

References

References used as a source of information to construct the chart showing the 'Metabolic pathways of the diseased potato' are provided below.

BIOSYNTHETIC PATHWAYS

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[Others](#)

Ceramide

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Cutin

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Elicitors

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Demonstrated that application of arachidonic, eicosapentaenoic, linoleic, linolenic and oleic acids to potato plants induced resistance to subsequent infection by P. infestans.
- Cohen Y, Gisi U, Niderman T. 1993. Local and systemic protection against *Phytophthora infestans* induced in potato and tomato plants by jasmonic acid and jasmonic acid methyl ester. *Phytopathology* 83, 1054-1062.
Jasmonic acid (JA) and jasmonic acid methyl ester (JME) applied as foliar sprays to potato plants protected them from subsequent infection by P. infestans. Systemin did not induce protection. JA and JME application caused an increase in accumulation of proteinase inhibitors and other PR proteins in treated leaves.
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In tobacco, expression of defence-related genes encoding proteinase inhibitor II, hydroxyproline-rich or glycine-rich glycoproteins, glucanase and chitinase can be induced by methyl jasmonate. Expression of the sesquiterpene cyclase (5-epi-aristolochene synthase) gene was not induced by methyl jasmonate. The synthesis of jasmonate via the LOX pathway is only part of a complex regulatory mechanism for the onset of many, but not all, defence reactions. There is no direct evidence whether these results can be extrapolated to potato.
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Fatty acid degradation, Lipoxygenase, and Oxylipin pathway

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However, in treated roots, very low, if any expression of these genes could be detected. In contrast, a novel root-specific pin2 homologue accumulated in the JA-treated root tissue which could not be detected in leaves. Application of okadaic acid and staurosporine indicated that a protein phosphorylation step is involved in the regulation of this differential response.

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Allene oxide cyclase catalyzes the cyclization of 12,13(S)-epoxy-9(Z),11,15(Z)-octadecatrienoic acid to 12-oxo-10,15(Z)-phytodienoic acid. The generation of 12-oxo-PDA from 13-HPOT occurs via two enzymes; allene oxide synthase (AOS; also called hydroperoxide dehydratase) which is associated with membranes, and allene

oxide cyclase (AOC) which is soluble.

Glycoalkaloids

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Quantified solanidine and solanthrene in S. tuberosum and tomatidine in S. brevidens and detected demissidine as a novel aglycone in hybrids. The authors hypothesised that the hydrogenase from S. brevidens produced demissidine from solanidine in the hybrids.
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chacoense.

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Halliwell-Asada pathway

- Price AH, Taylor A, Ripley S J, Griffiths, A., Trewavas, A. J. 1994. Oxidative signals in tobacco increase cytosolic calcium. *The Plant Cell* 6, 1301-1310.
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Mevalonic acid pathway

- Chappell J. 1995. Biochemistry and molecular biology of the isoprenoid biosynthetic pathway in plants. *Annual Review of Plant Physiology and Plant Molecular Biology* 46, 521-547.
Reviewed many aspects of the mevalonic acid pathway. Described a hypothetical model suggesting that classes of isoprenoids are synthesised by discrete metabolic channels. For example, entire metabolic channels for sterol and sesquiterpene biosynthesis are localised in the endoplasmic reticulum. Synthesis of other isoprenoids, such as carotenoids and long chain prenols of ubiquinone, require the coordinated activity of cytoplasmic and organellar biosynthetic channels with ubiquinone synthesised in the mitochondria and carotenoids etc in the chloroplasts.
- Choi D, Bostock RM, Avdiushko S, Hildebrand DF. 1994. Lipid-derived signals that discriminate wound- and pathogen-responsive isoprenoid pathways in plants: methyl jasmonate and the fungal elicitor arachidonic acid induce different 3-hydroxy-3-methylglutaryl-coenzyme A reductase genes and antimicrobial isoprenoids in *Solanum tuberosum* L. *Proceedings of the National Academy of Science USA* 91, 2329-2333.
Used gene-specific probes to study different HMGR genes (hmg1 and hmg2). Showed that methyl jasmonate can induce hmg1 expression and glycoalkaloid accumulation after wounding, and, importantly, reduce the abundance of hmg2 transcripts. Thus arachidonate and jasmonate-responsive pathways are distinct in relation to HMGR gene expression and isoprenoid product accumulation.
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Isolated three classes of cDNAs encoding HMGR (hmg1, hmg2 and hmg3) from potato. Demonstrated a suppression of hmg1 and an enhancement of hmg2 and hmg3 transcripts following elicitor treatment or inoculation with an incompatible race of P. infestans.

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Showed that the hmg1 promoter is differentially responsive to light in different organs and promoter activation by light deprivation is confined primarily to immature leaves. In contrast, expression of the hmg1 gene in roots is confined to the elongation zone and is not responsive to illumination.
- Ohnuma S, Hirooka K, Ohto C, Nishino T. 1997. Conversion from archael geranylgeranyl diphosphate synthase to farnesyl diphosphate synthase. *The Journal of Biological Chemistry*. 272, 5192-5198.
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- Scolnik PA, Bartley GE, 1996. A table of some cloned plant genes involved in isoprenoid biosynthesis. *Plant Molecular Biology Reporter* 14, 305-319.
Described the enzymes involved in the biosynthesis of isoprenoids in plants.
- Weissbecker B, Van Loon JJA, Posthumus MA, Bouwmeester HJ, Dicke M. 2000. Identification of volatile potato sesquiterpenoids and their olfactory detection by the two-spotted stinkbug *Perillus bioculatus*. *Journal of Chemical Ecology* 26, 1433-1445.
- Weissenborn DL, Denbow CJ, Laine M, Lang SS, Yang Z, Yu X, Cramer CL. 1995. HMG-CoA reductase and terpenoid phytoalexins: Molecular specialization within a complex pathway. *Physiologia Plantarum* 93, 393-400.
Reviews evidence from a number of plants that HMGRs are encoded by a small gene family.
- Yang Z, Park H, Lacy GH, Cramer CL. 1991. Differential activation of potato 3-hydroxy-3-methylglutaryl coenzyme A reductase genes by wounding and pathogen attack. *The Plant Cell* 3, 397-405.
Demonstrated that one isogene of the HMGR family is pathogen activated and is distinct from isogene(s) that are wound activated.
- Yokota T. 1997. The structure, biosynthesis and function of brassinosteroids. *Trends in Plant Science* 2, 137-143.
Shows some of the steps involved in the biosynthesis of sterols in plants.

Oxidative burst/free radicals

- Adam AL, Bestwick CS, Barna B, Mansfield JW. 1995. Enzymes regulating the accumulation of active oxygen species during the hypersensitive reaction of bean to *Pseudomonas syringae* pv. *phaseolicola*. *Planta* 197, 240-249.
Found five main isoforms of superoxide dismutase (SOD) in Phaseolus vulgaris which increased after inoculation with incompatible bacteria. Also showed the existence of four peroxidases.
- Arce DP, Tonon C, Zanetti ME, Godoy AV, Hirose S, Casalongue. 2006. The potato transcriptional co-activator StMBF1 is up-regulated in response to oxidative stress and interacts with the TATA-box binding protein. *J. Biochem Mol Biol* 39, 355-360.
- Deighton N, Johnston DJ, Glidewell SM, Lyon GD, Goodman BA. 1992. The involvement of oxygen-derived free radicals in the resistant response of potato tubers to *Erwinia carotovora*. *Protoplasma* 171, 167-169.
Demonstrated a rapid oxygen-requiring production of free radicals by potato tubers in response to infection by E. carotovora. They detected, by electron paramagnetic resonance (EPR) spectroscopy, a single radical adduct which had spectral characteristics of a lipid-derived radical.
- Doke N, Miura Y, Sanchez LM, Kawakita K. 1994. Involvement of superoxide in signal transduction: responses to attack by pathogens, physical and chemical shocks, and UV irradiation. In, *Causes of photooxidative stress and amelioration of defense systems in plants*. (Eds C.H.Foyer and P.M.Mullineaux). CRC Press, Boca Raton, Ann Arbor, London, Tokyo. 177-197.
Summarises the relationship between the hypersensitive response of potato to P. infestans and superoxide production.
- Kobayashi M, Ohura I, Kawakita K, Yokota N, Fujiwara M, Shimamoto K, Doke N, Yoshioka H. 2007. Calcium-dependent protein kinases regulate the production of reactive oxygen species by potato NADPH oxidase. *Plant Cell* 19, 1065-80.
- Lamb C, Dixon RA. 1997. The oxidative burst in plant disease resistance. *Annual Review of Plant Physiology and Plant Molecular Biology* 48, 251-275.
Reviews the literature on the oxidative burst in plant-pathogen interactions and suggests it is a central component of an integrated signalling system also involving salicylic acid and perturbations of Ca²⁺ which underlies the expression of disease resistance mechanisms.
- Langenkamper G, Manac'h N, Broin M, Cuine S, Becuwe N, Kuntz M, Rey P. 2001. Accumulation of plastid lipid-associated proteins (fibrillin/CDSP34) upon oxidative stress, ageing and biotic stress in Solanaceae and in response to drought in other species. *Journal of Experimental Botany* 52, 1545-1554.
Fibrillin/CDSP34 is induced in potato by Erwinia chrysanthemi.
- Mata CG, Lamattina L, Cassia RO. 2001. Involvement of iron and ferritin in the potato-*Phytophthora infestans* interaction. *European Journal of Plant Pathology* 107, 557-562.
- Mehdy MC, Sharma YK, Sathasivan K, Bays NW. 1996. The role of activated oxygen species in plant disease resistance. *Physiologia Plantarum* 98, 365-374.

Reviews the evidence demonstrating that the production of activated oxygen species is one of the earliest responses of plants to infection.

- Pobezhimova TP, Voinikov VK. 2000. Biochemical and physiological aspects of ubiquinone function. *Membr Cell Biol* 13, 595-602.
Suggests that ubiquinol (the reduced form of ubiquinone) functions as an antioxidant in cells.
- Rojas CM, Senthil-Kumar M, Wang K, Ryu CM, Kaundal A, Mysore KS. 2012. Glycolate oxidase modulates reactive oxygen species-mediated signal transduction during nonhost resistance in *Nicotiana benthamiana* and *Arabidopsis*. *Plant Cell* Jan 27.
Not yet demonstrated for potato but because of its occurrence in Nicotiana it is highly likely.
- Yun B-W, Feechan A, Yin M, Saidi NBB, Le Bihan T, Yu M, Moore JW, Kang J-G, Kwon E, Spoel SH, Pallas JA, Loake GJ. 2011. S-nitrosylation of NADPH oxidase regulates cell death in plant immunity. *Nature* 478, 264-8.

Pectin

- Bourlard T, Schaumann-Gaudinet A, Bruyant-Vannier M-P, Morvan C. 1997. Various pectin methyltransferase activities with affinity for low and highly methylated pectins. *Plant Cell Physiology* 38, 259-267.
- Ishii T. 1997. O-acetylated oligosaccharides from pectins of potato tuber cell walls. *Plant Physiology* 113, 1265-1272.
Describes the detection of some acetylated galacturonides from potato cell walls.
- McMillan GP, Hedley D, Fyffe L, Perombelon MCM. 1993. Potato resistance to soft rot erwinias is related to cell wall pectin esterification. *Physiological and Molecular Plant Pathology* 42, 279-289.
*Using potato clones derived from *S. brevidens* showed a correlation between pectin esterification and resistance to stem rotting by *E. carotovora*: pectin from the more resistant clones was more highly methylated. More recent data (unpublished) suggests that there is not a simple relationship between resistance and pectin methylation.*

Phenylpropanoid biosynthesis

- Belles JM, Garro R, Fayos J, Navarro P, Primo J, Conejero V. 1999. Gentisic acid as a pathogen-inducible signal, additional to salicylic acid for activation of plant defenses in tomato. *Molecular Plant-Microbe Interactions* 12, 227-235.
Detected gentisic acid in virus infected tomato.
- Bernards MA, Lewis NG. 1992. Alkyl ferulates in wound healing potato tubers. *Phytochemistry* 31, 3409-3412.

Showed that alkyl ferulate esters begin to accumulate 3 - 7 days after wounding potato tubers; these are associated with the suberin of wound periderm formation.

- Bernards MA, Lopez ML, Zajicek J, Lewis NG. 1995. Hydroxycinnamic acid-derived polymers constitute the polyaromatic domain of suberin. *The Journal of Biological Chemistry* 270, 7382-7386.
Studied the phenolic domain of suberin and suggested that it was almost exclusively comprised of a covalently-linked hydroxycinnamic acid-derived polymeric matrix.
- Brady JD, Fry SC. 1997. Formation of di-isodityrosine and loss of isodityrosine in the cell walls of tomato cell-suspension cultures treated with fungal elicitors or H₂O₂. *Plant Physiology* 115, 87-92
Treatment of tomato cells with resistance elicitors or H₂O₂ led to increases in Tyr-based oxidative coupling in the plant cell wall with the formation of di-isodityrosine. (Similar reactions probably occur in potato).
- Brady JD, Sadler IH, Fry SC. 1997. Pulcherosine, an oxidatively coupled trimer of tyrosine in plant cell walls: its role in cross-link formation. *Phytochemistry* 47, 349-353.
Isolated pulcherosine, a tyrosine-based trimer composed of isodityrosine and tyrosine oxidatively coupled via a biphenyl link, from tomato cell walls. Pulcherosine forms inter-polypeptide cross-links and/or wide intra-polypeptide loops.
- Chong J, Pierrel M-A, Atanassova R, Werck-Reichhart D, Fritig B, Saindrenan P. 2001. Free and conjugated benzoic acid in tobacco plants and cell cultures. Induced accumulation upon elicitation of defense responses and role as salicylic acid precursors. *Plant Physiology* 2001. 125, 318-328.
The pathway proposed is for tobacco; it may be similar in potato though not yet proven.
- Clarke DD. 1982. The accumulation of cinnamic acid amides in the cell walls of potato tissue as an early response to fungal attack. In, *Active Defense Mechanisms in Plants*. (ed, R. K. S. Wood). Plenum Press, New York, London.321-322.
Described the presence of amides of cinnamic acid and p-coumaric acid with tyramine or octopamine in potato tubers infected with P. infestans
- Delaney TP. 1997. Genetic dissection of acquired resistance to disease. *Plant Physiology* 113, 5-12.
Salicylic acid is converted to catechol by salicylate hydroxylase which is encoded by the nahG gene from Pseudomonas putida. This pathway therefore only occurs in genetically transformed plants.
- Dixon RA, Paiva NL. 1995. Stress-induced phenylpropanoid metabolism. *The Plant Cell* 7, 1085-1097.
Outlined the biosynthetic relationships among many classes of phenylpropanoids. Many phenolics accumulate in the vacuole as glycosides or other conjugates.
- Douglas CJ. 1996. Phenylpropanoid metabolism and lignin biosynthesis: from weeds to trees. *Trends in Plant Science* 1, 171-178.
A summary of the biosynthesis of phenylpropanoids leading to the production of

lignin in plants.

- El Hadrami A, Adam LR, Daayf F. 2011. Biocontrol treatments confer protection against *Verticillium dahlia* infection of potato by inducing anti-microbial metabolites. *Molecular Plant-Microbe Interactions* 24; 328-35.
Described the induction of rutin in potato and the detection of 2-PCPGCA.
- Friedman M. 1997. Chemistry, biochemistry, and dietary role of potato polyphenols. A review. *Journal of Agriculture and Food Chemistry* 45, 1523-1540.
Describes analytical and compositional aspects of phenolic compounds in potatoes; their biosynthesis, molecular genetics, and role in resistance to plant pathogens. Proposes a biosynthetic route to chlorogenic acid from cinnamic acid via cinnamoyl-D-glucose to p-coumaroyl-D-glucose and caffeoyl-D-glucose. Proposes a scheme to explain inhibition of enzymatic browning by cysteine and ascorbic acid.
- Henriquez MA, Adam LR, Daayf F. 2012. Alteration of secondary metabolites' profiles in potato leaves in response to weakly and highly aggressive isolates of *Phytophthora infestans*. *Plant Physiol Biochem* May 3.
- Jarvis AP, Schaaf O, Oldham NJ. 2000. 3-Hydroxy-3-phenylpropanoic acid is an intermediate in the biosynthesis of benzoic acid and salicylic acid but benzaldehyde is not. *Planta* 212, 119-126.
- Joos H-J, Hahlbrock K. 1992. Phenylalanine ammonia-lyase in potato (*Solanum tuberosum* L.). *European Journal of Biochemistry* 204, 621-629.
*Suggested that potato contains approximately 40 - 50 PAL genes/haploid genome. cDNA heterogeneity suggests that possibly more than 10 of these genes are potentially active. Mature leaves contained particularly low levels of PAL mRNA but infection by *Phytophthora infestans* caused a large transient increase. Describes two gene families, PAL1 and PAL2.*
- Keller H, Hohlfeld H, Wray V, Hahlbrock K, Scheel D, Strack D. 1996. Changes in the accumulation of soluble and cell wall-bound phenolics in elicitor-treated cell suspension cultures and fungus-infected leaves of *Solanum tuberosum*. *Phytochemistry* 42, 389-396.
Used HPLC to quantify pathogen- and elicitor-induced changes of potato phenolics. The largest changes were shown by soluble putrescine amides and cell wall-bound 4-hydroxybenzaldehyde and tyramine amides. Large amounts of coumaroyltyramine were secreted into the culture medium.
- King RR, Calhoun LA. 2005. Characterization of cross-linked hydroxycinnamic acid amides isolated from potato common scab lesions. *Phytochemistry* 66, 2468-2473.
- Kröner A, Marnet N, Andrivon D, Val F. 2012. Nicotiflorin, rutin and chlorogenic acid: phenylpropanoids involved differently in quantitative resistance of potato tubers to biotrophic and necrotrophic pathogens. *Plant Physiol Biochem* 15, 57C: 23-31.
- Lacombe E, Hawkins S, Van Doorselaere J, Piquemal J, Goffner D, Poeydomenge O, Boudet A-M, Grima-Pettenati J. 1997. Cinnamoyl CoA reductase, the first committed enzyme of the lignin biosynthetic pathway: cloning, expression and

phylogenetic relationships. *The Plant Journal* 11, 429-441.

Cinnamoyl CoA:NADP oxidoreductase (CCR) catalyzes the conversion of cinnamoyl CoA esters to their corresponding cinnamaldehydes.

- Lee H-i, Raskin, I. 1998. Glucosylation of salicylic acid in *Nicotiana tabacum* cv. Xanthi-nc. *Phytopathology* 88, 692-697.
Describes the activity of salicylic acid 2-O-glucosyltransferase, salicylic acid carboxyl glucosyltransferase and salicylic acid methyltransferase in infected tobacco.
- Lyon GD, McGill FM. 1988. Inhibition of growth of *Erwinia carotovora* in vitro by phenolics. *Potato Research* 31, 461-467.
Showed that the phenolic acids caffeic, cinnamic, ferulic, salicylic, sinapic, and vanillic, together with scopoletin and coniferyl alcohol inhibited growth of E. carotovora in vitro. Chlorogenic acid did not inhibit growth of E. carotovora in buffered nutrient broth.
- Malmberg A, Theander O. 1984. Free and conjugated phenolic acids and aldehydes in potato tubers. *Swedish Journal of Agricultural Research* 14, 119-125.
Used GC analysis to detect a wide range of free and conjugated phenolic acids and aldehydes in healthy potato tubers.
- Manosalva PM, Park SW, Forouhar F, Tong L, Fry WE, Klessig DF. 2010. Methyl esterase 1 (StMES1) is required for systemic acquired resistance in potato. *Molecular Plant-Microbe Interactions* 23, 1151-63.
- Mayer AM, Harel E. 1979. Polyphenol oxidases in plants. *Phytochemistry* 18, 193-215.
Critically reviews catechol oxidases and laccases (both classified as polyphenol oxidases) in plants; their purification, subcellular localisation and properties.
- Muhlenbeck U, Barz W. 1997. Cytochrome-P450-dependent formation of alpha-hydroxyacetovanillone from acetovanillone in *Solanum khasianum*. *Phytochemistry* 44, 865-867.
Studied the P450-dependent monooxygenase catalyzing the hydroxylation of acetovanillone.
- Negrel J, Lotfy S, Javelle F. 1995. Modulation of the activity of two hydroxycinnamoyl transferases in wound-healing potato tuber discs in response to pectinase or abscisic acid. *Journal of Plant Physiology* 146, 318-322.
Tyramine hydroxycinnamoyl transferase (THT) activity was strongly stimulated in potato tubers by pectinase and, to a lesser extent, by ABA. In contrast - hydroxypalmitic acid hydroxycinnamoyl transferase (HHT), which is associated with suberin biosynthesis, was induced by ABA but not by pectinase. Neither arachidonic nor jasmonic acids affected induction of THT or HHT activities.
- Negrel J, Pollet B, Lapierre C. 1996. Ether-linked ferulic acid amides in natural and wound periderms of potato tuber. *Phytochemistry* 43, 1195-1199.
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- Pallas JA, Paiva NL, Lamb C, Dixon RA. 1996. Tobacco plants epigenetically suppressed in phenylalanine ammonia-lyase expression do not develop systemic acquired resistance in response to infection by tobacco mosaic virus. *The Plant Journal* 10, 281-293.

PR proteins were not induced in systemic leaves of PAL-suppressed plants. De novo synthesis of salicylic acid and/or synthesis of other phenylpropanoids is required for the expression of resistance to TMV in systemic leaves.
- Razal RA, Ellis S, Singh S, Lewis NG, Towers GHN. 1996. Nitrogen recycling in phenylpropanoid metabolism. *Phytochemistry* 41, 31-35.

Proposes a scheme for nitrogen recycling in phenylpropanoid metabolism. Ammonium ions released by PAL during the conversion of phenylalanine to cinnamic acid is recycled in the biosynthesis of arogenic acid from prephenic acid.
- Rosler J, Krekel F, Amrhein N, Schmid J. 1997. Maize phenylalanine ammonia-lyase has tyrosine ammonia-lyase activity. *Plant Physiology* 113, 175-179.

Expression of a PAL-specific cDNA from maize in E. coli proved that phenylalanine ammonia-lyase (PAL) and tyrosine ammonia-lyase (TAL) activities reside in one polypeptide (unlike dicots) and imply that maize can produce p-coumaric acid from both phenylalanine and tyrosine. Potato does not possess TAL.
- Ryals JA, Neuenschwander UH, Willits MG, Molina A, Steiner H-Y, Hunt MD. 1996. Systemic acquired resistance. *The Plant Cell* 8, 1809-1819.

Proposed two alternative routes, involving either -oxidation or a non-oxidative pathway, by which cinnamic acid could be converted into benzoic acid in plants. These routes have not been confirmed in potato.
- Serra O, Figueras M, Franke R, Prat S, Molinas M. 2010. Unraveling ferulate role in suberin and periderm biology by reverse genetics. *Plant Signal Behav* 5; 953-958.
- Schmidt A, Grimm R, Schmidt J, Scheel D, Strack D, Rosahl S. 1999. Cloning and expression of a potato cDNA encoding hydroxycinnamoyl-CoA:tyramine N-(hydroxycinnamoyl)transferase. *The Journal of Biological Chemistry* 274, 4273-4280.

Provides structures of the hydroxycinnamic acid amides accumulating in cell walls and medium of suspension cultured cells.
- Schoch G, Goepfert S, Morant M, Hehn A, Meyer D, Ullmann P, Werck-Reichhart D. 2001. CYP98A3 from *Arabidopsis thaliana* is a 3'-hydroxylase of phenolic esters, a missing link in the phenylpropanoid pathway. *The Journal of Biological Chemistry* 276, 36566-36574.

This enzyme has not yet been confirmed in potato.
- Shulaev V, Silverman P, Raskin I. 1997. Airborne signalling by methyl salicylate in plant pathogen resistance. *Nature* 385, 718-721.

Showed that methyl salicylate, produced in many plants, is a major volatile produced by tobacco plants inoculated with tobacco mosaic virus.

- Stevens LH, Davelaar E, Kolb RM, Pennings EJM, Smit NPM. 1998. Tyrosine and cysteine are substrates for blackspot synthesis in potato. *Phytochemistry* 49, 703-707. *Describes the biosynthetic route for eumelanin and phaeomelanin*
- Szopa J, Wilczynski G, Fiehn O, Wenzel A, Willmitzer L. 2001. Identification and quantification of catecholamines in potato plants (*Solanum tuberosum*) by GC-MS. *Phytochemistry* 58, 315-320. *Identified dopamine, norepinephrine and normetanephrine.*
- Thipyapong P, Hunt MD, Steffens JC. 1995. Systemic wound induction of potato (*Solanum tuberosum*) polyphenol oxidase. *Phytochemistry* 40, 673-676. *Potato PPO can be systemically induced by wounding but only in tissues which normally express steady-state PPO mRNA.*
- Thygesen PW, Dry IB, Robinson SP. 1995. Polyphenol oxidase in potato. A multigene family that exhibits differential expression patterns. *Plant Physiology* 109, 525-531. *PPO catalyzes the conversion of monophenols to o-diphenols and o-dihydroxyphenols to o-quinones. The quinone products can then polymerize and react with amino groups of proteins causing black or brown pigments. PPO is present as a small multigene family in potato and each gene has a specific temporal and spacial pattern of expression.*
- van Gelder CWG, Flurkey WH, Wichers HJ. 1997. Sequence and structural features of plant and fungal tyrosinases. *Phytochemistry* 45, 1309-1323. *Provides a reaction scheme for tyrosinase showing both the cresolase and catecholase activity.*
- van Verk MC, Bol, JF, Linthorst HJ. 2011. WRKY transcription factors involved in activation of SA biosynthesis genes. *BMC Plant Biol* 11, 89.
- Wildermuth MC, Dewdney J, Wu G, Ausubel FM. 2001. Isochorismate synthase is required to synthesize salicylic acid for plant defense. *Nature* 414, 562-565. *Evidence is derived from experiments on Arabidopsis. There is no comparable experimental data yet for potato.*
- Zhang X-H, Chiang VL. 1997. Molecular cloning of 4-coumarate:coenzyme A ligase in loblolly pine and the roles of this enzyme in the biosynthesis of lignin in compression wood. *Plant Physiology* 113, 65-74. *Summarised the lignin biosynthetic pathway in gymnosperms.*

Phosphoinositide cascade

- Lemtiri-Chlieh F, MacRobbie EAC, Brearley CA. 2000. Inositol hexakisphosphate is a physiological signal regulating the K⁺-inward rectifying conductance in guard cells. *Proc. Natl. Acad. Sci. USA* 97, 8687-8692.
- Fruman DA, Meyers RE, Cantley LC. 1998. Phosphoinositide kinases. *Annual Review of Biochemistry* 67, 481-507.

- Liscovitch M, Cantley LC. 1994. Lipid second messengers. *Cell* 77, 329-334.
Reviews information on signalling pathways of lipid second messengers. Most of the information concerns animal cells.
- Lupu VD, Kaznatcheyeva E, Krishna UM, Falck JR, Bezprozvanny I. 1998. Functional coupling of phosphatidylinositol 4,5-bisphosphate to inositol 1,4,5-trisphosphate receptor. *The Journal of Biological Chemistry* 273, 14067-14070.
- Munnik T. 2001. Phosphatidic acid: an emerging plant lipid second messenger. *Trends in Plant Science* 6, 227-233.
- Munnik T, de Vrije T, Irvine RF, Musgrave A. 1996. Identification of diacylglycerol pyrophosphate as a novel metabolic product of phosphatidic acid during G-protein activation in plants. *The Journal of Biological Chemistry* 271, 15708-15715.
- Nakano T, Joh T, Narita K, Hayakawa T. 2000. The pathway of dephosphorylation of myo-inositol hexakisphosphate by phytases from wheat bran of *Triticum aestivum* L. cv. Nourin #61. *BioSci. Biotechnol. Biochem.* 64, 995-1003.
- Poovaiah BW, Reddy ASN, McFadden JJ. 1987. Calcium messenger system: Role of protein phosphorylation and inositol bisphospholipids. *Physiologia Plantarum* 69, 569-573.
Reviews information on the role of inositol phospholipids in signal transduction in plants.
- Raboy V. 2003. myo-Inositol-1,2,3,4,5,6-hexakisphosphate. *Phytochemistry* 64, 1033-1043.
- Riedel B, Morr M, Wu WI, Carman GM, Wissing JB. 1997. Metabolism of diacylglycerol pyrophosphate by suspension cultured *Catharanthus roseus* cells - identification and characterization of diacylglycerol pyrophosphatase in plants. *Plant Science* 128, 1-10.
Identification of DGPP phosphatase in a wide range of organisms.
- Saiardi A, Caffrey JJ, Snyder SH, Shears SB. 2000. The inositol hexakisphosphate kinase family. Catalytic flexibility and function in yeast vacuole biogenesis. *The Journal of Biological Chemistry* 275, 24686-24692.
- Wissing JB, Behrbohm H. 1993. Phosphatidate kinase, a novel enzyme in phospholipid metabolism. Purification, subcellular localization, and occurrence in the plant kingdom. *Plant Physiology* 102, 1243-1249.

Phosphorylation

- Arino J, Perez-Callejon E, Cunillera N, Camps M, Posas F, Ferrer A. 1993. Protein phosphatases in higher plants: multiplicity of type 2A phosphatases in *Arabidopsis thaliana*. *Plant Molecular Biology* 21, 475-485.
The authors suggest that a multiplicity of type 2A phosphatases might be differentially expressed in higher plants.

- Baizabal-Aguirre VM, de la Vara LEG. 1997. Purification and characterization of a calcium-regulated protein kinase from beet root (*Beta vulgaris*) plasma membranes. *Physiologia Plantarum* 99, 135-143.
Purified a calcium-regulated protein kinase (CRPK) associated with the plasma membrane of beet root cells. Calcium regulated kinases are likely to be present in all plants including potato.
- Bianchini GM, Stermer BA, Paiva NL. 1996. Induction of early mevalonate pathway enzymes and biosynthesis of end products in potato (*Solanum tuberosum*) tubers by wounding and elicitation. *Phytochemistry* 42, 1563-1571.
HMGR levels increased 30-fold following arachidonic acid treatment and 15-fold following wounding, but mevalonate kinase and mevalonate phosphate kinase only increased two- to four-fold following these treatments. While HMGR levels are extremely low in untreated tissues, the activities of the two kinases are relatively high suggesting to the authors that they do not serve as control points for the synthesis of terpenoids.
- Bolwell GP. 1992. A role for phosphorylation in the down-regulation of phenylalanine ammonia-lyase in suspension-cultured cells of French bean. *Phytochemistry* 31, 4081-4086.
Provided evidence that PAL activity in Phaseolus vulgaris is (partially) controlled by phosphorylation. [There is no comparable evidence concerning phosphorylation of PAL in potato but it seems likely that there will be some similarities].
- Carcamo JM, Pedraza A, Borquez-Ojeda O, Zhang B, Sanchez R, Golde DW. 2004. Vitamin C is a kinase inhibitor: dehydroascorbic acid inhibits IkappaBalpha kinase beta. *Molecular and Cellular Biology* 24, 6645-6652.
Work done on HeLa cells. No published evidence yet for plant cells
- Conrath U, Silva H, Klessig DF. 1997. Protein dephosphorylation mediates salicylic acid-induced expression of PR-1 genes in tobacco. *The Plant Journal* 11,747-757.
Using protein kinase and phosphatase inhibitors they showed that PR1 gene induction in tobacco can be mediated by dephosphorylation of serine/threonine residue(s) of two or more unidentified phosphoproteins. Protein phosphatase inhibitors okadaic acid and calyculin A blocked SA-mediated induction of PR-1 genes implying the involvement of a phosphoprotein downstream of SA. The protein kinase inhibitors K-252a and staurosporine induced PR-1 gene expression. K-252a also stimulated production of SA and it's glucoside, suggesting that another phosphoprotein acts upstream of SA. These results suggest that there are two (or more) phosphoproteins which function in the same signal transduction pathway leading to PR-1 gene induction.
- Felix G, Grosskopf DG, Regenass M, Boller T. 1991. Rapid changes of protein phosphorylation are involved in transduction of the elicitor signal in plant cells. *Proceedings of the National Academy of Science USA* 88, 8831-8834.
Showed that phosphorylation of protein substrates by K-252a-sensitive protein kinases is essential for transduction of elicitor signals in tomato cells and continuous phosphorylation of these proteins is required to maintain the elicited response.

- Hart GW, Kreppel LK, Comer FI, Arnold CS, Snow DM, Ye Z, Cheng X, Della Manna D, Caine DS, Earles BJ, Akimoto Y, Cole RN, Hayes BK. 1996. O-GlcNAcylation of key nuclear and cytoskeletal proteins: reciprocity with O-phosphorylation and putative roles in protein multimerization. *Glycobiology* 6, 711-716.
O-GlcNAcylated proteins are ubiquitous in all eukaryotes examined. The authors suggest a possible regulatory modification of some proteins involving a reciprocal relationship between phosphorylation of a hydroxyl moiety and its O-GlcNAcylation. If the system is truly widespread amongst eukaryotes then it is likely to be present in potato although there is no direct evidence.
- Hassan A, Okuta T, Kato M, Hatsugai N, Sano Y, Ishimori T, Okazaki K, Doullah MA, Shah MM. 2012. Alternaric acid stimulates phosphorylation of His-tagged RiCDPK2, a calcium-dependent protein kinase in potato plants. *Genetics and Molecular Research* May 10.
- Hirt H. 1997. Multiple roles of MAP kinases in plant signal transduction. *Trends in Plant Science* 2, 11-15.
Reviews the literature on MAP kinases involved in signal transduction caused by wounding, pathogens and abiotic stresses as well as the hormones abscisic acid, auxin and ethylene. Thus, pathways involving MAP kinases are common in signal transduction in all eukaryotes. MAP (mitogen-activated protein) kinases are serine/threonine protein kinases originally described in animals.
- Jonak C, Heberle-Bors E, Hirt H. 1994. MAP kinases: universal multi-purpose signaling tools. *Plant Molecular Biology* 24, 407-416.
Demonstrated the presence of MAP kinase, MAP kinase kinase and MAP kinase kinase kinase in plants and suggested that they appear to be involved in a number of physiological responses including ethylene signaling and auxin-induced cell proliferation.
- Katou S, Senda K, Yoshioka H, Doke N, Kawakita K. 1999. A 51 kDa protein kinase of potato activated with hyphal wall components from *Phytophthora infestans*. *Plant Cell Physiol* 40, 825-831.
- Kim JH, Kim WT, Kang BG, Yang SF. 1997. Induction of 1-aminocyclopropane-1-carboxylate oxidase mRNA by ethylene in mung bean hypocotyls: involvement of both protein phosphorylation and dephosphorylation in ethylene signalling. *The Plant Journal* 11, 399-405.
The protein kinase inhibitor staurosporine prevented ethylene-induced ACC oxidase gene expression whereas it recovered the ethylene-suppressed transcript level of ACC synthase suggesting that protein phosphorylation plays a role in the induction of ACC oxidase and suppression of ACC synthase by ethylene in mung bean hypocotyls. Biosynthesis of ethylene appears to occur via the same pathway in all higher plants and control through phosphorylation is therefore also likely to occur in potato.
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