



To eat or not to eat: premature sprouting (vivipary) in cereal and fruit crops

Jorge Hugo Cota-Sánchez 

Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, S7N 5E2, Canada. E-mail: hugo.cota@usask.ca

ABSTRACT. Vivipary also known as the precocious germination of seeds while still attached to the mother plant or fruit, it's a relatively common phenomenon in angiosperms. However, the proliferating seedlings though interesting to look at, deter customers from eating the fruits. Similarly, vivipary is an adverse phenomenon for the agroindustry because of the lowest quality and palatability of fruits as well as lower seed set and viability. This paper highlights the taxonomic occurrence of vivipary in cereal and crop plants and the detrimental effects of this phenomenon in agricultural crops. According to literature sources, there are 38 fruit crops in which vivipary has been reported. The families Cucurbitaceae, Poaceae, Rutaceae, and Solanaceae include the fruits with the highest incidence of vivipary in the markets.

Keywords: cereal and fruit crops; pre-harvest sprouting; premature germination; vivipary.

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Introduction

To eat or not to eat: that's the question... Just like the emulation of Hamlet's monologue, imagine that you are unpacking the fresh fruits you just bought in the street market and while cooking or peeling them you find unusual, maybe creepy looking filamentous whitish or greenish structures growing inside or around the fruit. Would you eat the fruit, or would you discard it? At first sight, such a disturbing discovery might discourage consumption of these weird fruits, but upon some scrutiny you realize that the fruits bear germinated seeds, some of which look more like seedlings. This phenomenon, it's known as precocious germination (PG) of seeds within the fruit and is called vivipary (Cota-Sánchez, 2004; 2022 and references therein). Even though traditional street markets are often the source of viviparous fruits, the goods exhibiting this condition are somewhat unpopular among people. The goal of this note is to promote the understanding of this natural phenomenon in crop plants, its economic implications, and the general ideas proposed for the occurrence of this event. Also, I present general ideas about making decisions on how to manipulate viviparous fruits.

In plants, vivipary it is a rare reproductive event implying that the typical process of germination went wrong as shown by seed germination within or outside the fruit and may make the viviparous fruits "defective." However, its bizarre occurrence may be an interesting finding for persons not familiar with the plant's physiological and germinative processes, which after all, leads to a fascinating incident that draws personal curiosity. To put in perspective vivipary in plants, it is convenient to briefly describe this reproductive mechanism in animals first, especially in placental mammals, which include humans. Etymologically, the Oxford Advanced Dictionary, indicates that the word vivipary derived from Latin (*vivus* = alive and *parus* = bearing), and according to Wagner, Kin, Muglia, and Pavličev (2014), this procreative event can be considered one of the most advanced developmental phases of intrauterine retention of the fetus. It is worth noting that vivipary is not unique to placental mammals; it also occurs in some reptiles, amphibians, insects, and fish (Blackburn, 1999).

In a viviparous organism, the embryo develops inside the maternal body or tissue which provides nourishment for the growing organism, rather than inside an egg (oviparous), which protects and nurtures the embryo outside the mother corpus. With these ideas in mind, vivipary in plants refers to the premature or pre-harvest sprouting (PHS), also known as pseudovivipary, when physiologically mature cereal grains germinate in the corn ear (Figure 1A) or panicle of the mother plant of wheat (Figure 1B) or rice (Figure 1C) and cryptovivipary when the germinated plantlets are concealed within the fruit body (Figure 2) and are

revealed once these are split open. One can see the funiculus, a small stem or thread that serves to anchor the ovule or developing seedling to the placenta of the fruit (see Figure 2A-H), which provides vascular supply. It is the equivalent of the umbilical cord in viviparous mammals, through which the developing embryo is attached to the maternal placenta to obtain nutrients.



Figure 1. Premature sprouting in the three major cereal crops. A. Corn (*Zea mays*). Photo: Jennifer Rees; B. Wheat (*Triticum aestivum*). Photo: Linda Watson; and C. Rice (*Oriza sativa*). Photo: Zu-hua He. Note the numerous germinated kernels showing the emerging greenish seedlings and whitish radicle (red arrows in 1C).

To answer the opening statement echoing Hamlet's monologue, despite the peculiar look, fruits exhibiting vivipary are safe to eat, but the decision will depend on personal gastronomic experiences and taste, and probably area of origin in the world. It can be expected that people from tropical and subtropical regions of the world would be exposed to wider fruit diversity and quite likely to frequent cases of viviparous fruits in the market. Thus, the likelihood of consuming these often so-called "spoiled" products will be higher, something that could be a strange affair for persons from northern temperate regions, where the assortment of fruits and produce available in the markets is more limited. In my experience, sprouted seeds/seedlings don't have specific flavor, other than bland, tender leafy shoots that give a reminiscence of tasting alfalfa sprouts.

But not to worry... If a consumer chooses not to discard the viviparous fruit but doesn't want to eat the sprouting seeds/seedlings, a good practice is to cut around the fruit and carefully remove the tiny plantlets from the maternal tissues and safely eat the fruit flesh. Thereafter, the seedlings could be transplanted, which could lead to an unusual but fun gardening learning experience at home while the growth of the baby viviparous seedlings is monitored. But why does this event happen, how widespread is this unusual reproductive mechanism in crop plants, and why should we be concerned about it from the agricultural perspective? These aspects are discussed next.

Incidence of vivipary in edible crop plants

Foremost, the occurrence of vivipary is associated with abnormal levels of moisture. When moisture is entrapped among the husks (in corn, for example), the damp conditions, in association with deficiency of the hormone abscisic acid (ABA) during fruit maturation, causes premature germination (Shu, Liu, Xie, & He, 2016; Wang et al., 2021) in the corn cob (Figure 1A) or inflorescences of wheat (Figure 1B), rice (Figure 1C), barley, sorghum, and other cereal crops. Similarly, vivipary in pecan increases up to 25-fold when the trees are irrigated compared to non-irrigated orchards (Wood 2015) confirming that moisture affects the regulating mechanisms for normal physiology of germination. There is, therefore, weak physiological dormancy in the seeds, which can be disrupted by adverse weather conditions during the harvesting time, such as heavy rain, that interfere with the natural hormonal levels that inhibit germination, particularly ABA. Obviously, there are genetic factors that in conjunction with hormonal levels control vivipary (both occurrence and suppression), a topic beyond the scope of this note.

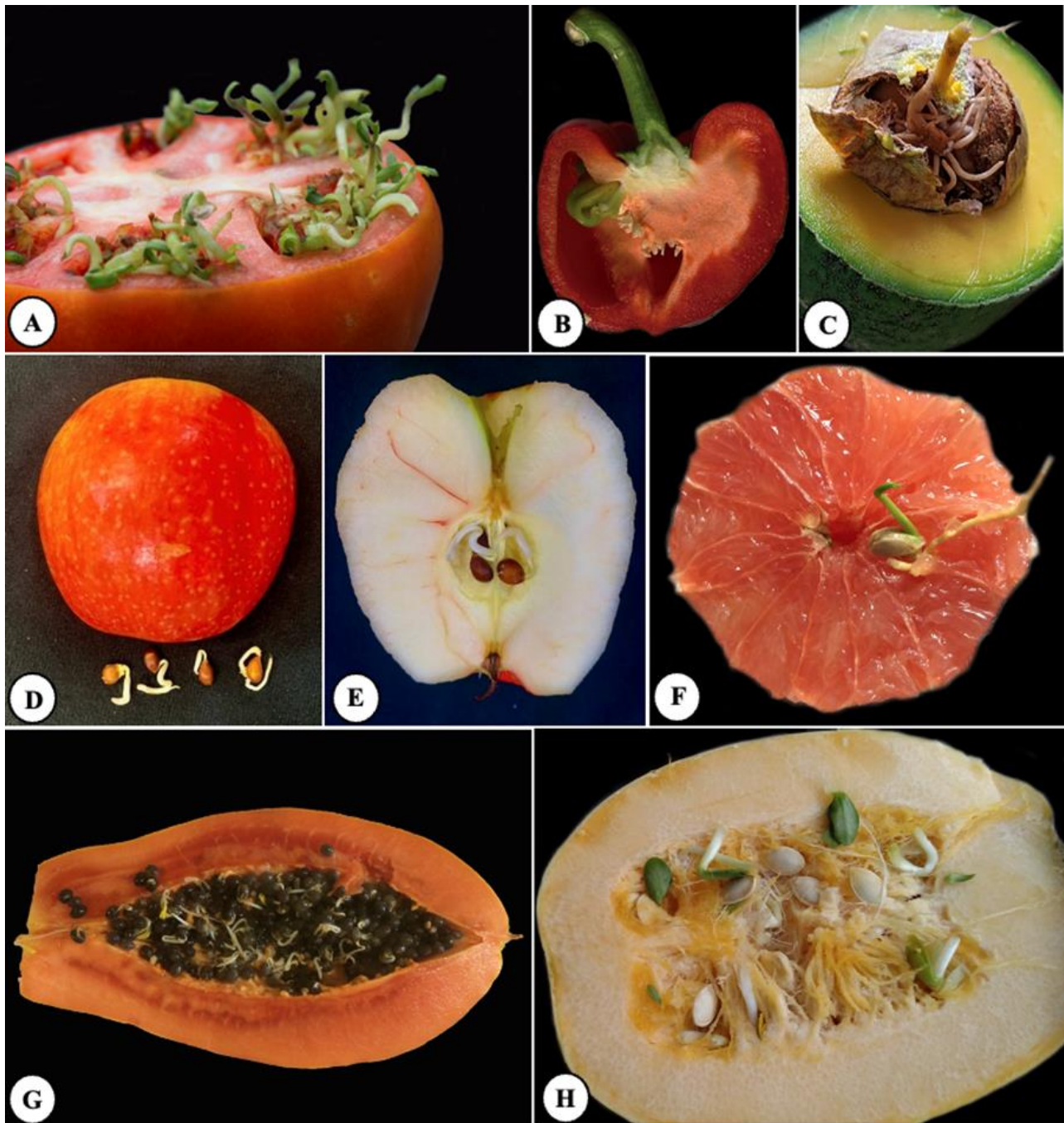


Figure 2. Representative fruit crops displaying vivipary in the form of cryptovivipary. Note the different germinative stages of viviparous seeds and seedlings inside the fruits. A: Tomato (*Solanum lycopersicum*). Photo: Kathy Clark; B: Sweet Bell Pepper (*Capsicum annuum*); C: Avocado (*Persea americana*). Photo: Diane Desenberg; D, E: Pink Lady Apple (*Malus domestica*); F: Grapefruit (*Citrus x paradisi*); G: Maradol Papaya (*Carica papaya*); and H: Spaghetti squash (*Cucurbita pepo* subsp. *pepo*). Photo: Bryan Overstreet.

To date, there are numerous cases of commercially grown crops exhibiting PHS and cryptovivipary. For instance, cereal crops, i.e., corn, wheat, rice (Figure 1A to C, respectively) in the grass family (Poaceae) exhibit the highest frequency of PHS, whereas cryptovivipary is most common in fruits such as include tomato (Figure 2A), bell pepper (Figure 2B), avocado (Figure 2C), apple (Figure 2D and E), grapefruit (Figure 2F), papaya (Figure 2G), and spaghetti squash (Figure 2H), to name a few.

Thus far, there are at least 38 crop species in which the natural occurrence of vivipary, both cryptovivipary and PHS, has been reported in the literature (Table 1). The plant families with higher frequency of cryptoviviparous crop species are the Cucurbitaceae, Cactaceae, Rutaceae, and Solanaceae. In addition to the crops listed in Table 1, several examples e.g., tangerine, pomegranate, and others, exist in the World Wide Web, e.g., <https://bitlybr.com/Ukj>, but no formal description is provided, hence, these cases were excluded from the table in this paper.

Overall, the incidence of vivipary is widespread in crops, including quite a few of the most useful domesticated species, e.g., maize, wheat, rice, tomato, orange, common beans (Table 1). Similarly, vivipary is equally quite pervasive in wild plant species. It occurs in numerous lineages, from ferns to gymnosperms to angiosperms (Cota-Sánchez, 2022). And its wide geographic range encompasses lineages with diverse life forms implying that this attribute has no habitat or ecological preferences in nature. Thus, its commonness in crop plants is not surprising.

Table 1. Taxonomic inventory by family of commercial cereal and fruit crops reported in literature as viviparous. The list focuses on major economic edible crops and excludes experimental papers involving induced vivipary.

Family	Common Name	Scientific Name	Reference
Anacardiaceae	Mango	<i>Mangifera indica</i> L.	Singh and Chauhan (2013)
Brassicaceae	Ethiopian mustard	<i>Brassica carinata</i> A. Braun	Sarla (1990)
Brassicaceae	Rape seed	<i>B. napus</i> L.	Ruan, Duan, and Hu (2000)
Caricaceae	Papaya	<i>Carica papaya</i> L.	Chakraborty and Chaudhuri (2008)
Cactaceae	Dragon fruit	<i>Selenicereus</i> spp.	Cota-Sánchez (2022)
Cactaceae	Garambullo	<i>Myrtillocactus geometrizans</i> (Mart.) Console	Cota-Sánchez (2022)
Cactaceae	Pitaya	<i>Stenocereus</i> spp.	Cota-Sánchez (2022)
Cucurbitaceae	Bottle gourd	<i>Lagenaria siceraria</i> (Molina) Stand.	Aya et al. (2019)
Cucurbitaceae	Chayote	<i>Sechium edule</i> (Jacq.) Sw.	Aung, Ball, and Kushad (1990)
Cucurbitaceae	Pickling melon	<i>Cucumis melo</i> L.	Rajendra (2017)
Cucurbitaceae	Spaghetti squash	<i>Cucurbita pepo</i> L.	This paper
Cucurbitaceae	Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum & Nakai	Singh and Sharma (1972)
Fabaceae	Common bean	<i>Phaseolus vulgaris</i> L.	Pryke (1978)
Fabaceae	Mung bean	<i>Vigna radiata</i> (L.) R. Wilczek	Thakur, Khethagoudar, and Nawalagatti (2022)
Juglandaceae	Pecan	<i>Carya illinoensis</i> (Wangenh.) K. Koch	Díaz (2013)
Lauraceae	Avocado	<i>Persea americana</i> Mill.	This paper
Malvaceae	Cacao	<i>Theobroma cacao</i> L.	Pence (1991)
Moraceae	Mulberry	<i>Morus nigra</i> L.	Mukherjee (1960)
Moraceae	Mysore jackfruit	<i>Artocarpus heterophyllus</i> Lam.	Habib (1973)
Palmae	Coconut	<i>Cocos nucifera</i> L.	Leka, Oma, and Nikkore (2013)
Pedaliaceae	Sesame	<i>Sesamum indicum</i> L.	Prasad and Gangopadhyay (2013)
Poaceae	Avena	<i>Avena fatua</i> L.	Hsiao and McIntyre (1988)
Poaceae	Barley	<i>Hordeum vulgare</i> L.	Pope (1949)
Poaceae	Corn	<i>Zea mays</i> L.	Neill, Horgan, and Rees (1987)
Poaceae	Rice	<i>Oryza sativa</i> L.	Fujita, Inokawa, and Ishii (1993)
Poaceae	Sorghum	<i>Sorghum bicolor</i> (L.) Moench	Ayyangar and Rao (1935)
Poaceae	Sugar cane	<i>Saccharum spontaneum</i> L.	Ragavan (1960)
Poaceae	Wheat	<i>Triticum aestivum</i> L.	Harada (1994)
Polygonaceae	Buckwheat	<i>Fagopyrum esculentum</i> Moench	Pirzadah, Malik, Tahir, and Rehman (2016)
Rosaceae	Apple	<i>Pyrus malus</i> L. = <i>M. domestica</i> Borkh.	Mani (1947)
Rosaceae	Bengal quince	<i>Aegle marmelos</i> (L.) Corrêa	Singh, Singh, Saroj (2018)
Rutaceae	Grapefruit	<i>Citrus x paradisi</i> Macfad.	Cota-Sánchez (2018)
Rutaceae	Lemon	<i>Citrus x limon</i> (L.) Osbeck	Jitendra and Chauhan (2011)
Rutaceae	Orange	<i>Citrus x sinensis</i> (L.) Osbeck	Jitendra and Chauhan (2011)
Sapindaceae	Litchie	<i>Litchi chinensis</i> Sonn.	Lal et al. (2021)
Solanaceae	Chili pepper	<i>Capsicum annuum</i> L.	Mohideem, Mussain, and Subbiah (1973)
Solanaceae	Eggplant	<i>Solanum melongena</i> L.	Singh and Khanna (1979)
Solanaceae	Tomato	<i>S. lycopersicum</i> L.	Cota-Sánchez (2018)

Agricultural and economic implications of vivipary in crop plants

Numerous fruits, especially staple foods represented by major cereal grains, have a significant role in human nutrition in numerous cultures globally. Some others, like those fruits in the cactus family, are of particular ethnobotanical importance and symbolism for some cultures (Cota-Sánchez, 2016), like Mesoamerica, for instance. In addition to being considered regionally emblematic, they are source of energy, minerals, vitamins, phytochemicals, and dietary fiber for consumers. However, the loss of seed dormancy leads to precocious germination, short shelf life, poor quality of viviparous crops/fruits, and ultimately economic losses for the agricultural industry.

The indicators of fruit quality include size, colour, shape, firmness, ease of peeling, seedless, fragrance, flavour, and nutritional properties, among others. These attributes in edible fruit crops are essential for superior market value. Similarly, vivipary alters the nutritional value of crops, and most importantly, it causes

reduced palatability and marketability (Cota-Sánchez, 2022); consequently, viviparous fruits are often removed from the harvest or the market shelves when this phenomenon is detected. Therefore, whether in the form of PHS or cryptovivipary, vivipary is an undesirable trait with adverse agronomical and financial consequences because it affects food production and might imperil food security, especially in geographic areas where crop and fruit diversity are limited.

Vivipary has also agronomic repercussions, such as lower crop yields and reduced number of normal, viable seeds for future crop seeding, trade market, or seedbanks. It can also negatively influence yield through its action on plant growth, development, and seedling establishment as shown in precociously germinated seedlings of tomato (Cota-Sánchez, 2018) and cacti (Cota-Sánchez and Abreu, 2007; García-Beltrán, Barrios, González-Torres, Cuza, & Toledo, 2021) experiencing high mortality rates after they are removed from the mother plant and transplanted in soil.

Because the high incidence of vivipary in crop species could potentially decimate fruit and seed production, several studies have investigated the prevention of precocious germination to circumvent its adverse effects as well as to find potential solutions to inhibit it in crop plants. For example, in pecan orchards and other fruit trees, the incidence of vivipary varies with crop load, irrigation, soil depth, tree crowding, and length of the growing season (Taylor, Kunene, & Pandor, 2020), but this event can be preventive with approaches involving appropriate irrigation and nitrogen fertilization (Wood, 2015) because it is an adaptive reproductive facultative response to excessive humidity (Chauhan, Bahuguna, Nautiyal, & Cota-Sánchez, 2018). Additionally, the occurrence of vivipary in cereal crops and other commercial fruit crops and the inherent desiccation intolerance nature of these seeds challenges traditional methods of *ex-situ* and *in-situ* conservation (Tweddle, Dickie, Baskin, & Baskin, 2003; Cota-Sánchez, 2018) and therefore tend to be absent from permanent seedbank collections (Rodríguez, Toorop, & Benech-Arnold, 2011).

Conclusion

Vivipary affects crop yield, fruit, and seed quality. It is, therefore, an undesirable attribute in crop plants because of the adverse effect on agronomic practices and problematic inclusion in seedbank repositories. Consequently, an improved research program dealing with germination behavior is essential for the prevention of this event to avert agro-economic losses. It will also facilitate the short or non-storability condition of viviparous seeds in permanent germplasm collections that can be used in *ex-situ* and/or *in-situ* restoration endeavors provided that precocious germination can be prevented to secure the survival of the next generation of crops.

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