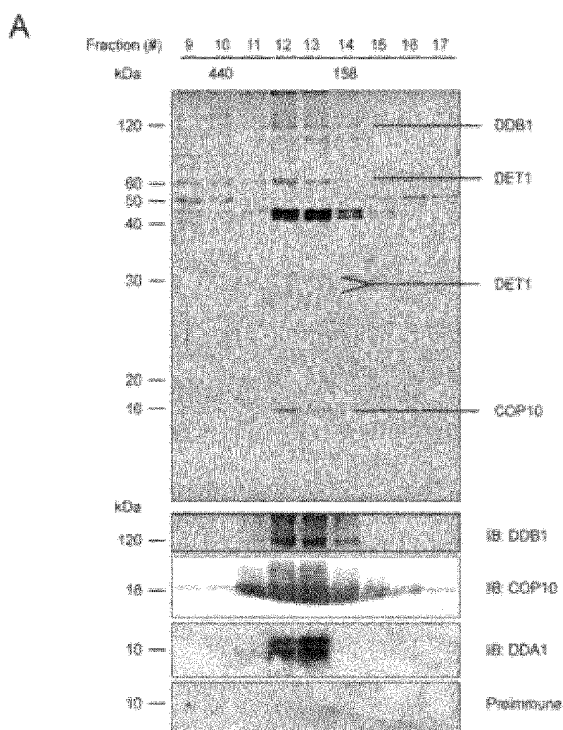




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[Continued on next page]

(54) Title: STRESS TOLERANT PLANTS



(57) **Abstract:** The invention relates to transgenic plants and methods for modulating abscisic acid (ABA) perception and signal transduction in plants. The plants find use in increasing yield in plants, particularly under abiotic stress.

FIGURE 1

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Stress Tolerant Plants

Field of the Invention

5 The invention relates to transgenic plants with improved phenotypic traits, including enhanced growth under stress conditions. The improved traits are conferred by altered ABA receptor signalling. Also within the scope of the invention are related methods, uses, isolated nucleic acids and vector constructs.

Introduction

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The ever-increasing world population and the dwindling supply of arable land available for agriculture fuels research towards increasing the efficiency of agriculture. Conventional means for crop and horticultural improvements utilise selective breeding techniques to identify plants having desirable characteristics. However, such selective breeding techniques have several drawbacks, namely that these techniques are typically labour intensive and result in plants that often contain heterogeneous genetic components that may not always result in the desirable trait being passed on from parent plants. Advances in molecular biology have allowed mankind to modify the germplasm of animals and plants. Genetic engineering of plants entails the isolation and manipulation of genetic material (typically in the form of DNA or RNA) and the subsequent introduction of that genetic material into a plant. Such technology has the capacity to deliver crops or plants having various improved economic, agronomic or horticultural traits. A trait of particular economic interest is growth, in that it is a determinant of eventual crop yield.

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Plants adapt to changing environmental conditions by modifying their growth. Plant growth and development is a complex process involves the integration of many environmental and endogenous signals that, together with the intrinsic genetic program, determine plant form. Factors that are involved in this process include several growth regulators collectively called the plant hormones or phytohormones. This group includes auxin, cytokinin, the gibberellins (GAs), abscisic acid (ABA), ethylene, the brassinosteroids (BRs), and jasmonic acid (JA), each of which acts at low concentrations to regulate many aspects of plant growth and development. Abiotic and biotic stress can negatively impact on plant growth leading to significant losses in agriculture. Even moderate stress can have significant impact on plant growth and thus yield of agriculturally important crop plants. Therefore, finding a way to improve growth, in particular under stress conditions, is of great economic interest.

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ABA has a central role in the control of seed germination and the regulation of responses to abiotic stresses, such as drought, high salinity and low temperatures (Chinnusamy et al., 2008; Hauser et al., 2011; Hirayama and Shinozaki, 2010). Plants respond to ABA in many ways, including closing stomata under drought stress, maintaining seed dormancy and inhibiting vegetative growth. For example, mutants with reduced ABA content or displaying insensitivity to ABA are more tolerant to salt stress during germination. ABA inhibits vegetative growth under stress conditions, in particular under drought conditions, when it accumulates to help plant survival through inhibition of other processes, including, stomata opening and plant growth. Thus, stress tolerance comes at the price of reduced growth and thus reduced yield. This has a particular impact on agriculture in temperate climates where limited water availability rarely causes plant death, but restricts biomass and seed yield. Moderate water stress, that is suboptimal availability of water for growth, can occur during intermittent intervals of days or weeks between irrigation events and may limit leaf growth, light interception, photosynthesis and hence yield potential. Leaf growth inhibition by water stress is particularly undesirable during early establishment.

ABA signaling is mediated by the PYR/PYL/RCAR family of ABA receptors, which allow direct ABA-dependent inhibition of clade A phosphatases type-2C (PP2Cs), for instance ABI1, HAB1, HAB2, PP2CA, which are key negative regulators of the pathway (Rubio et al., 2009; Saez et al., 2006). Inhibition of PP2Cs leads to activation of sucrose non-fermenting 1-related subfamily 2 (SnRK2) kinases, which, in turn, regulate transcriptional response to ABA by phosphorylating specific protein targets, including ABFs/AREBs transcription factors.

The CDD complex is conserved in humans where it has been termed DDD-E2 since it contains, in addition to DDB1 and DET1, a canonical E2 Ub conjugase (highly homologous to UEV COP10) and a small protein with no obvious motifs called DET1-, DDB1- Associated 1 (DDA1; (Pick et al., 2007)). Functional characterization of hDDA1 showed it acts as a positive regulator of multiple CRL4s, although the molecular basis of this activity remains completely unknown (Olma et al., 2009).

There is a need for methods for making plants with increased yield, in particular under moderate stress conditions. In other words, whilst plant research in making stress tolerant plants is often directed at identifying plants that show increased stress tolerance under severe conditions that will lead to death of a wild type plant, these plants do not perform well under moderate stress conditions and often show growth reduction which leads to unnecessary yield loss. The invention is aimed at addressing this need by providing transgenic plants and methods for manipulating stress response based on the findings that DDA1 binds ABA receptor PYL8 *in vivo* and facilitates its

proteasomal degradation when overexpressed in plants, and that overexpression of DDA1 mitigates the detrimental effects of ABA on plant growth and germination.

Summary of the invention

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The invention is directed to methods for modulating plant response to ABA. In certain embodiments, crop yield is maintained by ablating the detrimental effects of ABA on plant and seed development. In particular, the invention comprises compositions and methods for abolishing, disrupting or delaying ABA signaling or function. The compositions and methods are useful for abolishing, disrupting or delaying ABA function or effect in a tissue-preferred and/or developmentally-preferred manner to insulate vegetative and/or reproductive tissue from stress and adverse environmental conditions. This may advantageously alter the developmental time frame of certain tissues so as to minimize effects of abiotic stress. For example, the timing of certain aspects of endosperm development may be altered to avoid negative impacts of abiotic stress.

In a first aspect, the invention relates to a transgenic plant with an altered response to abscisic acid (ABA) wherein said plant expresses a nucleic acid construct comprising a DDA1 nucleic acid, preferably a plant DDA1 nucleic acid. In a second aspect, the invention relates to a product derived from a plant as defined herein. In another aspect, the invention relates to a vector comprising a DDA1 nucleic acid or a nucleic acid construct comprising a DDA1 nucleic acid, preferably a plant DDA1 nucleic acid.

In another aspect, the invention relates to a host cell comprising a vector according to the invention. In another aspect, the invention relates to a method for altering or reducing a plant response to ABA, said method comprising introducing into said plant and expressing a DDA1 nucleic acid or a nucleic acid construct comprising a DDA1 nucleic acid, wherein said DDA1 nucleic acid is preferably a plant DDA1 nucleic acid.

In another aspect, the invention relates to a method for modulating the interaction of a PYL receptor, for example PYL8, with ABA said method comprising introducing into said plant and expressing a DDA1 nucleic acid or a nucleic acid construct comprising a DDA1 nucleic acid, wherein said DDA1 nucleic acid is preferably a plant DDA1 nucleic acid. In another aspect, the invention relates to a method for reducing seed dormancy said method comprising introducing into said plant and expressing in said plant a DDA1 nucleic acid or a nucleic acid construct comprising a DDA1 nucleic acid, wherein said DDA1 nucleic acid is preferably a plant DDA1 nucleic acid.

In another aspect, the invention relates to a method for increasing yield and/or growth of a plant under stress conditions said method comprising introducing into said plant and expressing a DDA1 nucleic acid or a nucleic acid construct comprising a DDA1 nucleic acid, wherein said DDA1 nucleic acid is preferably a plant DDA1 nucleic acid.

5 In another aspect, the invention relates to a method for mitigating the impacts of stress conditions on plant growth and yield said method comprising introducing into said plant and expressing a DDA1 nucleic acid or acid or a nucleic acid construct comprising a DDA1 nucleic acid, wherein said DDA1 nucleic acid is preferably a plant DDA1 nucleic acid.

10 In another aspect, the invention relates to a method for producing a transgenic plant with improved yield/growth under stress conditions said method comprising introducing into said plant and expressing a DDA1 nucleic acid or a nucleic acid construct comprising a DDA1 nucleic acid, wherein said DDA1 nucleic acid is preferably a plant DDA1 nucleic acid. In another aspect, the invention relates to a use of a DDA1 nucleic acid or a nucleic acid construct comprising a DDA1 nucleic acid, preferably a plant DDA1 nucleic acid, in altering or reducing a plant response to ABA, improving yield/growth under stress conditions and altering a plants' stress response.

15 In another aspect, the invention relates to a method for increasing expression of a DDA1 nucleic acid in a plant, preferably a plant DDA1 nucleic acid compared to a control plant.

20 The term DDA1 nucleic acid as used herein designates any DDA1 nucleic acid from any organism. Preferred organisms are plants. According to the various aspects of the invention, the DDA1 nucleic acid may be AtDDA1, a functional variant or a homolog/ortholog thereof or a functional variant of such homolog/ortholog.

25 According to the various aspects of the invention, the stress is preferably water shortage, for example drought conditions, or salinity.

30 In another aspect, the invention relates to a plant with increased expression of an endogenous DDA1 nucleic acid wherein said endogenous DDA1 promoter carries a mutation introduced by mutagenesis or genome editing which results in increased expression of the DDA1 gene. In another aspect, the invention relates to plant with increased stability of the endogenous DDA1 protein wherein said endogenous DDA1 nucleic acid carries a mutation introduced by mutagenesis or genome editing which results in increased a DDA1 protein with increased stability.

35 In another aspect, the invention relates to a method for overexpressing a DDA1 plant nucleic acid, producing plants, a method for mitigating the impacts of stress conditions on plant growth and yield and a method for producing plants with improved yield/growth under stress conditions comprising the steps of mutagenising a plant population,

identifying and selecting a plant with an improved yield/growth under stress conditions and identifying a variant DDA1 promoter or gene sequence. In another aspect, the invention relates to a method for increasing expressing of a DDA1 plant nucleic acid, a method for mitigating the impacts of stress conditions on plant growth and yield and a method for producing a plant with improved yield/growth under stress conditions comprising the steps of altering the DDA1 promoter sequence using genome editing and identifying and selecting plants with an improved yield/growth under stress conditions. In another aspect, the invention relates to a method for increasing stability of a DDA1 plant polypeptide, a method for mitigating the impacts of stress conditions on plant growth and yield and a method for producing a plant with improved yield/growth under stress conditions comprising the steps of altering the endogenous DDA1 nucleic acid sequence using genome editing resulting in a mutant protein with increased stability and identifying and selecting plants with an improved yield/growth under stress conditions.

15

The invention is further described in the following non-limiting figures.

Figures

Figure 1. DDA1 associates with the CDD complex *in planta*.

(A) Gel filtration fractions obtained in the purification of the CDD complex from cauliflower were separated on a 15% SDS-PAGE gel and subjected to silver staining (upper panel) or to immunoblot analysis (4 lower panels). Antibodies used in each case are shown on the right side. The position of specific protein bands was determined according to data reported by Yanagawa et al., 2004.

(B) Isolation of DDA1-associated proteins by Tandem Affinity Purification (TAP) techniques. DDA1-TAP fusion was expressed and purified from transgenic cell cultures. Specific bands obtained were excised, trypsin-digested and analyzed by mass spectrometry.

(C) Proteins identified in (B) are listed. Accession numbers and names of proteins co-purified with DDA1, together with the number of positive identifications in two independent TAP experiments are shown.

(D-E) DDA1 interacts with DDB1 proteins in yeast two hybrid assays. DDA1 interaction with CDD complex components DDB1a and DDB1b (D), and DET1 and COP10 (E) was assessed. Growth of yeast transformed with the indicated constructs on selective plates is shown. Selective media contained different concentrations of 3-amino-1,2,4-triazole (3AT; ranging 0.5-10 mM). Previously reported DET1-DDB1a interaction was used as positive control. Empty vectors were used as negative controls.

(F) DDA1 interacts with the BPA domain in DDB1a. Interaction of DDA1 with a series of DDB1a deletion constructs, containing different domain combinations (represented in left panel), was assessed in yeast two hybrid experiments (right panel). Experimental conditions were as in (D-E).

5 **Figure 2.** DDA1-GFP fusion localizes in nuclei and plastids.

(A) Quantitative RT-PCR analysis of *DDA1-GFP* expression levels in three independent oeDDA1-GFP lines compared to endogenous DDA1 in wild-type plants.

(B) DDA1-GFP associates to FLAG-COP10 *in vivo*. Immunoprecipitation of DDA1-GFP fusions was performed using total protein extracts prepared from 8-d-old oeDDA1-GFP, oeFLAG-COP10 and oeDDA1-GFP/oeFLAG-COP10 seedlings. Total extracts (Input) and immunoprecipitates (IP) were subjected to immunoblot analysis with anti-GFP and anti-FLAG. Panels labeled with an asterisk in (B and C) correspond to non-specific bands used as loading controls.

(C) DDA1-GFP associates to CUL4 *in vivo*. Immunoprecipitation assays were performed as in (B) using protein extracts from 8-d-old wild-type (Col) and oeDDA1-GFP seedlings. Anti-GFP and anti-CUL4 antibodies (Chen et al., 2006) were used to detect DDA1-GFP and CUL4, respectively.

(D-H) Confocal fluorescence images of roots from 5-d-old oeDDA1-GFP seedlings. (E) corresponds to a detail of the picture shown in (D). Nuclei were labeled with 4',6-diamidino-2-phenylindole (DAPI) stain. Merge image (H) shows colocalization of DDA1-GFP fluorescence and DAPI stain.

(I-N) Confocal images of *N. benthamiana* epidermal cells expressing DDA1-GFP and a plastid (I-K) or endoplasmic reticulum (L-N) mCherry fluorescent marker (pt-rk CD3-99 and ER-rk CD3-959, respectively (Nelson et al., 2007)). DDA1-GFP localizes in both in nuclei and plastids in Arabidopsis roots and tobacco leaves. Stromules can be visualized as protuberances in plastids.

Figure 3. DDA1 is essential for female gametophyte development.

(A) A diagram of DDA1 genomic region shows the position of the G to A mutation identified in *dda1-1* plants, which affects the donor splice-site of the second intron and is predicted to impair proper splicing of DDA1 premRNA, yielding a truncated protein.

(B-C) Mature siliques of wild-type and *dda1-1* heterozygous plants (showing ~15% unfertilized ovules). Arrows indicate collapsed ovules. Scale bars represent 1 mm.

(D) Inflorescence images of 4-week-old wild-type and homozygous *dda1-1* plants. *dda1-1* lines show undeveloped siliques that do not set seeds. Scale bars represent 1 mm.

(E) Non-pollinated pistils from wild-type and homozygous *dda1-1* plants are undistinguishable. Scale bars represent 1 mm.

(F) Homozygous *dda1-1* mutants show aberrant ovule development. Nomarski images of cleared ovules from wild-type and homozygous *dda1-1* non-pollinated flowers. Scale bars represent 200 μm .

Figure 4. DDA1 interacts with ABA receptor PYL8.

- 5 (A) Y187 yeast cells transformed with pGBKT7-DDA1 were used to screen a cDNA library prepared from Arabidopsis seedlings in the pGADT7 vector and transformed into AH109 cells. Positive clones included truncated versions of ABA receptors PYL4 and PYL9. Yeast clones were grown in selective media containing different concentrations of 3AT (ranging 0.5 to 5 μM). Empty pGADT7 vector was used as negative control.
- 10 (B-C) DDA1 interaction with full length PYL8 (B), PYL4, PYL5, PYL6 or PYL9 (C) was assessed using yeast two hybrid experiments as in (A). Physical association between PYL8 and other components of the CDD complex (DDB1a, DDB1b, DET1 and COP10) was also tested (B).
- (D-E) Analysis of DDA1 and PYL8 interaction by BiFC. Confocal images of *N. benthamiana* epidermal cells expressing different construct combinations as indicated
- 15 were obtained. Reconstitution of YFP fluorescence indicates that the corresponding DDA1 and PYL8 constructs directly interact. YFP fluorescence, DAPI staining of nuclei, and merged images, including plastid autofluorescence in the far-red channel, are shown. Scale bars represent 10 μm .

20 **Figure 5.** DDA1-GFP over-expression reduces 3HA-PYL8 accumulation in both seedlings and seeds.

- (A) Proteasome inhibitor MG132 stabilizes 3HA-PYL8. 9-d-old oe3HA-PYL8 (T_0) seedlings (T_0) were treated or not during 2 h with 50 μM MG132.
- (B, C) Affinity purification of polyubiquitinated 3HA-PYL8. oe3HA-PYL8 protein extracts
- 25 were incubated with Ub-binding p62 resin or with empty agarose resin (negative control). Anti-Ub was used to detect total ubiquitinated proteins. Anti-HA allowed detection of 3HA-PYL8 and its ubiquitinated forms. Wild-type (Col) protein extracts were used as immunoblot controls. An asterisk indicates the position of a non-specific protein detected by anti-HA.
- (D, E) Time course of relative abundance of 3HA-PYL8 in 8-d-old seedlings treated with 10 μM cycloheximide (CHX) in the presence or absence of 50 μM ABA. Protein level analysis in (E) was carried out using ImageJ software.
- (F) Immunoblots showing increased accumulation of 3HA-PYL8 in the presence of proteasome inhibitor MG132.
- 35 Immunoblots in (A and F) were performed using anti-HA to detect 3HA-PYL8. Panels labeled with an asterisk show Ponceau staining of Rubisco as a loading control.

(G) Immunoblot analysis of 3HA-PYL8 levels in seeds corresponding to *oe3HA-PYL8/oeDDA1-GFP* and control (*oe3HA-PYL8*) plants. Both lines were in the *pyl8-1* background. Prior to protein extraction, imbibed seeds were maintained for 24 h in MS media with or without 3 μ M ABA. Anti-HA and anti-RPT5 antibodies were used to
5 detect 3HA-PYL8 and for loading control purposes, respectively.

(H) Protein level analysis of samples described in (F) was carried out using ImageJ software.

(I) Semiquantitative RT-PCR analysis to assess the expression levels of the *oe3HA-PYL8* and *DDA1-GFP* transgenes in samples described in (G). *ACTIN8 (ACT8)* was
10 used as a housekeeping reference gene.

Figure 6. DDA1 over-expressing plants show reduced sensitivity to ABA.

(A) The percentage of seeds that germinated (radicle emergence) in the presence of 0.5 μ M ABA at 72 h after sowing was compared for wild type (Col), *oeDDA1-GFP* and *oeHAB1* (ABA-insensitive control) lines.

15 (B) Percentage of seeds that germinated and developed green cotyledons and the first pair of true leaves at 5 d. Same genotypes as in A were compared.

(C) Quantification of ABA-mediated root growth inhibition. Same genotypes as in A were compared together with *pyl8-1* mutants.

20 (D, E) ABA-mediated shoot growth inhibition of seedlings that were either germinated on 0.5 μ M ABA or germinated on MS medium and transferred to 10 μ M ABA. Photographs from panel D or E were taken 10 or 20 d after sowing or after transferring seedlings to plates lacking or containing 10 μ M ABA, respectively.

(F) Reduced sensitivity to ABA-mediated inhibition of root growth from *oeDDA1-GFP* plants compared to Col wild type. Bars correspond to 1 cm.

25 (G, H) Percentage of seeds that germinated in the presence of 150 mM NaCl or 400 mM Mannitol at 5 d after sowing. ABA-insensitive *cra1* mutant plants were used as a control.

30 (I) Quantification of ABA-mediated shoot growth inhibition as displayed in (E). ABA-hypersensitive *hab1-1 abi1-2* double mutants were used as a control (Saez et al., 2006).

(J) Percentage of seeds that germinated and developed green cotyledons at 5 d in the presence of 1 μ M ABA and/or 10 μ M β -Estradiol (Estr). Genotypes corresponded to wild type (Col) plants, *cra1* mutants (Fernandez-Arbaizar et al., 2012) and plants expressing *DDA1* under the control of a β -Estradiol inducible promoter (*iDDA1*).

(K) Photographs of plants analyzed in (J) were taken 10 d after sowing. * $p < 0.01$ (Student's t test) with respect to the wild type in the same experimental condition. MS media (MS) was used as a control in all analyses.

Figure 7. Mutants in CDD complex components show enhanced sensitivity to ABA.

- 5 (A) Percentage of seeds that germinated (radicle emergence) in the presence of 0.5 μ M ABA at 4 d after sowing.
- (B) Percentage of seeds that germinated and developed green cotyledons and the first pair of true leaves at 7 d.
- (C) Photographs from representative seedlings taken 10 d after sowing.
- 10 (D) Quantification of ABA-mediated root growth inhibition of (1) Col wild type compared with (2) *hab1-1 abi1-2*, (3) *det1-1*, (4) *cop10-4* and (5) *ddb1a* mutants. Seeds were germinated on MS medium and transferred to 10 μ M ABA for 10 d.
- (E) Photographs of representative seedlings analyzed in D were taken 10 d after transferring seedlings to plates lacking or containing 10 μ M ABA. * $p < 0.01$ (Student's t
- 15 test) with respect to the wild type in the same experimental condition.
- (F) Immunoblot analysis of 3HA-PYL8 levels in seeds corresponding to wild type (*oe3HA-PYL8*) and *cop10-4* (*oe3HA-PYL8/cop10-4*) plants. Both lines were in the *pyl8-1* background. Prior to protein extraction, imbibed seeds were maintained for 24 h in MS media with or without 3 μ M ABA. Anti-HA and anti-RPT5 antibodies were used to
- 20 detect 3HA-PYL8 and for loading control purposes, respectively. Lower panels correspond to semiquantitative RT-PCR analyses to assess the expression levels of the *oe3HA-PYL8* transgene. *ACTIN8* (*ACT8*) was used as a housekeeping reference gene.
- (G) Protein level analysis of samples described in (F) was carried out using ImageJ
- 25 software.

Figure 8: Alignment of AtDDA1 and orthologs in other plants. The average sequence identity is 66%.

Figure 9: Phylogenetic tree.

30 Detailed description

The present invention will now be further described. In the following passages, different aspects of the invention are defined in more detail. Each aspect so defined may be combined with any other aspect or aspects unless clearly indicated to the contrary. In

35 particular, any feature indicated as being preferred or advantageous may be combined with any other feature or features indicated as being preferred or advantageous. The

practice of the present invention will employ, unless otherwise indicated, conventional techniques of botany, microbiology, tissue culture, molecular biology, chemistry, biochemistry and recombinant DNA technology, bioinformatics which are within the skill of the art. Such techniques are explained fully in the literature.

5

As used herein, the words "nucleic acid", "nucleic acid sequence", "nucleotide", "nucleic acid molecule" or "polynucleotide" are intended to include DNA molecules (e.g., cDNA or genomic DNA), RNA molecules (e.g., mRNA), natural occurring, mutated, synthetic DNA or RNA molecules, and analogs of the DNA or RNA generated using nucleotide analogs. It can be single-stranded or double-stranded. Such nucleic acids or polynucleotides include, but are not limited to, coding sequences of structural genes, anti-sense sequences, and non-coding regulatory sequences that do not encode mRNAs or protein products. These terms also encompass a gene. The term "gene" or "gene sequence" is used broadly to refer to a DNA nucleic acid associated with a biological function. Thus, genes may include introns and exons as in the genomic sequence, or may comprise only a coding sequence as in cDNAs, and/or may include cDNAs in combination with regulatory sequences. Thus, according to the various aspects of the invention, genomic DNA, cDNA or coding DNA may be used. In one embodiment, the nucleic acid is cDNA or coding DNA. The terms "peptide", "polypeptide" and "protein" are used interchangeably herein and refer to amino acids in a polymeric form of any length, linked together by peptide bonds.

For the purposes of the invention, "transgenic", "transgene" or "recombinant" means with regard to, for example, a nucleic acid sequence, an expression cassette, gene construct or a vector comprising the nucleic acid sequence or an organism transformed with the nucleic acid sequences, expression cassettes or vectors according to the invention, all those constructions brought about by recombinant methods in which either

(a) the nucleic acid sequences encoding proteins useful in the methods of the invention, or

(b) genetic control sequence(s) which is operably linked with the nucleic acid sequence according to the invention, for example a promoter, or

(c) a) and b)

are not located in their natural genetic environment or have been modified by recombinant methods, it being possible for the modification to take the form of, for example, a substitution, addition, deletion, inversion or insertion of one or more nucleotide residues. The natural genetic environment is understood as meaning the

natural genomic or chromosomal locus in the original plant or the presence in a genomic library. In the case of a genomic library, the natural genetic environment of the nucleic acid sequence is preferably retained, at least in part. The environment flanks the nucleic acid sequence at least on one side and has a sequence length of at least 50 bp, preferably at least 500 bp, especially preferably at least 1000 bp, most preferably at least 5000 bp. A naturally occurring expression cassette – for example the naturally occurring combination of the natural promoter of the nucleic acid sequences with the corresponding nucleic acid sequence encoding a polypeptide useful in the methods of the present invention, as defined above – becomes a transgenic expression cassette when this expression cassette is modified by non-natural, synthetic ("artificial") methods such as, for example, mutagenic treatment. Suitable methods are described, for example, in US 5,565,350 or WO 00/15815 both incorporated by reference.

The methods of the invention involve introducing a polypeptide or polynucleotide into a plant. "Introducing" is intended to mean presenting to the plant the polynucleotide or polypeptide in such a manner that the sequence gains access to the interior of a cell of the plant. The methods of the invention do not depend on a particular method for introducing a sequence into a plant, only that the polynucleotide or polypeptides gains access to the interior of at least one cell of the plant. Methods for introducing polynucleotide or polypeptides into plants are known in the art including, but not limited to, breeding methods, stable transformation methods, transient transformation methods, and virus-mediated methods. Methods are known in the art for the targeted insertion of a polynucleotide at a specific location in the plant genome.

A transgenic plant for the purposes of the invention is thus understood as meaning, as above, that the nucleic acids used in the method of the invention are not at their natural locus in the genome of said plant, it being possible for the nucleic acids to be expressed homologously or heterologously. However, as mentioned, transgenic also means that, while the nucleic acids according to the different embodiments of the invention are at their natural position in the genome of a plant, the sequence has been modified with regard to the natural sequence, and/or that the regulatory sequences of the natural sequences have been modified. Transgenic is preferably understood as meaning the expression of the nucleic acids according to the invention at an unnatural locus in the genome, i.e. homologous or, preferably, heterologous expression of the nucleic acids takes place. According to the invention, the transgene is stably integrated into the plant and the plant is preferably homozygous for the transgene. Thus, any off

spring or harvestable material derived from said plant is also preferably homozygous for the transgene.

5 The aspects of the invention involve recombination DNA technology and in a preferred embodiment exclude embodiments that are solely based on generating plants by traditional breeding methods.

10 The inventors have characterized Arabidopsis DDA1 (AtDDA1) and have demonstrated that overexpression of DDA1 in transgenic plants reduces the detrimental effects associated with ABA induced stress response when a plant is exposed to stress conditions.

15 The inventors have identified the proteins with which DDA1 interacts and demonstrated the function of DDA1 on a molecular level which forms the basis for the phenotype observed in the transgenic plants. The inventors have shown that DDA1 associates with the CDD complex and Cullin 4 Ring Ubiquitin Ligase (CUL4) and is able to interact with specific protein targets. DDA1 was found to physically bind ABA receptor PYL8 *in vivo* and facilitates its proteasomal degradation. In this way, DDA1, together with the other CDD components (CONSTITUTIVE PHOTOMORPHOGENIC10 (COP10) and
20 DEETIOLATED 1 (DET1)), acts as a negative regulator of ABA signaling. ABA treatment attenuates the effect of DDA1 on PYL8 degradation, suggesting that ABA not only activates PYL8 but also prevents its degradation, leading to increased ABA signaling. DDA1 function is also required for proper ovule development, indicating it may recognize additional targets involved in the control of plant reproduction. Thus,
25 DDA1 mediates recognition of specific targets of CUL4 as part of a substrate adaptor module that comprises the CDD complex.

30 Thus, in a first aspect, the invention relates to a transgenic plant with an altered response to ABA wherein said plant expresses a nucleic acid construct comprising a DDA1 nucleic acid sequence or a functional variant thereof. The DDA1 nucleic acid sequence is preferably an isolated plant DDA1 nucleic acid sequence. As explained elsewhere, this can be genomic DNA, cDNA or coding sequence. In another embodiment, the DDA1 nucleic acid sequence is an animal, for example a mammalian, DDA1 nucleic acid sequence.

35 The term "functional variant of a nucleic acid sequence" as used herein, for example with reference to SEQ ID No: 1, 2 or 3 or homologs thereof, refers to a variant gene

sequence or part of the gene sequence which retains the biological function of the full non-variant DDA1 sequence, for example confers increased growth or yield under stress conditions when expressed in a transgenic plant. A functional variant also comprises a variant of the gene of interest encoding a polypeptide which has sequence alterations that do not affect function of the resulting protein, for example in non-conserved residues. Also encompassed is a variant that is substantially identical, i.e. has only some sequence variations, for example in non-conserved residues, to the wild type sequences as shown herein and is biologically active.

Thus, it is understood, as those skilled in the art will appreciate, that the aspects of the invention, including the methods and uses, encompass not only a DDA1, for example a nucleic acid sequence comprising or consisting of SEQ ID NO: 1, 2 or 3 a polypeptide comprising or consisting of SEQ ID NO: 4, or homologs/orthologs thereof, but also functional variants of DDA1, for example of SEQ ID NO: 1, 2, 3 or 4 that do not affect the biological activity and function of the resulting protein. Alterations in a nucleic acid sequence which result in the production of a different amino acid at a given site that do however not affect the functional properties of the encoded polypeptide, are well known in the art. For example, a codon for the amino acid alanine, a hydrophobic amino acid, may be substituted by a codon encoding another less hydrophobic residue, such as glycine, or a more hydrophobic residue, such as valine, leucine, or isoleucine. Similarly, changes which result in substitution of one negatively charged residue for another, such as aspartic acid for glutamic acid, or one positively charged residue for another, such as lysine for arginine, can also be expected to produce a functionally equivalent product. Each of the proposed modifications is well within the routine skill in the art, as is determination of retention of biological activity of the encoded products.

Generally, variants of a particular DDA1 nucleotide sequence of the invention will have at least about 50%-99%, for example 85%, 86%, 87%, 88%, 89%, 90%, 92%, 94%, 95%, 96%, 97%, 98% or 99% or more sequence identity or similarity to that particular non-variant DDA1 nucleotide sequence, for example to SEQ ID NO: 1, 2, 3 or to the protein sequence SEQ ID NO:4 or homologs thereof, as determined by sequence alignment programs described elsewhere herein and known in the art. Methods of alignment of sequences for comparison are well known in the art. Thus, the determination of percent sequence identity between any two sequences can be accomplished using a mathematical algorithm, including but not limited to CLUSTAL, ALIGN program GAP, BESTFIT, BLAST, FASTA, and TFASTA.

A biologically active variant of a reference DDA1 protein may differ from that protein by as few as 1- 15 amino acid residues, as few as 1-10, such as 6-10, as few as 5, as few as 4, 3, 2, or even 1 amino acid residue. In certain embodiments, DDA1 proteins may be altered in various ways including amino acid substitutions, deletions, truncations, and insertions. Methods for such manipulations are generally known in the art. For example, amino acid sequence variants and fragments of the DDA1 protein can be prepared by mutations in the DNA. Methods for mutagenesis and polynucleotide alterations are well known in the art. See, for example, Kunkel (1985) Proc. Natl. Acad. Sci. USA 82:488-492; Kunkel et al. (1987) Methods in Enzymol. 154:367-382; U.S. Patent No. 4,873,192; Walker and Gaastra, eds. (1983) Techniques in Molecular Biology (MacMillan Publishing Company, New York) and the references cited therein. The deletions, insertions, and substitutions of the protein sequences encompassed herein are not expected to produce radical changes in the characteristics of the protein. When it is difficult, however, to predict the exact effect of a substitution, deletion, or insertion in advance of making such modifications, one skilled in the art will appreciate that the effect will be evaluated by routine screening assays.

For example, sequence identity/similarity values provided herein can refer to the value obtained using GAP Version 10 using the following parameters: % identity and % similarity for a nucleotide sequence using GAP Weight of 50 and Length Weight of 3, and the nwsgapdna.cmp scoring matrix; % identity and % similarity for an amino acid sequence using GAP Weight of 8 and Length Weight of 2, and the BLOSUM62 scoring matrix; or any equivalent program thereof.

As used herein, "sequence identity" or "identity" in the context of two polynucleotides or polypeptide sequences makes reference to the residues in the two sequences that are the same when aligned for maximum correspondence over a specified comparison window. When percentage of sequence identity is used in reference to proteins it is recognized that residue positions which are not identical often differ by conservative amino acid substitutions, where amino acid residues are substituted for other amino acid residues with similar chemical properties (e.g., charge or hydrophobicity) and therefore do not change the functional properties of the molecule. When sequences differ in conservative substitutions, the percent sequence identity may be adjusted upwards to correct for the conservative nature of the substitution. Sequences that differ by such conservative substitutions are said to have "sequence similarity" or "similarity".

Also, the various aspects of the invention the aspects of the invention, including the methods and uses, encompass not only a DDA1 nucleic acid, but also a fragment thereof. By "fragment" is intended a portion of the nucleotide sequence or a portion of the amino acid sequence and hence of the protein encoded thereby. Fragments of a nucleotide sequence may encode protein fragments that retain the biological activity of the native protein and hence act to modulate responses to ABA.

In one embodiment, the transgenic plant expresses a nucleic acid comprising, consisting essentially or consisting of AtDDA1 (CDS, cDNA or genomic DNA as defined in SEQ ID NO: 1, 2 or 3) or a functional variant thereof encoding a AtDDA1 polypeptide comprising, consisting essentially or consisting of SEQ ID NO: 4 or a functional variant thereof. However, the invention also extends functional homologs of AtDDA1. A functional homolog of AtDDA1 as shown in SEQ ID NO: 4 is a DDA1 peptide which is biologically active in the same way as SEQ ID NO: 4, in other words, for example it confers increased yield/growth under stress conditions when expressed in a transgenic plant. The term functional homolog includes AtDDA1 orthologs in other organisms, preferably other plant species. In a preferred embodiment of the various aspects of the invention, the invention relates specifically to AtDDA1 or orthologs of AtDDA1 in other plants. AtDDA1 homologs/orthologs include homologs in Arabidopsis. Homologs/orthologs of AtDDA1 are preferably selected from monocot or dicot plants, for example crop plants as further explained herein.

According to the various aspects of the invention, non-limiting preferred embodiments of homologs/orthologs of AtDDA1 as shown in SEQ ID NO: 1, 2, 3 and 4 include those shown in Fig. 8 and corresponding sequences for nucleic acids (CDS, cDNA or genomic DNA) and peptides according to SEQ ID NOs: 5-191 and also include a functional variants of these sequences. This list is non-limiting and other homologous DDA1 sequences of plants that are described herein, for example other DDA1 from preferred plants, such as crop plants, are also within the scope of the invention. DDA1 orthologs from cereals are one preferred embodiment. AtDDA1 orthologs in maize, rice, wheat, oilseed rape, sorghum, soybean, potato, tomato, grape, barley, pea, bean, field bean, lettuce, cotton, sugar cane, sugar beet, canola, broccoli or other vegetable brassicas or poplar are preferred embodiments within the scope of the aspects of the invention.

Thus, in one embodiment, the invention relates to a transgenic plant with an altered response to ABA wherein said plant expresses a nucleic acid construct expressing a peptide comprising, consisting essentially or consisting of a sequence selected from a sequence shown herein, specifically from SEQ ID Nos: 4, 8, 11, 14, 18, 22, 26, 30, 34,
5 38, 42, 45, 49, 52, 56, 60, 64, 68, 71, 75, 79, 83, 87, 90, 94, 98, 102, 106, 109, 112, 115, 119, 123, 126, 130, 133, 136, 139, 143, 147, 151, 155, 159, 163, 166, 169, 173, 177, 181, 184, 187, 191, 192 or a functional variant thereof. As described elsewhere, according to the invention, variants of a particular DDA1 nucleotide sequence of the invention, including of a homologs/orthologs of AtDDA1 as shown in SEQ ID NO: 1, 2,
10 3 and 4 have at least about 50%-99%, for example 85%, 86%, 87%, 88%, 89%, 90%, 92%, 94%, 95%, 96%, 97%, 98% or 99% or more sequence identity or similarity to that particular non-variant DDA1 nucleotide sequence. Corresponding nucleic acid sequences encoding these peptides and which can be used in expression constructs according to the aspects of the invention are shown herein.

15 In one embodiment of the transgenic plants, host cells and vectors of the invention, the homologs from glycine max, rice, sorghum and maize are disclaimed. In one embodiment, the sequences are not one of glycine max, rice, sorghum and maize as shown herein, for example any of SEQ ID Nos: 27-34, 140-147, 152-159 and 170-173.

20 The homolog of a AtDDA1 polypeptide has, in increasing order of preference, at least 25%, 26%, 27%, 28%, 29%, 30%, 31%, 32%, 33%, 34%, 35%, 36%, 37%, 38%, 39%, 40%, 41%, 42%, 43%, 44%, 45%, 46%, 47%, 48%, 49%, 50%, 51%, 52%, 53%, 54%, 55%, 56%, 57%, 58%, 59%, 60%, 61%, 62%, 63%, 64%, 65%, 66%, 67%, 68%, 69%,
25 70%, 71%, 72%, 73%, 74%, 75%, 76%, 77%, 78%, 79%, 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%, 89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99% overall sequence identity to the amino acid represented by SEQ ID NO: 4. In one embodiment, the overall sequence identity is at least 66%. Preferably, overall sequence identity or similarity to AtDDA1 as shown in SEQ ID NO: 1, 2, 3 and 4 is
30 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%, 89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99%, most preferably 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99%. In another embodiment, the homolog of a AtDDA1 nucleic acid sequence has, in increasing order of preference, at least 25%, 26%, 27%, 28%, 29%, 30%, 31%, 32%, 33%, 34%, 35%, 36%, 37%, 38%, 39%, 40%, 41%, 42%, 43%,
35 44%, 45%, 46%, 47%, 48%, 49%, 50%, 51%, 52%, 53%, 54%, 55%, 56%, 57%, 58%, 59%, 60%, 61%, 62%, 63%, 64%, 65%, 66%, 67%, 68%, 69%, 70%, 71%, 72%, 73%, 74%, 75%, 76%, 77%, 78%, 79%, 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%,

89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99% overall sequence identity or similarity to the nucleic acid represented by SEQ ID NO: 1, 2 or 3 or a variant thereof. In one embodiment, overall sequence identity is to the nucleic acid represented by SEQ ID NO: 1. In one embodiment, overall sequence identity is to the nucleic acid represented by SEQ ID NO: 2. In one embodiment, overall sequence identity is to the nucleic acid represented by SEQ ID NO: 3. Preferably, overall sequence identity is 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%, 89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99%, most preferably 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99%. The overall sequence identity is determined using a global alignment algorithm known in the art, such as the Needleman Wunsch algorithm in the program GAP (GCG Wisconsin Package, Accelrys).

In one embodiment, the homolog of a AtDDA1 polypeptide has, in increasing order of preference, at least 60%, 61%, 62%, 63%, 64%, 65%, 66%, 67%, 68%, 69%, 70%, 71%, 72%, 73%, 74%, 75%, 76%, 77%, 78%, 79%, 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%, 89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99%, preferably 85%-99% overall sequence identity to the amino acid represented by SEQ ID NO: 192 (DDA1 polypeptide consensus sequence). In one embodiment, a DDA1 homolog comprises one or more of the following domains: PHNFSQLRPSDPS (SEQ ID NO:193) or a domain with 95%, 96%, 97%, 98%, or 99% to this domain, RTLPPPDQVITTEAK (SEQ ID NO:194) or a domain with 95%, 96%, 97%, 98%, or 99% to this domain, NILLR (SEQ ID NO:195) or a domain with 99% to this domain and/or KLRPKRAA (SEQ ID NO:196) or a domain with 98% or 99% to this domain. In a preferred embodiment, the homolog comprises all of these domains or sequences with homologies to these domains as recited above.

Thus, in one embodiment of the various aspects of the invention, the DDA1 polypeptide comprises an amino acid having at least 50% sequence identity to DDA1 and which comprises an amino acid having at least 95% sequence identity to the amino acid represented by SEQ ID NO: 193, an amino acid having at least 95% sequence identity to the amino acid represented by SEQ ID NO: 194, an amino acid having at least 95% sequence identity to the amino acid represented by SEQ ID NO: 195 and/or an amino acid having at least 99% sequence identity to the amino acid represented by SEQ ID NO: 196. In one embodiment of the various aspects of the invention, the DDA1 polypeptide comprises an amino acid having at least 95% sequence identity to the amino acid represented by SEQ ID NO: 193, an amino acid having at least 95%

sequence identity to the amino acid represented by SEQ ID NO: 194, an amino acid having at least 95% sequence identity to the amino acid represented by SEQ ID NO: 195 and/or an amino acid having at least 99% sequence identity to the amino acid represented by SEQ ID NO: 196.

5

Suitable homologs or orthologs can be identified by sequence comparisons and identifications of conserved domains. The function of the homologue or ortholog can be identified as described herein and a skilled person would thus be able to confirm the function when expressed in a plant.

10

Thus, the nucleotide sequences of the invention and described herein can be used to isolate corresponding sequences from other organisms, particularly other plants, more particularly cereals. In this manner, methods such as PCR, hybridization, and the like can be used to identify such sequences based on their sequence homology to the sequences described herein. Sequences may be isolated based on their sequence identity to the entire sequence or to fragments thereof. In hybridization techniques, all or part of a known nucleotide sequence is used as a probe that selectively hybridizes to other corresponding nucleotide sequences present in a population of cloned genomic DNA fragments or cDNA fragments (i.e., genomic or cDNA libraries) from a chosen plant. The hybridization probes may be genomic DNA fragments, cDNA fragments, RNA fragments, or other oligonucleotides, and may be labeled with a detectable group, or any other detectable marker. Thus, for example, probes for hybridization can be made by labeling synthetic oligonucleotides based on the ABA-associated sequences of the invention. Methods for preparation of probes for hybridization and for construction of cDNA and genomic libraries are generally known in the art and are disclosed in Sambrook, et al., (1989) *Molecular Cloning: A Laboratory Manual* (2d ed., Cold Spring Harbor Laboratory Press, Plainview, New York).

20

25

Hybridization of such sequences may be carried out under stringent conditions. By "stringent conditions" or "stringent hybridization conditions" is intended conditions under which a probe will hybridize to its target sequence to a detectably greater degree than to other sequences (e.g., at least 2-fold over background). Stringent conditions are sequence dependent and will be different in different circumstances. By controlling the stringency of the hybridization and/or washing conditions, target sequences that are 100% complementary to the probe can be identified (homologous probing). Alternatively, stringency conditions can be adjusted to allow some mismatching in sequences so that lower degrees of similarity are detected (heterologous probing).

30

35

Generally, a probe is less than about 1000 nucleotides in length, preferably less than 500 nucleotides in length.

Typically, stringent conditions will be those in which the salt concentration is less than
5 about 1.5 M Na ion, typically about 0.01 to 1.0 M Na ion concentration (or other salts)
at pH 7.0 to 8.3 and the temperature is at least about 30°C for short probes (e.g., 10 to
50 nucleotides) and at least about 60°C for long probes (e.g., greater than 50
nucleotides). Duration of hybridization is generally less than about 24 hours, usually
about 4 to 12. Stringent conditions may also be achieved with the addition of
10 destabilizing agents such as formamide.

Thus, the methods, vector and plants of the invention encompass isolated DDA1
homologs/orthologs that modulate the plant response to ABA and which hybridize
under stringent conditions to the AtDDA1 or AtDDA1 homologs/orthologs described
15 herein, or to fragments thereof.

For example, according to the various aspects of the invention, a nucleic acid construct
comprising a nucleic acid encoding a DDA1 polypeptide may be expressed in said
plant by recombinant methods. In another embodiment, an exogenous DDA1 nucleic
20 acid from a first plant in a plant may be expressed in a second plant of another species
as defined herein by recombinant methods, for example AtDDA1 may be expressed in
a monocot plant, such as wheat. In another embodiment, a nucleic acid construct
comprising an endogenous nucleic acid encoding a DDA1 polypeptide may be
expressed a plant of the same species. For example, AtDD1 is expressed in
25 Arabidopsis, wheat DDA1 is expressed in wheat, maize DDA1 in maize and barley
DDA1 in barley.

In one embodiment according to the various aspects of the invention, the nucleic acid
construct comprises a regulatory sequence or element. According to the various
30 aspects of the invention, the term "regulatory element" is used interchangeably herein
with "control sequence" and "promoter" and all terms are to be taken in a broad context
to refer to regulatory nucleic acid sequences capable of effecting expression of the
sequences to which they are ligated. the term "regulatory element" also includes
terminator sequences which may be included 3' of the DDA1 nucleic acid sequence.
35 The term "promoter" typically refers to a nucleic acid control sequence located
upstream from the transcriptional start of a gene and which is involved in recognising
and binding of RNA polymerase and other proteins, thereby directing transcription of an

operably linked nucleic acid. Encompassed by the aforementioned terms are transcriptional regulatory sequences derived from a classical eukaryotic genomic gene (including the TATA box which is required for accurate transcription initiation, with or without a CCAAT box sequence) and additional regulatory elements (i.e. upstream activating sequences, enhancers and silencers) which alter gene expression in response to developmental and/or external stimuli, or in a tissue-specific manner. Also included within the term is a transcriptional regulatory sequence of a classical prokaryotic gene, in which case it may include a -35 box sequence and/or -10 box transcriptional regulatory sequences.

10

The term "regulatory element" also encompasses a synthetic fusion molecule or derivative that confers, activates or enhances expression of a nucleic acid molecule in a cell, tissue or organ.

15

A "plant promoter" comprises regulatory elements, which mediate the expression of a coding sequence segment in plant cells. Accordingly, a plant promoter need not be of plant origin, but may originate from viruses or micro-organisms, for example from viruses which attack plant cells. The "plant promoter" can also originate from a plant cell, e.g. from the plant which is transformed with the nucleic acid sequence to be expressed in the inventive process and described herein. This also applies to other "plant" regulatory signals, such as "plant" terminators. The promoters upstream of the nucleotide sequences useful in the methods of the present invention can be modified by one or more nucleotide substitution(s), insertion(s) and/or deletion(s) without interfering with the functionality or activity of either the promoters, the open reading frame (ORF) or the 3'-regulatory region such as terminators or other 3' regulatory regions which are located away from the ORF. It is furthermore possible that the activity of the promoters is increased by modification of their sequence, or that they are replaced completely by more active promoters, even promoters from heterologous organisms. For expression in plants, the nucleic acid molecule must, as described above, be linked operably to or comprise a suitable promoter which expresses the gene at the right point in time and with the required spatial expression pattern. For the identification of functionally equivalent promoters, the promoter strength and/or expression pattern of a candidate promoter may be analysed for example by operably linking the promoter to a reporter gene and assaying the expression level and pattern of the reporter gene in various tissues of the plant. Suitable well-known reporter genes are known to the skilled person and include for example beta-glucuronidase or beta-galactosidase.

35

The term "operably linked" as used herein refers to a functional linkage between the promoter sequence and the gene of interest, such that the promoter sequence is able to initiate transcription of the gene of interest.

5

For example, the nucleic acid sequence may be expressed using a promoter that drives overexpression. Overexpression according to the invention means that the transgene is expressed at a level that is higher than expression of endogenous counterparts driven by their endogenous promoters. For example, overexpression may be carried out using a strong promoter, such as a constitutive promoter. A "constitutive promoter" refers to a promoter that is transcriptionally active during most, but not necessarily all, phases of growth and development and under most environmental conditions, in at least one cell, tissue or organ. Examples of constitutive promoters include the cauliflower mosaic virus promoter (CaMV35S or 19S), rice actin promoter, 10 maize ubiquitin promoter, rubisco small subunit, maize or alfalfa H3 histone, OCS, SAD1 or 2, GOS2 or any promoter that gives enhanced expression. Alternatively, enhanced or increased expression can be achieved by using transcription or translation enhancers or activators and may incorporate enhancers into the gene to further increase expression. Furthermore, an inducible expression system may be used, 20 where expression is driven by a promoter induced by environmental stress conditions (for example the pepper pathogen-induced membrane protein gene CaPIMPI or promoters that comprise the dehydration-responsive element (DRE), the promoter of the sunflower HD-Zip protein gene *Hahb4*, which is inducible by water stress, high salt concentrations and ABA or a chemically inducible promoter (such as steroid- or ethanol-inducible promoter system). The promoter may also be tissue-specific. The 25 types of promoters listed above are described in the art. Other suitable promoters and inducible systems are also known to the skilled person.

In another embodiment, a root-specific promoter may be used. This is a promoter that 30 is transcriptionally active predominantly in plant roots, substantially to the exclusion of any other parts of a plant, whilst still allowing for any leaky expression in these other plant parts. Examples of root-specific promoters include promoters of root expressible genes, for example the promoters of the following genes: RCc3, Arabidopsis PHT1, Medicago phosphate transporter, Arabidopsis Pyk10, tobacco auxin-inducible gene, 35 beta-tubulin, LRX1, ALF5, EXP7, LBD16, ARF1, tobacco RD2, SIREO, Pyk10, PsPR10.

In a one embodiment, the promoter is a constitutive or strong promoter. In a preferred embodiment, the regulatory sequence is an inducible promoter, a stress inducible promoter or a tissue specific promoter. The stress inducible promoter is selected from the following non limiting list: the HaHB1 promoter, RD29A (which drives drought inducible expression of DREB1A), the maize rab17 drought-inducible promoter, P5CS1 (which drives drought inducible expression of the proline biosynthetic enzyme P5CS1), ABA- and drought-inducible promoters of Arabidopsis clade A PP2Cs (ABI1, ABI2, HAB1, PP2CA, HAI1, HAI2 and HAI3) or their corresponding crop orthologs.

10 In one embodiment, the promoter is CaMV35S.

Additional nucleic acid sequences which facilitate cloning of the target nucleic acid sequences into an expression vector may also be included in the nucleic acid construct according to the various aspects of the invention. This encompasses the alteration of certain codons to introduce specific restriction sites that facilitate cloning.

In another aspect, the invention relates to a non-transgenic plant with increased expression of DDA1 compared to a wild type plant wherein said endogenous DDA1 promoter nucleic acid or DDA1 nucleic acid carries a mutation introduced by mutagenesis which results in increased expression of the DDA1 gene or increased stability fo the DDA1 protein. The invention also relates to a method for increasing expression of DDA1, producing plants overexpressing DDA1, methods for mitigating the impacts of stress conditions on plant growth and yield and methods for producing plants with plant with improved yield/growth under stress conditions comprising the steps of mutagenising a plant population, identifying and selecting plants with an improved yield/growth under stress conditions and identifying a variant DDA1 promoter or gene sequence. In one embodiment such methods include exposing a plant population to a mutagen.

30 Mutagenesis procedures are well known in the art and include without limitation chemical mutagenesis and irradiation. In one embodiment, said chemical mutagen is selected from ethyl methanesulfonate (EMS), methylmethane sulfonate (MMS), N-ethyl-N-nitrosourea (ENU), triethylmelamine, N-methyl-N-nitrosourea (MNU), procarbazine, chlorambucil, cyclophosphamide, diethyl sulphate (DES), dimethyl sulfate, acrylamide monomer, melphalan, nitrogen mustard, vincristine, dimethylnitosamine, N-methyl-N'-nitro-nitrosoguanidine (MNNG), nitrosoguanidine, 2-aminopurine, 7,12 dimethyl-benz(a)anthracene (DMBA), ethylene oxide,

hexamethylphosphoramide, bisulfan, diepoxyalkanes (diepoxyoctane (DEO), diepoxybutane (BEB), and the like), 2-methoxy-6-chloro-9 [3-(ethyl-2-chloroethyl)aminopropylamino]acridine dihydrochloride (ICR-170) or formaldehyde. In another embodiment, mutagenesis is physical mutagenesis, such as application of
5 ultraviolet radiation, X-rays, gamma rays, fast or thermal neutrons or protons.

Isolated mutants of the wild type DDA1 gene nucleic acid sequence and DDA1 promoter nucleic acid sequence identified in this way are also included within the scope of the invention. Plants obtained by the method above are also included within the
10 scope of the invention.

In a further aspect, the invention relates to a method for producing a mutant plant expressing a DDA1 variant and which is characterised by one of the phenotypes described herein wherein said method uses mutagenesis and Targeting Induced Local
15 Lesions in Genomes (TILLING) to target the gene expressing a DDA1 polypeptide. According to this method, lines that carry a specific mutation are produced that has a known phenotypic effect. For example, mutagenesis is carried out using TILLING where traditional chemical mutagenesis is flowed by high-throughput screening for point mutations. This approach does thus not involve creating transgenic plants. The
20 plants are screened for one of the phenotypes described herein, for example a plant that shows improved yield/growth under stress conditions. A DDA1 locus is then analysed to identify a specific a DDA1 mutation responsible for the phenotype observed. Plants can be bred to obtain stable lines with the desired phenotype and carrying a mutation in a DDA1 locus.

25 Another technique that can be used for targeted DNA editing is Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR) (U.S. Patent No. 8,697,359, Ran et al incorporated by reference). The CRISPR system can be used to introduce specific nucleotide modifications at the target sequence. Originally discovered in bacteria,
30 where several different CRISPR cascades function as innate immune systems and natural defence mechanisms, the engineered CRISPR-Cas9 system can be programmed to target specific stretches of genetic code and to make cuts at precise locations. Over the past few years, those capabilities have been harnessed and used as genome editing tools, enabling researchers to permanently modify genes in
35 mammalian and plant cells.

Thus, the invention relates to a method for generating a DDA1 mutant nucleic acid encoding a mutant DDA1 polypeptide wherein said method comprises modifying a plant endogenous genome using CRISPR. The invention relates to a method for generating a DDA1 promoter mutant nucleic acid wherein said method comprises
5 modifying a plant endogenous genome using CRISPR. The method involves targeting of Cas9 to the specific genomic locus, in this case DDA1, via a 20nt guide sequence of the single-guide RNA. An online CRISPR Design Tool can identify suitable target sites (<http://tools.genome-engineering.org>, Ran et al. Genome engineering using the CRISPR-Cas9 system nature protocols, VOL.8 NO.11, 2281-2308, 2013). Target
10 plants for the mutagenesis/genome editing methods according to the invention are any monocot or dicot plants. Preferred plants are recited elsewhere herein.

Plants obtained through such methods are also within the scope of the invention.

15 In another aspect, the invention relates to a vector comprising a DDA1 nucleic acid sequence or nucleic acid construct comprising a DDA1 nucleic acid sequence. The DDA1 nucleic acid is preferably a plant DDA1 nucleic acid. The DDA1 nucleic acid may comprise SEQ D NO: 1, 2 or 3 a functional variant or homolog of SEQ D NO: 1, 2 or 3. Homologs/orthologs of AtDDA1 are defined elsewhere herein. Preferably, the vector
20 further comprises a regulatory sequence which directs expression of the nucleic acid. Expression vectors are well known in the art.

The invention also relates to an isolated host cell transformed with a nucleic acid or vector as described above. The host cell may be a bacterial cell, such as
25 *Agrobacterium tumefaciens*, or an isolated plant cell. The invention also relates to a culture medium or kit comprising a culture medium and an isolated host cell as described above.

The nucleic acid or vector described above is used to generate transgenic plants using
30 transformation methods known in the art. Thus, according to the various aspects of the invention, a nucleic acid comprising a DDA1 nucleic acid, for example SEQ D No. 1, a functional variant or homolog thereof is introduced into a plant and expressed as a transgene. The nucleic acid sequence is introduced into said plant through a process called transformation. The term "introduction" or "transformation" as referred to herein
35 encompasses the transfer of an exogenous polynucleotide into a host cell, irrespective of the method used for transfer. Plant tissue capable of subsequent clonal propagation, whether by organogenesis or embryogenesis, may be transformed with a genetic

construct of the present invention and a whole plant regenerated there from. The particular tissue chosen will vary depending on the clonal propagation systems available for, and best suited to, the particular species being transformed. Exemplary tissue targets include leaf disks, pollen, embryos, cotyledons, hypocotyls, 5 megagametophytes, callus tissue, existing meristematic tissue (e.g., apical meristem, axillary buds, and root meristems), and induced meristem tissue (e.g., cotyledon meristem and hypocotyl meristem). The polynucleotide may be transiently or stably introduced into a host cell and may be maintained non-integrated, for example, as a plasmid. Alternatively, it may be integrated into the host genome. The resulting 10 transformed plant cell may then be used to regenerate a transformed plant in a manner known to persons skilled in the art.

The transfer of foreign genes into the genome of a plant is called transformation. Transformation of plants is now a routine technique in many species. Advantageously, 15 any of several transformation methods may be used to introduce the gene of interest into a suitable ancestor cell. The methods described for the transformation and regeneration of plants from plant tissues or plant cells may be utilized for transient or for stable transformation. Transformation methods include the use of liposomes, electroporation, chemicals that increase free DNA uptake, injection of the DNA directly 20 into the plant, particle gun bombardment, transformation using viruses or pollen and microprojection. Methods may be selected from the calcium/polyethylene glycol method for protoplasts, electroporation of protoplasts, microinjection into plant material, DNA or RNA-coated particle bombardment, infection with (non-integrative) viruses and the like. Transgenic plants, including transgenic crop plants, are preferably produced 25 via *Agrobacterium tumefaciens* mediated transformation.

To select transformed plants, the plant material obtained in the transformation is, as a rule, subjected to selective conditions so that transformed plants can be distinguished from untransformed plants. For example, the seeds obtained in the above-described 30 manner can be planted and, after an initial growing period, subjected to a suitable selection by spraying. A further possibility is growing the seeds, if appropriate after sterilization, on agar plates using a suitable selection agent so that only the transformed seeds can grow into plants. Alternatively, the transformed plants are screened for the presence of a selectable marker such as the ones described above. 35 Following DNA transfer and regeneration, putatively transformed plants may also be evaluated, for instance using Southern analysis, for the presence of the gene of interest, copy number and/or genomic organisation. Alternatively or additionally,

expression levels of the newly introduced DNA may be monitored using Northern and/or Western analysis, both techniques being well known to persons having ordinary skill in the art.

5 The generated transformed plants may be propagated by a variety of means, such as by clonal propagation or classical breeding techniques. For example, a first generation (or T1) transformed plant may be selfed and homozygous second-generation (or T2) transformants selected, and the T2 plants may then further be propagated through classical breeding techniques. The generated transformed organisms may take a
10 variety of forms. For example, they may be chimeras of transformed cells and non-transformed cells; clonal transformants (e.g., all cells transformed to contain the expression cassette); grafts of transformed and untransformed tissues (e.g., in plants, a transformed rootstock grafted to an untransformed scion).

15 Thus, the invention relates to a method for producing a transgenic plant with improved yield/growth under stress conditions said method comprising

- a) introducing into said plant and expressing a nucleic acid construct comprising a DDA1 nucleic acid sequence, for example a nucleic acid sequence comprising SEQ ID NO: 1, 2, or 3 a functional variant or homolog of SEQ ID NO: 1, 2, or 3
- 20 b) obtaining a progeny plant derived from the plant or plant cell of step a).

The method may comprise the further steps of:

- exposing the plant to stress conditions, such as drought;
- assessing yield/growth;
- selecting a plant or part thereof with increased stress resistance/ improved
25 yield/growth;
- optionally harvesting parts of the plant.

The invention also relates to plants obtained or obtainable with said method.

In another aspect, the invention relates to a method for reducing a plant response to
30 ABA, said method comprising introducing into said plant and expressing a DDA1 nucleic acid or nucleic acid construct comprising a DDA1 nucleic acid, for example a nucleic acid comprising SEQ ID NO: 1, 2 or 3 or a functional variant or homolog of SEQ ID NO: 1, 2, or 3. The DDA1 nucleic acid is preferably a plant DDA1 nucleic acid sequence.

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In another aspect, the invention relates to a method for modulating the interaction of the receptor PYL8 with ABA in a plant or in vitro said method comprising introducing

into said plant or plant cell and expressing a DDA1 nucleic acid, for example a nucleic acid comprising SEQ ID NO: 1, 2, or 3 or a functional variant or homolog of SEQ ID NO: 1, 2, or 3. The DDA1 nucleic acid is preferably a plant DDA1 nucleic acid sequence. The interaction can be modulated by decreasing the presence of PYL8 as it will be degraded by DDA1.

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The method may comprise the further steps of:

- assessing the interaction of the receptor PYL8 with ABA;
- selecting a plant or part thereof with modulated interaction;
- optionally harvesting parts of the plant.

10

In another aspect, the invention relates to a method for increasing yield and/or growth of a plant under stress conditions said method comprising introducing into said plant and expressing a DDA1 nucleic acid, for example a nucleic acid comprising SEQ ID NO: 1, 2 or 3 or a functional variant or homolog of SEQ ID NO: 1, 2, or 3. The DDA1 nucleic acid is preferably a plant DDA1 nucleic acid sequence.

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The method may comprise the further steps of:

- exposing the plant to stress conditions, such as drought;
- assessing yield/growth;
- selecting a plant or part thereof with increased yield/growth;
- optionally harvesting parts of the plant.

20

In another aspect, the invention relates to a method for mitigating the impacts of stress conditions on plant growth, development and/or yield said method comprising introducing into said plant and expressing a DDA1 nucleic acid, for example a nucleic acid comprising SEQ ID NO: 1, 2 or 3 or a functional variant or homolog of SEQ ID NO: 1, 2, or 3. The DDA1 nucleic acid is preferably a plant DDA1 nucleic acid sequence.

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The method may comprise the further steps of:

- exposing the plant to stress conditions, such as drought;
- selecting a plant or part thereof with increased stress resistance;
- optionally harvesting parts of the plant.

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Preferred homologs of SEQ ID NO: 1, 2, or 3 are listed elsewhere, In one embodiment, the homologous nucleic acid encodes a peptide selected from SEQ ID NO: 4, 8, 11, 14, 18, 22, 26, 30, 34, 38, 42, 45, 49, 52, 56, 60, 64, 68, 71, 75, 79, 83, 87, 90, 94, 98, 102, 106, 109, 112, 115, 119, 123, 126, 130, 133, 136, 139, 143, 147, 151, 155, 159, 163, 166, 169, 173, 177, 181, 184, 187 or 191 or a functional variant thereof.

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According to the various aspects of the invention, the stress may be severe or preferably moderate stress. According to the various aspects of the invention, the stress is selected from biotic and abiotic stress. In one embodiment, the stress is drought or water deficiency. In another embodiment, the stress is salinity. In Arabidopsis research, stress is often assessed under severe conditions that are lethal to wild type plants. For example, drought tolerance is assessed predominantly under quite severe conditions in which plant survival is scored after a prolonged period of soil drying. However, in temperate climates, limited water availability rarely causes plant death, but restricts biomass and seed yield. Moderate water stress, that is suboptimal availability of water for growth can occur during intermittent intervals of days or weeks between irrigation events and may limit leaf growth, light interception, photosynthesis and hence yield potential. Leaf growth inhibition by water stress is particularly undesirable during early establishment. There is a need for methods for making plants with increased yield under moderate stress conditions. In other words, whilst plant research in making stress tolerant plants is often directed at identifying plants that show increased stress tolerance under severe conditions that will lead to death of a wild type plant, these plants do not perform well under moderate stress conditions and often show growth reduction which leads to unnecessary yield loss. Thus, in one embodiment of the methods of the invention, yield is improved under moderate stress conditions. The transgenic plants according to the various aspects of the invention show enhanced tolerance to these types of stresses compared to a control plant and are able to mitigate any loss in yield/growth. The tolerance can therefore be measured as an increase in yield as shown in the examples. The terms moderate or mild stress/stress conditions are used interchangeably and refer to non-severe stress. In other words, moderate stress, unlike severe stress, does not lead to plant death. Under moderate, that is non-lethal, stress conditions, wild type plants are able to survive, but show a decrease in growth and seed production and prolonged moderate stress can also result in developmental arrest. The decrease can be at least 5%-50% or more. Tolerance to severe stress is measured as a percentage of survival, whereas moderate stress does not affect survival, but growth rates. The precise conditions that define moderate stress vary from plant to plant and also between climate zones, but ultimately, these moderate conditions do not cause the plant to die. With regard to high salinity for example, most plants can tolerate and survive about 4 to 8 dS/m. Specifically, in rice, soil salinity beyond $E_{Ce} \sim 4$ dS/m is considered moderate salinity while more than 8 dS/m becomes high. Similarly, pH 8.8 - 9.2 is considered as non-stress while 9.3 – 9.7 as moderate stress and equal or greater than 9.8 as higher stress.

The DDA1 polypeptides described herein may be used alone or in combination with additional polypeptides or agents to increase stress tolerance in plants. For example, in the practice of certain embodiments, a plant can be genetically manipulated to produce
5 more than one polypeptide associated with increased stress, for example, drought tolerance.

Drought stress can be measured through leaf water potentials. Generally speaking, moderate drought stress is defined by a water potential of between -1 and -2 Mpa.
10 Moderate temperatures vary from plant to plant and specially between species. Normal temperature growth conditions for Arabidopsis are defined at $22-24^{\circ}\text{C}$. For example, at 28°C , Arabidopsis plants grow and survive, but show severe penalties because of "high" temperature stress associated with prolonged exposure to this temperature. However, the same temperature of 28°C is optimal for sunflower, a species for which
15 22°C or 38°C causes mild, but not lethal stress. In other words, for each species and genotype, an optimal temperature range can be defined as well as a temperature range that induces mild stress or severe stress which leads to lethality. Drought tolerance can be measured using methods known in the art, for example assessing survival of the transgenic plant compared to a control plant, or by determining turgor pressure, rosette
20 radius, water loss in leaves, growth or yield. Regulation of stomatal aperture by ABA is a key adaptive response to cope with drought stress. Thus, drought resistance can also be measured by assessing stomatal conductance (Gst) and transpiration in whole plants under basal conditions.

25 According to the invention, a transgenic plant has enhanced drought tolerance if the survival rates are at least 2, 3, 4, 5, 6, 7, 8, 9 or 10-fold higher than those of the control plant after exposure to drought and/or after exposure to drought and re-watering. Also according to the invention, a transgenic plant has enhanced drought tolerance if the rosette radius is at least 10, 20, 30, 40, 50% larger than that of the control plant after
30 exposure to drought and/or after exposure to drought and re-watering. The plant may be deprived of water for 10-30, for example 20 days and then re-watered. Also according to the invention, a transgenic plant has enhanced drought tolerance if stomatal conductance (Gst) and transpiration are lower than in the control plant, for example at least 10, 20, 30, 40, 50% lower.

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Thus in one embodiment, the methods of the invention relate to increasing resistance to moderate (non-lethal) stress or severe stress. In the former embodiment, transgenic

plants according to the invention show increased resistance to stress and therefore, the plant yield is not or less affected by the stress compared to wild type yields which are reduced upon exposure to stress. In other words, an improve in yield under moderate stress conditions can be observed.

5

The terms "increase", "improve" or "enhance" are interchangeable. Yield for example is increased by at least a 3%, 4%, 5%, 6%, 7%, 8%, 9% or 10%, preferably at least 15% or 20%, more preferably 25%, 30%, 35%, 40% or 50% or more in comparison to a control plant. The term "yield" in general means a measurable produce of economic value, typically related to a specified crop, to an area, and to a period of time. Individual plant parts directly contribute to yield based on their number, size and/or weight, or the actual yield is the yield per square meter for a crop and year, which is determined by dividing total production (includes both harvested and appraised production) by planted square meters. The term "yield" of a plant may relate to vegetative biomass (root and/or shoot biomass), to reproductive organs, and/or to propagules (such as seeds) of that plant. Thus, according to the invention, yield comprises one or more of and can be measured by assessing one or more of: increased seed yield per plant, increased seed filling rate, increased number of filled seeds, increased harvest index, increased number of seed capsules/pods, increased seed size, increased growth or increased branching, for example inflorescences with more branches. Preferably, yield comprises an increased number of seed capsules/pods and/or increased branching. Yield is increased relative to control plants.

In one embodiment, the methods relate to improving drought tolerance of plant vegetative tissue. In one embodiment, the methods relate to improving drought tolerance of plant non- vegetative tissue.

A control plant as used herein is a plant, which has not been modified according to the methods of the invention. Accordingly, the control plant has not been genetically modified to express a nucleic acid as described herein. In one embodiment, the control plant is a wild type plant. In another embodiment, the control plant is a plant that does not carry a transgenic according to the methods described herein, but expresses a different transgene. The control plant is typically of the same plant species, preferably the same ecotype as the plant to be assessed.

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A control plant or plant cell may thus comprise, for example: (a) a wild-type (WT) plant or cell, i.e., of the same genotype as the starting material for the genetic alteration

which resulted in the subject plant or cell; (b) a plant or plant cell of the same genotype as the starting material but which has been transformed with a null construct (i.e., with a construct which has no known effect on the trait of interest, such as a construct comprising a marker gene); (c) a plant or plant cell which is a non-transformed
5 segregant among progeny of a subject plant or plant cell; (d) a plant or plant cell genetically identical to the subject plant or plant cell but which is not exposed to conditions or stimuli that would induce expression of the gene of interest or (e) the subject plant or plant cell itself, under conditions in which the gene of interest is not expressed.

10

During seed development, ABA content increases and regulates many key processes including the imposition and maintenance of dormancy. ABA stimulates dormancy as well as adaptive responses to drought, cold and salt stress. As shown in the examples, DDA1 also controls PYL8 levels in seeds. Overexpressing DDA1-GFP seedlings were
15 less sensitive to NaCl- or mannitol- mediated inhibition of seed germination than the wild type (Fig. 6G-6H), indicating that DDA1 over-expression effect is also evident under stress conditions that increase endogenous ABA levels. Therefore, in another aspect, the invention relates to a method for reducing plant seed dormancy said method comprising introducing into said plant and expressing a DDA1 nucleic acid, for
20 example a nucleic acid comprising SEQ ID No: 1, 2 or 3 or a functional variant or homolog thereof. The DDA1 nucleic acid is preferably a plant DDA1 nucleic acid sequence. In another aspect, the invention relates to a method for modulating germination said method comprising introducing into said plant and expressing a DDA1 nucleic acid, for example a nucleic acid comprising SEQ ID No: 1, 2 or 3 or a functional
25 variant or homolog thereof. Thus, the method can be used to advance or initiate germination. The DDA1 is preferably a plant DDA1 nucleic acid sequence. In one embodiment, seed dormancy is reduced and germination is altered under stress, for example moderate stress conditions.

30 The terms "reduce" or "decrease" used herein are interchangeable. Seed dormancy for example is increased by at least a 3%, 4%, 5%, 6%, 7%, 8%, 9% or 10%, preferably at least 15% or 20%, more preferably 25%, 30%, 35%, 40% or 50%

The methods described above preferably contain the step of obtaining a progeny plant
35 derived from the plant or plant cell. The various methods of the invention may also include the additional step of evaluating growth and yield of the transgenic plant and comparing said phenotype to a control plant.

In another aspect, the invention relates to the use of a DDA1 nucleic acid sequence, for example a plant nucleic acid, for example a nucleic acid comprising or consisting of SEQ ID NO: 1, 2 or a functional variant or homolog, a vector comprising a DDA1 nucleic acid sequence, for example a nucleic acid comprising or consisting of SEQ ID NO: 1, 2 or 3 or a functional variant or homolog in reducing a plant response to ABA and/or increasing yield/growth under stress conditions. The DDA1 nucleic acid is preferably a plant DDA1 nucleic acid sequence.

The transgenic plant according to the various aspects of the invention, including the transgenic plants, methods and uses described herein may be a monocot or a dicot plant. The plant DDA1 nucleic acid according to the various aspects of the invention may be a monocot or a dicot plant DDA1 nucleic acid.

In one embodiment of the various aspects of the invention, the plant is a dicot plant. A dicot plant may be selected from the families including, but not limited to *Asteraceae*, *Brassicaceae* (eg *Brassica napus*), *Chenopodiaceae*, *Cucurbitaceae*, *Leguminosae* (*Caesalpinaceae*, *Aesalpinaceae*, *Mimosaceae*, *Papilionaceae* or *Fabaceae*), *Malvaceae*, *Rosaceae* or *Solanaceae*. For example, the plant may be selected from lettuce, sunflower, *Arabidopsis*, broccoli, spinach, water melon, squash, cabbage, tomato, potato, yam, capsicum, tobacco, cotton, okra, apple, rose, strawberry, alfalfa, bean, soybean, field (fava) bean, pea, lentil, peanut, chickpea, apricots, pears, peach, grape vine or citrus species. In one embodiment, the plant is oilseed rape.

Also included are biofuel and bioenergy crops such as rape/canola, corn, sugar cane, palm trees, jatropha, soybeans, sorghum, sunflowers, cottonseed, *Panicum virgatum* (switchgrass), linseed, wheat, lupin and willow, poplar, poplar hybrids, *Miscanthus* or gymnosperms, such as loblolly pine. Also included are crops for silage (maize), grazing or fodder (grasses, clover, sanfoin, alfalfa), fibres (e.g. cotton, flax), building materials (e.g. pine, oak), pulping (e.g. poplar), feeder stocks for the chemical industry (e.g. high erucic acid oil seed rape, linseed) and for amenity purposes (e.g. turf grasses for golf courses), ornamentals for public and private gardens (e.g. snapdragon, petunia, roses, geranium, *Nicotiana* sp.) and plants and cut flowers for the home (African violets, *Begonias*, chrysanthemums, geraniums, *Coleus* spider plants, *Dracaena*, rubber plant).

In one embodiment of the various aspects of the invention, the plant is a dicot plant. A monocot plant may, for example, be selected from the families *Arecaceae*,

Amaryllidaceae or *Poaceae*. For example, the plant may be a cereal crop, such as wheat, rice, barley, maize, oat, sorghum, rye, millet, buckwheat, turf grass, Italian rye grass, sugarcane or *Festuca* species, or a crop such as onion, leek, yam or banana.

5 In preferred embodiments of the various aspects of the invention the plant is a crop plant. By crop plant is meant any plant which is grown on a commercial scale for human or animal consumption or use.

10 In preferred embodiments of the various aspects of the invention the plant grain plant, an oil-seed plant, and a leguminous plant.

15 Most preferred plants according to the various aspects of the invention are maize, rice, wheat, oilseed rape, sorghum, soybean, potato, tomato, tobacco, grape, barley, pea, bean, field bean, lettuce, cotton, sugar cane, sugar beet, broccoli or other vegetable brassicas or poplar.

20 Polypeptide sequences for a non-limiting list of preferred AtDDA1 orthologs comprise or consist of SEQ ID NOs: 8, 11, 14, 18, 22, 26, 30, 34, 38, 42, 45, 49, 52, 56, 60, 64, 68, 71, 75, 79, 83, 87, 90, 94, 98, 102, 106, 109, 112, 115, 119, 123, 126, 130, 133, 136, 139, 143, 147, 151, 155, 159, 163, 166, 169, 173, 177, 181, 184, 187, 191, 192 or a functional variant thereof. Corresponding nucleic acids are set out herein. Alternatively, the AtDDA1 ortholog is a DDA1 isolated from any of the plants defined herein, preferably any crop plant, for example, but not limited to maize, wheat, oilseed rape, canola, sorghum, soybean, potato, tomato, tobacco, grape, barley, pea, bean, field bean, lettuce, cotton, sugar cane, sugar beet, broccoli or other vegetable brassicas or poplar.

30 In another aspect, the invention relates to a method for increasing expression of a DDA1 nucleic acid in a plant, preferably a plant DDA1 nucleic acid compared to a control plant by incorporating a heterologous nucleic acid which encodes a DDA1-related polypeptide. In one embodiment, expression is increased by a method comprising; crossing a first and a second plant to produce a population of progeny plants; determining the expression of the DDA1-related polypeptide in the progeny plants in the population, and identifying a progeny plant in the population in which expression of the DDA1-related polypeptide is increased relative to controls. In another embodiment, expression is increased by a method comprising; exposing a population of plants to a mutagen, determining the expression of the DDA1-related polypeptide in

one or more plants in said population, and identifying a plant with increased expression of the DDA1--related polypeptide. The methods can comprise sexually or asexually propagating or growing off-spring or descendants of the plant having increased DDA1-related polypeptide expression.

5

The term "plant" as used herein encompasses whole plants, ancestors and progeny of the plants and plant parts, including seeds, fruit, shoots, stems, leaves, roots (including tubers), flowers, and tissues and organs, wherein each of the aforementioned comprise the gene/nucleic acid of interest. The term "plant" also encompasses plant cells, suspension cultures, callus tissue, embryos, meristematic regions, gametophytes, sporophytes, pollen and microspores, again wherein each of the aforementioned comprises the gene/nucleic acid of interest.

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The various aspects of the invention described herein clearly extend to any plant cell or any plant produced, obtained or obtainable by any of the methods described herein, and to all plant parts and propagules thereof unless otherwise specified. The present invention extends further to encompass the progeny of a primary transformed or transfected cell, tissue, organ or whole plant that has been produced by any of the aforementioned methods, the only requirement being that progeny exhibit the same genotypic and/or phenotypic characteristic(s) as those produced by the parent in the methods according to the invention.

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The invention also extends to harvestable parts of a plant of the invention as described above such as, but not limited to seeds, leaves, fruits, flowers, stems, roots, rhizomes, tubers and bulbs. The invention furthermore relates to products derived, preferably directly derived, from a harvestable part of such a plant, such as dry pellets or powders, oil, fat and fatty acids, starch or proteins. The invention also relates to food products and food supplements comprising the plant of the invention or parts thereof.

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While the foregoing disclosure provides a general description of the subject matter encompassed within the scope of the present invention, including methods, as well as the best mode thereof, of making and using this invention, the following examples are provided to further enable those skilled in the art to practice this invention and to provide a complete written description thereof. However, those skilled in the art will appreciate that the specifics of these examples should not be read as limiting on the invention, the scope of which should be apprehended from the claims and equivalents thereof appended to this disclosure. Various further aspects and embodiments of the

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present invention will be apparent to those skilled in the art in view of the present disclosure.

5 All documents mentioned in this specification, including reference to sequence database identifiers, are incorporated herein by reference in their entirety. Unless otherwise specified, when reference to sequence database identifiers is made, the version number is 1.

10 "and/or" where used herein is to be taken as specific disclosure of each of the two specified features or components with or without the other. For example "A and/or B" is to be taken as specific disclosure of each of (i) A, (ii) B and (iii) A and B, just as if each is set out individually herein.

15 Unless context dictates otherwise, the descriptions and definitions of the features set out above are not limited to any particular aspect or embodiment of the invention and apply equally to all aspects and embodiments which are described. The invention is further described in the following non-limiting examples.

Examples

20 **DDA1 is present in vascular plants**

To investigate whether DDA1 is conserved across plant families, we searched for DDA1-related sequences in plant genomic databases (see Methods). We successfully retrieved DDA1 homologs from 49 different plant species and subspecies (Figure 8). On average, 66% aa sequence identity was found between DDA1 ortholog pairs. 25 Phylogenetic analyses showed that DDA1 is conserved in vascular plants, including pteridophyte *Sellaginella moellendorffii*, and could not be found in algae or in the moss *Physcomitrella patens* (Figure 9). In the case of Angiosperms, DDA1 was present in both monocots and dicots. In plant diploid species, *DDA1* was usually found as a single copy gene, although in some cases (e.g. corn, soybean and cotton) we found two 30 *DDA1* gene copies.

DDA1 is a component of the CDD complex in *Arabidopsis*

The CDD complex was originally isolated from floral meristems of cauliflower (a *Brassica* species related to *Arabidopsis*) using a biochemical purification procedure (Yanagawa et al., 2004). To determine whether DDA1 co-purifies with the CDD 35 complex, we subjected the original gel filtration fractions, corresponding to the last step of CDD purification, to SDS-PAGE followed by silver staining or immunoblots using a specific antibody raised against recombinant His-tagged DDA1 (Figure 1A). No

additional bands than those previously reported were detected by silver staining of the SDS-PAGE gel. However, DDA1 could be immunodetected in fractions corresponding to the CDD as three protein bands of lower MW (10 KDa) than expected (16 KDa), indicating that, although apparently partly degraded, DDA1 is present in purified CDD samples. To further confirm that DDA1 binds to the CDD complex, we isolated DDA1-associated proteins using Tandem Affinity Purification (TAP) techniques. For this, C-terminal TAP-tagged DDA1 was expressed and purified from two *Arabidopsis* cell cultures. The identity of proteins that co-purified with DDA1-TAP was determined using mass spectrometry analysis. Together with DDA1, TAP-purified samples contained all CDD complex components (Figure 1B-1C). In this regard, DDA1 was incorporated into CDD complexes that contained either DDB1a or DDB1b, as both proteins co-purified with DDA1-TAP. Next, we characterized DDA1 interaction with CDD complex components using yeast two-hybrid assays. In agreement with previous studies in mammalian systems (Jin et al., 2006; Olma et al., 2009; Pick et al., 2007), we found that DDA1 strongly binds to DDB1 proteins and that this interaction occurs through the β -propeller domain A (BPA) in DDB1 (Figure 1D-1F). Association of DDA1 into CDD complexes was likely mediated by DDA1-DDB1 physical interaction, since we did not observe direct binding of DDA1 to neither DET1 nor COP10 (Figure 1E). Upon DDA1-TAP purification, a DCAF protein (encoded by the At5g12920 locus; Lee et al., 2008) was also co-purified (Figure 1B-1C). This DCAF protein interacted with DDB1a in yeast two hybrid assays but not with DDA1, indicating that DDA1- DCAF association is indirect and likely mediated by DDB1 proteins (Figure 1E).

DDA1 localizes in nuclei and plastids and interacts *in vivo* with CUL4

DDA1 has been shown to localize in nuclei of mammalian cells (Olma et al., 2009). In order to analyze DDA1 subcellular localization *in planta*, we first generated *Arabidopsis* transgenic plants expressing the cDNA of DDA1 fused to GFP under the control of the CaMV 35S promoter (oeDDA1-GFP). Using these lines, we examined DDA1-GFP expression levels relative to endogenous DDA1 of wild-type plants by quantitative real-time RT-PCR (q-RT-PCR; Figure 2A). All three independent lines tested displayed high level of *DDA1-GFP* expression; ranging from 100- to 1000- fold the endogenous *DDA1* transcript level in wild-type plants. Confocal microscopy analysis showed a similar pattern of DDA1-GFP fluorescence in root cells of all oeDDA1-GFP lines analyzed (Figure 2D-2E). Thus, similar to previous studies in animals, DDA1-GFP was observed to localize in nuclei. Interestingly, DDA1-GFP accumulated in additional vesicular compartments unevenly distributed through the cytoplasm. To unveil the identity of these compartments we transiently co-expressed DDA1-GFP and different subcellular markers in *Nicotiana benthamiana* leaves using agroinfiltration techniques. We only

found co-localization of DDA1-GFP and a fluorescent marker of plastids (Figure 2F-2N). In agreement with our microscopy data, DDA1 is predicted to localize in both nuclei and chloroplasts according to protein subcellular localization prediction tools (SUBA3; <http://suba.plantenergy.uwa.edu.au/>). To test whether DDA1-GFP is able to associate with the CDD complex, we crossed oeDDA1-GFP plants (line 3; Figure 2A) with a previously described 3xFLAG epitope tagged-COP10 expressing line (FLAG-COP10) and conducted immunoprecipitation assays. As shown in Figure 2B, FLAG-COP10 coimmunoprecipitated with DDA1-GFP. Since DDA1 and COP10 do not directly interact, according to our yeast two hybrid assays (Figure 1E), we concluded that DDA1-GFP and FLAG-COP10 were incorporated in the same CDD complexes. Moreover, we detected CUL4 protein in DDA1-GFP immunoprecipitates using specific anti-CUL4 antibodies (Figure 2C). Taken together, these results indicate that DDA1, likely as part of the CDD, interacts with CUL4-containing (i.e. CRL4) complexes in plant nuclei, where both complexes are located (Chen et al., 2006; Molinier et al., 2008; Schroeder et al., 2002; Suzuki et al., 2002).

Null mutation of DDA1 causes ovule infertility

In order to functionally characterize DDA1 in plants, we searched for loss-of-function mutants in different *Arabidopsis* T-DNA insertion collections. All available lines contained the T-DNA integrated into non-coding regions in the *DDA1* gene and displayed transcript levels similar to those of wild-type plants (data not shown), which precluded their use in further studies. Similar results were found when *DDA1* gene silencing approaches were followed as all *Arabidopsis* transgenic lines obtained using two different RNA interference systems (Hilson et al., 2004; Karimi et al., 2002), displayed normal *DDA1* mRNA levels (data not shown). We then screened a permanent collection of chemically induced mutants (TILLer; <http://www.cnb.csic.es/~tiller/>; Martin et al., 2009) from which we isolated a heterozygous line that contained a point mutation (G to A) at the donor splice-site of the second intron (Figure 3A). This mutation, hereafter termed as *dda1-1*, is predicted to impair proper splicing of DDA1 premRNA and to yield a truncated translation product lacking the C-terminal half of the protein. In order to remove extraneous mutations, *dda1-1* plants were backcrossed with the wild-type seven times. Segregation analyses using the progeny of backcrossed plants showed that the frequency of homozygous *dda1-1* plants recovered was much lower (3.84%) than expected (25%), suggesting that loss of DDA1 function causes partial lethality of embryos or reduced gamete transmission efficiency. The latter seems to be the case since the siliques of heterozygous *dda1-1* mutants contained a larger number of unfertilized ovules (14.9%), compared to wild-type ones (4.3%), rather than an increased number of aborted seeds

(Figure 3B and 3C;). We aimed to test whether the transmission efficiency of the *dda1-1* mutation through any or both gametophytes (pollen and ovules) was altered. For this, reciprocal crosses between heterozygous *dda1-1* mutants and wild-type plants were carried out. Analysis of the F1 progeny showed that the transmission efficiency of the *dda1-1* allele through the pollen is reduced significantly, but not through the ovule . However, we observed ovule development defects when homozygous *dda1-1* plants were analyzed. Thus, although the homozygous mutants showed normal vegetative development and flowering, they were fully sterile (Figure 3D). Any attempt to fertilize homozygous *dda1-1* flowers using wild-type pollen failed, whereas fertilization could be attained when using mutant pollen and wild-type pistils (data not shown), indicating that *dda1-1* mutation reduces ovule fertility. Accordingly, dissection of non-pollinated pistils from homozygous *dda1-1* flowers showed they only contain arrested ovules (Figure 3E-3F). Taken together, these results indicate that DDA1 plays a role in the control of both gametophytes function, being essential for ovule development.

15

DDA1 physically interacts with PYR/PYL ABA receptors

The molecular basis of DDA1 activity is unknown. To get insights into its mechanism of action, we searched for proteins that interact with DDA1. With this aim, we conducted a yeast two-hybrid screen using DDA1 as bait. Thus, the full-length coding sequence of DDA1 fused to the binding domain of GAL4 was used to screen a cDNA library prepared from *Arabidopsis* seedlings. From over 15 million clones screened, 200 were identified as potential DDA1 interactors. Among them, 20 were subsequently confirmed by retransformation into yeast. Interestingly, among the DDA1 interactors we found two clones corresponding to members of the PYR/PYL/RCAR family of ABA receptors; PYL4 and PYL9 (Figure 4A). The clones isolated in our screen did not correspond to full-length versions of these proteins but rather to truncated ones (PYL4, aa 84-207; PYL9, aa 75-187). We aimed to determine whether DDA1 interacts with full length PYL4 and PYL9 and with other *Arabidopsis* PYR/PYL/RCAR family members using yeast two hybrid assays. Although we did not observe DDA1 binding to full length PYL4 and PYL9 (Figure 4C), suggesting that additional factors might be required for their interaction, we found that DDA1 strongly binds to PYL8, which we selected for further studies (Figure 4B).

To confirm that DDA1 and PYL8 interact *in planta*, we performed bimolecular fluorescence complementation (BiFC) assays. *N. benthamiana* leaves were coinfiltrated with *Agrobacterium tumefaciens* cells to express DDA1 and PYL8 fusions with the Nor C- portions of the yellow fluorescent protein (YFP). The infiltrated leaves were analyzed under the confocal fluorescence microscope 3 d after infiltration.

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Physical interaction between DDA1 and PYL8 was revealed by reconstitution of YFP fluorescence in cells coinfiltrated with constructs corresponding to DDA1:YFPC and YFPN:PYL8, whereas expression of DDA1 or PYL8 constructs alone did not restore the YFP fluorescence (Figure 4D). Interaction between DDA1 and PYL8 seemed to occur exclusively in nuclei, since fluorescent signal resulting from their interaction colocalizes with 4',6-diamidino-2-phenylindole (DAPI) staining (Figure 4D).

PYL8 ABA receptor is ubiquitinated and degraded by the proteasome

The CDD complex has been shown to facilitate ubiquitination and subsequent degradation of specific protein targets by the Ub-proteasome system (UPS) (Castells et al., 2010; Chen et al., 2006; Osterlund et al., 2000). To determine whether PYL8 is a substrate of the UPS, we treated *Arabidopsis* seedlings expressing a 3xHA-tagged PYL8 fusion (oe3HA-PYL8) with proteasome inhibitor MG132. Immunoblots using anti-HA antibodies showed increased 3HA-PYL8 protein accumulation in MG132- treated samples than in mock controls (Figure 5A). Moreover, upon proteasome inhibition several bands of high MW were detected, likely corresponding to ubiquitinated 3HA-PYL8 forms. To confirm PYL8 ubiquitination, Ub-conjugated proteins were purified from oe3HA-PYL8 plants using commercially available p62 resin (which displays affinity for Ub and binds it non-covalently). Immunoblots using anti-HA antibodies showed precipitation of 3HA-PYL8, as multiple high MW bands, when samples were incubated with p62 resin but not when the empty resin was used, indicating that 3HA-PYL8 is modified by poly-Ub chains *in planta* (Figure 5B-5C).

DDA1 overexpression promotes PYL8 protein degradation

Because PYL8 is targeted for degradation by the proteasome, and DDA1 and PYL8 physically interact, we investigated whether DDA1 mediates PYL8 destabilization. For this, we compared the rate of degradation of 3HA-PYL8 after treatment of plants with cycloheximide (CHX) with that in plants that over-express both DDA1-GFP and 3HAPYL8 (obtained by crossing between oe3HA-PYL8 and oeDDA1-GFP line 3; Figure 2A). DDA1-GFP over-expression increased 3HA-PYL8 degradation over the time compared to oe3HA-PYL8 controls (Figure 5D-5E). In these experiments, treatment of plants from both genotypes with MG132 attenuated 3HA-PYL8 destabilization, further confirming proteasomal control of PYL8 stability (Figure 5F). Interestingly, ABA treatments blocked 3HA-PYL8 degradation although this effect was reduced when DDA1-GFP was over-expressed. None of these effects on 3HA-PYL8 protein levels was caused by changes in the expression of the corresponding transgene, as indicated by semiquantitative RT-PCR analysis (Figure 5G).

It has been previously shown that PYR/PYL/RCAR ABA receptors accumulate in seeds where they mediate ABA inhibition of seed germination (Gonzalez-Guzman et al., 2012). Thus, we tested whether DDA1 also controls PYL8 levels in seeds. Immunoblots of protein extracts from imbibed seeds showed that DDA1-GFP over-expression decreases 3HA-PYL8 accumulation in both ABA-treated and non-treated seeds (Figure 5H-5J). Again, ABA led to increased accumulation of 3HA-PYL8. Taken together these results indicate that DDA1 and ABA play opposite roles in the control of PYL8 accumulation, whereas DDA1 facilitates PYL8 degradation, ABA prevents its destabilization.

10 **Overexpression of DDA1 reduces plant sensitivity to ABA**

Our data indicate that DDA1 facilitates degradation of PYL8, and likely that of other PYR/PYL/RCAR receptors with which it interacts, pointing to a negative regulatory role for DDA1 in ABA signalling. To test this hypothesis, we characterized several ABA responses in oeDDA1-GFP plants (line 3; Figure 2A), including ABA-mediated inhibition of seed germination, seedling establishment and root, and shoot growth. As a control, we used wild-type and oeHAB1 (over-expressing the PP2C phosphatase HAB1; used as ABA-insensitive control) plants in these experiments. oeDDA1-GFP plants showed a reduced response to ABA compared to wild-type plants in all cases, except for ABA-mediated inhibition of shoot growth (Fig. 6A-6I). In addition, oeDDA1-GFP seedlings were less sensitive to NaCl- or mannitol- mediated inhibition of seed germination than the wild-type (Fig. 6G-6H), indicating that DDA1 over-expression effect is also evident under stress conditions that increase endogenous ABA levels (Leung and Giraudat, 1998; Seo and Koshiba, 2002). To confirm that reduced sensitivity to ABA is due to DDA1 over-expression and not to an artifact caused by its fusion to GFP, we obtained *Arabidopsis* plants expressing the cDNA of *DDA1* under the control of a β -estradiol-inducible promoter (iDDA1; Fig 6J- 6K). Seed germination rates of iDDA1 plants grown in MS media supplemented or not with ABA or with β -estradiol were completely indistinguishable of those of wild-type plants. However, seedling establishment rate increased in the iDDA1 line compared to the wild-type when both ABA and β -estradiol were added to the media.

30 **Reduced CDD function causes ABA hypersensitivity**

Analysis of the effect of reduced DDA1 function in ABA signalling was hindered by the fact that homozygous *dda1-1* null mutants were infertile and under-represented in an F2 segregating population (~4% instead of 25%;). Additionally, RNAi approaches did not succeed to silence *DDA1*, as afore-mentioned. As an alternative, we sought to characterize mutants of other CDD components since DDA1 forms part of the CDD complex. Analysis of ABA responses showed that mutations that yield reduced function

of DDB1, DET1, or COP10 (note that their total loss of function is lethal; Bernhardt et al., 2010; Schroeder et al., 2002; Suzuki et al., 2002) caused an opposite ABA phenotype to that of DDA1 over-expressing plants. Thus, *ddb1a*, *cop10-4* and *det1-1* mutants showed increased response to ABA-mediated inhibition of germination and seedling establishment than wild-type plants. In the case of *det1-1* mutants, ABA hypersensitivity also extended to root growth responses (Figure 7A-7E). Next, we determined whether ABA hypersensitivity correlates with increased accumulation of PYL8 in plants showing reduced CDD function. For this analysis, we used *cop10-4* mutants as a representative of CDD deficient mutants. Immunoblots of protein extracts obtained from imbibed seeds showed that *cop10-4* mutation increases 3HA-PYL8 accumulation in both ABA-treated and non-treated seeds (Figure 7F-7G). Altogether, these results suggest that cooperation between CDD components exists to control ABA receptor stability and therefore, to regulate ABA responses.

DISCUSSION

Noteworthy, ABA and DDA1 seem to play opposite roles in the control of PYL8 stability; where ABA and DDA1 prevent and promote PYL8 degradation, respectively. Since ABA signaling is obviously strongly dependent on the activity of PYR/PYL/RCAR receptors, an ABA-dependent protection mechanism for receptor stability would serve to reinforce and sustain ABA signaling. In this context, DDA1-mediated degradation of PYL8 could contribute to desensitize the pathway when stress conditions disappear and ABA levels diminish. The molecular aspects underlying ABA-mediated protection of PYL8 are totally unknown. One possibility is that ABA binding-driven changes in receptor conformation disrupt DDA1-PYL8 interaction or PYL8 ubiquitination and/or degradation rates. Thus, it is known that PYL8 interacts in an ABA-dependent manner at least with five clade A PP2Cs in vivo (Antoni et al., 2013; Saavedra et al., 2010). The ternary complexes PP2C-ABA-PYL8 show high stability (Kd around 20-40 nM) and the interaction of PYL8 with ABA and the PP2C generates substantial changes in receptor conformation (Melcher et al., 2009; Santiago et al., 2009). Therefore, it is likely that such complexes protect PYL8 from DDA1-mediated degradation or effectively compete with DDA1-PYL8 interaction. Further biochemical and molecular studies should help us to unveil the precise details of such a protective mechanism.

Despite functional redundancy between PYR/PYL/RCAR ABA receptors, PYL8 has a prominent role in mediating ABA signaling at the roots (Antoni et al., 2013). Consistent with DDA1 control of PYL8 function, *oeDDA1-GFP* plants phenocopied the reduced sensitivity to ABA-mediated inhibition of root growth shown by *pyl8-1* mutants. Notably, DDA1 overexpression also altered responses that are regulated by highly redundant PYR/PYL/RCAR family members, including seed germination and seedling

establishment (Gonzalez-Guzman et al., 2012), suggesting an ampler role for DDA1 in controlling ABA receptor stability. In agreement with this, PYL4 and PYL9 were identified in a yeast two hybrid-based screen of DDA1 interactors. However, contrary to PYL8 results, full length versions of PYL4 and PYL9 did not bind DDA1 in yeast, which may suggest that additional factors are required for these interactions to occur *in vivo*. Indeed, we cannot exclude the possibility that DDA1 activity as part of CDD complexes is aided by other subunits, including other DCAF proteins. In fact, our TAP purification CDD complexes have been proposed to play a dual role in regulating CRL4 activity by enhancing the E3 activity of CRL4, likely through its COP10 subunit, and facilitating CRL4 target recognition (Yanagawa et al., 2004; Pick et al., 2007; Olma et al., 2009). In the latter case, it has been suggested that CDD complexes may act as adaptor modules for additional substrate receptors (Lau and Deng, 2012). Our results on the biochemical and functional characterization of *Arabidopsis* DDA1 strongly support this model. Thus, we found that DDA1 associates with the CDD complex and CUL4 *in vivo* and is involved in direct protein target recognition for ubiquitination and subsequent degradation by the proteasome. Although DDA1 association with plant CDD complexes was presumed (Chen et al., 2010), no direct evidence had been provided yet. Here, we demonstrate that DDA1 is a component of CDD using two approaches. First, we were able to detect DDA1 in biochemically purified CDD fractions. CDD purification yielded partially degraded COP10 and DET1 products, as seems to be the case for DDA1 too, which might have precluded its identification in the study by (Yanagawa et al., 2004). Second, we found all CDD components in TAP-purified DDA1 samples. Similar to its human counterpart, DDA1 association with CDD, and therefore CRL4, is mediated by its interaction with the BPA domain in DDB1 proteins (Jin et al., 2006; Pick et al., 2007). DDA1 biochemical activity has been a matter of discussion since its identification in mammalian systems (Pick et al., 2007; Olma et al., 2009; Chen et al., 2010). One hypothesis was that DDA1 might play a structural role as part of CDD/DDD-E2 complexes. However, DDA1 is apparently not required to maintain the integrity of these complexes, since the CDD complex could be reconstituted *in vitro* in the absence of DDA1 (Chen et al., 2006). Another possibility was that DDA1 might be necessary to activate certain CRL4s, by stabilizing DDB1 association with a specific subset of DCAFs. Indeed, immunoprecipitation assays showed that both endogenous and tagged hDDA1 associate with DDB1, CUL4 and several DCAF proteins, including Constitutively photomorphogenic 1 (COP1), AMBRA and Cockayne syndrome A (CSA) in human cells (Jin et al., 2006; Olma et al., 2009; Behrends et al., 2010). However, experimental evidence showing DDA1-mediated stabilization of DDB1- DCAF

complexes has not been provided. In this study, we propose a different function for DDA1 as a novel type of substrate receptor for CRL4 ubiquitin ligases. In this regard, we identified the first known target of DDA1 activity, the ABA receptor PYL8.

Despite functional redundancy between PYR/PYL/RCAR ABA receptors, PYL8 has a prominent role in mediating ABA signaling at the roots (Antoni et al., 2013). Consistent with DDA1 control of PYL8 function, *oeDDA1*-GFP plants demonstrated reduced sensitivity to ABA-mediated inhibition of root growth, as is also the case for *pyl8-1* mutants. Notably, DDA1 overexpression also altered responses that are regulated by highly redundant PYR/PYL/RCAR family members, including seed germination and seedling establishment (Gonzalez-Guzman et al., 2012), suggesting a broader role for DDA1 in controlling ABA receptor stability. In agreement with this, we found that DDA1 also interacts *in vivo* with PYL4 and PYL9, which may represent additional targets for DDA1. However, we did not observe interaction of DDA1 with PYL5 and PYL6 in yeast two hybrid assays, suggesting that a certain degree of specificity in DDA1 activity may exist. DDA1 function towards ABA receptors is very likely performed in the context of the CDD, as indicated by the increased sensitivity to ABA of mutants of other members of the complex. Accordingly, *cop10-4* plants accumulated higher levels of PYL8 protein than wild-type plants, as it is expected for plants with reduced DDA1 function. However, no other CDD component was able to interact with PYL8 under our experimental conditions, highlighting the specificity and preponderance of DDA1 in ABA receptor recognition. These results are consistent with a model in which the whole CDD complex acts as a substrate adaptor module for CRL4 where DDA1 mediates recognition of specific targets. It is noteworthy that ABA and DDA1 play opposite roles in the control of PYL8 stability where ABA and DDA1 prevent and promote PYL8 degradation, respectively. Since ABA signaling is obviously strongly dependent on the activity of PYR/PYL/RCAR receptors, an ABA-dependent protection mechanism for receptor stability would serve to reinforce and sustain ABA signaling, particularly during the early stages of signaling. However, at later stages, plant desensitization to ABA likely occurs in order to prevent the adverse effects of continuous ABA responses (i.e. growth reduction or stomatal closure). Accordingly, it has been shown that ABA reduces *PYL8* gene expression after 3 h of treatment (Saavedra et al., 2010). Interestingly, ABA treatment of *oeHA-PYL8* seeds for 24 h also reduced *HA-PYL8* transcript levels suggesting the implication of posttranscriptional control of *PYL8* mRNA by ABA. Our results on DDA1 further emphasize on the complexity and sophistication of the regulatory network that modulates ABA signaling. Thus, DDA1-mediated degradation of ABA receptors should also contribute to desensitize the pathway when stress conditions disappear and ABA levels diminish. This regulatory mechanism might

be also instrumental to impair ABA signaling during germination since it has been shown that ABA concentration in seeds is reduced upon imbibition. The molecular aspects underlying ABA-mediated protection of PYL8 remain unknown. This mechanism apparently does not imply disruption of the PYL8/DDA1 interaction or a reduction of DDA1 levels, but rather a decrease in PYL8 polyubiquitination rates. One possibility is that changes in receptor conformation driven by ABA-binding limit PYL8 ubiquitination. Thus, it is known that PYL8 interacts in an ABA-dependent manner at least with five clade A PP2Cs in vivo (Saavedra et al., 2010; Antoni et al., 2013). The ternary complexes PP2C-ABA-PYL8 show high stability (K_d around 20-40 nM), and the interaction of PYL8 with ABA and the PP2C generates substantial changes in receptor conformation (Melcher et al., 2009; Santiago et al., 2009). Therefore, it is possible that formation of such complexes may hide specific lysine residues on PYL8 and thereby interfere with its polyubiquitination. Further biochemical and molecular studies should help us to unveil the precise details of such a protective mechanism. Definition of the structural details of DDA1 binding to specific PYR/PYL/RCAR proteins in the presence of CDD and CRL4 complexes, and/or PP2Cs and ABA, will also help to elucidate how DDA1 substrate specificity is attained (note that DDA1 lacks WDxR motifs usually required for substrate interaction) and to better understand the modulation of ABA signaling based on the control of ABA receptor stability.

METHODS

Plant Materials and Growth Conditions

Arabidopsis plants used in this study, including mutants and transgenic plants, were of the Columbia-0 (Col-0) ecotype. Plants were grown in MS media (Murashige and Skoog, 1962) with 1% sucrose at 21°C under a 16-h-light/8-h-dark cycle using cool white fluorescent light conditions (100 mmol m⁻² s⁻¹). Specific treatments were performed as stated in each experiment (see below and figure legends). Mutants *cop10-4*, *det1-1*, *cra1*, *hab1-1*, *abi1-2*, *pyl8-1* and transgenic lines *oe3HA-PYL8*, *FLAGCOP10*, and *oeHAB1* have been previously described (Antoni et al., 2013; Fernandez-Arbaizar et al., 2012; Peeper et al., 1994; Suzuki et al., 2002; Yanagawa et al., 2004). The T-DNA insertion line corresponding to *ddb1a* was obtained from TAIR (<http://www.Arabidopsis.org>; SALK_038757). To generate transgenic plants expressing DDA1, the *DDA1* cDNA was amplified using Expand High Fidelity Polymerase (Roche) and Gateway-compatible primers: DDA1-BF 5'-GGGGACCACTTTGTACAAGAAAGCTGGGTAGAATAGTGAGCAACTTTAAGT CGA-3' (SEQ ID NO:197) and DDA1-BR 5'-GGGGACCACTTTGTACAAGAAAGCTGGGTATAAGCCCTGAGTAGATGAAGA

AGAAGACG-3' (SEQ ID NO:198). PCR products were cloned into the pDONR207 plasmid using Gateway BP reaction kits (Invitrogen) and verified by Sanger sequencing. Then, DDA1 cDNA was transferred, using Gateway LR reaction kits (Invitrogen), to pGWB5 (Nakagawa et al., 2007) and pMDC7 (Curtis and Grossniklaus, 2003) destination vectors. The resulting plasmids were used to generate oeDDA1-GFP and iDDA1 lines, respectively. In all cases, plant transformation was performed by transferring the corresponding constructs to *Agrobacterium tumefaciens* C58C1 (pGV2260) competent cells (Deblaere et al., 1985). Transformation of *Arabidopsis* plants was performed by the floral dip method (Clough and Bent, 1998). T1 transgenic seeds were selected based on corresponding selection markers and T3 homozygous progenies were used for further studies. Lines oeDDA1-GFP/oeFLAG-COP10, oe3HA-PYL8/*pyl8-1*/oeDDA1-GFP and oe3HA-PYL8/*pyl8-1*/*cop10-4* were generated by crossing the corresponding homozygous parental lines. F2 segregating progenies of these crosses were selected in the corresponding antibiotics to isolate homozygous plants for each construct. The *dda1-1* mutant was isolated by screening of an *Arabidopsis* TILLING (Targeting Induced Local Lesions IN Genomes) mutant collection (TILLer; Martin et al., 2009; <http://www.cnb.csic.es/~tiller/>). The *dda1-1* mutant, originally identified in a Landsberg *erecta* background, was introgressed into the Col-0 ecotype after seven sequential crosses. Plants harbouring the *dda1-1* mutation (either homo- or heterozygous mutants) could be identified by their distinctive restriction pattern compared to wild-type plants after genomic PCR using specific primers 5'-CTGGGTTTTGCTGCTTACTTGG-3' (SEQ ID NO:199) and 5'-TCCTACGAAATCCTGTGTTATG-3' (SEQ ID NO:200), and subsequent digestion with *HphI* (Roche). For BiFC experiments, *N. benthamiana* plants were grown in soil in the green house at 22°C under 16-h-light/8-h-dark photoperiod prior to agroinfiltration of leaves with the corresponding constructs.

Quantitative and semiquantitative RT-PCR

Quantitative RT-PCR experiments were performed using RNA extracted from Col-0 wild-type and oeDDA1-GFP plants. Three biological replicates, consisting of tissue pooled from 15-20 plants from different plates, were taken. RNA extraction and cleanup was done with RNeasy mini kit (Qiagen) and DNase digestion to remove genomic DNA contamination. cDNA was synthesized from 1 µg of total RNA using a high-capacity cDNA reverse transcription kit (Applied Biosystems). Ten µL from one-tenth diluted cDNA was used to amplify *DDA1* and the housekeeping gene *ACTIN8* using FastStart Universal Probe Master (Roche). Primers used were: DDA1-RTF 5'-CCCTCCGATCCTTCTAATCC-3', DDA1-RTR 5'- (SEQ ID NO:201) GCTGCGTATAAGAATGTTTTTCAC-3', ACT8-F 5'- (SEQ ID NO:202)

GGTACTGGAATGGTTAAGGC-3' and ACT8-R 5'- (SEQ ID NO:203)

GTCCAACACAATACCGGTTG-3'. (SEQ ID NO:204)

Quantitative PCRs were performed in 96-well optical plates in a 7300 Real Time PCR system (Applied Biosystems). The PCR conditions were as follows: 2 min at 50°C, 10 min at 95°C and 40 cycles of 15 s at 95°C and 30 s at 60°C.

Semiquantitative PCR experiments from seedlings were performed using RNA prepared as afore-mentioned. RNA extraction from seeds was carried out as previously described (Onate-Sanchez and Vicente-Carbajosa, 2008). cDNA from all tissues was synthesized as described above. Five µL of one-fifth diluted cDNA was used to amplify *DDA1-GFP*, *3HA-PYL8* and the housekeeping gene *ACTIN8* using the following primer: HA-F

5'-CTATGACGTCCCGGACTATGCA-3', *PYL8-R* 5'- (SEQ ID NO:205)

GGTGAAGAGAGATGATTGAAG-3', *DDA1-2F* 5'- (SEQ ID NO:206)

TCGTCCCTCCGATCCTTCTAATCC-3', *GFP-R* 5'- (SEQ ID NO:207)

CTTGCCGTAGGTGGCATCGC-3', *ACT8semi-F* 5'- (SEQ ID NO:208)

GGTACTGGAATGGTTAAGGC-3', *ACT8semi-R* 5'- (SEQ ID NO:209)

GTCCAACACAATACCGGTTG -3' (SEQ ID NO:210). The PCR conditions were as follows: 1 min at 94°C, 35 cycles of 15 s at 94°C, 1 min at 58-62°C, and 1 min 30 s at 72°C, and finally, 5 min at 72°C. 25

20 TAP assays

Cloning of a GS-tagged *DDA1* fusion under the control of the constitutive cauliflower tobacco mosaic virus 35S promoter and transformation of *Arabidopsis* cell suspension cultures were performed as previously described (Van Leene et al., 2007). TAP of protein complexes was done using GS tag (Burckstummer et al., 2006) followed by protein precipitation and separation, according to Van Leene et al. (2008). For the protocols of proteolysis and peptide isolation, acquisition of mass spectra by a 4800 MALDI TOF/TOF Proteomics Analyzer (AB SCIEX), and MS based protein homology identification based on the TAIR genomic database, we refer to Van Leene et al. (2010). Experimental background proteins were subtracted based on approximately 40 TAP experiments on wild-type cultures and cultures expressing TAP-tagged mock proteins GUS, RFP and GFP (Van Leene et al., 2010).

30 Microscopy analysis

For ovule observations, pistils from not-pollinated *Arabidopsis* flowers were opened longitudinally and observed using a Leica M165FC stereomicroscope. Photographs were taken with a Leica color camera DFC295. Then, pistils were cleared in chloral hydrate (2 mg mL⁻¹) and ovules were observed under a Leica DMR microscope with

differential interference contrast (DIC) optics (<http://www.leica.com>). Photographs were taken with an Olympus DP70 camera. To analyze DDA1-GFP subcellular localization, images of 5-d-old oeDDA1-GFP *Arabidopsis* roots and of *Nicotiana* leaves agroinfiltrated with DDA1-GFP and different organelle markers (Nelson et al., 2007), were visualized by a confocal microscope at 495-610 nm (Leica). To visualize nuclei, roots and *Nicotiana* leaves were submerged in a DAPI solution (1 µg mL⁻¹ DAPI in 100 mM phosphate buffer, 0.5% Triton X-100).

Yeast two hybrid experiments

The full length *DDA1* cDNA was cloned into the pGBKT7 (Gal4 DNA binding domain, BD; Clontech). This construct was used to screen a whole seedling cDNA library (Bustos et al., 2010) prepared in the pGADT7 vector (Gal4 activation domain, AD, Clontech) to detect DDA1-interacting proteins. To confirm protein interactions, plasmids were co-transformed into *Saccharomyces cerevisiae* AH109 cells, following standard heat-shock protocols (Chini et al., 2007). Successfully transformed colonies were identified on yeast synthetic drop-out lacking Leu and Trp; these colonies were resuspended in water and transferred to selective media lacking Ade, His, Leu and Trp. Plates without His were supplemented with different concentrations of 3-amino 1,2,4-triazole (3AT; ranging 0.5-10 mM). Yeast cells were incubated at 30°C during 6 days. Empty vectors were co-transformed as negative controls. To test the DDA1 interaction with specific DDB1a domains, DDB1a truncated versions were generated and cloned into the pGADT7 vector as follows: BPA (aa 16-350), BPB (aa 387-704), BPA+BPB (aa 16-704), BPC (aa 704-1002) and BPB+BPC (aa 350- 1002). Full length DDB1a was used as a positive control.

BiFC experiments

Different combinations of *A. tumefaciens* clones expressing fusion proteins YFPN:PYL8/DDA1:YFPC were co-infiltrated into the abaxial surface of 3-week-old *N. benthamiana* plants as described (Voinnet et al., 2003). The p19 protein was used to suppress gene silencing. The empty vectors were used as negative controls. Fluorescence was visualized in epidermal cells of leaves after 3 d of infiltration using a Leica sp5 confocal microscope. Nuclei were visualized after submerging the leaves in a DAPI solution (1 µg mL⁻¹ DAPI in 100 mM phosphate buffer, 0.5% Triton X-100).

Genetic analysis

To examine gametophytic transmission of the *dda1-1* mutant allele, reciprocal test crosses were performed between wild-type (Col-0) and heterozygous *dda1-1* mutant plants. Seeds harvested from crosses were germinated and grown on soil, and genomic DNAs from the F1 progeny were analyzed by PCR using the primer combination to detect the *dda1-1* mutation. Transmission efficiency (TE) of the mutant

allele via each type of gamete (TE male and TE female) was calculated as described previously (Howden et al., 1998).

Protein extraction, co-immunoprecipitation assays and immunoblots

For protein extraction from seedlings, proteins were extracted in buffer containing 50 mM Tris-HCl pH 7.4, 150 mM NaCl, 10mM MgCl₂, 1mM PMSF, 0,1%NP-40 and 1x complete protease inhibitor (Roche). After centrifugation at 16,000 g at 4°C, the supernatants were collected. This step was repeated twice. For protein extraction from seeds, seeds were frozen in liquid N₂ and then homogenized in buffer containing 7 M urea, 2 M thiourea, 4% 3-[(3-cholamidopropyl)dimethylammonio]-1-propanesulfonate (CHAPS; w/v), 18 mM Tris-HCl pH 7.5, 0,2% Triton X100, 1x complete protease inhibitor (Roche). After 10 min incubation at 4°C with rotation, DTT was added to protein extracts (14 mM final concentration), prior to 20 min incubation at 4°C. Extracts were clarified by centrifugation as afore-mentioned. Protein concentration in final supernatants was determined using a Bio-Rad Protein Assay kit. For in vivo co-immunoprecipitation assays, normalized seedling protein extracts were incubated with 5 µl anti-GFP antibody (Living colors Full length A.V. Polyclonal Antibody, Clontech) for 1 h at 4°C with rotation. 10 µl of protein A-coupled beads (prewashed twice with 0.1 M Glycine pH 2.7) were added to the samples and incubated for an additional hour at 4°C with rotation. After washing three times with 500 µL extraction buffer, samples were denatured, separated on SDS-PAGE gels and transferred onto polyvinylidene difluoride (PVDF) membranes (Millipore). Membranes were probed with different antibodies: anti-GFP-HRP (for DDA1-GFP detection, Milteny Biotec), monoclonal Anti-FLAG M2 (for FLAG-COP10; Sigma), anti-CUL4 (Chen et al., 2006). For immunodetection of 3HA-PYL8, anti-HA-HRP (Roche) was used. To confirm equal protein loading, membranes were stained with Ponceau reagent or immunoblotted using anti-RPT5 (Kwok et al., 1999).

CDD complex was purified as previously described (Yanagawa et al., 2004). For the analysis of purified CDD complex fractions, proteins in each fraction were separated onto 15% SDS-PAGE gels. Silver staining and immunoblots using anti-DDA1 antibodies were performed to visualize specific protein bands. For anti-DDA1 production see below.

Purification of recombinant proteins and antibody production

Recombinant His-DDA1 protein was expressed in the *Escherichia coli* BL21 (DE3) strain carrying a pET28-HisT7DDA1 construct. Bacteria were cultured in LB at 37°C to an optical density at 600 nm of 0.6, at which time protein expression was induced with 0.2 mM isopropyl-D-thio-galactopyranoside for 3 h. Cell lysis was performed using a French Press and lysates were clarified by centrifugation at 16,000 g for 30 min at 4°C.

His-DDA1 protein was purified from lysates with Ni-NTA-agarose beads under denaturing conditions (Qiagen) and eluted with a pH gradient as described by the manufacturer. Protein concentration in final eluates was determined using Bio-Rad Protein Assay kit. To raise anti-DDA1 antibodies purified His-DDA1 protein was introduced into two rabbits (1 mg/each). Rabbit preimmune serum was kept to check for anti-DDA1 specificity.

Affinity purification of ubiquitinated proteins.

Isolation of ubiquitinated proteins was performed as previously described (Manzano et al., 2008) with small modifications. Briefly, proteins were extracted from oe3HA-PYL8 plants using buffer BI (50 mM Tris-HCl pH = 7.5; 20 mM NaCl; 0.1% NP-40 and 5 mM ATP) plus plant protease inhibitors cocktail (Sigma), 1 mM of PMSF and 50 μ M MG132. Protein extracts were incubated with 40 μ L pre-washed p62-agarose (Wilkinson et al., 2001) or the agarose alone at 4°C during 4 h. Afterwards, the beads were washed 2 times with 1 mL BI buffer once more with 1 mL buffer BII (BI plus 200 mM NaCl) and proteins were eluted by boiling into 50 μ L SDS loading buffer. The eluted proteins were separated by SDS-PAGE and analyzed by immunoblotting using anti-Ub (Boston Biochem) to detect the presence of ubiquitinated proteins or anti-HAHRP (Roche) for 3HA-PYL8 detection.

***In vivo* protein degradation assays**

Seedlings were grown in MS solid media for 8 d and then transferred to liquid MS media containing 50 μ M cycloheximide (CHX; Sigma) in the presence or absence of 50 μ M ABA (Sigma). The effect of proteasome inhibition was tested by adding 50 μ M MG132 (Sigma) to the liquid MS. Whole plant samples were harvested at specific time points as indicated. Protein extraction and immunoblots were performed as aforementioned. ImageJ v1.37 software (<http://rsb.info.nih.gov/ij>) was used to analyze protein band intensity.

Seed germination and seedling establishment assays.

After surface sterilization of the seeds, stratification was conducted in the dark at 4°C for 3 d. Next, approximately 100 seeds of each genotype were sowed on MS plates lacking or supplemented with 0.5 μ M ABA, 150 mM NaCl or 400 mM Mannitol. In the analyses of iDDA1 lines, β -estradiol was added to media at 10 μ M final concentration as stated. To score seed germination, radical emergence was analyzed at 72 h and 96 h after sowing. Seedling establishment was scored at 5 and 7 d as the percentage of seeds that developed green expanded cotyledons and the first pair of true leaves.

Root and shoot growth assays.

Seedlings were grown on vertically oriented MS plates for 4 to 5 d. Afterwards, 20 plants were transferred to new MS plates lacking or supplemented with 10 μ M

concentration of ABA. The plates were scanned on a flatbed scanner after 10 d to produce image files suitable for quantitative analysis of root growth using ImageJ v1.37 software. As an indicator of shoot growth, the maximum rosette radius was measured after 20 d.

5 ACCESSION NUMBERS

Sequence data from this article can be found in the *Arabidopsis* Genome Initiative database under the following accession numbers: *DDA1* (At5g41560), *DDB1A* (At4g05420), *DDB1B* (At4g21100), *COP10* (At3g13550), *DET1* (At4g10180), *CUL4*(At5g46210), *PYL8* (At5g53160), *PYL4* (At2g38310), *PYL9* (At1g01360).

10 Accession numbers are incorporated by reference.

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Sequence listing

SEQ ID NO: 1 AtDDA1 nucleic acid sequence, CDS
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10 SEQ ID NO: 54 *Linum usitatissimum*, cDNA
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15 SEQ ID NO: 55 *Linum usitatissimum*, gDNA
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50 SEQ ID NO: 56 *Linum usitatissimum*
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55 SEQ ID NO: 57 *Ricinus communis*, CDS
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60 SEQ ID NO: 58 *Ricinus communis*, cDNA
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SEQ ID NO: 122 *Solanum lycopersicum*, gDNA

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SEQ ID NO: 142 *Zea mays* 1 gDNA

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 AAAA ACTTAGAGCTCTCTATAGTCTAGAATGATGTCACATATTA AAAACAACCACCGTTTGT TTAGACAA
 AAAAATGTTTTCCAATACTAAAGCCTGATAATTGATGCAATCCATCGATAATCAATGCAATCAGTTGAT
 20 ATTCAACAATTTTGGTTGATTTTCTATTTCTTTACCAACTTGACCAATATGCATGGGGTATTTACTA
 TATTTGTTGTATATTATGCTACAAATGGATGGTTATCTAGTATAATTTCCAATGTAGATTAGTGTAAATAT
 TAGTGGTGGGAAGAAAGACTTCAATGTTGACTTGTGTTAAATCAGTTAGGATACAATAGGCTTCAATGT
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 SEQ ID NO: 180 *Panicum virgatum* gDNA
 25 AAGGAAAGCGCTAACCACCAGCGGCAGACGAAGTGAGGGGAGCATCGCCGGACGCCGGAGTCAGAGACGG
 CGCGGCGATTCCGGCTCAACGAACCACCAGGGGAACAAGACGGGCGGTGGCGGC GCGGAGATGGGGAGCC
 CACTCGGCGGGTGGCCGTCGTACAACCCGCACAACCTTCAGCCAGCTCGTCCCGGCCGACCCCTCCGCTCA
 GCCCTCGGTCCGTCAGCACTTCCCTCTTTGGCGATCTCGTCTCTAATATACAGTAATTGACTGTCTCCA
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 30 TGTGACAACCTGCGCCCTCTTGTATCTGTATCTGCAATAAAAA ACTTCTTTAGTACTGTACTGCCCTTAT
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 35 CATATATATCCATTTAGAGTGACTCTAATGTTATTAGGTAGTTTTTATGTTCTTAACAGA ACTTCTATGCT
 GACAAGTGATAATTTAGGCTATGAAAGATATACTCTGTTGACCTCATGCTGATGCTGATGGTATGTTTCC
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 CCAATCAAGGTA ACTCCTTCCCATGTTCTTGAAAAAATGTTCTGTGTGCTGCTACCTGCTGTA AATGTAT
 CTTATTTTTATTTTCTCACTGTGCATTTTCCCGCAATTGAGATCATGCAATTA CTGTTTCGCAATAAGCCG
 40 AGAATTTCTTTTTCTGTCTATTTTAGTACTATGTAAGCTCAATATTGCAAAGTAGATCTTGTGAACCCGTT
 TGGCAAAGTTCTTAGCATGTTTCTCCATAAGATTTCTTTGCTCATGGTATATTGTGCTGCAAGTACAG
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 45 AGTGTCAAGTACTACCAGGTA CTGCCCCTTTTTCAATATCAAAGTTTACCAGGTAATGCATGCAGTGCAA
 TTTTTCTTTGATCTACATGGACAACAATTTCAATTTGCTAAATACTGCACATATAGTACTGATTCCAAAAT
 CTGAGGATGCTACTGATCTCTCACATTTATAGACCTATCAGCTTGACAAGTAGTATTTCCAAAATTTATCTC
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 CGAAGGAGTATCCATGATAACTTCTTATACACACAAAATCTCATTTCGAGCTCTACATAAAGATGGCAGGC
 50 CCTCCCTTTTTATTAAGCTGGACATTGCAAAGGCTTTTGACACTGTGCGATGGAATATCTGATGGAGGT
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 TCGGCTTTAGTCAATGGAGCACAACTCCAAAATTTAAGCACATGATCAGGTTAAGGCAGGGAGACCCCTT
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 CAACCTATACCAATACACACAAATATGGCAACGTTAAGAATAAGTTTTATTTGCCGATGATGCTGCAGTT
 55 TTTCTAAACCCAGTGAAAGAAGAGATTGATGTGATCAAAGAGGTAATTTCAGGCATTTGGAAATGCTTCTG
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 GCGTTGCTACCGGTGGCACAGAAACGCTCAGTTGCGGCCATCTTGATGTACACTTGTGGAATTTGTGGA
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 40 TATGCATGGGGTATTTACTATATTGTTGTATATTATGCTACAAAATGGATGGTTATACTGATAATTTCCAA
 TGTAGATTAGTGTAAATATTAGTGGTGGGAAGAAAGACTTCAATGTTGACTTGTGTTAAATCAGTTAG
 GATACAATAGGCTTCAATGTTGACTATAATATGTATGCTTATACTAAAAAAACTATGCTCTAACTGGT
 SEQ ID NO: 181 *Panicum virgatum*
 MGSPLGGWPSYNPHNFSQLVPPADPSAQPSNVTPATYIAAHRDPPPNQVITTEPRNILLRHFYQKSEKLR
 RPKRAAPDNLAPENNNKQPRGPVADVGSQSNARS
 45 SEQ ID NO: 182 *Phyllostachys edulis* CDS
 ATGGGGAGCCCCCTGGGTGACTGGCCGTCCTACAACCCGCACAACCTTCAGCCAGCTCGTCCCGGCCGACC
 CCTCCGCCAGCCCTCGAATGTCACACCAGCCACGTACATTGCGACGCATAGGACAGATCCACCTCCCAA
 TCAAGTGATAACAACACTGACTCTAGGAACATCCTGTTGAGGCATTTTTATCAAAAATCCGAGGAGAAGTTG
 AGGCCAAAGAGAGCCGACCCGACAATCTTACCCTGCAGAACAATTGCAAACAGCCAAGGGGCCCTGTTG
 50 CCGATGGTGGAAGCCAGTCAAGTAGTAGAAGCTAA
 SEQ ID NO: 183 *Phyllostachys edulis* cDNA
 GAAGAGGAAGAAGAAGAAGAAGAAGAAGGAAGCATCGGCGGTGGCGTCGCGGCGATGGGGAGCCCCCTGG
 GTGACTGGCCGTCCTACAACCCGCACAACCTTCAGCCAGCTCGTCCCGGCCGACCCCTCCGCCAGCCCTC
 GAATGTCACACCAGCCACGTACATTGCGACGCATAGGACAGATCCACCTCCCAATCAAGTGATAACAAC
 55 GACTCTAGGAACATCCTGTTGAGGCATTTTTATCAAAAATCCGAGGAGAAGTTGAGGCCAAAGAGAGCCG
 CACCGGACAATCTTACCCTGCAGAACAAATGCAAACAGCCAAGGGGCCCTGTTGCCGATGGTGGAAAGCCA
 GTCAAGTAGTAGAAGCTAAATCACCGCAGTGTTCCTCTCCTGCATCTCTTACGGTCTGTTGCGGCTGC
 TGCTGATGCATGTCATGCTACCTGTGTGGCTGTGTGCTTGTTC AAGCATGCGAAGCCCTCTCATTTCTCA
 60 TGTATTATCAAAAAGAGCTTGGATGCATGTACATACCTTCAGCGAGCCCTCAGTGGCGGTACCTTTTACA
 TGGCACTACTGCAGTCTCTTCTGAATATAATGTGCCACACTAGCCAACCTTGTGCTTTTGTATTGAAACAA
 AACCATGGCTCCATAATTGCGTTGCTTC

SEQ ID NO: 184 *Phyllostachys edulis*
 MGSPLGDWPSYNPHNFSQLVPADPSAQPSNVTPATYIATHRTDPPPNQVITTDNRNILLRHFYQKSEKLL
 RPKRAAPDNLTLQNNCKQPRGPVADGGSQSSSR

5 SEQ ID NO: 185 *Picea glauca* CDS
 ATGGGGTCATTGCTTGGAGATTGGCCCTCCTATAATCCGCACAATTTTCAGTCAGTTGAGGCCGTCGGATC
 CCTCGCATCCCTCGCAATTGACACCCGGTCACTTACTATCCTACTCATAATAGAACAGCACCCCCAGCACA
 CCAAGTAATTTCAACTGAGGCTACAAATATCCTTTTAAGGCAGTTTTATCAGCGAGCAGAAGAGAAGTTG
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10 SEQ ID NO: 186 *Picea glauca* cDNA
 AAGACACATGGATCGGTTCTGCACATGCAGCCGCGAGGATCTGCGTCCAGGCAGTGGCTGGAGACGGCCC
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15 TGGGTAATGACCGGTTCTGTTTTTCTGCTGTATTGGTTGAGTGGGTTGCCGTC AAGTGCAGATTCTAGAC
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 CTCATGTACATAATTTGGAATTTTCTGTTGTCAATCTCATGTACATAATTCGTGGATATAGTGGAAATCGG
 AATTTTCTGTACGTC

20 SEQ ID NO: 187 *Picea glauca*
 MGSLLGDWPSYNPHNFSQLRPSDPSPHSQLTPTVYYPTHNRTPAPAHQVISTEATNILLRQFYQRAEEKL
 KAKRPASDALVQEHMKNKHPKS

25 SEQ ID NO: 188 *Selaginella moellendorffii* CDS
 ATGGGTTCCCTTGGTGGCGATCTTCCCTTCGTACAACCCGCACAATTTTCAGCCAGTTGAGACCATCGGATC
 CTTCTCATCGCTCCCAACTCACACCCGCTCACTTATCACGCTACTCACGACCCGGACGATGCCTCCGGCGGA
 TCAAGTCACTCCACTGAAGCTACCAACATTTTGTGAGGCAGTTCTATCAAAAAGCCGATCACAAGCTC
 AAGTTGAAGCGCTCGGCCACCGATTTCGCTCTCGGGGATCACAAGCGTCCCAAGAGCACAACCTGCGCTC
 CAGAGAAGAGATGA

30 SEQ ID NO: 189 *Selaginella moellendorffii* cDNA
 GGCTCTTTTCCATGTTCATAGGAGGAGAGAGAAGGGACATTTCTTTTAGCTGCGGGGTTGCGATCGATCGA
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 CTCTCTAGAAAGCGCGAGATCTATCGTCTTCGTCGAGTAGCAACGCAAAGCGAAAAAGAGGTTTTCTTT
 TTGCGGAGGATCACAATGGGTTCCCTGCTGGGCGATCTTCTTCGTACAACCCGCACAATTTTCAGCCAGT

35 TGAGACCATCGGATCCTTCTCATCGCTCCCAACTCACACCCGCTCACTTATCACGCTACTCACGACCCGGAC
 GATGCCTCCGGCGGATCAAGTCACTCCACTGAAGCTACCAACATTTTGTGAGGCAGTTCTATCAAAAA
 GCCGATCACAAGCTCAAGTTGAAGCGCTCGGCCACCGATTTCGCTCTCGGGGATCACAAGCGTCCCAAGA
 GCACAACCTGCGCTCCAGAGAAGAGATGATCGCGAGTTCTCCCTGTACTTAACAAGCCCGCGATGGAAAA
 AAAAAACAGAGGTTGGCTACACAGGTTTGTGAGCAGAATCCATTTTCTCGATCTCTAAGCTTGTGAATAT

40 CTAGATCGACAATGGTAACTTTCTTTTAGAAA
 SEQ ID NO: 190 *Selaginella moellendorffii* gDNA
 GGCTCTTTTCCATGTTCATAGGAGGAGAGAGAAGGGACATTTCTTTTAGCTGCGGGGTTGCGATCGATCGA
 GCGAGAGGGAATCGGTGTGCGCCTTAAAAATCCTGGTTCGCTCTATCGGATAGAAGCGAGCGATCGTGTGCG
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45 CTCTCTAGAAAGCGCGAGATCTATCGTCTTCGTCGAGGATGTTGAGGTAATCTCTCCTTGTCTTCCCTC
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 TCTTTCGTTGTTCTTGTCTTACTGACCACATTTCTTTTTTTTTTTTTTTTTTTTTTTTTTTCAGCAACTCAC

50 ACCGCTCACTTATCACGCTACTCACGACCCGGACGATGCCCTCCGGCGGATCAAGGTAACCATCACCATAGC
 TTCGGAATTTGAGCTAACTTGTCTTTTGCAGTCACTCCACTGAAGCTACCAACATTTTGTGAGG
 CACTTCTATCAAAAAGCCGATCACAAGGTAAGTTCTTCCGATCAATGCTATGATTCAATCCTCACTCAC
 TCGAGTGTATGCAAGCAGCTCAAGTTGAAGCGCTCGGCCACCGATTTCGCTCTCGGGGATCACAAGCGTC

55 CCAAGAGCACAACTTTCGCTCCAGAGAAGAGATGATCGCGAGTTCTCCCTGTACTTAACAAGCCCGGAT
 GGAAAAAAAACAGAGGTTGGCTACACAGGTTTGTGAGCAGAATCCATTTTCTCGATCTCTAAGCTTGT
 GAATATCTAGATCGACAATGGTAACTTTCTTTTAGAAA

60 SEQ ID NO: 191 *Selaginella moellendorffii*
 MGSLLGDLPSYNPHNFSQLRPSDPSPHSRSLTPLYHATHDRTPMPADQVISTEATNILLRHFYQKADHKL
 KLKRSATDSPLGDHHRPKSTTCAPEKR

SEQ ID NO: 192 DDA1 consensus sequence

MGSS [LM] LGDWPSFDPHNFSQLRPSDFSSNPSKMPATYHPHTRSRTLPPDQVITTEAKNILLRHFYQ
RAEEKLRPKRAASENLLAPEHGCKQPRGPVAS [ST] SDTQSSASGRS

CLAIMS:

1. A method for increasing yield and/or growth of a plant under stress conditions said method comprising introducing and expressing in said plant a nucleic acid construct comprising a plant DDA1 nucleic acid sequence.
2. A method for reducing a plant response to abscisic acid (ABA), said method comprising introducing and expressing in said plant a nucleic acid construct comprising a plant DDA1 nucleic acid sequence.
3. A method for modulating the interaction of the receptor PYL8 with ABA said method comprising introducing and expressing in said plant a nucleic acid construct comprising a plant DDA1 nucleic acid sequence.
4. A method for reducing seed dormancy said method comprising introducing and expressing in said plant a nucleic acid construct comprising a plant DDA1 nucleic acid sequence.
5. A method for mitigating the impacts of stress conditions on plant growth and yield said method comprising introducing and expressing in said plant a nucleic acid construct comprising a plant DDA1 nucleic acid sequence.
6. A method for producing a transgenic plant with improved yield/growth under stress conditions said method comprising introducing and expressing in said plant a nucleic acid construct comprising a plant DDA1 nucleic acid sequence.
7. A method according to a preceding claim wherein said plant DDA1 nucleic acid sequence is a monocot or dicot plant DDA1 nucleic acid sequence.
8. A method according to a preceding claim wherein said plant DDA1 nucleic acid sequence comprises SEQ ID NO: 1, 2 or 3 or a functional variant or homolog of SEQ ID NO: 1, 2 or 3.
9. A method according to claim 8 wherein said homolog has at least 75% 70%, 71%, 72%, 73%, 74%, 75%, 76%, 77%, 78%, 79%, 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%, 89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99% overall sequence identity to the nucleic acid represented by SEQ ID NO: 1, 2 or 3 or wherein the peptide encoded by a homolog of SEQ ID NO: 1 has at least 75% 70%, 71%, 72%, 73%, 74%, 75%, 76%, 77%, 78%, 79%, 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%, 89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99% overall sequence identity to the amino acid represented by SEQ ID NO: 4.
10. A method according to claim 9 wherein said plant DDA1 nucleic acid sequence encodes a protein which comprises SEQ ID No: 4, 8, 11, 14, 18, 22, 26, 30, 34,

- 38, 42, 45, 49, 52, 56, 60, 64, 68, 71, 75, 79, 83, 87, 90, 94, 98, 102, 106, 109, 112, 115, 119, 123, 126, 130, 133, 136, 139, 143, 147, 151, 155, 159, 163, 166, 169, 173, 177, 181, 184, 187, 191 or a functional variant thereof.
11. A method according to any of claims 5 to 10 wherein said stress is abiotic stress.
- 5 12. A method according to claim 11 wherein said stress is moderate stress.
13. A method according to any of claims 11 or 12 wherein said stress is drought or salinity.
14. A method according to a preceding claim wherein said plant is a monocot or dicot plant.
- 10 15. A method according to a preceding claim wherein said plant is a crop plant or biofuel plant.
16. A method according to claim 15 wherein said crop plant is selected from maize, rice, wheat, oilseed rape, sorghum, soybean, potato, tomato, grape, barley, pea, bean, field bean, lettuce, cotton, sugar cane, sugar beet, broccoli or other
- 15 vegetable brassicas or poplar.
17. A method according to a preceding claim wherein said construct further comprises a regulatory sequence.
18. A method according to claim 17 wherein said regulatory sequence is a constitutive promoter, a strong promoter, an inducible promoter, a stress
- 20 inducible promoter or a tissue specific promoter.
19. A method according to claim 18 wherein said regulatory sequence is the CaMV35S promoter.
20. A transgenic plant with an altered response to ABA wherein said plant expresses a nucleic acid construct comprising a plant DDA1 nucleic acid sequence.
- 25 21. A plant according to claim 20 wherein said plant DDA1 nucleic acid sequence comprises SEQ ID No: 1, 2 or 3 or a functional variant or homolog thereof.
22. A plant according to claim 21 wherein said plant DDA1 nucleic acid sequence encodes a polypeptide comprising SEQ ID NO: 4, a functional variant or homolog thereof.
- 30 23. A plant according to claim 22 wherein said homolog has at least 75% 70%, 71%, 72%, 73%, 74%, 75%, 76%, 77%, 78%, 79%, 80%, 81%, 82%, 83%, 84%, 85%, 86%, 87%, 88%, 89%, 90%, 91%, 92%, 93%, 94%, 95%, 96%, 97%, 98%, or 99% overall sequence identity to the amino acid represented by SEQ ID NO: 4.
- 35 24. A plant according to claim 21 wherein said plant DDA1 nucleic acid encodes a protein which comprises SEQ ID No: 4, 8, 11, 14, 18, 22, 26, 30, 34, 38, 42, 45, 49, 52, 56, 60, 64, 68, 71, 75, 79, 83, 87, 90, 94, 98, 102, 106, 109, 112, 115,

- 119, 123, 126, 130, 133, 136, 139, 143, 147, 151, 155, 159, 163, 166, 169, 173, 177, 181, 184, 187, 191 or a functional variant thereof.
25. A plant according to any of claims 20 to 24 wherein said construct further comprises a regulatory sequence.
- 5 26. A plant according to any of claims 20 to 25 wherein said regulatory sequence is a constitutive promoter, a strong promoter, an inducible promoter, a stress inducible promoter or a tissue specific promoter.
27. A plant according to claim 26 wherein said regulatory sequence is the CaMV35S promoter.
- 10 28. A plant according to claim 27 wherein said regulatory sequence is a stress inducible promoter.
29. A plant according to claim 28 wherein said stress inducible promoter is selected from Hahb1, RD29A or rab17, P5CS1 or ABA- and drought-inducible promoters of Arabidopsis clade A PP2Cs, for example ABI1, ABI2, HAB1, PP2CA, HAI1, HAI2
15 and HAI3 or their corresponding crop orthologs.
30. A plant according to any of claims 20 to 29 wherein said plant is a monocot or dicot plant.
31. A plant according to any of claims 20 to 30 wherein said plant is a crop plant or biofuel plant.
- 20 32. A plant according to claim 31 wherein said crop plant is selected from maize, rice, wheat, oilseed rape, sorghum, soybean, potato, tomato, grape, barley, pea, bean, field bean, lettuce, cotton, sugar cane, sugar beet, broccoli or other vegetable brassicas or poplar.
33. Plant according to any of claims 20 to 32 wherein said plant has increased stress
25 resistance.
34. A product derived from a plant as defined in any of claims 20 to 33 or from a part thereof.
35. A vector comprising a plant DDA1 nucleic acid sequence.
- 30 36. A vector according to claim 35 wherein said plant DDA1 nucleic acid sequence is a nucleic acid corresponding to SEQ D NO: 1, 2 or 3 or a functional variant or homolog thereof.
37. A vector according to claim 35 or 36 further comprising a regulatory sequence which directs expression of the nucleic acid.
- 35 38. A vector according to claim 37 wherein said regulatory sequence is a constitutive promoter, a strong promoter, an inducible promoter, a stress inducible promoter or a tissue specific promoter.

39. A vector according to claim 38 wherein said regulatory sequence is the CaMV35S promoter.
40. A vector according to claim 38 wherein said regulatory sequence is a stress inducible promoter.
- 5 41. A vector according to claim 40 wherein said stress inducible promoter is selected from a Hahb1, RD29A or rab17, P5CS1 or ABA- and drought-inducible promoters of Arabidopsis clade A PP2Cs, for example ABI1, ABI2, HAB1, PP2CA, HAI1, HAI2 and HAI3 or their corresponding crop orthologs.
42. A host cell comprising a vector according to any of claims 34 to 41.
- 10 43. A host cell according to claim 42 wherein said host cell is a bacterial or a plant cell.
44. The use of a DDA1 plant nucleic acid sequence in reducing a plant response to ABA.
45. The use of a DDA1 plant nucleic acid sequence in reducing seed dormancy.
- 15 46. The use of a DDA1 plant nucleic acid sequence in increasing yield/growth of a plant under stress conditions.
47. The use according to any of claims 44 to 46 wherein said plant DDA1 nucleic acid comprises SEQ ID NO: 1, 2 or 3 or a functional variant or homolog thereof
- 20 48. A plant with increased expression of an endogenous DDA1 plant nucleic acid sequence wherein said endogenous DDA1 promoter carries a mutation introduced by mutagenesis or genome editing which results in increased expression of the DDA1 gene.
49. A plant with increased stability of the endogenous DDA1 polypeptide wherein said endogenous DDA1 nucleic acid sequence carries a mutation introduced by mutagenesis or genome editing and which results in increased stability of the DDA1 protein.
- 25 50. A method for increasing expression of a DDA1 plant nucleic acid sequence or improving stability of a DDA1 protein in a plant, producing plants, a method for mitigating the impacts of stress conditions on plant growth and yield and a method for producing plants with improved yield/growth under stress conditions comprising the steps of mutagenising a plant population, identifying and selecting plants with an improved yield/growth under stress conditions and identifying a variant DDA1 promoter or gene sequence.
- 30

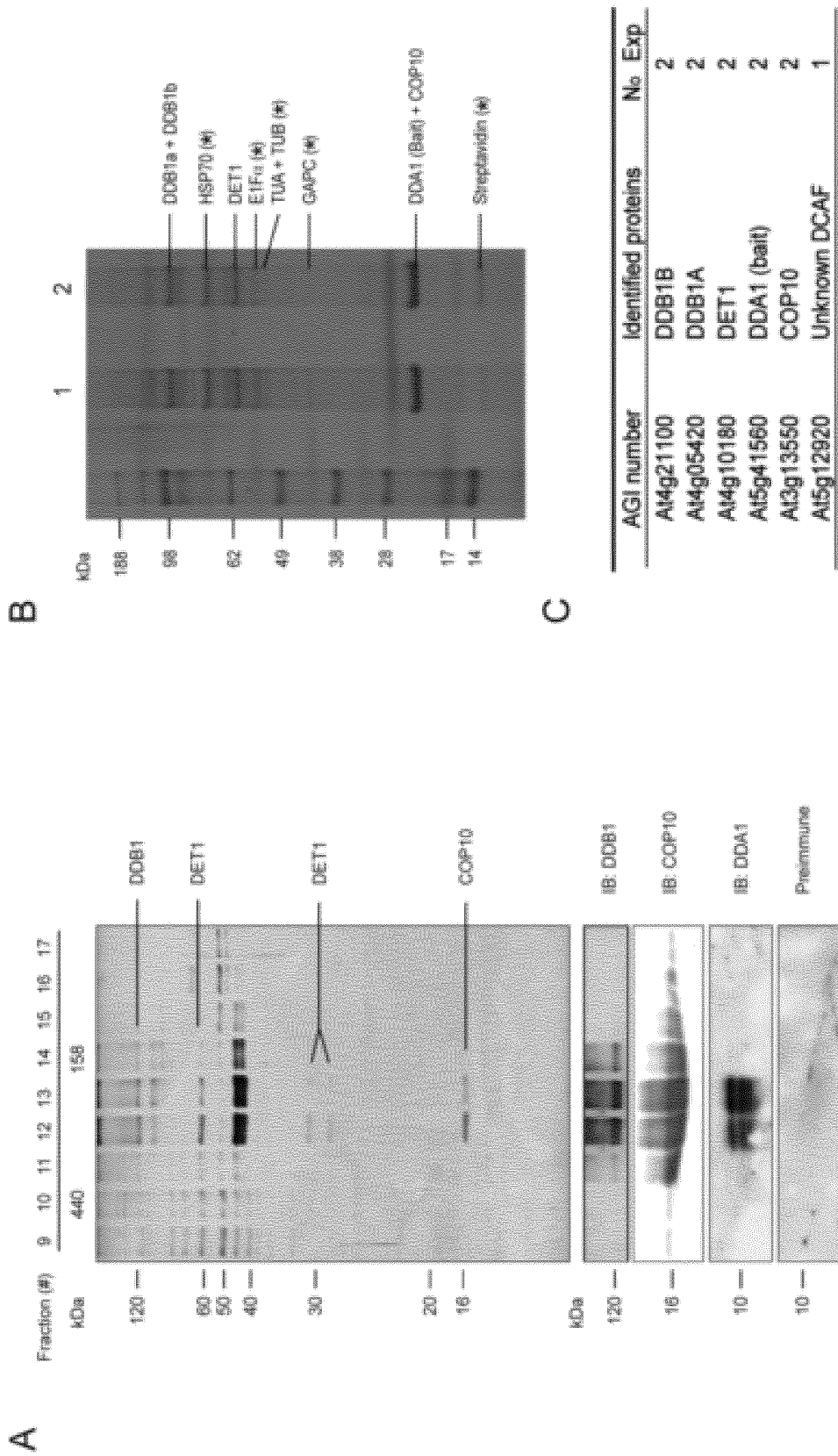


FIGURE 1

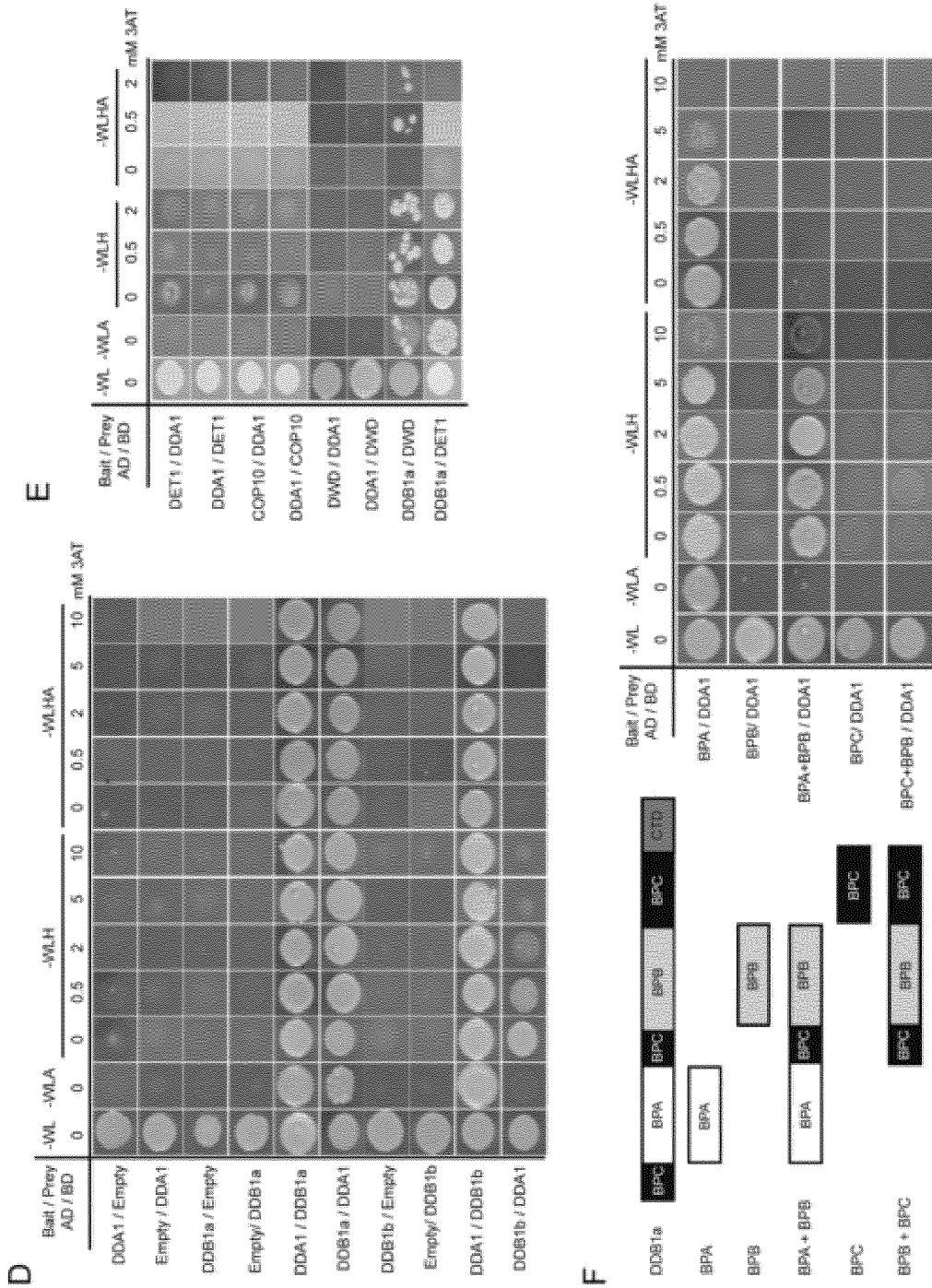


FIGURE 1

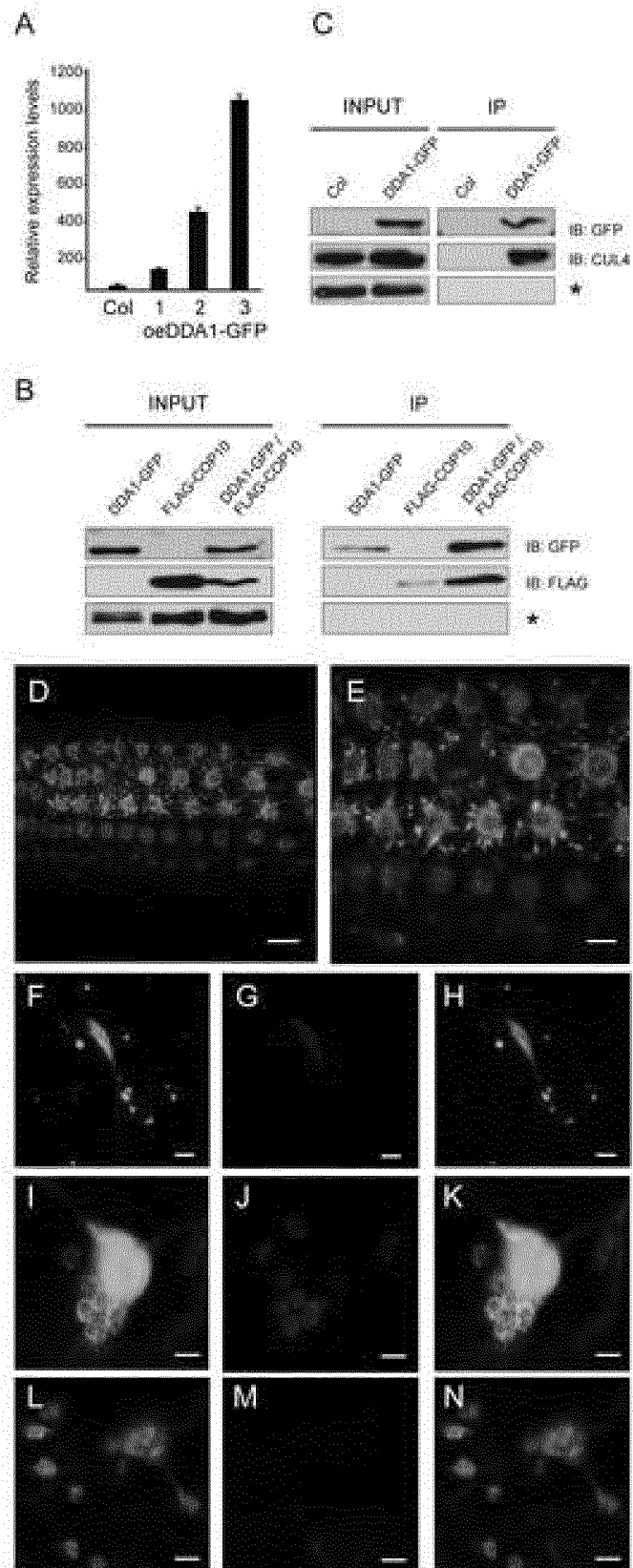


Figure 2

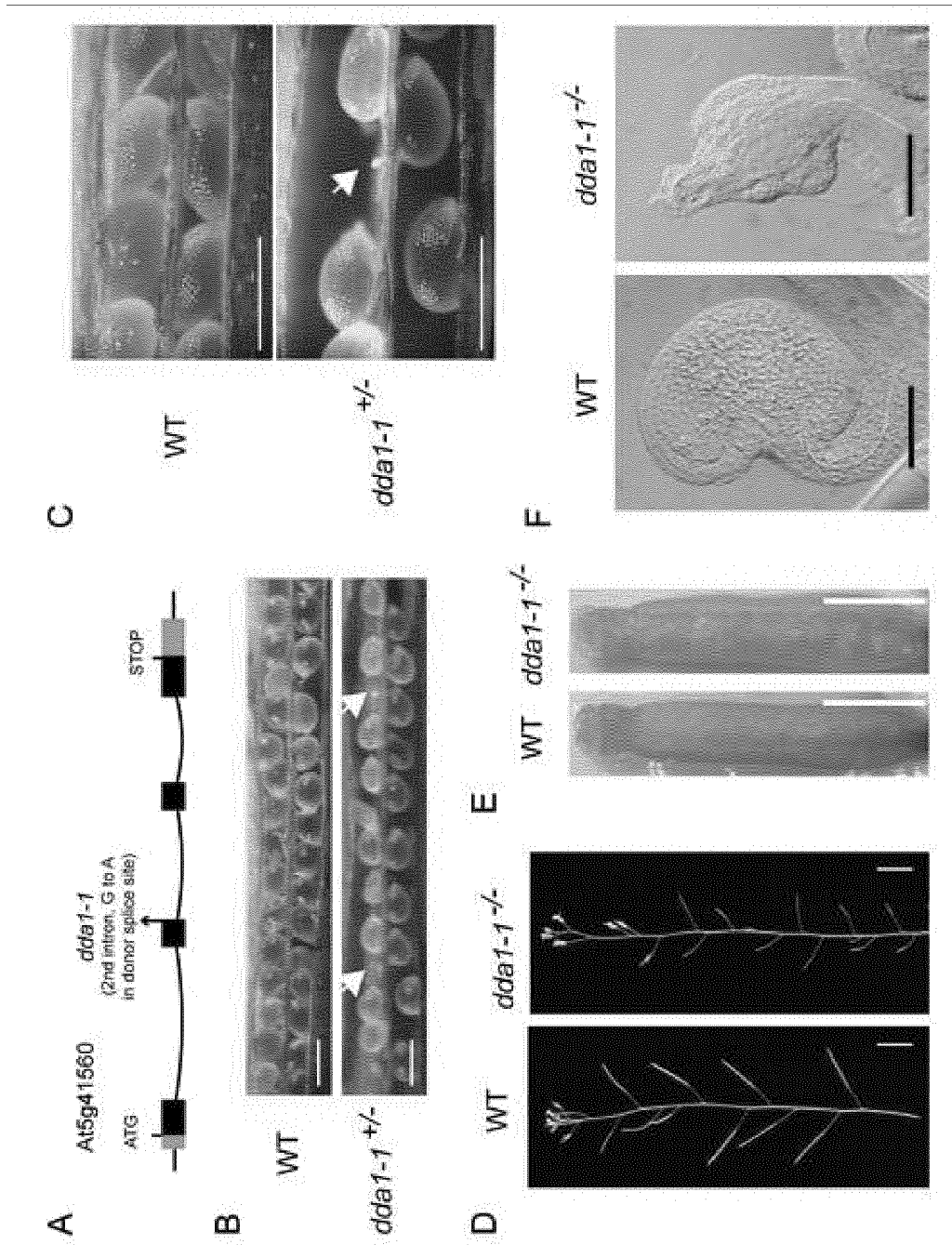
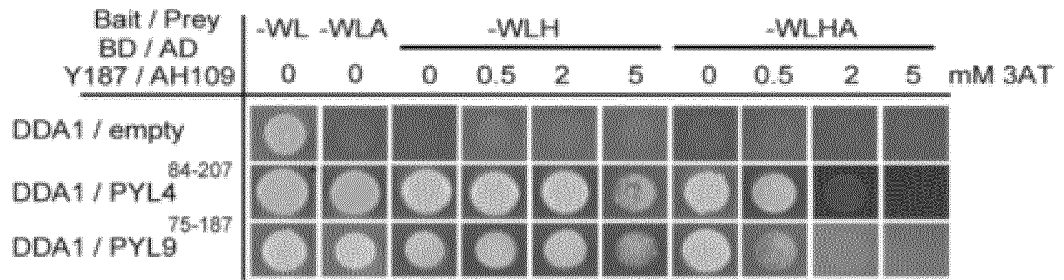


FIGURE 3

A



B

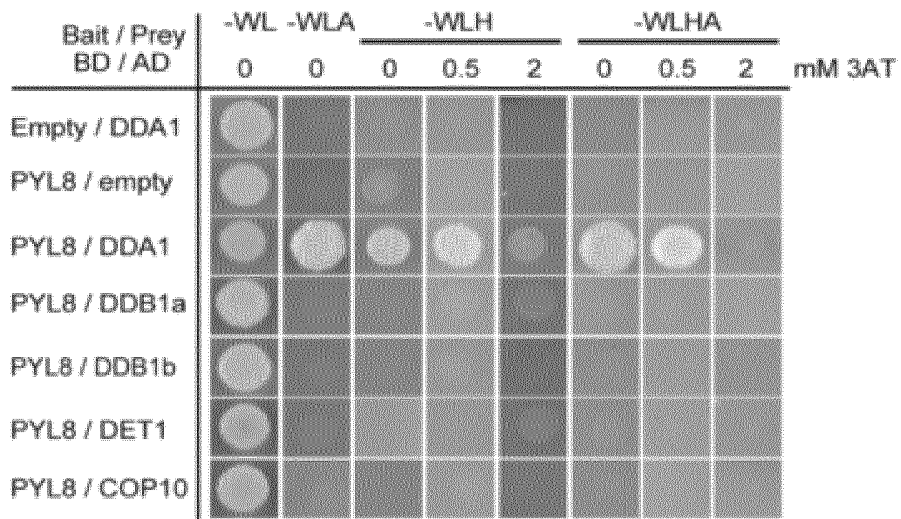


FIGURE 4

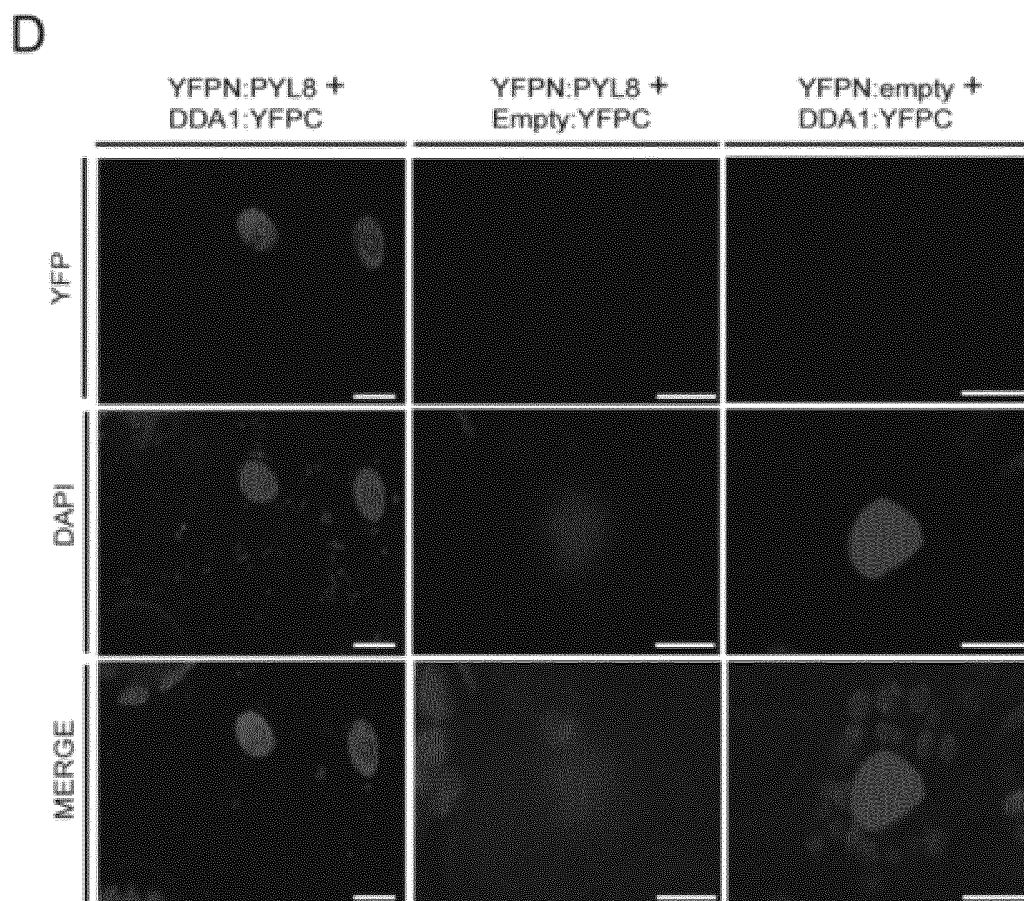
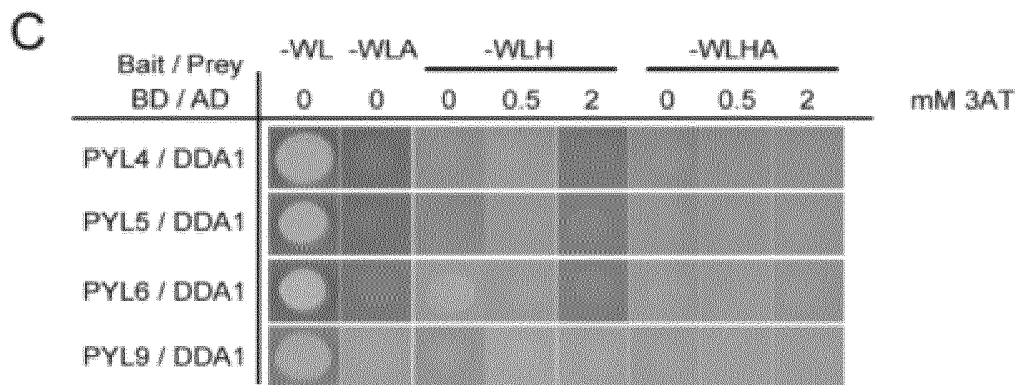
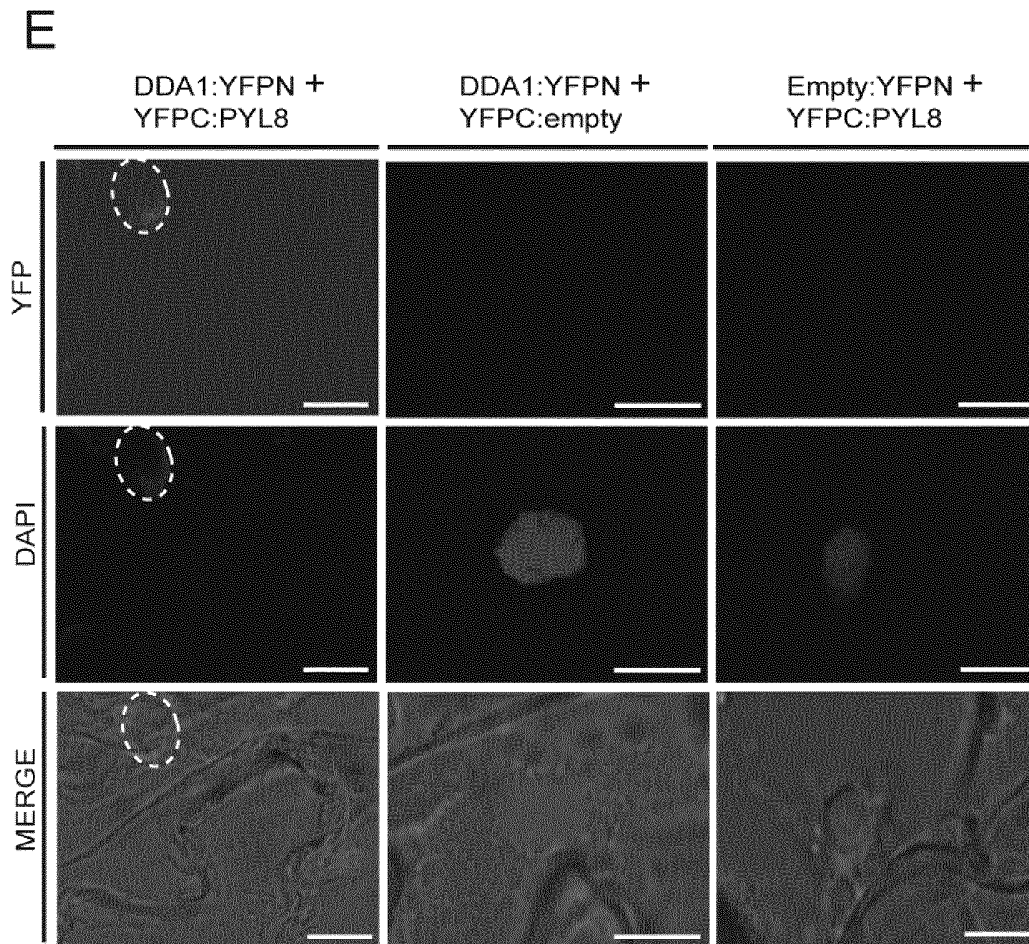


FIGURE 4

FIGURE 4



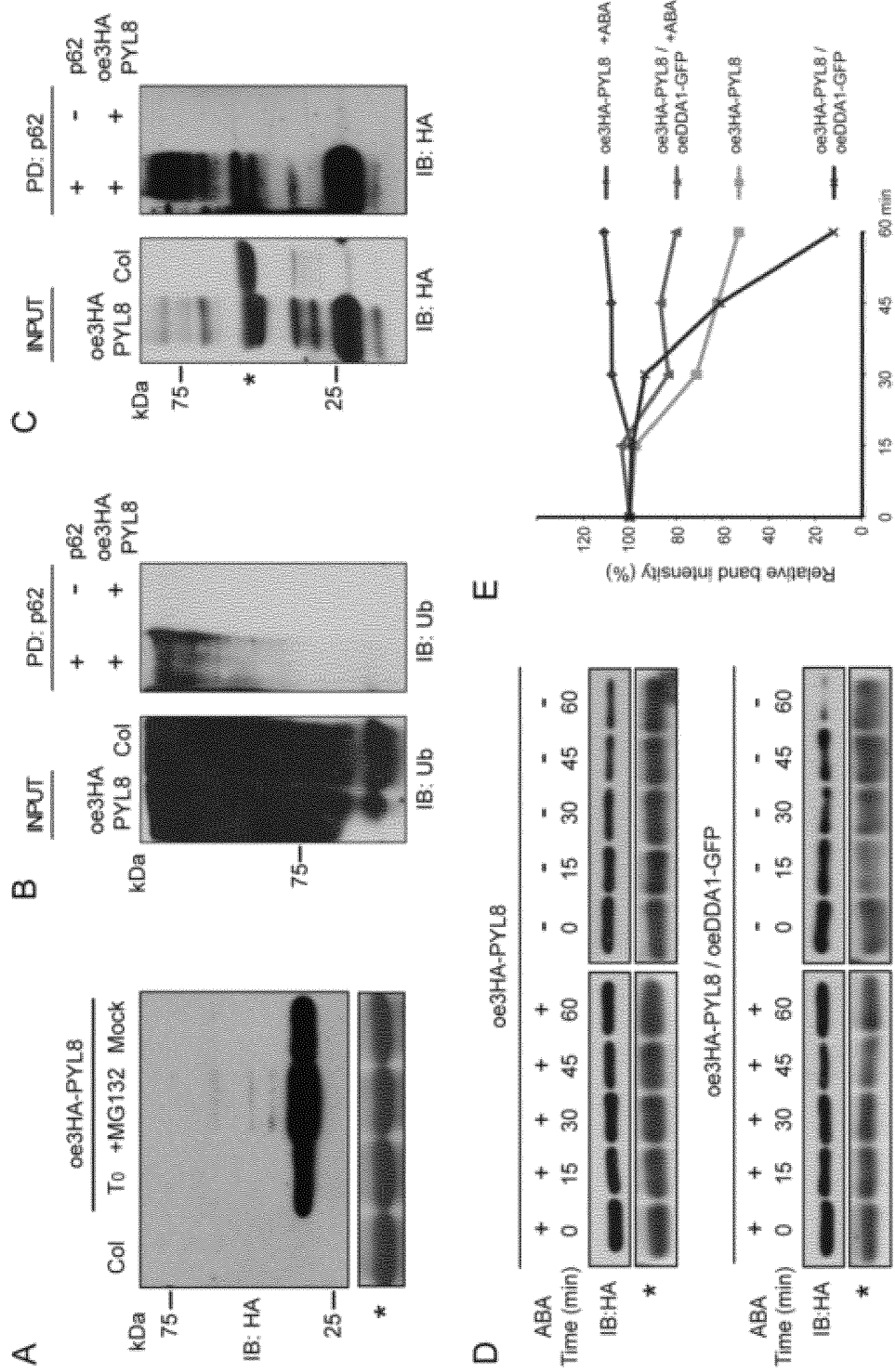


FIGURE 5

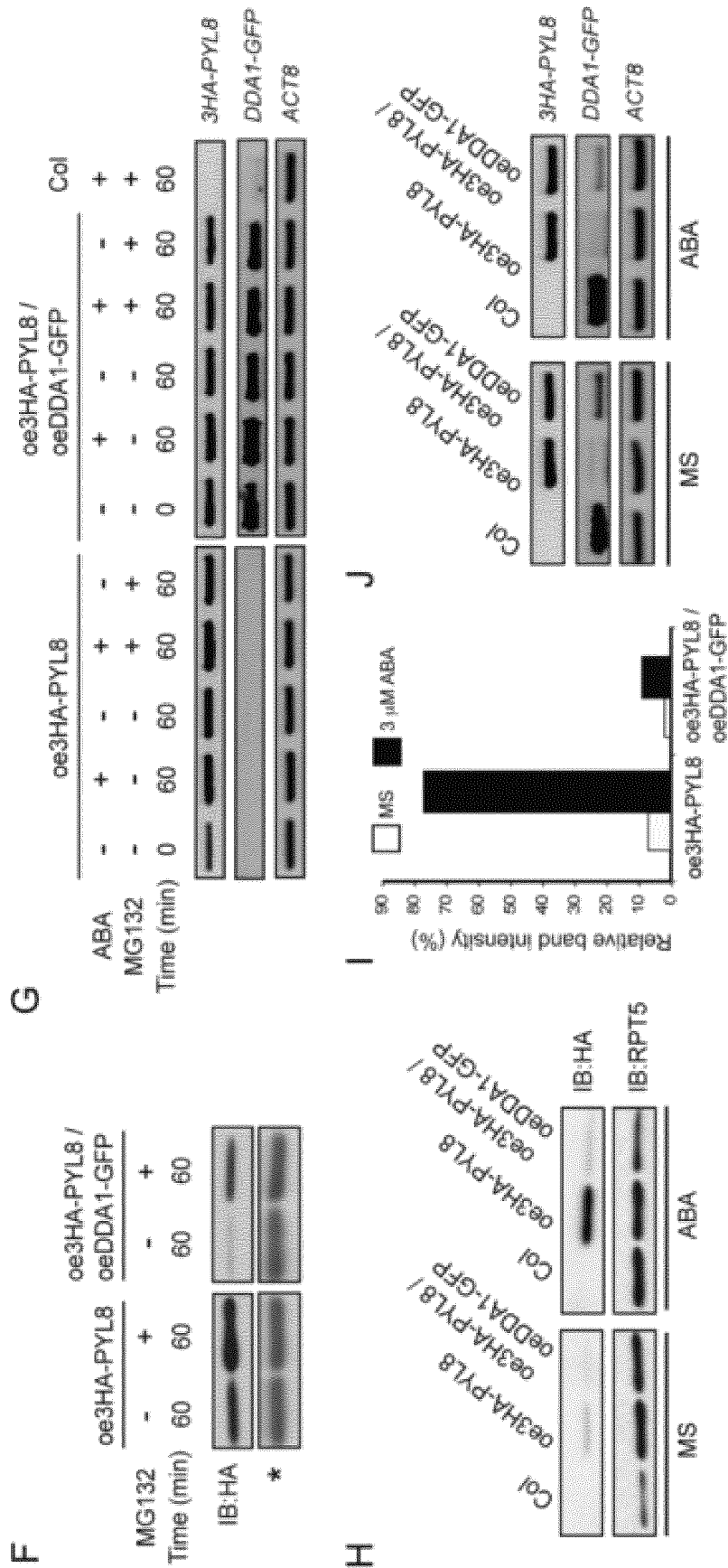


FIGURE 5

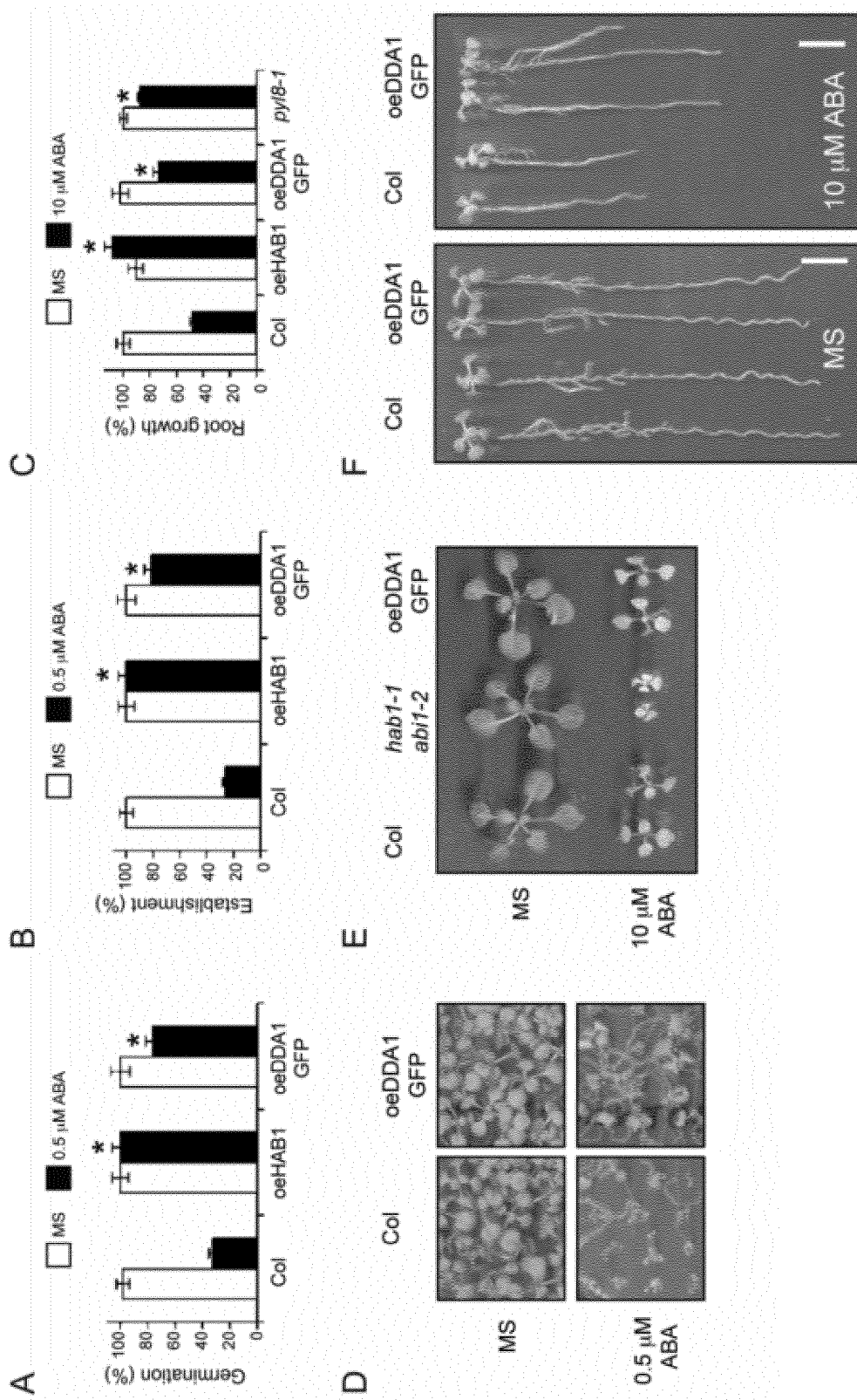


FIGURE 6

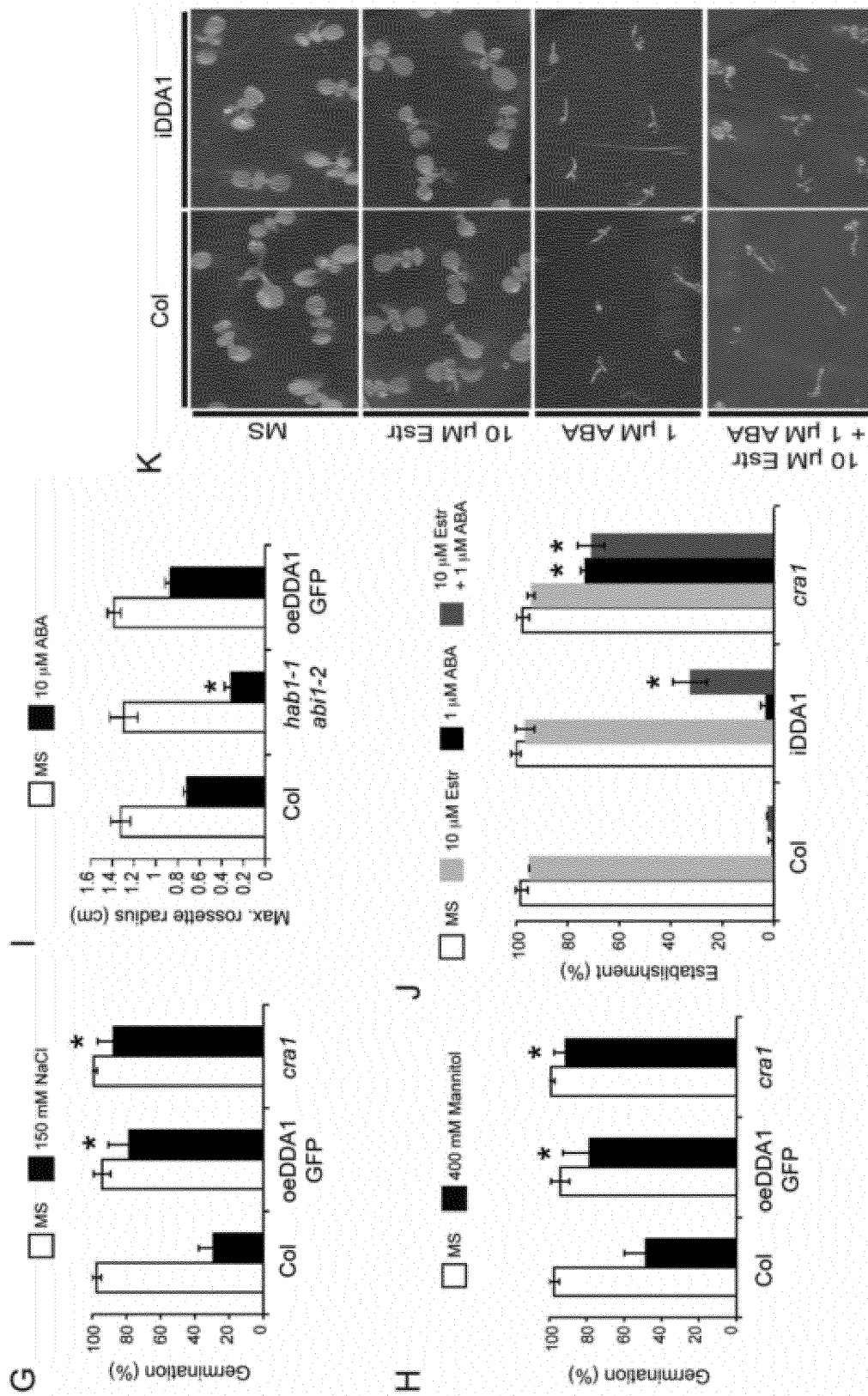


FIGURE 6

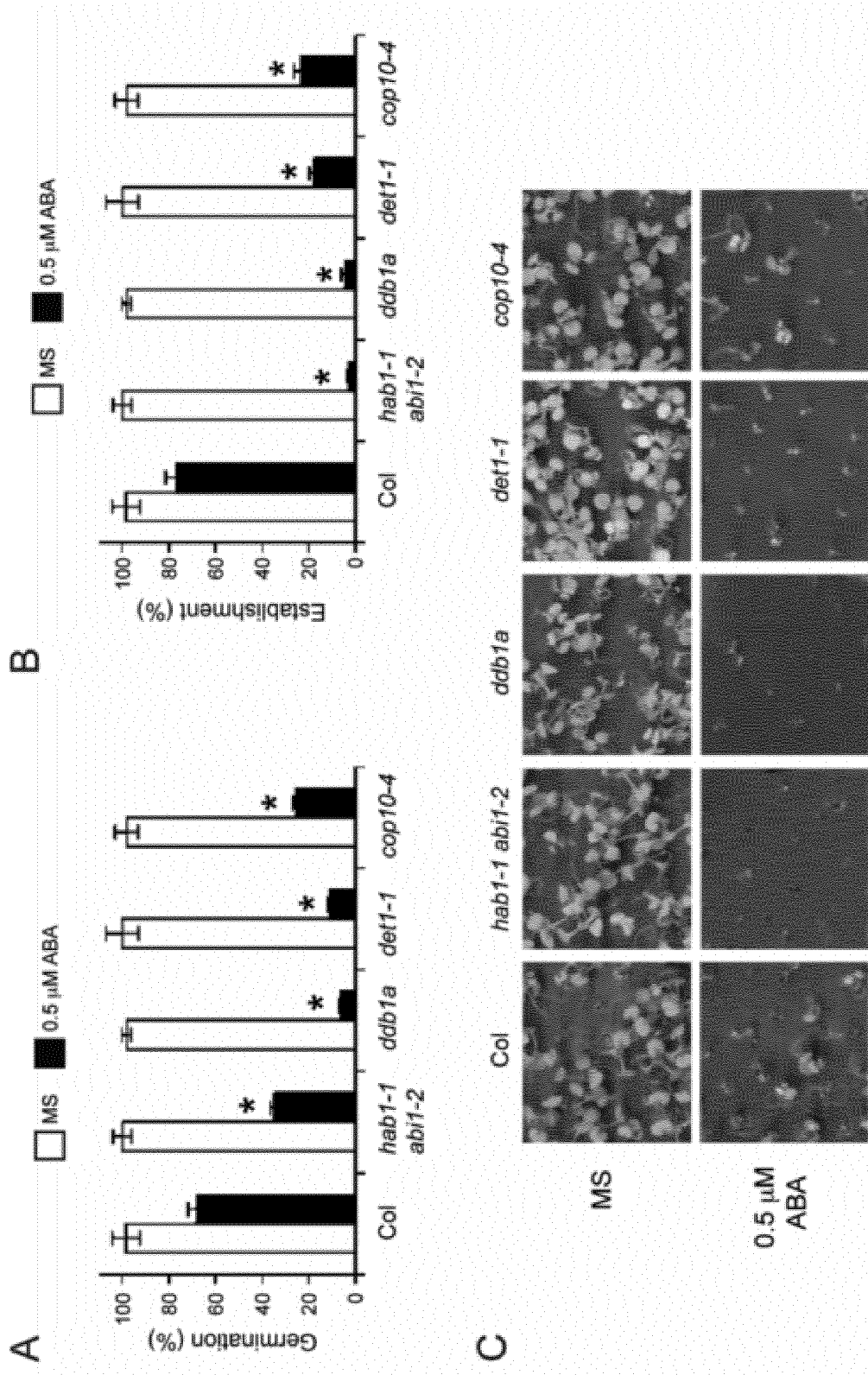


FIGURE 7

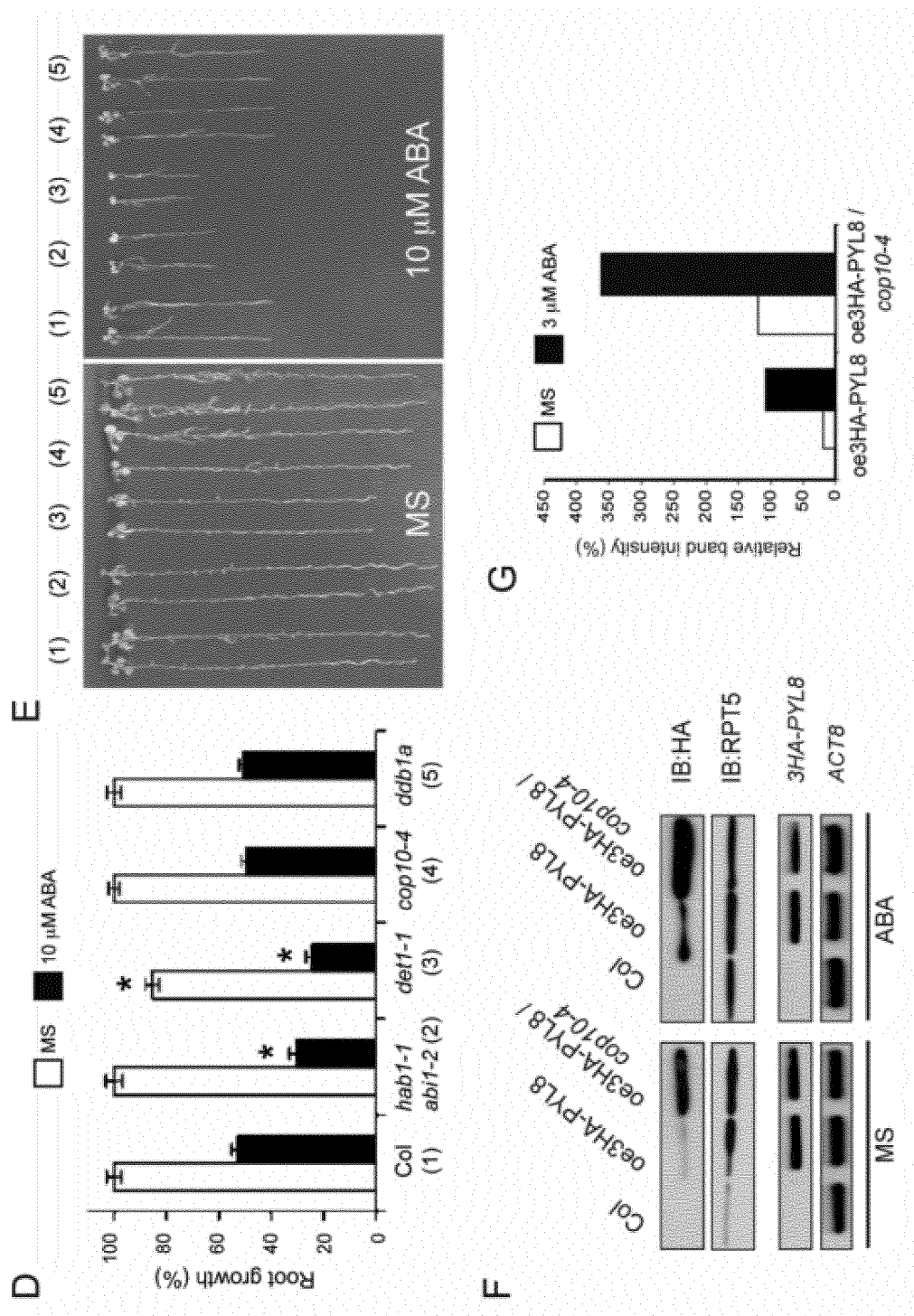


FIGURE 7

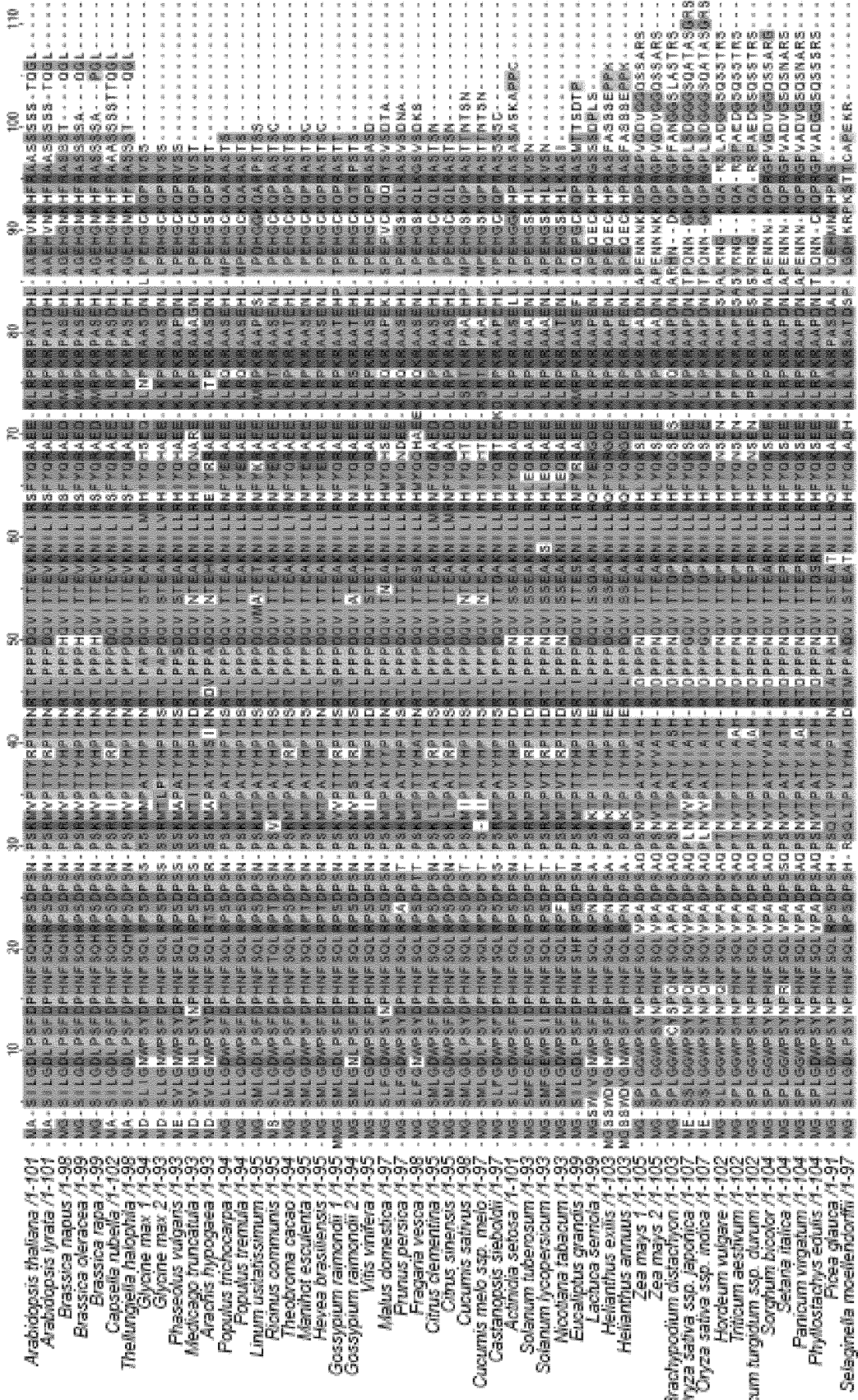


FIGURE 8

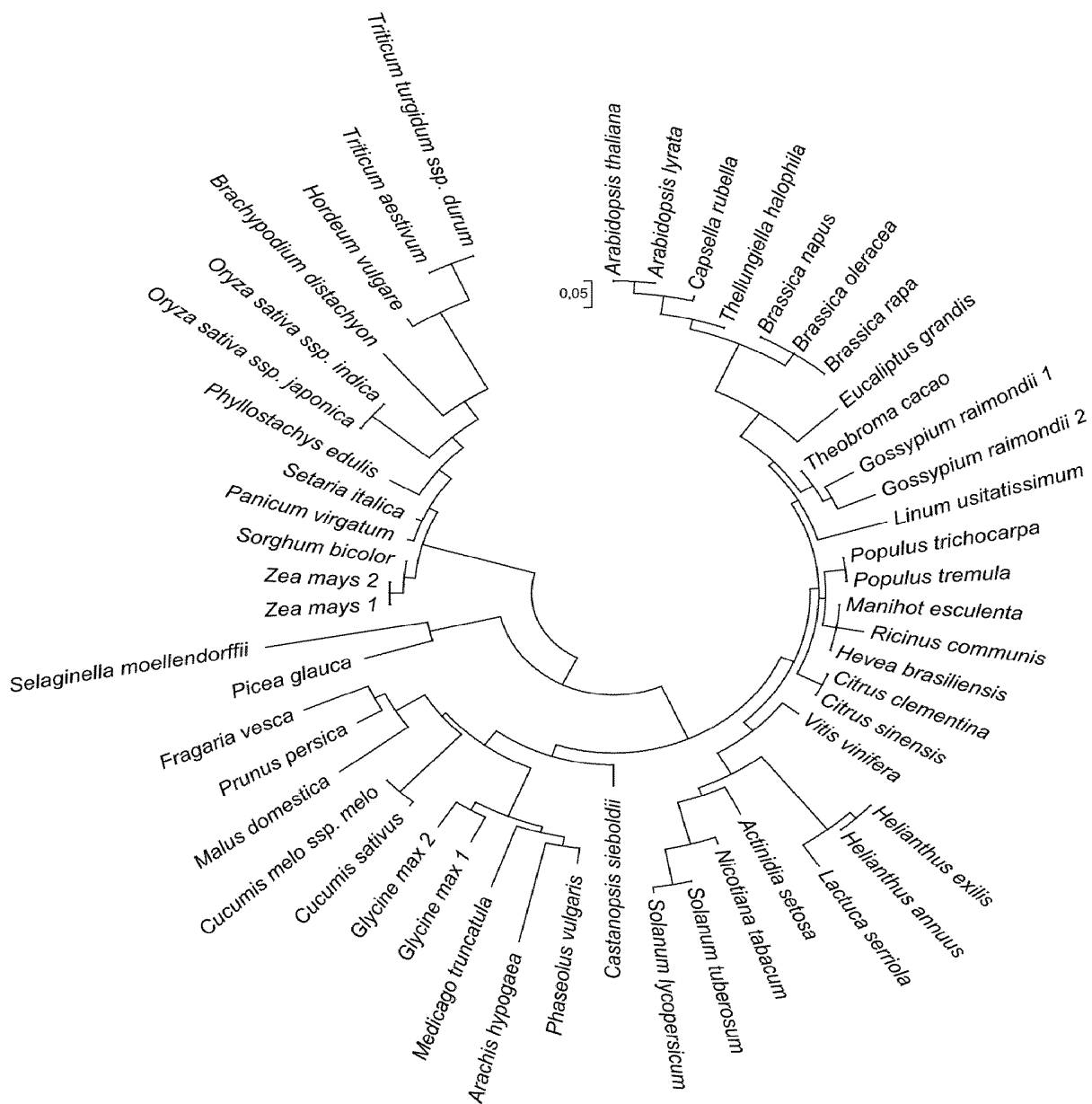


FIGURE 9

INTERNATIONAL SEARCH REPORT

International application No PCT/EP2014/061214

A. CLASSIFICATION OF SUBJECT MATTER INV. A01H5/00 C12N15/82 ADD.				
According to International Patent Classification (IPC) or to both national classification and IPC				
B. FIELDS SEARCHED				
Minimum documentation searched (classification system followed by classification symbols) A01H C12N				
Documentation searched other than minimum documentation to the extent that such documents are included in the fields searched				
Electronic data base consulted during the international search (name of data base and, where practicable, search terms used) EPO-Internal, BIOSIS, Sequence Search, EMBASE, MEDLINE, WPI Data				
C. DOCUMENTS CONSIDERED TO BE RELEVANT				
Category*	Citation of document, with indication, where appropriate, of the relevant passages	Relevant to claim No.		
X	EP 1 033 405 A2 (CERES INC [US]) 6 September 2000 (2000-09-06) Seq. ID Nos 76261 and 76263; abstract; paragraphs [0046], [0056], [0061], [0069]; pages 326 (paragraph [2279]) to 329; claims 1-34	20-33, 35-43		
X	----- US 2006/123505 A1 (KIKUCHI SHOSHI [JP] ET AL) 8 June 2006 (2006-06-08) Seq. ID No. 34210; claims 1-20; pages 12 and 13	20-33, 35-43		
X	----- US 2004/216190 A1 (KOVALIC DAVID K [US]) 28 October 2004 (2004-10-28) Seq. ID Nos 8841 and 8469; pages 3 and 6-9 ----- -/--	20-33, 35-43		
<table style="width: 100%; border: none;"> <tr> <td style="width: 50%; border: none;"><input checked="" type="checkbox"/> Further documents are listed in the continuation of Box C.</td> <td style="width: 50%; border: none;"><input checked="" type="checkbox"/> See patent family annex.</td> </tr> </table>			<input checked="" type="checkbox"/> Further documents are listed in the continuation of Box C.	<input checked="" type="checkbox"/> See patent family annex.
<input checked="" type="checkbox"/> Further documents are listed in the continuation of Box C.	<input checked="" type="checkbox"/> See patent family annex.			
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"A" document defining the general state of the art which is not considered to be of particular relevance "E" earlier application or patent but published on or after the international filing date "L" document which may throw doubts on priority claim(s) or which is cited to establish the publication date of another citation or other special reason (as specified) "O" document referring to an oral disclosure, use, exhibition or other means "P" document published prior to the international filing date but later than the priority date claimed	"T" later document published after the international filing date or priority date and not in conflict with the application but cited to understand the principle or theory underlying the invention "X" document of particular relevance; the claimed invention cannot be considered novel or cannot be considered to involve an inventive step when the document is taken alone "Y" document of particular relevance; the claimed invention cannot be considered to involve an inventive step when the document is combined with one or more other such documents, such combination being obvious to a person skilled in the art "&" document member of the same patent family			
Date of the actual completion of the international search	Date of mailing of the international search report			
30 September 2014	10/10/2014			
Name and mailing address of the ISA/ European Patent Office, P.B. 5818 Patentlaan 2 NL - 2280 HV Rijswijk Tel. (+31-70) 340-2040, Fax: (+31-70) 340-3016	Authorized officer Kurz, Birgit			

INTERNATIONAL SEARCH REPORT

International application No

PCT/EP2014/061214

C(Continuation). DOCUMENTS CONSIDERED TO BE RELEVANT		
Category*	Citation of document, with indication, where appropriate, of the relevant passages	Relevant to claim No.
A	<p>K. E. HUBBARD ET AL: "Early abscisic acid signal transduction mechanisms: newly discovered components and newly emerging questions", GENES & DEVELOPMENT, vol. 24, no. 16, 15 August 2010 (2010-08-15), pages 1695-1708, XP055143137, ISSN: 0890-9369, DOI: 10.1101/gad.1953910 the whole document, in particular pages 1695, 1696, 1700</p> <p>-----</p>	1-50
A	<p>WO 2007/011681 A2 (BASF PLANT SCIENCE GMBH; SARRIA-MILLAN RODRIGO [US]; GARR ERIC R [US];) 25 January 2007 (2007-01-25) abstract; pages 4-7; claims 1-48</p> <p>-----</p>	1,5-19
A	<p>MARTÁN BEATRIZ ET AL: "A high-density collection of EMS-induced mutations for TILLING in Landsberg erecta genetic background of Arabidopsis", BMC PLANT BIOLOGY, BIOMED CENTRAL, LONDON, GB, vol. 9, no. 1, 14 December 2009 (2009-12-14), page 147, XP021066514, ISSN: 1471-2229 cited in the application The whole document, in particular abstract; Table 2 and Figure 2</p> <p>-----</p>	48-50
X,P	<p>M. L. IRIGOYEN ET AL: "Targeted Degradation of Abscisic Acid Receptors Is Mediated by the Ubiquitin Ligase Substrate Adaptor DDA1 in Arabidopsis", THE PLANT CELL ONLINE, vol. 26, no. 2, 21 February 2014 (2014-02-21), pages 712-728, XP055142559, ISSN: 1040-4651, DOI: 10.1105/tpc.113.122234 The whole document, in particular abstract, pages 712, 713, 716, 717, 719, 725; Figure 7</p> <p>-----</p>	1-50

INTERNATIONAL SEARCH REPORT

Information on patent family members

International application No

PCT/EP2014/061214

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EP 1033405	A2	06-09-2000	NONE
US 2006123505	A1	08-06-2006	JP 2005185101 A US 2006123505 A1
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