Interactions of polyamines and phytohormones in plant response to abiotic stress

Oddziaływania poliamin i fitohormonów w odpowiedzi roślin na stres abiotyczny

Natalia Napieraj, Małgorzata Janicka, Małgorzata Reda
Department of Plant Molecular Physiology, Faculty of Biological Sciences, University of Wrocław, Kanonia 6/8, 50-328 Wrocław, Poland
natalia.napieraj2@uwr.edu.pl; malgorzata.janicka@uwr.edu.pl; malgorzata.reda@uwr.edu.pl

Table 1. Some representative evidence for interaction between PAs and plant hormones during plant growth and development. 6-BA, 6-benzylaminopurine; IAA, indole acetic acid; iP, isopentenyl adenine; NaSA, sodium salicylate.

Tabela 1. Niektóre reprezentatywne dowody interakcji między PA i hormonami roślinnymi podczas wzrostu i rozwoju roślin. 6-BA, 6-benzyloaminopuryna; IAA, kwas indolooctowy; iP, izopentenyloadenina; NaSA, salicylan sodu.

PAs-plant hormone crosstalk	Plant species	Exogenous treatment, gene mutation or over-expression	Effect (or outcome)	References
ABA	Maize	Exogenous ABA	Increased PAO activity, enhanced *PAO* expression	[50]
	Tomato	Exogenous ABA	Induced expression of *SlPAO2-4* genes, reduced expression *SlPAO1* gene and *SlPAO6-7* genes	[42]
	Cucumber	Exogenous ABA	Up-regulated expression of *CsSAMS1* and *CsSAMS2* in leaves, increased expression of *CsSAMS1* and inhibited expression of *CsSAMS2* in roots	[51]
	Rice	Exogenous ABA	Enhanced expression of *OsPAO1*	[52]
	Arabidopsis	Exogenous ABA	Up-regulated expression of *ADC2*, *ARGAH1*, *ARGAH2*, *AIH*, *CPA*, *SPDS2*, *SPMS*, *SAMDC1-2*, *PAO1-4*, *CuAOγ1*/*CuAO1*, *CuAOδ*	[43]
	Arabidopsis	Exogenous Spd and exogenous Spm	Increased ABA content, up-regulated *NCED3* expression	[53]
Auxin	Tomato	Exogenous IAA	Stimulated expression of *SlPAO2*, *SlPAO4* and *SlPAO7* genes, reduced expression of *SlPAO6*	[42]
	Arabidopsis	Exogenous IAA	Up-regulated expression of *ADC2*, *ACL5*, *SAMDC4*/*BUD2*, *PAO1*, *PAO2*, *PAO5*, reduced expression of *CuAOα2* and *CuAOα3*/*CuAO2*	[43]
	Arabidopsis	*acl5-1*	Up-regulation of genes related to auxin biosynthesis (*YUCCA2*), methylation (*IAMT1*), transport (*PIN-FORMED1* and *PIN6*) and signal transduction (*MP*/*ARF5*)	[47]
BRs	Tomato	Exogenous EBL	Modulated PAs content in plant organs	[54]
CKs	Cucumber	Exogenous KN	Increased Put content, decreased Spd content, reduced SAMDC activity and stimulated PAO activity	[55]
	Tomato	Exogenous 6-BA	Stimulated expression of *SlPAO2-5* genes and reduced expression of *SlPAO6-7* genes	[42]
	Rice	Exogenous iP	Up-regulated expression of *OsPAO1*, *OsPAO3*, *OsPAO5* and *OsPAO7*	[52]
	Arabidopsis	*bud2*	Enhanced CKs production, hypersensitivity to exogenous CKs	[56]

ETH	Tomato	Exogenous ethephon	Stimulated expression of *SlPAO1-2* genes and *SlPAO4* gene, decreased expression of *SlPAO5-7* genes	[42]
	Arabidopsis	Exogenous ACC	Enhanced expression of *ADC2* and reduced expression of *CuAOα2*	[43]
	Peach	Exogenous Spd	Decreased ETH content, enhanced expression of *ETR1* and *ERS1* in fruits	[46]
	Olive (ARB cv.)	Exogenous Put	Negatively regulated expression of *OeACO2* and *OeCTR1*, and positively regulated *OeERS1* expression in fruits	[57]
	Olive (ARB cv.)	Exogenous Spd	Up-regulated expression of *OeERS1*, down-regulated expression of *OeCTR1* and *OeEIL2* in fruits	[57]
	Grapes	Exogenous guazatine	Put accumulation, stimulated expression of *EIN3* and *EBF2* genes	[58]
	tomato	*Nr*	Enzymes of Put production responded to exogenous SA in a light- and ET-dependent manner	[44]
GAs	Pea	Exogenous GA3	Increased *ADC* expression, decreased *ODC* expression	[59]
	Grape	Exogenous GA3	Enhanced free Put content	[60]
	Tomato	Exogenous GA3	Up-regulated expression of *SlPAO2-3* genes and *SlPAO5* gene	[42]
	Rice	Exogenous GA	Up-regulated expression of *OsPAO5* and *OsPAO7*	[52]
	Arabidopsis	*ADC2*	Lower GA1, GA4 and GA9 content, reduced expression of genes related to GA biosynthesis (*AtGA20ox1*, *AtGA3ox1* and *AtGA3ox3*)	[45]
	Tomato	*ySAMdc*	Enhanced expression of genes encoding GA 2-oxidase and GA 20-oxidase and during fruit ripening	[61]
	Arabidopsis	Exogenous Put	Up-regulation *GA3ox1* expression	[53]
	Arabidopsis	Exogenous Spm	Reduced GA1 content, down-regulation *GA3ox1* expression	[53]
JAs	Tomato	Exogenous MeJA	Enhanced expression of *SlPAO1-2* genes and decreased expression of *SlPAO4* and *SlPAO6-7* genes	[42]
	Cucumber	Exogenous MeJA	Modulated expression of *CsSAMS1* and *CsSAMS2* genes in roots and leaves during treatment	[51]
	Rice	Exogenous JA	Up-regulated expression of *OsPAO1-3* and *OsPAO6-7*	[52]
	Arabidopsis	Exogenous MeJA	Enhanced expression of *ARGAH1*, *ARGAH2*, *PAO3* and *CuAOα3*/*CuAO2*	[43]
	Arabidopsis	Exogenous Spm	Up-regulation of JA biosynthesis genes (*LOX1-4*, *AOS*, *AOC1*, *AOC2*, *OPR3*, *OPCL1*, *CYP94B3*) and JA signaling genes (*JAZ1*, *JAZ5*, *JAZ6*, *JAZ7* and *JAZ10*)	[62]
	Arabidopsis	Exogenous tSpm	Up-regulation of JA biosynthesis genes (*LOX1-4*, *AOS*, *AOC1*, *AOC2*, *OPR3*, *OPCL1*, *CYP94B3*), JA signaling genes (*JAZ1*, *JAZ5*, *JAZ6*, *JAZ7*, *JAZ10* and *MYC4*) and JA response marker genes (*VSP2* and *PDF1.2*)	[62]
	Arabidopsis	Exogenous Spd	Lower JA content, reduced *AOS* expression	[53]
	Arabidopsis	Exogenous Spm	Lower JA content, enhanced *AOS* expression	[53]
SA	Tomato	Exogenous SA	Stimulated expression of *SlPAO2-4* genes and reduced expression of *SlPAO6-7* genes	[42]
	Cucumber	Exogenous SA	Enhanced expression of *CsSAMS1* and *CsSAMS2* in leaves	[51]
	Arabidopsis	Exogenous SA	SA modulated PAs content and PA metabolism gene expression	[63]

	Arabidopsis	*mpk6-2*	Decreased Put content	[63]
	Arabidopsis	Exogenous NaSA	Up-regulated expression of *ADC2*, *AIH*, *SPMS* and *PAO1*, down-regulated expression of *CuAOα2*, *CuAOα3*/*CuAO2* and *CuAOγ2*	[43]
	Arabidopsis	Exogenous PAs	Modulation of PAs biosynthesis and catabolism gene expression in *eds5* and *sid2* mutants	[53]

Table 2. A summary of evidence for interaction between PAs and plant hormones in response to abiotic stresses.

Tabela 2. Podsumowanie dowodów na interakcje między PA i hormonami roślinnymi w odpowiedzi na stresy abiotyczne.

Abiotic stress	PAs-plant hormone crosstalk	Plant species	Exogenous treatment, gene mutation or over-expression	Effect (or outcome)	References
Drought, osmotic stress	ABA ↔ PAs	*Vicia faba*	Exogenous PAs	Induced stomatal closure	[71]
	ABA ↔ PAs	*Vicia faba*	Exogenous ABA	Higher CuAO and NADPH oxidase activity leading to enhanced H_2O_2 production	[71]
	ABA ↔ PAs	*Arabidopsis*	Exogenous ABA	Higher expression of *AtPAO2* in guard cells	[72]
	ABA ↔ PAs	*Arabidopsis*	Exogenous PAs	Induced stomatal closure, enhanced NO and ROS levels in guard cells due to NADPH oxidase and AO activity	[73]
	ABA ↔ PAs	*Arabidopsis*	*aba2*, *abi1*	No observed dehydration-inducible expression of *ADC2*, *SPDS1* and *SPMS*	[74]
	ABA ↔ PAs	*Arabidopsis*	-	Presence of ABREs in promoter regions of *ADC2*, *SPDS1* and *SPMS* genes	[75]
	ABA ↔ PAs	*Arabidopsis*	-	Enhanced expression of ABA-inducible and drought-responsive genes (*RD29A* and *RD22*) and PAs biosynthesis genes (*ADC1*, *ADC2*, *SPDS1*, *SPDS2*, *SPMS* and *SAMDC1*)	[66]
	ABA ↔ PAs	Rice	-	Presence of putative cis-acting elements, such as ABRE, LTRE, MYB and W-box, in the promoter region of *SAMDC* gene	[76]
	ABA ↔ PAs	Rice	*OsHSFA3*	Higher ABA level, increased PAs content, up-regulation of *ADC1*, *ADC2*, *SPDS1* and *SPMS* expression	[77]
	ABA ↔ PAs	*Lotus tenuis*	*ADC*	Increased Put content, expression of *NCED* gene and ABA accumulation	[78]
	ABA ↔ PAs	Wheat	Exogenous Put	Enhanced expression of *NCED*	[79]
		Wheat (drought-susceptible cv.)	Exogenous Spm	Further escalation in ABA level	[80]
	ABA ↔ PAs	Wheat (drought-resistant cv.)	Exogenous Spd	Reduced ABA level	[80]

	ABA ↔ PAs	Wheat	Exogenous ABA	Enhanced expression of *ADC*, decreased expression of *SPDS* and *PAO*	[79]
	ETH ↔ PAs	Wheat	Exogenous Spd and exogenous Spm	Reduction of ETH evolution rate, increased CKs and ABA level	[81]
	ETH ↔ PAs	Wheat	Exogenous Put	Increased ETH evolution rate, excessive ABA accumulation	[81]
	JAs ↔ PAs	Rice	Exogenous MeJa	Negatively regulation of *OsAdc*, *OsSamdc* and *OsSpds* genes	[82]
	JAs ↔ PAs	Maize	Exogenous Spd	Decreased MeJA content	[37]
	CKs ↔ PAs	Maize	Exogenous Spd	Increased ZR content	[37]
	GAs ↔ PAs	Wheat	Exogenous Spd and exogenous Spm	Higher GA (GA1+GA4) content during seed germination	[81]
	GAs ↔ PAs	Bentgrass	Exogenous Spm	Increased GA1 content	[83]
	GAs ↔ PAs	Bentgrass	Exogenous Spd	Increased GA4 and GA20 content	[83]
Salt stress	ABA ↔ PAs	*Arabidopsis*	*SAMDC1*	Improved expression of ABA-induced genes (*NCED* and *RD29A*)	[19]
	ABA ↔ PAs	*Arabidopsis*	*spms*, *acl5*/*spms*	Decreased *NCED3* expression	[19]
	ABA ↔ PAs	*Arabidopsis*	*atpao5-3*	Higher ABA content, up-regulated expression of *NCED* and *RD29B*	[62]
	BRs ↔ PAs	Tomato	Exogenous EBL	Increased PAs level in the middle leaf and fruits, higher Spm level in the stem higher (Spd+Spm)/Put ratio in the fruits	[54]
	BRs ↔ PAs	Lettuce	Exogenous DI-31	Enhanced PAs accumulation in shoots, reduced Spd and Spm content in roots	[84]
	BRs ↔ PAs	Canola	Exogenous EBL	Increased accumulation of Put in cotyledons and reduced in hypocotyls and radicles, reduced H_2O_2 content, decreased DAO activity and increased PAO activity	[12]
	ETH ↔ PAs	Rice	Exogenous Put	Enhanced ETH production	[65]
	ETH ↔ PAs	Tobacco	*AS-ZmPAO*	Up-regulation of *ACCSyn* and *ACCOx* gene expression	[4]
	ETH ↔ PAs	Tomato	*Nr*	Lower Spm content, enhanced DAO, and PAO activity	[44]
	JAs ↔ PAs	Cucumber	Exogenous Spd	Decreased JA content	[85]
	JAs ↔ PAs	*Arabidopsis*	*atpao5-3*	Increased JA accumulation	[62]
	CKs ↔ PAs	*Vigna sinensis*	Exogenous KN	Increased PAs content	[86]
	GAs ↔ PAs	Cucumber	Exogenous Spd	Enhanced *GT-3b* expression, increased GA3 level, increased activity of GA3-oxidase and GA20-oxidase, upregulated expression of genes related to GA biosynthesis	[31]
Heavy metal stress	BRs ↔ PAs	Radish	Exogenous EBL	Increased Put content, decreased Spd content	[54]
	BRs ↔ PAs	Mustard	Exogenous EBL	Increased PAs level in leaves	[87]
	BRs ↔ PAs	Mustard	Exogenous EBL and SA	Increased Spd level in roots	[88]
	ETH ↔ PAs	Wheat	Exogenous Put	Improved root elongation, decreased ACS activity and ETH level	[6]

	ETH ↔ PAs	Cucumber	Exogenous 2-OHMT	Higher PAs content, reduction of PAO activity, increased *CS-ERS* expression	[7]
Low-temperature stress	ABA ↔ PAs	Tomato	Exogenous Put	Increased ABA level and *LeNCED1* expression, role of ABA in Put-induced tolerance	[33]
	ABA ↔ PAs	*Arabidopsis*	*adc*	Reduced ABA accumulation, lower *NCED* expression, down-regulation of ABA-regulated genes	[10]
	ABA ↔ PAs	*Arabidopsis*	*adc*	Reduced ABA level, decreased ABA-dependent gene induction, decreased freezing tolerance	[89]
	JAs ↔ PAs	Zucchini	Exogenous MeJA	Higher Put content, lower Spd and Spm content	[90]
	JAs ↔ PAs	Rice	Exogenous MeJA	Shoots: increased Put and Spm content, reduced Spd content, increased ADC activity, reduced ODC and SAMDC activity; roots: increased Put and reduced Spd content, increased ADC and SAMDC activity, reduced ODC activity	[30]
	CKs ↔ PAs	*Indica-japonica* hybrid rice	Exogenous Spd	Higher ZR content	[91]
	GAs ↔ PAs	*Indica-japonica* hybrid rice	Exogenous Spd	Higher GA3 content	[91]