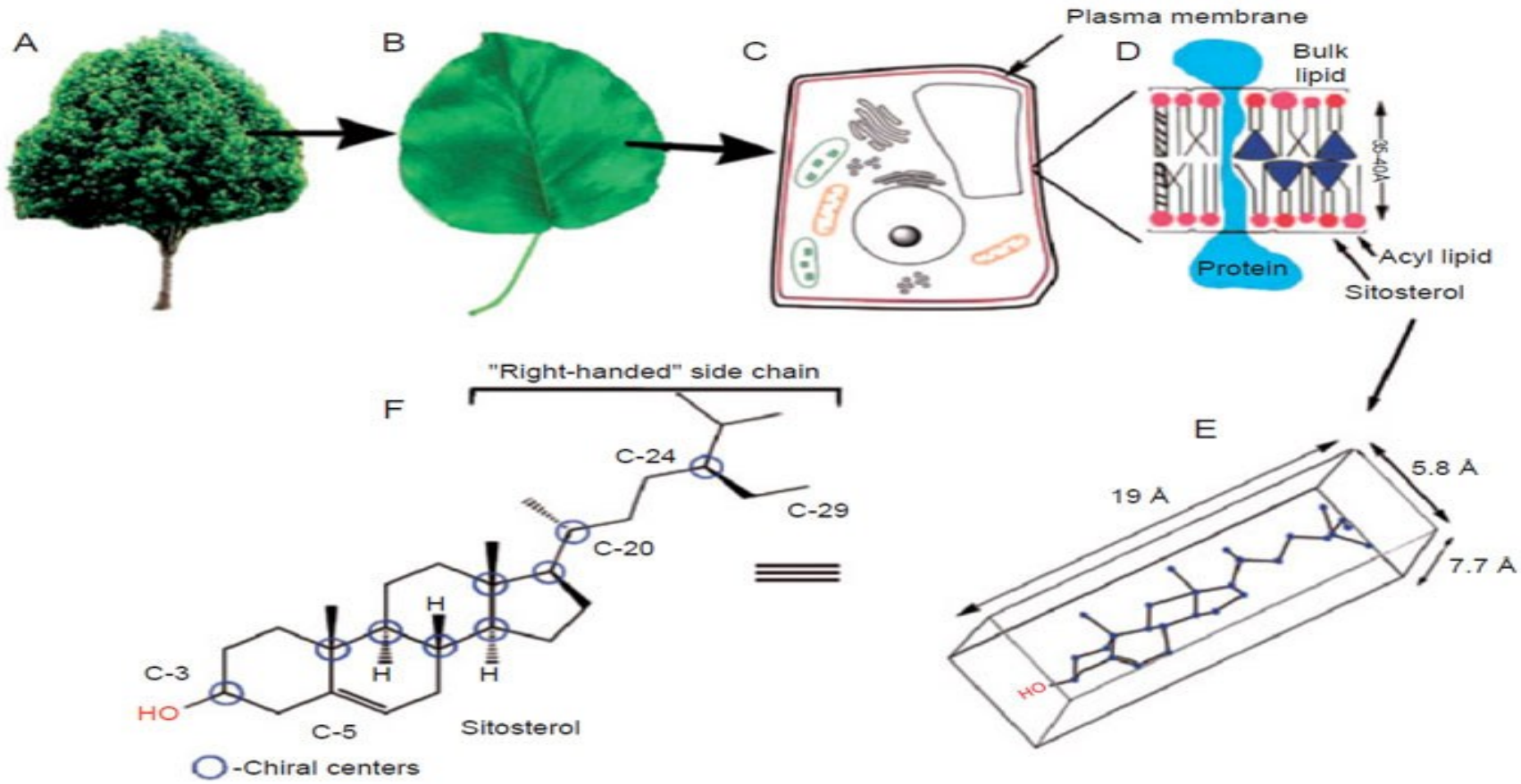
IN THE NAME OF GOD



- Plants sense stimuli from their environment through changes in membranes.
- Biotic and abiotic stressors can alter cell membrane structure and composition.

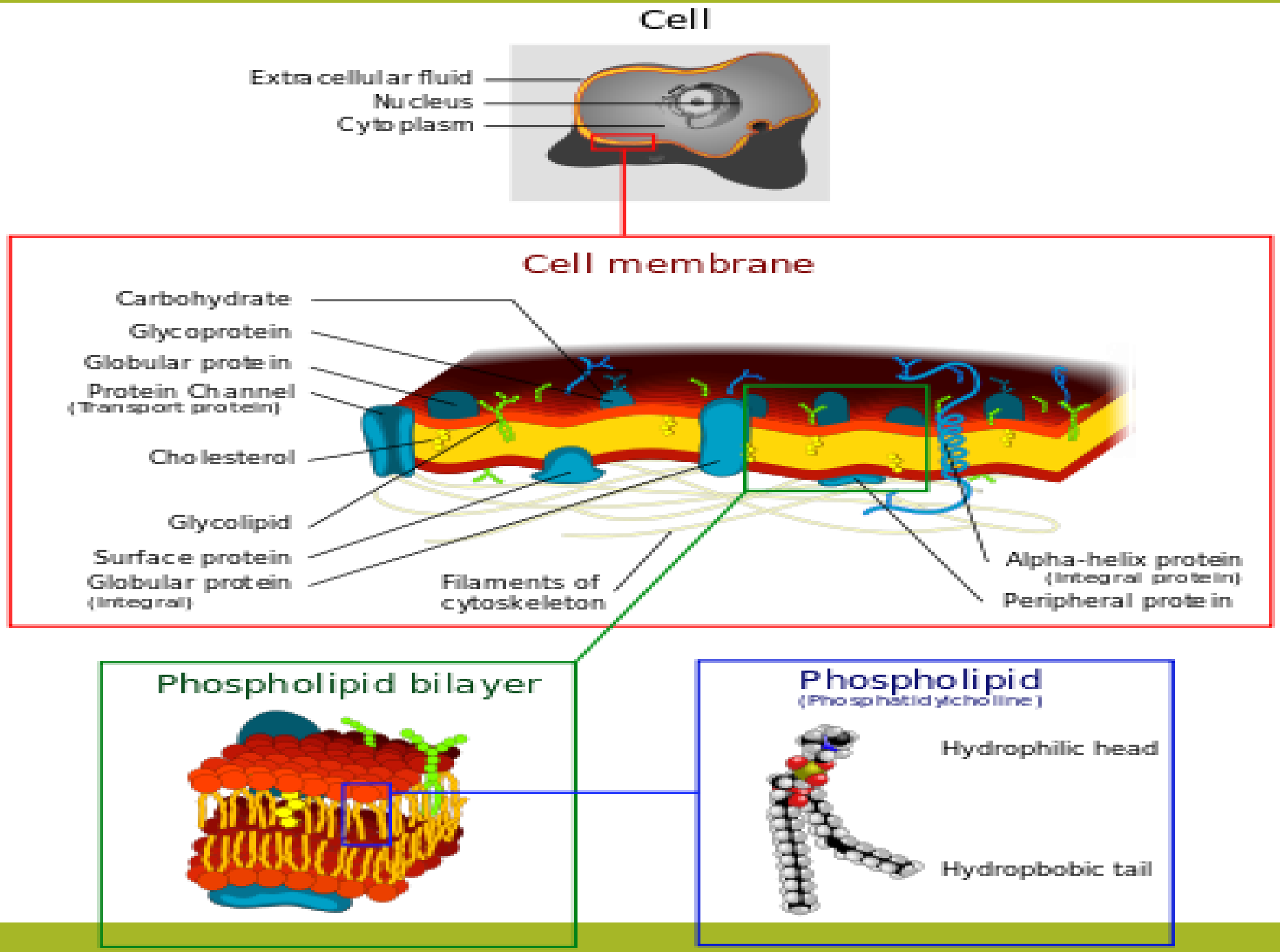
Chemical and Physical Changes in Membranes

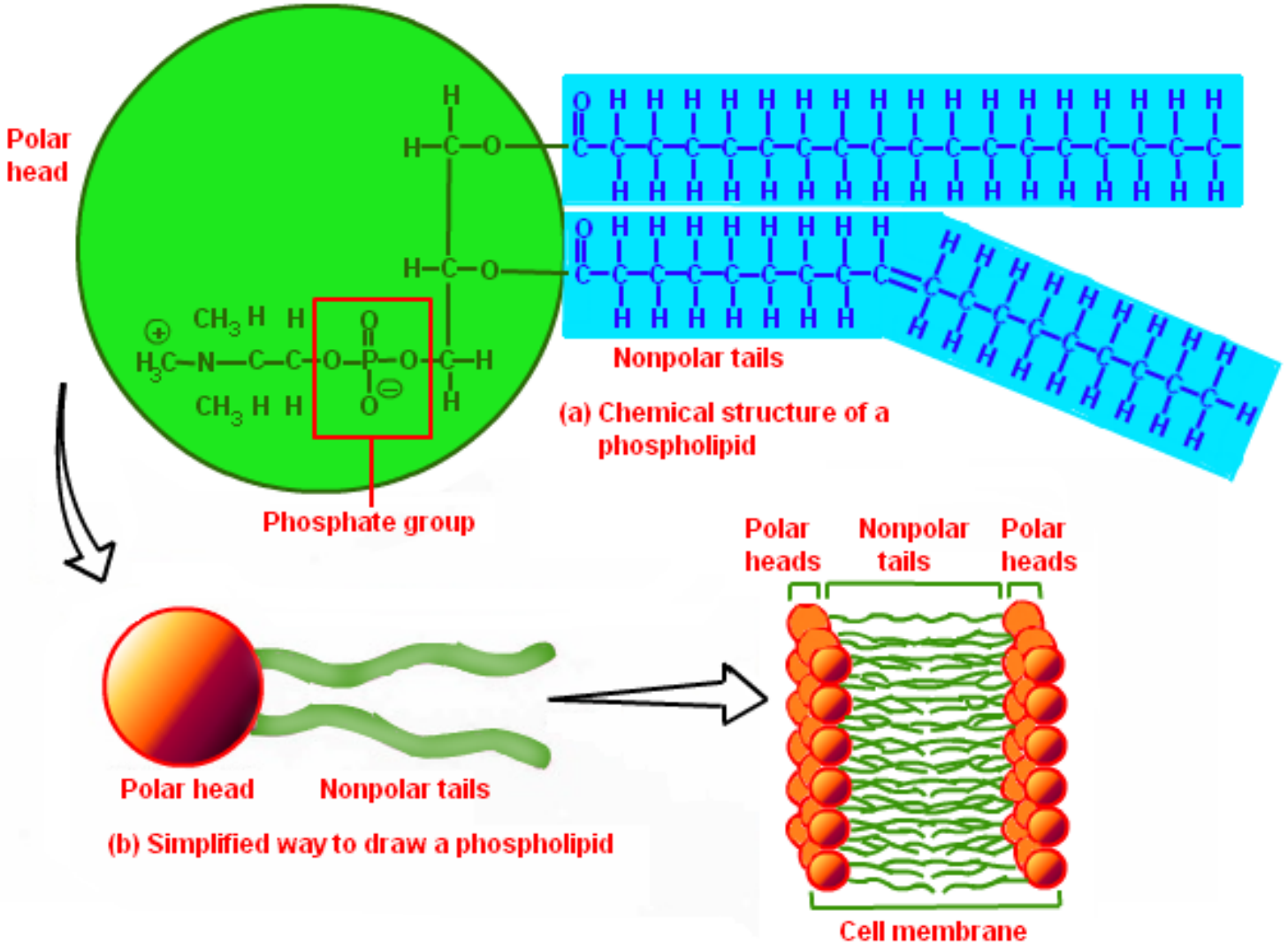
Maintenance of the requisite physical properties and functionality of cell membranes is essential for preservation of quality during the storage life of fresh vegetables. Water loss and the consequent loss of turgor pressure which cause wilting and undesirable textural changes are in part attributable to increased permeability of the plasmalemma and tonoplast.

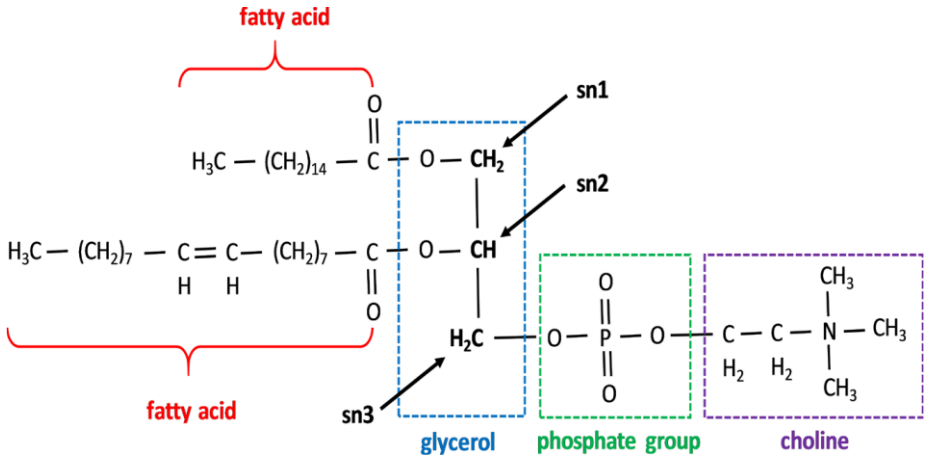
A number of postharvest physiological disorders, such as chilling injury, involve both increased water loss and leakage of electrolytes across cell membranes. In addition to their important barrier properties, membranes serve to compartmentalize various life functions of the plant cell .The enzymatic activity of individual membranes, which is essential to their specific role in the cell, is greatly influenced by the composition of the lipid matrix.

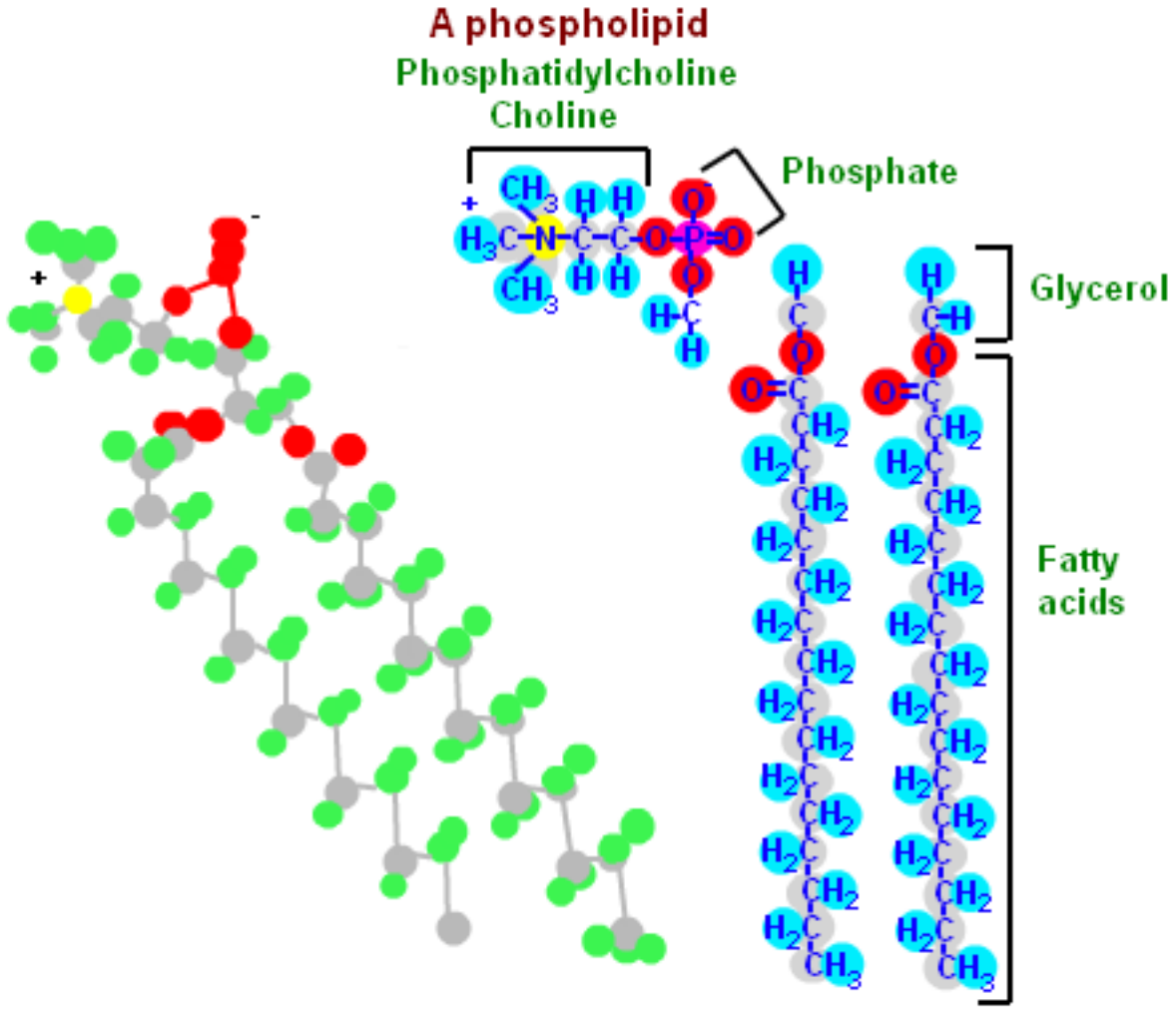
membranes play a critical role in many vital activities, including energy transfer, hormone binding, signal transduction, plant-pathogen interactions, and transport of ions, other solutes, and macromolecules between compartments.

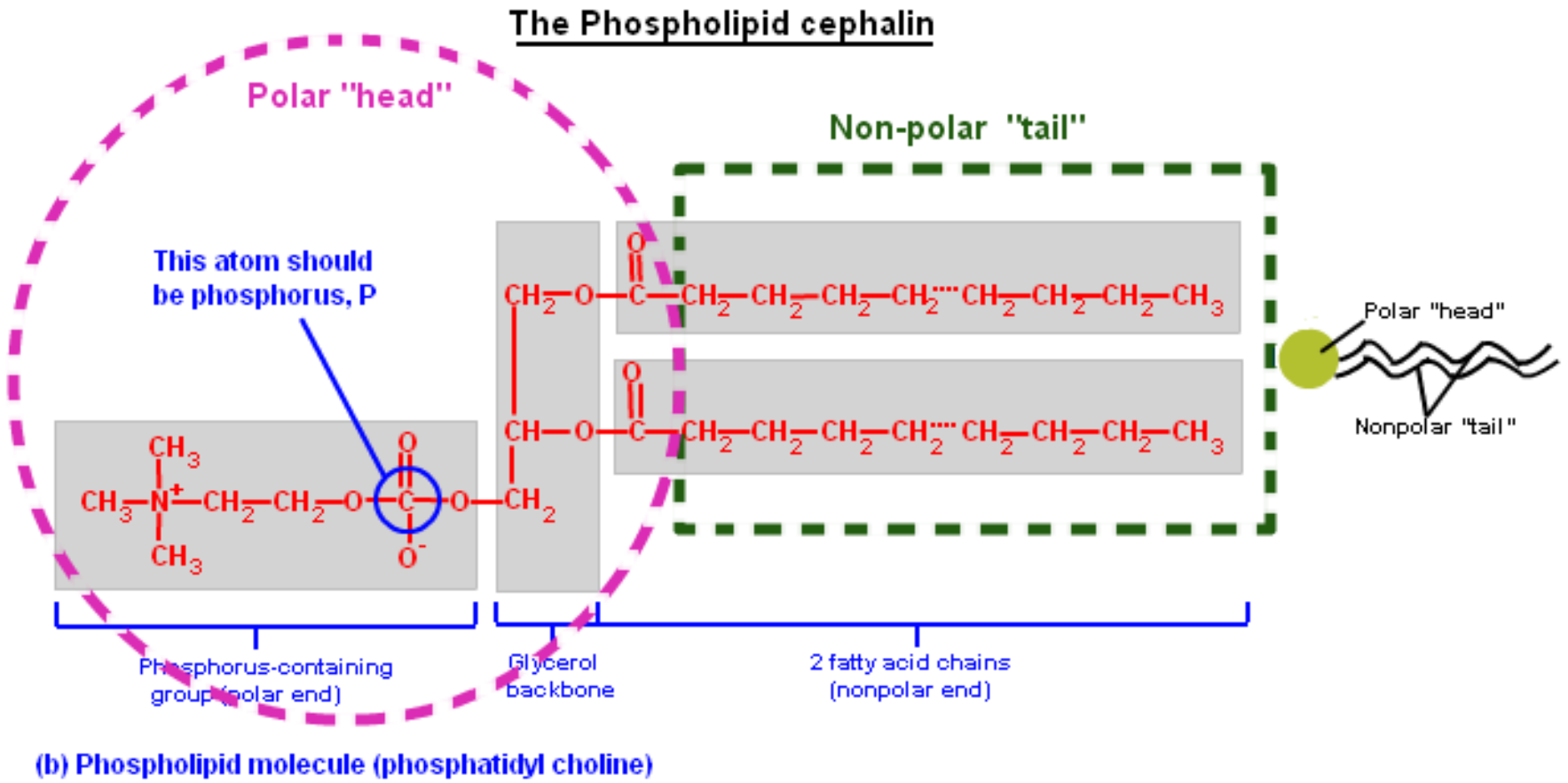
relatively little attention, prior to the 1980s, was focused on changes in membrane lipid metabolism during the course of postharvest life. Over the past decade, however, there has been a flow of activity in this area, much of it addressing the processes involved in membrane deterioration during normal and stress-induced senescence.


Cell
Extracellular fluid
Nucleus
Cytoplasm
Cell membrane
Carbohydrate
Glycoprotein
Globular protein
Protein Channel
(Transport protein)
Cholesterol
Glycolipid
Surface protein
Globular protein
(Integral)
Filaments of
cytoskeleton
Alpha-helix protein
(Integral protein)
Peripheral protein
Phospholipid bilayer
Phospholipid
(Phosphatidylcholine)
Hydrophilic head
Hydropbobic tail

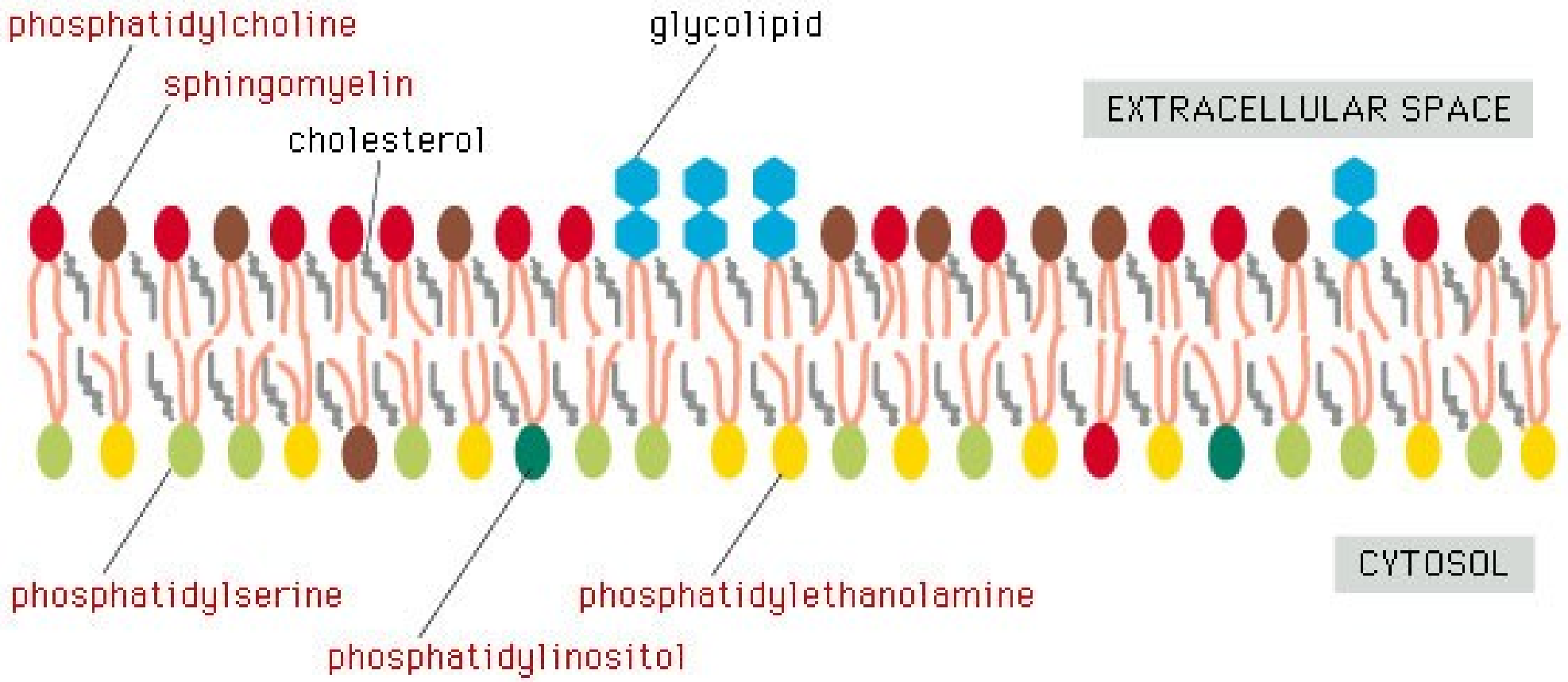

Polar head
Nonpolar tails
(a) Chemical structure of a phospholipid
Phosphate group
Polar heads
Nonpolar tails
Polar heads
Polar head
Nonpolar tails
(b) Simplified way to draw a phospholipid
Cell membrane

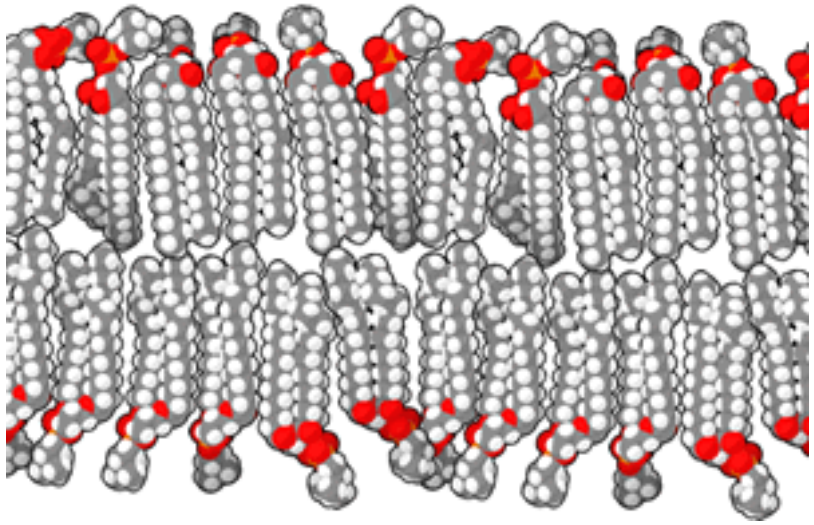

fatty acid
sn1
sn2
sn3
fatty acid
glycerol
phosphate group
choline

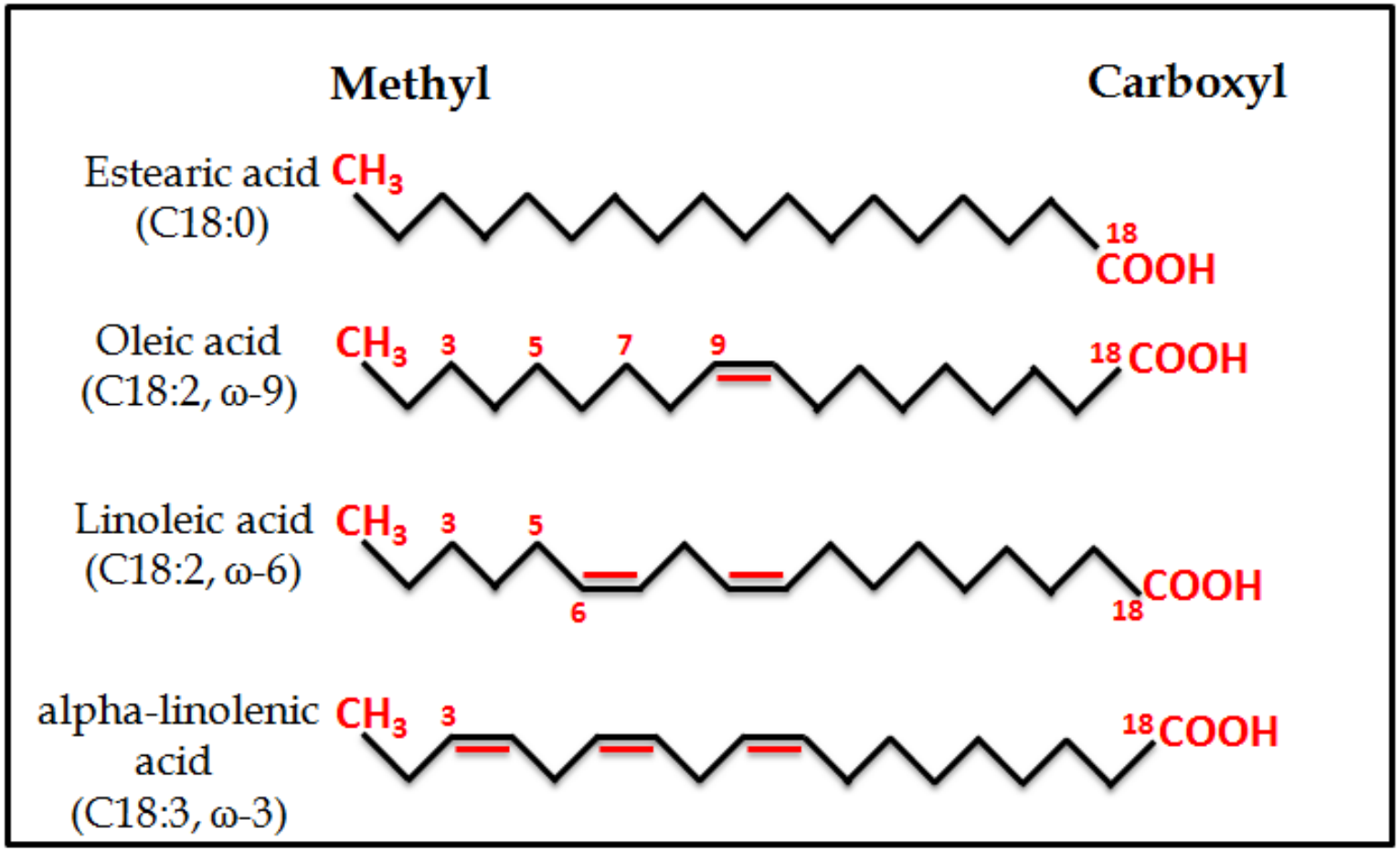

A phospholipid
Phosphatidylcholine
Choline
Phosphate
Glycerol
Fatty acids

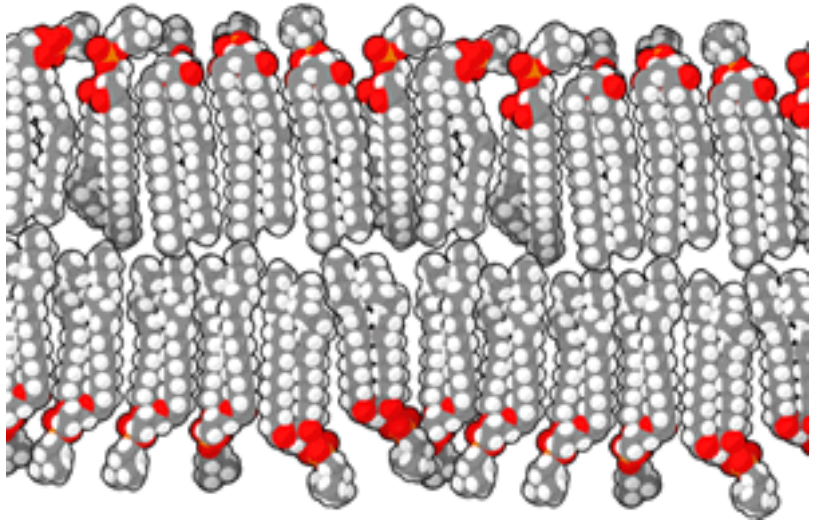


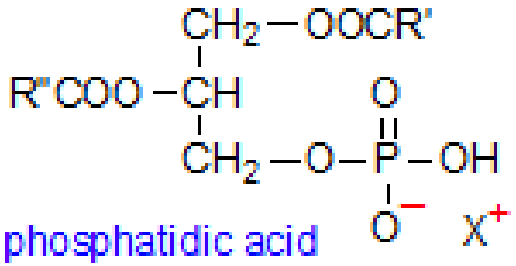
(b) Phospholipid molecule (phosphatidyl choline)


phosphatidylcholine
sphingomyelin
cholesterol
glycolipid
EXTRACELLULAR SPACE
CYTOSOL
phosphatidylserine
phosphatidylinositol
phosphatidylethanolamine
©1998 GARLAND PUBLISHING



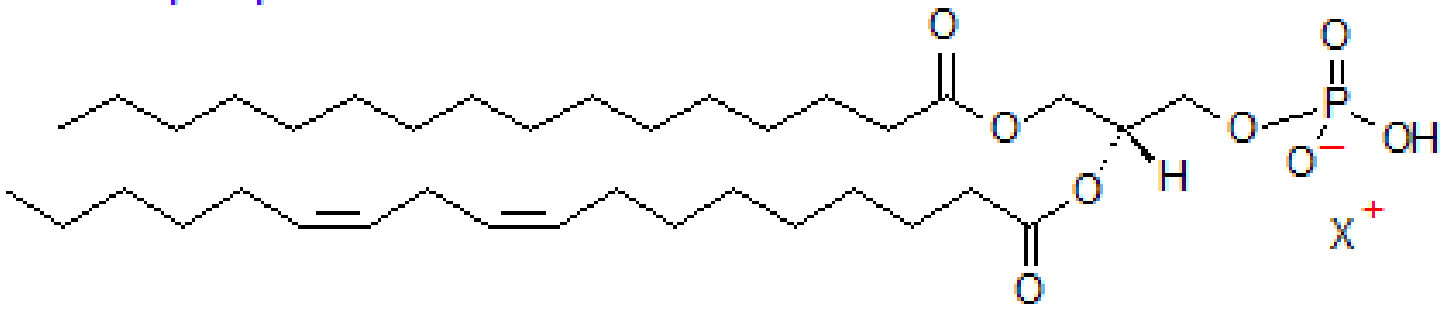

Methyl
Carboxyl
Estearic acid
(C18:0)
CH3
18
COOH
Oleic acid
(C18:2, ω-9)
CH3
3
5
7
9
18
COOH
Linoleic acid
(C18:2, ω-6)
CH3
3
5
6
18
COOH
alpha-linolenic
acid
(C18:3, ω-3)
CH3
3
18
COOH



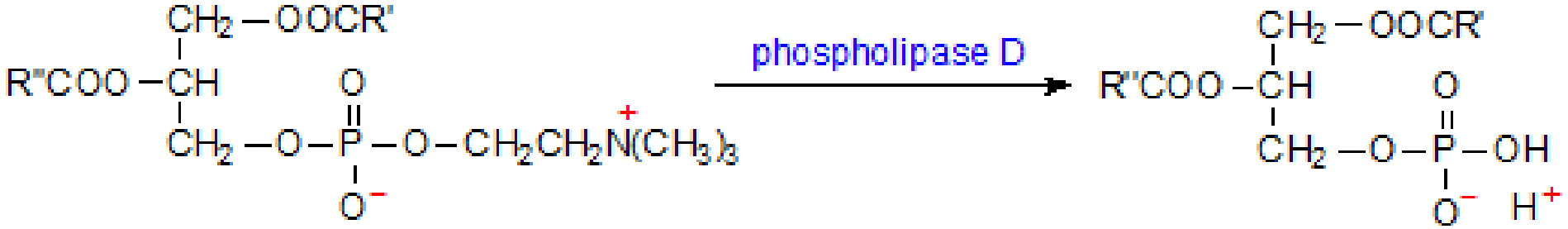


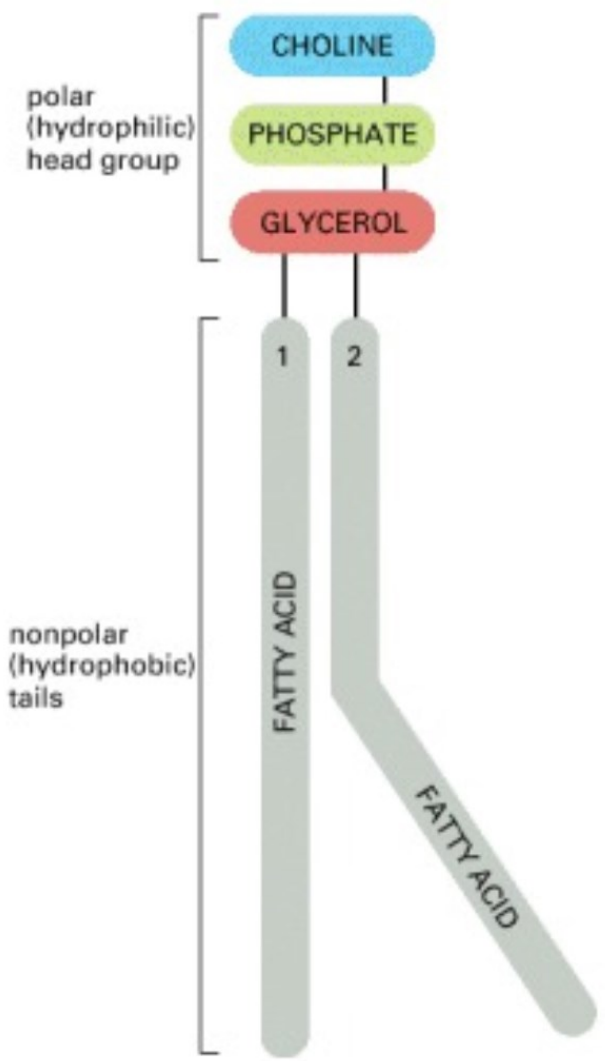
phosphatidic acid

(where X = H, Na, K, Ca, etc)

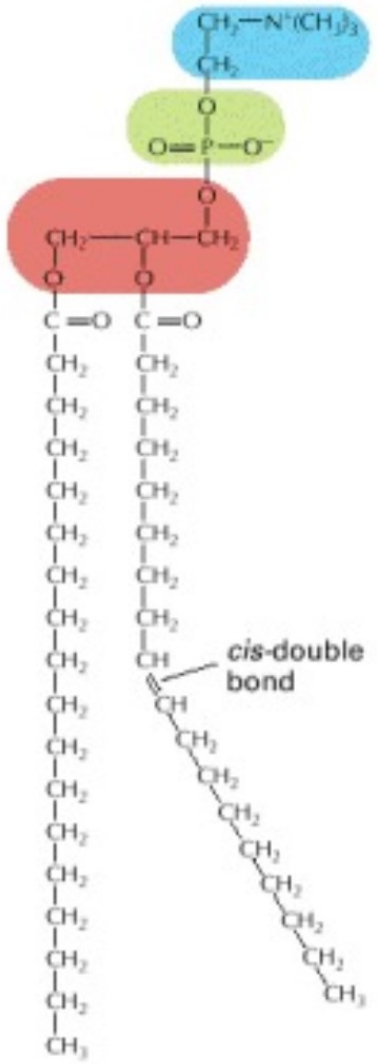


1-hexadecanoyl,2-(9Z,12Z)-octadecadienoyl-*sn*-glycero-3-phosphate

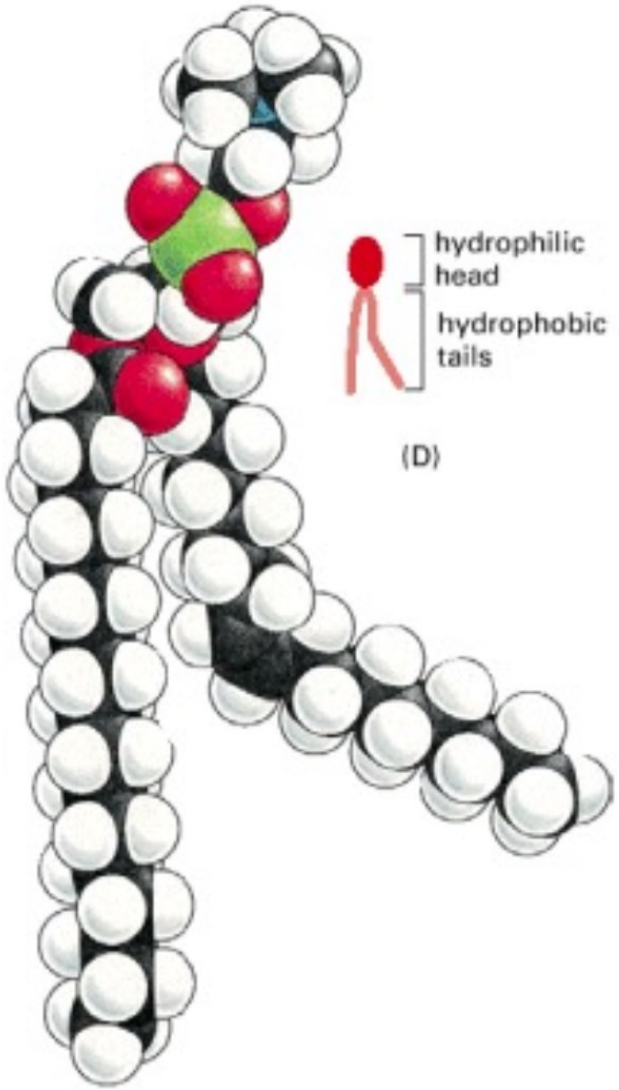



CHOLINE
PHOSPHATE
GLYCEROL
polar
(hydrophilic)
head group
1
2
FATTY ACID
FATTY ACID
nonpolar
(hydrophobic)
tails

(A)

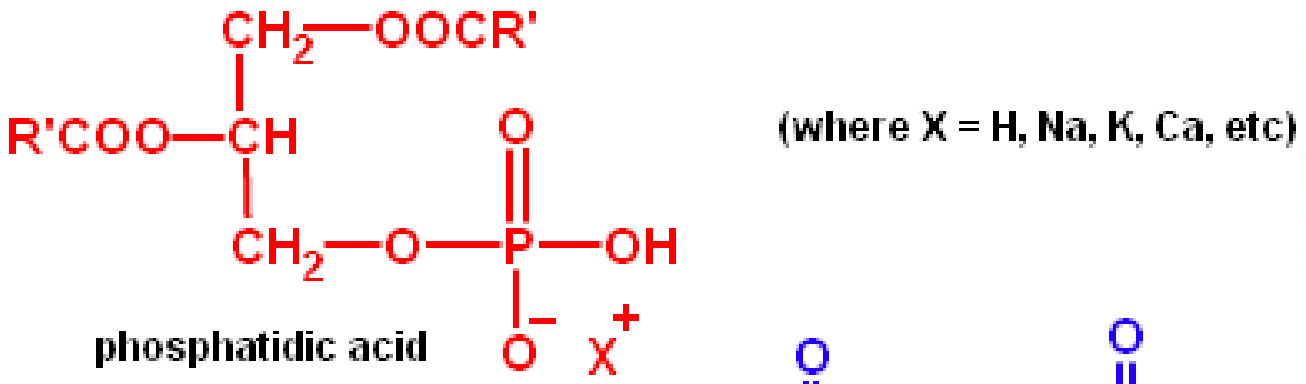

cis-double
bond

(B)


hydrophilic
head
hydrophobic
tails

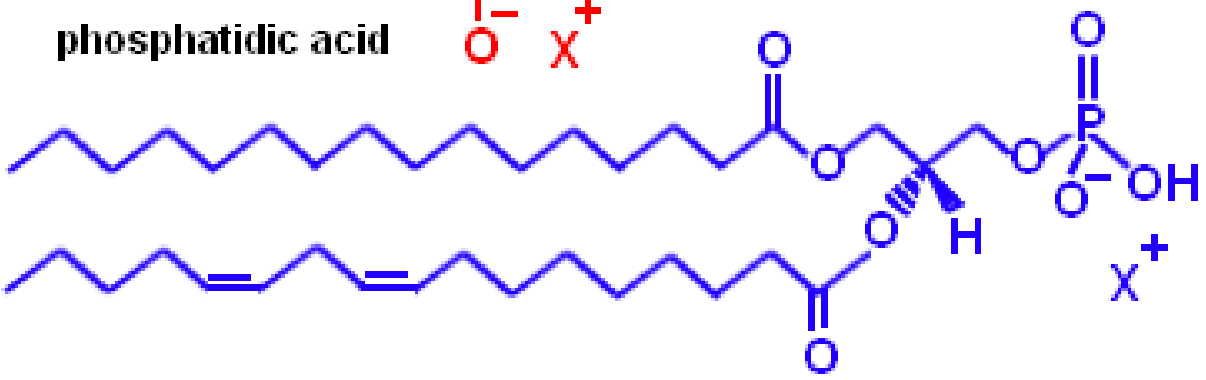
(D)

(C)

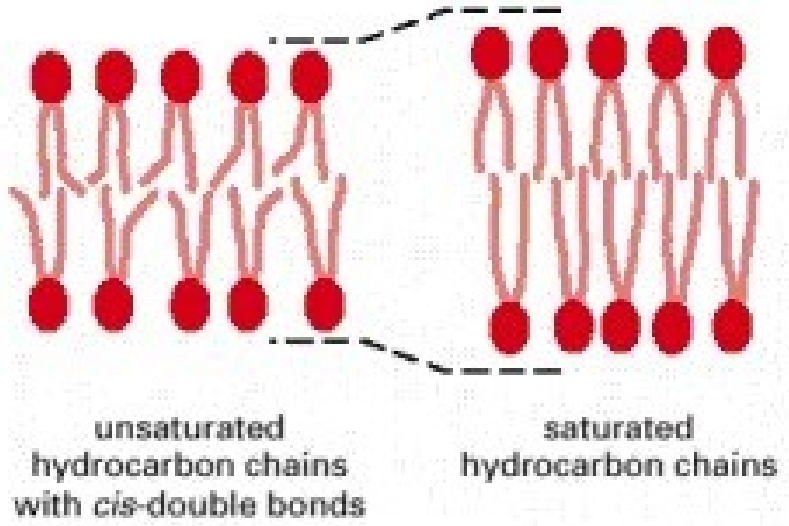


phosphatidic acid

(where X = H, Na, K, Ca, etc)



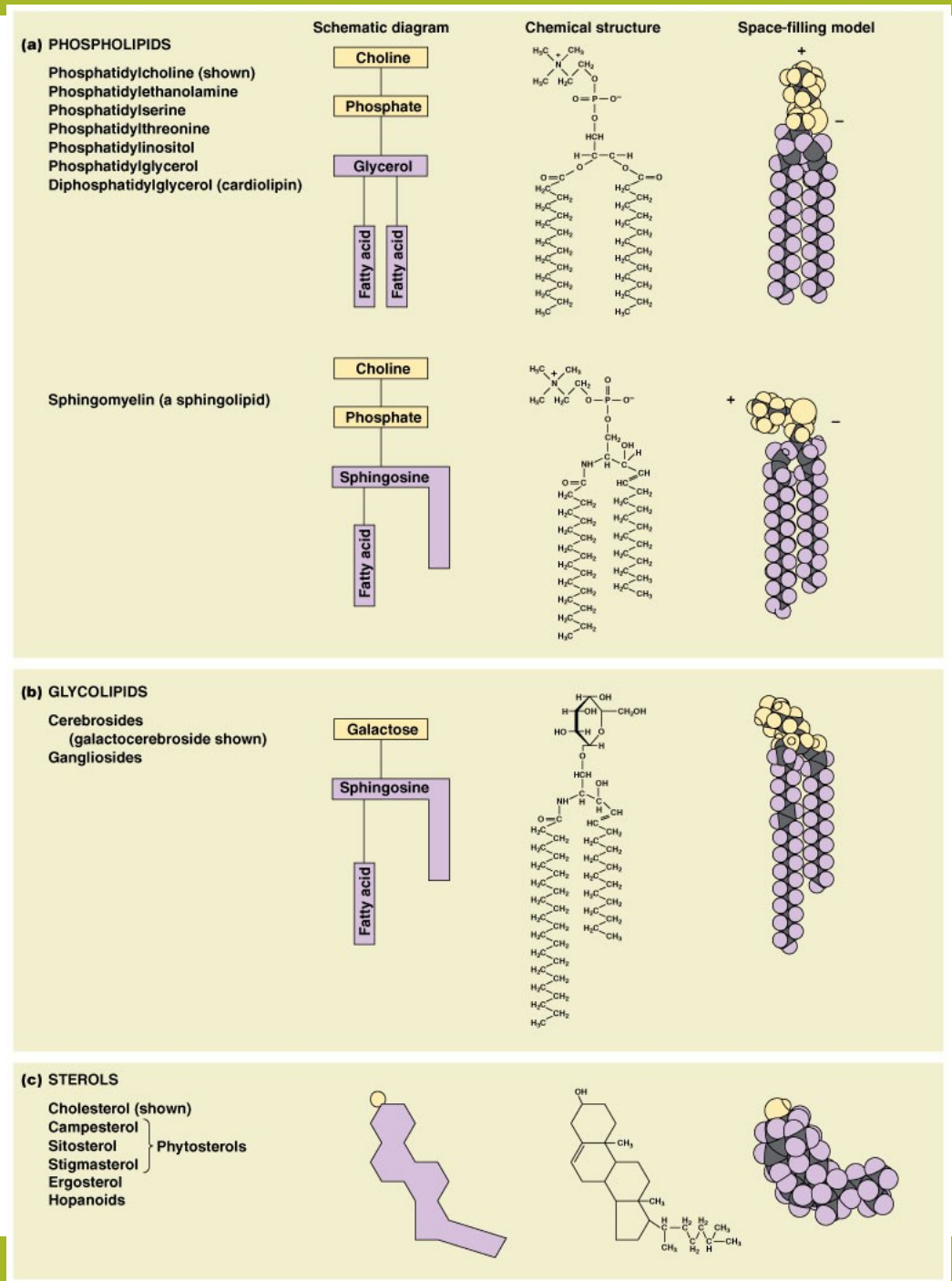
1-hexadecanoyl,2-(9Z,12Z)-octadecadienoyl-sn-glycero-3-phosphate

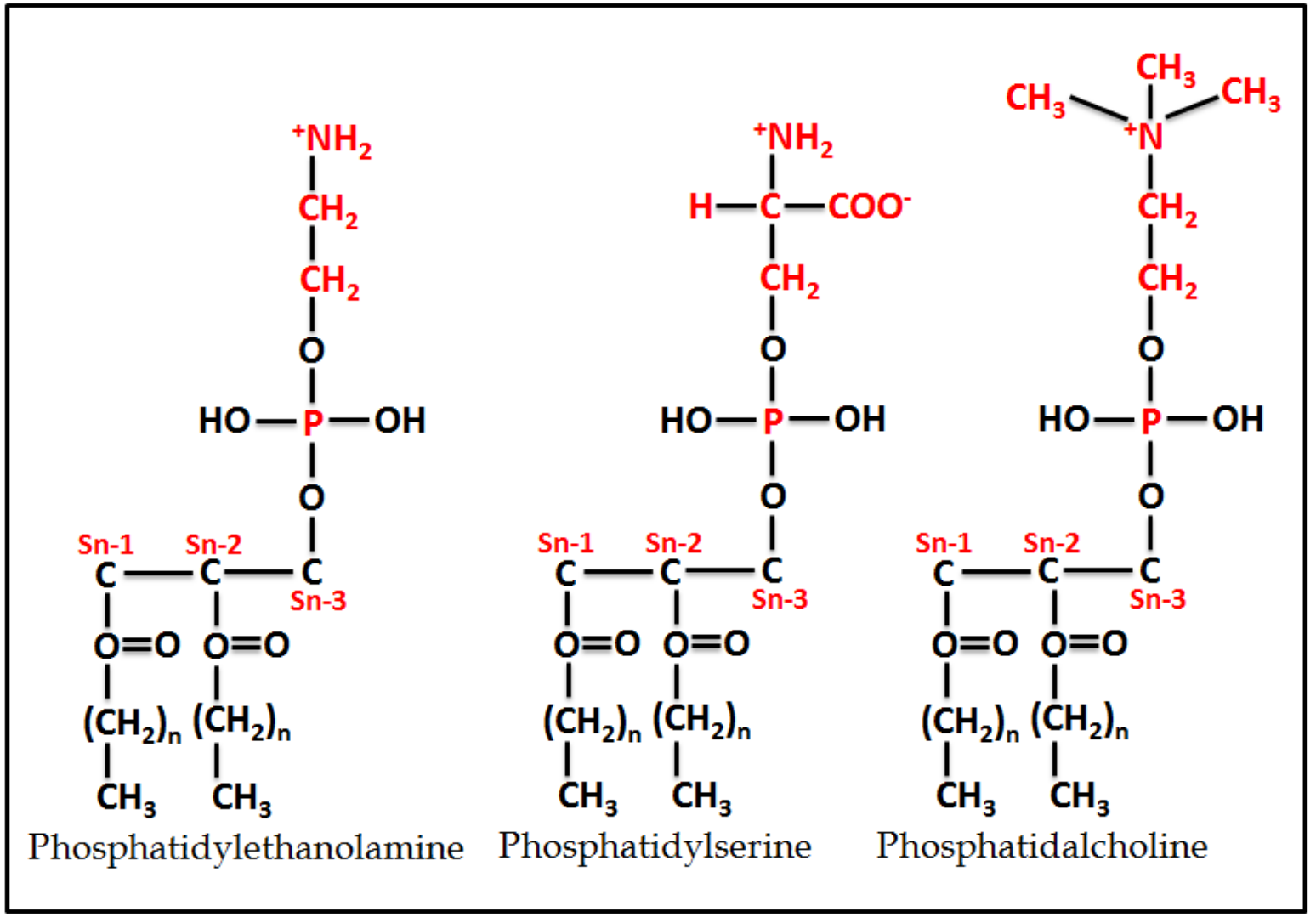


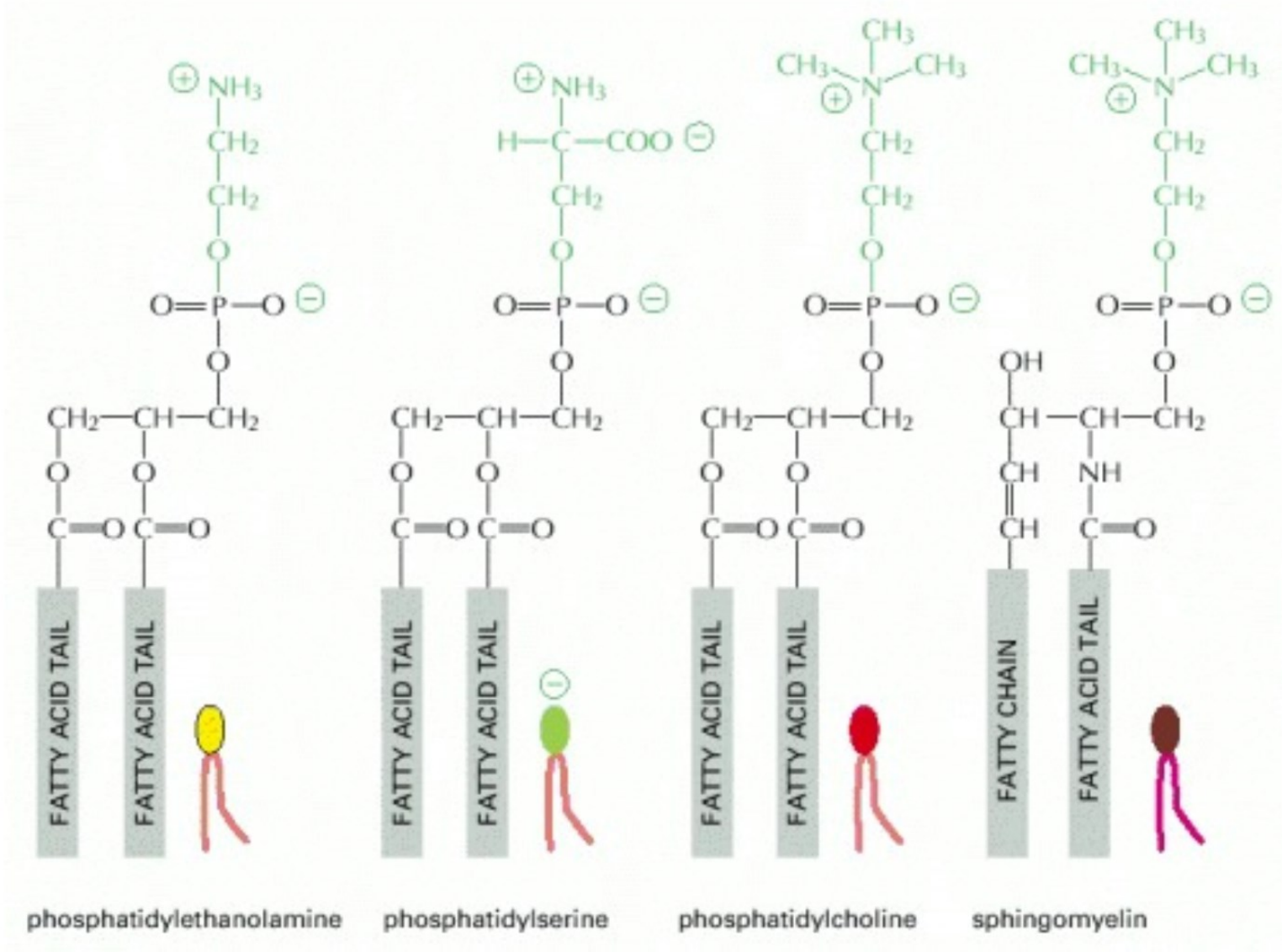
unsaturated hydrocarbon chains with *cis*-double bonds

saturated hydrocarbon chains

GL, are associated mostly with the chloroplast membranes, and PL is a constituent of other membranes of the cell, particularly the plasma membrane.




+NH2
CH2
CH2
O
HO—P—OH
O
Sn-1
Sn-2
Sn-3
C—C—C
O=O O=O
(CH2)n (CH2)n
CH3 CH3
Phosphatidylethanolamine
+NH2
H—C—COO-
CH2
O
HO—P—OH
O
Sn-1
Sn-2
Sn-3
C—C—C
O=O O=O
(CH2)n (CH2)n
CH3 CH3
Phosphatidylserine
CH3
CH3
CH3
+N
CH2
CH2
O
HO—P—OH
O
Sn-1
Sn-2
Sn-3
C—C—C
O=O O=O
(CH2)n (CH2)n
CH3 CH3
Phosphatidalcholine


FATTY ACID TAIL
FATTY ACID TAIL
FATTY ACID TAIL
FATTY ACID TAIL
FATTY ACID TAIL
FATTY ACID TAIL
FATTY CHAIN
FATTY ACID TAIL
phosphatidylethanolamine
phosphatidylserine
phosphatidylcholine
sphingomyelin

The main components of biological membranes are lipids. Recently, lipids and fatty acids (FAs) have been found to be signaling molecules and/or precursors giving rise to other molecules related to abscission and/or senescence .

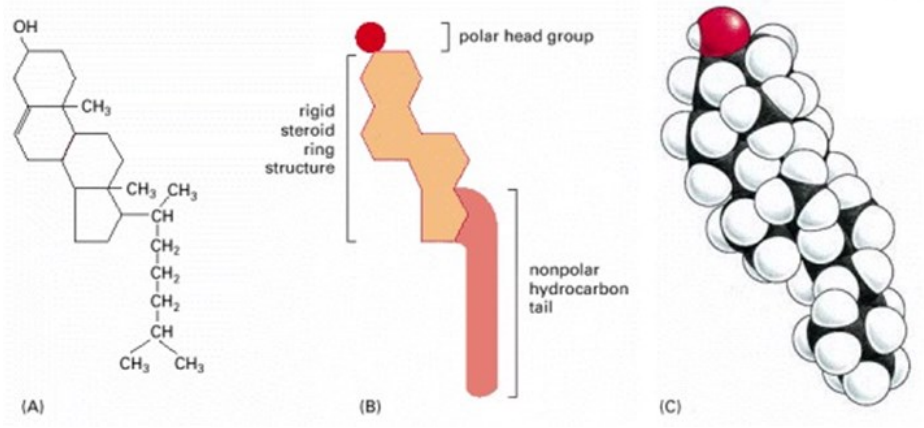
- Membrane Lipids: Classes

- Three classes of membrane lipids
  1) phospholipids (PLs) - most prominent component *
  2) glycolipids (GLs) - addition of carbohydrate/sugar group
  3) sterols - rings in their structure hydrophobic e.g. cholesterol, ergosterol, and phytosterols

- The fatty acids tails can be of differing length and (saturation or) number of double bonds (12 - 20 carbon atoms long)

* PLs are the primary membrane lipids, whereas GLs tend to be associated mostly with the chloroplast membranes.

- Functioning of the lipid bilayer and thus the membrane is affected by temperature.
  Transition temperature (Tm): temperature at which a membrane changes between the fluid and gelled state
  The Tm is effected by
  1) the length of the fatty acids
  2) the number of double bonds &
  3) the proportion of sterols (e.g. cholesterol)



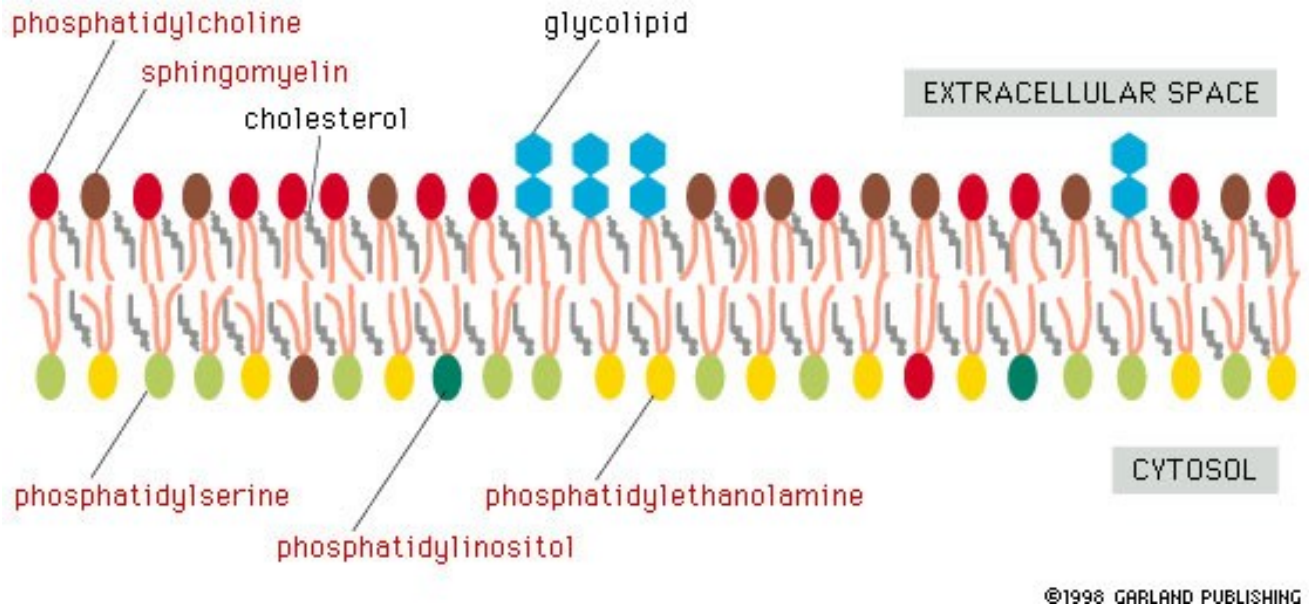
In contrast to animal and fungal cells, which contain only one major sterol, plant cells synthesize a complex array of sterol mixtures in which sitosterol, stigmasterol and 24-methylcholesterol often predominate.
Sitosterol and 24-methylcholesterol are able to regulate membrane fluidity and permeability.

In contrast, stigmasterol might be specifically required for cell proliferation.

Lipid Composition and Physical Properties of Plant Cell Membranes

- Phospholipids (PL), mainly phosphatidylcholine (PC) and phosphatidylethanolamine (PE), usually compose the bulk of the lipid matrix in plant cell membranes .
- The fluidity of the lipid bilayer is determined to a large extent by the fatty-acid composition and positional distribution (molecular species) of the PL.
- A change in the phase (liquid-crystalline to gel) or fluidity of a biomembrane affects both the permeability to water and small solutes and the activity of enzymes embedded in the lipid bilayer.

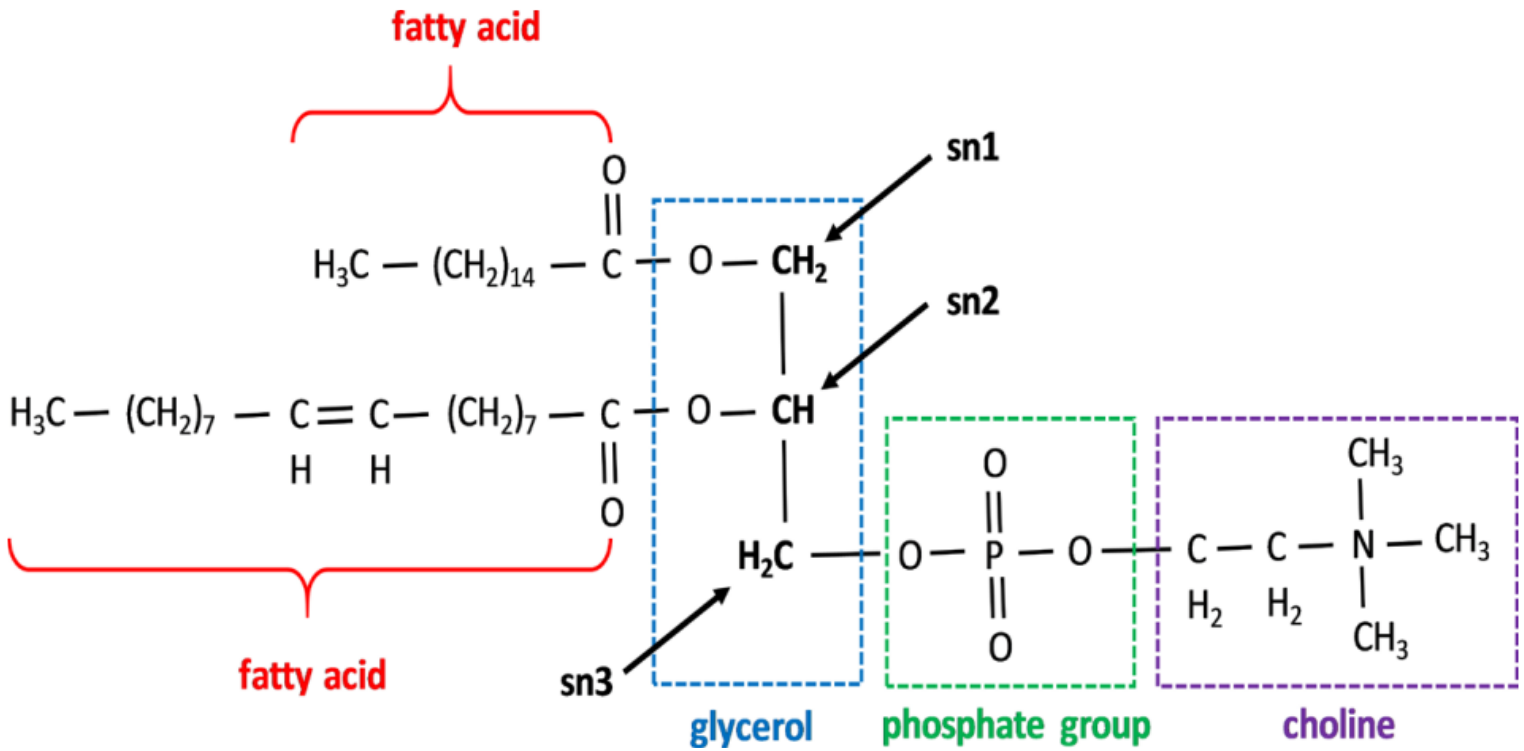
- In plant cells as in animal cells, the plasma membrane is enriched in sterols by more than fivefold relative to other cell membranes.
- Sterol-PL interactions influence various membrane functions, including simple diffusion, carrier mediated diffusion, and active transport, and also modulate the activities of membrane bound enzymes or receptors.



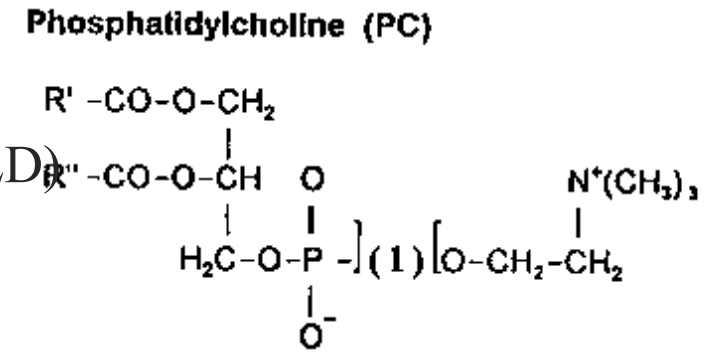
The Senescence Cascade of Membrane Phospholipid Catabolism

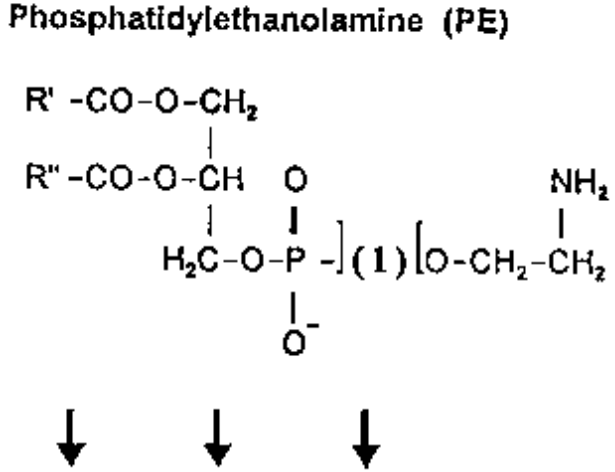
Much of the research on the role of membrane lipid metabolism in postharvest ripening, senescence, and deterioration of quality has focused on the cascade of enzymes involved in PL hydrolysis and fatty-acid peroxidation.

Hydrolysis and peroxidation of PL are thought to play a major role in the sequence of deteriorative events.

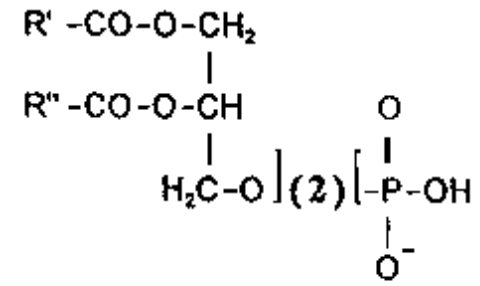

fatty acid
sn1
sn2
sn3
fatty acid
glycerol
phosphate group
choline

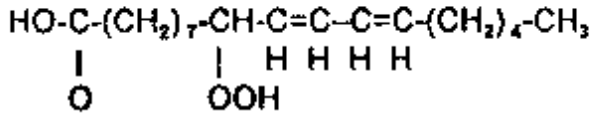
phospholipase D (PLD)

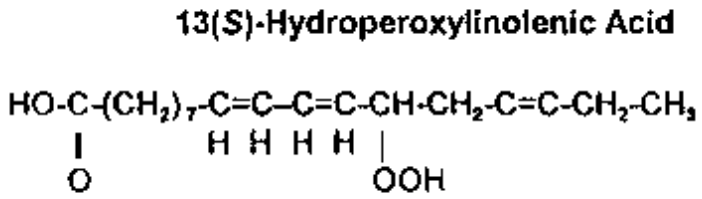




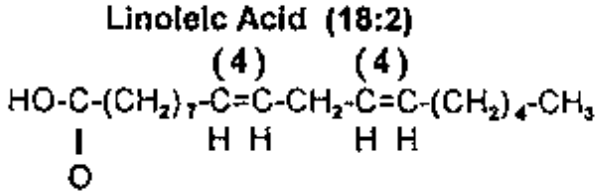
phosphatase

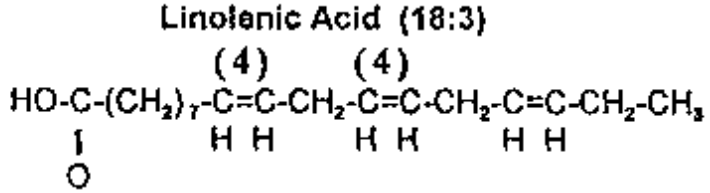


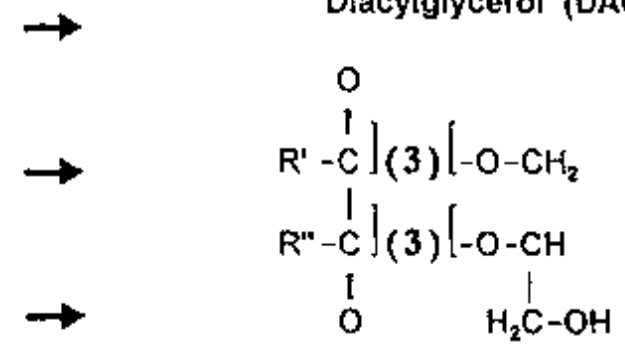




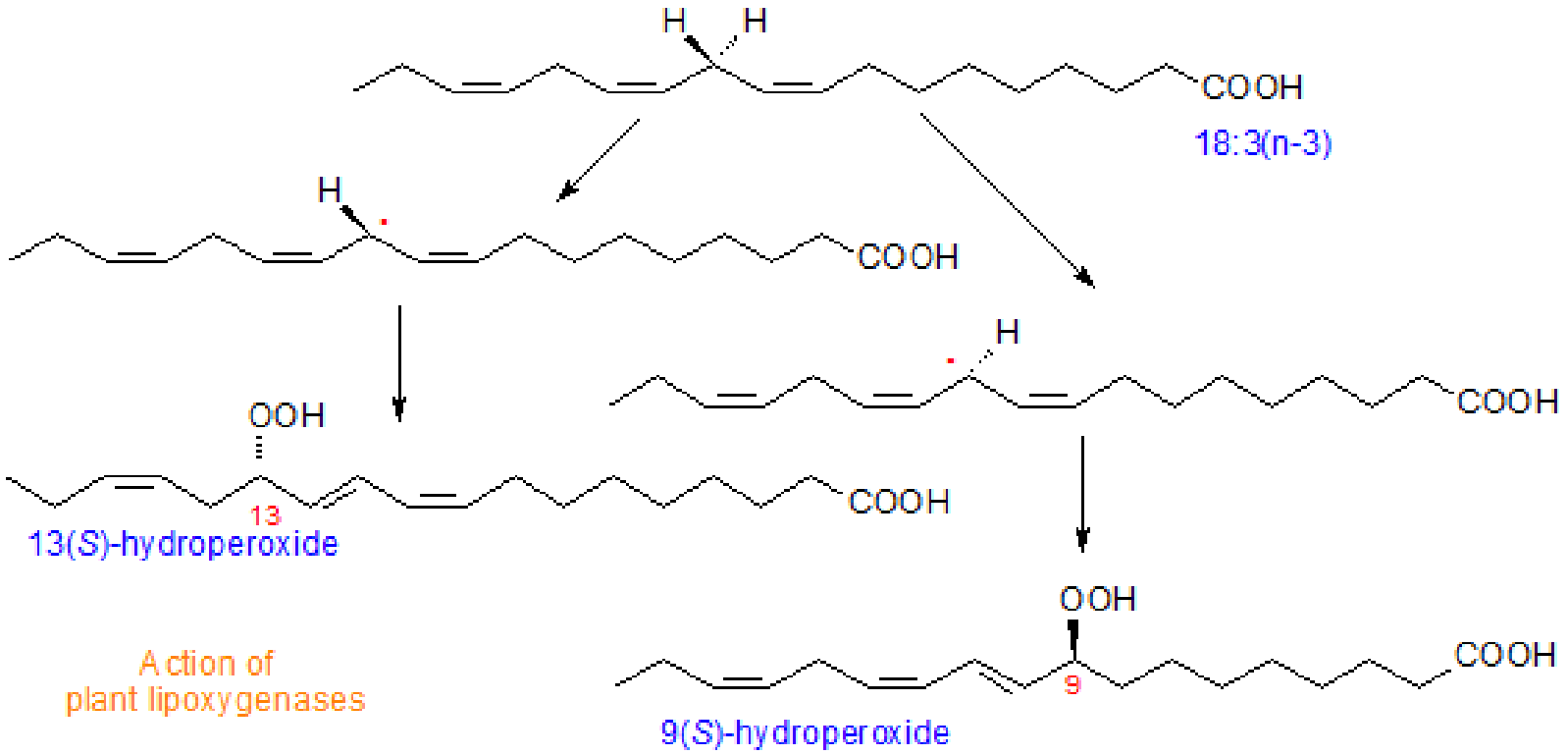
lipoxygenase (LOX).

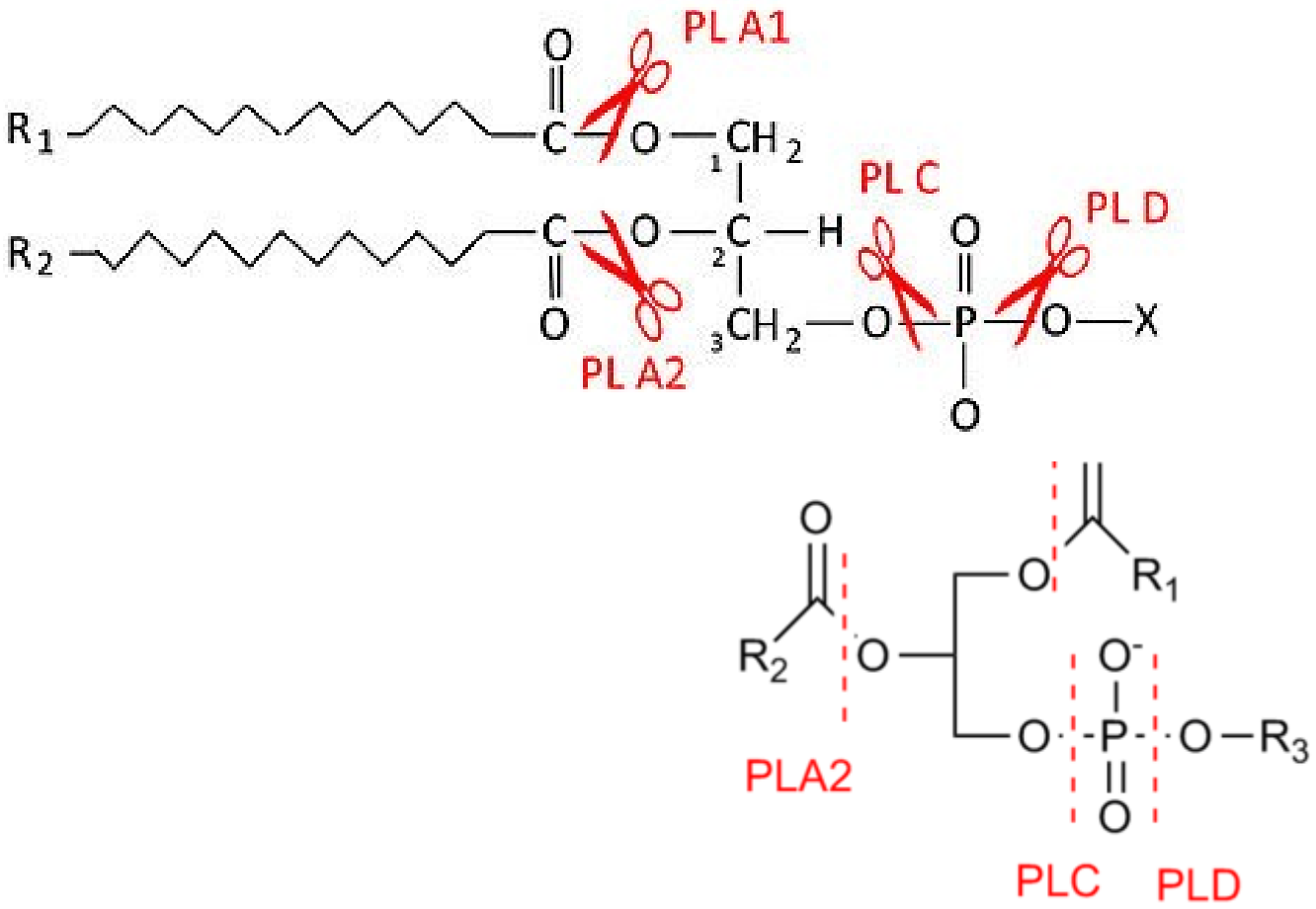


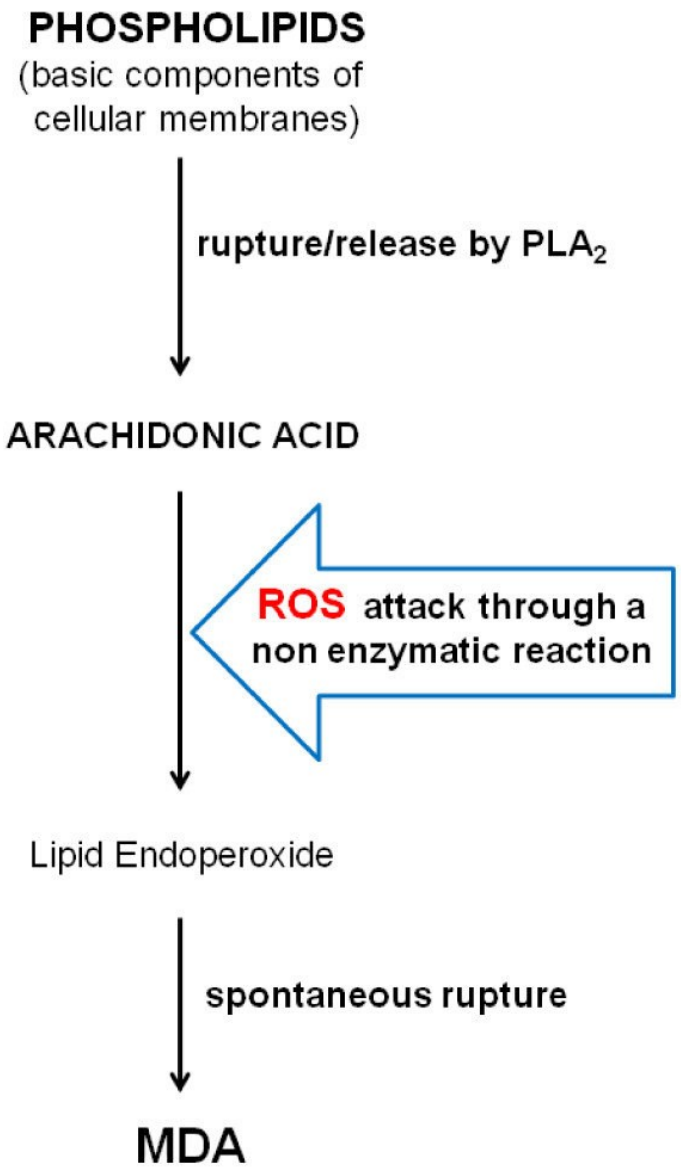




Lipolytic acyl hydrolase (LAH)


H
H
COOH
18:3(n-3)
H
COOH
H
COOH
OOH
COOH
13
13(S)-hydroperoxide
Action of
plant lipoxygenases
OOH
COOH
9
9(S)-hydroperoxide


PL A1
PL C
PL D
PL A2
PLA2
PLC
PLD


PHOSPHOLIPIDS
(basic components of cellular membranes)
rupture/release by PLA2
ARACHIDONIC ACID
ROS attack through a non enzymatic reaction
Lipid Endoperoxide
spontaneous rupture
MDA

senescence cascade begins with removal of polar head groups by phospholipase D (PLD), yielding phosphatidic acid (PA), which in turn is dephosphorylated to diacylglycerol (DAG).

Lipolytic acyl hydrolase (LAH) then cleaves DAG, yielding free fatty acids .

These disrupt membrane structure, and the di- and tri-enoic acids (linoleic and linolenic, 18:2 and 18:3) serve as substrates for lipoxygenase (LOX).

- Because the LOX reaction results in formation of a highly reactive hydroperoxide and may also generate superoxide radicals, a prominent role for this enzyme in plant senescence has been postulated.
- The fatty acid hydroperoxides produced by LOX can perturb the membrane bilayer directly, or break down to yield toxic volatiles and free radicals that attack additional membrane components.

As plant tissues age and senesce, an consequence in harvested organs, the balance of membrane lipid metabolism is shifted in PL catabolism, via the pathway showed above. This results in an overall loss of PL, altered PL class composition, an increase in the sterol to PL ratio, a decline in unsaturation of PL fatty acids, and as just mentioned, accumulation of lipid catabolites, including phosphatidic acid (PA), free fatty acids, and fatty-acid hydroperoxides. All of these changes contribute to a decrease in membrane bilayer fluidity and therefore a loss of optimal membrane function.

Reactive Oxygen Species

Although increased PL catabolism is clearly important with respect to maintenance of quality, it has become evident in recent years that the ability of plant tissues to manage with oxidative stress may be even more critical. Reactive oxygen species (ROS), including superoxide anion, hydrogen peroxide, and hydroxyl radical, pose a major threat to the integrity of membrane lipids as well as other cellular components.

- These ROS are generated in the course of normal oxidative metabolism, but their production is often increased under adverse conditions such as water deficit and temperature stress

- Plant cells produce antioxidant compounds (e.g., carotenoids, tocopherols, ascorbic acid, glutathione, and flavonoids), plus a complement of enzymes such as superoxide dismutase, catalase, and glutathione and ascorbic acid peroxidases, which serve to detoxify potentially damaging ROS.
- Over the course of storage, and depending upon pre-harvest, handling, and postharvest conditions, these natural defenses in vegetable tissues are often eventually declined. As a result, unchecked free radical–mediated reactions disrupt cell membranes, leading to cell death and tissue damage.
- it is probable that the tissue damage and increased susceptibility to postharvest decay associated with storage disorders such as chilling injury involve ROS and oxidative stress

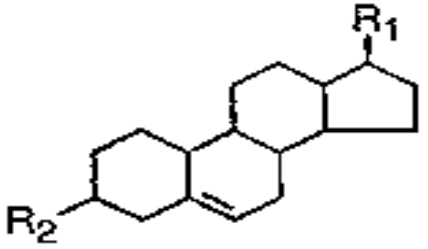
Other Changes in Lipid Composition with Ripening

- In addition to PL catabolism and ROS-induced lipid peroxidation, other changes in membrane lipid composition occur during postharvest life, some in response to low temperature and/or controlled atmosphere (CA) storage, which may have an important role in regulating membrane structure and function.

Examples include:

- increased desaturation of glycerol lipid fatty acids;
- modification of the proportions of PL polar head groups (e.g., choline and ethanolamine);
- changes in the amount, composition and conjugation of membrane sterols.

Sterol Nucleus



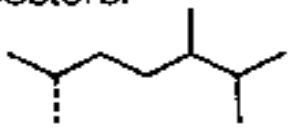
Alkyl Side Chain

Cholesterol

R_1 =

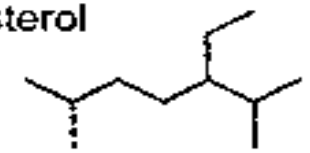
Campesterol

R_1 =



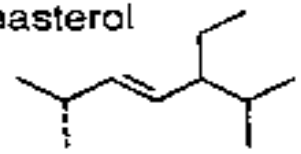
Sitosterol

R_1 =



Stigmasterol

R_1 =



Sterol Lipid 3β-Substituent

Free Sterol (FS)

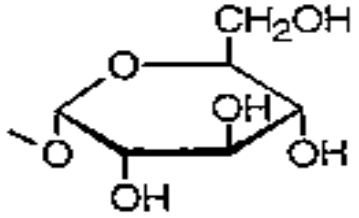
R_2 = OH

Steryl Ester (SE)

R_2 = -O-C(=O)-$(CH_2)_{14}CH_3$

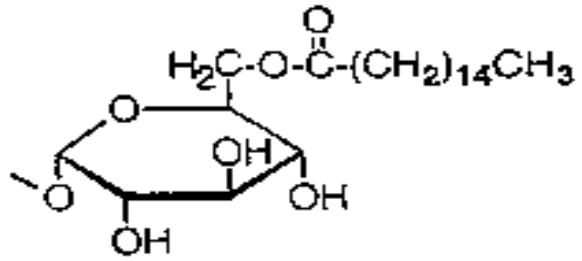
Steryl Glycoside (SG)

R_2 =

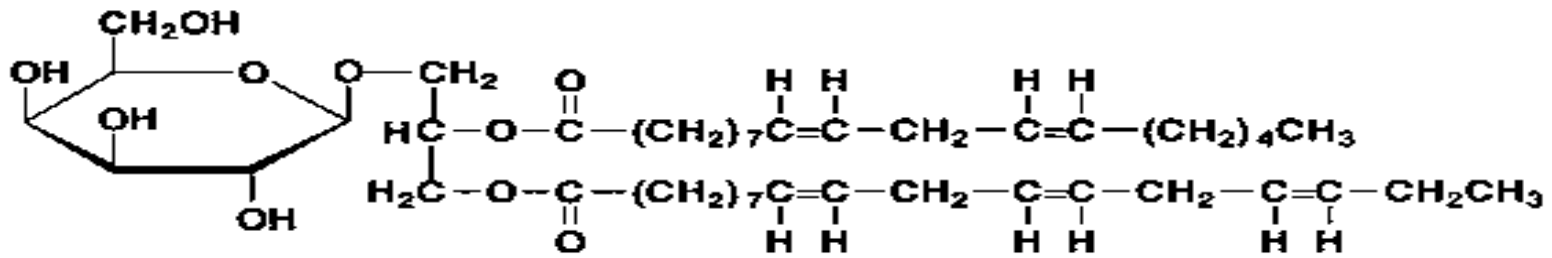


Acylated Steryl Glycoside (ASG)

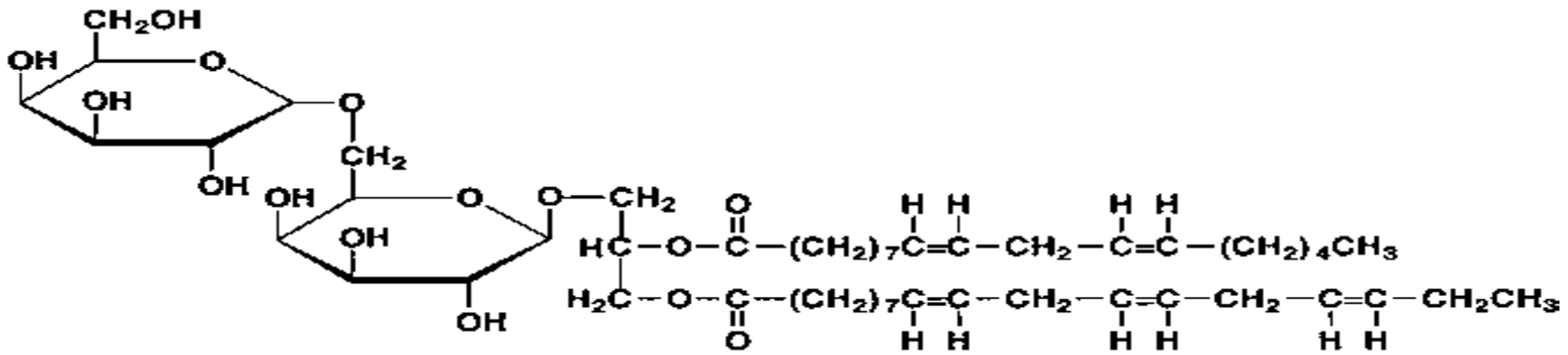
R_2 =



Monogalactosyldiacylglycerol (**MGDG**)



Digalactosyldiacylglycerol (**DGDG**)



Structures of the two predominant glycoglycerolipids in chloroplast membranes, monogalactosyl-diacylglycerol (MGDG) and digalactosyl-diacylglycerol (DGDG). MGDG is most concentrated in the thylakoids, whereas DGDG is more abundant in the membranes. Both lipids include a high percentage of linoleic and linolenic acids.

Fruit Ripening and Chilling Injury

- Increased permeability, manifest as a greater rate of electrolyte leakage, has also often been cited as evidence of chilling-induced damage of the plasma membrane in chilling-sensitive fruits. However, there are quite a few contradictions in the literature with regard to whether increased ion leakage is induced by prolonged chilling or only after subsequent rewarming.
- In any case, most recent evidence indicates that a significant increase in permeability occurs only after rewarming, and coincides with membrane lipid degradation and development of injury symptoms such as water soaking of the tissues

- One important factor that may be involved in apparent increased membrane permeability, both with the progression of ripening and the onset of chilling injury, is a decline in or inhibition of H- and Ca2-ATPase activities in cell membranes.
- The sensitive H-ATPase maintains an electrical potential and a proton gradient across the plasma membrane that are necessary for uptake of K and other solutes, whereas Ca2-ATPase serves to extrude free cytosolic Ca2 and thereby maintain the submicromolar Ca2 concentration required for normal cell function. Thus, impairment of these ion transporters would ultimately result in loss of viability and tissue injury. It is logical to assume that the senescence-related increase in membrane lipid fluidity and lipid phase transitions that arise as a result of increased PL catabolism alter the conformation of membrane proteins, and thus affect their enzymatic activity.

- Surely one of the most complex changes associated with fruit ripening is the transformation of chloroplasts in mature-green fruit into chromoplasts in fully ripened fruit.The entire process entails a temporally regulated series of events that begins with :

- degradation of chlorophyll, dismantling of the photosynthetic granal thylakoid membranes and mobilization of starch reserves from specialized vacuoles, and synthesis of large amounts of carotenoids that are incorporated into crystalline structures.

In terms of postharvest quality attributes, plastid transformation can be highly desirable, as in tomatoes and red peppers, or detrimental, as in green bell peppers and cucumbers, where yellowing negative factors in marketing. In fact, there is a some evidence indicating that chilling-induced aberrations in lipid metabolism in chloroplasts are a primary determinant of chilling sensitivity in a number of fruits, including tomato and pepper.

Antioxidant enzymes and fatty acid composition as related to disease resistance in postharvest loquat fruit

Two cultivars of loquat fruit were stored at 20 C for 10 days to investigate the relationship between disease resistance, and fatty acid composition and activities of endogenous antioxidant enzymes. The results showed that decay incidence increased with storage time in both cultivars. A significantly lower disease incidence was observed in ‘Qingzhong’ fruit than in ‘Fuyang’, suggesting ‘Qingzhong’ had increased disease resistance. Meanwhile, ‘Qingzhong’ fruit also had lower levels of superoxide radical and hydrogen peroxide, and lower lipoxygenase activity, but higher levels of linolenic and linoleic acids and higher activities of catalase (CAT) and ascorbate peroxidase (APX) compared with ‘Fuyang’. These results suggest that the higher levels of linolenic and linoleic acids and the higher activity of CAT and APX have a role in disease resistance of postharvest loquat fruit.

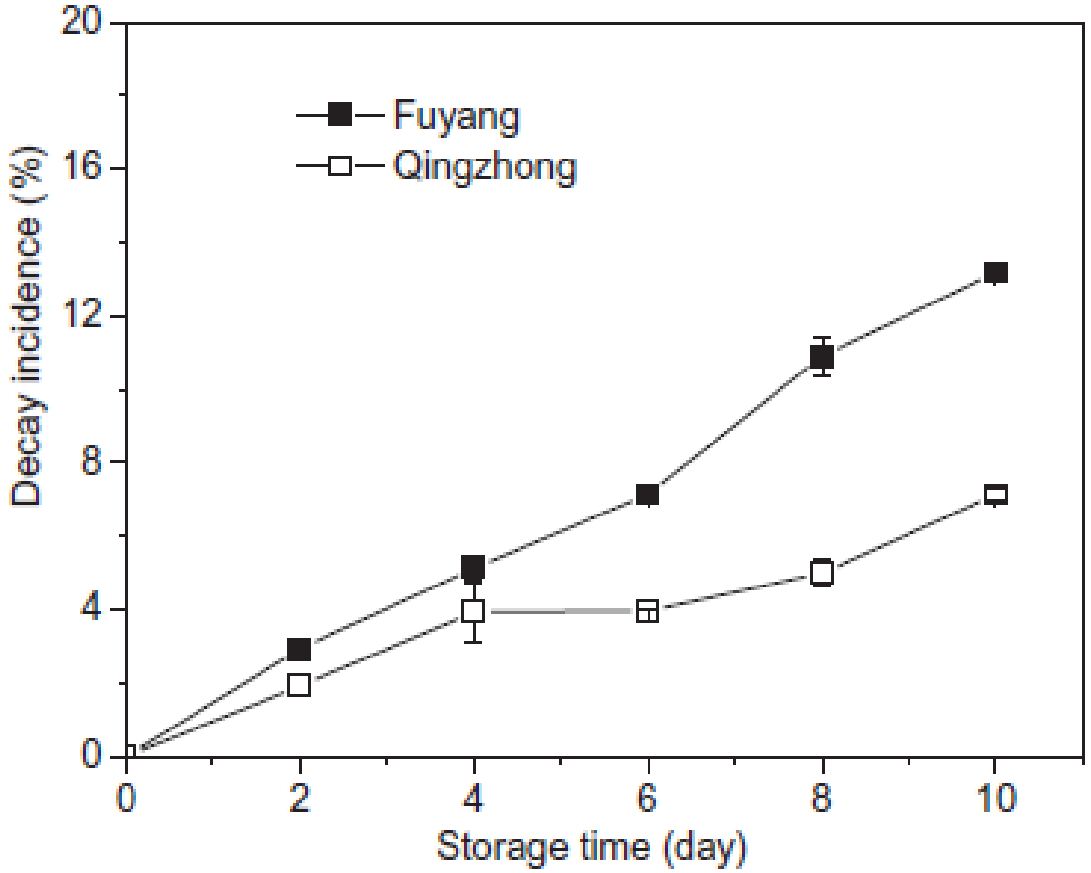
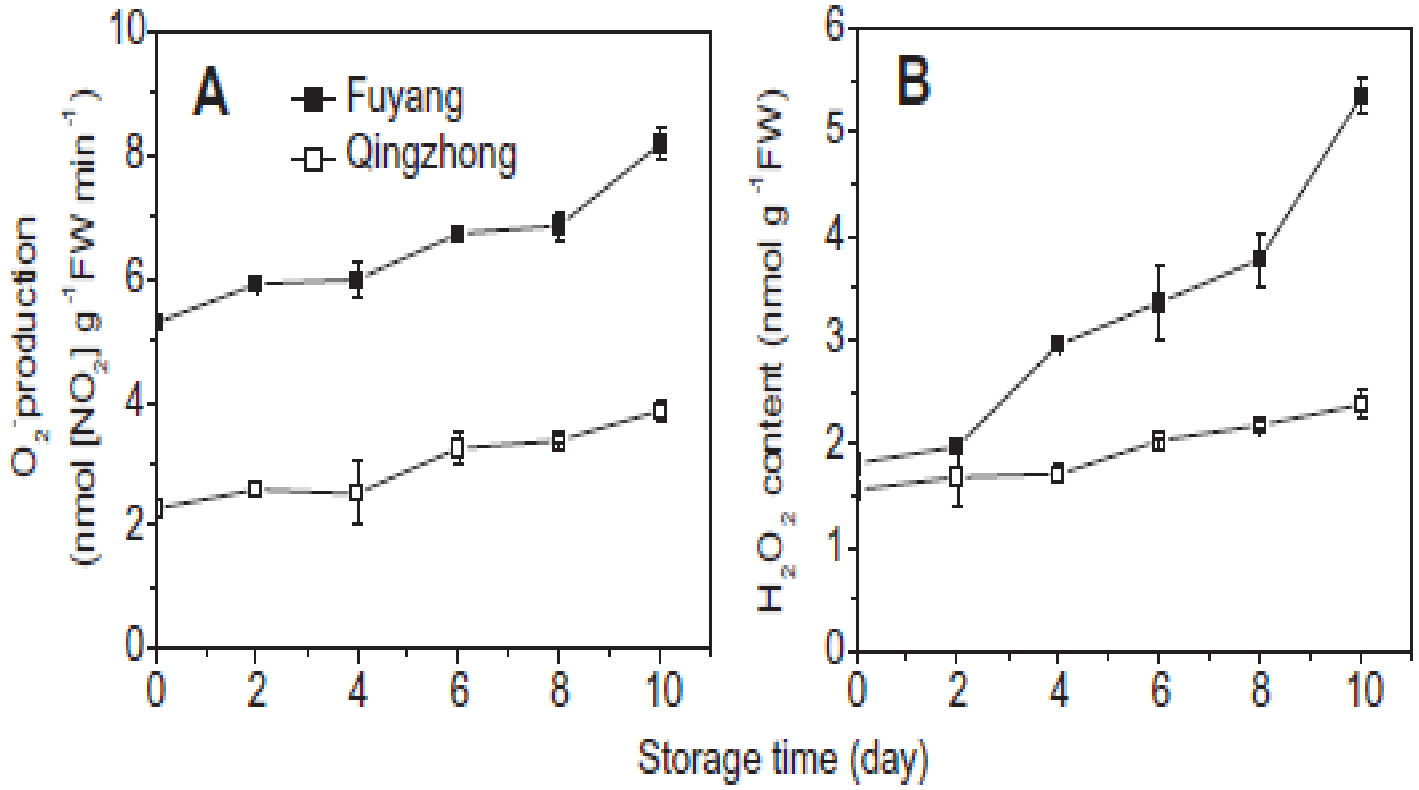
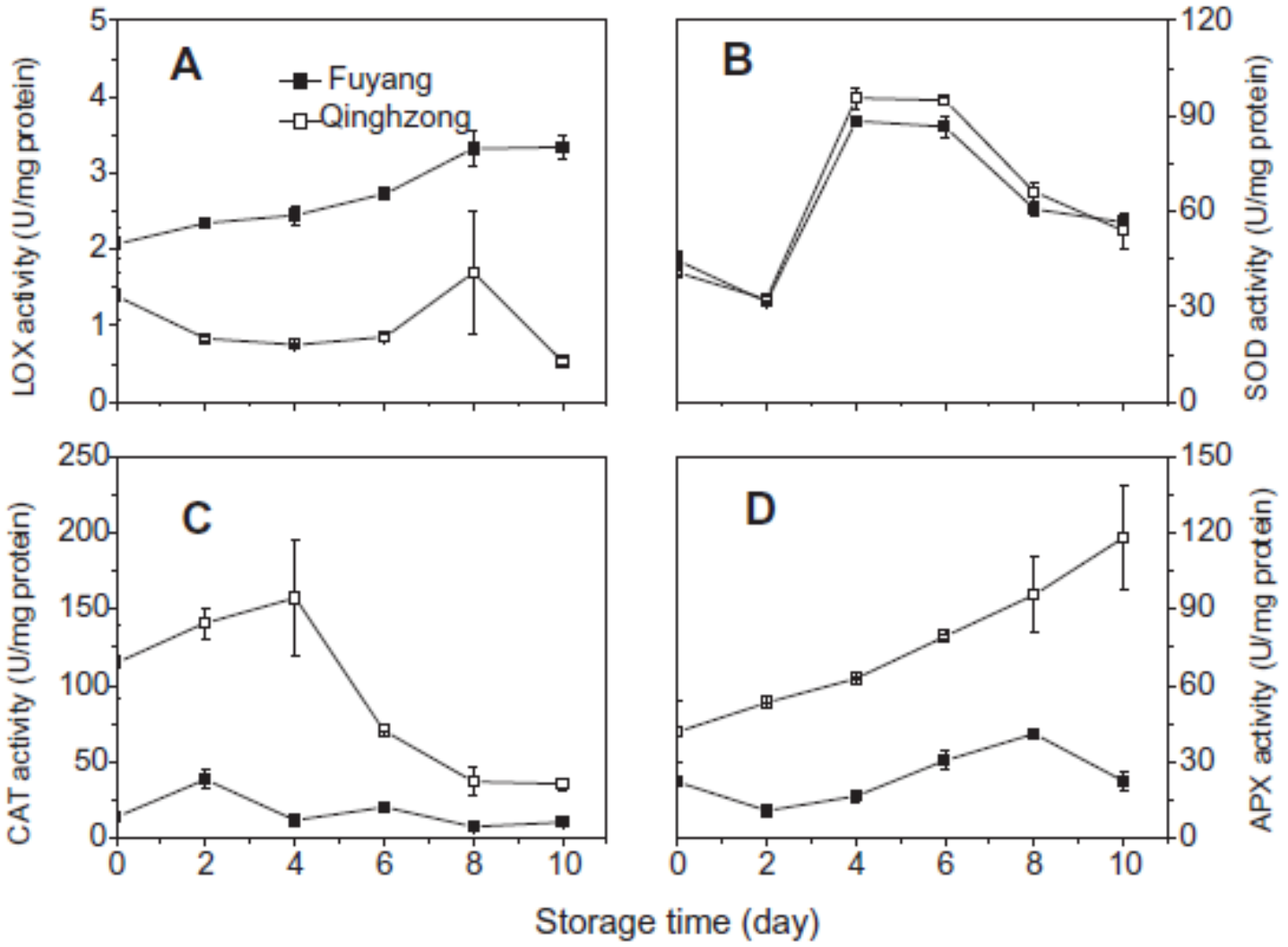


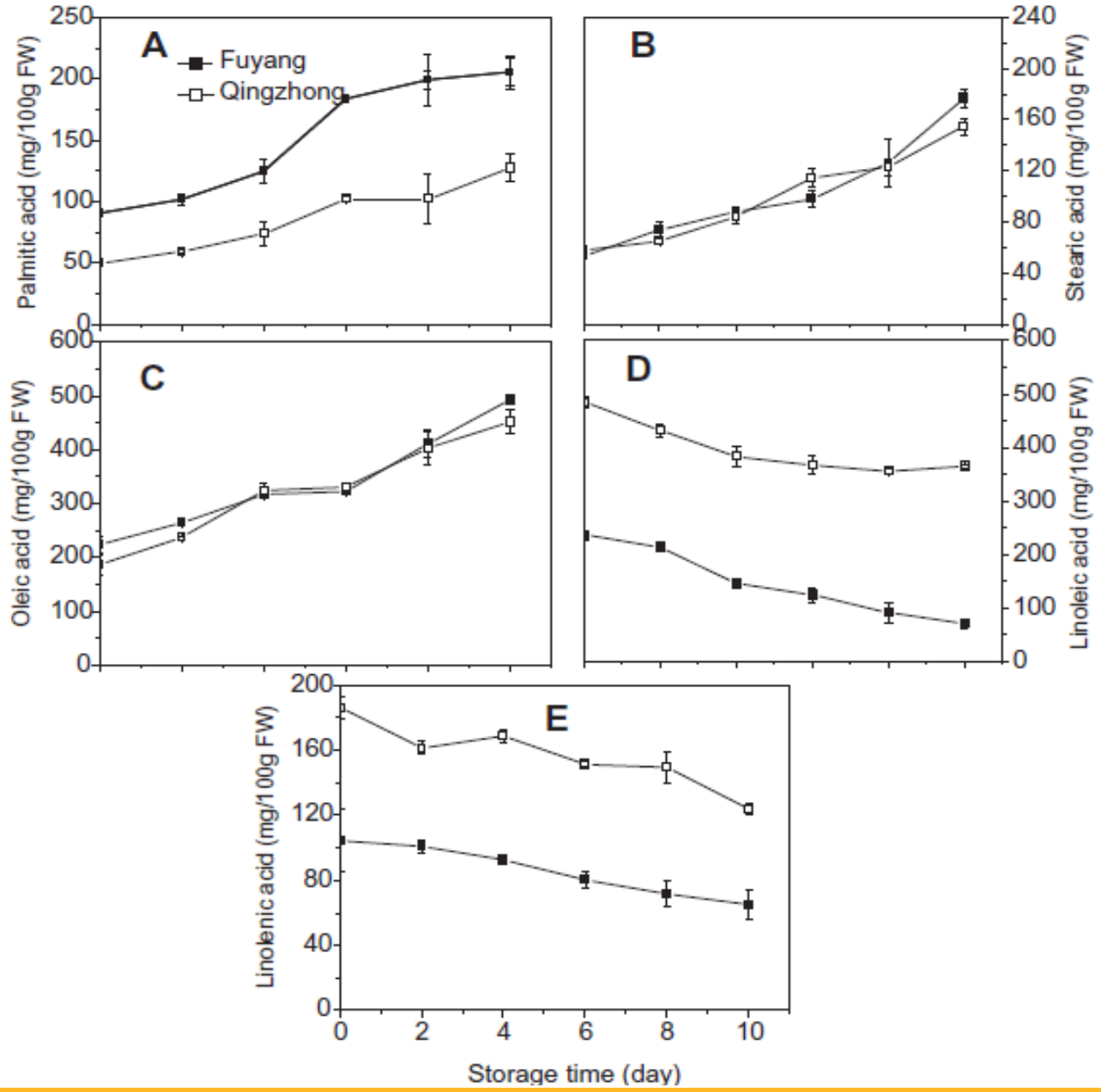
Fig. 1. Changes of decay incidence of 'Fuyang' (■) and 'Qingzhong' (□) loquat fruit during storage at 20 °C. Values are the means ± SE of triplicate samples of ten fruit each. Vertical bars represent the standard errors of the means.

$$\text{Decay incidence } (\%) = [(1 \times N_1 + 2 \times N_2 + 3 \times N_3) \times 100/(3 \times N)]$$

where N was the total number of fruit measured and N_1, N_2, and N_3 were the numbers of fruit showing the different severities of decay.


A
Fuyang
Qingzhong
O_2^- production
(nmol [NO_2] g^{-1}FW min^{-1})
B
H_2O_2 content (nmol g^{-1}FW)
Storage time (day)
0
2
4
6
8
10


A
B
C
D
Fuyang
Qinghzong
LOX activity (U/mg protein)
SOD activity (U/mg protein)
CAT activity (U/mg protein)
APX activity (U/mg protein)
Storage time (day)


A
Fuyang
Qingzhong
Palmitic acid (mg/100g FW)
B
Stearic acid (mg/100g FW)
C
Oleic acid (mg/100g FW)
D
Linoleic acid (mg/100g FW)
E
Linolenic acid (mg/100g FW)
Storage time (day)

Low temperature alters plasma membrane lipid composition and ATPase activity of pineapple fruit during blackheart development

Yuchan Zhou · Xiaoping Pan · Hongxia Qu · Steven J. R. Underhill

Received: 28 July 2013 / Accepted: 17 December 2013 / Published online: 4 January 2014

Abstract Plasma membrane (PM) plays central role in triggering primary responses to chilling injury and sustaining cellular homeostasis. Characterising response of membrane lipids to low temperature can provide important information for identifying early causal factors contributing to chilling injury. To this end, PM lipid composition and ATPase activity was found to inhibit the PM ATPase activity of pineapple fruit in vitro. Modification of membrane lipid composition and its effect on the functional property of plasma membrane at low temperature were discussed in correlation with their roles in blackheart development of pineapple fruit.

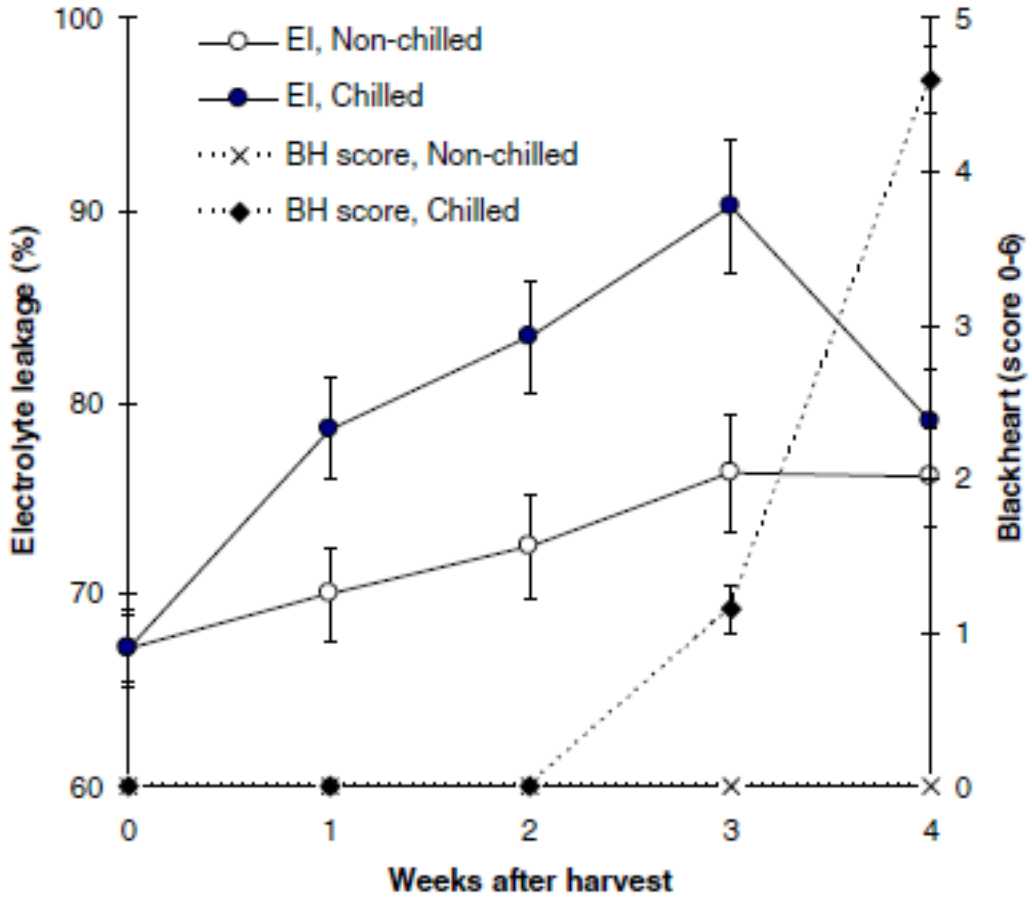


Fig. 1 Effect of low temperature on blackheart development and electrolyte leakage of pineapple fruit. Non-chilled, continuous 25 °C; Chilled, 3 week storage at 10 °C followed by 1 week at 25 °C. *EI* electrolyte leakage, *BH* blackheart. All values represent mean±SE of nine biological replicates

Table 1 Activities of marker enzymes in plasma membrane fraction isolated from pineapple fruit

Marker enzyme		1 Week		2 Week	
ATPase	Harvest	25 °C	10 °C	25 °C	10 °C
no addition	311.21±18.05	280.47±12.39	265.21±14.73	326.00 ±16.81	220.37±13.44
Vanadate-sensitive ATPase (PM)	281.01±13.05***ab***	250.97±11.99***abc***	239.09±10.53***c***	290.67±10.94***a***	194.67±7.10***d***
Nitrate-sensitive ATPase (tonoplast)	21.23±1.40	19.69±1.27	17.88±0.88	21.19±1.12	15.22±0.96
Azide-sensitive ATPase (mitochondria)	4.40±0.16	3.67±0.23	3.30±0.15	5.22±0.22	3.46±0.17
NADH cyt c reductase (ER)	3.97±0.26	3.67±0.19	3.17±0.18	4.27±0.26	2.86±0.14
Latent IDPase (Golgi apparatus)	18.28±1.08	16.84±0.86	15.11±0.84	19.47±1.22	12.07±0.57

PM plasma membrane, *ER* endoplasmic reticulum, *Latent IDPase* latent inosine diphosphatase. Activities of ATPase and Latent IDPase are presented as nmol Pi/min/mgProtein, the NADH cyt c reductase activity is presented as nmol cyt/min/mgProtein. All values represent the mean ± SE of six biological replicates. Values with different letter are significantly different ($P<0.05$)

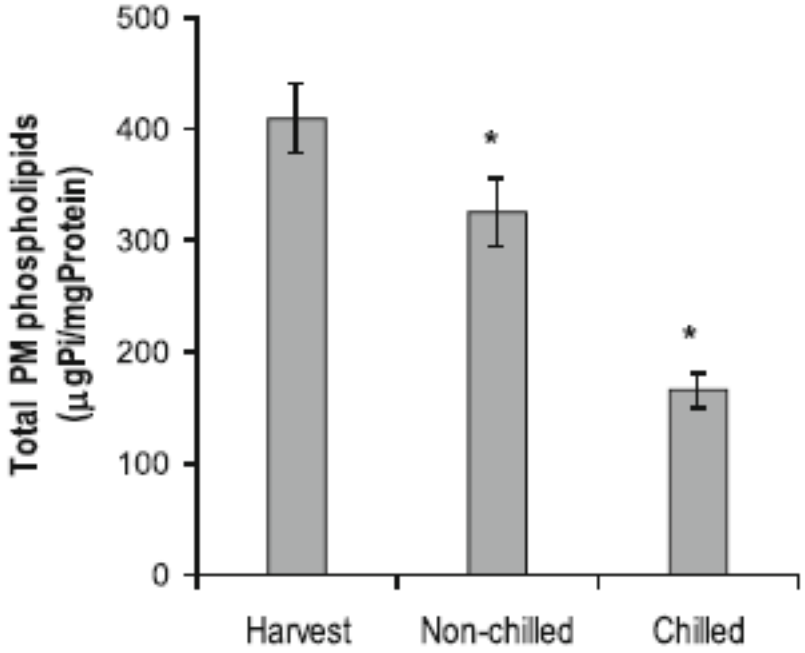


Fig. 2 Effect of low temperature on the total phospholipids of plasma membrane isolated from pineapple fruit. Non-chilled, 25 °C 2 week; Chilled, 10 °C 2 week. *PM* plasma membrane; All values represent mean ± SE of six biological replicates (*$P<0.05$)

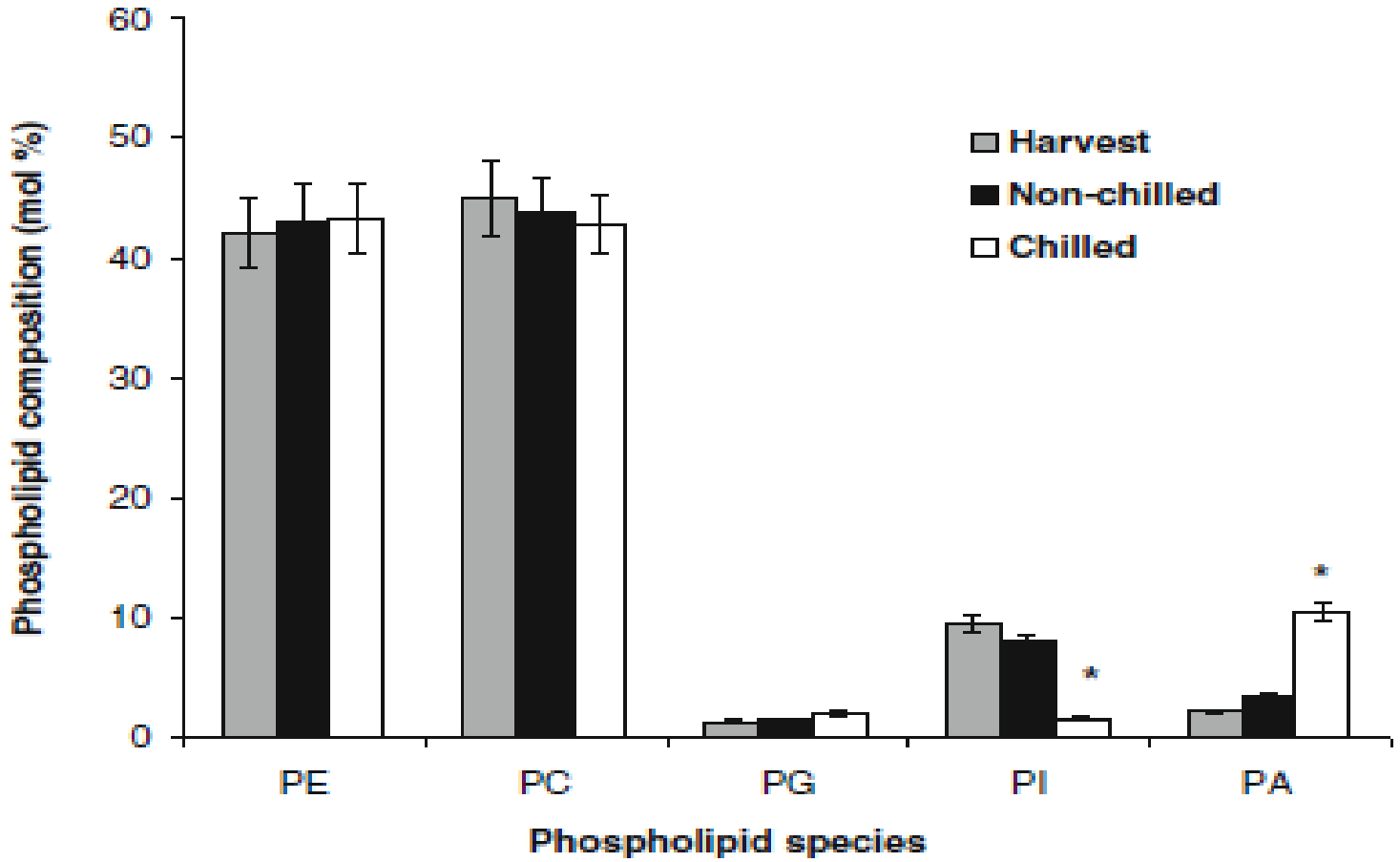
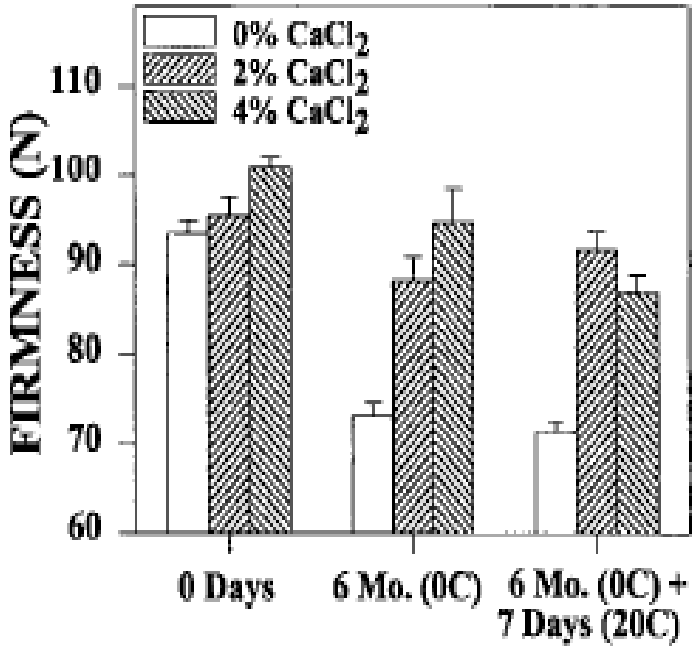
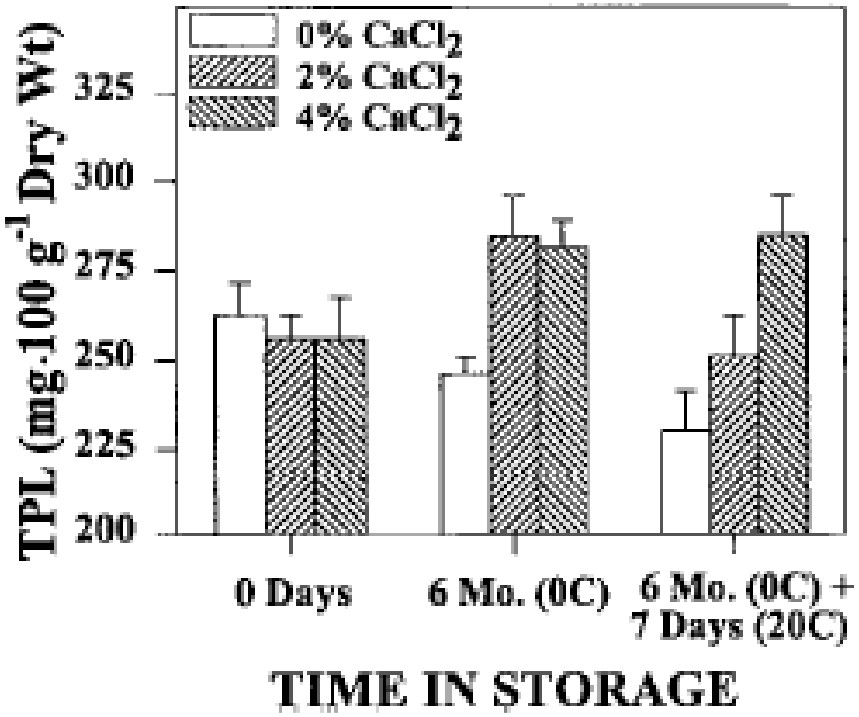


Fig. 3 Effect of low temperature on phospholipid composition of plasma membrane from pineapple fruit. Non-chilled, 25 °C 2 week; Chilled, 10 °C 2 week. *PC* phosphatidylcholine, *PE* phosphatidylethanolamine, *PG* phosphatidylglycerol, *PI* phosphatidylinositol, and *PA* phosphatidic acid; All values represent mean ± SE of six biological replicates (*$P<0.05$)

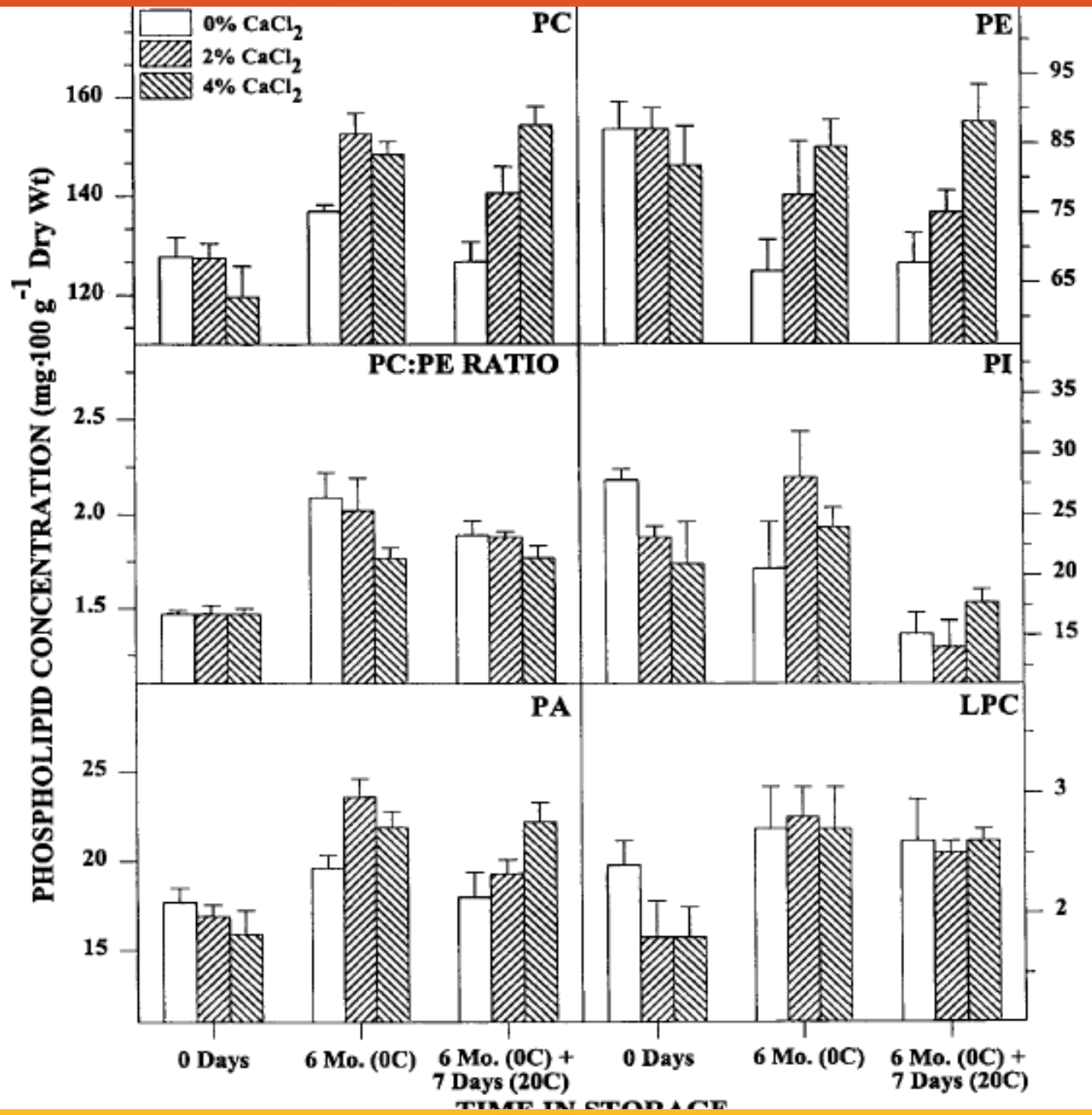
Postharvest Calcium Infiltration Delays Membrane Lipid Catabolism in Apple Fruit

Postharvest changes in membrane lipids of Ca^{2+}-infiltrated apples (*Malus domestica* Borkh. cv. Golden Delicious) have been evaluated. Calcium infiltration (2% or 4% w/v $CaCl_2$) improved fruit firmness retention over control (water-infiltrated) fruit following 6 months of 0 °C storage and after 7 subsequent days at 20 °C. During cold storage, total phospholipid (primarily phosphatidylcholine and phosphatidylethanolamine) and acylated steryl glycoside concentrations increased in Ca^{2+}- infiltrated fruit but decreased in control fruit. Seven days following transfer from cold storage to 20 °C, total phospholipid concentration remained highest in fruit infiltrated with 4% $CaCl_2$. Free sitosterol and steryl glycoside concentrations were generally increased with increasing infiltrated Ca^{2+} concentration throughout the postharvest evaluation period. Greater conservation of specific membrane lipid components in the Ca^{2+}-infiltrated fruit, both during and after low-temperature storage, may contribute to the well-known beneficial effects of Ca^{2+} infiltration in maintaining apple quality.


0% CaCl2
2% CaCl2
4% CaCl2
FIRMNESS (N)
110
100
90
80
70
60
0 Days
6 Mo. (0C)
6 Mo. (0C) +
7 Days (20C)


0% CaCl2
2% CaCl2
4% CaCl2
TPL (mg.100 g-1 Dry Wt)
325
300
275
250
225
200
0 Days
6 Mo. (0C)
6 Mo. (0C) +
7 Days (20C)
TIME IN STORAGE

.


0% CaCl2
2% CaCl2
4% CaCl2
PC
PE
PC:PE RATIO
PI
PA
LPC
PHOSPHOLIPID CONCENTRATION (mg·100 g-1 Dry Wt)
160
140
120
95
85
75
65
2.5
2.0
1.5
35
30
25
20
15
25
20
15
3
2
0 Days
6 Mo. (0C)
6 Mo. (0C) + 7 Days (20C)
0 Days
6 Mo. (0C)
6 Mo. (0C) + 7 Days (20C)
TIME IN STORAGE

.

- This research suggested smaller losses in total membrane lipid components and increased membrane integrity in Ca infiltrated as compared to control fruit.
- Because membrane lipid alterations are viewed as a central factor in the senescence of plant tissues, conclude that Ca may serve a key role in delaying apple fruit quality losses after Ca infiltration, especially by delaying membrane lipid catabolic processes.

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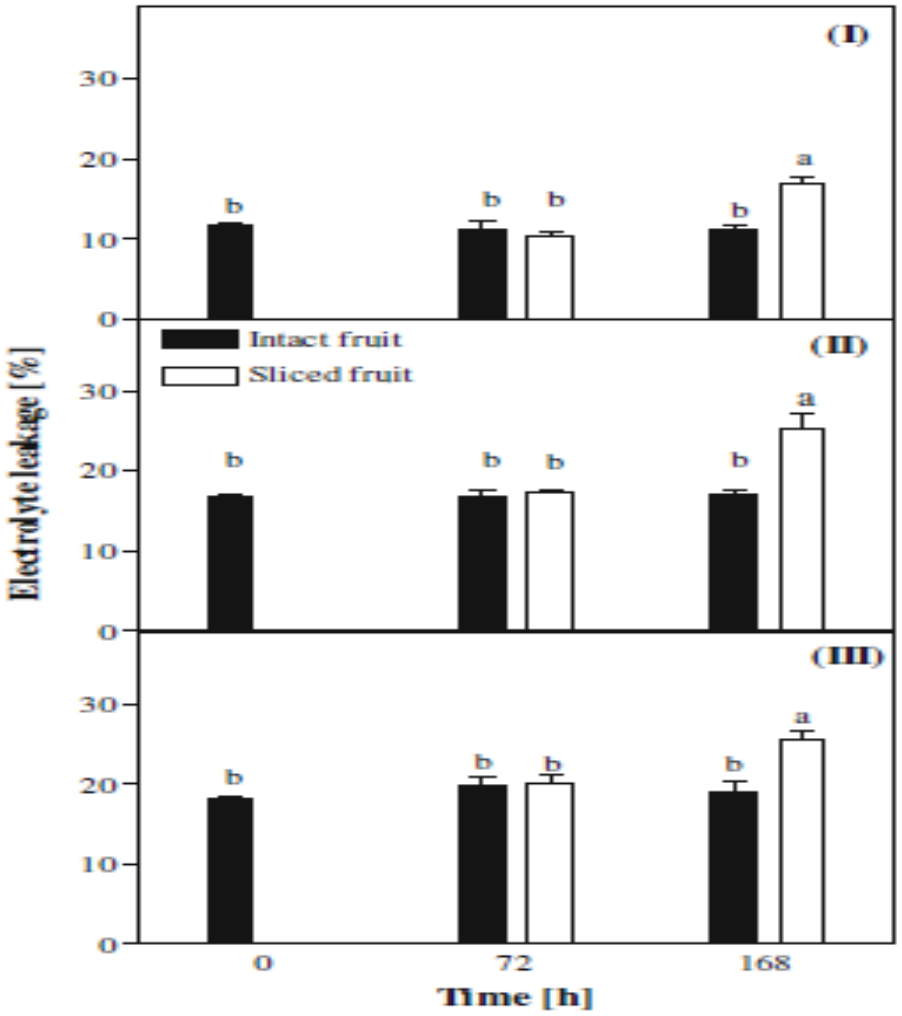
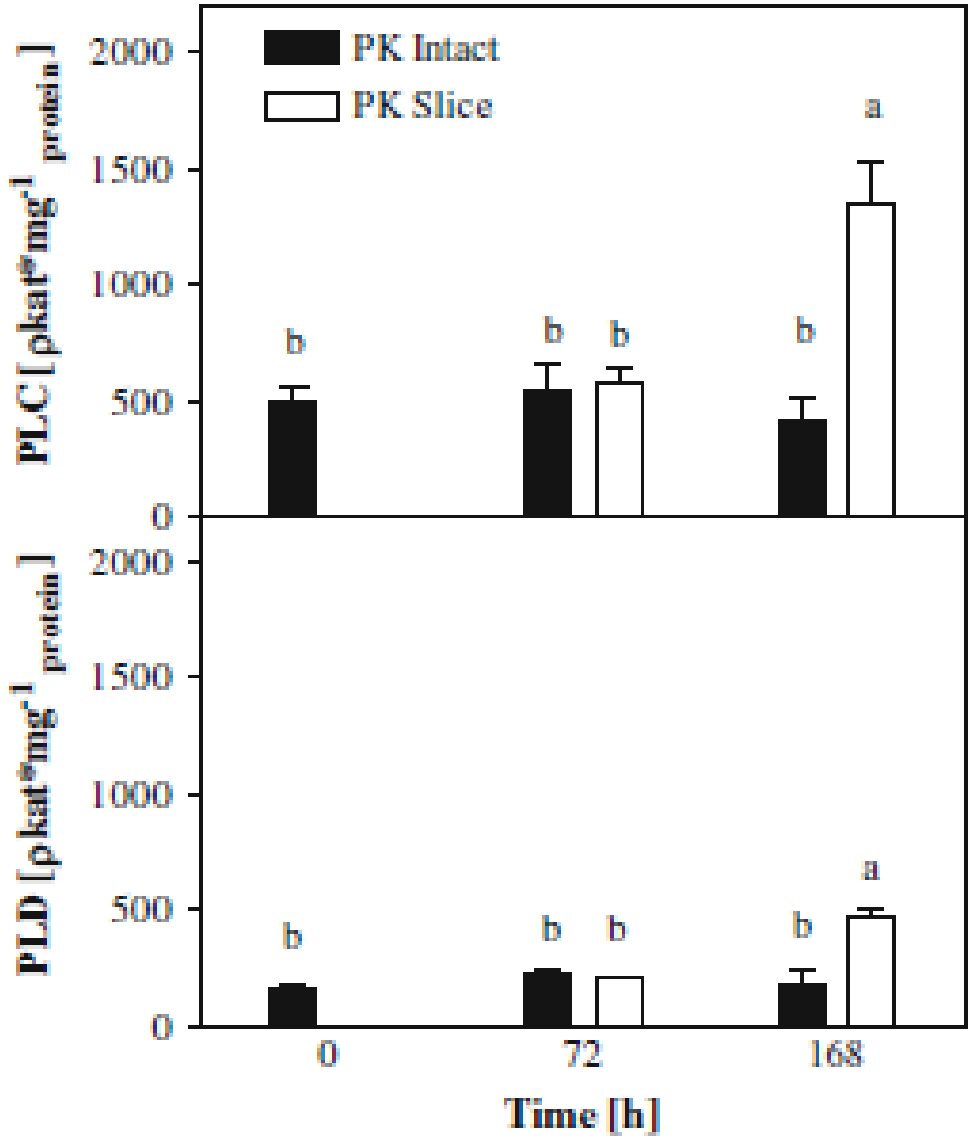
Effect of temperature and ripening stages on membrane integrity of fresh-cut tomatoes




PK Intact
PK Slice
PLC [pkat*mg-1protein]
PLD [pkat*mg-1protein]
2000
1500
1000
500
0
b
b
b
b
a
b
b
b
b
a
0
72
168
Time [h]

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Review

The fruit cuticle as a modulator of postharvest quality

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ABSTRACT

The composition and structure of fruit surface tissues have a noticeable influence on the postharvest storage potential of fruit, inasmuch as they behave as a barrier against drying, chemical attack, mechanical injuries and microbial infection. The cuticle is made of cutin, a biological insoluble polyester, embedded in an impermeable wax complex, and its inner side interacts intimately with the underlying epidermal cell walls. The cuticle plays a decisive role in plant development, being the first communication system with the surrounding biotic and abiotic environment. Published reports on the composition and biosynthesis of fruit cuticles are comparatively scarce, and many knowledge gaps exist on the part cuticles play in quality determination and postharvest performance. This review aims at collecting available information in relation to the role of the fruit cuticle as a determinant factor of some important traits related to postharvest quality, including water loss, susceptibility to physical and biological stresses, and decreased

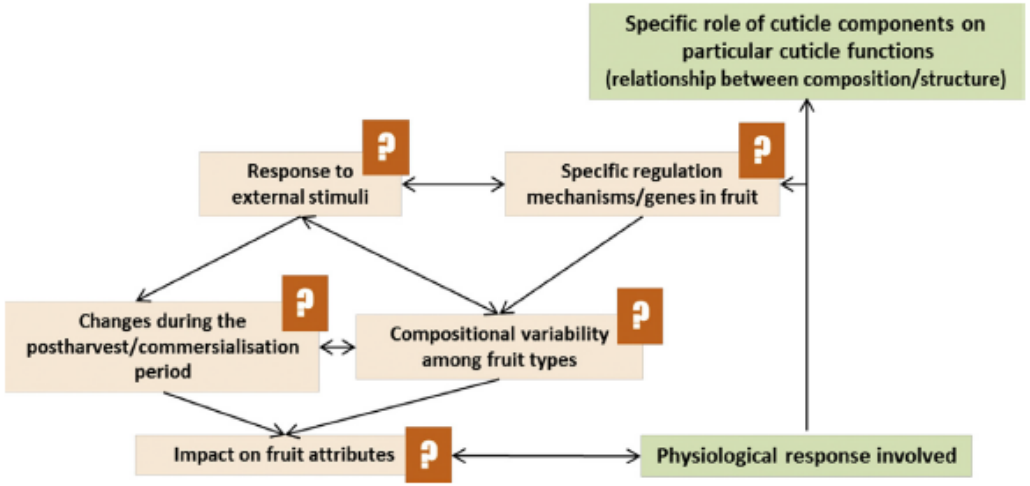

Fig. 1. Major unanswered questions on the interactions between cuticle characteristics and fruit quality attributes impacting postharvest management.

ed by epicuticular waxes, both amorphous and crystalline. On ner side of the cuticle, cutin is mixed with pectin and glucan ccharides from the epidermal cell walls, the composition of closely resembles that of primary cell walls (López-Casado 2007). The cuticle also contains cutan, a non-ester network of aliphatic compounds assembled mainly by ether bonds. t reviews have summarised available information on the osition and biosynthesis of cutin and cuticular waxes (Kunst

development, prior to the onset of the ripening process and fi quently before the fruit has attained maximum size, resulting decreased amounts of cuticle per surface area and thus in reduc cuticle thickness in ripe fruit (Rosenquist and Morrison, 198 Comménil et al., 1997; Belding et al., 1998; Dong et al., 2012; l et al., 2012). In some cases, early-arrested deposition of cuticu components and the associated decline in cuticle thickness caus microcracks as surface strain increases when fruit expand (S