LITERATURE REVIEW: FACTORS INFLUENCING POLLINATION OF PECANS FOR COMMERCIAL PRODUCTION

E. Lötze

TABLE OF CONTENTS

LITERATURE REVIEW: Factors influencing pollination of pecans for commercial production 1

Staminate inflorescence 4

Pistillate inflorescence 5

Pollination 7

Pollen germination 12

Fertilization 13

Fruit drop 14

PLANT FACTORS 17

Cultivar 17

Physical manipulations 18

Vegetative growth 20

Alternate bearing 21

Reserve status 22

Fertilization 23

Irrigation 26

Plant Growth Regulators 26

ENVIRONMENTAL FACTORS 27

Temperature 27

Rain 28

Relative humidity (RH) 29

Heat units (HU) 29

Wind 29

MANAGEMENT PRACTICES 29

Planting distance and orchard design 29

Conclusions 29

References 30

PECAN PHENOLOGY AND BEARING HABITS

The reproductive potential of deciduous fruit trees refers to the innate ability to produce reproductive organs such as flowers, and thus fruit, with the intent to survive and reproduce. In pecan, previous studies indicated an important role of inviable pollen (Woodroof, 1930; Adriance, 1931), metaxenia (pollen influences), female selection and heterosis (Romberg and Smith, 1946) and the degree of dichogamy (Stuckey, 1916; Smith and Romberg, 1940; Madden and Brown, 1973) in fruit set.

In pecans [*Carya illinoinensis* (Wangenh. K. Koch)], male (staminate) and female (pistillate) flowers occur on the same tree (monoecious) and exhibits heterodichogamy (Grauke and Thompson, 1996a). Heterodichogamy is a system where one or more dichogamous mating-types are present within a population (Stout, 1928). This involves the differential maturation of the male and female organs between individuals. Therefore, trees were divided into two groups: "Protandrous" (Type I) which is when pollen from the male flowers is shed before the female flowers are receptive, and "Protogynous" (Type II), where female flowers are receptive to pollen before pollen is shed from the male flowers (Knuth, 1906). This system is useful for diploid species as it ensures cross-pollination between individuals (Thompson and Romberg, 1985) and enable selection of compatible cultivars based on their flowering maturity windows. However, later it was shown that this simple two-class classification is not accurate in older pecan orchards (> 30 years) and thus needed an alternative system (Worley et al., 1992)

Adriance (1931) observed a seasonal effect on the maturation of reproductive organs. Cultivars Delmas, Shley, Stuart and Burket responded to seasonal changes and displayed either prodandry or protogyny, in contrast with Texas Prolific, San Saba, Moore and Alley that were always protandrous, irrespective of the climate. Temperature and rainfall seemed to be the critical factors determining this difference in maturity of the flowers, whereas wind and relative humidity (RH) influenced pollen shedding and the duration of sigma receptivity. The temperature effect was quantified as heat units (base 4.4 °C) for the first four months of the year (Jan - Apr) in the Northern hemisphere. In seasons that were cooler, with more rainfall during bloom, protogyny was more prominent than in hot and dry seasons. 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 HU requirement of pistillate flowers varied more between seasons than for staminate flowers and the environmental conditions during spring impacted considerably on bloom.

Thus, although the maturity dates of staminate and pistillate flowers are influenced by weather conditions in spring, staminate flowers were more responsive that the pistillate flowers which indicated 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.

Sufficient pollination is defined as an effective pollination of receptive pistillate flowers with intent to minimise crop losses (Wood, 1996). If sufficient cross-pollination occurs within an orchard, pollination related crop-losses should be minimal (Wood, 2000). After such pollination, other factors that lead to decreases in yield, such as the effect of plant growth regulators on flowering, the different fruit drop periods, nutritional status of the tree and the importance of reserves in storage organs, can be evaluated.

Floral induction is a function of a chemical or hormonal signal to the buds 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 (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).

In the southern hemisphere, bud swell in pecans start during August. The male inflorescence (catkin) comprising three stalks with approximately 72 individual staminate flowers (protandrous cultivars) and approximately 123 individual staminate flowers (protogynous) per catkin (Woodroof, 1924), emerges during the first week of September. This is shortly followed by pistillate flower emergence at the end of October. Pistillate flower differentiation occurs during bud swell (Wetztein and Sparks, 1984). It may take between 6-8 weeks from bud swell until fertilization is complete. Pollen dispersal is highly weather dependant, but fruit set is generally complete end of November, where after nut growth will begin and continue for up to 9 weeks until water stage**.** Shell hardening and nut-fill is complete around end of February, taking approximately three weeks. At this stage shuck-split will take place which indicates the start of the harvesting period, ending in middle June. Trees then enter dormancy after natural leaf drop end of July. Yearly fluctuations might be present due to climatic differences.

Male flower initiation starts during the previous year's vegetative phase and will continue until dormancy in July. Female flower initiation starts in January and ends in July. The sprouting of a differentiated bud will reveal male inflorescence first, followed by vegetative structures (leaves) ending in a terminal female inflorescence, in most cases if sufficient carbohydrates are present. Therefore, fruit is borne terminally on the current years' growth.

Staminate inflorescence

Studies regarding staminate flower initiation and development has seen little attention in literature when compared to pistillate flower development. The first study on staminate flower development was performed by Stuckey (1916), on 33 pecan cultivars. He divided these into two groups based on the length and size of the catkins, length of the bracts and time of pollen shedding. Staminate flowers are produced more regularly than pistillate flowers (Wood and Payne, 1983), as they are buffered by being exposed to environmental conditions for longer (two seasons) compared to pistillate flowers, where development depends only on the previous season's growing conditions (Lockwood and Sparks, 1978). Staminate flowers are also dependent on substrates for two seasons, compared to the one season in the case of pistillate flowers (Lockwood and Sparks, 1978). They are also produced more regularly compared to pistillate flowers, which are rarely produced without staminates (Woodroof, 1930). Staminate flowers differentiate during summer to early fall, in the lateral, axillary buds during the season prior to pollen being shed (Woodroof, 1924) and, according to Adriance (1931), it is unlikely that pollen can be deficient as result of retarded differentiation. It was only later understood that protogynous and protandrous cultivars differ in their period of catkin development. Protogynous cultivars initiate anthers on the catkins during spring when pollen is shed, but protandrous cultivars do so in the summer prior to pollen shed (Wetzstein and Sparks, 1984). Therefore, protogynous cultivars are identified by longer and thinner catkins than in protandrous cultivars (Woodroof, 1924).

Catkin primordia are initiated approximately after two weeks of active growth in spring (Haulik and Holtzhausen, 1988b). According to Woodroof (1930), differences between the catkin differentiating in the two types of cultivars was only observed after summer and by early winter, group I had clearly differentiated bracts and anthers, which lagged in type II until the following spring. Anther differentiation in type I cultivars occurred four to six months before dehiscence, whereas in type II, this occurred about six weeks before dehiscence. Later studies (Smith and Romberg, 1940; Wetzstein and Sparks, 1984) showed that, in Georgia (USA), type I cultivars differentiated inflorescence initials just after bud break, followed by the

development of stamen primordia and bracts a month thereafter. Three to four months thereafter (midsummer), anthers primordia were formed although they only became bilobed the next season. Type II cultivars also initiated flower primordia and bracts soon after bud break, but the rest of the flower development only occurred the next season. In South Africa (Roodeplaat), catkin differentiation phases corresponded with the latter reports, but grouping of cultivars were made according to catkin length (Haulik and Holtzhausen, 1988b) and contradicted grouping according to dichogamy reported in the USA and in Kwa-Zulu Natal (RSA) (Wolstenholm and Storey, 1970).

Although pollen yield per catkin on a fresh weight (FW) basis can be low, the amount of pollen recovered per catkin is primarily dependent on the maturity of the catkin (Yates et al., 1991). Woodroof (1930) found between 100 and 400 individual florets in a single catkin and reported that the number of catkins produced are in proportion to the number of nodes on the specific shoot. Each individual staminate flower consists of one central bract and two lateral bracteoles. Furthermore, each staminate flower can have three to seven stamen, composed of an anther (containing the pollen) and stalk/filament which attaches the anther to the flower. Each anther has four thecae (pollen sacs) when mature. Up to 365 individual ball-shaped pollen grains of about 50 µm in diameter can be found in each of the thecae (Woodroof, 1930).

If catkins around the basal position of a cluster were removed, and the cluster bagged for two months, one lateral bud on each new shoot produced a group of catkins. These catkins were thus younger, being produced on the current season's growth, and appeared to have developed normally, but the pollen arrived too late for pollination.

Pistillate inflorescence

Pistillate flowers normally develop in spring, from lateral buds near the terminal, on the current season's shoots (Woodroof and Woodroof, 1926). Thus, differentiation occurs at the same time as vegetative growth (Feb/Mar NH) (Madden et al., 1969). Buds rendered sub-terminal after dormant pruning almost always produced pistillate flowers and true terminal buds are usually vegetative (Shuhart, 1927). Terminal buds of pecan were previously grouped into one of four groups: Type 1 is a true terminal bud and normally produces vegetative growth, these buds are abundant on young, non-bearing trees. Types 2, 3 and 4 are false terminals and pistillate flowers are normally produced in Types 2 and 3 when in a terminal position and Types 2, 3 and 4 when in a lateral position close to the end of a shoot. These buds are typical on older, bearing trees (Shuhart, 1927). The inflorescence is a spike, consisting of one to six flowers. Commonly the inflorescence is erroneously called a cluster. Pistillate flowers consist of a bilobed stigma on a

stigmatic disc that is surrounded by three bracteoles and a bract that is fused at the base to create the involucre (shuck) (Manning, 1940). The number of flowers on a spike can greatly increase when adverse climatic conditions, such as prolonged drought, are encountered (Wood, 2000). The number of pistillate flowers in an inflorescence is positively correlated to shoot vigour (Sparks and Madden, 1985). Individual flowers are between 5.5 mm to 8 mm in length, with four distinct tapering bracts that vary in length depending on the cultivar (Woodroof and Woodroof, 1926). The receptive stigmas have various shapes and colours and are covered with an exudate that consist of various organic and inorganic molecules that secure pollen grains to the stigmatic surface (Lord and Russel, 2002). Some researchers believe that the colour of the stigma is an indication of receptivity, but later studies by Woodroof and Woodroof (1926) have shown that it is cultivar specific and not related to receptivity. Under normal circumstances the pistillate flowers differentiate during spring, eight to ten days before bud break (Sparks, 1992) following a period of exposure to low temperatures (between -1.7 °C and -2.2 °C), but the differentiation period can vary due to differences in climatic conditions (Shuhart, 1927; Amling and Amling, 1983). Pistillate flowers have the ability to differentiate from basal lateral buds, when the terminal and upper lateral buds were damaged by frost or insects (Woodroof and Woodroof, 1926; Shuhart, 1927). 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 basal flowers may be ready for pollination, while some of the terminal flowers may still only show papillae, or small underdeveloped flower buds. Most terminal flowers generally do not reach maturity and drop (Woodroof and Woodroof, 1926). The period of receptivity is reflected in the ability of pollen to stick to a stigma, therefore it is a useful indication when selecting compatible cultivars for an orchard. Under normal circumstances, the receptivity period of a single stigma is approximately five days (Woodroof, 1930). However, the period of receptivity is highly responsive to changes in weather conditions and variation in development of the bearing shoots (Smith and Romberg, 1940). The receptivity period of flowers within a single inflorescence is approximately two days (Smith and Romberg,1941), however later studies by Wood et al. (1997) found that, within a single tree, it can take between four and ten days for all the flowers to become receptive.

In the pistillate flower, approximately eight weeks after differentiation, the stigma encloses the ovarian cavity and initiates the development of the ovary. However, the time of pollination and development of the ovary can vary substantially between cultivars and seasons. Nevertheless, within 12h after pollination, germination and pollen tube growth towards the ovarian cavity occurs. The pollen tube may enter the embryo sac when it is mature via the

chalaza or micropylar end and 46h after pollination, the pollen tubes have entered the ovarian cavity. At 22 h after pollination, pollen tubes were observed below the bracts of the calyx. Fertilization of the egg occurred between 10 and 15 d after pollination in 'Stuart' when nuts were on average 6.5 to 8.08 mm long and had a diameter between 2.0 and 2.87 mm (Ramming, 1968).

In contrast, the time between pollination and ovule fertilization varies and was estimated between four days and seven weeks, depending on circumstances (Wolstenholme and Story, 1970). It was also observed that a significant amount of nut drop or abortion occurred at the time of fertilization (Adriance, 1931; Smith and Romberg, 1940; Wolstenholme and Storey, 1970) and ascribed to a lack of fertilization.

When pollen tube growth was prevented via excising of the style, after pollination at the beginning of May (NH) in 'Stuart', the most abscission occurred between mid to end of June. At this time of pollination, nuts were on average 6.1 mm long with diameter 1.93 mm. Pollen tube growth passed the point just below the flower bracts between 6 and 9h after pollination. A higher percentage abscission was recorded in clusters with excision 0 – 4 h compared to > 6h after pollination when evaluated 36 to 47 d after treatment (Ramming, 1968). All nuts from treatments where stigmas were excised before 6 h after pollination abscised by beginning of July. Where excision was done > 52h after pollination, a few nuts remained.

With regard to the shape of the flower, the following characteristics increase efficiency for wind pollen collection: i) an exposed sigma with a small diameter that increases pollen collection and minimises the surface boundary layer, ii) a cone shaped stigma that increases the surface area, without compromising the stigma diameter (Woodroof and Woodroof, 1936) and iii), rounded papillate surface cells (Wetzstein, 1990).

Sequential seasons of over cropping may inhibit the initiation of pistillate flowers in varying degrees (Sparks, 1983), even though alternate bearing can also be influenced by the environmental conditions in addition to crop load (Sparks, 1996; 1997).

Results from Iran confirmed that self-pollination resulted in reduced yields, but there was no significant effect on the number of nuts per cluster with different pollen sources (Ajamgard et al., 2017).

Pollination

Sufficient pollination is also important in pecan to ensure high yields. Pecans are wind-pollinated which implies that under normal circumstances they should receive enough pollen

to produce a satisfactory crop (Smith and Romberg, 1940). According to Woodroof (1924), the number of pollen grains produced per tree was calculated as 2.9 x10^{10}, others reported between 1550 and 2000 pollen grains per flower (Hamilton and Romberg, 1933; Madden and Brown, 1975), whereas the number of pollen grains produced per catkin was reported as approx. 2.5 mil. (Madden et al., 1969).

Compatible cultivars need to be in close proximity to each other for successful cross-pollination, as pollen is usually disseminated within 100 – 150 m from the parent plant, although longer distances from 200 m (Woodroof and Woodroof, 1927) to 900 m (Woodroof, 1930) were recorded. Wood (1997) found that fruit set in 'Desirable' pecans decreased sigmoidally as the distance from the 'Stuart' polliniser increased, therefore insufficient pollination can be found in standard block-type orchards, where the cross-pollinator might be planted too far from the main cultivar, contrary to what was previously believed (Marquard, 1992b). This emphasized the importance of the correct number of pollinisers within an orchard, as well as pollinisers that are of the correct genotype for successful fertilization (Wood and Marquard, 1992). It is possible for fruit to set through self-pollination in the case of incomplete dichogamy, but this often results in smaller and lighter nuts (Marquard, 1988). Under self-pollination, pecan yield is 35 – 75% lower with nut quality severely reduced (Polles et al., 1980). Complete dichogamy will result in a self-sterile cultivar, as there is no overlap between pollen shed and pistil receptivity. Some commercial cultivars which are presumed self-sterile are: Big Z, Bradley, Caddo, Chicksaw, Grabohl, Ivey, Maramec, Mahan Stuart, Moneymaker, Oconee, Osage, Owens, Pawnee, Robinson, Sumner, Tejas and Wichita (Worley et al., 1992), but flowering patterns may vary due to environmental conditions (Wood et al., 1997).

In addition, pollen is usually shed when the trees have leaved out, reducing actual distribution to within the tree (containment effect), or to adjacent trees. This furthermore emphasises the important role of wind movement during pollination to ensure efficient coverage of the orchard (McCarthy and Quinn, 1990).

Worley et al. (1992) identified the flower maturity windows of 80 high-value cultivars in an attempt to increase the pollination percentage within commercial orchards after a decline in fruit set was observed in some orchards. When trees are chosen to be planted within an orchard as a complementary cultivar, it is important to take flower maturity windows into consideration, because the tree age/size as well as climatic conditions have a significant impact on the flower maturity during the pollination period (Wood, 1997). Younger trees have an earlier and longer flower maturity window than older trees of the same cultivar. Furthermore, 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. Cultivar selection is thus strongly influenced by the climatic conditions in a specific production region due to the large variation that occurs in pollen maturity and pollen shedding patterns (Wood and Marquard, 1992; Wood et al., 1997; Wood, 1997).

The dispersal of pollen within a tree occurs acropetally, 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). The weather conditions during pollen release are important to determine if pollination can be regarded as sufficient. Abnormally high or low temperatures influence the timing of pollen release (Wood et al, 1997). Woodroof (1930) found the ideal relative humidity (RH) and temperature range for pollen dispersal to be 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. The inability of pollen to be shed at RH higher than 85% is thought to be an adaptation to prevent pollen from being shed when it is raining, as this would severely inhibit the wind dispersal of pollen (Yates and Sparks, 1993). Once the appropriate temperature and RH combination is achieved, the anthers will dry out, causing the pollen sacs to split longitudinally and release the pollen (Woodroof, 1930). In most cases, the prevailing wind is enough to set the pollen free, but a gentle agitation of the branches will also set free clouds of pollen (Wood, 2000). Depending on weather conditions, pollen dispersal can take from three to more than ten days. It is, however, important to note that conditions that favour pollen dispersal i.e., dry, and hot air, will also lead to a shortened receptivity of the pistillate flowers due to the pistils losing their moist and sticky surface to which the pollen adheres (Wood, 2000).

Pollen can also be stored for hand/artificial pollination. Successful fruit set with stored pollen was reported by Yates and Sparks (1990) for pollen stored for 1, 2 and 3 years at -80 °C or 1 year at -196 °C, but pollen quality may be compromised if collected during severe drought conditions. Pollen viability was more accurately quantified by fruit set than in vitro germination.

The pecan is a monoecious, dichogamous and wind pollinated tree (Sparks, 2000a). Pollination is important as it enables fertilization, which enables development of a seed and fruit from the flowers. The timing of pollination is important, as the stigmatic surface of the pistil is only receptive for pollen for a short period of time (Zhang et al., 2015). Pollination is critical and a lack of pollination will result in yield reduction (Conner, 2007).

Several factors influence the pollination of pecan trees including tree age, with older trees flowering at different times than younger trees; tree height, the duration of pollination and the receptivity window, which also shortens with tree age (from 2 – 18 to 2 – 12 d); flower position, with interior and lower positions maturing more quickly, bud break, which influence flowering and climate conditions (Adriance, 1931; Conner, 2007; Wood, 2000; Woodroof, 1930). In addition, Wood (2000) reported that pollination of 'Wichita' is influenced by the distance of the trees from a pollinator, which can lead to reduced kernel quality due to self-pollination if the distance to the pollinator is too far.

Pollen distribution and dispersal of pecan occurs with wind, but differs between cultivars (Wood, 2000). Catkins located in the lower positions of the tree usually shed first and those at the top shed last with the pollen release proceeding from the base to the tip of the tree (Wood, 2000). Lower relative humidity and higher temperatures will ensure moderate turbulence and adequate wind movement, which will increase pollination (Sparks, 2005). Woodroof (1928) concluded that pollen was not shed if RH exceeded 85% or under low temperatures, whereas Smith and Romberg (1940) observed a lack of dehiscence of anthers during rain or foggy conditions. The mechanism of anther dehiscence was affected by the high RH, but it did not affect the ripening of the pollen. Heavy shedding usually followed a period of high RH.

Pecans are unlike most deciduous fruit trees, with the restriction of female flower development to the spring of its anthesis. Stored substrates are decreasingly allocated from the base to the terminus in spring (Sparks, 2005), resulting in weak pistillate flower development on weaker shoots that will lead to abortion of the cluster during the first drop (Sparks, 2005). Pistillate flower development is crucial for fruit development and is produced from substrates that accumulated from the previous year's growth. The final number of pistillate flowers is determined at bud break (Sparks, 1996). Thus, the maximum number of pistillate flowers are determined by the previous seasons growing conditions, not only the tree health and growth, but also environmental factors influencing the tree's productivity (Sparks, 1996). The production of staminate flowers occur before the development of the pistillate flowers, but this is not advantageous, as pecans are normally cross-pollinated, which is promoted by dichogamy and ensures the availability of sufficient pollen once the pistillate flowers are produced (Sparks, 2005). The flowers develop at different times, which causes the pollen production or female flowers to be past maturity when the male flowers are only yet reaching maturity (Ajamgard, 2017). This emphasizes the importance of the selection of cross pollinators to reduce chances of inadequate pollination with resulting low nut production or poorly developed nuts (Connor

2007; Zhang et al., 2015). Cross-pollination (dichogamy) is often complete in colder climates and incomplete in warmer climates (Sparks, 2005). When incomplete pollination occurs, it will result in fruit drop. Along with fruit drop, kernel development is also suppressed (Ravindran et al., 2008) and yields can be reduced by up to 75% (Conner, 2007) with reduced nut set and kernel percentage. Ajamgard (2017) showed that the number of nuts per cluster was significantly reduced by self-pollination of different cultivars.

There is a considerable variation in the length of the period of stigma receptivity between seasons and cultivars and stigmas within a cluster become receptive within a very short time span (Smith and Romberg, 1940). This is primarily a function of growth and development of shoots bearing pistillate clusters. Shoots on slow-growing trees showed a more uniform flower development and growth initiation compared to faster growing trees and therefore the total length of the receptive period of stigmas varied. This observation also held true for staminate flowers.

Pollen storage is required under certain circumstances i.e. trees maturing late, the need for pollen for breeding purposes, climatic conditions influencing the pollination window and require supplemental pollination (Bennet et al., 1986) and the heterodichogamous nature of the pecan (Yates et al., 1991). Although pollen can be stored for up to three (Yates and Sparks, 1990) to eight (Conner, 2011) years under laboratory conditions (-80 to -196 °C), it is not feasible for commercial application and an alternative storage protocol was investigated (Yates et al., 1991). It was possible to store ‘Stuart’ and ‘Desirable’ pollen at -12 °C for two years after freshly collected pollen was oven dried at 35 °C. Precaution should be taken to reduce pollen moisture prior to and during storage to ensure long-term viability. The dehydration of the pollen before storage increased the longevity of the pollen and thus it is recommended to include this process in the protocol for storage. After drying, pollen needs to be packaged in moisture-proof containers for storage.

For in vitro pecan pollen germination, Connor (2011) proposed a re-hydration of the stored pollen in a humidified chamber of four to 24 h prior to testing. Various germination media have been proposed, i.e. the hanging drop or well, germination on a membrane support and germination on a solidified agar or gel. To further simulate natural germination conditions, borate, sucrose and calcium can be added to the medium (Connor, 2011).

In China, stage V (anthers turning yellow and a 90% angle between bracts and catkin rachis) was identified as the optimal time for pollen collection and the receptivity of the stigma began from stage II (increased dehisced angle), with a peak when the angle reaches 90%.

Receptivity was reported as two to three days and could be quantified by measuring the sigma peroxidase activity (Zhang et al., 2015).

A study on 12 cultivars in the USA showed that all un-pollinated nuts dropped between 38 and 45 d after the last date of sigma receptivity (Smith and Romberg, 1940).

Pollen germination

According to Woodroof (1930), anther dehiscence is primarily determined by RH and secondary, temperature. 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). Therefore, pollen dispersal in the field can be erratic over time, even when environmental conditions are similar (RH and temperature).

Once pollen is released and land on an appropriate stigma surface – the various phases of germination are initiated: rehydration, pollen tube formation and pollen tube elongation (Heslop-Harrison et al., 1975). However, germination is often analysed as only the last two processes.

Pollen becomes rehydrated on the stigmatic surface approximately 1 h after pollination in pecan (Wetzstein and Sparks, 1989). Within 3 h, the germ tubes will reach a similar or higher grain diameter (Wetzstein and Sparks, 1989; Marquart, 1992). The germ tubes can penetrate the stigmatic surface as soon as 2 h after pollination to elongate to below the junction of the stigma and floral bracts, within 7 h after pollination (Hinrichs and Ramming, 1973). The maximum pollen tube formation and elongation in vivo occurred at 26 °C for ‘Cheyenne’ and in vitro, at 27 °C for ‘Cape Fear’. However, in this study, the interaction between temperature and hydration and pollen tube development as sequential event was not analysed. To investigate the effect of temperature and RH on anther dehiscence and pollen germination, ‘Desirable’ and ‘Stuart’ were selected for a study in Georgia (Yates and Sparks, 1993). The detached anthers and pollen were exposed to a range of RH (56, 33, 64 and 97%) and temperature (10, 21, 27 and 33 °C) regimes to assess the interaction between these factors and pollen dispersion and germination. A decrease in RH and increase in temperature resulted in an increase in pollen dispersal in the field, as well as in detached anthers under laboratory conditions. Inhibition of dehiscence of anthers due to high RH, could be reduced by high temperatures and inhibited by low temperatures, with low RH. Furthermore, the effect of temperature on specific germination phases were evaluated by varying pollen dehydration temperatures from 3 to 42 °C, whilst keeping the incubation temperature during pollen tube development constant at 25 °C. After 2h of rehydration, maximum tube formation occurred at

15 °C, whilst maximum tube length occurred at 29 °C. When all pollen was rehydrated at a constant 25 °C and the incubation temperature during tube development varied, the maximum tube formation occurred at 15 °C and differed from maximum tube length attained at 33 °C. Rehydrate conditions did not influence the morphology of the tubes, but during incubation of tube development, no tubes developed at 3 °C, whereas abnormal development was observed at 42 °C. The adverse effect on tube development at the lowest temperature could be reversed when pollen was transferred to 25 °C, but not for the highest temperature abnormality.

Fertilization

The fertilization process begins when pollen grains land on the sticky surface of the stigma. The exudates found on the surface of a receptive stigma hydrates the pollen grain within approximately one hour, which leads to the pollen grain losing its flattened shape and becoming more rounded (Wetzstein and Sparks, 1989). It is, however, important to note that the arrival time of the pollen on a receptive stigma highly affects the success of pollination. Pollen arriving on the stigma after other pollen grains have started to germinate has very little chance at fertilization (Mulcahy and Mulcahy, 1987). Successful pollination is characterized by an observable darkening of the stigmatic surface after about 24 hours, due to the degeneration of the stigmatic surface. With pollination now complete, the pollen grains germinate and produce a pollen tube over a period of about three hours where after extensive pollen tube growth can be identified on the stigma after approximately 8 to 12 hours (Wetzstein and Sparks, 1989). Marquard (1992a) determined the average growth rate of a pollen tube to be approximately 150 $\mu m.h^{-1}$ between three- and eight-hours post pollination. In addition, the pollen arriving first on the stigma has the best chance for successful fertilization and this declined to less than 3 % after 24h after arrival Marquard (1992a). Moderate temperatures (26°C) result in a growth rate roughly three times higher than at relatively high (30°C) or low (22°C) temperatures. In vivo pollen tube growth at 26 °C was also more than three times that of growth at 22 °C. After the pollen tube has extended past the stigmatic cells, it rapidly grows towards the ovule where fertilization will take place. Fertilization, as described by McKay (1947), is the polar fusion of two nuclei with one of the two male gametes approximately four hours after pollination. This results in the formation of the triploid endosperm that is also referred to as the liquid endosperm and acts as a food source for the developing embryo. The second male gamete fuses with the haploid female gametophyte (egg) to form a diploid zygote (Wilhelmi and Preuss, 1999) approximately four to seven days after pollination (McKay, 1947; Haulik and Holtzhausen, 1988a). There are however various studies on the subject of when fertilization occurs after

pollination: Woodroof (1928) described it to be five to six weeks after pollination. Adriance (1931) found it to be four weeks after pollination and Shuhart (1927; 1932) found it to be two weeks after pollination. Haulik and Holtzhausen (1988a) reported observation of the egg nucleus between 18 and 22 d after pollination, with an inactive zygote for at least 40 d under South African conditions. The pollen parent determines the nut weight and volume of pecans (Romberg and Smith, 1946; Sparks and Madden, 1985; Wolstenholme, 1969).

It is common practice to apply pesticides early in the season as a preventative measure against disease and insect damage and these sprays often overlap with the pollination period. Early season fruit drop is the result of a lack of pollination and conversely, a lack of fertilization (Hamilton, 1942). This coincides with the Stage-II fruit drop period as later proposed by Sparks and Madden (1985). Therefore, the effect of pesticide sprays on fruit drop are of economic importance to the producer. Agricultural pesticides has shown to have a negative effect on pollen germination in other fruit crops, (Church and Williams, 1977; Bristow and Windom, 1987; Redalen, 1980; Bristow and Shawa, 1981) and the application of triphenyltin hydroxide, benzimidazole, and phosalone ,for example, were found to inhibited pollen germination in pecans through restricting pollen hydration and pollen tube elongation in both in vivo and in vitro studies, with the former showing a less pronounced effect (Wetzstein, 1990). Furthermore, treating pecan trees with propiconazole, a fungicide, can lead to a significant decrease in leaf area through inhibiting leaf expansion by causing major modifications in the cellular organization of the mesophyll cells (Wetzstein et al., 2002), which could possibly affect pollination.

Fruit drop

During pollination, if the stigma receives excessive pollen, as is the case in controlled crosses, it can lead to the abortion of fruit within weeks after being pollinized (Romberg and Smith, 1950) although this phenomenon has only been observed in certain Walnut (*Juglans sp.*) cultivars and not in pecans as of yet. For successful fruit set only a small amount (more than 5%) of live pollen is needed (Marquard, 1992b). Crop losses due to incomplete fertilization may present itself as the premature abortion of fruit or the production of nuts where the kernel is absent (Wood, 2017). These nuts, referred to as “pops” in the pecan industry, are sorted from the filled nuts via aspirators in processing facilities. Pollination plays an important role in fruit abortion, with the degree and specific pattern of fruit drop correlated with a specific pollination problem (Wood, 2000). Four fruit drop periods can occur within the pecan development period (Sparks and Madden, 1985). Stage-I fruit drop, as first described by Woodroof and Woodroof

(1926), is the abscission of pistillate flowers from a terminal spike on a shoot during full bloom due to their weak and underdeveloped nature, therefore the term “bloom drop” is frequently used. Abortions are also more common on the distal than proximal section of the spike (Yates and Sparks, 1994). Pistillate flower abortion and not a lack of pistillate flowers, is the main reason for alternate bearing. Furthermore, pistillate flower abortion is suggested to be due to incomplete development of the flowers (Sparks and Heath, 1972; Sparks and Madden, 1985; Woodroof en al., 1928) and not a lack of pollination (Sparks and Madden, 1985). 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). This was further confirmed by an increase in pistillate flower production and decrease in abortion with increasing shoot vigour (Sparks, 1988). Insufficient access to carbohydrates and/or minerals is the main cause of this fruit drop period (Yates and Sparks, 1994). 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 thus limited for flower development under these conditions and this is more prominent in an ‘off’ year, when low-vigour shoots are a familiar sight, abortion is high and low assimilate reserves occur (Lockwood and Sparks, 1978; Sparks, 1983). This limited nutrient status also resulted in undeveloped floral structure in the aborted pistillate flowers which was illustrated in SEM studies on ‘Wichita and ‘Desirable’ in Georgia (Yates and Sparks, 1994). Flower anatomy was quantified during all four drop stages. No tissue necrosis was observed in any of the samples, but anatomical differences occurred between aborted and non-aborted flowers. The diameter, length and weight of the intact, aborting flowers were significantly lower than in intact, non-aborting flowers. The integument in aborting flowers was i) less extended over the nucellus of the ovule, ii) the number of parenchyma nucellus cell layers lateral to the embryo sac were lower and iii), embryo sacs deflated compared to the in the non-aborting flowers (Yates and Sparks, 1994).

The effect of late-spring frost on shoot growth, flowering and fruit retention also plays a role in fruit drop (Wells, 2008). During the first fruit drop period, the average shoot length on frost-damaged trees is shorter and there are fewer fruit per inflorescence, therefore the flower drop recorded on frost damaged trees was most likely due to weak flowers. The effect of frost is 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. The Stage-II fruit drop period occurs during the fruit elongation phase, before rapid fruit enlargement takes place, and begins at approximately 14 days after pollination, and 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 as this fruit drop period overlaps with that of non-pollinated trees (Sparks and Madden, 1985). Furthermore, this drop is also observed in self-pollinated trees, which suggest that this type of drop is due to insufficient pollen availability. The Stage-III fruit drop period occurs at approximately 54 to 90 days after pollination, which McKay (1947) found to correspond with the first and subsequent divisions of the diploid zygote. Therefore, this drop is most likely due to the inability of the zygote to divide thus leading to the abortion of the embryo. The Stage-IV, and final, fruit drop is much less aggressive and is rarely noticed in orchards. It is associated with abortion of the embryo, which leads to a shrivelled appearance of the embryo without any apparent discolouration of the seed coat or any other tissues surrounding the embryo (Sparks and Madden, 1985). Yates and Sparks (1995) later revised this model and proposed that Stage-III and -IV be renamed as the endosperm and embryo drops, respectively. Through morphological studies of the flowers during the pollination period it was found that ovules from aborting fruit had no cellular endosperm at the Stage-III drop. The Stage-IV drop as proposed by Sparks and Madden (1985) was confirmed by their morphological studies.

The four fruit drop periods contribute to a decrease in profitability of an orchard. This decrease in potential income to the producer has led to fruit drop or abortion becoming an important research subject for the industry. A single cause for the Stage-II fruit drop, which is often the most economically important, has not been identified yet. Previous research has, however, identified that exposure to ethylene during this period can induce major fruit drop (Kays et al., 1975; Wood, 1983; Khalil et al., 2016). Stage-II fruit drop could thus be managed chemically, either through the inhibition of ethylene biosynthesis or through altering the receptivity of ethylene receptors within plant tissues. Aminoethoxyvinylglycine (AVG) is naturally occurring in plants and is commercially produced through a process of fermentation and formulated as ReTain®. It is commercially available and is used in the deciduous fruit industry to reduce ethylene biosynthesis through competitive inhibition of 1-aminocyclopropanecarboxylate synthase (ACC synthase), which is the rate limiting enzyme in the endogenous biosynthesis of ethylene in higher plants (Yu et al., 1979). ReTain® prevents unwanted fruit drop in pecans (Wood et al., 2009). 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. However, this effect was absent when applied to 'Desirable' trees with a light crop load. Consequently, the effectivity of ReTain® was evaluated again in a commercial 'Desirable' orchard (Wood, 2011a), where the opposite was found, and it was concluded that the use of ReTain® during an "on" year was questionable after use in a previous "off" year. The 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®.

Woodroof and Woodroof (1926) reported that the position of the shedding was determined by the number of nuts per cluster. According to them, basal flowers are differentiated first, at the terminal end of a cluster. There are thus always un-developed flowers that are shed soon after the pollination period due to a lag in development, which rendered them non-receptive at this time. In contrast, with regard to nut drop in the cluster at the time of pollination, Adriance (1931) reported that in all clusters, one to three immature nuts at the apical end are shed along with the tip of the peduncle. There does not appear to be a regular drop order in the cluster. However, in later studies on open pollinated clusters, there seemed to be an established relationship, indicating the basal flower or nut was the most likely to drop, followed by other positions (Adriance, 1931). In addition, Adriance (1931) confirmed that there were also immature flowers at the base of the cluster, which never reached full development and shed without being pollinated, in 'Texas Prolific'.

In un-pollinated nuts, the abscission layer was well defined by three weeks after receptivity (Adriance, 1931). The shrivelling of a whole cluster is usually associated with a lack of reserve nutrients after an 'on' year (Woodroof and Woodroof, 1926), or mechanical damage caused by insects or wind (Adriance, 1931).

PLANT FACTORS

Cultivar

Rohla et al. (2007) also stated that cultivar choice affects alternate bearing, with early fruit-ripening cultivars having a lower alternate bearing habit than late-ripening cultivars.

Some cultivars are more likely to produce abnormal flowers after a spring freeze than others, which may be influenced by the phenology of bud break. Cultivars where abnormal flowering was observed in Georgia (USA) included Schley, Stuart, Desirable, Farley, Moneymaker, Success, Pabst and Mahan (Wells, 2008) and those where abnormal flowering were not observed included Curtis, Teche, Moor, Van Deman or Frotscher. This abnormal

flowering behaviour is temperature dependent, with a critical temperature of -1.7 and -2.2 °C (Wells, 2008) in spring.

In pecan, studies indicated no evidence of pollen-stylar incompatibility or selectivity of pollen tubes with regard to fertilization of the egg cells. As long as stigmas were receptive when pollen was applied, fruit set was satisfactory (Romberg and Smith, 1946), although it was always lower in self-fertilization conditions.

Wood et al. (1997) also indicated a significant three-way interaction (location x cultivar x season) which influenced the reproductive and vegetative characteristics of the pecan. The developmental phases proved to be very sensitive to the environment and implied that the timing of critical phenological stages like flower maturity may differ between seasons and result in failure of cross-pollination in otherwise complementary cultivars. The prominent climate parameters winter chilling and HU in spring furthermore enhanced cultivar differences (Grauke and Thompson, 1996b). In contrast with previous studies, their extended research indicated that the type of dichogamy by these 80 cultivars was constant for each location during the evaluation period, but the degree of completeness of pollination varied as did the receptivity windows. The strongest correlation between growth- and reproductive parameters was between the starting date of pollen shedding and date of reproductive maturity. Therefore, cultivars with early maturing flowers (staminate and pistillate) tended to be protandrous and exhibit longer pollination windows and vice versa.

They recommended the following 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. They did not indicate whether pollinators should be in alternate rows or planted in the row, alternating with main cultivar.

Physical manipulations

Summer pruning redirects the allocation of resources through the removal of vegetative sinks. Summer pruning could therefore increase the allocation of carbohydrates and other substances to the roots, and other organs, in an effort to increase their rate of development as is the case in sweet cherry (Measham et al., 2013). In apples, the rejuvenation response that summer pruning induces, can consist of the mobilization and redistribution of nutrients and phytohormones which could lead to the breaking of axillary buds, the inhibition of flower induction and later induction of dormancy (Saure, 1987). These responses are, however, dependent on tree vigour as well as the earliness and severity of the pruning cuts. The theories behind the timing of

pruning cuts differ quite drastically. Some suggest that later pruning might lead to a higher accumulation of nutrients with a corresponding increase in the formation of flower buds, while others suggest that summer pruning might have the opposite effect, where it could increase the breaking of axillary buds. This depletes carbohydrate reserves as it leads to the formation of secondary shoots rather than flower buds. Fruit set in apples, for example, is improved by early summer pruning (Quinlan and Preston, 1971). Pinching may promote flower formation in apples and often needs successive pinching of the secondary and tertiary shoots to be effective (Gardner et al., 1952). Pinching often leads to less regrowth, more flowers and thicker stems when compared to heading cuts (Lord et al., 1979). Locally, a pilot trial involving pinching of current season shoots on young, non-bearing 'Wichita' trees resulted in a consistent increase in lateral growth on pinched shoots, whereas non-pinched trees grew long and unproductive shoots during the first season (one-year old trees) (Snyman, 2021). During the second season, with more shoot growth (two-year old trees), a further increase in lateral branching resulted from the pinching that indicated a potential of more bearing units the following season.

Hedging on an annual cycle produced higher nut yields when compared to bi-annual or eight-yearly cycles, and considerably higher yields when compared to orchard thinning strategies where trees were removed to decrease orchard crowding (Wood and Stahmann, 2004). However, when physical manipulations are restricted to annual or bi-annual hedging and topping of trees, it may lead to a very dense tree canopies, thus limiting light penetration into the tree. This can cause a tree to become unproductive as bearing surfaces decrease and limbs ultimately die. The solution therefore is selective limb pruning. Pruning trees will increase the shoot vigour resulting in an increase in fruit set and a decrease in fruit drop (Sparks, 1988). The removal of large limbs reduces overall yield for a number of years and could stimulate vigorous regrowth close to the pruning wound. This could in turn cause more shading within the canopy (Reid, 1924).

Leaf area and crop load are the primary factors that determine the reserve status of the tree. Some reports indicated an optimum leaf:nut ration as eight to 10 (Crane et al., 1935). Hinrichs (1962) confirmed this when he defoliated trees before early September (NH) and prevented pistillate flower differentiation the following spring which resulted in a reduced (20 – 50%) number of catkins. This effect was carried over into the second season after defoliation.

Prolific cultivars, such as Wichita, require crop control, otherwise alternate bearing can occur because of overbearing (Sparks, 2000a). Extreme fruit set causes poor kernel development and quality and is accentuated by shuck decline in excessive fruiting trees (Sparks

et al., 1995). This will result in reduced pistillate bloom and fruit set the following season (Sparks, 2000a).

Significant depletion of reserves occurs with the presence of fruit on the tree, which creates additional stress in the second half of the growth cycle, with only 20% or less of the total dry weight reaching a maximum during the development of the kernel. 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. This pattern is described as alternate or irregular bearing, because environmental conditions can also affect return bloom, (Sparks, 2005).

Carbohydrate reserves are also affected by heavy cropping and the depletion of nitrogen (N), phosphorus (P) and potassium (K) reserves. The depletion of N, P, K reserves are associated with premature defoliation, caused by the high demand of rapidly growing fruit that cannot be met by uptake from the soil alone and must be supplemented by reserves from the leaves. This will cause a gradual decline in leaf reserves if an 'off' year cannot refill these reserves (Sparks, 2005). Hand thinning of high crop loads in August (SH) resulted in a high return bloom the following season.

The balance between energy in a tree usually shifts from vegetative to reproductive growth during the season, but this can be changed by severe environmental conditions. Drought stress before the beginning of kennel development will result in fruit abortion to protect the tree, but leaf abscission will not occur (Sparks, 1989). However, after kernel development, seed production will be prioritised over tree survival (Sparks, 1989) and leaf, but not fruit abscission, will occur.

Vegetative growth

Shoot growth indicates the physiological conditions of a tree and is an important factor in final yield and nut quality. The optimum shoot length for maximum yield efficiency varies between cultivars in pecans (Amling, 1959; Taylor, 1966) and a pecan shoot may produce between 24 and 48 catkins (Woodroof, 1924; 1926). The most productive shoots were defined as moderately vigorous (10.2 – 38.01cm) (Crane, 1930; Finch and Crane, 1931; Taylor, 1966), with the shoot diameter between the fourth and fifth nodes from the terminal, indicating the potential productivity (Taylor, 1966). The diameter varied between cultivars, with the highest productivity between 3.4 and 8.3 mm.

The formation of incomplete developed flowers was due to limited shoot growth in 'Desirable' and 'Wichita' (USA) (Yates and Sparks, 1994). The aborting flowers had embryo sacs, but showed no flower or integument necrosis as is common in abscised walnut flowers.

Alternate bearing

Various cultural and management practices including nutrition, light and water management, vegetation control and fruit thinning have been applied to reduce alternate bearing intensity, but none could eliminate alternate bearing completely (Smith, 2010). The main factors responsible for alternate bearing include the level of carbohydrate reserves within the tree, a dual mechanism of carbohydrate balance and phytohormones, and endogenous hormone growth regulators from the fruit and leaves (Wood, 1996).

Pecan productivity, regardless of an 'on' or 'off' year, is dependent on the success or failure of flowering. The flowering process is complex and involves several environmental and endogenous cues (Thompson et al., 2019). Thompson et al. (2019) investigated the effect of exogenous applied plant growth regulators, such as gibberellic acid, for the mitigation of alternate bearing in pecan trees. They reported an increase in the number of flowers per shoot increasing (125.3 %) after treatment with GA_3 (2X), compared to controlled 'Western' shoots (applied three times between June to July) in a study conducted in Mesilla Valley, USA.

Furthermore, the reduction in return bloom of the subsequent season is dependent on the intensity of the crop load and trees with a moderate crop load had a more pronounced effect compared to trees with a heavy or light crop load (Schmidt et al., 2009). Krezdorn (1955) found a strong relationship between foliar K and P accumulation and depletion and alternate bearing. During large cropping years, trees had a higher concentration of K and P due to higher reserves from the previous year. In addition, the concentrations of K and P increased faster in trees with a low compared to high crop load (Krezdorn, 1955). Smith (2010) found no increase in pecan yield with applied K, but Wells and Wood (2007) showed that a critical N:K ratio of 2:1 reduced alternate bearing. Additionally, increased yields with excessive N, reduced nut yield and quality, and enhanced alternate bearing (Wells and Wood, 2007).

Thus, a relatively short period remains to store carbohydrates and reserves for the next season's development and a lack of management of this process may further increase the onset of alternate bearing.

Haulik and Holtzhausen (1987) reported a nut:leaf ratio of 23 for various cultivars under South African conditions, which differed substantial from previous reports of between 4.5 and 13 leaves per nut (Crane et al., 1934; Harris and Smith, 1957; Wolstenholm, 1972), with

recommendation to use 10 as a basis. Nevertheless, they found no direct correlation between the leaf:nut ratio and alternation in spite of trends in 'Moore' showing a higher yield with ratio 2, than the poor yield associated with a ratio of 1.7.

Reserve status

Stored carbohydrates (CHO reserves) within the roots of deciduous fruit trees play a key role in a variety of physiological processes, most importantly it supports the initial growth of trees during bud break and initial growth in spring before enough CHO can be produced. Pecans, as with stone fruits, rely on CHO reserves due to them flowering before the canopy is fully developed (Westwood, 1978). During spring, reserves are translocated from the shoot base to the terminal (Lockwood and Sparks, 1978), which often results in underdeveloped pistillate flowers on weak shoots (Sparks, 1988; Yates and Sparks, 1994) and aborting clusters during the first drop (Sparks, 1988; Sparks and Madden, 1985). Pistillate abortion under these conditions serve as a survival mechanism during stressful periods, by reducing crop load.

Lockwood and Sparks (1987) observed radioactivity in both male and female flowers after $^{14}CO_2$ was fed to bearing trees, which confirmed that initial growth is dependent on CHO reserves. Carbohydrates are the predominant assimilate reserve present in pecans (Smith and Waugh, 1938), but nitrogenous (N) reserves are worth mentioning as they play a key role in the total reserves of a tree (Titus and Kang, 1982). Crop load in pistachio (*Pistacia vera* L.) is directly correlated to the amount of N reserves stored in the tree during the previous winter (Picchioni et al., 1997) and the majority of N that is used for the spring canopy growth flush and flowering of pistachio is from stored N reserves (Weinbaum et al., 1994). Pecans tend to use stored N reserves in spring, followed by a rapid uptake of N after the endogenous reserve pool is depleted (Acuña-Maldonado et al., 2003). The majority of N used for annual structures (fruit and leaves) is obtained from stored N sources (Smith et al., 2007). Therefore, it is important for producers to follow an annual N fertility program to inhibit the depletion of N reserves, which would have a definite impact on the current and future season's production.

Maintaining healthy foliage through autumn is of utmost importance with regard to root growth and the accumulation of all reserves. Worley (1979) demonstrated that defoliation of pecans during September (NH) would lead to depletion of starch within the smaller roots even though most of the reserves would be replenished during regrowth. This would undoubtedly have an influence on the production of both staminate and pistillate flowers during spring. When leaves are removed from a tree before natural abscission has occurred, the metabolic N that could potentially be remobilized and transported to roots and other tissues, is lost entirely.

If this is not replaced via nutritional amendments, it can be expected that the tree will show deficiency symptoms. Therefore, the late-season photosynthesis that occurs is important for normal starch accumulation, and the period leading up to final leaf drop presents an ideal opportunity to increase reserves with the help of nutrient amendments, whether it be soil applied or foliar sprays. Carbohydrate reserves within the roots will only increase after the competition for photosynthates has decreased (Loescher et al., 1990), thus during the pre-harvest period for pecans, when nut growth slows down. In the case where an insufficient supply of carbohydrate reserves is present in the roots, N deficiencies can become apparent due to a lack of CHO substrates needed for active root growth. In pecans, active root growth is severely inhibited by a lack of reserves as roots depend on these reserves for the first two months of the growing season (Lockwood and Sparks, 1987).

Fertilization

Fertilizer management in pecan is often overlooked (Weckler et al., 2015). Whilst excessive application of fertilizers promotes pest and disease incidence, a lack of nutrition will result in poor nut development and growth and may induce alternate bearing (Weckler et al., 2015).

Snyman (2021) performed a pilot trial on additional fertilization in a young, bearing 'Wichita' orchard in the Northern Cape with aim to increase fruit set/nut retention. Trees were without any deficiency symptoms, visual or foliar analyses. A single annual balanced foliar nutrient application during March, in addition to commercial fertilization, had no effect on yield efficiency in June. However, when this was supplemented by an early season nutrient soil drench (balanced nutrient combination) in September, also in addition to commercial fertilization, it resulted in significant increase in yield efficiency the following season. This was not related to a significant increase in fruit set, or to severe B and Zn deficiencies in the orchard. One possible explanation was that the foliar application in March, during the water stage of fruit development, may have increased the reserve status of the trees indirectly via an increase in photosynthesis or via an increase in the nutrient status of the leaves and the effect was only visible the following season. This needs further investigation.

Pecans responded positively to fertilization and increase in stem diameter and tree height, especially during the early years of planting compared to trees in their natural habitat (Burner et al., 2013). However, fertigation with N may cause root damage to newly planted pecan trees during establishment if the irrigation and delivery rates are not properly managed (Wells, 2015). Excessive nickel (Ni) and soil levels of Zn, copper (Cu), calcium (Ca), magnesium (Mg) and manganese Mn can lead to deficiency (Wood, 2006).

Zn-deficiency symptoms are usually characterized by the shortened internodes giving the tree branches a “rosette” foliar feature, with a reduced leaf area, wavy leaf margins with interveinal leaf necrosis and chlorosis (Heerema and Walworth, 2016). Zn deficiencies also cause reduced flowering intensity, reduce pistillate flowering and the final number of fruit set, which severely reduces nut production (Hu and Sparks, 1991). Zn deficiencies can also cause impairments in the development of the reproductive structures, decrease carbonic anhydrase and lead to low stomatal conductance (Hu and Sparks, 1991). These impairments reduced the number of fruit produced per branch and drastically decreased the development of fruit and delayed nut maturation (Hounnou, 2019; Fronza et al., 2018).

Delayed bud break and dieback on the current year’s shoots caused by a Mn imbalance was observed in ‘Western Schley’, Southeast Arizona (Núñez-Moreno, 2012). Along with the delayed bud break, lateral branches produce smaller catkins which later die, leaves turn pale with curled leaflets causing a reduced leaf size and canopy cover and leads to early defoliation and even dieback of branches (Núñez-Moreno, 2012). Reproductive characteristics are also affected by Mn toxicity, as well as the growth of the shoots. Affected trees only had an average of 7 % fruiting shoots versus 86 % of unaffected trees. The annual shoot growth was also affected, with only 2 cm versus 13 cm shoot growth of unaffected trees, with the shorter shoots showing signs of ‘rosette’ symptoms (Núñez-Moreno, 2012). Most of the symptoms occured early in the season and indicated that the Mn was redistributed from reserves, which could be affected by the previous year’s growth (Núñez-Moreno, 2012).

With regard to the reproductive biology of pecans, N is the most dominant element. The number of nuts per tree will dramatically increase as N levels in the tree increases over a wide range, above visible deficiency (Sparks, 2000a). This increased N, no details about set were available, resulted in 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.

Four distinct reproductive drops occur in pecans (Wood et al., 2010). Observations indicate that a low K concentration may be the cause of Stage II fruit drop of pecans, since stage II is associated with the absence of zygotes, as well as ovule tissue structural problems, caused by physiological stresses (Wood et al., 2010). This postulate is further supported by evidence demonstrating increased nutmeat yields and quality and reduced fruit drop (Wood et al., 2010). In years with a high crop load, K deficiency is a common problem in pecans and is visible as interveinal chlorosis of the older leaves (Wood et al., 2010).

Smith (2010) showed a relationship between leaf necrosis and defoliation, P and K concentrations below 1 %, because of a high demand for K and P during fruit development. A

concentration of 1 % leaf K, according to Smith (2010), should be sufficient to support fruit development. P and K play an important part in the accumulation in leaves and fruit of alternate bearing pecan trees, since a depletion of P and K reserves from a heavy demand, such as fruit development, might be a factor in alternate bearing (Krezdorn, 1955). Years of large crop loads in pecan resulted in leaf necrosis and partial early defoliation on the fruiting shoots (Smith, 2010). These shoots had lower P and K concentrations than the non-fruiting shoots. Necrotic symptoms on leaves would lead to defoliation and reduced nut weight, and therefore kernel quality. This defoliation, specifically premature defoliation, reduces the pistillate development of the following year and can initiate an alternate bearing cycle (Smith, 2010).

In a K deficient tree, developing fruit and foliage compete for available potassium, which could potentially trigger the abscission of fruit (Wood et al., 2010). During rapid fruit growth, K accumulates in fruit at a high rate, with a simultaneous loss from leaves (Smith, 2009) which could induce leaf scorching and defoliation if a deficiency is pre-existent (Sparks, 1977). Furthermore, when the endogenous K concentration of the fruit is 1.25% dry weight or less, it can induce a fruit drop period that coincides with the Stage-II drop period. Potassium is widely accepted to be the most important nutrient in pecan fruit and is especially high in the shuck tissue. During the fruit enlargement period the K concentration can increase up to eight times, which is present before this period (Sparks, 1985).

The premature abscission of flowers and fruit in tree crops is related to deficiencies in boron (B) because reproductive structures have a very high demand for B (Dell and Huang, 1997). Fruit set and fruit quality of various fruit and nut crops are increased through foliar B applications, e.g., an increase in fruit set of almonds [*Prunus dulcis* (Mill. D.A. Webb)] (Nyomora et al., 1997), and in ‘Italian’ prune (*Prunus domestica* L.) (Batjer and Thompson, 1949) and ‘Anjou’ pear (*Pyrus communis* L.) (Hanson et al, 1985.). Kernel quality of macadamia [*Macadamia integrifolia* (Maiden and Betche)] was improved by foliar B applications (Stephenson and Gallagher, 1987). The total mass of almond nuts increased with a simultaneous decrease in the hull percentage (Nyomora et al., 1999). Correct timing of foliar applied B is notably more important than the frequency of applications when trying to improve fruit retention. Applications during the pre-pollination stage has the best chance of increasing leaf B concentration, fruit retention and percentage kernel in ‘Desirable’ pecans (Wells et al., 2008). However, the efficacy is highly dependent of tree age and the environmental conditions. Leaf B concentration did not necessarily correspond with an increase in fruit retention or the quality of kernels, because the transportation of B is restricted to the xylem in pecans and it is therefore mediated by the transpiration stream (Wells et al., 2008), further emphasizing the

need for foliar applications during drought periods. In contrast, Kilby et al. (1998) found no effect of foliar B applications in Arizona on 'Western Schley' with sufficient foliar levels and high yields. However, they applied the B with a Zn spray and did not find any indications of B uptake in the leaves with their approach.

Water-stage fruit-split is a common problem in thin-shelled pecan cultivars for example: 'Oconee', 'Sumner', 'Wichita', 'Frotcher' and 'Farley' and occurs during the period preceding kernel filling, also referred to as "late water stage" where the turgor pressure within the liquid endosperm is increasing (Prussia et al., 1985) while the shell is hardening (Allison et al., 1987). The characteristic longitudinal split is caused by the rapidly expanding cotyledon within the ovule. The damaged nuts abort and drop approximately 7 days after splitting (Wood and Reilly, 1999), resulting in decreases in marketable product. The effect of foliar B and nickel (Ni) sprays on the incidence of water-stage fruit-split has been evaluated by Wells and Wood (2008). A number of nutritional factors contribute to water-stage fruit-split and timely foliar applications of either B or Ni decreases the severity of water-stage fruit-split in pecans (Wells and Wood, 2008).

Zinc (Zn) deficiencies have no effect on the abortion of fruitlets during the fruit growth period of 'Stuart' pecans, but it will rather increase the number of fruits that die and consequently dry in situ (Hu and Sparks, 1990). Zinc deficiencies greatly reduced fruit development rates and lead to a delay in shuck dehiscence, which can introduce logistical problems during harvest. Catkin development is strongly influenced by the Zn status of trees. Catkins produced from 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).

Irrigation

If the drought stress occurs before the onset of kernel development, it would lead to fruit abortion, but not leaf abscission (Ravindran et al., 2008).

Plant Growth Regulators

Wood (2011b) examined the influence that different plant growth regulators (PGRs) have on pistillate flower initiation in mitigation of alternate bearing of pecan trees. Pecans can exhibit up to three consecutive "on" years before a definite "off" year is encountered (Wood et al., 2003). Wood (2011b) proposed a model to explain pistillate flower initiation within pecans. According to the model there are three sequential phases of chromatin modification which control the initiation of pistillate flowers, the first of which is when florigen, produced in the

leaves, is translocated via the phloem which then acts as a level-1 signal to initiate phase-one chromatin modification, which leads to induction processes within bud primordia. The second phase chromatin modification is regulated by translocated phytohormones from leaves and/or fruit, which act within the primordia environment during the post-induction period. It functions as a "cytokinin-GA ratio" based level-2 signal, which is modulated by auxin and ethylene concentrations. The phase-three modification of chromatin is regulated by the concentration of one or more non-structural carbohydrates that act within the primordia environment during the vernalization period as a level-3 signal enabling pistillate flower development before anthesis. This three-stage model identifies possible avenues that can be used to manipulate pistillate flower development to enable producers to control alternate bearing and to harvest better quality fruit. Therefore, it is possible to manipulate flowering via application of different phytohormones to regulate the level-2 signalling pathway as was shown by Wood (2011b). Gibberellic acid (GA_3) and auxin [*B*-napththaleneacetic acid (NAA)] inhibit floral initiation, whereas prohexadione-calcium (3-oxido-5-oxo-4-propionylcyclohex-3-enecarboxylate), ethephon and a cytokinin [6-benylamino purine (6-BA)] together with a auxin transport inhibitor [2,3,5-triodobenzoic acid (TIBA)] promote pistillate flower initiation when applied before the kernel filling period (Wood, 2011b).

Applications of AVG (Retain®) to enhance nut retention on young, bearing 'Wichita' and 'Navaho' orchards in the Northern Cape, were investigated over three consecutive seasons (Snyman, 2021). At these high concentrations with various application times, AVG only increased nut retention significantly compared to the control in one season, for one site ('Wichita') and this did not affect yield. This confirmed varying results regarding cultivar, crop load-, concentration-interaction and timing of applications reported before by Wood et al. (2009) and Wood (2011).

ENVIRONMENTAL FACTORS

Temperature

High temperatures and low moisture during spring resulted in early maturity of staminate flowers, in contrast with cooler, dry conditions that promoted early maturity in pistillate flowers according to Morris (1925) as sited by Mullenax (1970), but this was contested by others. Flowering in pecans is primarily controlled by temperature, with higher temperatures resulting in earlier flowering (Han, 2018). Climate conditions, such as long photoperiods, high light intensity and water supply, longer growing seasons, carbon dioxide and warm temperature (no

parameters were given) also influence the juvenile length of seedlings and these climate conditions can promote growth leading to a reduced juvenility time, which can lead to earlier fruit production (Sherman and Beckman, 2003).

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. This coincided with the morphological development of the pistillate flower – when the inflorescence apex was just about to broaden. Freeze damage at this stage resulted in malformed pistillate flowers that aborted. The same temperatures during anthesis did not influence the morphological development. However, Sparks (1992) recommended further studies to confirm this observation.

Climate can also influence pollination of pecans. Temperatures near freezing can damage and kill female flowers and catkins. The degree of impact will depend upon the severity of the damage caused by the duration of the temperature near freezing point or below. These dead flowers will impact pollination and the overall nut production. The rate of flowering is also influenced by temperature. Temperature not only alters the date of pollen shedding, but also disrupts the timing of flower maturity between the male and female flowers (Wood et al., 1997). Pollen dispersal is influenced by the climate and a combination of dry air at relatively high temperatures and wind will shorten the release by the anthers, again, no set parameters were mentioned (Wood, 2000). These conditions will also influence the pistil's receptivity period.

Rain

Rainfall directly and indirectly determines production, by influencing the soil moisture and pollination directly and indirectly (Sparks, 1997). The duration and intensity of the rain will determine the severity of damage. Rain can wash away the pollen from female flowers. Moist and cool conditions can also lead to protracted and delayed dispersal of pollen, with wet conditions and lowered humidity leading to an immense release of pollen (Wood, 2000). Germination of pollen before it reaches the stigma was also reported when rain occurred during the flowering period in Israel.

Deviations in climate and weather are some of the major reasons for alternative bearing (Sparks, 1983). Climate conditions such as prolonged cloudy days and rainfall events, as well as severe short-term droughts, can induce irregular bearing for the following year, especially during a heavy crop year (Sparks, 1996).

Relative humidity (RH)

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, prior to unfavourable night temperatures which is often associated with spring (Yates and Sparks, 1993).

Heat units (HU)

Delayed bud break leads to protracted pollination and causes varying nut maturity resulting in multiple or delayed harvests (Sparks, 2000b). 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).

Wind

Wind also influences pollination directly as the pecan is wind pollinated with tree height increases the efficiency of wind pollination, because of the velocity that increases with height (Sparks, 2000b). 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 (Israel). No mention of exact temperatures occurred.

Soil moisture

Low soil moisture can also reduce the stomatal conductance, photosynthetic rate, transpiration, fluorescence and the chlorophyll content of pecan (Othman et al., 2014).

MANAGEMENT PRACTICES

Planting distance and orchard design

Tree spacing influences management practices and decisions, by increasing the difficulty of spraying and harvesting (Andales et al., 2006), pollination, thinning, orchard establishment, future maintenance, and labour costs (Fronza et al., 2018). Canopy density can also increase via management practices like continuous hedging, which stimulates high amounts of regrowth and potential excessive interior shading, often resulting in reduced yields (Sparks, 2000b).

CONCLUSIONS

The initial research on basic morphology and anatomy was performed in the early 1900's but were accurately documented and is still relevant today. It established a clear understanding of

the complexities of the reproductive flower organs that are required to interpret the contribution of these organs in insufficient fruit set and poor yields and illustrations of the organs can be used for further studies. New technology and methodology may contribute towards improved colour imaging of the organs and three dimensional construction thereof may prove beneficial when treatments which influence the anatomy or require labelling of mineral elements i.e zink, are applied and need to be quantified visually. Factors influencing the act of pollination were also investigated and quantified extensively in the USA and can be used, in conjunction with more recent papers from other regions, as point of reference to address fruit set challenges under local conditions. As environmental conditions and management practises differ between production regions, challenges with fruit set and yield will require *in situ* studies and a comprehensive (holistic) approach to determine the main factors influencing these processes for specific cultivars to plan future trials to address these challenges.

Acknowledgements

I am grateful for the contributions from the theses of MSc students TJ Snyman and AS Oberholzer and their co-supervisors Prof KI Theron and Dr NJ Taylor that were referred to in this review.

REFERENCES

Acuña-Maldonado, L.E., Smith, M.W., Maness, N.O., Cheary, B.S., Carroll, B.L. and Johnson, G.V., 2003. Influence of nitrogen application time on nitrogen absorption, partitioning, and yield of pecan. Journal of the American Society for Horticultural Science, 128(2): 155- 162.

Adriance, G.W., 1931. Factors influencing fruit setting in the pecan. Botanical Gazette, 91: 144-166.

Ajamgard, F., Rahemi, M. and Vahdati, K., 2017. Determining the Pollinizer for Pecan Cultivars. Journal of Nuts, 8(1):41-48.

Allison, J.M., Prussia, S.E., Daniell, J.W. and Tollner, E.W., 1987. Measuring the internal pressure of maturing pecans. Transactions of American Society of Agricultural Engineers, 30: 1869-1872.

Amling, H.J. and Amling, K.A., 1983. Physiological differentiation of pistillate flowers of pecan and cold requirements for their initiation. Journal of the American Society for Horticultural Science, 108: 196-198.

Andales, A., Wang, J., Sammis, T., Mexal, J., Simmons, L., Miller, D. and Gutschick, V., 2006. A model of pecan tree growth for the management of pruning and irrigation. Agricultural Water Management, 84(1-2):7-88.

Annon, 1982. Studies on pollination of pecan varieties in Israel. The Peacan Quarterly, 16(4): 26-30.

Batjer, L.P. and Thompson, A.H., 1949. Effects of boric acid sprays during bloom upon the set of pear fruits. Proceeding of the American Society for Horticultural Science 53: 141-142.

Bennet, T., Koflanovich, T. and Stahmann III, W.J., 1986. Pecan growers' experiences with artificial pollination. Western Pecan Conference Proceedings, 20: 8-10.

Bristow, P.R. and Shawa, A.Y., 1981. The influence of fungicides on pollen germination and yield of cranberry. Journal of the American Society for Horticultural Science, 106(3): 290-292.

Bristow, P.R. and Windom, G.E., 1987. Effects of selected fungicides, insecticides, and adjuvants on in vitro germination of highbush blueberry pollen. Plant Disease, 71: 326-328.

Burner, D., Brauer, D., Snider, J., Harrington, C. and Moore, P., 2013. Phenological responses of juvenile pecan and white oak on an upland site. Agroforestry Systems, 88(1):141-155.

Church, R.M. and Williams, R.R., 1977. The toxicity to apple pollen of several fungicides, as demonstrated by in vivo and in vitro techniques. Journal of Horticultural Science and Biotechnology, 52: 429-436.

Conner, P., 2007. Pecan Pollination. University of Georgia-Tifton campus, Horticulture Department. 3.

Connor, P.J., 2011. Optimization of in vitro pecan pollen germination. HortScience, 46(4): 561-576.

Crane, H.L., Hardy, M.B., Loomis, N.H. and Dodge, F.N., 1934. Effect of nut thinning on size, degree of filling and annual yield of pecans. Proceedings of the American Society of Horticultural Sciences, 32: 29-32.

Dedekind, R., 2020. Investigating the vegetative development and yield of pecan (MSc Thesis), Stellenbosch University, Stellenbosch. South Africa.

Dell, B. and Huang, L., 1997. Physiological response of plants to low boron. Plant Soil, 193: 103-120.

Finch, A.H. and Crane, H.L., 1931. Physiological factors associated with the productiveness of pecan shoots. Nat. Pecan Growers Association Bulletin, 29:98-107.

Fronza, D., Hamann, J., Both, V., Anese, R. and Meyer, E., 2018. Pecan cultivation: general aspects. Ciência Rural, 48(2).

Grauke, L.J. and Thompson, T.E., 1996a. Pecans and hickories. Janick, In: J. and Moore, J. (eds.). Fruit breeding. Vol 3. Wiley, New York. p. 185-239.

Grauke, L.J. and Thompson, T.E., 1996b. Variability in pecan flowering. Fruit varieties journal, 50: 140-150.

Hamilton, J. 1942. Studies of premature dropping of pecan nuts. Proceeding of the American Society for Horticultural Science, 40: 159-160.

Hamilton, P.T. and Romberg, L.D., 1933. Methods of controlling pollination in the pecan. Journal of Agricultural Research, 40(5): 287-296.

Hanson, E.J., Chaplin, M.H. and Breen, P.J., 1985. Movement of foliar applied boron out of leaves and accumulation in flower buds and flower parts of 'Italian' prune. HortScience, 20: 747-748.

Haulik, T.K. and Holtzhausen, L.C., 1987. Evaluation of five pecan cultivars [*Carya illinoensis* (Wang.) R. Koch] for yield, precocity, alternate bearing, leaf:nut ration and length of growing season in the Transvaal middle veld. South African Journal Plant Soil, 4(2): 70-74.

Haulik, T.K. and Holtzhausen, L.C., 1988a. Megagametogensis and embryology of the pecan (*Carya illinoensis*). South African Journal Plant Soil, 5(4):200-204.

Haulik, T.K. and Holtzhausen, L.C., 1988b. Anatomy of staminate flower ontogeny of the pecan as determined by scanning electron microscopy. South African Journal Plant Soil, 5(4):205-208.

Harris, O.W. and Smith, C.L., 1957. Chemical thinning of pecan nut crops. Proceedings of the American Society for Horticultural Science, 70: 204-208.

Heerema, R. and Walworth, J., 2016. Soil-applied zinc-EDTA: photosynthesis in 'Wichita' pecan grown on an alkaline and calcareous soil. Acta Horticulturae, 1109:89-94.

Heslop-Harrison, J., Knox, R.B., Heslop-Harrison, Y, and Mattsson, O. 1975. Pollen-wall proteins: Emission and role in incompatibility responses. In: J.G. Duckett and P.A. Racey (eds.). The biology of the male gamete. Academic, London. p 189-202.

Hinrichs, H.A. and Ramming, D.W., 1973. Flowering and nut development of pecans. Proceedings of the Oklahoma Pecan Growers Association, 21-28.

Hounnou, L., Wade Brorsen, B., Biermacher, J. and Rohla, C., 2019. Foliar applied zinc and the performance of pecan trees. Journal of Plant Nutrition, 42(5):512-516.

Hu, H. and Sparks, D., 1990. Zinc deficiency inhibits reproductive development in 'Stuart' pecan. HortScience, 25(11): 1392-1396.

Hu, H. and Sparks, D., 1991. Zinc Deficiency Inhibits Chlorophyll Synthesis and Gas Exchange in `Stuart' Pecan. HortScience, 26(3):267-268.

Isbell, C.L., 1928. Growth studies on the pecan. Alabama Agricultural Experimentation Station Bulletin 266: 1-63.

Kays, S.J., Crocker, T.F. and Worley, R.E., 1975. Concentration dependencies of ethylene on shuck dehiscence and fruit and leaf abscission of *Carya illinoensis*. Journal of Agricultural Food Chemistry, 23: 1116-1118.

Khalil, S.K., Mexal, J.G., Khalil, I.H., Wahab, S., Rehman, A., Hussain, Z., Khan, A., Khan, A.Z. and Khattak. M.K., 2016. Foliar ethephon fruit thinning improves nut quality and could manage alternate bearing in pecan. The Pharmaceutical and Chemical Journal, 3(4): 150-156.

Kilby, M.W. Neja, R. and Call, R., 1998. Foliar applications of Boron to Pecan Trees Does not affect fruit set. Citrus and Deciduous Fruit and Nut Research Report, 95-97 (http://hdl.handle.net/10150/220575.

Knuth, P. 1906. Handbook of flower pollination. Vol 3. Claredon Press, Oxford. Translation by J.R.A. Davis.

Krezdorn, A.H., 1955. The nutrient status of pecan leaves in relation to alternate bearing. Texas Pecan Growers Association, 34:43-53.

Kudan, A., Tuzcu, O., Bayazit, S., Yildirim, B. and Imrak, B., 2013. Studies on the chilling requirements of pecan nut (*Carya illionensis* Koch) cultivars. African Journal of Agricultural Research, 8(24):3159-3165.

Lockwood, D.W. and Sparks, D., 1978. Translocation of ^{14}C from tops and roots of pecan in the spring following assimilation of $^{14}CO_2$ during previous season. Journal of the American Society for Horticultural Science, 103: 45-49.

Loescher, W.H., McCamant, T. and Keller, J.D., 1990. Carbohydrate reserves, translocation, and storage in woody plant roots. HortScience, 25(3): 274-281.

Lord, W.J., Greene, D.W. and Damon, R.A., 1979. Flowering of young apple trees following summer pruning. Journal of the American Society for Horticultural Science, 104: 540-544.

Lord, E.M. and Russel, S.D., 2002. The mechanisms of pollination and fertilization in plant. Annual Review of Cell and Developmental Biology, 18: 81-105.

Madden, G.D., Brison, F.R. and McDaniel, J.C., 1969. Pecans. In: R.A. Jaynes (ed.), Handbook of North American nut trees. 163 – 189. Humphrey Press, Geneva, NY.

Madden, G.D. and Brown, E.J., 1973. Blossom dates of selected pecans. Pecan Quarterly, 7: 17-19.

Manning, W.E., 1940. The morphology of the flowers of the Juglandaceae. II. The pistillate flowers and fruit. American Journal of Botany, 27: 839-852.

Marquard, R.D., 1988. Outcrossing rates in pecan and the potential to increase yields. Journal of the American Society for Horticultural Science, 113: 84-88.

Marquard, R.D., 1992a. Pollen tube growth in *Carya* and temporal influence of pollen deposition on fertilization success in pecan. Journal of the American Society for Horticultural Science, 117(2): 328-331.

Marquard, R.D., 1992b. Fruit set of pecan requires a low percentage of live pollen in controlled pollination. HortScience, 27(5): 473.

McCarthy, B.C. and Quinn, J.A., 1990. Reproductive ecology of Carya (Juglandaceae): phenology, pollination, and breeding system of two sympatric tree species. American Journal of Botany, 77(2): 261-273.

McKay, J.W., 1947. Embryology of pecan. Journal of Agricultural Research, 74: 263-284.

Measham, P.F., MacNair, N., Quentin, A.G. and Bound, S.A., 2013. To cut or not to cut: The role of extension growth in fruit quality. International Society for Horticultural Science XII International Cherry Symposium, Spain, 23-27 June.

Mulcahy, D.L. and Mulcahy, G.B., 1987. The effects of pollen competition. American Scientist, 75: 44-50.

Mullenax, R.H., 1970. Bud ontogeny, flowering habits, and disease resistance studies of pecan, *Carya Illinoensis* (Wang.) K.Koch. PhD Thesis. Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College. Tennessee, USA.

Núñez-Moreno, H., Walworth, J. and Pond, A., 2012. Field identification and characterization of manganese toxicity in 'Western Schley' pecan trees. Acta Horticulturae, 938:291-298.

Nyomora, A.M.S., Brown, P.H. and Freeman, M., 1997. Fall foliar-applied boron increases tissue boron concentration and nut set of almond. Journal of the American Society for Horticultural Science, 122: 405-410.

Nyomora, A.M.S., Brown, P.H. and Krueger, B., 1999. Rate and time of boron application increase almond productivity and tissue boron concentration. HortScience, 34: 242-245.

Othman, Y., Steele, C., VanLeeuwen, D., Heerema, R., Bawazir, S. and St. Hilaire, R., 2014. Remote sensing used to detect moisture status of pecan orchards grown in a desert environment. International Journal of Remote Sensing, 35(3):949-966.

Polles S.G.; Long W.J.; Mullenax R.H., 1980. Flowering dates of several pecan cultivars and selections in the Central and Delta areas of Mississippi. Pecan-South (USA), 7(1): 38-41.

Prussia, S.A., Campbell, D.T., Tollner, E.W. and Daniell. J.W., 1985. Apparent modules of elasticity of maturing pecans. Transactions of American Society of Agricultural Engineers, 28:1290-1296.

Quinlan, J.D. and Preston, A.P., 1971. The influence of shoot competition on fruit retention and cropping of apple trees. Journal of Horticultural Science, 46: 525-534.

Ramming, D.W., 1968. Pollen tube growth and development in relation to chemical thinning of pecan nuts. MSc thesis. Faculty of the Graduate College of the Oklahoma State University, Oklahoma, USA.

Ravindran, C., Sharma, M. and Kher, R., 2008. Present status and problems of pecan nut (*Carya illinoinensis (*wang*.) K. Koch*) cultivation in Jammu and Kashmir. Acta Horticulturae, 772:179-182.

Redalen, G. 1980. Effects of fungicides on pollen germination and fruit set in raspberries. Gartenbauwissenschaft, 45(6): 248-251.

Reid, C.A., 1924. Further notes on pecan pruning. Proceedings of the Georgia-Florida Pecan Growers Association, 18: 44-49.

Rohla, C., Smith, M., Maness, N. and Reid, W., 2007. A Comparison of Return Bloom and Non-structural Carbohydrates, Nitrogen, and Potassium Concentrations in Moderate and Severe Alternate-bearing Pecan Cultivars. Journal of the American Society for Horticultural Science, 132(2):172-176.

Romberg, L.D. and Smith, C.L., 1946. Effect of cross-pollination, self-pollination and sib-pollination on the dropping, volume and kernel development of pecan nuts and vigour of the seedlings. Proceedings of the American Society of Horticultural Science, 47: 130-138.

Romberg, L.D. and Smith, C.L., 1950. Progress report on the breeding of new pecan varieties. Proceedings Texas Pecan growers Association. 29, 12-21.

Saure, M.C., 1987. Summer pruning effects in apple – a review. Scientia Horticulturae, 30: 253-282.

Schmidt, T., Elfving, D., McFerson, J. and Whiting, M., 2009. Crop Load Overwhelms Effects of Gibberellic Acid and Ethephon on Floral Initiation in Apple. HortScience, 44(7):1900-1906.

Schuhart, D.V., 1927. The morphological differentiation of the pistillate flowers of the pecan. Journal of Agricultural Research, 35:687-696.

Schuhart, D.V., 1932. Morphology and anatomy of the fruit of hicoria pecan. The Botanical Gazette, 93 (1): 1-20.

Sherman, W. and Beckman, T., 2003. Climatic adaptation in fruit crops. Acta Horticulturae, 622:411-428.

Smith, M., 2010. Relationship of leaf necrosis and defoliation to phosphorus and potassium concentrations in selected tissue and to certain fruit quality parameters of pecan. Scientia Horticulturae, 125(2):117-122.

Smith, C.L. and Romberg, L.D., 1940. Stigma receptivity and pollen shedding in some pecan varieties. Journal of Agricultural Research, 60(8): 551-564.

Smith, C.L. and Romberg, L.D., 1941. Pollen adherence as a criterion of the beginning of stigma receptivity in the pecan. Proceedings of the Texan Pecan Growers Association, 21: 38-45.

Smith, M.W., Wood, B.W. and Ruan, W.R., 2007. Recovery and partitioning of nitrogen from early spring and midsummer applications to pecan trees. Journal of the American Society for Horticultural Science, 132(6): 758-763.

Snyman, T.J., 2021. Investigating the Reproductive Potential and Yield of Pecans [*Carya illinoinensis* (Wangenh. K. Koch)] under South African conditions. MSc Agric thesis, Faculty of AgriScience, Stellenbosch University.

Sparks, D., 1977. Effects of fruiting on scorch, premature defoliation, and nutrient status of 'Chickasaw' pecan leaves. Journal of the American Society for Horticultural Science, 102(5), 669-673.

Sparks, D., 1983. Threshold leaf levels of zinc that influence nut yield and vegetative growth in pecan. HortScience. https://doi.org/10.21273/HORTSCI.28.11.1100.

Sparks, D., 1988. Effect of shoot vigour on pistillate flower production and abortion in 'Stuart' pecan. HortScience, 23: 570-571.

Sparks, D. 1989. Drought induces fruit abortion in pecan. HortScience, 24:78–79.

Sparks, D., 1992. Abnormal flowering in pecan associated with freezing temperature. HortScience, 27(7): 801-803.

Sparks, D., 1993. Chilling and heating model for pecan budbreak. Journal of the American Society for Horticultural Science, 118(1):29-35.

Sparks, D., 1996. A Climatic Model for Pecan Production under Humid Conditions. Journal of the American Society for Horticultural Science. https://doi.org/10.21273/JASHS.121.5.908.

Sparks, D., 1997. A Model for Predicting Pecan Production under Arid Conditions at High Elevations. Journal of the American Society for Horticultural Science. https://doi.org/10.21273/JASHS.122.5.648

Sparks, D., 2000a. Fruit set in pecan, *Carya illinoinensis*. Acta Horticulturae, 527: 35-48.

Sparks, D., 2000b. Pecan in warm climate. In: Temperate Fruit Crops in Warm Climates Springer, Dordrecht. pp. 381-403.

Sparks, D., 2005. Adaptability of pecan as a species. HortScience, 40(5):1175-1189. DOI: 10.21273/HORTSCI.40.5.1175.

Sparks, D. and Heath, J.L., 1972. Pistallate flower and fruit drop of pecan as function of time and shoot length. Hortscience, 7: 402-404.

Sparks, D. and Madden, G.D. 1985. Pistillate flower and fruit abortion in pecan as a function of cultivar, time and pollination. Journal of the American Society for Horticultural Science, 110: 219-223.

Stephenson, R.A. and Gallagher, E.C., 1987. Effects of foliar applied boron sprays on yield and quality of macadamia. Scientia Horticulturae, 32: 97-103.

Stout, A.B., 1928. Dichogamy in flowering plants. Bulletin of the Torrey Botanical Club, 55: 141-153.

Stuckey, H.P., 1916. The two groups of varieties of the *Hicoria* pecan and their relation of self-sterility. Georgia Agricultural Experimental Station bulletin, 124: 127-148.

Taylor, G.G., 1966. The relation of terminal growth to fruiting in pecans. MSc thesis, Graduate school of the Oklahoma State University, USA.

Thompson, T.E. and Romberg, L.D., 1985. Inheritance of heterodichogamy in pecan. Journal of Hereditary, 76(6): 456-458.

Titus, J.S. and Kang, S.M., 1982. Nitrogen metabolism, translocation and recycling in apple trees. Horticultural Reviews, 4: 204-246.

Weckler, P., Jones, C., Bowser, T., Hardin, J., Ning Wang, Franzen, A., Mathanker, S., Maness, N. and Smith, M., 2015. Technologies for enhancing pecan production and processing. Acta Horticulturae, 1070: 235-243.

Weinbaum, S.A., Picchioni, G.A., Maraoka, T.T., Brown, P.H. and Ferguson, L., 1994. Nitrogen usage, accumulation of carbon and nitrogen reserves, and the capacity for labelled fertilizer nitrogen and boron uptake varies during the alternate-bearing cycle in pistachio. Journal of the American Society for Horticultural Science, 119: 24-31.

Wells, M.L., 2008. Response of 'Desirable' and 'Kiowa' pecan to a late-spring freeze. HortTechnology, 18(3): 455-459.

Wells, L., 2015. Growth and Nitrogen Status of Young Pecan Trees Using Fertigation. HortScience, 50(6):904-908.

Wells, M.L., Conner, P.J., Funderburk, J.F. and Price, J.G., 2008. Effects of foliar-applied boron on fruit retention, fruit quality, and tissue boron concentration of pecan. HortScience, 43(3): 696-699.

Wells, M.L. and Wood, B.W., 2008. Foliar boron and nickel applications reduce water-stage fruit-split of pecan. HortScience, 43(5): 1437-1440.

Westwood, M.N., 1978. Temperate-zone pomology. Freeman, San Francisco.

Wetzstein, H.Y., 1990. Stigmatic surface degeneration and inhibition of pollen germination with selected pesticidal sprays during receptivity in pecan. Journal of the American Society for Horticultural Science 115(4): 656-661.

Wetzstein, H.Y. and Sparks, D., 1984. The morphology of staminate flower differentiation in pecan. Journal of the American Society for Horticultural Science, 109: 245-252.

Wetzstein, H.Y. and Sparks, D., 1989. Stigma-pollen interactions in pecan. Journal of the American Society for Horticultural Science 114: 355-359 (abstr.).

Wilhelmi, L.K. and Preuss, D., 1999. The mating game: Pollination and fertilization in flowering plants Curr. Opin. Plant Biol. 2, 18-22.

Wolstenholme, B.N., 1969. Effects of self-pollination on fruit set and nut drop of the pecan at Pietermaritzburg. Agroplantae, 1: 189-194.

Wolstenholme, B.N. and Storey, J.B., 1970. Fruit development. The Pecan Quarterly, 4(4): 15-19.

Wood, B.W., 1983. Fruit thinning of pecan with ethephon. HortScience, 18: 53-54.

Wood, B.W., 1989. Pecan production responds to root carbohydrates and rootstock. Journal of the American Society for Horticultural Science. https://agris.fao.org/agrisrearch/search.do?recordid=us8923049#:~:text=journal%20of%20the, issn%20%3a%200003%2d1062.

Wood, B.W., 1995. Relationship of reproductive and vegetative characteristics of pecan to previous-season fruit development and postripening foliation period. Journal of the American Society for Horticultural Science. https://doi.org/10.21273/JASHS.120.4.635

Wood, B.W., 1996. Cross-pollination in pecan orchards. HortScience, 31: 583.

Wood, B., W. 1996. Canopy Morphology of Pecan Cultivars. HortScience, 31(1):139-142.

Wood, B.W. 1997. Source of pollen, distance from pollinizer and time of pollination affects yields in block-type pecan orchards. HortScience, 32(7): 1182-1185.

Wood, B., 2000. Pollination Characteristics of Pecan Trees and Orchards. HortTechnology, 10(1):120-126.

Wood, B.W., 2011a. Influence of Aminoethoxyvinylglycine (AVG) on yield and quality of nut crops from a commercial pecan orchard. HortScience, 46(4): 586-589.

Wood, B.W., 2011b. Influence of plant bioregulators on pecan flowering and implications for regulation of pistillate flower initiation. HortScience, 46(6): 870-877.

Wood, B.W., 2017. Flavonoids, alkali earth, and rare earth elements affect pecan pollen germination. HortScience, 52(1): 85-88.

Wood, B., 2015. Regulation of vivipary in pecan. Acta Horticulturae, 1070:33-42.

Wood, B.W., Conner, P.J. and Worley, R.E., 2003. Relationship of alternate bearing intensity in pecan to fruit and canopy characteristics. HortScience, 38: 361-366.

Wood, B.W., Lombardini, L. and Heerema, R.J., 2009. Influence of aminoethoxyvinylglycine on pecan fruit retention. HortScience, 44(7): 1884-1889.

Wood, B.W. and Payne, J.A., 1983. Flowering potential of pecan. HortScience, 18(3): 326-328.

Wood, B.W. and Marquard, R.D., 1992. Estimates of self-pollination in pecan orchards in the Southeastern United States. HortScience 27(5): 406-408.

Wood, B., Smith, M., Worley, R., Anderson, P., Thompson, T. and Grauke, L., 1997. Reproductive and vegetative characteristics of pecan cultivars. HortScience, 32(6):1028-1033.

Wood, B., Wells, L. and Funderburke, F., 2010. Influence of Elevating Tree Potassium on Fruit Drop and Yield of Pecan. HortScience, 45(6):911-917.

Wood, B.W., Wells, L. and Funderburke, F., 2010. Influence of elevating tree potassium on fruit drop and yield of pecan. HortScience, 45: 911-917.

Wood, B.W., Smith, M.W., Worley, R.E., Anderson, R.E., Thompson, T.E. and Grauke, L.J., 1997. Reproductive and vegetative characteristics of pecan cultivars. HortScience, 32: 1028-1033.

Woodroof, J.G., 1924. The development of pecan buds and quantitative production of pollen. Georgia Agricultural Station Bulletin, 144: 134-161.

Woodroof, N.C., 1928. Development of the embryo sac and young embryo of hicoria pecan. American journal of botany. https://doi.org/10.1002/j.1537-2197.1928.tb09436.x

Woodroof, J.G., 1930. Studies of the staminate inflorescence and pollen of Hicoria pecan. Journal of Agricultural Research, 40: 1059-1104.

Woodroof, J.G. and Woodroof. N.C., 1926. Fruit-bud differentiation and subsequent development of the flowers in the Hicoria pecan. Journal of Agricultural Research, 33(7): 677-686.

Woodroof, J.G. and Woodroof. N.C., 1927. Distance pecan pollen is carried by wind for practical purposes. Georgia-Florida Pecan Growers Association, 21: 43-44.

Woodroof, J. and Woodroof, N., 1934. Pecan root growth and development. Journal of Agricultural Research, 49(6):511-530.

Worley, R.E., 1979. Fall defoliation date and seasonal carbohydrate concentration of pecan wood tissue. Journal of the American Society for Horticultural Science, 104: 195-199.

Worley, R.E., Dove, S.K., Mullinix, B.G., Jr. and Smith, M., 1992. Long-term dichogamy of 80 pecan cultivars. Scientia Horticulturae, 49: 93-101.

Worley, R.E. and Mullinix. B., 1997. Selective limb pruning of large pecan trees reduces yield but improves nut size and tree characteristics. HortScience, 32(1): 50-52.

Yates, L.E. and Sparks, D., 1990. Three-year-old pecan pollen retains fertility. Journal American Society for Horticultural Science, 115(3): 359-363.

Yates, I.E. and D. Sparks, 1992. Pecan cultivar conversion by grafting onto roots of 70-year-old trees. HortScience, 27: 803-807.

Yates, I.E. and Sparks, D., 1993. Environmental regulation of anther dehiscence and pollen germination in pecan. Journal of the American Society for Horticultural Science, 118(8): 699-706.

Yates, I.E. and Sparks, D., 1994. Anatomy differs for aborting and non-aborting pistillate flowers in pecan. Journal of the American Society for Horticultural Science, 119(5): 949-955.

Yates, I.E. and Sparks, D., 1995. Morphology of postpollination fruit abortion in pecan. Journal of the American Society for Horticultural Science, 120(3): 446-453.

Yates, I.E., Sparks, D., Connor, K. and Towill, L., 1991. Reducing pollen moisture simplifies long-term storage of pecan pollen. Journal of the American Society for Horticultural Science, 116(3): 430-434.

Yu, Y.B., Adams, D.O. and Yang, S.F., 1979. 1-aminocyclopropanecarboxylate synthase, a key enzyme in ethylene biosynthesis. Archives of Biochemistry and Biophysics, 198: 280-286.

Zhang, R., Peng, F., Liang, Y., Hao, M., and Li, Y., 2015. Flowering and pollination characteristics of Chinese-grown pecan (*Carya illinoinensis*). Acta Horticulturae, 1070:43-51.