

Protective Function of Lipid Rafts

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ABSTRACT

The study of lipid rafts allowed us to take a new look at the morphology, organization and functioning of membranes, both of animal and plant origin. However, lipid rafts and their function in the cell membranes of plants are poorly understood in comparison with the membranes of animal cells. The protective function of the plant cell is of great importance for the body as a whole because plants lead an attached mode of life. To date, it is known that lipid rafts are involved in the membrane mechanisms of cell protection in response to negative effects. In this review, we summarized the literature data showing the participation of lipid rafts of plant membranes (plasmalemma, Golgi complex membranes, chloroplasts, mitochondria, and vacuoles) in the protective function of cells.

Keywords: plant, membrane, stress, lipid rafts.

Article type: Research Article.

INTRODUCTION

At present, it has been understood that different cell membranes have similarities in structural organization and chemical composition. Understanding this allows us to consider the body as a system of uniform structural elements. Violation of any of the factors of the molecular organization of this system may be unfavorable for the organism (Filek *et al.* 2017). It is known that due to the lipid component, the cell membrane system is able to activate protective mechanisms. Lipids, being an integral part of all biological membranes, play an important role in the biochemical processes of the cell. It turns out that the lipid composition of membranes is carefully optimized by evolution, and therefore the lipid profile of membranes changes depending on the type of tissue, cell, and organelle (Cassim *et al.* 2018; Kleiman *et al.* 2021). The study of certain physical properties of lipids led researchers to a new theory of the organization of biological membranes. Lipids can form partially isolated areas of the bilayer that have special structural properties. This concept was further developed by Simons and Ikonen, who later put forward the revolutionary theory of "lipid rafts". The main idea is that certain areas of the membrane are self-organized into cholesterol-rich "rafts" in which lipids are in a different phase state, liquid-ordered, i.e. they are denser than other areas of the membrane, and therefore freely drift in the surrounding space (Simons & Ikonen 1997). Currently, sterol-rich sections of the membrane are called domains, sometimes with the prefix micro - or nano-, depending on the size. In English-language literature, these domains are called "raft", which means "raft" (Goñi 2018). However, the most commonly used name in the scientific literature is "lipid raft", given by Simons and Ikonen in the 1990s. Membrane microdomains were defined as ordered, nanoscale (10-200 nm), heterogeneous, highly dynamic domains that can participate in the regulation of cellular processes (Pike 2006) at

a Symposium on lipid rafts and cell function (Keystone Symposium of Lipid Rafts and Cell Function) in 2006. To date, it is known that lipid rafts are plastic in relation to such parameters as size, shape, and localization in the cell. It was found that the size of rafts could vary and change depending on the concentration of lipids in the cell, external conditions, and the active state of the membrane. In this connection, it is necessary to distinguish between two main classes of membrane domains "nanodomains" (size 10-200 nm), the fusion of which leads to the formation of larger structures "microdomains" (> 200 Nm) (Pleskova *et al.* 2015). A number of researchers believe that rafts in cells are short-lived aggregates with an average of no more than 1 minute, containing more than 1000 lipid molecules and having an almost circular shape, which quickly (in seconds) recovers after its perturbation. In addition, the thickness of rafts exceeds the thickness of the surrounding membrane by 0.5-1.0 nm (Bhatia *et al.* 2016; Rosetti *et al.* 2017). Lipid rafts have a different density and melting point from the membrane, so they can "float" on the surface of a liquid-disordered membrane (Lu & Fairn 2018). This property of rafts was revealed during the treatment of membranes with detergents. In this case, the lipid part of the membrane located in the liquid disordered phase is dissolved, and the raft lipids located in the liquid ordered phase retain their integrity. This is due to the presence of sterols, sphingolipids, and lipids with saturated acyl chains in rafts (Schroeder *et al.* 1998). This resistance to dissolution in the detergent was originally the definition of a lipid raft. Over the past two decades, the concept of lipid rafts has become extremely popular among cell biologists, and these structures have been proven involved in a wide variety of cellular functions and biological processes (Santos & Preta 2018). Currently, the presence of lipid rafts in prokaryotic and eukaryotic organisms has been proven (Cascianelli *et al.* 2008; Toledo *et al.* 2018). The role of lipid rafts in cell protection mechanisms is well considered in animal organisms. Lipid rafts have been studied more recently in plant organisms. In this connection, there are not many data on lipid rafts of plants. The aim of this work was to generalize the literature data on the participation of lipid rafts of various cell membranes in plant defense mechanisms.

Participation of lipid rafts in the protective mechanisms of plant cells

It is known that all plant cell membranes participate in a set of metabolic and energy processes that maintain and reproduce the entire cellular system under normal and stressful conditions, while each membrane performs its own specific function. Currently, it has been shown that lipid rafts in plant cells are found in the plasmalemma, mitochondrial membranes, chloroplasts, vacuoles, and Golgi complex (Lefebvre *et al.* 2007; Laloi *et al.* 2007; Ozolina *et al.* 2013; Yoshida *et al.* 2013; Nesterov *et al.* 2017). However, the lipid rafts of the plasmalemma are the most studied; there are few data on the lipid rafts of other membranes. In particular, information on chloroplast and mitochondrial rafts appeared in 2017.

Animal cells are studied more actively, so lipid rafts are detected in the plasmalemma, the membranes of the nuclei, mitochondria, Golgi complex, and in the membranes of the endoplasmic reticulum (Santos & Preta 2018). The protective function of plants is of great importance because they lead an attached mode of life. Membranes are actively involved in the response of cells to negative effects. In this connection, much attention is paid to the study of the membrane structure. As a result, the study of lipid rafts of plant cell membranes allowed us to understand the functions that cell membranes perform better. Recently, researchers have proved the participation of membrane rafts in the response of plant cells to biotic and abiotic stress (Hao *et al.* 2014). *Plasmalemma*, being the outer cell membrane, is the first to react to negative effects using various mechanisms in which lipid rafts are involved. The study of the composition of plant plasmalemma lipid rafts showed the presence of a variety of proteins responsible for various functions directly or indirectly involved in responses to stress. For example, the lipid rafts of the plasma membrane of tobacco leaves contain up to 145 proteins, of which more than 30 have not been identified. Of the identified proteins, 36 are involved in transport processes, 34 in signaling, and 17 proteins are involved in intercellular transport (Morel *et al.* 2006). 270 proteins were found in the plasma membrane of alfalfa roots. Many of them can be classified by functions: 43 signaling, 65 transport, 21 associated with redox regulation, 30 associated with the cytoskeleton, 111 have several functions, and 22 functions are still unknown (Lefebvre *et al.* 2007; Arekhi *et al.* 2020). Currently there is information about the functional and physiological characteristics of the individual proteins investigated in stress conditions. It is assumed that the predominant distribution of PIP-type aquaporins in sterol-rich domains (lipid rafts) is regulated by the traffic of sterol-rich vesicles and/or by the interaction of aquaporins with lipid "raft" proteins, which allows regulating the activity of water transport at the membrane level. It is noted that low-temperature hardening of Arabidopsis plants results in an increase in the proportion of PIP aquaporins and p-type ATP phases in lipid rafts. This may be due to the need for rapid water release from the cell to prevent the formation of intracellular ice (Fan *et al.* 2015). The response mechanisms of

the plasmalemma to stress involve not only the proteins that make up rafts, but also the lipids that are their basis. Recent studies have shown that cold acclimatization leads to changes in the lipid profile of raft structures. The proportion of phospholipids decreases and the proportion of sphingolipids and sterols increases. Together, these results show that cold acclimatization induces changes in the composition of lipids in rafts, which leads to changes in the thermodynamic properties and physiological functions of lipid rafts, which, consequently, affects the resistance of plants to low temperatures (Takahashi *et al.* 2016, Momeni, A.R 2018, Adejoke, H.T 2019, Naderi, D 2021, Saadatmand, M 2021). *Plasmodesmata* play a key role in the interaction of plants with pathogens. Pathogens are transported from the site of infection to the conducting system that carries their long-distance transport through the plant. It is known that one of the ways to influence the transport capacity of plasmodesmata is the deposition of callose at their stoma (Leslie *et al.* 2016).

It is proved that the pathogenesis in plant cells the content of callose increases. At the same time, a correlation was noted between the content of callose in the host cells and the plant's resistance to the spread of the pathogen. It has also been shown that the more resistant the plant, the greater the layer of callose deposits around the site of infection (Ellinger *et al.* 2013). The mechanism is that callosa can reduce the diameter of the transport channel, thereby making it more difficult for the pathogen to spread. Currently, it is proved that lipid rafts play an important role in the synthesis and accumulation of callose in plasmodesmata (Iswanto & Kim 2017). In lipid rafts, proteins that regulate the binding and turnover of callose in plasmodesmata (PDCB1 and PDBG2) are localized. It was shown that a violation of the formation of lipid rafts affects the accumulation of callose that affects the functions of the plasmodesma, including the interaction with pathogens (Grison *et al.* 2015; Iswanto & Kim 2017). In addition, defects in the lipid rafts of the plasmalemma also affect the activity of the remorin protein. To date, it has been established that remorin is a specific raft-associated protein that is localized in the plant membrane (Jarsch & Ott 2011; Ott 2017). Previously, the functions of this protein were unknown, but now their role in the interaction of plants and microorganisms has been proven. It has been shown that remorins inhibit the movement of the virus in potato leaves by interacting with the virus protein TGBp1 (Perraki *et al.* 2018). It has also been shown that the accumulation of raft-associated remorin protein (MtSYMREM1) is observed when plants are infected with a bacterium of the Rhizobiaceae family (Lefebvre *et al.* 2010). An interesting fact is that the immobilization of pathogens is preceded by the appearance of mobile cytosolic vesicles-endosomes, a few hours after inoculation (Haney *et al.* 2011). Interaction sites between the pathogen and the host cell are overgrown with vesicles, which are formed by receptor-mediated endocytosis. Then the endosomes with the pathogen are delivered to the lysosomes where their degradation occurs (Parton & Richards 2003). In addition, endocytosis is of great importance, both under normal conditions of plant life, and under stress. This is because endocytosis is involved in such important cellular processes as signal transmission and nutrient uptake (Paez Valencia *et al.* 2016). Recent evidence proves that two endocytic pathways have been identified in plants: clathrin-mediated endocytosis and membrane microdomain-associated endocytosis (microdomains-lipid rafts). Membrane microdomain or raft-linked endocytosis is involved in important processes for plants such as symbiotic infection with bacteria, internalization of sucrose transporters and proteins involved in the response to salinification, regulation of the activity of proteins that initiate cellular responses to extracellular cues (Fan *et al.* 2015).

Chloroplasts and mitochondria are semi-autonomous, two-membrane cell organoids that are involved in important cellular processes. It is known that *chloroplasts* play an important role in the life of plants. Chloroplast membranes, like other membranes, are involved in the cell's defense mechanisms in response to negative effects. This is because during stress, plants need to maintain the photosynthetic efficiency of chloroplasts for normal growth and development (Liu *et al.* 2018). In addition to chloroplasts, the cell also has a two-membrane, semi-autonomous organelle. *Mitochondria* are central to the metabolism of plant cells. They are not only a source of energy and metabolic intermediates for the cell, but they are also involved in the biosynthesis of certain coenzymes and cofactors, as well as lipids. Mitochondria can regulate their metabolism by adapting to their environment. Finally, mitochondria are involved in retrograde signaling and programmed cell death in response to external stimuli of both abiotic and biotic nature (Rao *et al.* 2017). Recently, the presence of lipid rafts in the membranes of chloroplasts and mitochondria of different types of halophytes has been proven. The study revealed a difference in the composition of raft-specific lipids in halophytes that differ in the salt accumulation strategy, which suggests that the functional role of these structures is related to the nature of salt tolerance and makes it possible to assume the participation of rafts in plant adaptation to abiotic environmental factors (Nesterov *et al.* 2017; Nesterov *et al.* 2017). Currently, it has been proven that *vacuole* perform functions that are important for plants, both under normal conditions and under stress (accumulation of nutrients, degradation of products of metabolism, detoxification of

substances harmful to the cell, etc.). Similarly, to animal cell lysosomes, plant vacuoles participate in programmed cell death (Dickman *et al.* 2017). According to recent data, rafts of the vacuolar membrane can participate in the functions performed by the vacuole (Ozolina *et al.* 2013; Yoshida *et al.* 2013). It is proved that tonoplast lipid rafts contain proteins that provide transport of metabolites through the vacuolar membrane, such as V-ATPase, ion transporters, sugar transporters, Ca-ATPase, aquaporins. In this connection, it is concluded that rafts are involved in the main function of the tonoplast - the regulation of membrane transport processes. It is known that this function can play a great role in certain types of stress. In addition, proteins involved in autophagy processes (DRP1A, 1C, 2A, and 2B) were found in rafts of the vacuolar membrane (Nestyorkina *et al.* 2016; Yoshida *et al.* 2017). Studies of the *Golgi complex* membrane have shown that it is involved in protein secretion, which is necessary for intracellular processes and cell interaction with the environment. Further work on the structure of the membrane of this organelle showed that it contains lipid rafts. The researchers concluded that a violation in the structure of lipid rafts of the Golgi complex membranes might affect the effectiveness of the secretory pathway. This conclusion was made based on experiments conducted to regulate the synthesis of raft specific lipids (Laloi *et al.*, 2007).

CONCLUSION

The plant response to stress is a complex reaction of cell membranes. In this connection, in this work, we considered the contribution of lipid rafts of various plant cell membranes in protective mechanisms. Plants cell membrane is the most studied in this line of research. It is proved that the lipid rafts of plant plasma lemma contain proteins involved in the body's response to stress. The lipid rafts of chloroplasts and mitochondria are the least studied. The contribution of these structures to plant protection from stress is determined by changes in the lipid component of rafts. In general, plant lipid rafts are involved in protective mechanisms. The role of lipid rafts is shown in interaction with microorganisms using the remorin protein; in transport processes (important for negative effects) using aquaporin proteins and proton pumps; in cold and salt stability by changing the lipid composition of rafts. Thus, the results obtained to date allow us to evaluate the participation of lipid rafts in the protective mechanisms of plant cell membranes in response to negative effects. In addition, the analysis of these results reveals directions for further research of the structure and functioning of plant cell membranes (search for lipid rafts in the nuclear membrane and the membrane of the endoplasmic reticulum, etc.). The work was carried out with partial use of funds from the grant MK-666.2020.11 on the equipment of the Shared-Use Equipment Center "Bioanalytics" of the Siberian Institute of Plant Physiology and Biochemistry SB RAS (Irkutsk).

REFERENCES

- Adejoke, HT, Louis, H, Amusan, OO & Apebende, G 2019, A review on classes, extraction, purification and pharmaceutical importance of plants alkaloid. *Journal of Medicinal and Chemical Sciences*, 2: 130-139.
- Arekhi, M, Terry, LG, John, G, F, Al-Khayat, JA, Castillo, AB, Vethamony, P & Clement, TP 2020, Field and laboratory investigation of tarbat deposits found on Ras Rakan Island and northern beaches of Qatar, *Science of The Total Environment*, 735, 139516.
- Bhatia, T, Cornelius, F & Ipsen, JH 2016, Exploring the raft-hypothesis by probing planar bilayer patches of free-standing giant vesicles at nanoscale resolution, with and without Na, K-ATPase, *Biochimica et Biophysica Acta (BBA)-Biomembranes*, 1858: 3041-3049.
- Cascianelli, G, Villani, M, Tosti, M, Marini, F, Bartocchini, E, Viola Magni, M, & Albi, E 2008, Lipid microdomains in cell nucleus. *Molecular Biology of the Cell*, 19: 5289-5295.
- Cassim, AM, Gouguet, P, Gronnier, J, Laurent, N, Germain, V, Grison, M, Boutté, Y, Gerbeau-Pissot, P, Simon-Plas, F & Mongrand, S 2019, Plant lipids: Key players of plasma membrane organization and function. *Progress in Lipid Research*, 73: 1-27.
- Dickman, M, Williams, B, Li, Y, de Figueiredo, P, & Wolpert, T 2017, Reassessing apoptosis in plants, *Nature Plants*, 3: 773-779.
- Ellinger, D, Naumann, M, Falter, C, Zwikowics, C, Jamrow, T, Manisseri, C, Somerville, SC, and Voigt, CA 2013, Elevated early callose deposition results in complete penetration resistance to powdery mildew in *Arabidopsis*, *Plant Physiology*, 161: 1433-1444.
- Fan, L, Li, R, Pan, J, Ding, Z, & Lin, J 2015, Endocytosis and its regulation in plants, *Trends in Plant Science*, 20: 388-397.

- Fan, W, Li, J, Jia, J, Wang, F, Cao, C, Hu, J, & Mu, Z 2015, Pyrabactin regulates root hydraulic properties in maize seedlings by affecting PIP aquaporins in a phosphorylation-dependent manner. *Plant Physiology and Biochemistry*, 94: 28-34.
- Filek, M, Rudolphi-Skórska, E, Sieprawska, A, Kvasnica, M & Janeczko, A 2017, Regulation of the membrane structure by brassinosteroids and progesterone in winter wheat seedlings exposed to low temperature. *Steroids*, 128: 37-45.
- Goñi, FM 2019, "Rafts": a nickname for putative transient nanodomains, *Chemistry and Physics of Lipids*. 218: 34-39,
- Grison, MS, Brocard, L, Fouillen, L, Nicolas, W, Wewer, V, Dörmann, P, Nacir, H, Benitez-Alfonso, Y, Claverol, S, Germain, V, & Boutté, Y 2015, Specific membrane lipid composition is important for plasmodesmata function in Arabidopsis. *The Plant Cell*, 27: 1228-1250,
- Haney, CH, Riely, BK, Tricoli, DM, Cook, DR, Ehrhardt, DW & Long, SR 2011, Symbiotic rhizobia bacteria trigger a change in localization and dynamics of the Medicago truncatula receptor kinase LYK3, *The Plant Cell*, 23: 2774-2787.
- Hao, H, Fan, L, Chen, T, Li, R, Li, X, He, Q, Botella, MA & Lin, J, 2014, Clathrin and membrane microdomains cooperatively regulate RbohD dynamics and activity in Arabidopsis, *The Plant Cell*, 26: 1729-1745.
- Iswanto, ABB & Kim, JY 2017, Lipid raft, regulator of plasmodesmal callose homeostasis, *Plants*, 6: 15.
- Jarsch, IK & Ott, T 2011, Perspectives on remorin proteins, membrane rafts, and their role during plant–microbe interactions, *Molecular Plant-Microbe Interactions*, 24: 7-12.
- Kleiman, BM, Koptur, S & Jayachandran, K 2021, Beneficial Interactions of Weeds and Pollinators to Improve Crop Production, *Journal of Research in Weed Science*, 4: 151-164.
- Laloi, M, Perret, AM, Chatre, L, Melsner, S, Cantrel, C, Vaultier, MN, Zachowski, A, Bathany, K, Schmitter, JM, Vallet, M, & Lessire, R 2007, Insights into the role of specific lipids in the formation and delivery of lipid microdomains to the plasma membrane of plant cells, *Plant Physiology*, 143: 461-472.
- Lefebvre, B, Furt, F, Hartmann, MA, Michaelson, LV, Carde, JP, Sargueil-Boiron, F, Rossignol, M, Napier, JA, Cullimore, J, Bessoule, JJ, & Mongrand, S 2007, Characterization of lipid rafts from Medicago truncatula root plasma membranes: a proteomic study reveals the presence of a raft-associated redox system, *Plant Physiology*, 144: 402-418,
- Lefebvre, B, Timmers, T, Mbengue, M, Moreau, S, Hervé, C, Tóth, K, Bittencourt-Silvestre, J, Klaus, D, Deslandes, L, Godiard, L, & Murray, JD 2010, A remorin protein interacts with symbiotic receptors and regulates bacterial infection, *Proceedings of the National Academy of Sciences*, 107: 2343-2348,
- Leslie, ME, Rogers, SW, and Heese, A 2016, Increased callose deposition in plants lacking Dynamin-Related Protein 2B is dependent upon Powdery Mildew Resistant 4, *Plant Signaling & Behavior*, 11: e1244594,
- Liu, X, Zhou, Y, Xiao, J, & Bao, F 2018, Effects of chilling on the structure, function and development of chloroplasts, *Frontiers in Plant Science*, 9: 1715.
- Lu, SM & Fairm, GD 2018, Mesoscale organization of domains in the plasma membrane—beyond the lipid raft. *Critical Reviews in Biochemistry and Molecular Biology*, 53:192-207,
- Melsner, S, Molino, D, Batailler, B, Peypelut, M, Laloi, M, Wattelet-Boyer, V, Bellec, Y, Faure, JD & Moreau, P 2011, Links between lipid homeostasis, organelle morphodynamics and protein trafficking in eukaryotic and plant secretory pathways, *Plant Cell Reports*, 30: 177-193,
- Momeni, AR, Samimi, HA, Vaezzadeh, H 2018, Eutectic mixture choline chloride–chloroacetic acid: a new and efficient catalyst for synthesis of 3, 4-dihydropyrimidin-2-ones. *Chemical Methodologies*, 2: 260-269,
- Morel, J, Claverol, S, Mongrand, S, Furt, F, Fromentin, J, Bessoule, JJ, Blein, JP & Simon-Plas, F 2006, Proteomics of plant detergent-resistant membranes. *Molecular & Cellular Proteomics*, 5: 1396-1411.
- Naderi, D, Jami, R & Rehman, F 2021, A Review of RNA Motifs, Identification Algorithms and their Function on Plants, *Journal of Plant Bioinformatics and Biotechnology*, 1: 28-40.
- Nesterov VN, Nesterkina IS, Nurminskij VN, Bogdanova ES, Ozolina NV, Rozencvet, OA 2017, Detection and investigation of lipid rafts in the membranes of halophyte cell organelles, *Experimental plant biology: fundamental and applied aspects: annual meeting of the RSPB, Crimea, Sudak, September 18-24*, p. 56.
- Nesterov, VN, Nestyorkina, IS, Rozencvet, OA, Ozolina, NV & Salyaev, RK 2017, Detection of lipid-protein microdomains (rafts) and study of their functional role in chloroplast membranes of halophytes, *Reports of the Academy of Sciences*, 476: 350-352.

- Nestyorkina, IS, Ozolina, NV, Baduev, BK, Fyodorova, GA, Nurminskij, VN, Spiridonova, EV & Salyaev, RK 2016, Table beet vacuolar membrane rafts contain V-H⁺ - ATP-ase, *Biologicheskie membrany*, 33: 450-453,
- Ott, T 2017, Membrane nanodomains and microdomains in plant–microbe interactions, *Current Opinion in Plant Biology*, 40: 82-88.
- Ozolina, NV, Nesterkina, IS, Kolesnikova, EV, Salyaev, R, Nurminsky, VN, Rakevich, AL, Martynovich, EF & Chernyshov, MY 2013, Tonoplast of *Beta vulgaris* L, contains detergent-resistant membrane microdomains, *Planta*, 237: 859-871.
- Paez Valencia, J, Goodman, K & Otegui, MS 2016, Endocytosis and endosomal trafficking in plants, *Annual Review of Plant Biology*, 67: 309-335.
- Parton, RG & Richards, AA 2003, Lipid rafts and caveolae as portals for endocytosis: new insights and common mechanisms, *Traffic*, 4: 724-738,
- Perraki, A, Gronnier, J, Gouguet, P, Boudsocq, M, Deroubaix, AF, Simon, V, German-Retana, S, Zipfel, C, Bayer, E, Mongrand, S & Germain, V 2018, REM1, 3's phospho-status defines its plasma membrane nanodomain organization and activity in restricting PVX cell-to-cell movement, *PLoS Pathogens*, 14: e1007378,
- Pike, LJ 2006, Rafts defined: a report on the Keystone Symposium on Lipid Rafts and Cell Function, *Journal of Lipid Research*, 47: 1597-1598,
- Pleskova, SN, Krylov, VN & Deryugina, AV 2015, Functional features of planar rafts and caveola in cellular physiology, *Advances in Modern Biology*, 135: 590-598,
- Rao, RSP, Salvato, F, Thal, B, Eubel, H, Thelen, JJ & Møller, IM 2017, The proteome of higher plant mitochondria, *Mitochondrion*, 33: 22-37.
- Rosetti, CM, Mangiarotti, A & Wilke, N 2017, Sizes of lipid domains: What do we know from artificial lipid membranes? What are the possible shared features with membrane rafts in cells?, *Biochimica et Biophysica Acta (BBA)-Biomembranes*, 1859: 789-802,
- Saadatmand, M & Abbasi, F 2021, Evaluating Factors Affecting Reproductive Success by Intrauterine Fertilization: The Cases in Qom University Jihad Center, 2018-2019, *Progress in Chemical and Biochemical Research*, 4: 148-159,
- Santos, AL & Preta, G 2018, Lipids in the cell: organisation regulates function, *Cellular and Molecular Life Sciences*, 75: 1909-1927,
- Schroeder, RJ, Ahmed, SN, Zhu, Y, London, E & Brown, DA 1998, Cholesterol and sphingolipid enhance the Triton X-100 insolubility of glycosylphosphatidylinositol-anchored proteins by promoting the formation of detergent-insoluble ordered membrane domains, *Journal of Biological Chemistry*, 273: 1150-1157.
- Simons, K & Ikonen, E 1997, Functional rafts in cell membranes, *Nature*, 387: 569-572.
- Takahashi, D, Imai, H, Kawamura, Y & Uemura, M 2016, Lipid profiles of detergent resistant fractions of the plasma membrane in oat and rye in association with cold acclimation and freezing tolerance, *Cryobiology*, 72: 123-134,
- Toledo, A, Huang, Z, Coleman, JL, London, E & Benach, JL 2018, Lipid rafts can form in the inner and outer membranes of *Borrelia burgdorferi* and have different properties and associated proteins, *Molecular Microbiology*, 108: 63-76.
- Yoshida, K, Ohnishi, M, Fukao, Y, Okazaki, Y, Fujiwara, M, Song, C, Nakanishi, Y, Saito, K, Shimmen, T, Suzuki, T & Hayashi, F 2013, Studies on vacuolar membrane microdomains isolated from Arabidopsis suspension-cultured cells: local distribution of vacuolar membrane proteins, *Plant and Cell Physiology*, 54: 1571-1584.

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