Factors influencing pollination and thus flower and fruit/nut drop in Pecan

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Introduction

Pollination of the pistillate flower is the first activity that is required for fruit set. However, this is also influenced by various factors before pollination i.e. development of the staminate and pistillate flowers, conditions conducive to pollen shedding, as well as especially weather conditions. An extensive review of all factors influencing this process is available from SAPPA (Lötze, 2022). In this paper, the aim was to summarise the main factors influencing pollination under commercial conditions.

Pollination process

Initially, pecan cultivars were categorized into a simple two-class classification (prodandrous or protogynous). However, this is not accurate in older pecan orchards (> 30 years) (Worley et al., 1992) and we need an alternative system to correctly classify mature orchards to allow correct selection of suitable combinations for cross-pollination for the long term.

Pollination

Several factors influence pollination of pecan trees including tree age, tree height, the duration of pollination and the receptivity window, flower position and bud break (Adriance, 1931; Conner, 2007; Wood, 2000; Woodroof, 1930). Younger trees flower at different times than older trees and this may affect pollination success as orchards mature. The pollination window shortens with tree age (from 2 – 18, to 2 – 12 days) and flowers inside and at the bottom of the canopy mature sooner than in the other positions. In addition, winter chilling and the following spring temperatures will influence bud break and thus pollination.

Pollination is also dependent on the duration of the receptivity of the stigma. Under normal circumstances, the receptivity period of a single stigma is approximately five days (Woodroof, 1930). Although the receptivity period of flowers within a single inflorescence is approximately two days (Smith and Romberg, 1941), within a single tree, four to 10 days may be required for all flowers to become receptive (Wood, 1997). Furthermore, the period of receptivity is highly responsive to changes in weather conditions and variation in development of the bearing shoots (Smith and Romberg, 1940).

Flowers should receive enough pollen to produce a satisfactory crop under normal climatic conditions (Smith and Romberg, 1940) as approximately 2.5 mil. pollen grains are produced per catkin (Madden et al., 1969).

Peak pollen release periods vary within a tree, between staminate inflorescences, between trees of the same cultivar and between cultivars (Wetzstein and Sparks, 1986; Yates and Sparks, 1992). This result in erratic pollen dispersal under field conditions, even when environmental conditions like RH and temperature, are similar.

The pollen that arrives at the stigma is dehydrated and needs to be rehydrated before the pollen tube can start to grow. Pollen tube growth can be identified on the stigma after approximately 8 to 12 h (Wetzstein and Sparks, 1989). This process is weather dependent. After 2h of rehydration, maximum tube formation occurred at 15 °C, whilst maximum tube length occurred at 29 °C.

Pollen germination can be inhibited by certain pesticides, when applied during pollination, which restricts pollen hydration and tube elongation and will ultimately impact on fruit set (Wetzstein, 1990).

Fertilization

Successful fertilization is symbolised by the formation of an embryo. It may take between six to eight weeks from bud swell until fertilization is complete. In fertilization of pecan, the time of pollination and development of the ovary vary substantially between cultivars and seasons. Nevertheless, within 12 h after pollination, germination and pollen tube growth towards the ovarian cavity occurs. Approximately 22 h after pollination, pollen tubes can be observed below the bracts. Fertilization of the egg occurred 10 to 15 days after pollination in 'Stuart', but can occur between four days and seven weeks, depending on circumstances (Wolstenholme and Storey, 1970).

A significant amount of nut drop or abortion is associated with the time of fertilization. This can be due to a lack of fertilization (Adriance, 1931; Smith and Romberg, 1940; Wolstenholme and Storey, 1970), or incomplete fertilization, presented as the premature abortion of fruit or the production of nuts where the kernel is absent (Wood, 2017).

Cross-pollination

The timing of critical phenological stages like flower maturity may differ between seasons and result in failure of cross-pollination in otherwise complementary cultivars (Rohla et al., 2007). Cross-pollination (dichogamy) is often complete in colder climates and incomplete in warmer climates (Sparks, 2005), that may result in fruit drop.

Cultivar choice also affects alternate bearing, with early fruit-ripening cultivars having a lower alternate bearing habit than late-ripening cultivars. Ajamgard (2017) showed that the number of nuts per cluster was significantly reduced by self-pollination of different cultivars. It is therefore recommended to follow this strategy to avoid pollination issues: i) select cultivars based on performance within the region and ii), to plant two or more complimentary cultivars based on the pistillate flower receptivity period of the main cultivar and iii) also observe the shift in phenological phases associated with maturing orchards.

Hand pollination

Pollen can be stored for hand/artificial pollination, but it is important to follow the correct protocol to ensure satisfactory fertilization. This protocol is discussed in detail in a report that is available from SAPPA (Lötze and Lötze, 2022). In addition to the protocol conditions, pollen viability is severely compromised if it is collected during severe drought conditions.

Fruit drop

Stage-I fruit drop (Woodroof and Woodroof ,1926), is the abscission of pistillate flowers from a terminal spike on a shoot during full bloom due to weak and underdeveloped growth of the flower, therefore the term “bloom drop” is frequently used. The number of pistillate flowers on a spike is correlated positively with shoot vigour (Isbell, 1928; Finch and Crane, 1931; Sparks, 1988; Sparks and Heath, 1972; Sparks and Madden, 1985) and shoot vigour is inversely related to pistillate abortion (Sparks, 1988; Sparks and Heath, 1972; Sparks and Madden, 1985). Abortions are also more common on the distal than proximal section of the spike (Yates and Sparks, 1994).

The Stage-II fruit drop period, 14 days after pollination, can continue up until 45 days after pistillate flowers lose their receptivity to pollen (Smith and Romberg, 1941). This fruit drop period is most likely due to a lack of fertilization of the female gamete and not insufficient pollen availability.

Stages- III and IV drop involve endosperm and embryo drop, respectively. Thus, incomplete fertilization in Stage-III fruit drop occurs approximately 54 to 90 days after pollination and is mainly associated with the inability of the zygote to divide, leading to the abortion of the embryo, whereas Stage-IV is associated with abortion of the embryo.

Pollen distribution

Mechanism

The dispersal of pollen within a tree occurs from the base towards the top of the tree (Smith and Romberg, 1940). Furthermore, within a single shoot, the pollen is released from the base of the shoot towards the tip (Wood, 2000). This complicates determination of time of pollination in a commercial orchard.

Protandry vs protogyny

Adriance (1931) observed a seasonal effect on the maturation of reproductive organs in cultivars Delmas, Shley, Stuart and Burket that responded to seasonal changes and displayed either protandry or protogyny, in contrast with Texas Prolific, San Saba, Moore and Alley, which were always protandrous, irrespective of the climate. In cooler seasons, with more rainfall during bloom, protogyny was more prominent than in hot and dry seasons. Thus, contradicting the formal classification of cultivars in only one of the classes and this will have an important effect on successful pollination in mature orchards.

Distance

Pollen is usually disseminated within 100 – 150 m from the parent plant and Wood (1997) confirmed that fruit set in ‘Desirable’ decreased sigmoidally as the distance from the ‘Stuart’ polliniser increased. Therefore, insufficient pollination can occur in standard block-type orchards where the cross-pollinator might be planted too far from the main cultivar (Wood, 1997). This may be aggravated further by unfavourable weather conditions during pollination. In addition, pollen is usually shed when the trees have leaved out, thus leaf area also reduces the potential distribution of pollen to and within a tree (containment effect), or to adjacent trees. This will reduce the distance of pollen distribution considerably compared to the open areas, where this could potentially happen over hundreds of meters.

Viability

Viability of pollen is influenced by the condition of its origin or mother plant (nutrient and carbohydrate status), health status (pest and diseases), canopy density, as well as weather conditions during dehiscence. The ideal relative humidity (RH) and temperature range for pollen dispersal is between 40% and 70% and 21°C and 31°C, respectively. RH higher than 85% will inhibit pollen release, because the anthers do not dehisce.

Flowers

Floral induction is a function of a chemical and/or hormonal signal to the bud and is influenced by the current crop, in contrast with flower development that is primarily influenced by the reserve status during spring (Sparks, 2000a; 2003). A vegetative shoot will produce more pistillate flowers than a fruiting shoot during the following spring, irrespective of the carbohydrate reserve status, which may be similar for both shoots, indicating the role of a hormonal signal (Amling and Amling, 1983). This was true for adjacent shoots on a single branch, as well as shoots on the same tree. After induction, root carbohydrates are primarily responsible for flower development (Lockwood and Sparks, 1978), with the amount regulating the degree of return bloom (Worley, 1979; Wood, 1989, 1995).

Temperature and rainfall are the critical factors determining the difference in maturity of the flowers, whereas wind and RH influence pollen shedding and the duration of sigma receptivity.

The maturity dates of staminate and pistillate flowers are influenced by weather conditions in spring. Staminate flowers are more responsive that the pistillate flowers, which indicate a seasonal preference for protandry. In a cold or dry season (winter), opening of the staminate flowers may be retarded sufficiently to allow complete differentiation of the pistillate flowers.

Staminate (male) flower

Staminate flowers are dependent on reserves for two seasons, compared to the one season in the case of pistillate flowers, which develop on the current growth (Lockwood and Sparks, 1978). The amount of pollen recovered per catkin is primarily dependent on the maturity of the catkin and not the reserve status of the flower (Yates et al., 1991).

Pistillate (female) flower

Buds rendered sub-terminal after dormant pruning almost always produce pistillate flowers and, true terminal buds, are usually vegetative (Shuhart, 1927). The number of flowers on a spike can increase substantially when adverse climatic conditions, such as prolonged drought, occurs (Wood, 2000). Because the number of pistillate flowers in an inflorescence is correlated to shoot vigour (Sparks and Madden, 1985), an increase in pistillate flower production and decrease in abortion is usually associated with increasing shoot vigour (Sparks, 1988).

When assimilate reserves are low, pistillate flower development may be reduced or prevented due to the terminal position of the inflorescence on a shoot. Nutrients are limited for flower development under these conditions and this is more prominent in an ‘off’ year, when low-vigour shoots are associated with high abortion and low assimilate reserves (Lockwood and Sparks, 1978; Sparks, 1983). Insufficient access to carbohydrates and/or minerals is the main cause of this fruit drop period (Yates and Sparks, 1994).

Pistillate flowers have the ability to differentiate from basal lateral buds when terminal and upper lateral buds are damaged by frost or insects (Woodroof and Woodroof, 1926; Shuhart, 1927). This will ensure some pollination in spite of extensive damage to buds in these positions. The pistillate flowers mature from the base of the inflorescence towards the tip and, within a single inflorescence, different stages of differentiation can be observed. The ripening and development sequence of pistillate flowers in a cluster was contested in literature. However, most terminal flowers generally do not reach maturity and will drop (Woodroof and Woodroof, 1926).

Vegetative growth

Younger trees, with higher vegetative growth, have an earlier and longer flower maturity window than older trees of the same cultivar. Shoots on slow-growing trees have a more uniform flower development and growth initiation compared to faster growing trees and, therefore, the total length of the receptive period of stigmas and development of staminate flowers, will vary. Furthermore, canopy density can increase with certain management practices like continuous hedging, which stimulates high amounts of regrowth and potential excessive interior shading, often resulting in reduced yields (Sparks, 2000b).

Defoliation of trees before early September (NH) prevented pistillate flower differentiation the following spring, resulting in a reduced (20 – 50%) number of catkins, reduced pistillate bloom and fruit set (Sparks, 2000a). Fortunately, this is not a familiar natural phenomenon.

The potential productivity of a shoot was quantified by measuring shoot diameter between the fourth and fifth nodes from the terminal by Taylor (1966). Although the ideal diameter varied between cultivars, the highest productivity was recorded for diameters between 3.4 and 8.3 mm.

Limited shoot growth in ‘Desirable’ and ‘Wichita’ (USA) resulted in the formation of incomplete developed flowers (Yates and Sparks, 1994). Thompson et al. (2019) reported an increase in the number of flowers per shoot increasing (125.3 %) after treatment with GA_3, which further illustrated the important contribution of shoot length towards yield.

Reproductive (harvest)

The maximum number of pistillate flowers are determined by the previous season’s growing conditions, not only the tree health and growth, but also the environmental factors influencing the tree’s productivity (Sparks, 1996). With excessive fruiting, pistillate development can be totally inhibited, or suppressed in the following season, resulting in an ‘off’ year, with weak and absent flowers. However, alternate bearing is influenced by environmental conditions and crop load (Sparks, 1996; 1997). In addition, sequential seasons of over cropping may inhibit the initiation of pistillate flowers in varying degrees (Sparks, 1983). Hand thinning of high crop loads in August (SH) resulted in a high return bloom the following season, similar to what is experienced in other deciduous crops. This is at present not a common practice in commercial pecan production.

Climate

Tree age/size and climatic conditions have a significant impact on the flower maturity during the pollination period (Wood, 1997). An increase in spring temperatures shortens the flowering period by advancing the flower maturity of both staminate and pistillate flowers, by two to five days. The same increase in temperature also leads to a shorter pollen dispersal period and a shorter period of receptivity of the pistillate flowers.

Adriance (1931) also reported that the variation between varieties with respect to heat units (HU) until maturity of the staminate flowers was much higher (less difference in blossom date; longer developmental phase) than for the maturity of pistillate flowers, and was not affected by tree age.

The effect of late-spring frost on shoot growth, flowering and fruit retention contributes towards fruit drop (Wells, 2008). The flower drop recorded on frost damaged trees was most likely due to weak flowers. The effect of frost is also cultivar specific, as frost-damaged ‘Desirable’ trees exhibit reduced shoot length and a decrease in fruit retention even though a number of pistillate flowers were produced from secondary buds. In comparison, damaged ‘Kiowa’ trees produce longer shoots, but failed to produce any pistillate flowers on secondary buds.

Delayed bud break that is associated with insufficient winter chilling leads to protracted pollination. The date of budburst is also important and depends on the growing degree hours (GDH) as well as the chilling requirement (Kudan et al., 2013). Sparks (1993) reported that unusually low temperatures approximately three weeks before bud break caused abnormal flowering in 'Desirable'. Induction of abnormal flowering was the result of critical low temperatures (-1.7 to -2.2°C) during a critical stage of development (8 – 10 d before 50 % bud break) in the pistillate bud development, during early spring. Freeze damage at this stage resulted in malformed pistillate flowers that aborted later.

Depending on weather conditions, pollen dispersal can take three to more than 10 days. A decrease in RH and increase in temperature resulted in an increase in pollen dispersal in the field. However, weather conditions that favour pollen dispersal i.e., dry, and hot air, will unfortunately also lead to a shortened receptivity of the pistillate flowers (Wood, 2000).

Wind and high temperatures (low RH) will advance flowering, but catkins are prone to stop growth and dry out without releasing pollen under these conditions in Israel (Anonymous).

Temperature not only alters the date of pollen shedding, but also disrupts the timing of flower maturity between the male and female flowers (Wood, 1997). Flowering in pecans is primarily controlled by temperature, with higher temperatures resulting in earlier flowering (Han, 2018). Smith and Romberg (1940) observed a lack of dehiscence of anthers during rain or foggy conditions. Rain can also wash away the pollen from female flowers, or rain occurring during the flowering period will results in pollen germinating before it reaches the stigma in Israel (Anonymous). Moist and cool conditions lead to protracted and delayed dispersal of pollen, with wet conditions and lowered humidity leading to an immense release of pollen thereafter (Wood, 2000). Pollen release during mid-morning following a decrease in RH ensures suitable temperatures for pollen hydration, termination and tube elongation and penetration of the stigma (Yates and Sparks, 1993). The mechanism of anther dehiscence was affected by the high RH, but it did not affect the ripening of the pollen.

Drought stress before the beginning of kennel development will result in fruit abortion, without leaf abscission, to protect the tree (Sparks, 1989; Ravindran et al., 2008). In contrast, when drought stress occur after kernel development, seed production will be prioritised over tree survival (Sparks, 1989) and leaf, but not fruit abscission, will occur.

Hormones

A single cause for the Stage-II fruit drop, the most economically important drop, has not been identified, but exposure to ethylene during this period induced major fruit drop. ReTain® caused a substantial increase in fruit retention in 28-year-old ‘Desirable’ trees with a moderate to heavy crop load when applied approximately seven days after pistillate flower receptivity is concluded. Differences in responses were attributed to a potassium (K) deficiency in the young ‘Desirable’ fruit and the influence that crop-load has on the efficacy of ReTain®. In contrast, under Northern Cape conditions, no consistent results were obtained on nut retention or yield with the application of ReTain® on ‘Wichita’ and ‘Navaho’ (Snyman, 2021). The trees were relatively young and the yields probably too low to influence nut retention in the ‘off’ year cycle when Wood (2011a, b) reported a favourable effect. No mentioning was made of the nutrient status of the trees Snyman (2021).

Nutrition

Krezdorn (1955) found a strong relationship between foliar K and phosphorus (P) accumulation and depletion and alternate bearing. Wells and Wood (2008) showed that a critical N:K ratio of 2:1 reduced alternate bearing. In years with a high crop load, K deficiency is a common problem in pecans (Wood et al., 2010).

Zinc (Zn) deficiencies had no effect on the abortion of fruitlets during the fruit growth period of ‘Stuart’ pecans, but increased the number of fruits that die and consequently dry *in situ* (Hu and Sparks, 1990). Catkins produced on branches with a severe Zn deficiency were on average shorter, weighed less and pollen release was progressively retarded with increasing Zn deficiency (Hu and Sparks, 1990). Zn deficiencies also caused reduced flowering intensity, reduce pistillate flowering and the final number of fruit set and may cause impairments in the development of the reproductive structures (Hu and Sparks, 1991)

A manganese (Mn) imbalance delayed bud break, lateral branches produce smaller catkins which later die, leaves turned pale with curled leaflets causing a reduced leaf size and canopy cover which lead to early defoliation and even dieback of branches (Núñez-Moreno, 2012). Reproductive characteristics were influence negatively by Mn toxicity.

Shoot growth and number and nuts per tree dramatically increased as nitrogen (N) levels in the tree increased over a wide range, above visible deficiency (Sparks, 2000a). Furthermore, there was an increase in pistillate formation and less abortion of flowers, indicating the importance of N on the fruit set of the current year’s growth.

Boron (B) applications during the pre-pollination stage increased leaf B concentration, fruit retention and percentage kernel in ‘Desirable’ pecans (Wells et al., 2008). However, leaf B concentration did not necessarily correspond with an increase in fruit retention.

A supplemental foliar nutrient application in March to the commercial soil application in September (SH), did not affect nut retention of ‘Wichita’ in the Northern Cape, but did increase yield the following season (Snyman, 2021).

Conclusion

Successful pollination of the stigma is the first step towards realising a crop. Under local conditions, SAPPA reported concern regarding varying commercial yields from different production regions during the last few seasons. To address this concern, a literature review on pollination of pecans was conducted. Thus summary highlights the factors contributing to successful pollination and indicators to determine where in the process potential interventions can be made to address these concerns in future. The next step will be to analyse existing climate and field data and relate this to yield for potential solutions.

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