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Review

Apple pollination: A review

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ABSTRACT

Pollination is a key event for fruit set. Worldwide, there has been an increasing interest in apple pollination. Apple pollen grains are elliptical and tricolpate. Pollen germination is highly dependent on temperature. Most apple pollination occurs through cross-pollination; however, some cultivars have been reported to self-pollinate. Most apple cultivars have a gametophytic self incompatibility (GSI) system; however, others are semi compatible, or fully self compatible. The most common insect pollinator of apple is the honey bee. Other effective pollinator species include Hymenopterans, Dipterans and Coleopterans. Wind seems not to be an effective mechanism for pollination. Environmental conditions such as temperature, rain and high wind speed negatively affect pollination. This article reviews recent developments in our knowledge of apple pollination focusing on recently developed cultivars growing in the tropics.

Contents

1. Introduction

The apple is the most ubiquitous of temperate fruits and has been cultivated in Europe and Asia from antiquity (Janick et al., 1996; Adachi et al., 2009). Orchards are now found from Siberia and northern China, where winter temperatures fall to −40 °C, to high elevations in Colombia and Indonesia straddling the equator, where two crops can be produced in a single year (Janick, 1974). The center of origin of apples is Asia (Forsline et al., 2003), particularly the Republic of Kazakhstan (Dzhangaliev, 2010). Most wild apple species are found in the mountains of central and inner Asia, western and southwestern China, the Far East, and Siberia (Ignatov and Bodishevskaya, 2011). Apple cultivation dates back to a few centuries B.C. to the Greeks and Romans. Greeks and Romans were growing apples at least 2500 years ago (Hancock et al., 2008). The Romans spread the apple across Europe during their invasions (Hancock et al., 2008). Its introduction to the Americas by European colonists began in the 16th and 17th centuries. Nowadays, apples are commercially produced in numerous countries and have great

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economic importance. The accepted scientific name for apple is *Malus* × *domestica* Borkh. It is also named *Malus domestica* Borkh. The cultivated apple is likely the result of interspecific hybridization (Forsline et al., 2003). Its primary wild ancestor is *Malus sieversii* found from the Heavenly Mountains (Tien Shan) on the border between western China and the former Soviet Union to the edge of the Caspian sea (Forsline and Aldwinckle, 2004; Hancock et al., 2008). The number of species in the genus *Malus* is uncertain and still controversial (Pereira-Lorenzo et al., 2009). Harris et al. (2002) reported 55 species, Zhou (1999) reported 30–35 species, Robinson et al. (2001) 25–47 species, Janick et al. (1996) reported 37 and Forsline et al. (2003) reported 27 primary apple species. Apples have been introduced into temperate, subtropical and tropical environments worldwide. There are over 6000 regionally important cultivars and land races across the world, but a few major cultivars dominate worldwide.

Pollination is a key event in plant reproduction, stimulating ovary growth and development. Pollination is the mechanical transfer of pollen from anthers to stigmas within a plant species and is a prerequisite to the fertilization of the ovules to initiate development of seeds and fruit. Successful pollination is an important event for apple diversification among different countries for it is critical for dependable fruit production. The current article discusses apple pollination in a wide range of environments. It reviews available information on pollen morphology, germination, tube growth, compatibility related features, cross-pollination, self-pollination and insect pollination in tropical, subtropical and temperate climates.

2. Pollen morphology

Anthesis is the opening of flowers coupled with anther dehiscence and pollen grain release (Jackson, 2003). Pollen grains are dormant, resistant structures containing lipid reserves for germination and early growth but are quickly dehydrated after anther dehiscence and must absorb water to germinate when deposited on stigmas (Jackson, 2003). When dry, they are ellipsoidal and tricolpate (Fig. 1) with three germinal furrows extending almost the full length of the grain (Adams, 1916; Currie et al., 1997). They swell when wet and become more globular in shape (Adams, 1916). The exine, or outer, layer of the typical pollen grain has a striated pattern and sometimes bears small pores on its surface. Estimated average pollen length is about 40 μm and width about 20 μm (Currie et al., 1997). It is heavy and not readily carried by wind (Dennis, 2003). The quantity of pollen produced by a cultivar depends on its flower production and the yield of pollen per flower (Jackson, 2003).

3. Pollen germination, fertilization and physiology

Pollen germination is the first of a series of steps leading to subsequent ovule fertilization, fruit development and growth. It occurs soon after a pollen grain contacts the floral stigmatic surface (Fig. 2). The stigma has a wet surface composed of extracellular secretions from its papilla cells, which collapse after anthesis (Sedgley, 1990). The hydrated pollen grain germinates in the secretion pool on the stigmatic surface, and the emergent pollen tube begins to grow through the interstitial material of the transmitting tract (Jackson, 2003). 'Recognition' of incompatibility takes place here to select the most compatible pollen grain (Fig. 2) (Stösser et al., 1996; Jackson, 2003). Pollen germination on apple stigmas is mediated by a series of complex processes that involve proteins and other molecules. RNA, protein and polyamine concentrations within a pollen grain remain relatively unchanged before germination. After germination, they begin to decrease (Bagni et al., 1981). Mature pollen grains contain two generative nuclei and the tube cell nucleus. Once compatible pollen grains are deposited on stigmas, germination proceeds with pollen tube elongation, each carrying a tube nucleus and two generative nuclei down each style into the ovaries (Dennis, 2003). Pollen tube growth is mediated by proteins, but many details remain to be fully elucidated. Some of these proteins interact with stylar glycoproteins to anchor the pollen tube to the pollen/stylar extracellular matrix (Di Sandro et al., 2010). An extracellular form of the calcium-dependent protein-crosslinking enzyme TGase (transglutaminase) is involved in the apical growth of *Malus domestica* pollen tube (Di Sandro et al., 2010). This protein possibly interacts with the pollen tube and style during fertilization (Di Sandro et al., 2010); yet, further research is required to fully elucidate the mechanisms of various proteins involved in pollen tube growth. Another group of molecules, polyamines, which are organic compounds having two or more amino or nitrogen containing groups are also necessary during pollen tube growth (Speranza and Calzoni, 1980; Bagni et al., 1981). Their role may be related to the structure and assembly of vegetative cell walls (Berta et al., 1997; Lenucci et al., 2005); however, the precise role of polyamines secreted from the germinating pollen tube and their interaction with the pollen/stylar extracellular matrix is also not completely understood (Di Sandro et al., 2010). After continuous tube cell elongation, they enter the micropyles (a small opening on the surface of each ovule) and penetrate where they rupture, releasing the two generative nuclei in each. One nucleus unites with the egg cell in each ovule to produce the diploid zygote and the other unites with the two polar nuclei in the embryo sac, producing a triploid nucleus. The resulting zygote passes through successive cell divisions that occur rapidly to produce the embryo. The triploid nuclei divide to form a nuclear-free, liquid endosperm (Dennis, 2003; Jackson, 2003).

The rate of pollen germination is affected by temperature and varies with the source of pollen (Jackson, 2003). Percent germination of 'Manchurian' crabapple pollen and 'Golden Delicious' apples on the stigmatic surface of 'Golden Delicious' pistils increased with increasing temperature from 13 to 29 °C in the first 24 and 48 h after pollination, respectively (Yoder et al., 2009). Pollen germination is directly correlated with physiological temperatures in the 24 h following its deposition on stigmas (Williams and Maier, 1977), but higher temperatures are detrimental. Dry 'Golden Delicious' apple pollen subjected to a range of temperatures (40, 50, 60, 70, 80 or 90 °C) at different time intervals (0, 1/6, 1/3, 2/3, 1, 2, 4, 8, 26, 24, or 48 h) displayed the lowest germination rates (18.7%) after 1/3 h at the highest temperature, 90 °C (Marcucci et al., 1982). Pollen grains exposed to 50, 60, 70 and 80 °C for 1 h resulted in 68.7; 70.3; 55. 4 and 47.9% germination, respectively and were reduced to 57.6; 11.5; and 0% (for both 70 °C and 80 °C) after 16 h. In cross pollination of 'M.9' with 'Marubakaido' in Brazil, pollen germination began on the stigma 12 h after pollination, and 83% germination of deposited pollen was observed after 24 h at 25 °C (Dantas et al., 2002). Pollen tube growth rate also increases linearly with increasing temperatures from 0 to 40 °C (Jefferies and Brain, 1984). The time necessary for pollen to reach the ovary is a measure of the effectiveness of pollination. Pollen tube growth typically takes two days (48 h) to reach the ovary under typical temperature conditions (Namikawa, 1923; Yoder et al., 2009). de Albuquerque et al. (2010a) evaluated pollen tube growth in 34 crosses between Brazilian apple cultivars. Tube growth was observed 120 h after pollen deposition on the stigma; however, these authors failed to provide information about the temperature at which tube growth occurred; Moreover, 50–100% of the pollen tubes reached the ovaries (in most of the studied cultivars), but low compatibility was found between 'Imperatriz' × 'Daiane' (16%). Pollen germination ranged from 59 to 73% in cultivars such as Princesa, Condessa, Eva, Baronesa, Fred Hough, Imperatriz, Daiane, Duquesa, Gala and Suprema (de Albuquerque et al., 2010a). The effective pollination period (EPP) is determined by the longevity of the egg apparatus