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Differential display analysis of gene expression in plants

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Abstract. This review deals with the application of differential display to investigate gene expression in plants. A substantial articles reports the isolation and profiling of various genes expressed in cells using this technique. Genes involved in physiological events, stress responses, signal transduction and secondary metabolism have been isolated and characterized. Some of the isolated genes encode transcription factors, membrane proteins and rare enzymes that were previously difficult to purify. These results suggest that differential display is a powerful tool used to investigate the rare genes involved in the plant life cycle without using information from proteins.

Key words. Differential display; plant gene; secondary metabolism; chemotype.

Introduction

The differential display (DD) was first reported by Liang and Pardee [1]. This method can be used to amplify low-abundance transcripts by polymerase chain reaction (PCR). It was statistically indicated that 80–120 primer combinations would be sufficient to cover all the transcript populations in cells [2]. This technique possesses the following advantages over other similar techniques: it is based on simple and established methods, it does not require biochemical information about proteins, more than two samples can be compared simultaneously, and only a small amount of starting material is needed. In the last 10 years, DD has been used to isolate genes from plants which are involved in physiological events, signal transduction, stress response and secondary metabolism. With DD, scientists have been able to isolate genes encoding membrane proteins and transcription factors; these genes occur in small amounts, thus are typically difficult to identify. Differential display has also been used to inclusive profiling of genes expressed in particular plant cell types.

Gene expression in physiological events

The DD analyses of plant gene expression in various physiological events are summarized in table 1. An expression profile of the genes responding to phytohormones [3–18] and related to decapitation [19], dormancy [20, 21], cell cycle [22, 23] and programmed cell death [24–28] were imaged, and some of the genes were characterized. In these studies, several regulatory factors were isolated. The genes expressed during morphological development such as embryogenesis [29–34], flower development [35–41] and fruit maturation [42, 43] were profiled, and tissue-specific gene expression in endosperm [44], seed coat [45], fiber [46], root tip [47] and haustrium [48] was investigated. These experiments allowed scientist to isolate the genes for homeobox proteins and their target sequences and tissue-specific enzyme genes. Gene expression during fruit ripening was studied [49–52]. Photoregulation mediated by phytochromes was profiled [53, 54], and genes involved in photoperiodic regulation [55–57] and circadian rhythm [58] were isolated. Genes used in productivity [59–64] and nutrient metabolism [65, 66] were also isolated.

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Isolation of genes involved in stress response

Application of differential display to stress response in plants is summarized in table 2. The stress response genes affected by environmental factors such as ultraviolet (UV) light exposure, extreme temperatures, oxygen, salt and desiccation was isolated using by DD and characterized [67–85]. The genes involved in signal transduction mediated by salicylic acid [86, 87] and methyljasmonic acid [88–90], and in wounding [91–94], were profiled. Genes specifically expressed under elicitor treatment [95–101] – and chemical induction [102] – were isolated using DD. Several defense genes which are expressed in response to attacks by pathogens [103–113] and herbivores [114, 115] were obtained. In plant-microbe interactions such as symbiosis, induced genes were isolated and characterized [116–122]. Information about the functions of these genes will provide agriculturally valuable leads.

Isolation of genes involved in secondary metabolism

Genes involved in secondary metabolism are expressed at relatively low levels in comparison with primary metabolism. Also, secondary pathways consist of multiple catalytic steps. That makes it time- and energy-consuming to purify each of the responsible catalytic enzymes, and only limited information about proteins involved in secondary metabolism has been available. Because their expression profiles is restricted to particular cells, genetically defined lines, developmental stages and induction, they can be analyzed using DD.

DD has been used to isolate genes involved in secondary metabolism from different chemically defined phenotypes (chemotypes) and through inductive conditions such as elicitor treatments (summarized in table 3).

Isolation of novel genes from chemotypes

Chemotypes exhibiting different patterns of secondary products with similar genetic background have been genetically defined in phytochemical studies. Anthocyanin production is used to define two distinct forms of the plant, *Perilla frutescens* var. crispa (perilla). In the red form, anthocyanin pigments, mainly malonyl shisonin, accumulate in epidermal cells of leaves and stems, whereas anthocyanin pigments do not accumulate in the green form. At least three loci were believed to control pigmentation in the upper and lower epidermis of leaves and stems [123]. Anthocyanins are produced through two stages of biosynthetic reactions. The early-stage reactions are involved in the formation of anthocyanidin 3-*O*-glucoside, which is the first stable, colored metabolite in anthocyanin biosynthesis. The late stage involves modification of anthocyanin molecules such as glycosylation, acylation and methylation. The diversity of the modifications in the late stages determines the type of anthocyanins synthesized. However, the peptide sequences of the modifying enzymes were unavailable owing to low quantity and/or instability of the enzyme, thus making them difficult to purify. Screening strategies using heterologous forms were unsuccessful. The genes that were expressed specifically in the red form were isolated by comparing messenger RNA (mRNA) DD profiles between red and green perilla forms. Five complementary DNA (cDNA) fragments expressed specifically in the red form were isolated. Using these fragments as probes for library screening, the cDNAs encoding UDP-glucose:anthocyanin 5-*O*-glucosyltransferase (5-GT) [124] and anthocyanidin synthase [125] were isolated. Glucosylation at the 5-*O*-position affects stabilization of anthocyanin molecules and the formation of copigmentation complexes. This results in flowers with bright reddish-purple color rather than a dull violet or pure red when 5-*O*-glycosylation does not take place. Thus, 5-GT is one of the most important enzymes modifying flower color to a purple hue. The 5-GT cDNA encodes a polypeptide of 460 amino acids, exhibiting a low homology with the sequences of several glucosyltransferases, including UDP-glucose:anthocyanidin 3-*O*-glucosyltransferase (3-GT).

To identify the biochemical function of the encoded proteins, these cDNAs were expressed in *Saccharomyces cerevisiae* cells. Yeast extracts containing the recombinant protein catalyzed the conversion of anthocyanidin 3-*O*-glucosides into corresponding anthocyanidin 3,5-di-*O*-glucosides with UDP-glucose as a cofactor, thus indicating the identity of the cDNA encoding 5-GT. Several biochemical properties (optimum pH, K_m values and sensitivity to inhibitors) were similar to those reported previously for 5-GTs from plant extracts. Southern blot analysis indicated the presence of two copies of 5-GT genes in the genomes of both red and green forms of *P. frutescens*. The accumulation of the 5-GT mRNA was detected in the leaves of red forms but not in green forms and was induced by exposure to light. This characteristic was observed for other genes involved in anthocyanin biosynthesis in *P. frutescens*. Moreover, 5-GT homologue genes were isolated from several other plant species, and substrate specificity was investigated.

Similarly way, the cDNA encoding flavone synthase II was isolated from *Gerbera* hybrids of two different chemogenetically defined lines with the dominant (*fns*+) or recessive (*fns fns*) alleles at the locus *Fns* using DD[126]. An *fns*+ specific cytochrome P450 fragment was isolated using selective DD PCR with upstream primers based on the conserved heme binding region. Microsomes from yeast cells expressing this isolated transcript catalyzed the direct formation of flavones from their respective precursor flavanones.

Table 1. Application of differential display technique for physiological events in plants.

Physiological events	Plant species	Tissue or cells used, and treatment	Obtained gene or encoded protein	Ref.
Phytohormone response				
auxin	*Nicotiana tabacum*	auxin treatment	AUX/IAA gene family	3–5
	Pinus taeda	adventitious root induced with IBA	α-expansin homologue	6
cytokinin	*Nicotiana tabacum*	protoplast culture, BAP+/–	unknown	7
	Arabidopsis thaliana	etiolated seedlings, cytokinin +/–	response-regulator homologue	8
	Zea mays	detached leaves, cytokinin +/–	response-regulator homologue	9
gibberellin (GA)	*Oryza sativa*	GA +/–	ubiquitin-conjugating enzyme, histon H3, replication protein A1 ortholog, Ca^{2+}-ATPase	10–13
	Zea mays	wild-type/dwarf mutant, GA +/–	proline-rich protein	14
	Lycopersicom, *esculentum*	GA deficient mutant, GA +/–	vacuolar H^{+}-ATPase	15
ethylene	*Lycopersicom esculentum*	ethylene +/–	LEA-like protein	16
	Arabidopsis thaliana	*etr1* mutant, ethylene +/–	nuclear protein	17
abscisic acid (ABA)	*Vicia faba*	guard cells, ABA +/–	unknown	18
Decapitation	*Medicago truncatula*	nodule from decapitated/ control plants	RNA-binding homologue	19
Dormancy	*Avena fatua*	dormant/nondormant embryos	glutathione peroxidase-like protein	20
	Pisum sativum	dominant axillary buds, decapitation	unknown	21
Cell cycle	*Arabidopsis thaliana*	proliferative cell /growth-arrested cells	molecular markers	22
		synchronized cell-division	histone H2A.F/Z family	23
Programmed cell death (PCD)	*Hordeum vulgare*	dark induced senescence	proteinase inhibitor, 4-hydroxy-phenylpyruvate dioxygenase	24
	Phaseolus vulgaris	yellow/green leaves	receptor-like protein kinase	25
	Lycopersicom esculentum	camptothecin-induced PCD	PIRIN homologue, GST-like protein, AuX/IAA early-auxin-responsive gene, RSI-I, proline-rich protein	26, 27
	Arabidopsis thaliana	yellow/green leaves	β-glucosidase homologues, strictosidine synthase homologue, lipid transfer protein, aspartate aminotransferase, protease I, cytochrome P450, DimI, hin1	28
Morphological development				
embryogenesis	*Solanum melongena*	somatic embryogenesis	unknown	29
	Brassica napus	young embryo	MADS domain protein (AGAMOUS-like)	30
	Arabidopsis thaliana	developing seed	novel embryo-specific genes	31
	Zea mays	proembryo/microspore	unknown	32
	Daucus carota	embryogenic/nonembryogenic cells	thaumatin-like protein, proline-rich protein	33
	Lycopersicom esculentum	growth regulator supplement	molecular markers	34
flower	*Arabidopsis thaliana*	*ap3 pi* mutant	target gene of APETALA3/PISTILLATA	35
		pi/pi ag floral homeotic mutants	endo-1,4-β-D-glucanase	36
		abi3 fus3 double mutant	gene set negatively regulated by *ABI3 FUS3*	37
	Dendrobium hybrid	floral transition	MADS-box genes	38
	Malus domestica	flower/leaves	auxin-inducible SAUR genes, ligno-stilene α, β-dioxygenase	39
	Arabidopsis thaliana	flowers, wild-type/*coi1* mutant	myrosinase-binding proteins	40
	Petunia hybrida	nectary tissue	unknown membrane protein	41
fruit	*Malus domestica*	developing fruit/flower buds	homeobox gene	42
	Vitis vinifera	berry/leaf	AGAMOUS, SHATTERPROOF	43

Table 1 (continued)

Physiological events	Plant species	Tissue or cells used, and treatment	Obtained gene or encoded protein	Ref.
Development	*Zea mays*	endosperm/embryo	unknown	44
	Pisum sativum	seed coat/leaves	MADS box transcription factor	45
	Gossypium	immature fibers/stripped ovules	acyl carrier protein	46
	Psium sativum	root tip	H1 histone, H1 histone-like protein	47
	Cuscuta japonica (holoparasitic plant)	haustrium formation	low molecular weight heat shock protein	48
Fruit ripening	*Fragaria chiloensis*	fruit	ripening related genes	49
	Rubus idaeus	fruit	ripening related genes	50
	Capsicum annuum	fruit	cytochrome P450, thionin homologue, defensin against *Colletotrichum gloeosporioides*	51, 52
Photoregulation	*Adiantum capillus-veneis*	spores, red/red-blue / blue light irradiation	profiling, cell wall-associated extensins	53
	Arabidopsis thaliana	wild-type/*phy-A* mutant, far-red light irradiation	phytochrome-regulated genes	54
Photoperiodic regulation	*Pharbitis nil*	flower-inductive darkness	CONSTANS orthologue, function unknown	55, 56
	Solanum tuberosum	tuberizing	drought-stress-responsive tylakid protein	57
Circadian rhythm	*A. thaliana*	circadian rhythm	circadian-clock-controlled genes	58
Reproductive function				
pollination	*Nicotiana tabacum*	pollination	receptor-like protein kinase	59
heterosis	*Triticum aestivum*	hybrid/inbreds	RNA-binding protein	60
self-incompatibility	*Petunia inflata*	S-halotypes pollen	S-RNase-related protein	61
apomixes	*Pennisetum ciliare*	ovules with apomictic/sexual gametophytes	apomixes-related genes	62
	Hieracium piloselloides	autonomous embryogenesis/ mature ovules	DEFICIENS homologue	63
	Paspalum notatum	apomictic/sexual plants	unknown	64
Nutrient	*Spinacia oleracea*	glucose feeding	hexokinase on outer envelope of plastid membrane	65
	A. thaliana	nitrate stress	high-affinity nitrate transporter	66

Table 2. Application of differential display technique for stress response in plants.

Stress treatments	Plant species	Obtained gene or encoded protein	References
UV	parsley	glutathione S-transferase	67
(UV-B)	*Pisum sativum*	short-chain alcohol dehydrogenase	68
(UV-C)	grapefruit	isoflavone reductase-like protein	69
Light	*Arabidopsis thaliana*	dehydration responsive protein, actin2, embryogenesis related, metallothionein, β-1,3-galactosyltransferase homologue	70
Heat	*A. thaliana*	low molecular weight heat shock protein	71
	Hordeum vulgare	peroxisomal type ascorbate peroxidase	72
	Lycopersicom esculentum	unknown	73
	Triticum aestivum	expression patterns of HSP16.9 and HSP70 families	74, 75
Cold	*Euphorbia esula* (leafy spurge)	glicine-rich RNA-binding protein	76
Hydrogen peroxide	*A. thaliana*	H_2O_2-induced genes	77
Ozone	*A. thaliana*	unknown	78
	Betula pendula (birch)	mitochondrial phosphate translocator	79
Anoxia	*Oryza sativa* (flood-tolerant)	novel gene family	80
Salt	*Hordeum vulgare*	nuclease I	81
	Mesembryanthemum crystallium (common ice plant)	ribosome-inactivating protein, PEPc kinase	82, 83
	Brassica napus	EREBP/AP2-type transcription factor	84

Table 2 (continued)

Stress treatments	Plant species	Obtained gene or encoded protein	References
Desiccation/rehydration	*Sporobolus stapfianus* (desiccation-tolerant)	GTP-binding protein	85
Salicylic acid (SA)	*Capsicum annuum (leaf)*	putative acyl-CoA synthase	86
	Nicotiana tabacum (cell culture)	UDP-glucose: flavonoid glucosyltransferase	87
Methyljasmonic acid-related			
coronatine	*Arabidopsis thaliana*	unknown	88
	(wild-type/*coi1* mutant)	tyrosine aminotransferase	89
z-jasmone	*Phaseolus vulgaris*	α-tublin isoform	90
Wounding	*A. thaliana* (*coi1* mutant)	flavoprotein oxidoreductase homologue, wound-induced genes	91, 92
	N. tabacum	WRKY transcription factor, high-charged protein	93, 94
Elicitor treatment			
CaMV gene VI protein	*A. thaliana*	altered expression pattern	95
elicitor from *Scerotinia sclerotiorum*	*Daucus carota*	extracellular glycoprotein	96
yeast extract	*Glycine max*	cinnamate 4-hydroxylase	97
chitosan	slash pine	profiling	98
hyphal wall components	*N. tabacum*	LRP-receptor-like protein (membrane protein)	99
cryptogein		β-type proteasome subunit, transformer-2-like SR-related protein	100
elicitor from rice blast fungus	*Oryza sativa*	rab-specific GDP-dissociation inhibitor	101
Chemical induction (probenazole) infection	*O. sativa*	nucleotide-binding protein	102
Colletotrichum trifolii	*Medicago sativa*	defense-related protein, tree pollen allergen homologue	103
Phytophthora infestans	*Solanum tuberosum*	putative peroxidase, NAC domain protein, pathogen-induced genes	104
Phytophthora sojae	*G. max*	basic peroxidase	105
Pseudomonus syringae		chalcone isomerase, ubiquitin, signalling molecule, G-6-P dehydrogenase, leucin-rich protein	106
mollicutes	*Catharanthus roseus*	genes involved in photosynthesis, sugar transport, stress response, phytosterol synthesis	107
Plasmopara halstedii	*Helianthus annuus*	auxin-induced gene homologue	108
Paenibacillus polymyxa	*A. thaliana*	drought-stress-responsive defense genes	109
TMV	*N. tabacum* (resistant/susceptible lines)	WRKY transcription factor	110
Meloidogyne incognita (nematode)	*A. thaliana*	trypsine inhibitor, peroxidase, mitochondrial uncoupling protein, endomembrane protein, 20S proteasome α-subunit, diaminopimelate decarboxylase	111
Heterodera schanttii (cyst nematode)	*A. thaliana*	infection-responsive genes	112
Heterodera glycines (cyst nematode)	*G. max* (resistant/susceptible plants)	polygalacturonase	113
Herbivore attack	*Nicotiana attenuata*	insect-responsive genes	114, 115
Symbiosis			
Sinorhizobium	*Medicago sativa* (xenobiotic treated)	copper transporter homologue, 60S ribosomal protein	116
Rhizobium lori	*Lotus japonicus*	nodule specific protein phosphatase, peptide transporter, nodule-specific P450	117
Azorhizobium caulinodans	*Sesbania rostrata*	hydroxyprolin-rich cell wall protein, chitinase, chalcone reductase	118
Nod factor treatment	*Medicago truncatula*	annexin	119
	Vicia sativa	leghemoglobin	120
Glomus mosseae	*Pisum sativum* (defective mutant)	proline-rich protein	121, 122

Table 3. Application of differential display to secondary metabolism in plants.

Species	Differential condition	Obtained gene	References
Perilla frutescens	red and green formas	anthocyanin 5-*O*-glucosyltransferase anthocyanidin synthase Myc-transcriptional factor	124, 125 [M.Yamazaki et al., unpublished],
Gerbera hybrids	chemogenetic defined lines, cytochrome P450 targeted PCR	flavone synthase II	126
Glycine max	cell suspension cultures untreated or treated with yeast extract, cytochrome P450-targeted PCR	cinnamate 4-hydroxylase, dihydroxyptero-carpan 6α-hydroxylase, flavonoid 6-hydroxylase	97, 127, 128
Taxus cuspidata	MeJA induction, cytochrome P450-targeted PCR	taxane 10β-hydroxylase	129

Isolation of novel genes from induced cells

As described previously, some secondary products are induced by addition of elicitors or signal compounds in cell suspension cultures. In soybean, production of pterocarpans such as glyceollin is inducible by pathogen infection or elicitor treatment. From induced cells elicited with yeast extract, cinnamate 4-hydroxylase, dihydroxypterocarpan 6-hydroxylase and another novel flavonoid 6-hydroxylase were isolated using DD [97, 127, 128]. In these reports, selective DD PCR targeted to cytochrome P450 was performed. Similarly, the cDNA encoding a cytochrome P450 enzyme, taxane 10 β-hydroxylase, involved in taxol biosynthesis was isolated using DD to examine cell cultures treated with and without methyljasmonic acid [129]. In these studies, physiologically induced genes needed to be distinguished from secondary metabolism genes. For this purpose, selective DD PCR using anchored primers with increased annealing temperature was carried out.

Conclusion

mRNA differential display is a powerful technique for isolating of cDNAs specifically expressed in particular types of cells or induced in cells by stress. Even genes that express at low levels, such as transcriptional factors, can be cloned after isolating them using this technique. Also, DD has been used in modified form to meet the demands of different experimental designs.

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