (FAO, 2021). No data have been published on Fabaceae flower evolution but their diversification started approximately 60 million years ago and the most important clades separated some 50 million years ago (Lavin, 2005). The Fabaceae family was reorganized into six subfamilies, comprising c. 19 000 species (LPWG, 2017). Among them, *Medicago truncatula* and *Cicer arietinum* belong to the Trifoleae and Cicereae Tribes, respectively and the ABC model in these species has been studied in detail (Weller and Macknight 2018).

The aim of this review is to scrutinize the current state of knowledge on "ABC" model at Sophoreae, Phaseoleae, Dalbergieae and Genisteae tribes. Moreover, we examine the role of non-coding RNAs on floral development at Cajaninae subtribe, Dalbergieae and Genisteae tribes.

Sophoreae tribe

Sophoreae includes approximately 122 species in 14 genera. It is an early-branched Papilionid, often regarded as "primitive" or "basal", alongside the Swartzieae tribe (Cardoso *et al*. 2013). Within this tribe, the genus *Sophora* comprises approximately 50 species (Song *et al*. 2008). This genus has a variation in the order of development of floral organs, differing from the standard sequential pattern of sepals, petals, stamens and carpels (Tucker 2006). In *Sophora tetraptera* and within the subfamily Papilionoideae, the variations include a precocious carpel initiation, delayed petal development and late development with interrupted floral organ development (Song *et al*. 2008). Also, the developmental order is acropetal among whorls and unidirectional from the abaxial side in the whorls of sepals, petals and stamens (Benlloch *et al*. 2009). This unusual pattern of initiation and development of the floral organs in *S. tetraptera* is interesting because it suggests that the expression of ABC genes varies according to the initiation, differentiation and development of different types of floral organs (Song *et al*. 2008). Indeed, the sequence analysis of the putative floral identity genes of *S. tetraptera* suggests that *StLFY*, *StAP1*, *StPI* and *StAG* are homologues to *LFY/FLO*, *AP1/SQUA*, *PI/GLO* and *AG/PLE* for *Arabidopsis* and *Antirrhinum*, respectively (Chanderbali *et al*. 2010). In addition, Southern blot analyses have revealed that there is a single copy of *StAP1*, *StPI* and *StAG* genes in the *S. tetraptera* genome and two copies of *StLFY* (Song *et al*. 2008).

In *S. tetraptera*, the expression of class A gene *StAP1* is strictly limited to floral primordia during floral development

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and to sepals and petals after floral differentiation (Song *et al.* 2008). Meanwhile, the expression of *StPI*, a class B homolog gene, is limited to the petals and stamens; with the homolog of the class C gene, *StAG*, being expressed in stamens, carpels and seeds (Song *et al*, 2008). These expression patterns are completely consistent with the defined functions of these genes in *Arabidopsis* and *Antirrhinum* (Song *et al.* 2008). Even though the same genes appear to regulate the flowering process in Sophoreae, the sequential pattern of gene expression has been demonstrated to differ from that of *Arabidopsis* and *Antirrhinum* on which the ABC model is based (Song *et al.* 2008).

Song *et al.* (2008) have suggested that the ABC genes could also be required during the later stages of flower

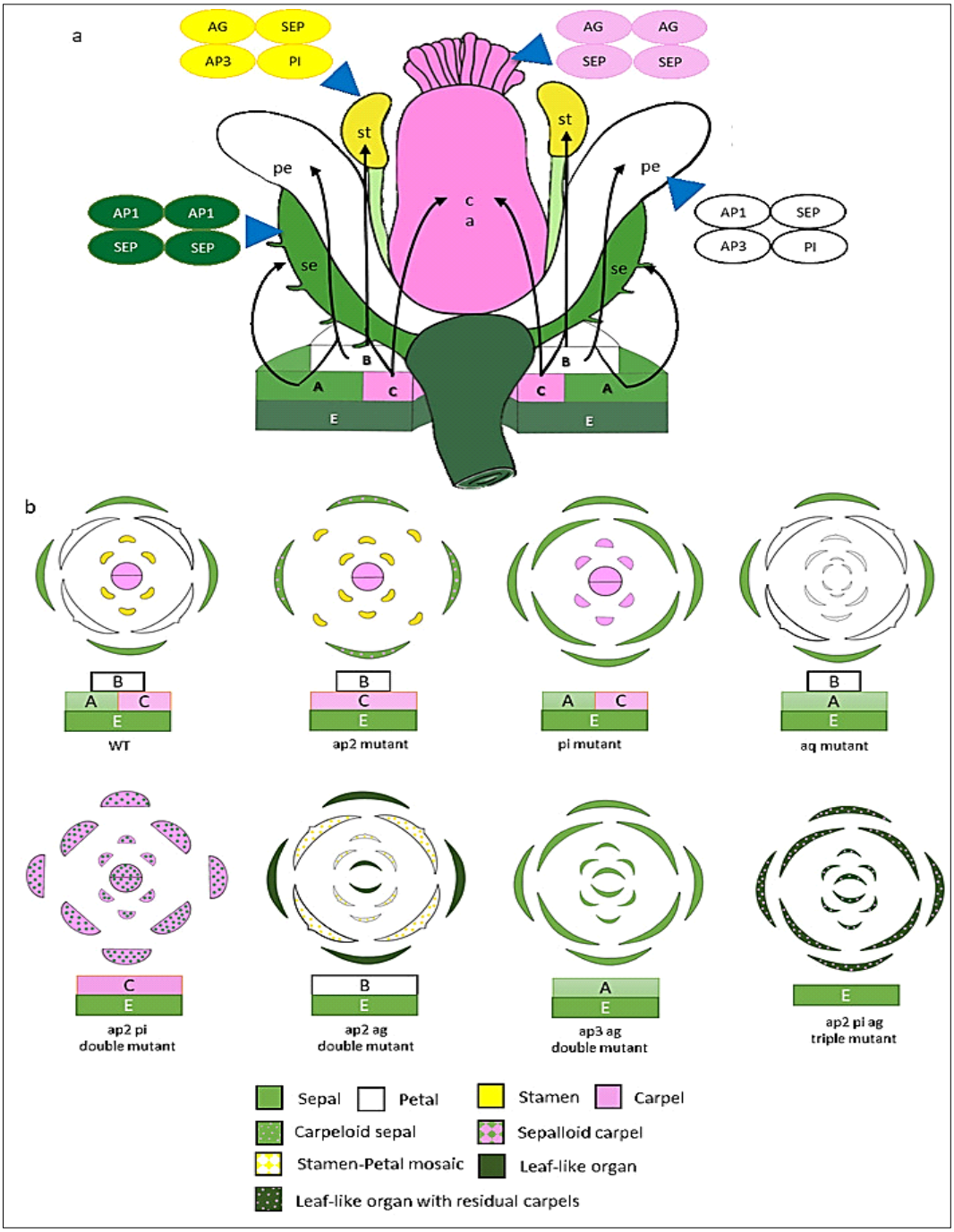

Fig 1: ABC model and floral organ identity in *Arabidopsis thaliana.* a) Class A gen: *APETALLA 1* (*AP1*), *APETALLA 2* (*AP2*); Class B gen: *APETALLA 3* (*AP3*), *PISTILLATA* (*PI*); Class C gene: *AGAMOUS* (*AG*) and Class E gene: *SEPALLATA* (*SEP*). se: sepals; pe: petals; st: stamens; ca: carpels. b) Wild type, single, double and triple mutant flowers are shown, adapted from Alvarez-Buylla *et al.* (2010).

development. This is supported by the findings in *Arabidopsis*, in which *AG* appears to be functionally redundant with SHATTERPROOF (*SHP*) and SEEDSTICK (*STK*) (Song *et al.* 2008). However, it has to be considered that the role of *AG* in the development of Arabidopsis fruit has not yet been fully described. In species such as *Impatiens balsamina*, the homologous gene *IbAG*, is expressed in the floral meristem until the ovule production, not being expressed afterwards (Ordidge *et al.* 2005). Thus, in *S. tetraptera*, in which the floral identity genes: *StAP1*, *StPI* and *StAG* show low initial expression levels that increase only after the onset of differentiation of floral organs, it has been proposed that these genes could work as the main barrier for the differentiation of floral organs (Song *et al.* 2008).

Phaseoleae tribe

Cajaninae subtribe

Pigeonpea [*Cajanus cajan* (L.) Millsp.] belongs to Cajaninae subtribe and it was domesticated in India no earlier than 3,500 years ago (Kassa *et al.* 2012). Moreover, it has many wild relatives such as *C. scarabaeoides*, *C. sericeus*, *C. acutifolius* and *C. albicans* (Khoury *et al.* 2015) (Table 1). Summarizes the 13 homologous genes for the ABC model in *C. cajan*. Related to the ABCDE model proposed by Theißen *et al.* (2016), *STK* has not been identified. On the other hand, Kumar *et al.* (2021) were able to report only one copy of the *FLC* and *SVP* genes, while three paralogs of *SOC1*were found in the *C. cajan* genome. *CcMADS1.5* is one paralog of *SOC1* and it was found to be missing in *C. scarabaeoides*, *C. platycarpus* and *C. cajanifolius*. Finally, Das *et al*. (2020) were able to report long non-coding RNAs (lncRNAs) and miRNAs during the process of flower development in *C. scarabaeoides*.

Glyciniae subtribe

Glycine max and *Glycine soja* belong to the Glyciniae subtribe. In regards to the ABCDE model proposed by Theißen *et al.* (2016), a total of 12 MADS box genes were identified as homologs for *G. max* and *G. soja* (Table 2). As in other species *AP1* is in charge of the development of petals and sepals, while *AP3* and *PI* are involved in that of petals and stamens and Class C AG is involved in the formation of stamens, carpels and ovules. Regarding Class D, *SHP1* and *SHP2* are involved in the development of ovules, While Class E, homologs *SEP1, SEP2, SEP3* and *SEP4* have also been (Vasquez-Regalado, 2021). In addition, *AP2* and some genes of the floral transition process were identified (Table 2). This data is in agreement with the study of Jung *et al.* (2012), who also identified *WUS*, *LFY* and *SPL3* genes. On the other hand, Chi *et al.* (2011) were able to isolate and characterize *GmAP1,* which is specifically expressed in sepals and petals. In addition, Machado *et al.* (2020) identified two genes similar to *AG* and three genes similar to *PI*. According to Chi *et al.* (2017), *GmAGL1* is expressed in carpel and its overexpression causes carpel loss. On the other hand, *GsLFY* showed a high expression in sepals and stamens but having a weak expression in petals and carpels (Guo *et al.* 2017). On the other hand, Huang *et al.* (2009), state that *GmSEP1* is possibly involved in the development of petals. Finally, *GmMADS28*, a class E homolog, can control the number of floral organs and petal identity, producing stamen sterility when it is ectopically expressed (Huang *et al.* 2014). Furthermore, *chicken toes-like leaf and petalody flower* is a novel and critical pleiotropic regulator of leaf and flower development (Zhao *et al.* 2017).

Phaseolinae subtribe

The information on the genetic mechanism that explains the identity of the floral organs is scarce in *Vigna* and *Phaseolus*. However, 13 and 11 homologs were found for classes A, B, C, D and E, respectively (Theiben *et al*. 2016) as is detailed in Table 3. Lin *et al*. (2020) also described *VrSE1* in *V. radiata*, which belongs to class C, modulating cell division in petals and cell expansion in style. On the other hand, integrative genes such as *SOC1* and *FUL* that work as promoters flower transition (Torti and Fornara, 2012). Furthermore, *Squamosa Promoter Binding protien-like 8* and

Table 1: *Cajanus cajan* ABC homologues genes.

Species	Gene name	Identity (%)	Coverage (%)	E-value	Bit-score	NCBI accession
Cajanus	*SEP1*	74.81	99.6	3.00E-125	355	XP-020202290.1
cajan	*SEP2*	74.7	99.6	1.00E-132	374	XP-020202290.1
	SEP3	77.73	99.59	7.00E-131	369	XP-020229786.1
	SEP4	55	99.6	1.00E-91	270	XP-020202290.1
	AG	72.2	95.45	2.00E-125	355	XP-020203368.1
	AP1	71.26	99.58	1.00E-121	345	XP-020229986.1
	AP2	66.04	68.05	1.00E-136	402	XP-020237263.1
	AP3	55.41	99.12	6.00E-92	269	XP-029130909.1
	FUL, AGL8	69.55	98.77	4.00E-116	331	XP-020234496.1
	PI	61.24	99.52	1.00E-86	253	XP-020220122.1
	SHP1, AGL1	63.74	99.58	1.00E-116	334	XP-020234730.1
	SHP2, AGL5	72.57	95	3.00E-119	339	XP-020234730.1
	SOC1, AGL20	70.7	99.53	7.00E-96	278	XP-029128017.1

Blast parameters: E-value=1xE^{-50}, identity > 50% and coverage > 50% (Vasquez-Regalado, 2021).

SPL9 are able to modulate the expression of *SEP3* and *MADS 32* (Gou *et al*. 2019).

Dalbergieae tribe

Dalbergieae is regarded as basal Papilionoideae subfamily of Fabaceae. Flower development in this taxon shows a deviation from that of other Papilionoideae. Organ inception is principally acropetal, with a precocious carpel inception. The whorls develop in different manners, with a helicoidal initiation in *Dalbergia brasiliensis* sepals and a lateral stamen development in *Pterocarpus rotundifolius*. These patterns appear at initiation and late stage in ontogenesis, rather than at mid-stage, which is opposed to the unidirectional order usually seen in Papilionoideae (Klitgaard, 1999). These variations seem to be controlled at a genetic level by genes of the ABC model. Indeed, the genetic studies in *Arachis hypogaea* have focused on the regulation of pod formation by MADS-box genes (Li *et al.* 2016). Some of these genes have been cloned by Mei *et al.* (2005), who states that they are related to flower morphogenesis in *A. hypogaea*.

Regarding Class A, Alyr *et al.* (2020) have characterized a genomic region involved in pod and seed size reduction, providing insights into the flowering regulation in *A. hypogaea*. They studied *Aradu.DN3DB*, a gene that codes for the transcriptional regulator STERILE APETALA-like (*SAP*), demonstrating that its expression can negatively regulate *AG* expression in the perianth whorls. In *A. thaliana*, *SAP* is required for the maintenance of floral identity acting in a similar manner to *AP1*, with severe aberrations in inflorescences being caused by its loss of function, leading to sterile flowers with small petals (Byzova *et al.* 1999). On the other hand, the expression of *AP2* has been proved to be significantly increased in response to drought (Dang *et al.* 2012). Additionally, the expression profile of *A. hypogaea* studied by Li *et al.* (2016) showed that *SPL* proteins are capable of interacting with different coding genes belonging to the MADS-box family. This gene has also been reported to have floral homeotic A function (Theißen *et al.* 2016).

Recently, Vasquez-Regalado (2021) has performed a study in comparative genomics to find orthologs in the flowering pathway among 13 different species of legumes, where the data for ABC model in *Arachis* is summarized in (Table 4). On the other hand, the AG expression seems to be highly affected by environmental factors. In a study about Ca^{2+} regulation in *A. hypogaea*, the expression of AG related gene called MADS transcription factor family was downregulated in plants grown in free-calcium-sufficient treatment (Yang *et al.* 2017). In *A. hypogaea*, Kumar and Reddy (1997)

Table 2: *Glycine* spp. homologues genes for ABC model.

Species	Gene name	Identity (%)	Coverage (%)	E-value	Bit-score	NCBI accession
Glycine max	*SEP1*	71.38	99.61	1.00E-120	344	XP-003552609.1
	SEP2	72.83	99.6	9.00E-129	364	NP-001238296.2
	SEP3	78.14	99.59	6.00E-131	369	XP-006579433.1
	SEP4	55.73	99.6	2.00E-93	274	XP-006585806.1
	AG	72.2	95.47	8.00E-126	356	XP-006597496.1
	AP1	70.87	99.58	2.00E-120	343	XP-003547792.1
	AP2	64.51	68.89	5.00E-134	395	XP-014631052.1
	AP3	55.41	99.12	6.00E-93	271	XP-014629918.1
	FUL, AGL8	66.4	98.8	5.00E-112	321	XP-014630194.1
	PI	61.24	99.52	3.00E-87	255	NP-001235385.1
	SHP1, AGL1	64.55	95.93	3.00E-111	320	XP-006575666.1
	SHP2, AGL5	70.2	95.98	4.00E-116	332	XP-025985172.1
	SOC1, AGL20	69.81	99.05	2.00E-95	276	XP-006587879.1
Glycine soja	*SEP1*	71.11	99.61	8.00E-119	339	XP-028213065.1
	SEP2	72.83	99.6	9.00E-129	364	XP-028216322.1
	SEP3	78.14	99.59	6.00E-131	369	XP-028232724.1
	SEP4	54.58	99.6	4.00E-90	266	XP-028196021.1
	AG	72.61	95.47	5.00E-127	359	XP-028202774.1
	AP1	70.87	99.58	2.00E-120	343	XP-028206839.1
	AP2	65.78	68.42	7.00E-135	397	XP-028210310.1
	AP3	55.41	99.12	6.00E-93	271	XP-028227507.1
	FUL, AGL8	68.72	98.77	1.00E-116	333	XP-028228976.1
	PI	61.24	99.52	3.00E-87	255	XP-028198374.1
	SHP1, AGL1	63.64	99.59	2.00E-112	323	XP-028245899.1
	SHP2, AGL5	71.73	94.63	4.00E-118	337	XP-028199253.1
	SOC1, AGL20	69.81	99.05	2.00E-95	276	XP-028247912.1

Blast parameters: E-value=1xE^{-50}, identity > 50% and coverage > 50% (Vasquez-Regalado, 2021).

Table 3: *Phaseolus vulgaris* and *Vigna* spp. ABC homologues.

Species	Gene name	Identity (%)	Coverage (%)	E-value	Bit-score	NCBI accession
Phaseolus vulgaris	*SEP1*	74.81	99.6	4.00E-126	358	XP-007151389.1
	SEP2	78.28	99.54	3.00E-121	343	XP-007151388.1
	SEP4	53.41	99.6	4.00E-91	268	XP-007139420.1
	AG	71.37	93.88	2.00E-122	348	XP-007147970.1
	AP1	62.89	99.59	1.00E-106	308	XP-007153481.1
	AP3	52.05	91.88	1.00E-67	207	XP-007157955.1
	FUL, AGL8	69.39	98.79	1.00E-118	338	XP-007138377.1
	PI	60.77	99.52	5.00E-86	252	XP-007161433.1
	SHP1, AGL1	61.15	92.65	7.00E-104	301	XP-007147970.1
	SHP2, AGL5	65.96	92.65	5.00E-103	298	XP-007147970.1
	SOC1, AGL20	64.58	99.31	5.00E-58	178	XP-007155575.1
Vigna angularis	*SEP1*	75.29	99.6	1.00E-126	359	XP-017437560.1
	SEP2	74.02	99.6	5.00E-132	372	XP-017437560.1
	SEP3	77.33	99.59	9.00E-130	366	XP-017441201.1
	SEP4	56.15	99.18	2.00E-89	264	XP-017426583.1
	AG	71.78	95.42	8.00E-122	346	XP-017434003.1
	AP1	65.10	99.59	1.00E-113	325	XP-017426838.1
	AP2	67.69	65.83	8.00E-134	394	XP-017408128.1
	AP3	50.89	94.47	9.00E-69	210	XP-017426472.1
	FUL, AGL8	69.11	99.19	8.00E-119	338	XP-017420721.1
	PI	60.77	99.52	6.00E-86	252	XP-017429903.1
	SHP1, AGL1	62.64	99.59	9.00E-114	327	XP-017436853.1
	SHP2, AGL5	70.71	93.52	8.00E-116	331	XP-017436851.1
	SOC1, AGL20	70.00	94.55	6.00E-93	270	XP-017441729.1
Vigna radiata	*SEP1*	75.29	99.6	1.00E-126	359	XP-014522871.1
	SEP2	74.02	99.6	5.00E-132	372	XP-014522871.1
	SEP3	77.73	99.59	8.00E-131	369	XP-014522692.1
	SEP4	55.13	99.6	3.00E-92	271	XP-014522871.1
	AG	71.78	95.42	8.00E-122	346	XP-022642889.1
	AP1	71.26	99.58	1.00E-121	345	XP-014507468.1
	AP2	67.23	65.58	5.00E-133	392	XP-014510210.1
	AP3	56.03	99.12	3.00E-90	265	XP-014500756.1
	FUL, AGL8	69.39	99.19	7.00E-119	338	XP-014492976.1
	PI	60.77	99.52	6.00E-86	252	XP-014504222.1
	SHP1, AGL1	62.27	97.98	1.00E-113	326	XP-022642936.1
	SHP2, AGL5	70.00	93.55	1.00E-114	328	XP-022642936.1
	SOC1, AGL20	68.06	98.58	3.00E-95	276	XP-014490257.1
Vigna unguiculata	*SEP1*	75.67	99.6	6.00E-128	362	XP-027923541.1
	SEP2	73.62	99.6	4.00E-132	372	XP-027923541.1
	SEP3	78.14	99.59	2.00E-131	370	XP-027917203.1
	SEP4	55.51	99.6	2.00E-93	274	XP-027923541.1
	AG	71.78	95.04	2.00E-123	350	XP-027931268.1
	AP1	70.87	99.58	2.00E-121	345	XP-027920653.1
	AP2	66.49	67.37	6.00E-134	395	XP-027919703.1
	AP3	50.89	94.47	1.00E-68	209	XP-027910413.1
	FUL, AGL8	69.67	98.78	6.00E-119	338	XP-027942348.1
	PI	60.77	99.52	6.00E-86	252	XP-027939831.1
	SHP1, AGL1	62.64	99.59	2.00E-115	330	XP-027931173.1
	SHP2, AGL5	70.59	95.04	3.00E-115	329	XP-027931174.1
	SOC1, AGL20	68.06	98.58	1.00E-95	276	XP-027926066.1

Blast parameters: E-value =1xE^{-50}, identity > 50% and coverage > 50% (Vasquez-Regalado, 2021).

identified a single copy of AG homologous that was tissue specific during flower bud formation. These findings support the hypothesis that the AG locus is related to environmental response. In fact, some of its introns are capable of producing non-coding RNAs that are capable of interacting with different targets at a molecular level (Wu *et al.* 2018).

Genisteae tribe

In a *Lupinus albus* population derived from Kiev Mutant and P27174 is found homologs to class A (*Lup009441*, *Lup020693*), homologs to class C (*AGL8, AGL21, AGL24, AGL38, AGL42, AGL65, AGL80*) and homologs to class D (*SEP2, SEP3, SEP4*); which are related to ABC model (Rychel-Bielska *et al.* 2021). Moreover, genes from the ABC model have also been found in the genome of *L. angustifolius* Tanjil cultivar (Hane *et al.* 2017). With this information, Taylor *et al.* (2019) have studied insertion and deletion mutations in the regulatory regions of the major flowering gene LanFTc1, a homolog of Arabidopsis *FT*. They have further identified transcription factor binding site motifs of *AGL9* and *PI* that are expressed during early vegetative growth in *L. angustifolius* (Taylor *et al.* 2019). Genes of the ABC model have also been related to the vernalization response in *L. angustifolius*, including *SEP3, SEP4* and

Table 4: ABC genes for *Arachis* spp. homologues.

Species	Gene name	Identity (%)	Coverage (%)	E-value	Bit-score	NCBI accession
Arachis	*SEP1*	74.43	99.60	9.00E-125	354	XP-015946308.1
duranensis	*SEP2*	73.12	99.60	2.00E-130	368	XP-015946308.1
	SEP3	75.71	99.59	2.00E-124	353	XP-015958021.1
	SEP4	55.04	98.82	2.00E-89	265	XP-015965819.1
	AG	70.78	90.26	8.00E-119	340	XP-015958103.1
	AP1	74.86	80.18	1.00E-97	284	XP-020988998.1
	AP2	54.6	99.80	4.00E-138	405	XP-015963905.1
	AP3	56.71	99.12	2.00E-91	267	XP-015933798.1
	FUL, AGL8	60.57	99.18	7.00E-98	285	XP-015945915.1
	PI	61.9	99.52	2.00E-87	256	XP-015935244.1
	SHP1, AGL1	60.75	96.95	1.00E-107	313	XP-020982823.1
	SHP2, AGL5	69.71	92.91	7.00E-113	324	XP-015973264.1
	SOC1, AGL20	71.23	99.53	1.00E-97	282	XP-020996506.1
Arachis	*SEP1*					
hypogaea	*SEP2*	73.62	99.60	1.00E-127	361	XP-025650095.1
	SEP3	75.71	99.59	2.00E-124	353	XP-025640165.1
	SEP4	55.04	98.82	2.00E-89	265	XP-025654902.1
	AG	69.17	91.51	3.00E-123	351	XP-025683569.1
	AP1	74.86	72.65	7.00E-97	283	XP-025623911.1
	AP2	62.21	89.95	7.00E-134	390	XP-025627263.1
	AP3	56.71	99.12	2.00E-91	267	XP-025612265.1
	FUL, AGL8	63.95	98.46	4.00E-110	317	XP-025617010.1
	PI	61.9	99.52	2.00E-87	256	XP-025613621.1
	SHP1, AGL1	62.45	96.44	4.00E-110	317	XP-025667576.1
	SHP2, AGL5	68.16	94.86	1.00E-112	323	XP-025667576.1
	SOC1, AGL20	70.75	99.53	3.00E-97	281	XP-025696001.1
Arachis	*SEP1*	51.37	89.33	2.00E-79	243	XP-025640943.1
ipaensis	*SEP2*	70.23	99.60	1.00E-122	349	XP-016194431.1
	SEP3	72.94	99.60	8.00E-128	362	XP-016194431.1
	SEP4	75.3	99.59	5.00E-125	354	XP-016191072.1
	AG	56.2	98.78	2.00E-92	272	XP-016202921.1
	AP1	71.19	90.26	2.00E-119	341	XP-016191305.1
	AP2	68.75	70.22	2.00E-87	259	XP-016193748.1
	AP3	56.71	99.12	3.00E-91	267	XP-016165389.1
	FUL, AGL8	60.74	98.53	6.00E-105	304	XP-016193748.1
	PI	61.43	99.52	3.00E-87	255	XP-016165746.1
	SHP1, AGL1	62.45	96.53	4.00E-110	318	XP-020962677.1
	SHP2, AGL5	68.16	94.86	1.00E-112	323	XP-020962678.1
	SOC1, AGL20	70.75	99.53	4.00E-97	280	XP-020977335.1

Blast parameters: E-value= $1xE^{-50}$, identity > 50% and coverage > 50% (Vasquez-Regalado, 2021).

AGL15 (Nelson *et al.* 2017). In addition, Fig 2 shows *Arabidopsis* homolog genes for class A, B and C. All of these genes, with the exception of *AP2*, are classified as MADS-box type genes (Theißen *et al.* 2016) and possibly encode or interact with transcription factors that contain highly conserved DNA domains in *Lupinus* (Delgado-Benarroch *et al.* 2009). In addition, *L. angustifolius* ABC model (Fig 2) is conceptualized under the floral development mechanism proposed by Bouche *et al.* (2016).

Other genes affecting the flowering process in the genus *Lupinus* have been published. Thus, Rychel-Bielska *et al.* (2021) reported the presence of homologs for *CO*, *FT*, *MFT*, *PIF4*, *SKIP1* and *VIP3* in *L. albus*. The same *FT* gene has a homolog (*FTc1*) responsible for vernalization and it is located at locus *Ku* in *L. luteus* (Lichtin *et al.* 2020). Meanwhile, in *L. angustifolius*, there is evidence of similar roles for the homolog *LanFTc1*, which is associated with vernalization response and flowering time (Taylor *et al.* 2019).

Genisteae non coding RNA controlling floral development

The ABC genes can interact with plant hormones (Chandler, 2011), transcription factors (Krishnamurthy *et al.* 2015) and noncoding RNAs (ncRNAs) such as microRNAs (miRNAs) (Luo *et al.* 2013). These noncoding sequences are capable of regulating processes involved in floral development (Budak *et al.* 2020). The ncRNAs include two major groups: lncRNAs and small RNAs (sRNAs).

The sRNAs include several different types of RNA, including miRNAs and small interference RNA (siRNA). Some miRNA, such as *miR172*, have been shown to repress the expression of genes belonging to class A of the ABC

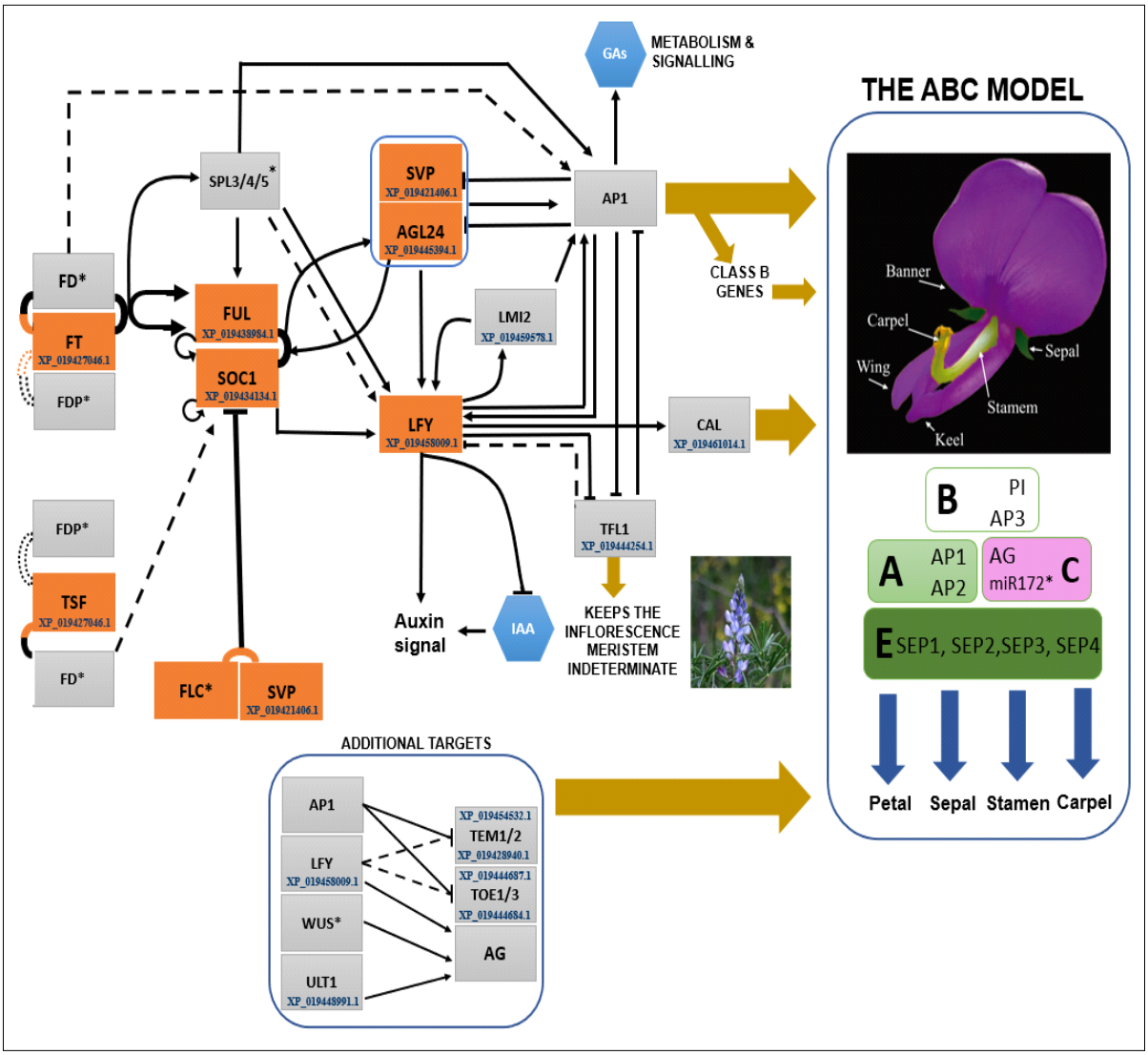

Fig 2: *Lupinus angustifolius* ABC model. Depicted according to Bouche *et al.* (2016) and gene annotation according to Vasquez-Regalado, 2021. (*) genes that do not meet these parameters E-value= $1xE^{-50}$, identity > 50% and coverage > 50%. Eli Livne authorizes the use of *L. angustifolius* inflorescence picture.

a)

Database	Gene	% identity	evalue	bit score	Transcript	Species
Arabidopsis thaliana	EL0144	78.26	5.00E-17	93.5	ma-XR_004214849.1	*Cucumis sativus*
		78.01	4.00E-13	80.5	ma-XR_002273036.1	*Prunus persica*
		76.77	5.00E-12	76.8	LSAT_LNC003922.2	*Lactuca sativa*
		76.77	5.00E-12	76.8	LSAT_LNC003922.1	*Lactuca sativa*
		75.52	4.00E-08	63.9	FTRINITY_DN52533_c1_g7_i1	*Lupinus luteus*

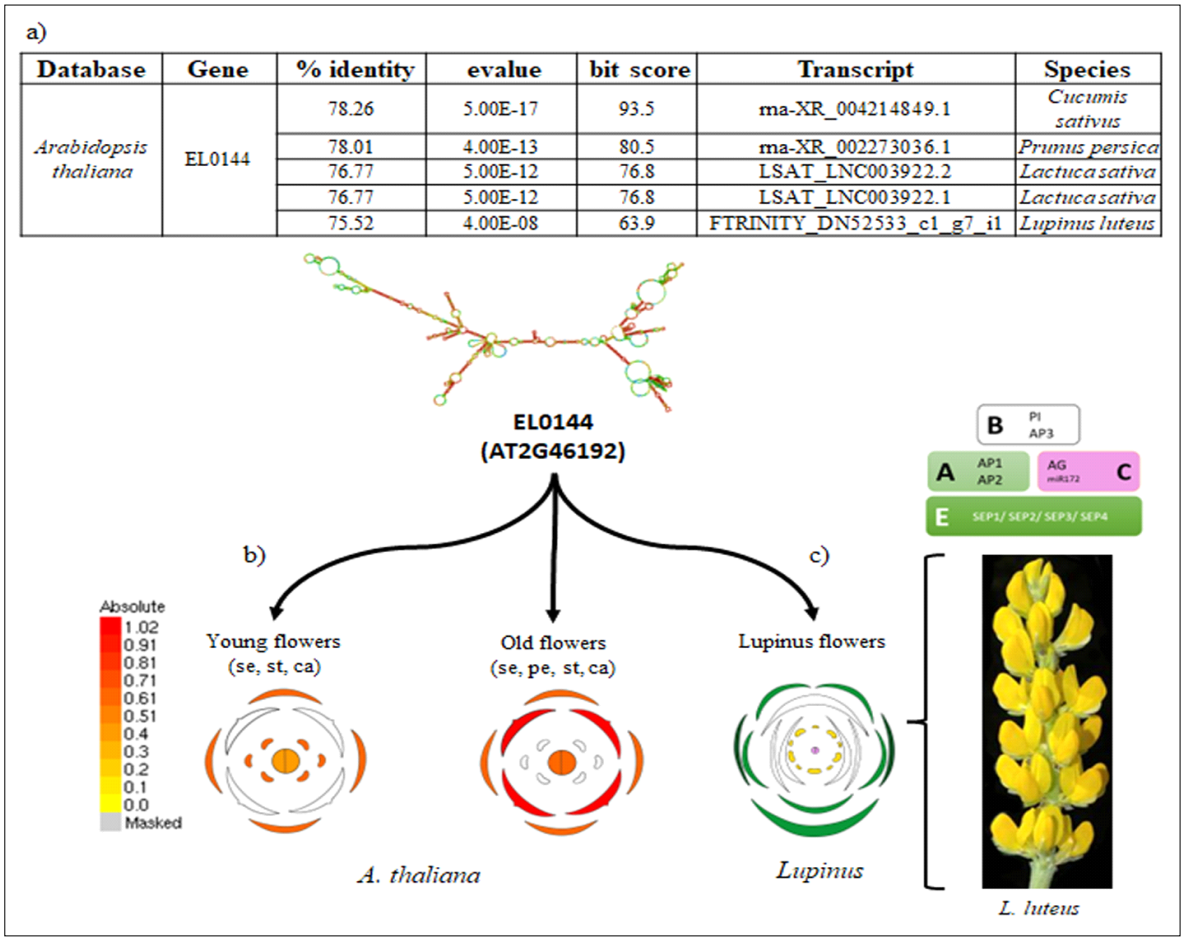

Fig 3: Non-coding RNA in Lupinus floral development. a) EL0144 (AT2G46192) homologue in *L. luteus*. b) EL0144 (AT2G46192) expression patterns in *A. thaliana* flowers, adapted from Sullivan *et al* (2019). c) No validate function of lncRNA EL0144 in *L. luteus* flower (The floral formulas follow the format proposed by Prenner *et al.* 2010).

model of flower development, including *AP2*, in sepals and petals (Chen, 2004). Besides, it has been demonstrated that some miRNAs and siRNAs can interact with auxin response factor (ARF) in *Arabidopsis thaliana* (Marín *et al.* 2010). Glazinska *et al.* (2019) reported miRNA and siRNA that are involved in flower development in *L. luteus*. They also reported 46 differential expressed miRNAs that were found while comparing the upper and lower flowers. Furthermore, two lncRNAs are involved in the regulation of *FLC* (Yamaguchi and Abe 2012).

In *L. angustifolius*, the transcript rna-XR_002106613.1 reported in PLncDB V2.0 (Jingjing *et al.* 2021) is homologous to lncRNA EL0144 (AT2G46192) (Fig 3). According to TAIR (Berardini *et al.* 2015), this transcript is expressed at different levels, in particular sepals, stamens and carpels, which suggests that the expression of this gene could affect functional genes belonging to the ABC model in *Lupinus* (Fig 3). AT2G46192 has been demonstrated to have differential expression in response to several conditions. Mergner *et al.* (2020) have reported that this transcript is upregulated in flower pedicels and flowers and is found in carpels and petals *Arabidopsis*. On the contrary, it is downregulated in *Arabidopsis* under drought, heat and salinity stress (Di *et al.* 2014). In particular, its repression is notable in the pollen of *Arabidopsis* knockout cyclic nucleotide-gated cation channel 16 mutants exposed to heat stress (Rahmati *et al.* 2018). These findings suggest that besides regulating flower development, lncRNA EL0144 could also be involved in abiotic stress responses.

CONCLUSION

Based on the results of this review, key genes for the molecular control of ABC model in Fabaceae are proposed. Moreover, EL0144 (AT2G46192), a non-coding RNA, is involved in the floral development and homologues were found in *L. luteus*, *C. sativus*, *L. sativa* and *P. persica*. Although they need to be validated, the study of non-coding RNA evolution may uncover important regions and highlight the features that drive their functions. After three decades, it is still critical to understand ABC model because high seed yield and food safety depend on flower bud development. However, there is a question that needs to be answered at the genetic level: Are class A genes, a key step in floral evolution that forced the BC model to create new whorls

(sepals and petals) to favor pollination through pollinators and avoid the sexual incompatibility present in several families of angiosperms to consolidate the evolution of mating systems in flowering plants?

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