Plant lipids in space:
a survey paper of research

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Introduction

Plant oils are important for both nutrition as well as industrial purposed. One market research study valued the global oilseed market as USD 293.56 billion in 2022, forecasting a compound annual growth rate of 5.5% between 2023 to 2030 reach about USD 450.52 billion in valuation by 2030 (Databridge Market Research, 2022).

Given the valuable commercial value of oilseed market, a tremendous amount of research has been conducted over the decades to improve oil content in oilseed plants (see Sagun et al., 2023, for a current summary). For example, a study demonstrates the potentials of increasing oil content at the expense of starch production in potato via genetic engineering (Liu et al., 2017; Xu, 2019). In another study, scientists identified genetic factors in the plant *Arabidopsis thaliana,* enriching the current understanding of the negative correlation between oil and protein content in seeds (Jasinski et al, 2018).

Over the past several decades, it has become possible to grow plants in microgravity in space. It is, therefore, natural to ask: Would growth in microgravity affect the oil content in oilseed plants? If so, could these microgravity effects be applied to improve oilseed production on Earth? Unfortunately, as of today, no research studies have been conducted on investigating oil content of oilseed plants grown in space (Kordyum & Hasenstein, 2021). However, a handful of studies have shown that there was a delay in seed maturation and a change in lipid reserve metabolism in seeds grown under microgravity. The goal of this paper is to provide a summary of the results of those microgravity experiments.

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Lipids in Plants

Most plants store their oils in seeds. Plants producing seeds or fruits with high levels of oils or other commercially useful fats are called oilseed plants. Oils, proteins and carbohydrates are major energy reserves for the seed embryo in germination and post-germinative growth before photosynthesis can take place.

Major oilseed plants such as soybean, rape, and sunflower store their oils as lipids[1] in the cotyledon (part of the embryo inside the seed of a plant) as TAG (triacylglycerol) during seed development (Nguyen, 2016, Ch 3.2, p. 246; Kigel, 1995, Ch. 7, p 173). High activity level of TAG biosynthesis occurs only during a short window (usually about two weeks) (Beaudoin & Napier, 2003, p 268). In a study of Arabidopsis, a model for flowering plants, the regulator genes WRI1 that controls other genes of oil biosynthesis had the highest expression between 6 to 8 days after flowering and started to decline after 10 days of flowering. After that, the accumulation and synthesis of protein started to take place in the seed (Kanai et al., 2016, p. 1242). The timing of lipid and protein synthesis in developing seeds varies, depending on plant species.

Lipid-related studies in microgravity

The growth cycle of plants starts with seed germination, a process in which a plant grows from a seed into a seedling. Germination starts when the dry seed absorbs (imbibes) water. Then the seedling uses the oils, carbohydrates and proteins stored in the seed as food supply to support its growth.

A microgravity study showed that the lipid utilization in Arabidopsis seeds were delayed during seed germination in microgravity. In microgravity samples, there was over 15% of the lipid volume in cotyledon symplast compared to less than 7% in control samples (Briarty & Maher, 2004). The symplast of a plant is the inner part of the plasma membrane, which is essential in transporting water and solutes between cells. Their result is consistent with studies conducted in a clinostat environment. A clinostat is a rotational device that can simulate microgravity while on Earth. For example, lipid content increased in cotyledon tissue (seed leaves) in soybean seedlings exposed to 6 days of clinorotation (Brown & Piastuch, 1994). Lipid metabolic modification was also observed in a study on rapeseed seedlings on clinorotation (Aarrouf et al., 1999). In addition, lipid droplets confluenced into large aggregates were observed in the roots of *Lepidium sativum*, commonly known as garden cress (Hensel 1980).

In a microgravity study, spores of the fern Ceratopteris richardiito were exposed to microgravity aboard NASA shuttle flightSTS-93 (Salmi & Roux, 2008). One of the findings in their study, which was consistent with other studies, was that the genes involved in lipid mobilization in plants altered their expression in microgravity environment. Based on their study and other studies on microgravity effects

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[1] While there is no exact definition of lipids, a commonly used definition based on their physical properties is the following: "as oily, fatty, waxy organic compounds, which, while insoluble in water, are readily soluble in organic solvents" (Murphy, 2005, page 4).

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on Arabidopsis, the authors suggest that "*changes in the utilization of reserve lipids in microgravity occur in ferns as well as angiosperms and may, in fact, be universal to plants*." (Salmi & Roux, 2008).

Epigenetics studies in microgravity

Plants have various ways to adapt to stresses in the environment. In addition to mutations in DNA sequences, phenotypic changes in plants can also be caused by changes in gene expression without any DNA modifications. This type of changes is called epigenetic change, which can be inherited across generations (Iwasaki & Paszkowski, 2014).

Scientists have confirmed that DNA methylation, a type of epigenetic changes, was observed in *Arabidopsis thaliana* plants grown from seeds aboard the space station. A study in 2019 found that epigenetic changes in *Arabidopsis thaliana* plants in microgravity were organ-specific where higher level of methylation were observed in leaves instead of roots (Zhou et al., 2019). Another study observed that the changes in gene expression were widespread (Nakashima et al., 2023).

In a similar study conducted on Arabidopsis thaliana seedlings grown in a Chinese recoverable scientific satellite, it was shown that DNA methylation was detected in root length, flowering time and silique length phenotypes in the first generation offspring of seedlings grown in space. However, only root length phenotypic change was retained in the second generation of the offspring and no longer observed in the third generation (Xu et al., 2021).

The upcoming findings from NASA’s Plant Habitat-03A experiment will shed light on whether epigenetic changes induced by environmental stresses in microgravity environment can pass from one generation to another (NASA, 2022, Oct. 28).

While the application of epigenetics on crop breeding is still at its early stage (Tonosaki et al., 2022), the question of how heritable epigenetics changes is an important one with both space and commercial implications. Understanding how plants adapt to stress in space environment will help not only astronauts growing plants for food in space, but also farmers to grow plants to adapt to increasingly harsh environmental conditions on earth. For a review on epigenetics and crop improvement, see Varotto et al. (2020), Bilichak (2016) and Fresnedo-Ramírez (2023).

So far, studies have suggested that epigenetic changes and how heritable they are depend on specific phenotypes. If so, it would be interesting to ask the following questions: do spaceflight environments induce epigenetic changes in lipid synthesis in developing seeds, lipid metabolism in seed germination? How heritable are these the changes across generations?

If so, then it would be further interesting to ask if spaceflight environments induce epigenetics changes in lipid metabolism in plants and how heritable the changes are across generations. Hopefully, the answers to these questions will increase our understanding on how to increase lipid content to benefit mankind.

References

Aarrouf, J., Darbelley, N., Demandre, C., Razafindramboa, N. & Perbal, G. (1999). Effect of Horizontal Clinorotation on the Root System Development and on Lipid Breakdown in Rapeseed (*Brassica napus*)

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Seedlings. *Plant and Cell Physiology*, 40(4), pp. 396–405. https://doi.org/10.1093/oxfordjournals.pcp.a029555

Beaudoin, F., Napier, J.A. (2003). 8 Biosynthesis and compartmentation of triacylglycerol in higher plants. In G. Daum. (Ed.), *Lipid Metabolism and Membrane Biogenesis. Topics in Current Genetics*, Vol. 6. Springer. https://doi.org/10.1007/978-3-540-40999-1_9

Bilichak, A., & Kovalchuk, I. (2016). Transgenerational response to stress in plants and its application for breeding, *Journal of Experimental Botany*, 67(7), 2081–2092. https://doi.org/10.1093/jxb/erw066

Briarty, L.G., & Maher, E. P. (2004). Reserve Utilization in Seeds of Arabidopsis thaliana Germinating in Microgravity. *International Journal of Plant Sciences*, 165(4), 545–551. https://doi.org/10.1086/386379

Brown C. S. & Piastuch, W. C. (1994). Starch metabolism in germinating soybean cotyledons is sensitive to clinorotation and centrifugation. *Plant Cell & Environment*, 17(3), 341–344. https://doi.org/10.1111/j.1365-3040.1994.tb00301.x

Databridge Market Research. (2022, Dec). *Global Oilseeds Market—Industry Trends and Forecast to 2030*. https://www.databridgemarketresearch.com/reports/global-oilseeds-market.

Fresnedo-Ramírez, J., Anderson, E. S., D'Amico-Willman, K. M., & Gradziel, T. M. (2023). A review of plant epigenetics through the lens of almond. *The Plant Genome*, 16(4). https://doi.org/10.1002/tpg2.20367

Hensel, W. & Sievers, A. (1980). Effects of prolonged omnilateral gravistimulation on the ultrastructure of statocytes and on the graviresponse of roots. *Planta*, 150 (4), 338-346. https://doi.org/10.1007/BF00384664

Iwasaki, M. & Paszkowski J. (2014). Epigenetic memory in plants, *The EMBO Journal*, 33(18), 1987-98. https://doi.org/doi: 10.15252/embj.201488883

Jasinski, S., Chardon, F., Nesi, N., Lécureuil, A., & Guerche, P. (2018). Improving seed oil and protein content in Brassicaceae: some new genetic insights from Arabidopsis thaliana. *Oilseeds & fats Crops and Lipids,* 25(6): D603. https://doi.org/10.1051/ocl/2018047

Kanai, M., Mano, S., Hayashi, M., & Nishimura, M. (2016). Chapter 6 Designing Novel Breeding Strategies for Producing High-Oil Crops Based on a Molecular Understanding of Triacylglycerol Metabolism. In S. Araujo & A. Balestrazzi, *New Challenges in Seed Biology - Basic and Translational Research Driving Seed Technology*. IntechOpen. https://doi.org/doi: 10.5772/64465

Kigel, J. (1995). Seed Development and Germination Books in Soils, Plants, and the Environment. CRC Press.

Kordyuma, E., Hasenstein, Karl. (2021). Life Sciences in Space Research, 29, 1–7. https://doi.org/10.1016/j.lssr.2021.01.003

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Liu, Q., Guo, Q., Akbar, S., Zhi, Y., El Tahchy, A., Mitchell, M., Li, Z., Shrestha, P., Vanhercke, T., Ral, J.P., Liang, G., Wang, M.B., White, R., Larkin, P., Singh, S., & Petrie, J. (2017). Genetic enhancement of oil content in potato tuber (Solanum tuberosum L.) through an integrated metabolic engineering strategy. *Plant Biotechnolgy Journal*, 15, 56–67. https://doi.org/10.1111/pbi.12590

Miquel, M., Browse, J. (1995). Lipid Biosynthesis in Developing Seeds. In J. Kigel & G. Galili (Eds.), *Seed Development and Germination Books in Soils, Plants, and the Environment,* (pp. 169–194). Marcel Dekker, Inc.

Murphy, D. (2005). The study and utilization of plant lipids: from margarine to lipid rafts. In D. Murphy, (Eds.), *Plant Lipids: Biology, Utilisation and Manipulation* (p. 4). Blackwell Publishing.

Nakashima, J., Pattathil, S., Avci, U., Chin, S., Sparks, J. A., Hahn, M. G., Gilroy, S., & Blancaflor, E. B. (2023). Glycome profiling and immunohistochemistry uncover changes in cell walls of *Arabidopsis thaliana* roots during spaceflight. *NPJ Microgravity*. 9(1), 1–13. https://doi.org/10.1038/s41526-023-00312-0

NASA. (2022, Oct. 28*). Surviving Space: Extreme Plant Adaptation*. https://science.nasa.gov/science-research/biological-physical-sciences/surviving-space-extreme-plant-adaptation/

Nguyen, QT., Kisiala, A., Andreas, P., Neil Emery, R.J., & Narine, S. (2016). Soybean Seed Development: Fatty Acid and Phytohormone Metabolism and Their Interactions. *Current Genomics*, 17(3), 241–260. https://doi.org/10.2174/1389202917666160202220238

Sagun, J. V., Yadav, U. P., & Alonso, A. P. (2023). Progress in understanding and improving oil content and quality in seeds. *Frontier Plant Science,* 14(1116894). https://doi.org/10.3389/fpls.2023.1116894

Salmi, M. L., & Roux, S. J. (2008). Gene expression changes induced by space flight in single-cells of the fern *Ceratopteris richardii*. *Planta*, 229(1), 151–159. doi:10.1007/s00425-008-0817-y

Tonosaki, K., Fujimoto, R., Dennis, E. S., Raboy, V., & Osabe, K. (2022). Will epigenetics be a key player in crop breeding? *Frontiers in Plant Science*, 13, 2022. https://doi.org/10.3389/fpls.2022.958350

Varotto, S., Tani, E., Abraham, E., Krugman, T., Kapazoglou, A., Melzer, R., Radanović, A., & Miladinović, D. (2020). Epigenetics: possible applications in climate-smart crop breeding. *Journal of Experimental Botany*, 71(17), 5223–5236. https://doi.org/10.1093/jxb/eraa188

Xu, P., Chen, H., Hu, J., & Cai, W. (2021). Potential evidence for transgenerational epigenetic memory in *Arabidopsis thaliana* following spaceflight. *Communication Biology*, 4, 835. https://doi.org/10.1038/s42003-021-02342-4

Zhou, M., Sng, N.J., LeFrois, C. E., & Paul, A. L., & Ferl, R. J. (2019). Epigenomics in an extraterrestrial environment: Organ-specific alteration of DNA methylation and gene expression elicited by spaceflight in Arabidopsis thaliana. *BMC Genomics*. 20, 205. https://doi.org/10.1186/s12864-019-5554-z

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