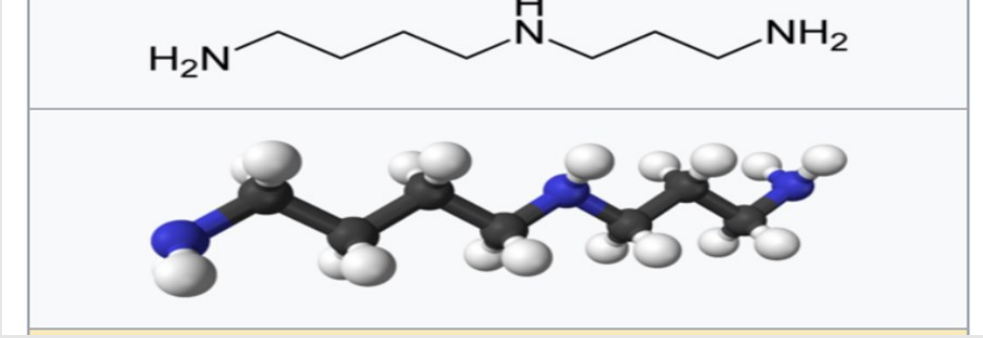
IN THE NAME OF GOD

What are polyamines?



PAs are positively charged nitrogenous compounds derived from amino acids.

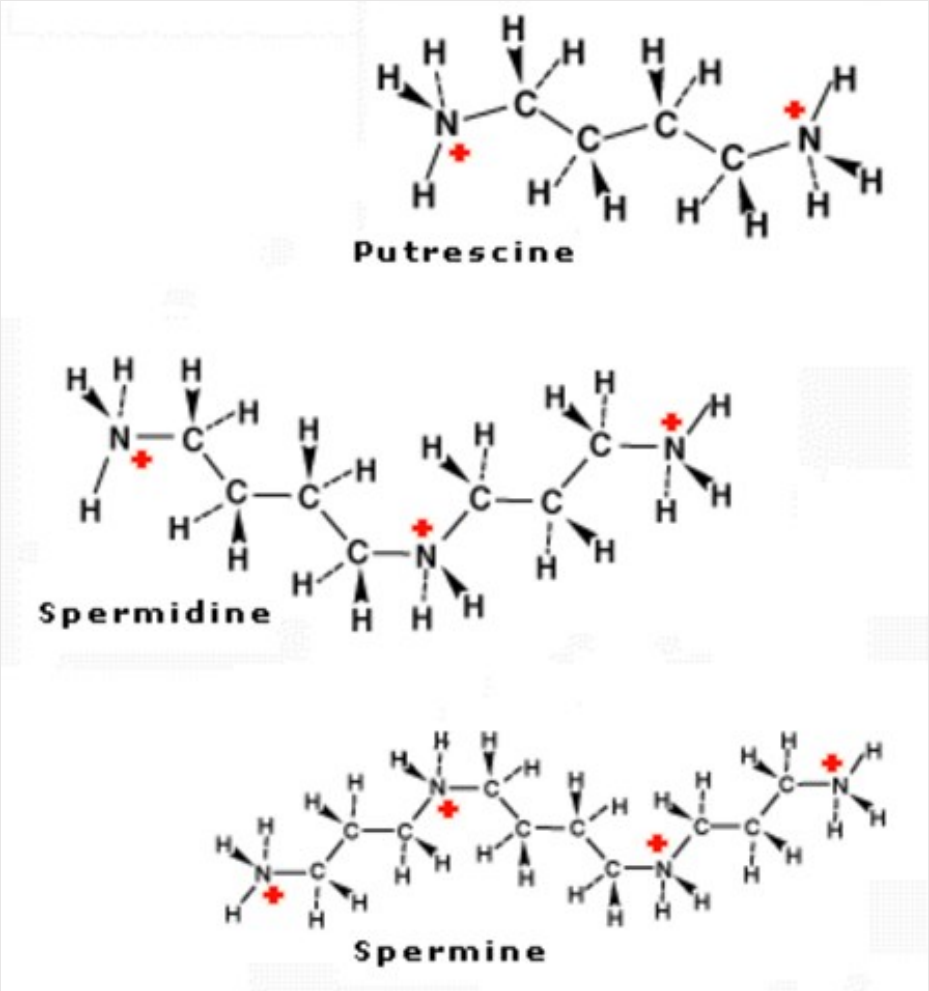
Polyamines (PAs) are present in all eukaryotic cells (both animal and plant) and have important roles in several biological functions related with cell growth and differentiation.

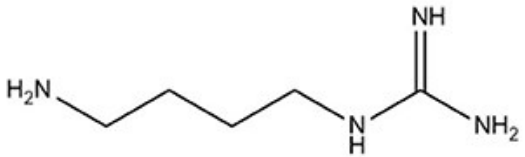
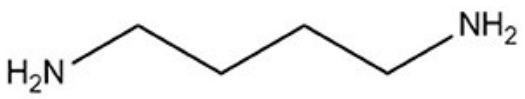
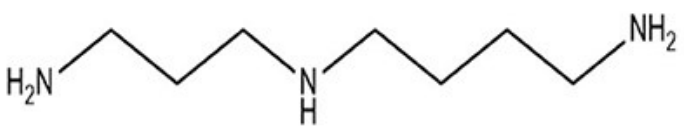
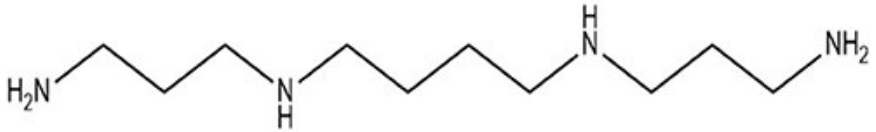
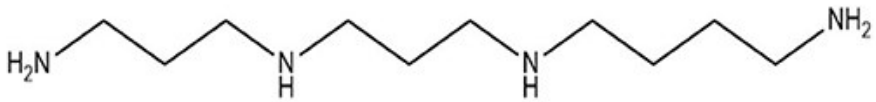
In plant organs, the main PAs are putrescine (PUT),spermidine (SPD) and spermine (SPM) .

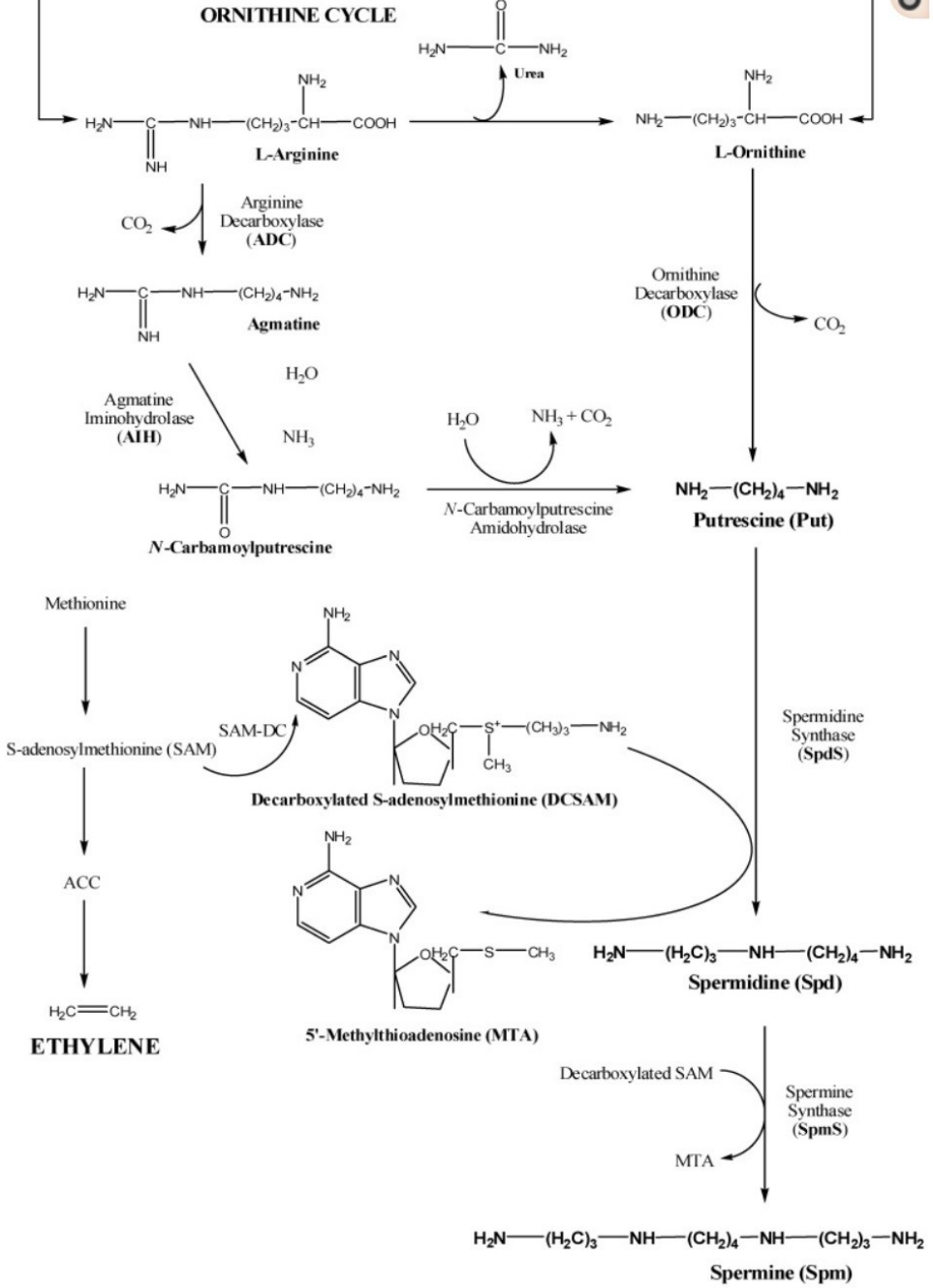
These PAs are involved in a wide range of growth and developmental process, such as cell division, dormancy breaking, germination, development of flower buds, fruit set, growth and ripening, as well as in plant responses to environmental stresses including chilling injury (CI).

Types of polyamine in plants

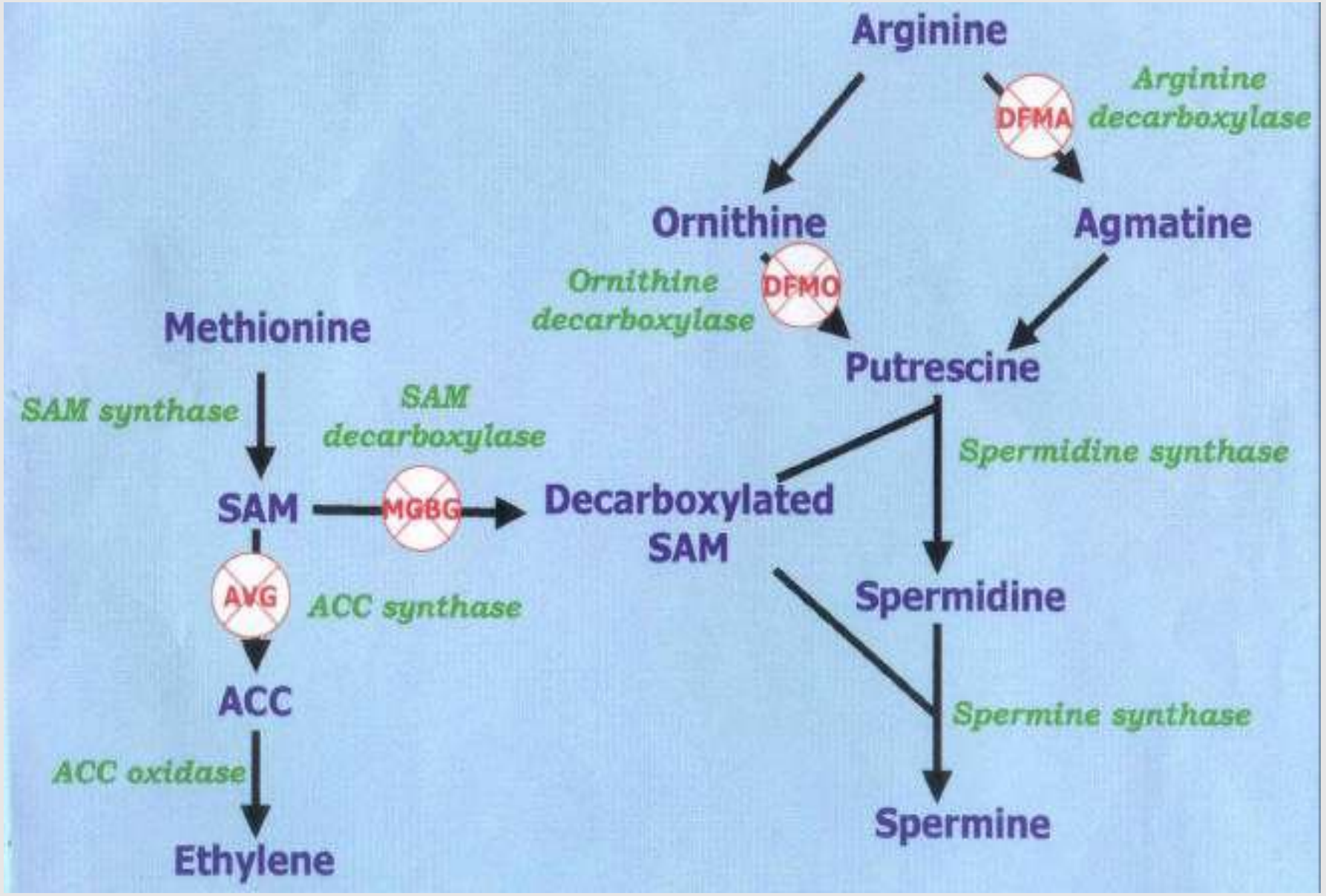
- Putrescine (PUT)
- Spermidine (SPD)
- Spermine (SPM)
- Cadaverine
- Homospermidine
- Caldopentamine
- Canavalmine
- Aminobutyl canavalmine
- Aminopropyl canavalmine
- 1,3-diaminopropane
- Norspermidine (caldine)
- Norspermine (thermine)

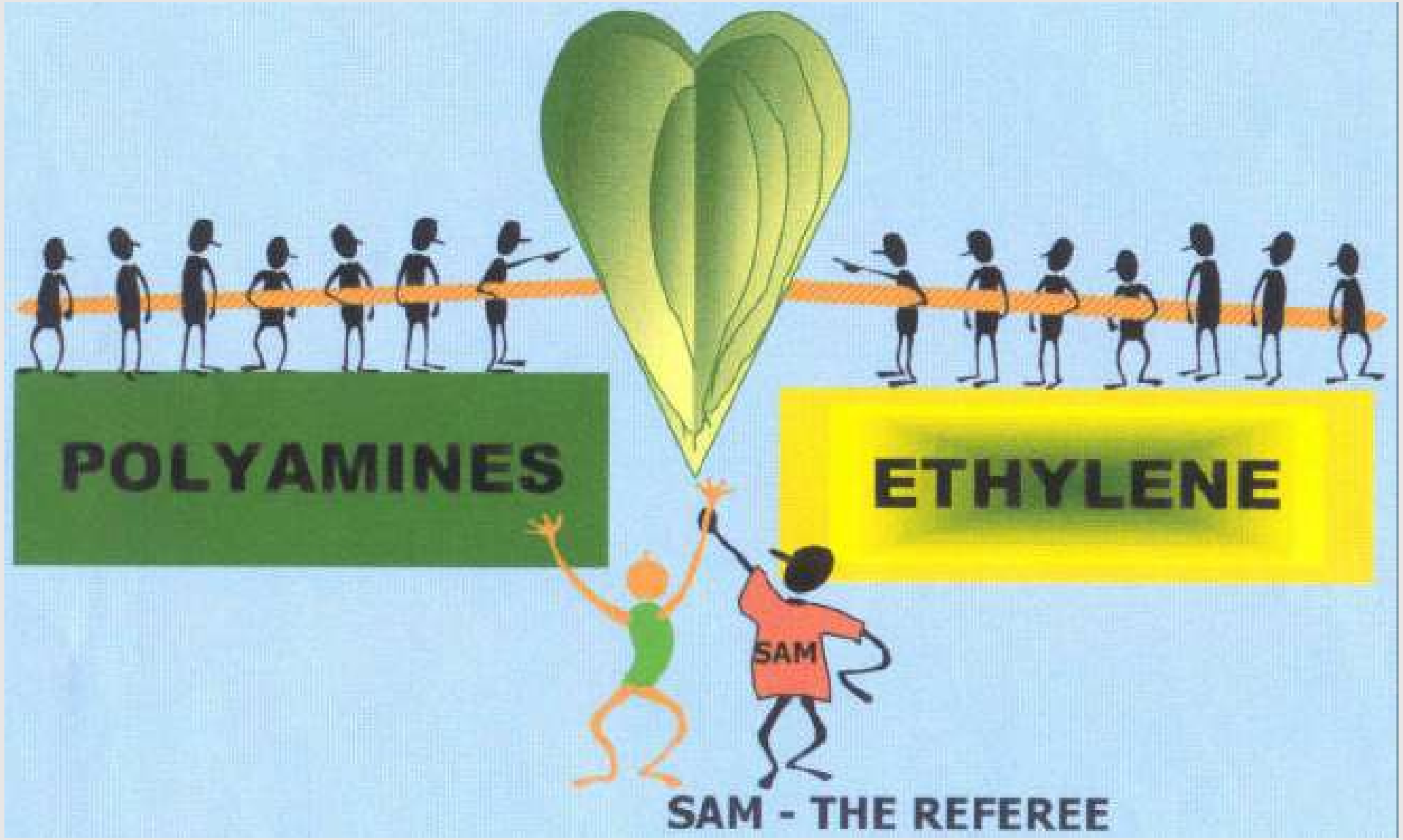


Name	Structure	Molecular formula	Source
Agm		$C_5H_{14}N_4$	ubiquitous
Put		$C_4H_{12}N_2$	Ubiquitous
Spd		$C_7H_{19}N_3$	Ubiquitous
Spm		$C_{10}H_{26}N_4$	Ubiquitous
Cad		$C_5H_{14}N_2$	Legume plants
Tspm		$C_{10}H_{26}N_4$	–


ORNITHINE CYCLE
Urea
L-Arginine
L-Ornithine
Arginine Decarboxylase (ADC)
Agmatine
Ornithine Decarboxylase (ODC)
Agmatine Iminohydrolase (AIH)
N-Carbamoylputrescine
N-Carbamoylputrescine Amidohydrolase
Putrescine (Put)
Methionine
S-adenosylmethionine (SAM)
SAM-DC
Decarboxylated S-adenosylmethionine (DCSAM)
Spermidine Synthase (SpdS)
ACC
ETHYLENE
5'-Methylthioadenosine (MTA)
Spermidine (Spd)
Decarboxylated SAM
Spermine Synthase (SpmS)
MTA
Spermine (Spm)

Biosynthetic Pathways of Important Polyamines




POLYAMINES
ETHYLENE
SAM
SAM - THE REFEREE

Distribution and Localization of PAs in Plants

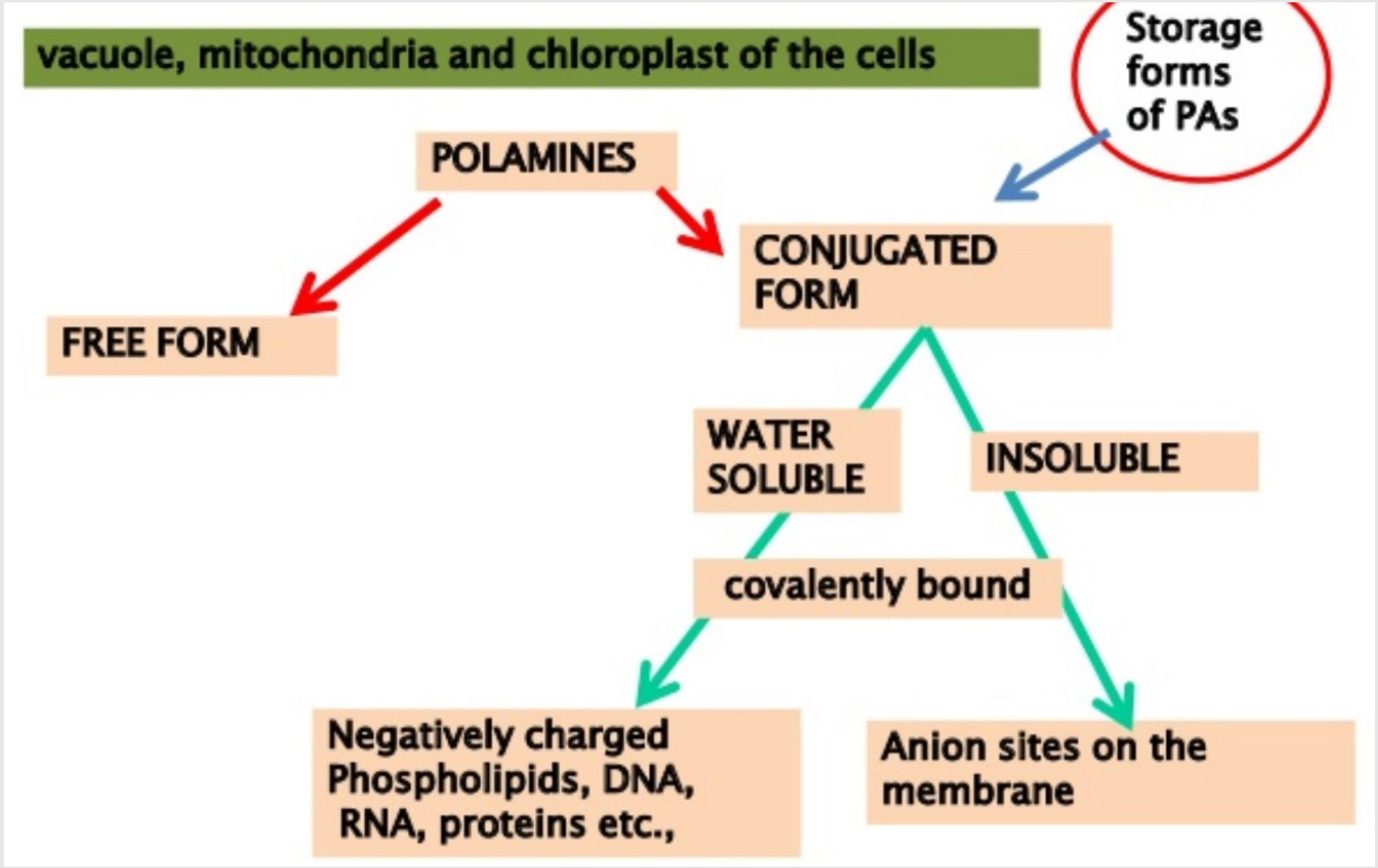
PA's are distributed in all vegetative and reproductive plant organs

- Roots
- Stems
- Leaves
- Flowers (pollen, stamens, pistils)
- Seeds (embryo and endosperm)
- Seedlings
- Tubers
- Meristem
- Xylem Phloem
- Parenchyma tissues

Polyamines show tissue- and organ-specific distribution patterns in plants. For example, the most abundant PA in leaves was found to be Put, and its levels were three times higher than those of Spd and Spm, whereas Spd was found to be the most abundant PA in other organs .

Vacuole, **mitochondria** and **chloroplast** of the cells

Different types of PAs also show different localization patterns within cells. In carrot cells, Put was found to accumulate in the cytoplasm, and Spm in the cell wall.


vacuole, mitochondria and chloroplast of the cells
Storage forms of PAs
POLAMINES
FREE FORM
CONJUGATED FORM
WATER SOLUBLE
INSOLUBLE
covalently bound
Negatively charged Phospholipids, DNA, RNA, proteins etc.,
Anion sites on the membrane

Role of Endogenous Polyamines in Fruit Development and Ripening

PAs are involved in the overall physiological process from floral development to fruit growth and ripening.

PAs are also related to flower genders or fertility as well as to the pollen germination and pollen tube growth and promote flowering of some plants under noninductive conditions.

Inaddition, a clear relationship has been reported between the concentration of free PAs (mainly Spd and Spm) in the apricot ovary and the ovule development, its viability, and fruit set.

Similarly, spray treatments of date palm tree at bloom phase with 0.45 mM Put, alone or in combination with 2% potassium citrate, increased fruit set and fruit retention percentages.

In a similar way, fruit retention was increased in mango tree by Put, Spd, and Spm treatments, especially with Spm when applied at full blossom stage. This effect has been ascribed to the increased levels of endogenous PAs in the fruitlets and pedicels making them less prone to abscise, especially during the initial 4–6 weeks of heavy fruitlet abscission, by inhibiting endogenous ethylene biosynthesis, which is the known trigger in abscission.

Moreover, PA treatments have also led to improved fruit volume and weight in date and apricot fruits, due to the PA effects on increasing fruit sink strength and favoring phloem sugar translocation towards them.

The high PA concentration soon after full bloom has been related to the high growth rate and active cell division. However, in avocado mesocarp cells continue to divide as long as the fruit remains attached to the tree and nevertheless PAs also decreased during fruit growth.

The decrease in PAs at late stages of fruit growth has been regarded as a signal for fruit ripening, although a few exceptions exist.

Moreover, since ethylene and PAs share their common precursor, it is normally accepted that they compete each other during fruit development and ripening and then diminution in Spd and Spm during fruit ripening may be a consequence of SAM diversion to ACC for ethylene biosynthesis, concomitantly with the increase of Put.

Effects of Pre- and Postharvest Polyamine Application on Fruit Ripening and Quality Attributes

According to consumers the term “quality” can be defined as a fruit with a perfect shape, size, color, firmness, aroma, and absence of defects such as cuts, bruises, or decay. However, fruits are appreciated not only because of their attractive sensorial properties, but also because of their nutritional and health benefits, due to their antioxidant compound content with the beneficial role in the prevention of degenerative diseases.

Several experiments have shown that preharvest and postharvest treatments with PAs during the fruit growing season can decrease ethylene production and delay the ripening process in a wide range of fruit species.

- Inhibit biosynthesis of ethylene and reduce respiration rate
- Increase fruit firmness
- Reduce chilling injury
- Retard colour changes
- Reduce mechanical damage
- Maintain antioxidant enzyme activity
- Reduce physiological weight loss (PWL)
- Delay senescence

Ethylene Production

- Field applications of 1 mM Spd on peach trees at 41 days after full bloom led to a lower accumulation of ACO and ACS transcripts at harvest, in accordance with their effect on inhibiting ethylene biosynthesis.
- preharvest foliar spray treatment of plum trees with Put delayed and inhibited both ethylene production and respiration rate during postharvest storage, these effects being higher as Put concentration increased from 0.1 to 2 mM, and also evident after a 6-week period of cold storage.
- The inhibitory effects of exogenous PAs in ethylene production have been ascribed to both the competitive biosynthesis mechanism between ethylene and PAs and to the inhibition of ACC synthase and ACC oxidase.
- The failures of PA treatments on inhibiting synthesis of ethylene in some fruits may be due to their high levels of ethylene production. The delayed postharvest ripening process as a consequence of PA treatments has been also observed in nonclimacteric fruits.

Fruit Quality Parameters

Pre- and postharvest PA treatments have shown to have beneficial effects on fruit quality attributes. Thus foliar spray with Put and Spm to apricot trees increased yield, fruit weight, and fruit volume compared with fruits from control trees. In addition, at harvest time, fruits of treated trees with both Put and Spm had a significantly higher total soluble solids (TSSs) concentration and they were firmer than fruits of control trees, whereas fruit total acidity (TA) was lower in fruits from PA treated trees, showing that PAs could be recommended in cultural practices to enhance the production of apricot tree orchards and improve fruit quality.

Foliar spray treatments of peach trees 19 days before fruit harvest with Put (10 mM), Spd (0.1, 1, and 5 mM), or Spm (2 mM) markedly slowed down the softening process, while only Spd affected the accumulation of TSS, leading to lower levels at harvest as compared with control fruits.

However, in apricot, both Put and Spd were effective in reducing fruit softening during cold storage.

Several mechanisms have been postulated to explain the increased fruit firmness after Put treatment.

- ✓ One is supported by decreased activity of cell wall hydrolytic enzymes involved in softening, such as endo- and exo-polygalacturonase (PG), pectin esterase (PE), and pectin methyl esterase (PME). Thus Spm at the dose of 1.0 mM effectively maintained grape berry firmness during long-term cold storage, because the enzymatic activity of PME was effectively. Accordingly in peach fruit it has been shown that the effect of PA treatment on reducing fruit softening is due to a strong downregulation of genes responsible for fruit softening, such as those codifying for PG and PME.
- ✓ Other mechanisms involve the PA capacity to cross-link pectic substances in the cell wall, producing rigidification and also blocking the access of such degrading enzymes reducing the rate of softening during storage.

postharvest Put treatments decreased the weight loss throughout storage in plum cultivars with respect to those observed in control fruits, as well as Put or Spm treatment of table grape, which was attributed to the improved biophysical properties of the berries by means of stabilization and consolidation of both cell integrity and permeability as a consequence of Spm treatment manifested as lower electrolyte leakage during storage.

Another effect of PA treatments is amelioration of chlorophyll breakdown in several fruits, such as lemon and apricot, which is an indicator of reduced senescence rate. exogenous PAs retarded chlorophyll loss in muskmelon by reducing the hydrolytic activities acting on chloroplast thylakoid membranes.

Similarly, Put treatments reduced color change during low-temperature storage in a wide range of plum cultivars, the effect being also attributed to lower chlorophyll degradation and delay in the senescence process. The effects of PAs on retarding color evolution were in the order: SPM4+ > SPD3+ > PUT2+, following the order of their available number of cations, which has been argued as the reason for their difference in effectiveness.

Taking into account data of the observed parameters relating to fruit quality (firmness, color, TSS, and TA), as well as the visual appearance of the fruits, it could be concluded that PA treatment, either at pre- or postharvest time, delayed the postharvest ripening process, with a net effect on maintaining fruit quality attributes and increasing the fruit shelf life. These effects could be because PA treatments led to increases in endogenous Put and Spd concentrations, as have been shown in lemon, peach, apricot plum, and pomegranate.

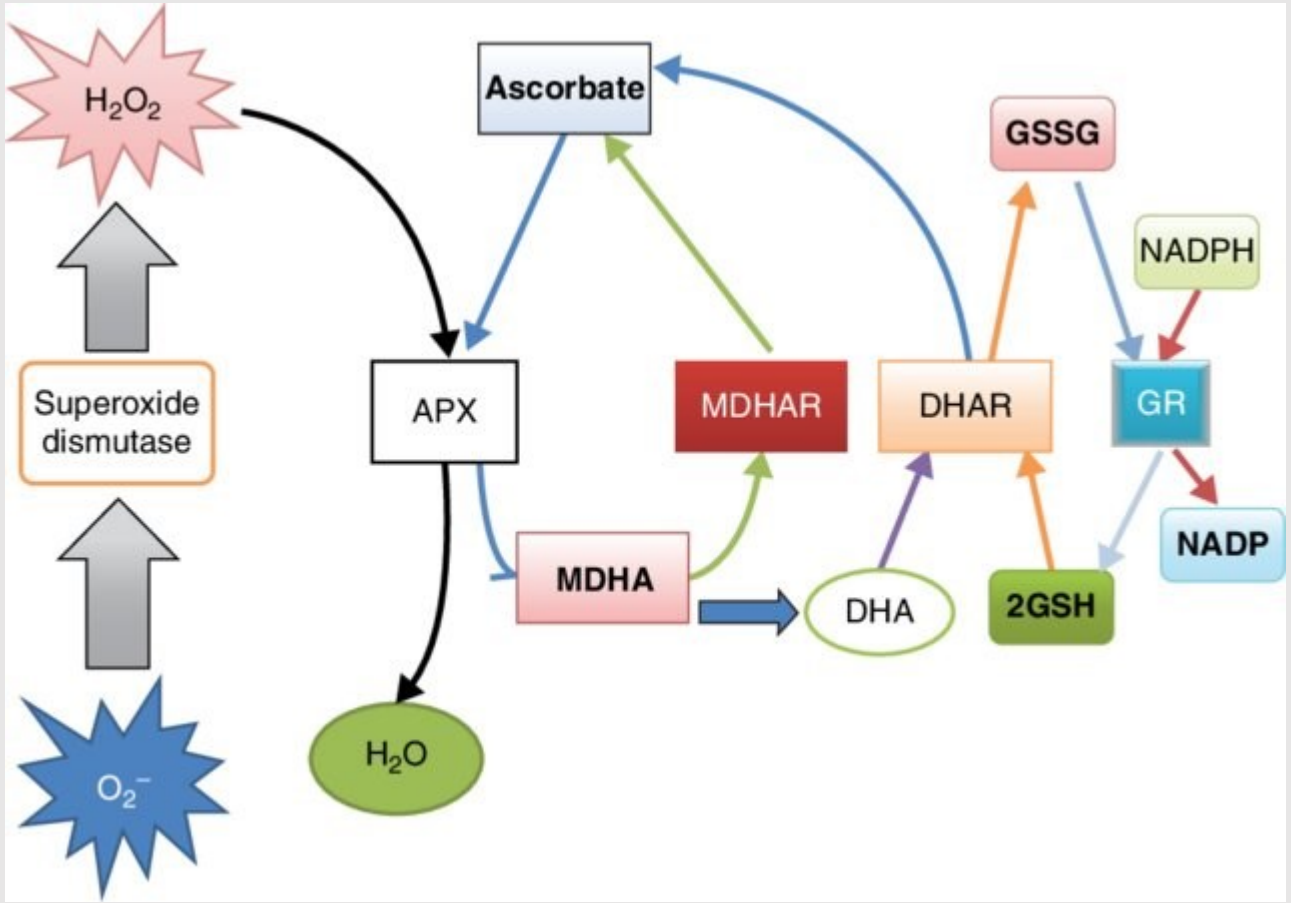
Bioactive Constituents With Antioxidant Activity

Positive correlation between putrescine concentrations and antioxidant activity of fruit.

Moreover, treatments with Put, Spd, or Spm at concentrations of 0.01, 0.1, and 1 mM of mango trees by foliar spraying at final fruit set stage led to fruits with significantly higher total carotenoids in the pulp at harvest time as compared with fruits from control trees, the maximum increase being observed with Put treatments (95%) followed by Spd (33%).

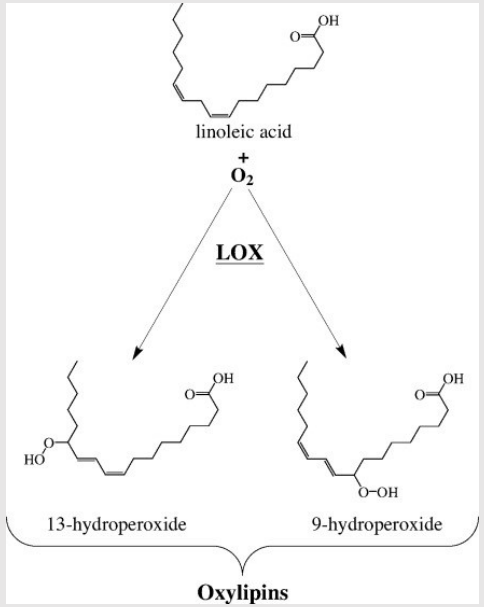
Pomegranate treated with 2 mM Put by the immersion method retained higher anthocyanin, ascorbic acid, and tannin concentrations and antioxidant activity than control fruits, the effects being increased when Put was applied in combination with carnauba wax.

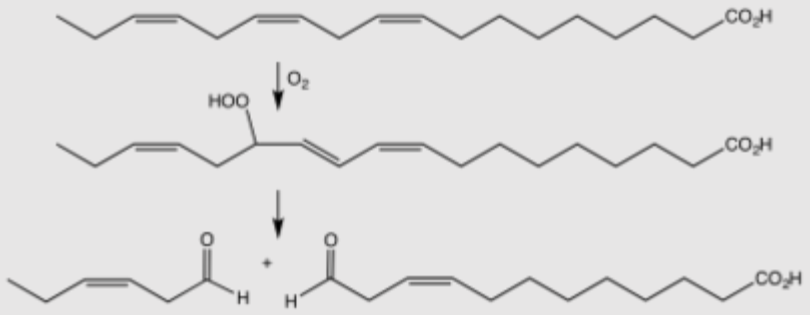
The enhancement of total antioxidant activity found in pomegranate arils after PA treatments could be attributed to the PA capacity acting as effective scavengers of free radicals, and even to their role on the superoxide dismutase (SOD)/ascorbate–glutathione cycle.



Delay senescence

- Activated oxygen free radicals cause per oxidative damage to all membranes and hasten senescence.
- Polyamines (PAs) are effective scavengers of these free radicals produced by lipoxygenase (LOX) and phospholipase-D (PL-D).
- PAs have been considered as antisenescence agents.





Polyamines and Chilling Injury

Many tropical and subtropical fruits suffer physiological alterations know as chilling injury (CI) when stored at low temperatures, usually below 10–12°C depending on commodities.

Chilling symptoms mainly develop during shelf life after removing fruits from low-temperature storage and are manifested as surface pitting, flesh browning and mealiness in apricot, failure of fruit to ripen, or uneven or slow ripening, accelerated senescence and ethylene production, shortened storage or shelf life, compositional changes affecting flavor and texture, loss of growth or sprouting capability, wilting, and increased decay due to leakage of plant metabolites, which encourage growth of microorganisms, especially fungi.

Cell membranes are the first cell structures affected by CI, which change from a flexible liquid-crystalline phase to a solid gel structure at chilling temperatures, leading to losses of the cell membrane semipermeability and functionality. In addition, disorganization of mitochondria and chloroplast occurs, which sets off a cascade of secondary reactions, including ethylene production, increased respiration, reduced photosynthesis, and interference with energy production, accumulation of toxic compounds, such as ethanol and acetaldehyde, and altered cellular structure.

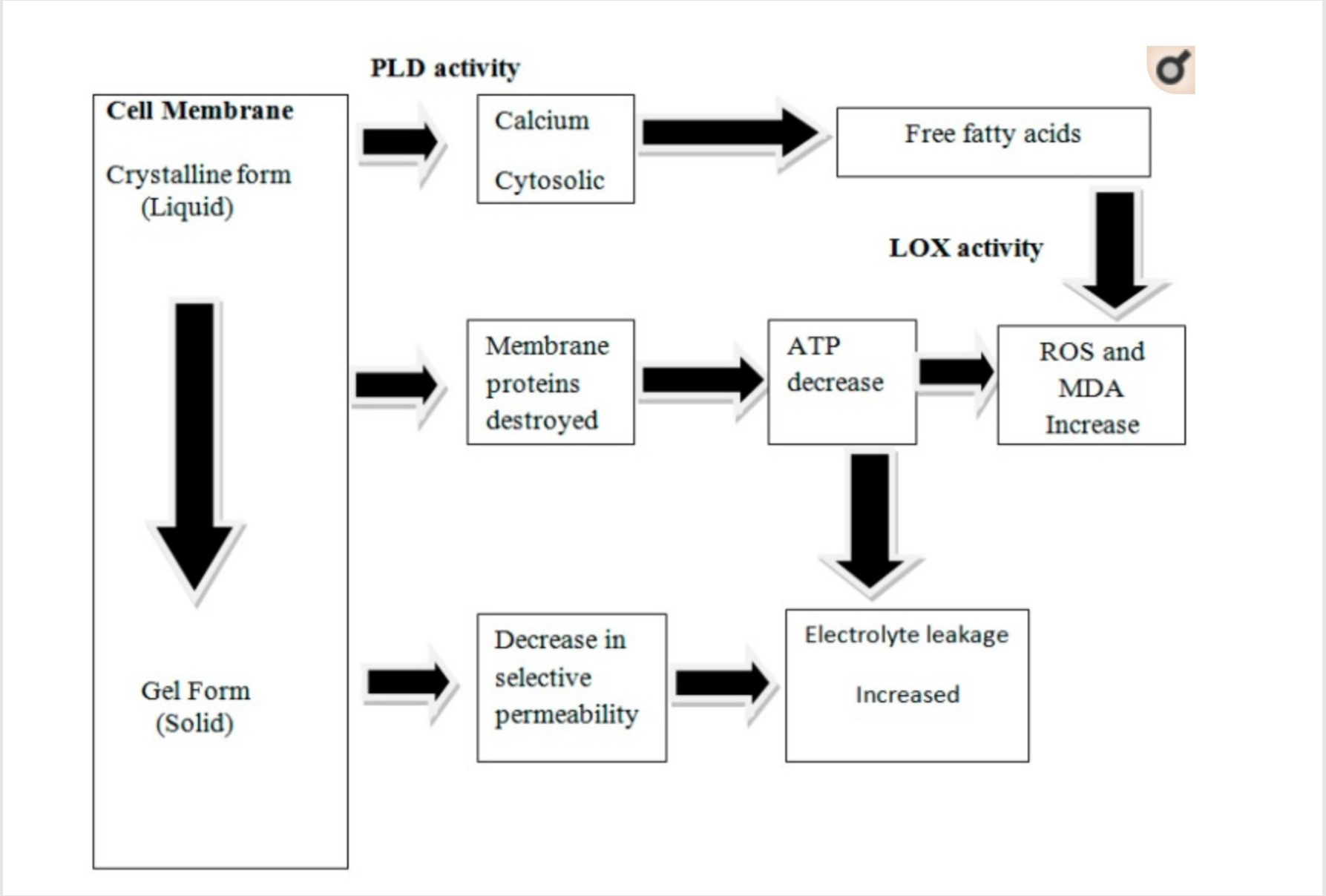
It has been found that membrane lipid composition changes during storage, with losses of saturated and unsaturated fatty acids and reduction in the ratio of unsaturated/saturated fatty acids, affecting membrane permeability and causing leakage of intracellular water, ions, and metabolites, which can be monitored by determining electrolyte leakage (EL).

Thus EL is a measurement of loss of semipermeability of cell membranes, which increases as a consequence of membrane damage, and has been widely used as an indicator of CI .

Another indicator of the structural integrity of the plant membranes is malondialdehyde (MDA), which is a secondary end product of the oxidation of the membrane polyunsaturated fatty acid, and increases in chilling injured fruit and vegetable tissues.

In addition, increases in phospholipase-d and lipoxigenase activities, responsible for the degradation of unsaturated fatty acids, reduced cell membrane integrity and therefore increased CI impact.

Membrane lipid peroxidation can be also stimulated by radical oxygen species (ROS) generated as a consequence of chilling stress.


PLD activity
Cell Membrane
Crystalline form
(Liquid)
Calcium
Cytosolic
Free fatty acids
LOX activity
Membrane
proteins
destroyed
ATP
decrease
ROS and
MDA
Increase
Gel Form
(Solid)
Decrease in
selective
permeability
Electrolyte leakage
Increased

PAs, as polycationic molecules at physiological pH, can bind strongly to anionic components of the cell membranes, such as phospholipids, leading to stabilization of the bilayer surface. Then, as the maintenance of membrane stability at low temperature is an important factor for plant resistance to cold stress.

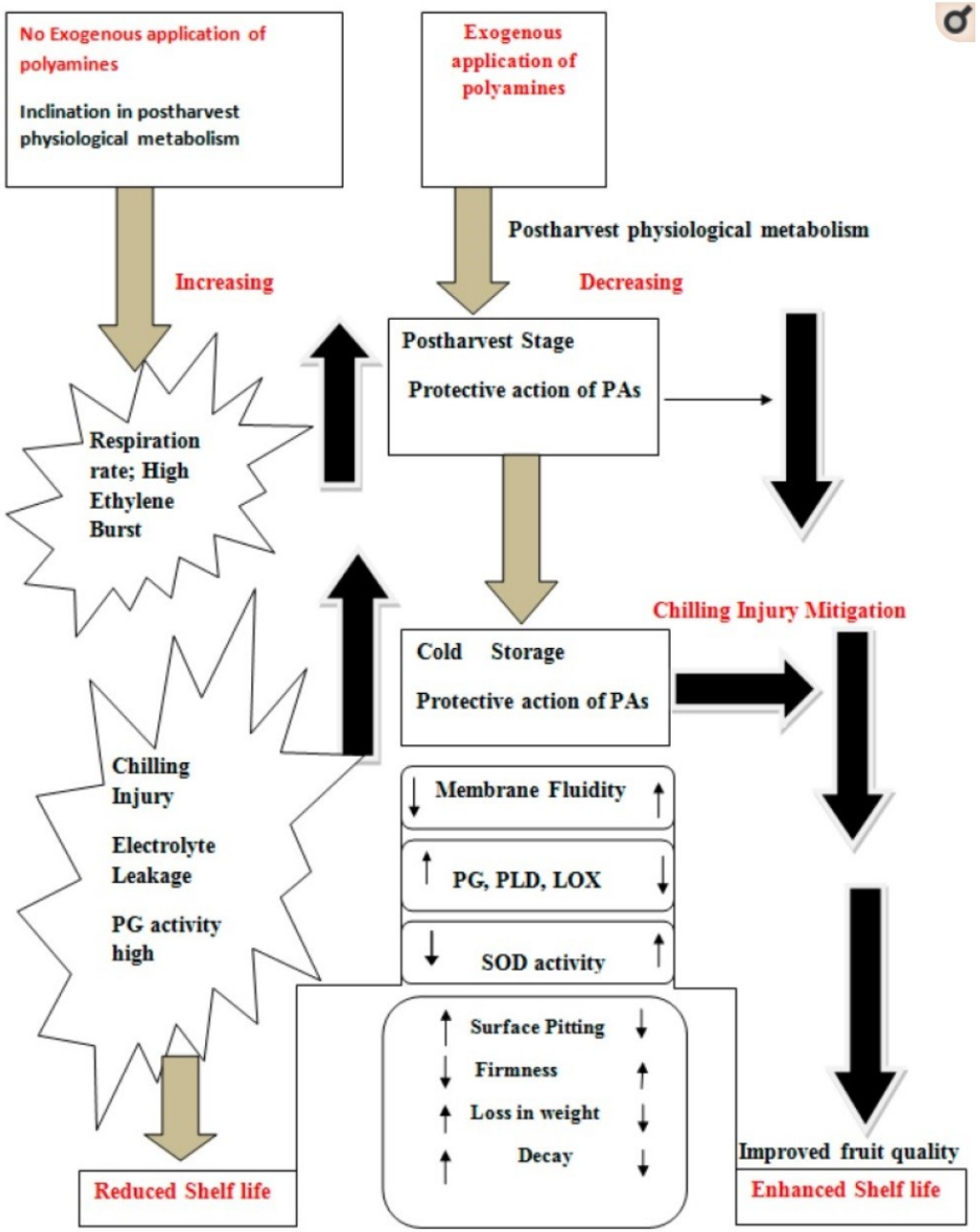
In addition, PAs exhibit antioxidant activity by scavenging ROS, leading to enhanced membrane stability and integrity under CI stress. In this sense, increases in Put concentration have been found in several fruits suffering CI, such as lemon, orange, lime, grapefruit, pepper, tomato, peach, pepino, and zucchini, among others.

Thus PAs could work as free radical scavengers, stabilizing membranes by means of ionic interactions to provide protection against chilling stress, this effect being greater as the number of positive charges per molecules is increased, that is, Spm > Spd > Put.

Heat treatments have been also effective on decreasing CI by increasing PA concentration in a wide range of fruits. In Fortune mandarins, temperature pretreatments for 3 days above 20°C increased progressively both Put and Spd levels in flavedo, as did temperature treatment, and reduced CI.

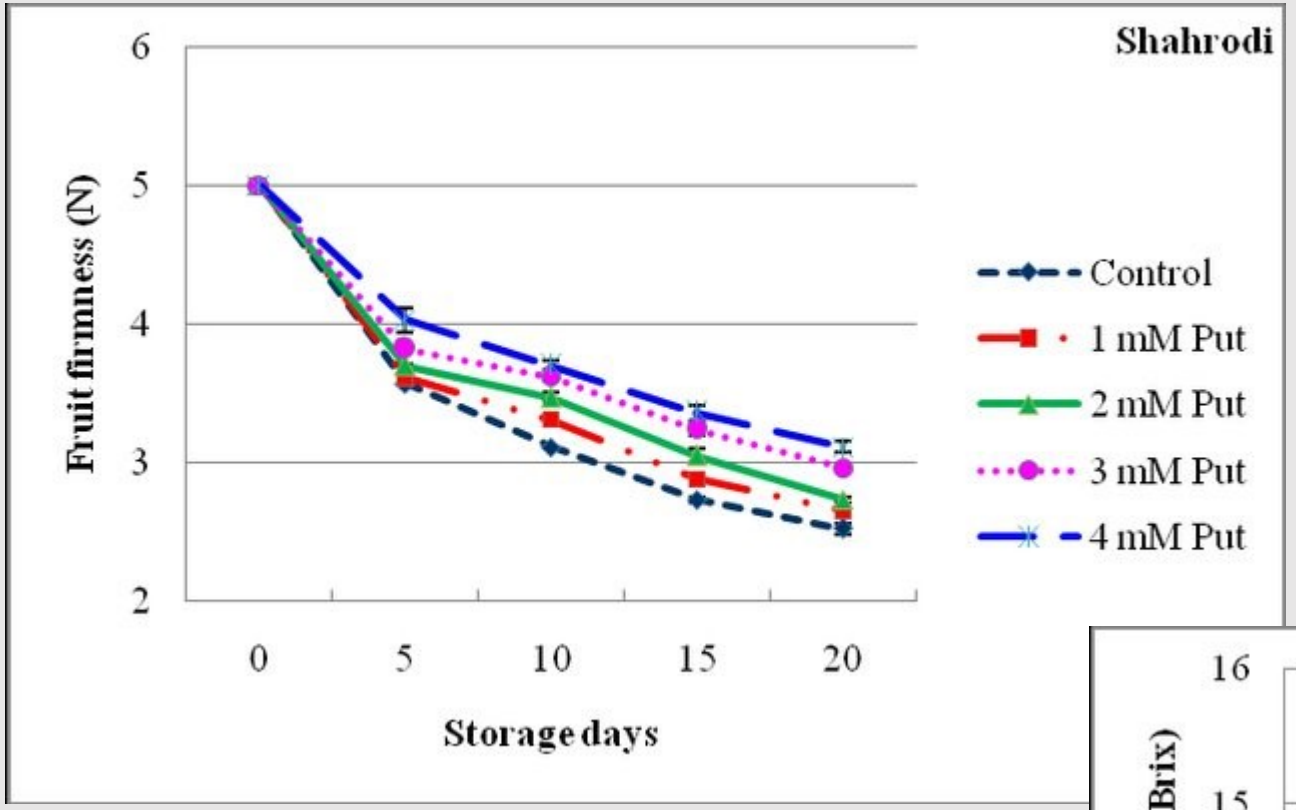
In some fruits, Put treatment was more effective than those of Spd or Spm and its effects on improving fruit chilling tolerance have been attributed to enhancement of betaine and proline concentrations, which can act not only as osmoprotectants but also as a membrane stabilizer contributing to the stabilization and integrity of cellular membranes under chilling stress.

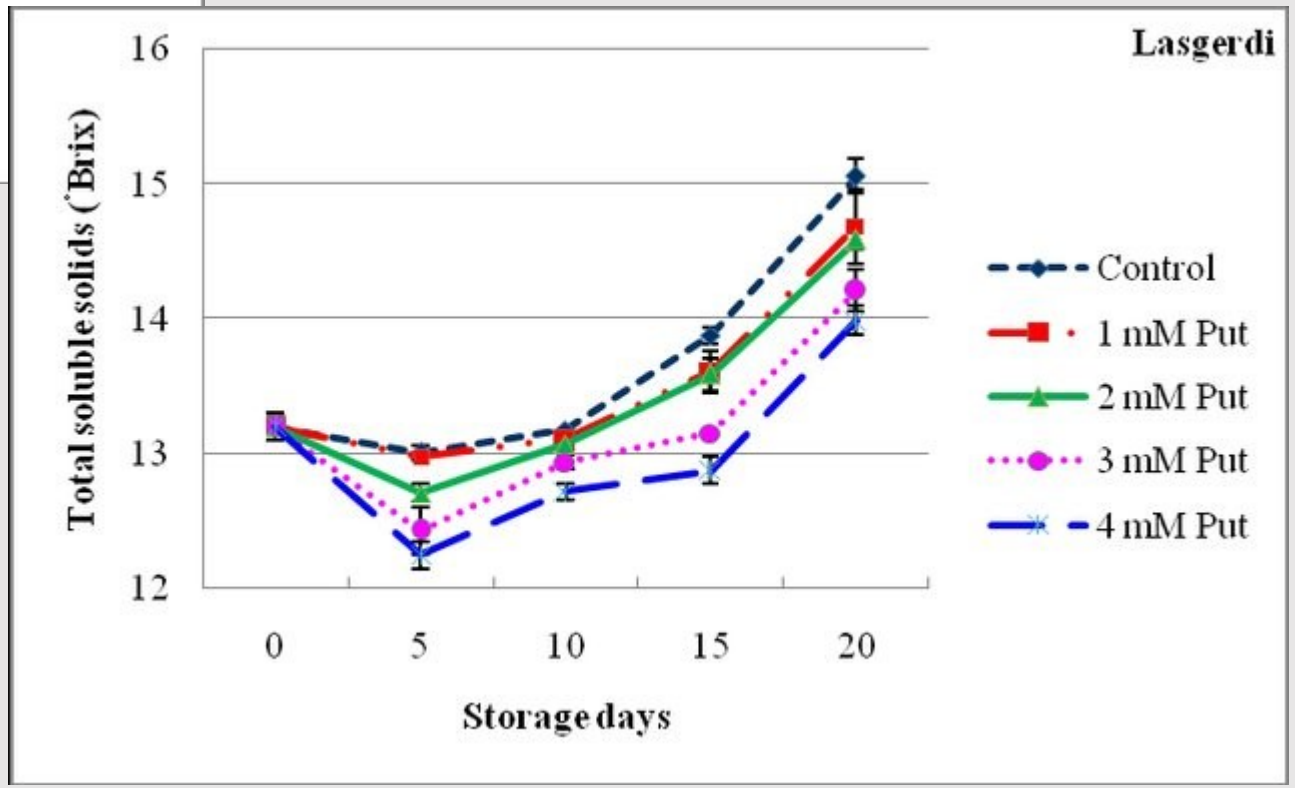
Thus, PAs may be involved in reducing CI due to their ability to preserve membrane integrity, both by lowering the membrane phase transition temperature fluidity and by retarding lipid peroxidation, resulting in increased cell viability, due to their membrane-binding capacity and/or antioxidant properties. Thus the increases of PAs occurring in chilling injured fruits could be a natural defense mechanism of fruit tissues against this stress, although this effect itself may not be totally accurate if the increase in PAs is not high enough.

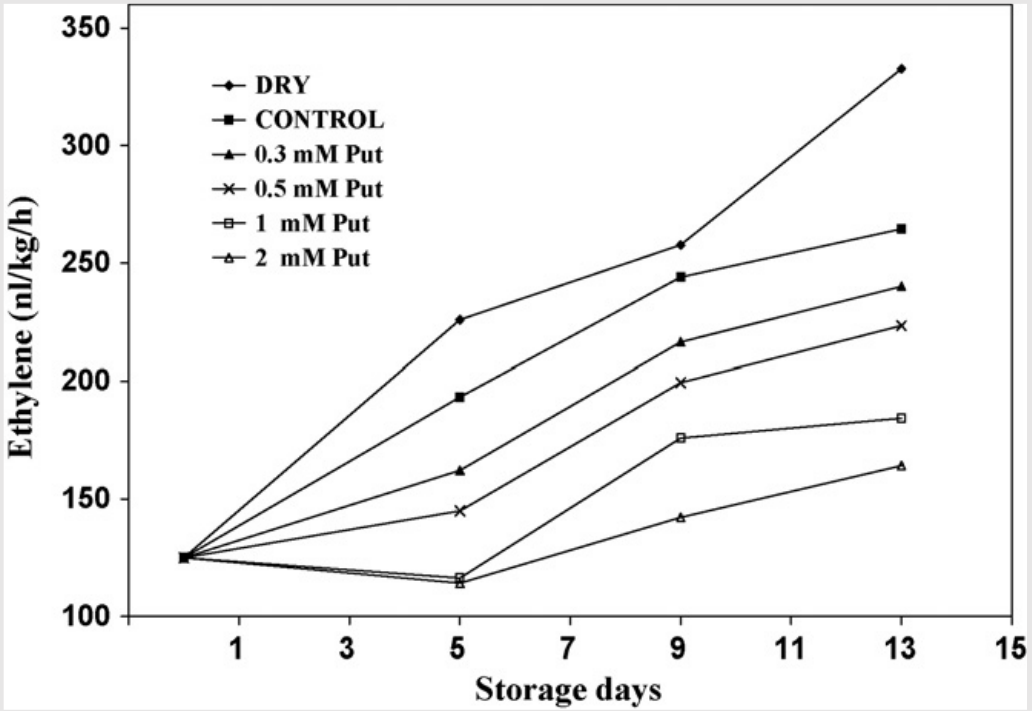

No Exogenous application of polyamines
Inclination in postharvest physiological metabolism
Exogenous application of polyamines
Postharvest physiological metabolism
Increasing
Decreasing
Postharvest Stage
Protective action of PAs
Respiration rate; High Ethylene Burst
Chilling Injury Mitigation
Cold Storage
Protective action of PAs
Chilling Injury
Electrolyte Leakage
PG activity high
Membrane Fluidity
PG, PLD, LOX
SOD activity
Surface Pitting
Firmness
Loss in weight
Decay
Reduced Shelf life
Improved fruit quality
Enhanced Shelf life

Summary of effect of PAs on postharvest physiology and quality of fruits.

		mM	
Mango	SPM	0.5 mM	Reduction in weight loss, decrease in softness, decrease in respiration rate
	SPM and PUT	0.5, 1 mM	Reduced weight loss, reduced fruit colour
	PUT	2.0 mM	Reduced physiological weight loss, improved blend of TSS, acidity and palatability rate
	PUT	2.0 mM	Inhibition of ethylene release, respiration rate, fruit softening, suppression of cell wall enzymes *endo*, *exo*-PG and *EGase*, modulation of antioxidant enzymes: SOD CAT, POX, overall fruit quality maintained
Plum	PUT	1 mM	Increased firmness peel and flesh firmness, decreased ethylene and CO_2 evolution. SPD acted as physiological marker against mechanical damage
	PUT	1 mM	Reduction in ethylene release and soluble solids, increased fruit and flesh firmness, and extended storability
Pomegranate	PUT or SPD	1 mM	Maintained fruit firmness, enhanced shelf life, reduced husk scald, prevented skin browning
	PUT or SPD	1 mM	Heat treatment induced PA induction, reduction in fruit softening, CI mitigation
	PUT + Carnauba wax	2 mM Ratio (1:10)	Low respiration rate, ethylene release and CI, no discoloration of fruit peel, fruit firmness maintained, mitigation in pitting surface
Strawberry cv. Selva	PUT	1 mM 2 mM	Reduced weight loss and ethylene release and maintained firmness
"Valencia" oranges	PUT + Methyl jasmonate	5 mM + 10 µmol	Lowered enzymatic activity and chilling injury
	SPD	1, 1.5 mM	Maintained TSS, tritatable acidity, flavour index


Shahrodi
Fruit firmness (N)
6
5
4
3
2
0
5
10
15
20
Storage days
Control
1 mM Put
2 mM Put
3 mM Put
4 mM Put


Lasgerdi
Total soluble solids (˚Brix)
16
15
14
13
12
0
5
10
15
20
Storage days
Control
1 mM Put
2 mM Put
3 mM Put
4 mM Put

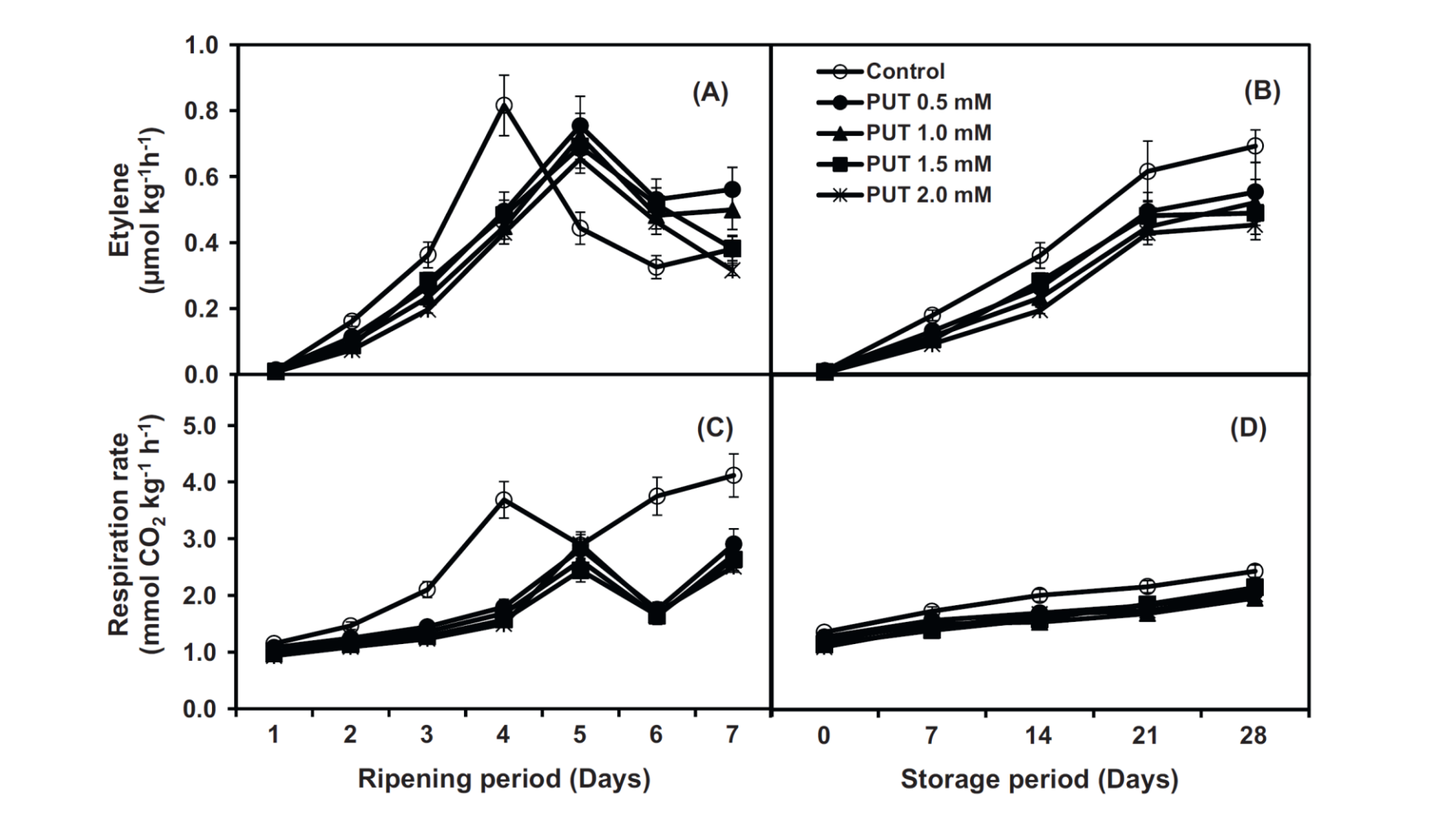


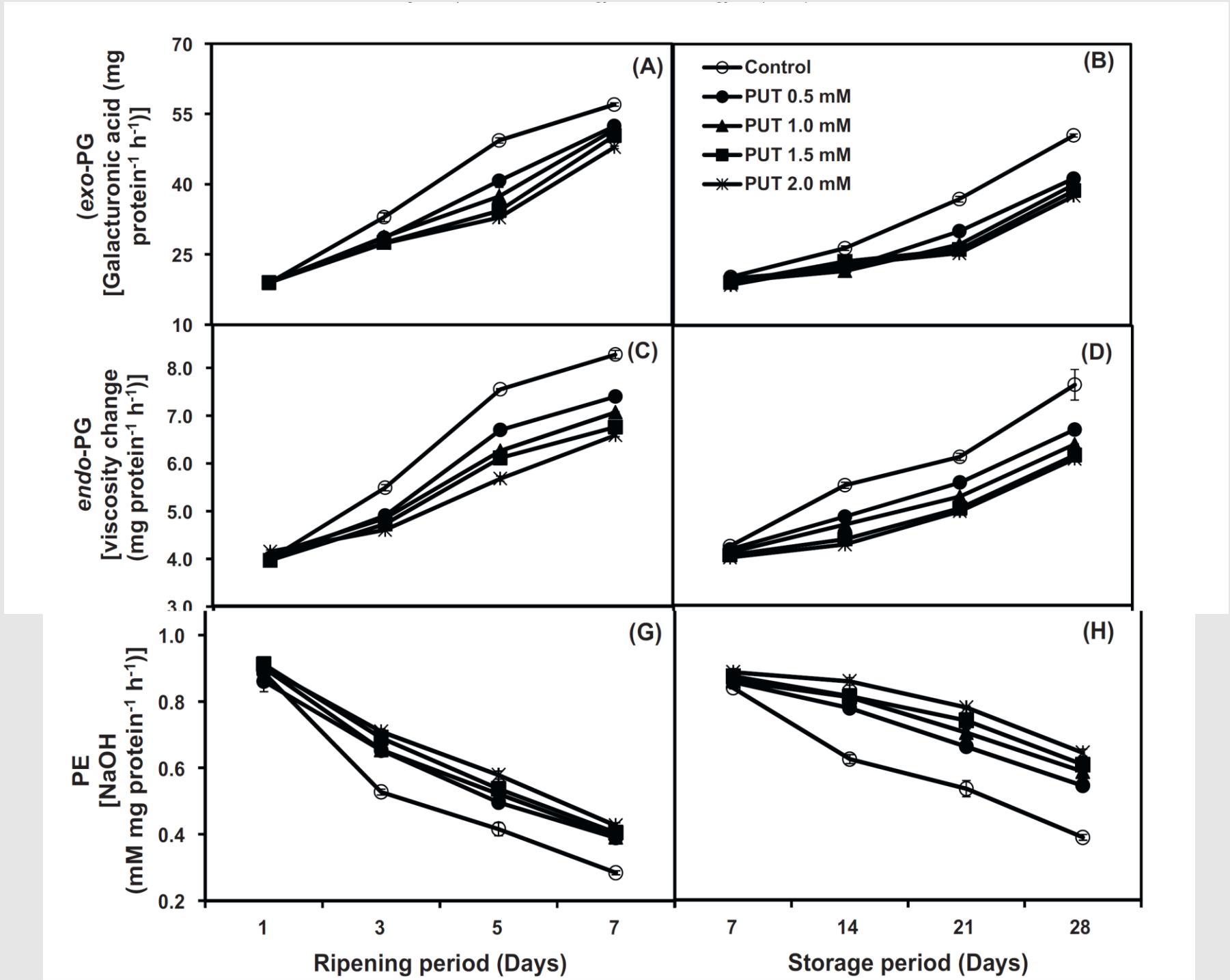
Effect of putrescine on ethylene production by strawberry fruits, cv.Selva, during storage.

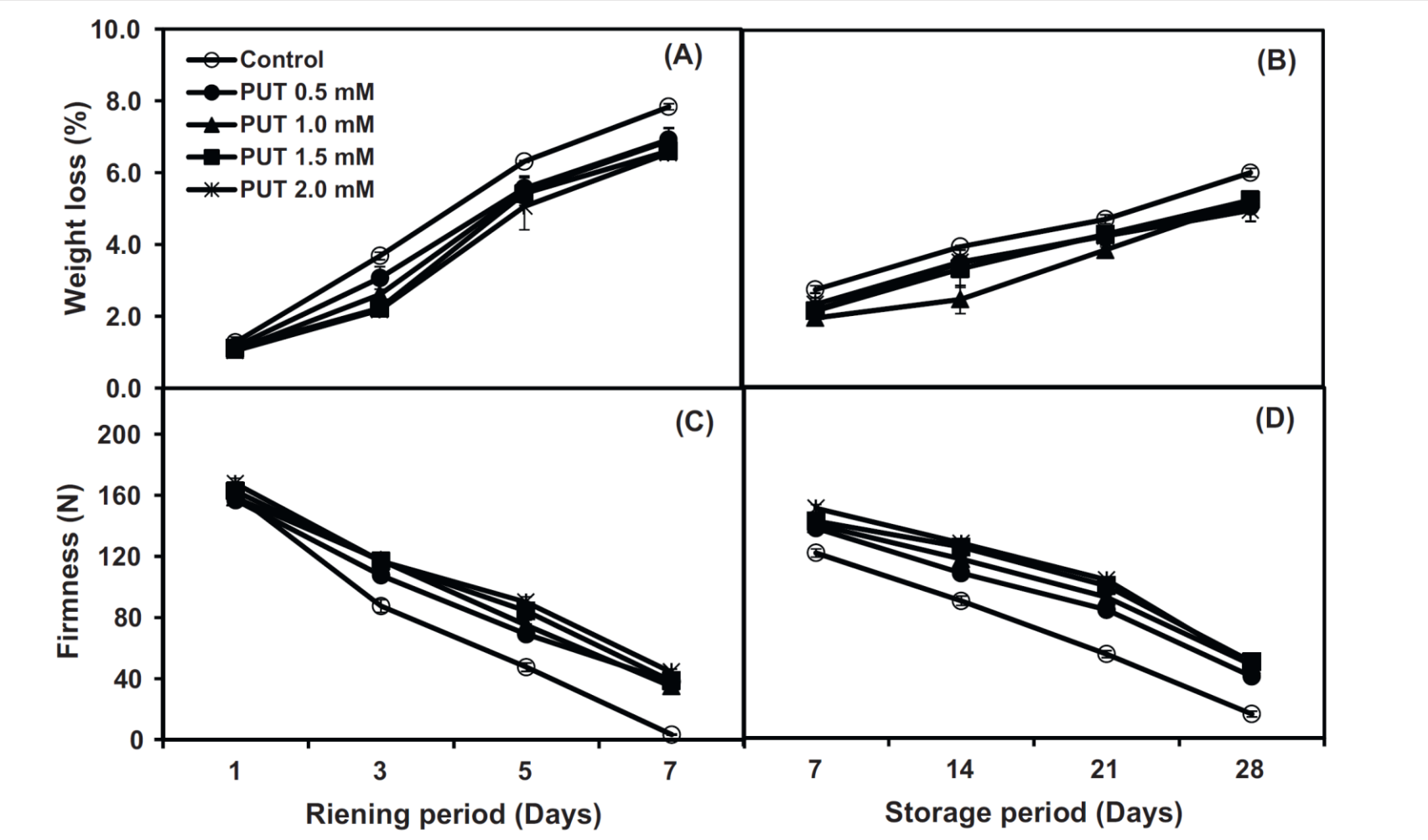
Reduce respiration rate

- After harvest fruits are live and continue respiration
- It converts stored sugars into energy
- PAs reduced respiration also retards softening

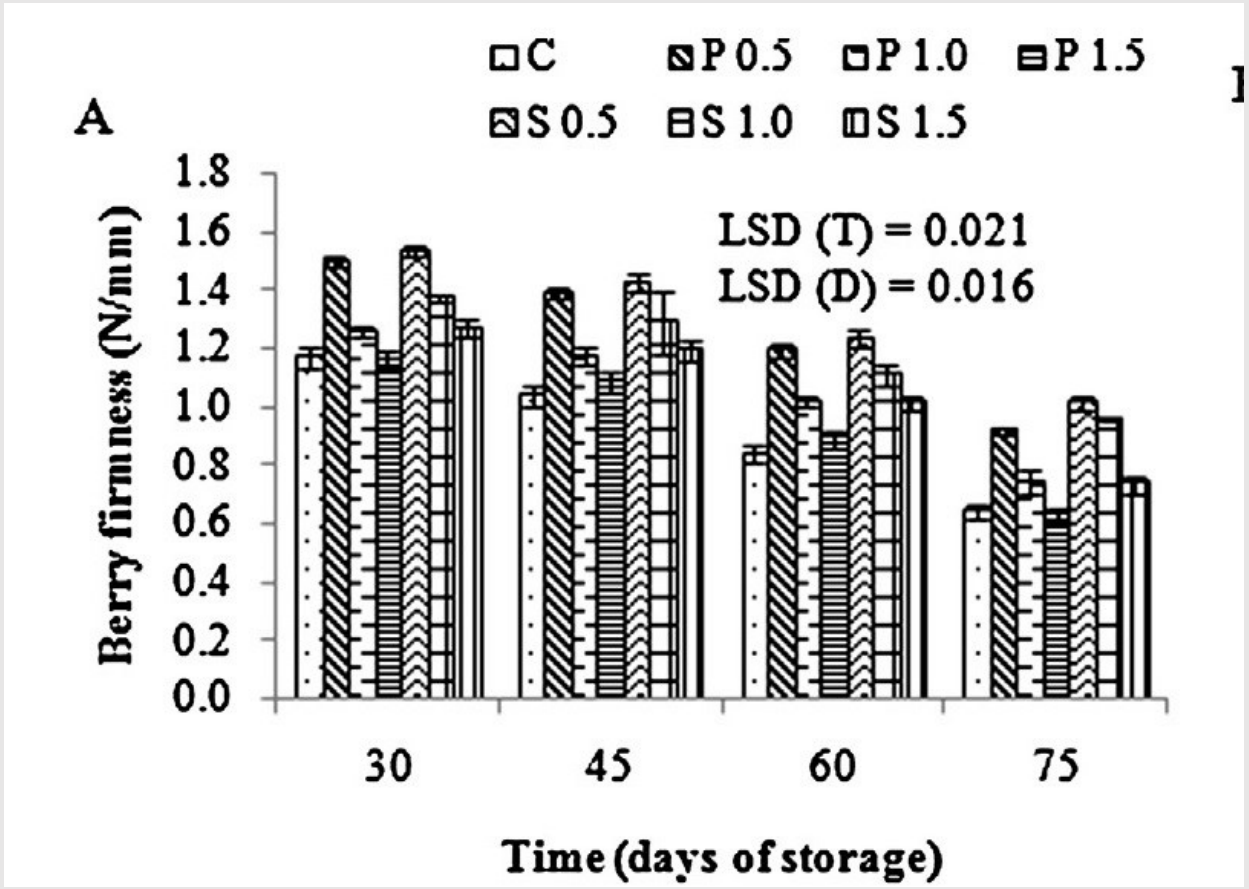
Effect of postharvest application of putrescine (T) on ethylene production (A and B) and respiration rate (C and D) of ‘Samar Bahisht Chaunsa’ mango fruit during ripening (RP) at ambient conditions and cold storage.




(A)
(B)
(C)
(D)
(G)
(H)
Control
PUT 0.5 mM
PUT 1.0 mM
PUT 1.5 mM
PUT 2.0 mM
(exo-PG [Galacturonic acid (mg protein-1 h-1)]
endo-PG [viscosity change (mg protein-1 h-1)]
PE [NaOH (mM mg protein-1 h-1)]
70
55
40
25
10
8.0
7.0
6.0
5.0
4.0
3.0
1.0
0.8
0.6
0.4
0.2
1
3
5
7
14
21
28
Ripening period (Days)
Storage period (Days)


Control
PUT 0.5 mM
PUT 1.0 mM
PUT 1.5 mM
PUT 2.0 mM
(A)
(B)
(C)
(D)
Weight loss (%)
Firmness (N)
10.0
8.0
6.0
4.0
2.0
0.0
200
160
120
80
40
0
1
3
5
7
7
14
21
28
Riening period (Days)
Storage period (Days)

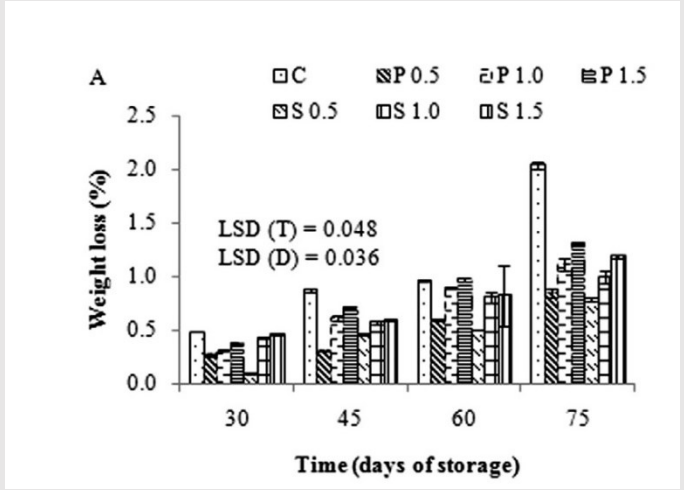
Variation in firmness of grape cv. FlameSeedless during cold storage (3–4◦C, 90–95% RH) in relation to postharvest treatment with different concentrations of putrescine and spermidine.

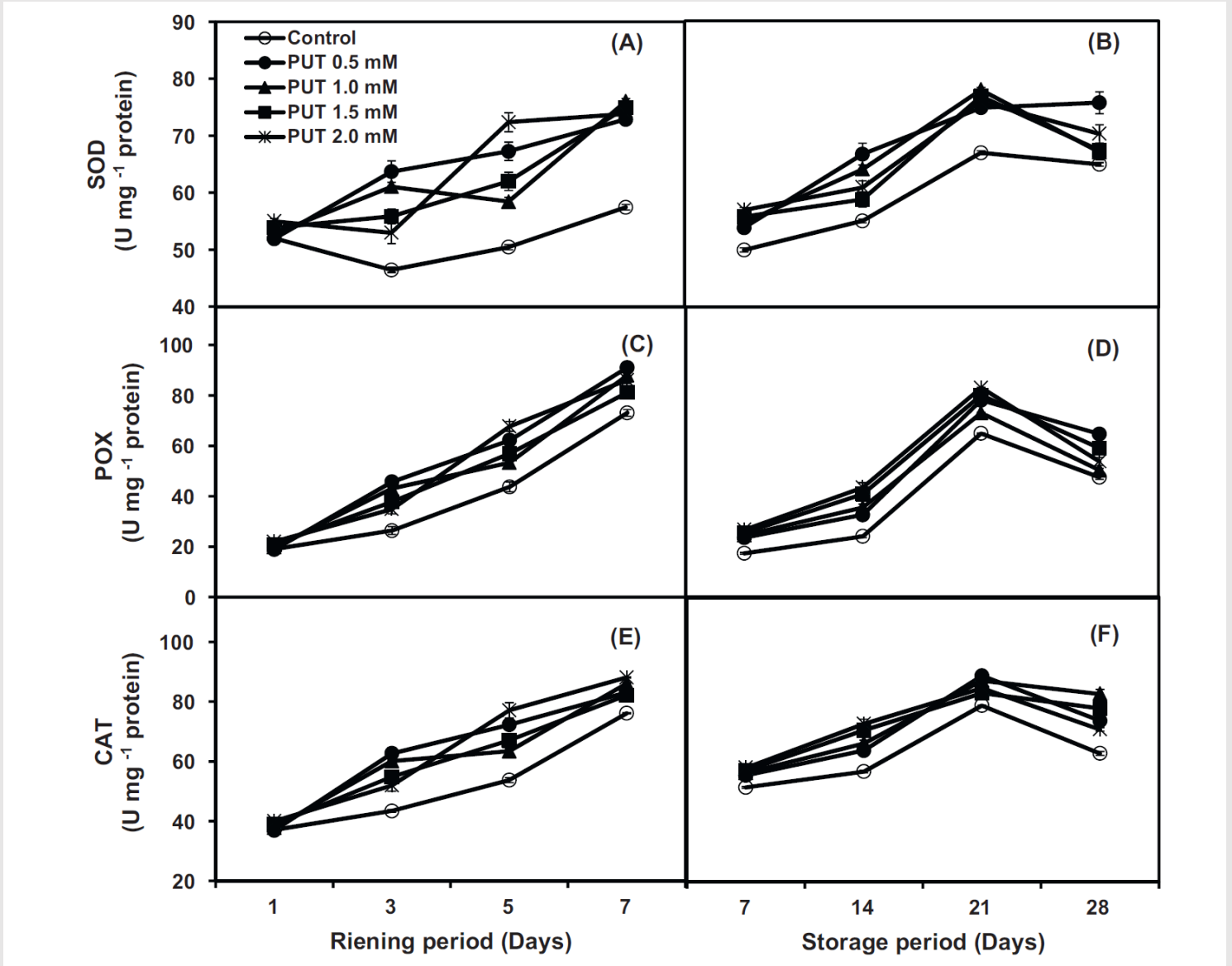


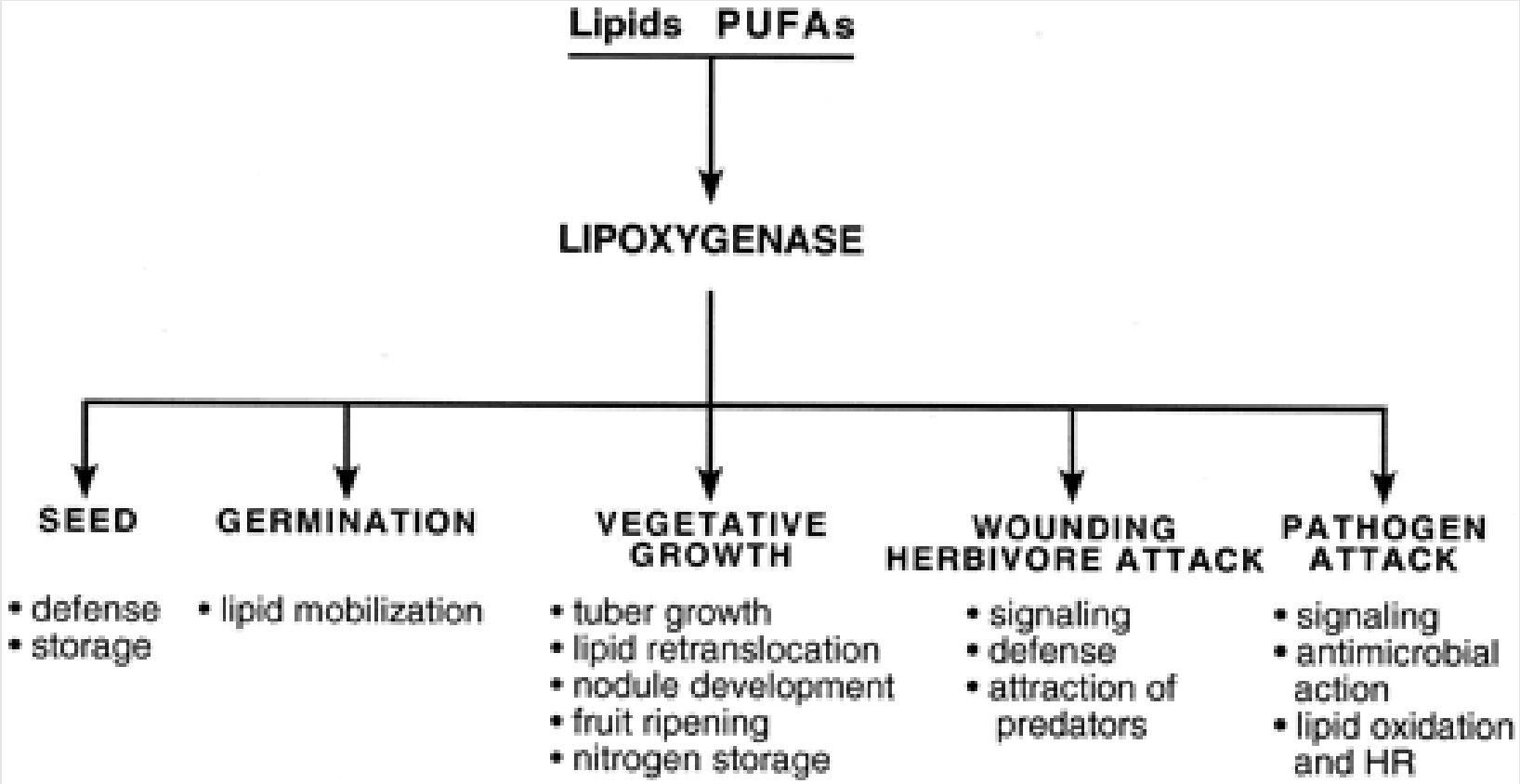
Retard colour changes

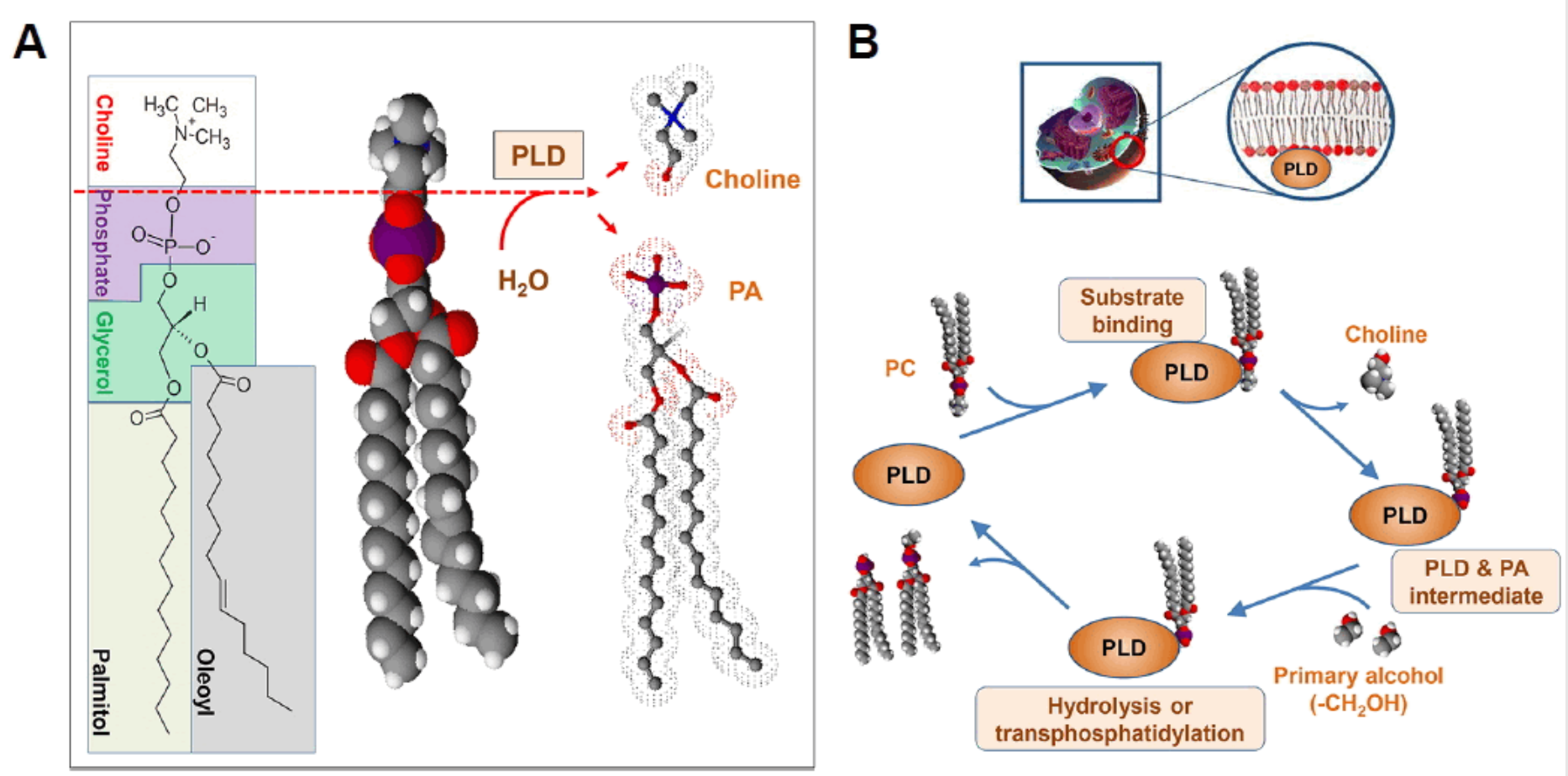
- Accumulation of carotenoids and anthocyanins
- Carotenoids are natural fat-soluble pigments derived from isoprene.
- PAs retarded chlorophyll breakdown and carotenoid biosynthesis.
- PUT delay colour development during storage.

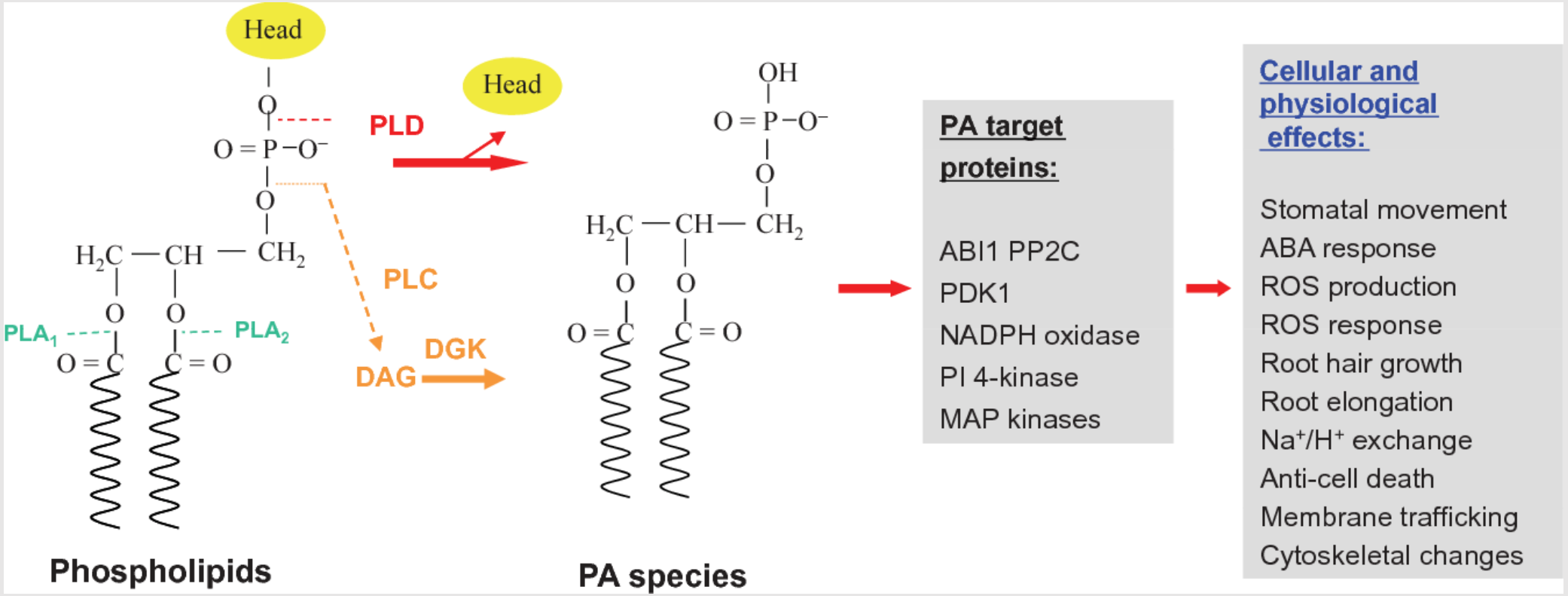
Lower pectin methylesterase (PME) activity was found in fruittreated with putrescine or spermidine (Fig. 1B). It is well knownthat changes in the pectin matrix affect cell wall structure duringfruit ripening and senescence (Deytieux-Belleau et al., 2008). In thiscontext, PME activity constitutes a key control point for both theassembly and disassembly of pectin networks. The modificationsof pectin chains by the action of PME determine the accessibility ofthe galacturonans to degradation by polygalacturonases (Barnavonet al., 2001). During the first 45 days of storage, no significantincrease in PME activity was detected. However, a surge of PMEactivity was observed after this point which may be considered asa signal for induction of rapid softening/accelerated ripening in thisnon-climacteric fruit. Reduced activity of fruit softening enzymesFig. 2. Variation in weight loss (A), berry shatter (B), decay incidence (C) and membrane electrolyte leakage (MEL, D) of grape cv. Flame Seedless during cold storage (3–4◦C,90–95% RH) in relation to postharvest treatment with different concentrations of putrescine and spermidine. Vertical bars represent ± S.E. of pooled mean. C: control (0.0 mM),P: putrescine (mM), S: spermidine (mM), T: treatment, D: days.




Control
PUT 0.5 mM
PUT 1.0 mM
PUT 1.5 mM
PUT 2.0 mM
(A)
(B)
(C)
(D)
(E)
(F)
SOD (U mg -1 protein)
POX (U mg -1 protein)
CAT (U mg -1 protein)
90
80
70
60
50
40
100
80
60
40
20
0
100
80
60
40
20
1
3
5
7
7
14
21
28
Riening period (Days)
Storage period (Days)


Lipids PUFAs
LIPOXYGENASE
SEED
• defense
• storage
GERMINATION
• lipid mobilization
VEGETATIVE GROWTH
• tuber growth
• lipid retranslocation
• nodule development
• fruit ripening
• nitrogen storage
WOUNDING HERBIVORE ATTACK
• signaling
• defense
• attraction of predators
PATHOGEN ATTACK
• signaling
• antimicrobial action
• lipid oxidation and HR


A
Choline
Phosphate
Glycerol
Palmitol
Oleoyl
PLD
H_2O
Choline
PA
B
PLD
PC
Substrate binding
PLD
Choline
PLD
PLD
PLD & PA intermediate
PLD
Primary alcohol (-CH_2OH)
Hydrolysis or transphosphatidylation


Head
PLD
Head
PLC
DGK
DAG
PLA1
PLA2
Phospholipids
PA species
PA target proteins:
ABI1 PP2C
PDK1
NADPH oxidase
PI 4-kinase
MAP kinases
Cellular and physiological effects:
Stomatal movement
ABA response
ROS production
ROS response
Root hair growth
Root elongation
Na+/H+ exchange
Anti-cell death
Membrane trafficking
Cytoskeletal changes

Reduce chilling injury

- Chilling injury (CI) are exposed to low but non-freezing temperatures either before or after harvest
- CI shows skin browning, pitting, increased electrolyte leakage
- PAs can enhance chilling tolerance of tissues
- PAs linkage to cell membrane caused membrane stability
- Postharvest dip application of PAs has been reported to inhibit CI in apricot, mango

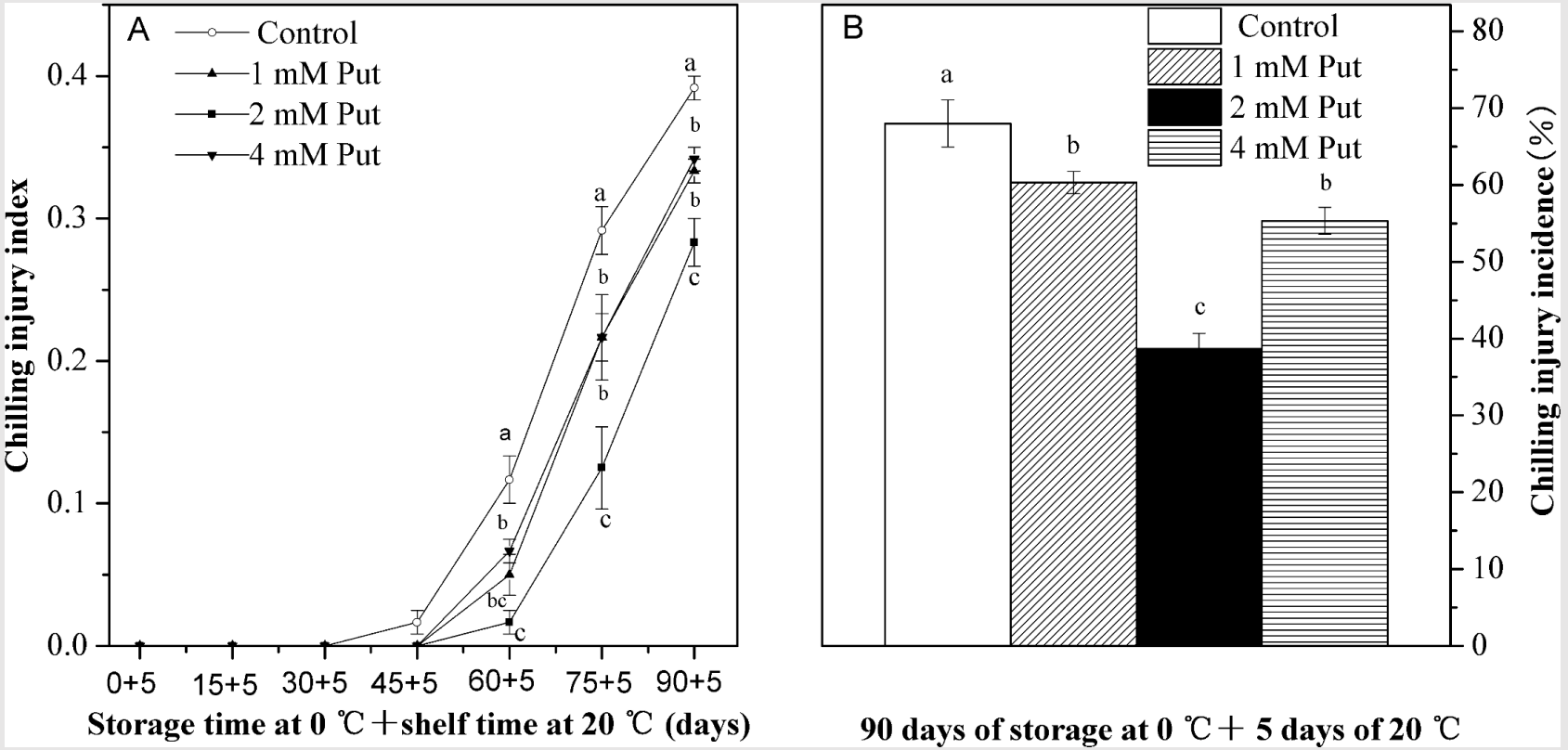
Conclusion

PAs are positively charged nitrogenous compounds derived from amino acids and commonly used PAs are putrescine (PUT), spermidine (SPD) and spermine (SPM).

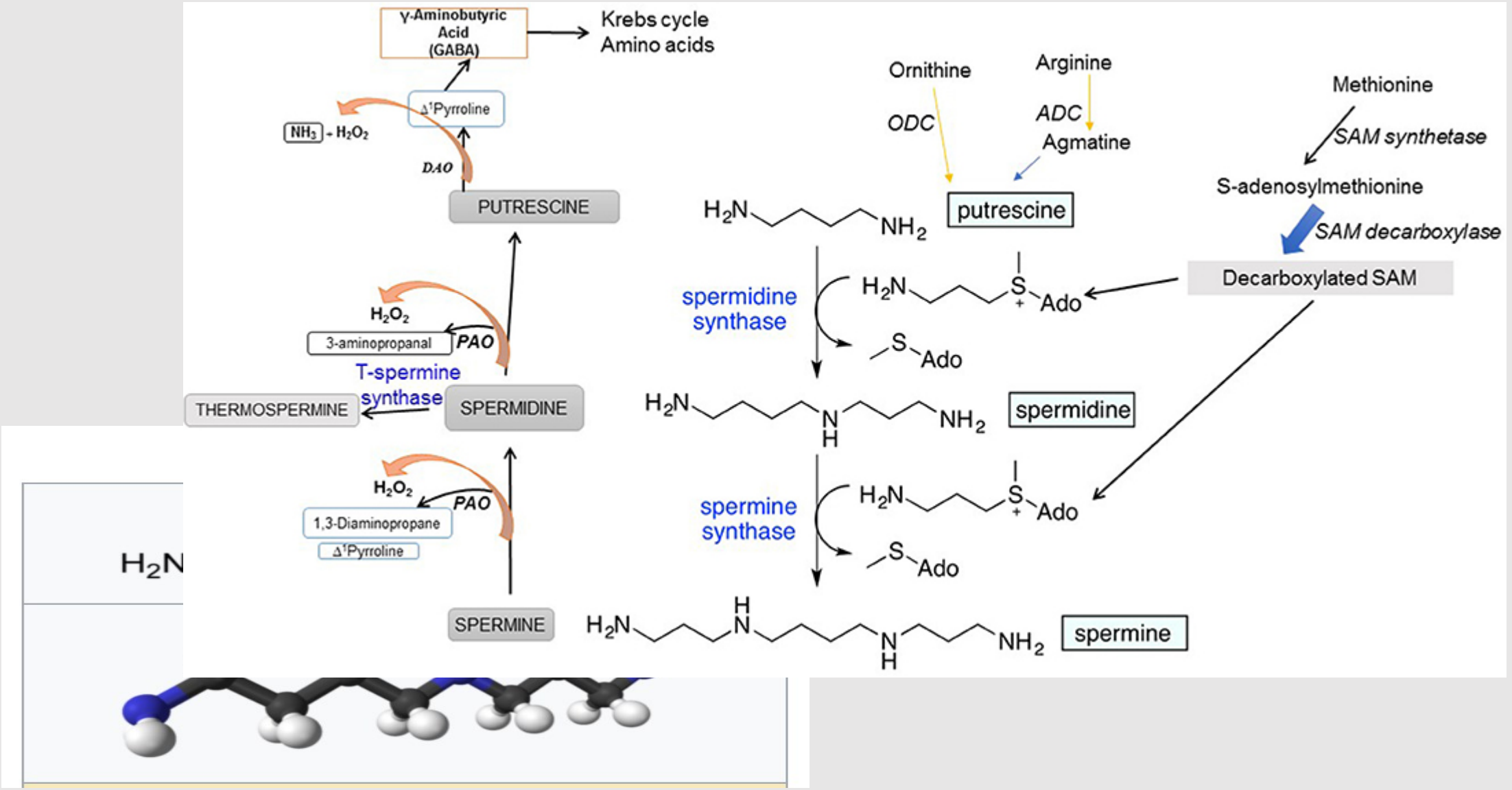
PAs significantly inhibit ethylene biosynthesis, delay senescence, retard colour changes and reduce respiration rate, chilling injury, physiological weight loss (PWL), mechanical damage while, increase fruit firmness and maintain antioxidant enzyme activity.

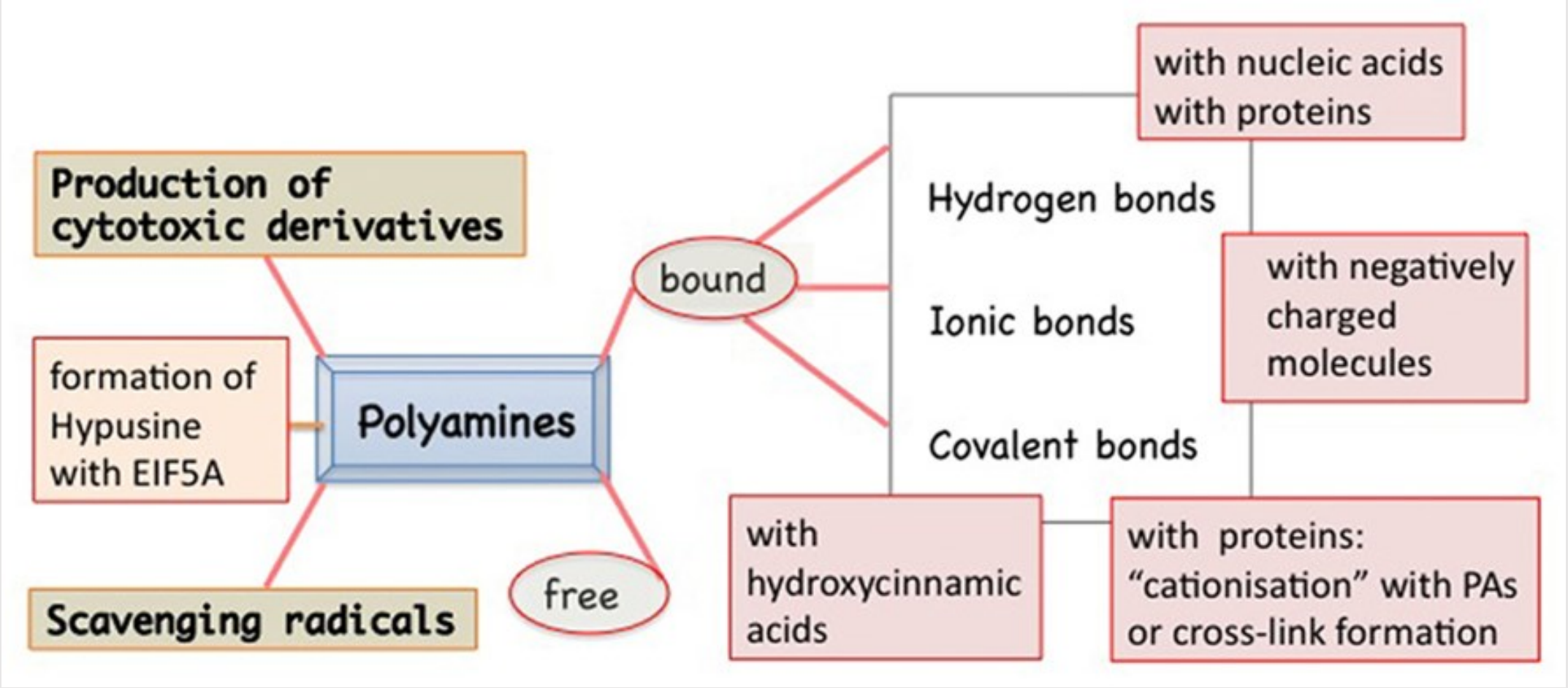
PAs either endogenously or exogenously both helps in suppression of ethylene production during fruit ripening and significantly increase shelf life of the fruits for distant markets.

Fig 1. Chilling injury symptoms of ‘Hongyang’ kiwifruit.
Representative pictures of ‘Hongyang’ kiwifruit after 90 days of cold storage followed by 5 days of shelf life at 20°C. (A) normal kiwifruit. (B) skin showing the brown symptom of CI (arrow). (C) normal flesh of kiwifruit. (D) flesh of kiwifruit showing the grainy symptom (arrow). (E) the cross-section of the normal flesh. (F) the cross-section of the flesh showing the grainy symptom (arrow). (G)the longitudinal section of the normal flesh. (H) the longitudinal section of the flesh showing the grainy symptom (arrow).



Effects of exogenous Put treatment on chilling injury index (A) and chilling injury incidence (B) of 'Hongyang' fruit. Kiwifruit were respectively immersed in 0 mM (control), 1 mM, 2 mM and 4 mM putrescine (Put) for 10 min, and then storage at 0°C followed with another 5 days shelf life at 20°C. Chilling injury incidence was assessed at day 90.


γ-Aminobutyric Acid (GABA)
Krebs cycle
Amino acids
Δ¹Pyrroline
NH₃ + H₂O₂
DAO
PUTRESCINE
H₂O₂
3-aminopropanal
PAO
T-spermine synthase
THERMOSPERMINE
SPERMIDINE
H₂O₂
1,3-Diaminopropane
PAO
Δ¹Pyrroline
SPERMINE
Ornithine
ODC
Arginine
ADC
Agmatine
putrescine
spermidine synthase
S-Ado
spermidine
spermine synthase
S-Ado
spermine
Methionine
SAM synthetase
S-adenosylmethionine
SAM decarboxylase
Decarboxylated SAM



- In fact, these polycations are able to form linkages of various types and strength with several molecules. In addition to ionic linkages with negatively charged molecules, interactions may occur by electrostatic linkages, causing conformational stabilization/destabilization of DNA, RNA, chromatin, and proteins.
- The intracellular free PA pool depends on its synthesis and also on several metabolic pathways including degradation, conjugation, and transport.
- PAs can be conjugated either with small molecules, especially hydroxycinnamic acids to form soluble Pas, or with high molecular mass substances, such as hemicelluloses, lignin, or protein of the cell wall to form cell wall-bound PAs and could serve as a pool of free Pas.