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Review

Besides and Beyond Flowering: Other roles of *euAP2* genes in plant development

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Abstract: *EuAP2* genes are famous for their role in flower development. A legacy of the founding member of this subfamily of transcription factor, whose mutants lacked petals in *Arabidopsis*. However, studies of other *euAP2* genes in several species have accumulated evidence highlighting the diverse roles of *euAP2* genes in other aspects of plant development. Here, we emphasize other developmental roles of *euAP2* genes in various species and suggest a shift from regarding *euAP2* genes as just flowering genes to consider the global role they may be playing in plant development. We hypothesize that their almost universal expression profile and pleiotropic effects of their mutation suggest their involvement in fundamental plant development processes.

Keywords: EuAP2 genes; Flowering; Plant Development

Introduction

APETALA2 (AP2) genes are named after a series of *Arabidopsis* mutants characterized by homeotic transformations of their sepals to leaves and petals to staminoid petals. Analysis of the *ap2* mutants along with other floral mutants gave birth to the ABC model of flower development where *AP2* is classified as an A-class gene [1,2].

The forerunner AP2 protein was cloned and characterized in *Arabidopsis* [3] . The *Arabidopsis* AP2 protein comprising 432 amino acids (aa) is mainly characterized by the possession of two AP2 domains, each made up of 68-aa that with an 18-aa core conserved section that forms an amphipathic α-helix . The two AP2 domains called AP2-R1 and AP2-R2 (R for Repeat) have 53% amino acid identity and 69% amino acid homology. Their 18-aa core conserved sections show 83% amino acid homology [3]. Sequence analysis of the AP2 gene showed that it has a domain that can activate RNA polymerase II transcriptions factor and another domain that is a putative nuclear localization signal. The presence of these domains served as evidence to suggest that the AP2 protein is a transcription factor [3,4].

Following the cloning and characterization of the *AP2* gene, other genes encoding two AP2 domains were identified in Arabidopsis [5-7]. About the same time, ethylene-responsive element binding proteins (EREBPs) from tobacco were shown to contain a conserved DNA binding domain [8]. Sequence comparison by alignment of EREBPs (aka ethylene responsive factor (ERF)) and AP2 domains revealed they were related [4,5]. This relationship subsequently lead to the classification of genes having AP2/EREBPs domains into one superfamily of transcription factors called Apetala 2/Ethylene Response Factor (AP2/ERF) [9,10]. The AP2/ERF superfamily is divided into four subfamilies based on the number of AP2 domains and sequence similarity (Figure 1).

The AP2/ERF superfamily of transcription factors is one of the largest in most plant species whose genome sequences have been analysed [11]. The superfamily is divided into subfamilies viz; AP2, ERF, RAV and Soloist. Functional analysis of proteins belonging to AP2/ERF superfamily suggests that while genes belonging to AP2 and RAV subfamily are generally involved with developmental processes, ERF subfamily genes have been largely implicated in stress response processes [12-14].

AP2-subfamily is further divided into *euAP2* and *ANTEGUIMENTA (ANT)* lineages (Figure 1.). *EuAP2* lineage genes are distinguished from *ANTEGUIMENTA (ANT)* lineage genes by their possession of miRNA 172 binding sequence towards their C-terminal. They also lack 10 and 1 amino acid insertions found respectively in the first and second AP2 domains of *ANT* lineage genes [13].

The forerunner *Arabidopsis* AP2 protein belong to the euAP2 lineage. Genome-wide analysis shows that the euAP2 lineage is made up of six genes in *Arabidopsis* [13]. These six genes have been actively studied in the context of their role floral ontogeny. The six members of this lineage in *Arabidopsis* have been linked with aspects of flowering such as floral meristem and organ identity, flowering time, [15-17]. For recent update on the ABC floral model see [18,19] and references therein. However, functional characterization in *Arabidopsis* and several other plant species suggest that e*uAP2* genes are involved in other developmental processes besides flower development. Here, we present a summary of their expression profiles in various plant species, and attempt to summarize evidence that underscore the roles of *euAP2* genes in other aspects of plant development. By highlighting other roles of *euAP2* genes in plant developmental processes, we aim to bring attention to their possible involvement in global and fundamental plant developmental process(es).

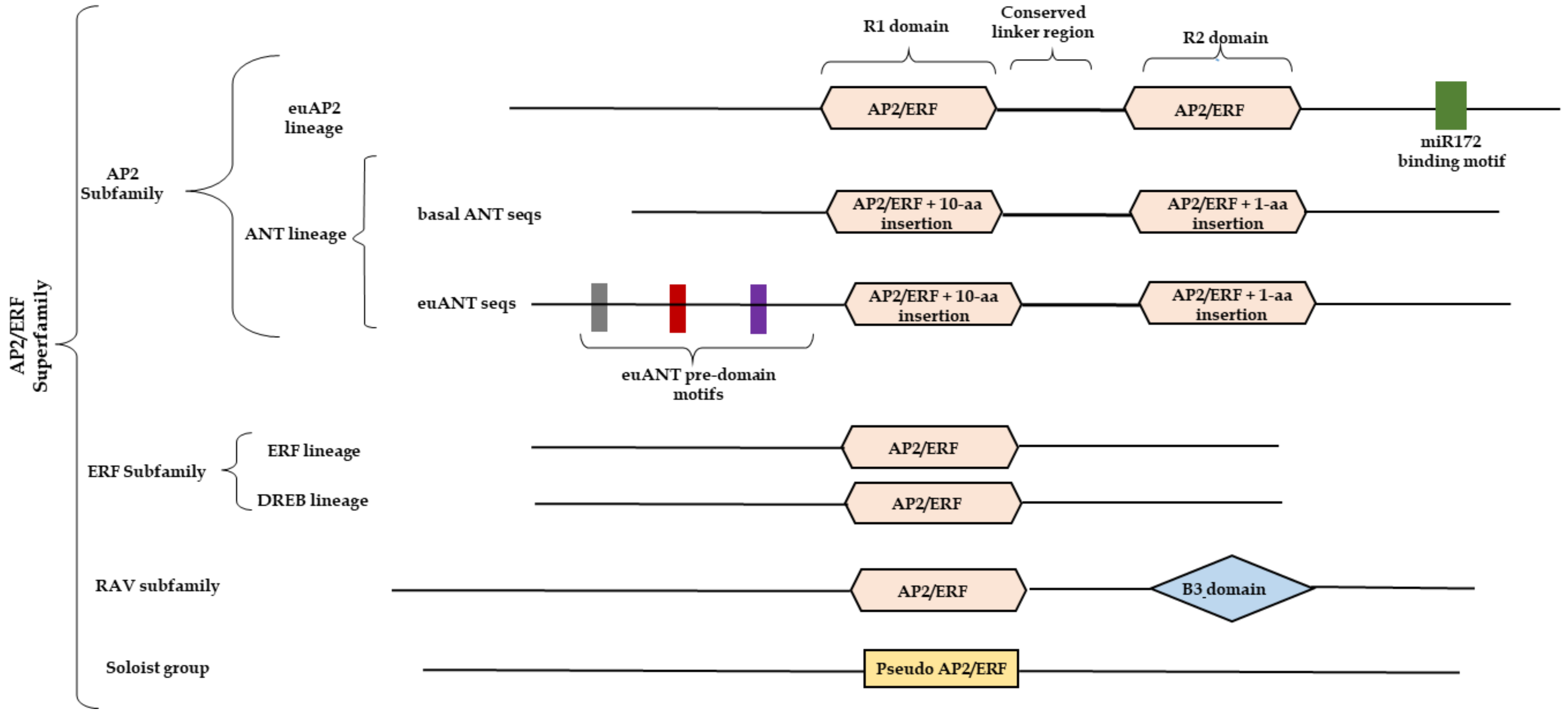

Figure 1. Structure of AP2/ERF Transcription factor superfamily. *EuAP2* genes belong to the AP2 subfamily. They are distinguished from ANT lineage genes by the presence of miR172 binding site. Not to scale. Adapted from Kagaya *et al*, (1999) [52] and Kim *et al* (2005)[13].

Expression of *euAP2* genes

EuAP2 genes are found expressed in almost all plant tissues (Figure 2). However, there are differences between individual genes in their expression profiles within species. Their expression profile suggest a prominent gene that is more highly expressed in all tissues compared to others. This gene is called *AP2* in *Arabidopsis*, *INDETERMINATE SPIKELET* (*IDS)* in maize, *RICE STARCH REGULATOR 1* (*RSR1*) in rice, *Q* in wheat, and *SLAP2a* in tomato. This gene has been functionally characterized in the species listed. From such studies we learn that mutations in this prominent *euAP2* gene leads to pronounced phenotypes [3,20-23].

Mutations in other *euAP2* genes that are expressed quite broadly but less highly than the prominent *euAP2* gene lead to no or less pronounced phenotypes. This has prompted the suggestion that they play redundant roles [17,24]. Interestingly, one or two *euAP2* gene(s) in various species are not universally expressed (Figure 2). They may be found not expressed in one or two organs. A loose consensus is that they are not expressed in mature fruits and seeds.

However, mRNA expression profile of *euAP2* genes should be interpreted carefully because miR172 has been proven to regulate translation of euAP2 mRNA into protein [15-17,25,26].

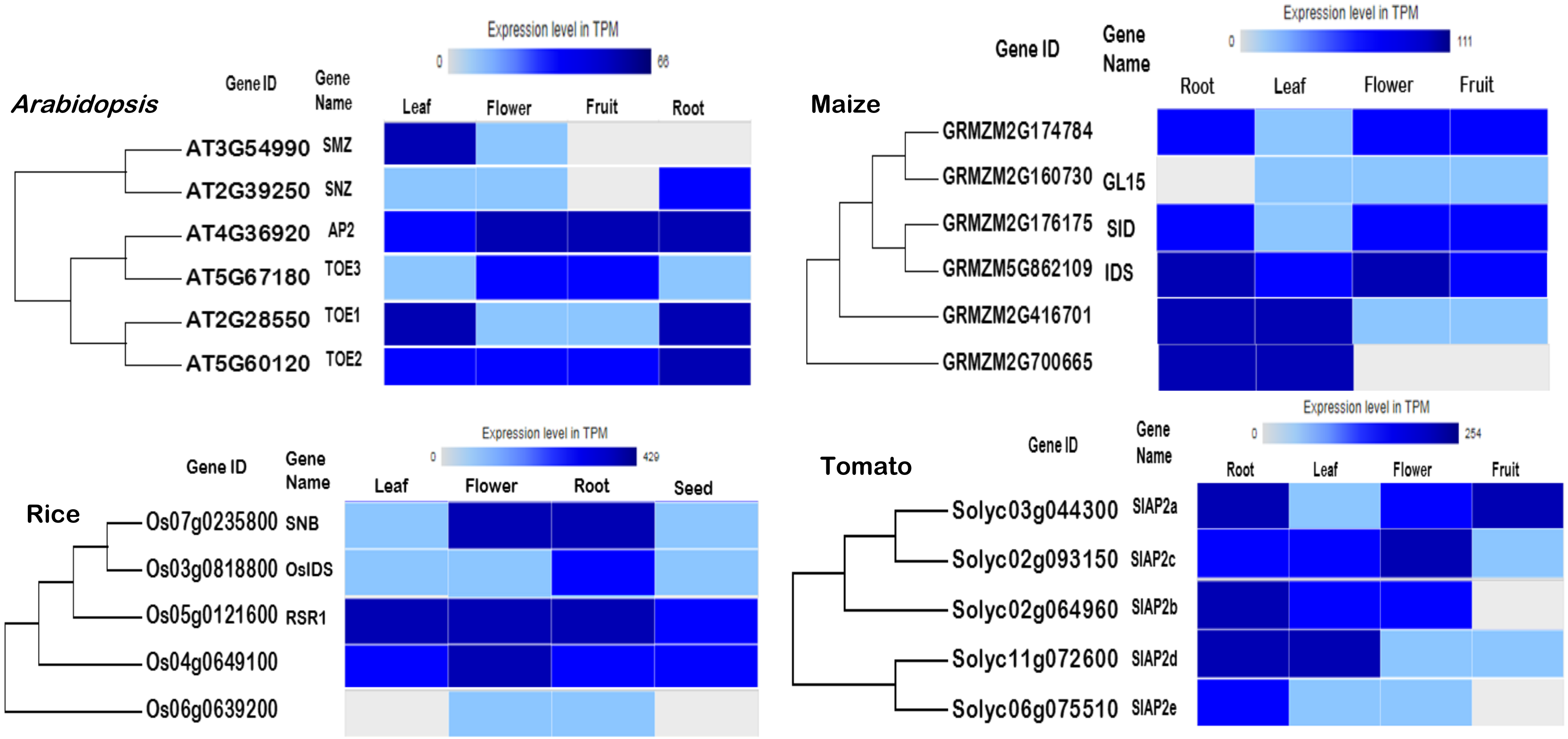

Figure 2. Expression Profile of *euAP2* genes in selected Monocot and dicot species. The expression profile of all the *euAP2* genes in root, leaf, flower and fruit of *Arabidopsis*, maize, rice and tomato. Irrespective of species, some *EuAP2* genes are expressed in all the tissues surveyed, while one or two are not expressed in some tissues. The expression profiles were sourced from Expression Atlas (www.ebi.ac.uk/gxa/home) from the following experiments; *Arabidopsis* (Liu et al. 2012) [27], maize (Stelpflug et al. 2016) [28], rice (Sakai et al. 2011)[29] and tomato (Tomato Genome Consortium).

Briefly on miR172 regulation of *euAP2* genes

A careful study of literatures reporting miR172 regulation of *euAP2* genes suggest a seeming pattern of partial or total tempo/spatial regulation of *euAP2* genes by miR172 at critical steps in the development of reproductive plant tissues. Apparently, *euAP2* genes are freely expressed in various tissues during early vegetative growth stage. However, as the plant approaches reproductive stage, miR172 is recruited to regulate expression of *euAP2* genes in timely and spatially restricted manner leading to the development of normal reproductive tissues [15,16,24-27]. Hence, ectopic autologous and heterologous over-expression of miR172 interrupts the vegetative growth stage activities of *euAP2* genes and leads to precocious transition to reproductive stages in plants [17,28].

MiR172 regulation of *euAP2* genes is very efficient even when *euAP2* genes are over-expressed [16,17]. However, the regulatory ability of mir172 on *euAP2* genes is very sensitive to base mismatches on the complimentary binding sequence on *euAP2* gene mRNA. One base substitution on the mir172 binding site is enough to render an *euAP2* gene resistant to miR172 regulation [26].

It appears that mir172 only regulates *euAP2* genes [17]. This can be exploited in future studies by over-expressing mir172 to study the developmental roles of *euAP2* genes in any plant species.

Roles of *euAP2* Genes in Plant Development

Fruit Development

Functional analyses have shown that AP2-like genes are involved in tomato fruit development in two similar but independent studies [22,29]. In both studies, expression of tomato *AP2* gene; *SlAP2a* was suppressed by RNA inhibition. Tomato *AP2* gene (*SlAP2a*) was shown to affect the colour of ripe fruits. Ripe wild type fruits were totally red in colour while *SIAP2a-RNAi* fruits had uneven orange colour when ripe [22,29]. In these two studies, the investigators showed that the observed differences in the pigmentation of ripe tomato fruits can, in addition to other factors, can be attributed to increased β-carotene to lycopene ratio in *SIAP2a-RNAi* fruits compared to the wild type.

Fruit softening and disintegration was also observed to occur earlier and rapidly in *SIAP2a-RNAi* tomato fruits than in wild type fruits [29].

Mature green tomato fruits of *AP2i-1* lines were shown to have abnormal shape with indentations and uneven surface that splits open when ripe compared to wild type fruits which were round in shape and had smooth surface. [29].

In *Arabidopsis* whose fruit is a silique, null *ap2* mutant fruits were found to possess larger replum compared to wild type. The lignin layer of the valve margin of *ap2* fruits were also found to have more and larger cells compared to wild type [30]. The authors suggested that AP2 negatively regulate replum development thereby preventing its overgrowth. They also reported AP2 to repress valve margin lignification [30].

The *Q* gene in wheat is an *euAP2* gene reported to be a major domestication gene that confers various agronomic traits that gives wheat its prominence among temperate cereals [21,31]. Wheat *Q* gene is known to be associated with grain yield and yield components such as grain shape, grain threshability, thousand grain weight (TGW), glume shape and tenacity, [21,31-33].

The effects of *Q* in wheat processing quality was recently reported by Xu et al. (2018)[34]. They mapped a new allele of *Q* called Q^{c1} from a wheat mutant (*S-Cp1-1*) characterized by dense spike. Their results demonstrated higher significant values in four wheat grain processing parameters in the mutant compared to wild-type. Remarkably, the new allele correlated with about 60 g kg^{-1} increase in grain protein content (GPC) compared to *Q*. When used to make bread, loafs from the *Q* mutant dough were larger compared to wild-type [34].

RICE STARCH REGULATOR 1 (*RSR1*) has been demonstrated to negatively regulate starch synthesis genes in developing endosperm of rice grain [23]. Overexpression of *RSR1* severely downregulate starch synthesis genes leading to abnormal amylopectin structure and increased gelatinization temperature. On the other hand, *rsr1* mutants had larger grain size, increased grain mass and yield [23].

Triticum aestivum RICE STARCH REGULATOR 1 (*TaRSR1*) an orthologue of *RSR1* has also been reported to negatively regulate a group of important starch synthesis related genes during endosperm development in wheat [35]. In another study, Liu et al. (2016) [36], used barley stripe mosaic virus—virus induced gene-silencing (BSMV-VIGS) to silence *TaRSR1*. Their results confirmed that *TaRSR1* negatively regulates critical starch synthesis related genes in wheat endosperm. This manifested in significant increase in grain starch contents, one thousand kernel weights, grain length and width of BSMV-VIGS-TaRSR1-infected wheat plants compared to wild-type.

Seed Development

Arabidopsis AP2 (*AtAP2*) gene is known to play roles in seed coat morphology. [3,37]. The seed epidermal cells of *ap2-6* null mutants are rectangular in shape contrasting hexagonal shaped epidermal cells of wild type seeds. Developmental analysis by Western *et al.*, (2001)[37], revealed that the outer integument development proceeds normally in *ap2-6* seed coats until about 4 days after pollination (DAP). At this point further differentiation is terminated, so that at maturity, epidermal and sub-epidermal cell types and structures such as columella are absent. Consequently, mucilage synthesis, storage and secretion is absent or very limited in the seed coat of *ap2* seeds [3,37,38].

In similar studies, about the same time, two groups reported that *AtAP2* influenced seed shape, size, mass, content and yield in *Arabidopsis* [39,40]. Seeds of *ap2* mutant plants were larger in size and had more weight compared to wild type seeds. Increase in seed weight and size in *ap2* plants were also accompanied by increase in total seed protein and total seed oils content compared to wild type seeds [39].

Ohto *et al.*, (2005) [40], also reported that *ap2* mutant embryos were larger and irregularly shaped compared to wild type embryos. They concluded that *AP2* affects embryo cell number and size.

Heteroblasty

Heteroblasty can be defined as the occurrence of plant organs that bear anatomical, physiological and morphological differences compared to identical organs earlier formed on same plant [41,42]. Following germination, an *Arabidopsis* plant usually produces rosette leaves separated by short internodes. Then the internode elongates and producing cauline leaves along the way before terminating in inflorescence [43]. The differences between *Arabidopsis* rosette and cauline leaves demonstrates heteroblasty.

EuAP2 genes have been associated with leaf heteroblasty in *Arabidopsis* and maize [16,17,41,44]. *Arabidopsis* null mutants for *euAP2* genes produce lesser number of rosette leaves compared to wild-type plants. This was observed in single and multiple null *ap2* mutants. However, the number of cauline leaves produced were identical between multiple null *ap2* mutants and wild-type plants. In addition, hexuple null *ap2* mutant plants showed early formation of trichomes on their lower leaf surface signifying precocious transition from vegetative to reproductive phase [17].

Heteroblastic effects of Glossy15 (*GL15*), an *euAP* gene, on maize leaves is well documented [41,44]. Post-germination, a maize plant will first produce 5-6 juvenile leaves. Subsequent leaves are called adult leaves. Maize juvenile and adult leaves are distinct in some features such as cell wall characteristics, epidermal cell morphology, fine structure and histo-chemistry of epicuticular waxes. Over-expression of *gl15* leads to increase in the number of juvenile leaves consequently delaying transition from vegetative to reproductive phase [41].

Inflorescence Architecture and Meristem determinacy

The activities of *euAP2* genes in determining inflorescence architecture in grass species have been reported in maize, rice, wheat and barley [20,24-27]. See Bommert and Whipple (2017) [45], for a discussion of the role of *euAP2* genes in grass inflorescence architecture and meristem determinacy.

Plant Height

Plant height has been reported to be affected by the *Q* gene in wheat [31]. The *Q* gene gives rise to shorter plants by producing shorter culm lengths [46,47].

Cleistogamy

Flowers that are self-pollinated because they remain closed at maturity are cleistogamous. In cereals like barley, wheat and rice a pair of lodicule lie below the carpel and swell at maturity, forcing the lemma and ovary apart, which results in open (chasmogamous) flowers at maturity. Over-expression of *Cleistogamy 1* (*Cly1*), an *euAP2* gene in barley has been shown to lead to cleistogamy [48,49]. In *Cly1* mutants, the lodicule does not enlarge at maturity but remain small leaving the florets tightly closed.

Pleiotropic effects of *euAP2* genes may be evidence for their role(s) in a fundamental developmental pathway

There is little doubt that *euAP2* genes are pleiotropic, at least some of them are pleiotropic. This is evident from their expression profile and the number of developmental defects that is manifest with their mutation or mis-regulation. We think this may point to their involvement in a fundamental pathway during a plant’s life. A pathway as fundamental as sugar metabolism as reported in *Arabidopsis* [40,50]. A pathway that is universal but employed differently by different plant species. As an example, mutation in petunia and tomato *euAP2* genes did not result in lack of petals (*APETALA*) as in *Arabidopsis*, even though petunia *AP2* (*PhAP2*) was able to restore normal petals in *Arabidopsis ap2* mutants [22,29,51].

Conclusion

EuAP2 genes are almost universally expressed in plants. They are involved in quite a number of developmental processes in plants, suggesting their part in a fundamental developmental pathway. It is possible that many other developmental effects of *euAP2* are not yet reported because of researchers’ focus on specific tissues. We therefore encourage a more holistic approach in characterization of AP2 mutants. Such an approach will facilitate the understanding of their roles in plant development, and exploitation for domestication and biotechnological purposes.

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