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Identification of auxin responsive genes in *Arabidopsis* by cDNA array

BAO Fang, HU Yuxin & LI Jiayang Q94 A

Institute of Genetics, Chinese Academy of Sciences, Beijing 100101, China

Correspondence should be addressed to Li Jiayang (e-mail: jyli@genetics.ac.cn)

Abstract **The plant hormone auxin influences a variety of developmental and physiological processes. But the mechanism of its action is quite unclear. In order to identify and analyze the expression of auxin responsive genes, a cDNA array approach was used to screen for genes with altered expression from *Arabidopsis* suspension culture after IAA treatment and was identified 50 differentially expressed genes from 13824 cDNA clones. These genes were related to signal transduction, stress responses, senescence, photosynthesis, protein biosynthesis and transportation. The results provide the molecular evidence that auxin influences a variety of physiological processes and pave a way for further investigation of the mechanism of auxin action. Furthermore, we found that the expression of a *ClpC* (regulation subunit of Clp protease) was repressed by exogenous auxin, but increased in dark-induced senescing leaves. This suggests that *ClpC* may be a senescence-associated gene and can be regulated by auxin.**

Keywords: cDNA array, auxin responsive genes, *Arabidopsis thaliana*, *ClpC*, senescence-associated genes.

Auxin influences a variety of developmental and physiological processes, including cell division and expansion, vascular tissue differentiation, lateral root formation, tropism and leaf senescence. Although the physiological effects of auxin have been extensively studied, the molecular mechanisms of auxin action is poorly understood. Within the past decade, two complementary strategies have been used and produced remarkable results. One is to characterize mutants defective in auxin response, which led to the establishment of the ubiquitin-proteasome pathway in regulation of auxin responses[1]. The other strategy is to study auxin-regulated gene expression, resulting in the identification of several classes of early auxin response genes[2]. However, the function of early auxin response genes and genes downstream of them are still unclear, target proteins of the ubiquitin-proteasome pathway have not been identified, and the interactions between the ubiquitin-proteasome pathway and early auxin response genes are waiting to be dissected. Identification of auxin responsive genes in a global way will be helpful for further understanding of molecular mechanism of auxin action and the auxin signal transduction pathways.

Auxin represses leaf senescence processes. But the regulation of senescence-associated genes by auxin has not been reported yet. Leaf senescence process involves a sequence of degradative processes and is highly regulated. A variety of genes, such as genes encoding proteases and RNases, have been identified to be senescence-inducible[3]. Plant Clp (chloroplast protein) protease is a highly selective protease in chloroplast[4]. Although several of its subunits have been suggested to have a role in the senescence process, some other subunits are not induced by senescence and the role of Clp protease in plant senescence remains unknown[5].

Here, we reported that 50 auxin responsive genes in *Arabidopsis thaliana* were identified and analyzed among 13824 cDNA clones with a cDNA array method[6] and a *ClpC* gene repressed by auxin was further characterized.

1 Materials and methods

(i) Plant material. *Arabidopsis thaliana* ecotype Columbia (Col-0).

(ii) Suspension culture and plant hormone treatments. Suspension culture was established as previously described[7]. After hormone starvation for 48 h, suspension cells were treated with 5 μmol/L indole-3-acetic acid (IAA) for 0, 1 and 3 h, respectively. RNA were extracted and used in preparation of cDNA probe with reverse transcription approach. For Northern blot analysis, suspension cells were treated with 5 μmol/L IAA and 100 μmol/L abscisic acid (ABA) for 0, 1, 2, 4 and 8 h, respectively.

(iii) cDNA array. The cDNA array procedure was performed as previously described[7]. Each of the 13824 cDNA clones from an *Arabidopsis* seedling cDNA library was deposited on reinforced nitrocellulose filters (Schleicher & Schuell, Germany) with additional two duplicates for each cDNA clone by Biomek 2000 system (Beckman, USA). Three sets of the arrayed filters were prepared. Filters were probed with [α-^{32}P]-dCTP labelled first strand cDNA. The reverse transcription procedure was done as previously described[7]. The signals were analyzed with Phosphoimager (Molecular Dynamics, USA).

(iv) RNA preparation and Northern blot analysis. Total RNA was isolated according to the guanidinium-thiocyanate-chloroform extraction procedure[8]. RNA samples were stored at −20℃ after quantification.

15 μg total RNA of each sample was fractionated in a formaldehyde agarose gel, blotted onto Hybond-N$^+$ nylon filters (Amersham Pharmacia, USA) and immobilized by baking at 80℃ for 2 h. Hybridization was performed as previously described[9]. Signals were analyzed with phosphoimager (Molecular Dynamics, USA). All data shown were calibrated against the loaded RNA stained with ethidium bromide (EtBr).

(v) Sequence analysis. Differentially expressed cDNA clones were subcloned into a pBluescript II SK(+)

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vector and sequenced with a DYEnamic Direct dGTP cycle seq kit (Amersham Pharmacia, USA) on an ABI373A DNA sequencer (Perkin Elmer, USA). Nucleotide or amino acids homology was blasted against Genbank database.

(vi) Induction of leaf senescence in dark. The last four leaves (leaves 5—8) were detached from Col-0 plants forming 8 rosette leaves and submerged completely in either distilled water or 5 μmol/L IAA in darkness for 3 d. Samples were taken once a day and frozen in liquid nitrogen. Control leaves were detached from plants on the last day of treatment.

2 Results

(i) Identification of auxin responsive clones. To identify genes responsive to auxin, we took the cDNA array approach to monitor gene differential expression of Col-0 suspension cells treated with 5 μmol/L IAA for 0, 1 and 3 h. First strand cDNA probes reverse-transcripted from total RNA were hybridized with high-density filters containing 13824 cDNA clones and differentially expressed clones were selected. To reduce the possible false positives caused by the difference of sample deposit among filters, hybridization was performed twice with changed filters and only those clones that showed similar expression patterns in the two hybridizations were chosen (fig. 1).

To confirm the differential expression of the selected clones, Northern blot analyses were performed for 27 clones, and 21 clones were found to have similar responses as in cDNA array (fig. 2), indicating that the cDNA array method was reliable in monitoring differential expression of genes.

Based on the verification of Northern blotting analysis, 50 differentially expressed clones were identified from 13824 cDNA clones, 25 of them were induced by IAA, and the other 25 clones were repressed.

(ii) Analysis of auxin responsive genes. Based on sequence homology, 16 clones (7 clones were repressed and 9 induced) were novel genes, and the remaining 34 clones were classified into 6 groups based on the functions of their homologous genes, including genes related to signal transduction, stress responses, senescence, photosynthesis and CO_2 fixation, protein translation and translocation and genes have not been grouped yet (table 1).

(iii) Preliminary analysis of the *ClpC* gene expression. The auxin-repressed clone, J2, represents an *Arabidopsis ClpC* gene whose function was unknown. ClpC was the regulation subunit of Clp protease, and several subunits of Clp protease were related to senescence[5]. Expression of the *ClpC* was analyzed by Northern blot to demonstrate whether it is a senescence-associated gene. When suspension cells were treated with 5 μmol/L IAA, *ClpC* mRNA level was decreased within 1 h and reached the lowest level at 4 h (about 30% of the control, fig. 3(a)).

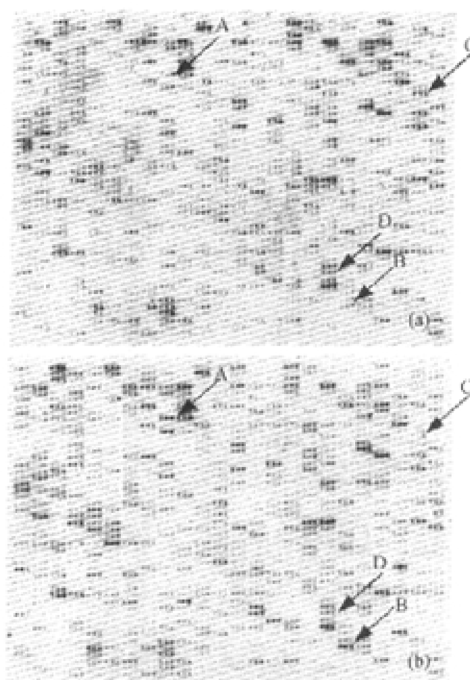

Fig. 1. Identification of auxin responsive genes by using cDNA array. (a) Control; (b) treatment with 5 μmol/L IAA for 3 h. Arrows indicate the differentially expressed clones: A and B are exogenous auxin induced clones; C and D are exogenous auxin repressed clones.

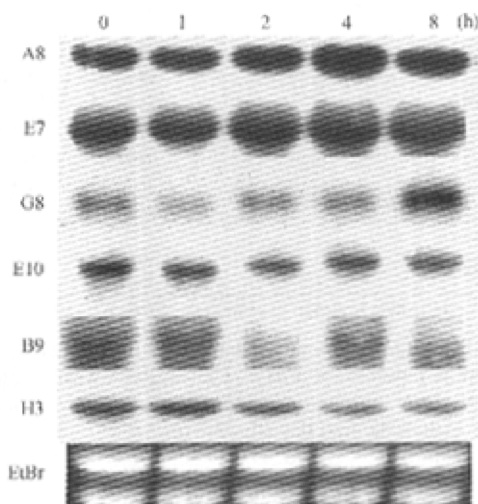

Fig. 2. Northern hybridization of some auxin responsive clones. RNA were isolated from Col-0 suspension cells treated with 5 μmol/L IAA for 0, 1, 2, 4 and 8 h, respectively. 15 μg total RNA was loaded in each lane.

When treated with 100 μmol/L ABA, *ClpC* was induced after 4 h and accumulated more than 6 fold compared to the control at 8 h (fig. 3(b)). In dark-induced senescing leaves, *ClpC* mRNA level increased rapidly within the

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Table 1 *Arabidopsis* genes regulated by auxin

Clone No.	Expression	Homolgous gene /protein	Accession No.	Identity(%)
Related to signal transduction				
F8	repressed	*CaM 2*	U19925	97a)
E10	repressed	Myb-related transcription factor	Z68157	95a)
H2	induced	*AtCNGC2*	AF067798	88a)
B3	repressed	*Smt3*	X99609	93a)
Related to stress responses				
A5, D5	repressed	*Catalase 1*	AF021937	97a)
H3	repressed	*AtMEKK1*	D50468	96a)
B1	repressed	*Ferritin1*	AF229850	98a)
C1	repressed	*At-RSH3*	AF225704	96a)
F10	repressed	*Hsl Pro-1*	AAB95282	75b)
Senescence associated genes				
J2	repressed	*ClpC*	AB017063	96a)
B9, D9	repressed	*Atgsr2*	S69727	100a)
Related to photosynthesis and CO_2 fixation				
A3, C9	induced	*Cab*	AF143691	100a)
D4	induced	NAC2-like protein	AL132964	74b)
A1	induced	Phosphate/triose-phosphate translocator	AF097648	98a)
B4, G8	induced	*GapA*	M64117	80a)
J3	induced	Phosphoenolpyruvate carboxykinase	PC2167	90a)
E4	induced	Carbonic anhydrase	X65541	94a)
Related to Protein translation and translocation				
E7	induced	*EF-1 α-A4*	X16432	89a)
A7	induced	*HSC70*	X74604	90a)
E1	induced	Putative clathrin heavy chain	AAF01510	98b)
Others				
B53	repressed	*AtCDC5*	D58424	90a)
F5	induced	Chloroplast RNA binding protein	D31712	98a)
G9, G10	induced	Putative cytochrome P450	O22203	98a)
D2	repressed	Methionine synthase	U97200	96a)
A2	induced	Putative copper methylamine oxidase	AC007087	79a)
H5	induced	Adenylate translocator	X65549	90a)
F1	repressed	Aminomethyltransferase precursor	AC002131	59b)
Unknown				
16 clones	repressed/induced			

a) Nucleotide sequence; b) amino acid sequence.

first day (5.2 fold compared to T0 control) and leaves treated in darkness for 3 days, *ClpC* mRNA was 11 fold of control. IAA inhibited the induction of *ClpC* by senescence with in the first day (fig. 3(c)).

3 Discussion

The auxin affects a variety of processes in plant growth and development. In order to investigate the mechanism of auxin action, it is necessary to study auxin responsive genes systematically. With a cDNA array method, we have identified auxin responsive genes with suspension culture of *Arabidopsis*. We employed suspension culture as material because plant suspension cells react to auxin rapidly[10] and the interference of other growth regulators can be eliminated in this system. The cDNA array method makes it possible to monitor gene differential expression systematically and effectively. This approach has been proved to be highly accurate[6] (fig. 2) and used successfully in the identification of brassinisteriod responsive genes[7, 11].

(i) Auxin responsive genes. The identified auxin responsive genes include genes related to signal transduction, stress response, senescence and photosynthesis, and consist with the physiological function of auxin. It is interesting that two signal transduction genes, *Calmodulin 2* (*CaM2*) and cyclic nucleotide-gated cation channel, cng channel (*AtCNGC2*) are repressed by auxin. *AtCNGC2*

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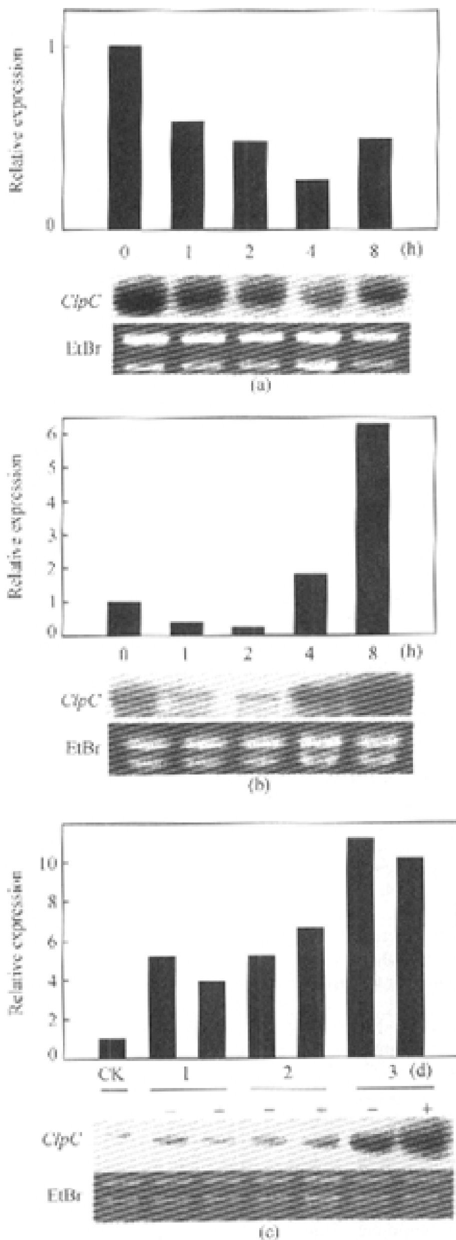

Fig. 3. Expression pattern of *ClpC*. (a) Col-0 suspension cells treated with 5 μmol/L IAA for 0, 1, 2, 4 and 8 h; (b) Col-0 suspension cells treated with 100 μmol/L ABA for 0, 1, 2, 4 and 8 h; (c) induction of leaf senescence in dark for 0, 1, 2 and 3 d. –, without IAA; +, 5 μmol/L IAA.

encodes a pore-forming subunit of cng channel protein[12]. It facilitates the conductance of cations, such as K^+, Ca^{2+}, or Na^+ across cell membranes upon the direct binding of cAMP or cGMP. Animal cng channels transform the alteration of cytosolic cAMP or cGMP level into cell membrane potential or cation flux and trigger the signal transduction cascade[13]. The regulation of *AtCNGC2* and *CaM2* suggests that auxin might act through a Ca^{2+} or Ca^{2+}/CaM dependent signal pathway. Auxin might also regulate gene expression through Myb-related transcription factors. Smt3 (suppressor of *mif2*) is a ubiquitin-like molecule. The regulation of *smt3* expression suggests a possible point for auxin signal to feed into the ubiquitin pathway.

Several evidence implied some kind of cross-talk between auxin and stress responses. Early auxin response family *GH2/4*-like genes can be induced not only by auxin but also by a variety of stress signals[14]. Genes involved in IAA metabolism, such as *nitrilase 2* (*NIT2*) and *IAA-Ala hydrolase* (*IAR3*), can be induced by wounding[15] or pathogens[16], and lead to the increase of free IAA. Five stress-inducible genes are found to be auxin responsive. *Arabidopsis* homologue of *MEKK* (*ATMEKK1*) encodes a mitogen-activated protein kinase kinase kinase (MAPKKK), which can be induced by cold and osmotic stress[17]. *At-RSH3* is a homolog of *E. coli RelA/SpoT* gene, which is recently identified in plants[18]. In bacteria, RelA/SpoT regulates the level of (p)ppGpp, which plays a central role in bacterial stringent response. The characterization of *At-RSH3* suggests that a rapid plant (p)ppGpp mediated response to stress may also exist in plants[18]. Catalase 1 catalyzes the dismutation of H_2O_2 produced as a consequence of environment insults. Genes encoding catalase can be induced by variety of environment stresses[19]. *Fer1* (*ferritin1*) is induced by cold[20] and plays a role in plant tolerance to oxidative damage and pathogens[21].

Auxin represses leaf senescence. *Atgsr2* encodes a glutamine synthetase in chloroplast[22], involving in the recycle of nitrogen from senescence leaves to developing leaves. *Atgsr2* can be induced by senescence and is a senescence-associated gene.

AtCDC5 is a homolog of yeast *cdc5*+. It is expressed at meristem of shoots and roots and has been suggested to have a similar function in cell cycle as cdc5+and promotes the transition from G2 into M phase[23]. Auxin may affect cell division or the initiation of lateral roots through *AtCDC5*.

Early reports showed that IAA promoted photosynthesis and CO_2 fixation in leaves or in isolated chloroplast[24]. Genes involved in chloroplast biogenesis and photosynthesis (chlorophyll a/b binding protein, Cab) and CO_2 fixation (phosphate/triose-phosphate translocator, phosphoenolpyruvate carboxykinase) are induced by auxin. Besides, genes involved in peptide synthesis (elongation factor-1a-A4, EF-1a-A4) and protein translocation (clathrin heavy chain and Heat shock cognate 70, HSC70) are also up-regulated by IAA treatment.

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The identification of auxin responsive genes shows that genes related to cell growth or cell division are up-regulated by auxin, while genes involved in senescence or stress response are down-regulated. The results are consistent with the function of auxin to promote growth and repress senescence, and they pave a way for further investigation of auxin mechanism.

(ii) *ClpC* is induced in senescing leaf. Clp protease is a highly selective protease in chloroplast, which consists of two types of subunits, the regulatory subunit ClpC and the catalytic subunit ClpP[4]. Several subunits of Clp protease have been characterized in plant[25—27]. Clp protease may be composed of complicated combinations of subunits[5]. Regulatory subunit ERD1 and catalytic subunits nClpP5 and pClpP have been found to participate in the degradation of proteins in senescing chloroplast but other subunit such as *AtClpC* is not induced by senescence[5]. Until now there is no report about the function and expression pattern of the auxin-responsive *ClpC*. Because senescence-associated genes are induced significantly in dark treated detached leaves[28], we examined the expression of the *ClpC* in dark-induced senescing leaves to study if this *ClpC* is related to senescence process. We found that the expression of *ClpC* was increased significantly during dark treatment and exogenous application of IAA repressed the accumulation of its mRNA (fig. 3(c)). Treatment with ABA also induced the expression of *ClpC* (fig. 3(b)). These results indicate that the *ClpC* might be a senescence-associated gene.

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作者： BAO Fang， HU Yuxin， LI Jiayang

作者单位： Institute of Genetics, Chinese Academy of Sciences, Beijing 100101,China

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