STICK-TIGHTS AND VIVIPARY IN PECANS

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TABLE OF CONTENTS

1 DEFINITIONS AND SCOPE OF THE LITERATURE REVIEW

Stick-tights is a term used to define a lack of shuck split in some nuts, which results in the nut being retained in the green shuck on the tree at harvest time. In some cases, the kernel is underdeveloped, although in other cases the kernel is well developed and mature. Whilst the lack of shuck split in nuts with underdeveloped kernels is attributed to a lack of ethylene production required for shuck split, normally produced by a mature kernel, the factors underlying a lack of shuck split in nuts with mature kernels is currently unknown. The incidence of stick-tights is typically associated with stress during the kernel filling and shuck dehiscence stages.

Vivipary or pre-harvest sprouting is used to define the premature germination of seeds whilst still attached to the parent plant. Viviparous seeds do not undergo the same degree of internal desiccation, organelle differentiation, membrane stabilisation or metabolic quiescence, as compared to non-viviparous seeds and have thus not completed the maturation phase of seed development (Farnsworth, 2000). Preharvest sprouting, on the other hand, is the germination of physiologically mature seed when the environment is humid (Black et al., 2006). In pecan, viviparous seeds have typically not achieved maturity prior to sprouting and sprouting is not solely linked to a humid environment and therefore germination of pecan seed whilst on the tree is most accurately described as vivipary, according to Wood (2015). Vivipary in pecans often occurs in green stick-tights, where the kernel has matured or filled to some degree and where there is on some occasions still liquid endosperm in the seed. This is often attributed to two conditions, 1) high humidity between the shell and shuck and 2) high temperatures during

ripening (Wells, 2017). The degree of vivipary has been found to vary with crop load, irrigation, tree crowding, soil depth and length of the growing season. In addition, the longer the nut remains on the tree, the greater the chance of vivipary.

This literature review will attempt to assimilate the available literature (mainstream science and grower bulletins or grey literature) on stick-tights and vivipary to summarise the current state of knowledge of these phenomena in pecans. Focus will be on abiotic factors contributing to these phenomena, although biotic factors (insects and disease) can play a role in the decline of shucks. Management practices that can reduce the incidence of these disorders will also be discussed in relation to nut growth and the phenological cycle. Where possible, literature from other crops will be summarised, in an attempt to fully understanding the underlying mechanisms in pecan, with the aim of reducing these profit-limiting problems in pecan. It should be noted that there is a fair amount of conjecture in trying to explain the underlying mechanisms responsible for causing stick-tights and vivipary. Considerably more research is required to test these hypotheses of modes of action and possible avenues for future research are outlined in the conclusions. Before discussing these disorders, nut development and germination will be described, as this knowledge is critical for understanding casual factors for stick-tights and vivipary.

2 PECAN NUT DEVELOPMENT AND GERMINATION

Some of the most common physiological disorders in pecans are stick-tights, shuck-dieback, water stage fruit split and pre-germination/vivipary. These disorders can be a result of a number of factors, which include insufficient irrigation or drought stress, over-irrigation, poor fertilization, a heavy crop load, and pests and diseases (Call et al., 2006). In order to understand the underlying causes of these disorders, it is important to understand nut development and factors important to ensure the normal development of nuts (Figure 1). Flowering normally occurs in October/November (southern hemisphere) and at this stage some flowers can be prematurely shed. This shed can include (a) rudimentary flowers located near the shoot tip; (b) normal flowers that were not pollinated, and (c) pollinated flowers in which nutlets did not develop because food reserves were depleted during early growth or because of unfavourable soil water conditions. This is the first period of “nut drop” and can be cultivar dependent and usually goes unnoticed by the grower. The degree of drop is often inversely proportional to the shoot length or stress level imposed on the tree during the previous season (Wells, 2017). The process of fertilization takes approximately 2-6 days following pollination, which is unusually long, as it normally occurs within a few hours in most

plants. In December there is typically a second nut drop period, which is associated with incomplete fertilization or in other words poor fruit set. Double fertilization occurs in the pecan nut, whereby one sperm nucleus fuses with the egg nucleus to form an embryo and another sperm nucleus fuses with polar nuclei to form endosperm, which will nourish the embryo. This process offers two possibilities for premature nut shedding, which may occur at different times (unfertilized nuts usually drop before those where the endosperm fails to develop). Firstly, if the egg cell is not fertilized, premature shedding will occur, due to the lack of an embryo. Secondly, if the endosperm does not form properly there will be premature shedding due to a lack of nutritional support for the embryo. Approximately 25% of the total nut crop is shed during the first and second nut drop periods and is dependent on environmental stresses and pollination. Cross pollination is key for reducing fruit drop, as fruit drop has been shown to be correlated with self-pollination. Self-pollination increases the chances of fruit abortion and poor kernel development (Sparks, 2005).

Following normal fertilization, the nut starts to increase in size and after approximately 80-90 days final fruit size is reached (February). Final fruit size can only be impacted during this stage (Stage I of fruit growth) and factors impacting final fruit size include soil water, the availability of nitrogen and zinc and environmental conditions. Zinc seems to be more critical for nut survival during nut sizing than kernel development (Hu and Sparks, 1990). When all other factors are not limiting, hot days and warm nights encourage rapid nut growth, but size is also influenced by crop load, pollination and position of the nut on the tree. An orchard which has insufficient cross-pollination, is overcrowded, with much of the tree shaded, and has a heavy crop load will have reduced nut size, with the larger nuts found towards the top of the tree, where maximum sunlight is intercepted.

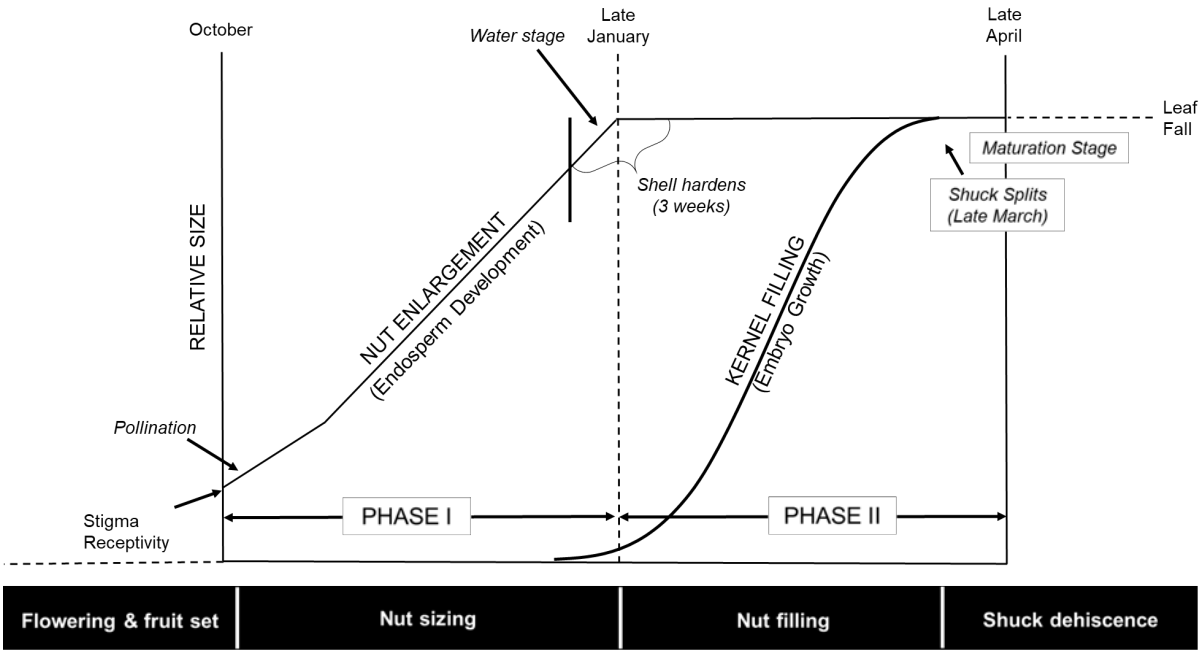

Figure 1 Pecan nut development (adapted from Herrera, 1990)

Stage I is also the stage of rapid endosperm development and from December to February the endosperm is rich in growth substances and sugars and is known as the water stage. Interestingly, embryo growth (later to become the kernel) is very slow during this stage, but by the end of Stage I it will have reached its final size. The seed coat or integuments grow slowly initially (first 50-70 days) following fertilization. In January the growth rate of the integuments increases and expands into the fissures of the packing material, forcing them against the surrounding walls. The pressure exerted by the liquid endosperm forces the integument into the available space within the shell. The integument becomes the seed coat 30 days later, and encloses the growing embryo. Once the embryo has attained full size, the ovary has completed its enlargement, and the pecan nuts will soon begin to harden. In late January shell hardening begins and is complete by middle to late February. Hardening begins at the apex of the nut and then progresses towards the base.

It is at this stage, the end of Stage I, that the third nut drop (late February to March) takes place. The percentage drop can be between 8-10% of large sized nuts and is thought to occur due to embryo abortion. If the embryo aborts after the shell hardens, the nut usually matures, but will be hollow (often leading to stick-tights). Although the exact causal factors for embryo abortion are unknown, the following situations seem to contribute to embryo abortion: 1) A severe drought or water stress. 2) A prolonged period of excess moisture or waterlogging. 3) Hot, dry winds which increase water loss by increasing the pecan tree moisture requirements due to high transpiration rates. 4) Insects which puncture the ovary wall, the future nut shell,

and cause nuts to fall in 3 or 4 days. 5) Physical damage that results in a disturbance of the ovary wall or shell of the nut (Byford and Herrera, 2005a).

Phase II occurs from shell hardening (or end of water stage) until the shuck splits. During this stage there is no further increase in nut size, as the hard shell prevents this, but the kernel develops, absorbing the endosperm and fills out by the end of March (3 weeks after shell hardening), ending when the hull or shuck splits along the four sutures. During the early stages the shuck increases in thickness and the kernel will continue to fill, provided the shuck remains green. Most of the storage material is translocated to the kernels in the last 6 weeks of kernel filling. This relatively short period of time, represents a severe drain on the reserves of the tree, especially considering the fact that the kernel is filled with oil and a given mass of oil requires 2.25 to 2.5 times its mass in carbohydrates. Any factor which impacts the carbohydrate resources of a tree will therefore influence nut filling. A high-quality kernel contains 73–75% oil, 12–15% protein, 3–4%, water and 1.5% minerals, which represents a significant drain on tree carbohydrate supplies. The opening of the shuck allows both the shuck and nut to dry. Moisture content of the nut declines from 30% at shuck opening to 8-12% at early harvest or 3.5-5% when trees reach dormancy. The release of the nut from the shuck depends on the dryness of the air and the nut shape, with round nuts tending be retained more in the shuck.

As mentioned above, nut development in pecans is an exhaustive process, that can impose a great deal of stress on the tree, due to the high energy requirements of filling nuts (Smith et al., 1993). The degree to which nuts are filled, or how developed the kernels are at harvest, is determined by a rather large number of interrelated factors. These factors are summarised as follows, 1) The size of the crop in relation to the leaf area will determine if the tree is capable of producing sufficient photoassimilates to fill the nuts. If there are too many nuts per unit leaf area, then the nuts may not fill properly. In addition, excessive secondary vegetative growth will also impact nut growth, as this growth utilises important carbohydrate reserves. 2) Large nuts also require more photoassimilates to fill the nuts and thus in seasons where conditions favour the development of a large number of large nuts, these nuts may be poorly filled. 3) The canopy should also be healthy and vigorous for optimal photoassimilate production. This includes nutritional deficiencies and pests and/or diseases which damage the foliage. Growers should therefore try and maximise canopy growth in early spring and summer by ensuring adequate nitrogen and irrigation before bud break, followed by zinc applications to prolong shoot growth. Correct irrigation scheduling is important for ensuring adequate soil water for uptake by the trees to maximise photosynthesis and nutrient uptake. Proper nutrition is therefore also vital. 4) The size of the crop in the previous season and how well they were

filled can influence production in the current season, as a large crop of well-filled nuts will deplete the tree of reserves by the time the nuts are harvested. Ensuring an optimal nutritional status of the tree following harvest is important to maintain a healthy canopy in order to replenish these reserves and ensure adequate production of female flowers in the following season. Premature defoliation will therefore have a negative effect on yield and quality. In early maturing varieties this is easier to achieve, as there is a greater post-harvest period to replenish reserves. 5) The prevailing weather conditions can also impact nut filling. Prolonged dry spells or drought will reduce kernel filling, mostly through a reduction in photosynthesis as a result of stomatal closure. Hot weather, which causes shuck sunscald or burning will also impact nut filling. This occurs on the north or north-west sides of the trees that are exposed to afternoon sun and have a sparse canopy, thereby exposing the nuts to the hot afternoon sun. 6) Cross-pollination or heterosis has been reported to be important for good nut size and nut filling, with self-pollinated nuts having poorly filled kernels.

Shortly after nut filling has been completed, the dehiscence period starts, during which the shuck separates from the nut (Kays, 1978). This process starts at the tip of the nut and progresses towards the stem end. This is followed by the development of the shuck abscission zone, the splitting of the shuck, the start of the change in colour of the kernel, the opening of the shuck and finally nut drop. These steps do not always follow on from one another and many can overlap. Initially the seed remains attached to the shuck via vascular strands (Sparks and Yates, 1995), but with time these strands gradually separate, which facilitates the drying process of the nut, which can last up to 2 weeks. The nut will then either fall from the tree or the tree can be mechanically shaken to release nuts within the dried husk.

It is thought that this long drying period prevents the drop of a non-dormant seed that would otherwise germinate during a warm autumn period (Sparks, 2005). This is often observed on the tree during hot autumns and is referred to as vivipary. Seed dormancy ensures that the seed will only germinate once conditions are suitable for growth (i.e. in Spring) and it is suggested that seed germination of pecans is regulated by both heating and chilling (Sparks, 1974; Wolstenholme, 1974). Understanding pecan seed germination and factors required for successful germination is important when trying to understand the causes of vivipary, which will be discussed later. Contrary to the report by Sparks (2005) on pecan seed dormancy, Dimalla and Van Staden (1978) provided good evidence to suggest that pecan seeds are not physiologically dormant, but rather have a mechanical restriction to germination. Although the shell of a pecan appears to be a formidable barrier, Dimalla and Van Staden (1976) and Van Staden and Dimalla (1976) demonstrated that it does not impede the transfer of water or gases, both of which are required for germination. Rather, radicle protrusion is restricted by

the shell, which acts as a mechanical barrier. Dimalla and Van Staden (1976) and Van Staden and Dimalla (1976) also found no additional benefit of cold stratification of the nuts, with no difference in germination between nuts dried to a low moisture content following harvest and immediately germinated and those stored at 5ºC for up to 10 months. In addition, pecan nuts removed from shucks at maturity were capable of germination when incubated at 30 ºC (Dimalla and Van Staden, 1976; Van Staden and Dimalla, 1976) and remained viable for an extended period of time, provided they were stored correctly to prevent rancidity. Importantly, the optimum temperature for pecan germination is between 30 and 35 ºC (Van Staden and Dimalla, 1976) and at this temperature the mechanical effect of the shell is almost completely nullified. Interestingly, although the number of cultivars evaluated was limited, Dimalla and Van Staden (1976) found no differences in germination requirements between nuts of cultivars adapted to cooler conditions and those adapted to warmer conditions. Although, King and Roberts (1980) described pecan seeds as recalcitrant, they don't quite fit the absolute definition of recalcitrancy. Berjak et al. (1989) defined recalcitrant seeds as those seeds undergoing no maturation drying at the final phase of development, tolerate very little post-shedding desiccation and are often chilling-sensitive. Pecan does tolerate post shedding desiccation (the nuts start drying once the shuck opens) and is not chilling sensitive, as seeds can be stored at 5 ºC without loss of quality. The drying of the nuts as the shuck opens and storing nuts in a low humidity environment is therefore key to avoiding germination following harvest.

3 CAUSES OF STICK-TIGHTS IN PECANS

Stick-tights in pecan occur when shucks remain green on the tree and fail to open (Figure 2). In some cases, the kernel fails to develop, whilst in others the kernel is mature. In general, kernel abortion typically occurs during the water stage, leaving only the seed coat within the nut. The shuck does not open in nuts where the kernel fails to develop, as a result of a lack of ethylene due to embryo abortion. Typically, the mature kernel produces ethylene which causes the shuck to split, along predetermined sutures or abscission zones. When the kernel is mature in stick-tights, the kernel remains extremely moist and the seed coat is darkened (Wells, 2017). There is still a lack of understanding as to why shuck split is delayed when the nuts inside are mature, but may perhaps be related to hormonal imbalances that are associated with vivipary, as these nuts often germinate whilst on the tree. As a result, some of the factors leading to stick-tights with mature kernels may contribute to vivipary. Interestingly, this disorder is not only limited to pecans but occurs to varying degrees in macadamias, walnut and almond.

Figure 2 Examples of stick-tights in pecans. The poorly filled kernel is visible in the right hand image http://northernpecans.blogspot.com/2016/11/stick-tights-when-pecan-kernel-doesnt.html)

In order to understand the occurrence of stick-tights, the role of the shuck in nut growth and the process of shuck split need to explained. The shuck plays an important role in the development of the kernel, as nutrients required for the development of the kernel and shell are transported through the shuck (Shuhart, 1932). Stress caused by a heavy crop load, is often manifested in poor quality fruit and shuck deterioration that may result in premature shuck opening and/or stick-tights in some instances. This is usually first noticeable in February to March, with stick-tights first characterized by black markings on the shuck (Call et al., 2006).

Shuck dehiscence is a three step process, with each step segregated in time from two to several days (Sparks and Yates, 1995). The first step involves the shuck separating from the shell and the development of shell markings, both of which develop from the distal end (pointed end of the nut, away from where it is attached to the tree). This is followed by the start of the abscission of the sutures from the distal end, which separates the shuck into four quarters. The final step is when the vascular system partially detaches from the dorsal surface or upper surface of the shuck, which begins at the proximal end of the nut (end attached to the tree). It is at this point that the shuck will start to dry. The separation of the nut from the shuck therefore involves three abscission zone 1) between the shuck and the shell, 2) between the sutures and 3) between the vascular system and the shuck. Factors impacting any of these

processes could lead to stick-tights. Environmental stresses can accelerate maturation of the preformed abscission zones resulting in premature shuck opening (Sparks et al., 1995), which is important for early harvest technology. Exogenous applications of ethylene hastens shuck opening (Kays et al., 1975) and suggests a role for ethylene in the regulation of shuck dehiscence, as has been demonstrated by Lipe and Morgan (1972). Typically, the mature kernel produces ethylene, which causes the shuck to split and thus the failure of the embryo to produce ethylene usually results in stick-tights. Stein et al. (1986) demonstrated that trunk injections of ethephon were able to cause shuck dehiscence, but only when applied during the critical stage of shuck separation from the nut. There was little impact on leaf drop when trunk applications were made at this stage.

Stick-tights are best prevented by avoiding late season stress, which is most often related to water stress, either too little or too much (drought or waterlogging). Other stresses include crowded trees, lack of sunlight reaching the nuts or prolonged cloudy conditions, poor soils, poor weed control (Call et al., 2006), an early freeze, low heat units during the growing season, excessive N, low Zn levels, and excessive nut production or heavy crop loads (Carroll et al., 2015). The greater the leaf area per nut, the better the chance that the nuts will be well filled and the lower the chance of stick-tights. Studies have shown that each nut requires 8-10 functional leaves to adequately fill the nuts (Carroll et al., 2015). Fruit thinning may therefore be an option during heavy bearing years. According to Byford and Herrera (2005b), drought stress can be cultivar/variety dependent, with ‘Wichita’ trees being more susceptible to water stress than ‘Western Schley’, causing them to have more stick-tights at the end of the season. Late watering of pecan, up until the leaf drop stage, reduces stick-tights and increases a clean nut drop. Núñez-Moreno et al. (2017) found that at higher rates of N the incidence of stick-tights increased in ‘Western Schley’ trees in Arizona. Hu and Sparks (1990) demonstrated that shuck dehiscence was delayed and the rate of dehiscence was drastically reduced as Zn deficiency increased (Figure 3). These authors suggested that the impact of Zn on shuck dehiscence may be indirect through the negative impact of Zn deficiencies on kernel development, which in turn impacts ethylene production that is required to trigger dehiscence. The correlation between kernel development and maximum shuck dehiscence with regards to shoot Zn concentration demonstrates that the stick-tights in this case were mostly associated with nuts which had failed to fill properly (Hu and Sparks, 1990) (Figure 4).

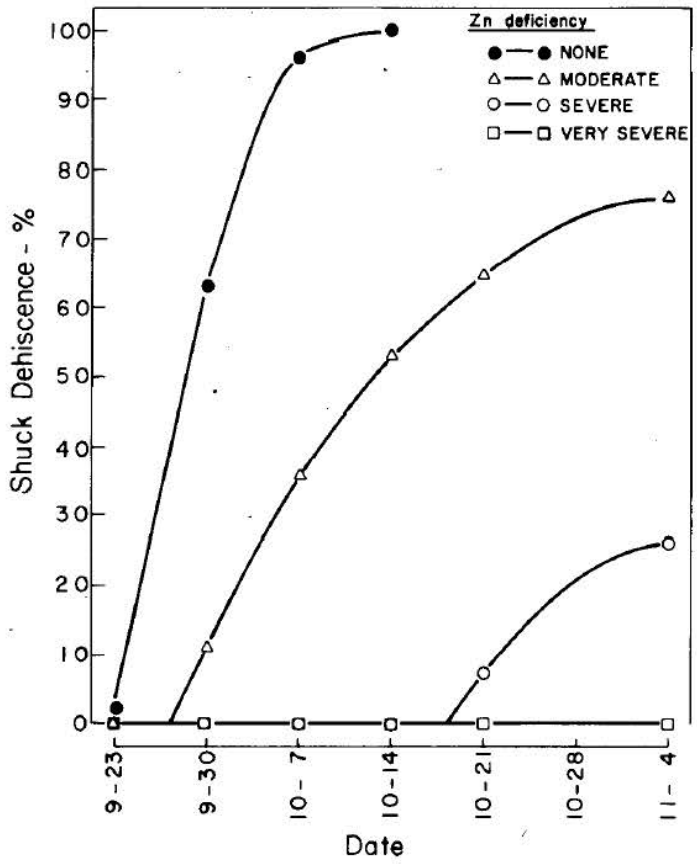

Figure 3 Effect of severity of Zn deficiency on shuck dehiscence of 'Stuart' pecan in Georgia, USA (Hu and Sparks, 1990)

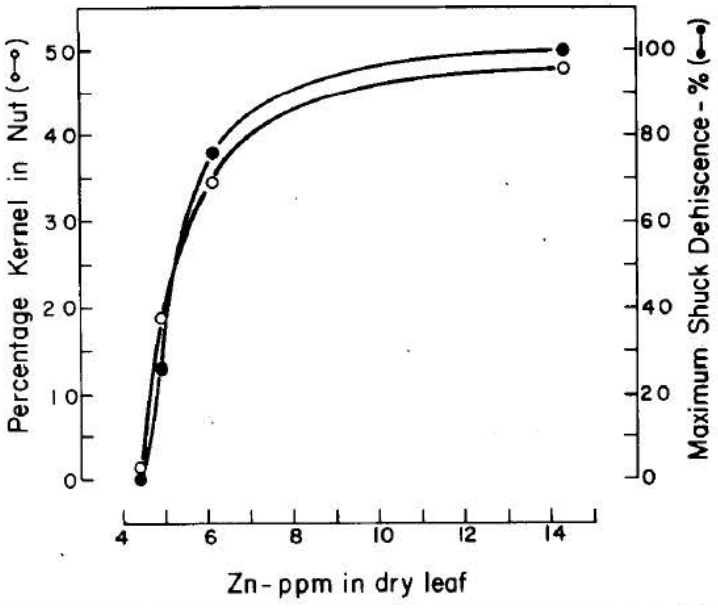

Figure 4 Influence of Zn in leaves of the supporting shoot on kernel development and shuck dehiscence in 'Stuart' pecan in Georgia, USA (Hu and Sparks, 1990)

Early kernel abortion as a result of heavy crop loads can also lead to shuck decline, which is proposed to be the result of the acceleration of normal senescence. The shucks can blacken if this occurs early in fruit development and they may fall from the tree. It is important to note that this can also occur without any pathogen. Years of high crops loads are generally associated with severe shuck decline, while very little shuck decline is found in years with low crop loads (Sparks et al., 1995). Shuck decline also seems to increase as the tree ages and could be associated with a decrease in the nut to leaf ratio, as the tree matures. Sparks et al. (1995) demonstrated that midseason fruit removal decreased the incidence of shuck decline. Percentage kernel also increased with an increased percentage of fruit thinned. However, these authors also suggested that fruiting stress alone was unlikely to be solely responsible for shuck decline and that an additional stress factor combined with fruiting stress to bring about the observed level of shuck decline. These stress factors could include inadequate sunlight penetration throughout the canopy and water stress, either waterlogging or drought. Decline has been observed to be worse in shaded parts of the tree or in crowded areas of the orchard, as opposed to open areas (Sparks et al., 1995). If stress occurs during the early stages of kernel development the impact on kernel quality can be quite severe. However, if the stress occurs late in the season close to nut maturity, there is little impact on kernel quality.

Figure 3 Development of shuck necrosis or shuck decline (Heerema et al., 2010)

Data from a water stress experiment on the University of Pretoria's Hatfield Experimental farm (Water Research Commission and SAPPA co-funded project K5/2814//4) has shown that water stress during kernel filling significantly increases the % of unfilled kernels (wafers and air pocket) and reduced the mass of nuts (higher number of nuts per kg) (

Table 1 and Table 2). In the 2017/2018 significant rainfall during the shuck dehiscence period resulted in minimal stress being achieved during this period and there was no impact on stick-tights (

Table 1). However, in the 2018/2019 season significant water stress was achieved during shuck dehiscence and the % stick-tights significantly increased (Table 2). This confirms that water stress during this stage can cause an increase in the incidence of stick-tights. Although stress during nut filling increased the % unsound kernel, there was no recorded impact on stick-tights. It is possible that stress at this early stage could have caused shuck decline rather than delayed shuck dehiscence.

Table 1 The impact of water stress at different phenological stages on quality parameters of pecans for the 2017/2018 season

Treatment	Diameter (mm)	No. of nuts/kg	Kernel % (halves)	Kernel % (pieces)	Kernel %	Moisture %	Wafer/air pockets %
Control	19 ± 0.04a	163.0 ± 4.2a	37.2 ± 2.2a	18.0 ± 2.68a	55.2 ± 0.64a	2.2 ± 0.11a	15.8 ± 0.32a
Flowering and nut set	19 ± 0.18a	166.0 ± 5.44a	29.6 ± 4.86a	24.8 ± 4.63a	54.3 ± 0.79a	2.5 ± 0.22a	15.4 ± 0.38a
Nut sizing	19 ± 0.34a	160.1 ± 5.85a	36.9 ± 2.97a	18.6 ± 2.56a	55.5 ± 0.6a	2.3 ± 0.08a	15.4 ± 0.47a
Nut filling	19 ± 0.33a	176.8 ± 1.89b	38.5 ± 4.18a	17.0 ± 3.27a	56.5 ± 1.18a	2.1 ± 0.07a	24.1 ± 0.42b
Shuck dehiscence	19 ± 0.13a	164.3 ± 4.61a	36.9 ± 3.78a	17.5 ± 2.69a	54.4 ± 1.15a	2.3 ± 0.03a	15.5 ± 0.61a

Table 2 The impact of water stress at different phenological stages on quality parameters of pecans for the 2018/2019 season

Treatment	Diameter (mm)	No. of nuts/kg	Kernel %	Moisture %	Unsound Kernel (% pops)	Wafer/air pockets %	Stick-tights %
Control	21 ± 0.19a	137 ± 0.74a	58.4 ± 0.57a	3 ± 0.59a	2.5 ± 0.47a	13.9 ± 0.34a	6.2 ± 0.76a
Flowering and nut set	21 ± 0.64a	135 ± 1.32a	62.0 ± 1.09a	2.2 ± 0.09a	2 ± 0.43a	14.1 ± 0.44a	6.8 ± 0.73a
Nut sizing	19 ± 1.13a	159 ± 1.61b	57.0 ± 0.64a	2.0 ± 0.18a	1.6 ± 0.32a	14.7 ± 0.46a	7.2 ± 0.58a
Nut filling	21 ± 0.41a	152 ± 0.89b	58.0 ± 0.46a	2.0 ± 0.17a	7.9 ± 0.68b	22.3 ± 0.67b	7.1 ± 0.67a
Shuck dehiscence	21 ± 0.68a	139 ± 1.45a	57.0 ± 0.55a	2.0 ± 0.07a	2.9 ± 0.67a	14.3 ± 0.43a	14.4 ± 1.25b

Stick-tights are also an issue in almond, where a number of nuts can remain on the tree following mechanical harvest. This is seen as problematic as they can harbour pests over the winter period. Cajales (2011) indicated that the number of stick-tights can be manipulated with certain levels of water stress at specific times of the season, with stress between hull split and harvest causing a significant number of stick-tights The number of stick-tights was affected by the severity of the stress, with a strong linear increase in stick-tights with midday stem water potential (MSWP) below -3.0 MPa, reaching a maximum of approximately 0.33 stick-tights per kg of harvested nut, when MSWP reached -5.5 MPa (Figure 5). According to these results, the number of stick-tights can potentially be reduced when preharvest water stress is avoided in almonds. As with pecans, the incidence of poorly filled hazelnuts increased under water deficits (Bignami et al., 2008).

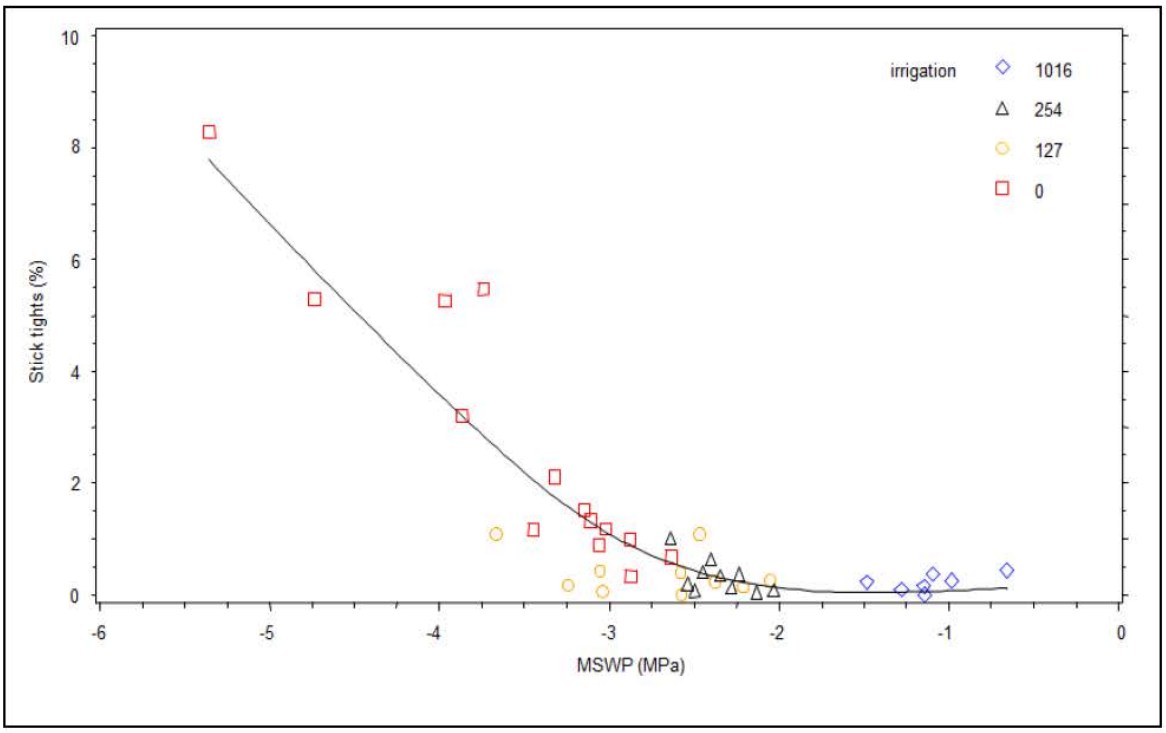

Figure 5 Stick-tights (%) as a function of average midday stem water potential (MSWP) determined in July (Cajales, 2011). The different irrigation treatments are mm applied irrigation during a season.

4 CAUSES OF VIVIPARY IN PECANS

Vivipary refers to the germination of seeds while still attached to the mother plant. Vivipary is found in a large number of angiosperm plants, including several economically important species. Most commercially grown grain crops exhibit vivipary under unusually hot and wet

conditions. There are also a number of trees that are known to be viviparous, although there are very few reports of vivipary in commercial tree crops. Farnsworth (2000) suggests that vivipary is more common in plants with a particular morphological profile, which includes 1) large seeds, which occur singly in a fruit, 2) seeds which have a hard endocarp surrounded by fleshy tissue that maintains the internal water content, 3) directed dispersal species (a seed dispersal strategy which allows plants to reach specific habitats that are favourable for survival), 4) species with long adult life spans, 5) those that are less specialised to microhabitats and 6) those adapted to moist habitats. As pecan fits most of these criteria, it is highly likely that this specie will be prone to vivipary under the right conditions (Wood, 2015). Vivipary tends to be almost exclusively found in species which originate from hot, humid areas; riverine, coastal or swamp environments; or at the very least, areas with mild winters where water is available. In these areas vivipary can be highly advantageous, with seeds having germinated before dispersal having a head-start over those that have to wait for conducive conditions on the ground before germinating, as well as being able to use maternal resources for a longer period. In some cases, vivipary may be present because of a lack of selection pressure against the trait under the above-mentioned conditions (Farnsworth, 2000). Pecan is a good example of this, with varieties bred out of wild populations in the more tropical Southern parts of the natural range of the species (Southern varieties) being susceptible to vivipary, whilst Northern varieties, developed from populations in the colder North of the range, do not generally exhibit vivipary (Díaz, 2013; Ou et al., 1994; Sparks, 2005). Cross-pollination may also play a role and incidence of vivipary seems to be lower when Southern varieties are pollination by Northern varieties (Ou et al., 1994).

While vivipary may be an adaptation to take advantage of a particular set of conditions and increase survival in the wild; in cultivated pecans it is a cause of economic loss (Figure 6). The process of germination uses stored carbohydrates for growth and in the process causes blackening of the embryonic region (the region where the two kernel sections are attached), a condition commonly known as embryo rot. Such nuts are completely unmarketable (Sparks et al., 1995; Wood, 2015). In some cases vivipary related crop loss can be >70% in parts of the USA (Wood, 2015). In North America this disorder is usually most severe in the hotter production regions, which include lower San Joaquin Valley of California, lower elevations in Arizona, portions of the mid- to lower Rio Grande Valley of Texas, and lower elevation arid regions of northern Mexico. In these warmer pecan production areas, where vivipary is fairly common, producers may “green harvest” their pecans before normal shuck split and before kernels have initiated germination. “Green harvest” creates additional processing expense because, unlike the traditional pecan harvest, it requires mechanical removal of the unsplit pecan shucks and drying of the nuts. Vivipary also seems much more prevalent in the hotter

pecan production regions in South Africa, located in the west of the country (Personal communication Hardus du Toit).

Figure 6 Premature germination or vivipary in pecan nuts (photos by Hardus du Toit)

While the genetic potential for vivipary is always present, especially in Southern pecan cultivars (genotypes originated from the warmer southern areas of the USA), the trait is only expressed under particular environmental and management conditions. Northern varieties (genotypes originated from the colder northern areas of the USA) are typically adapted to a shorter growing period (160-180 days) as compared to Southern varieties (190-220 days), with seed from Southern varieties germinating more readily than Northern varieties (Ou et al., 1994). It is very common in 'Wichita', 'Western Schley', 'Burkett', 'Mahan', 'Cheyenne', 'GraKing', 'Shawnee', 'Choctaw', 'GraTex', 'Oconee', and 'Pawnee', but relatively rare in 'Sioux', 'Caddo' and 'Squirrel's Delight' in the United States (Wood, 2015). In general, a combination of high NO_3^-, high seed moisture, warm night temperatures and low abscisic acid (ABA) concentration, appear to be especially powerful triggers for vivipary in plants. The availability of late season nitrogen, low soil pH and Mo deficiency increased vivipary in maize (Farwell et al., 1991). In addition, vivipary in pecan is favoured by a high crop load, long growing season, delayed shuck opening and splitting (vivipary is not always linked to stick-tights) and the duration of time nuts are on the tree before harvesting. It has also been linked to irrigation (excessive irrigation or rainfall leading to waterlogged conditions close to harvest or abnormally dry conditions), vigorous trees, particular soil characteristics, sunlight conditions, excessive nitrogen fertilisation during the later stages of nut development, and high temperatures at the end of the season (Díaz, 2013; Wood, 2015). Sparks et al. (1995) demonstrated that fruiting stress in 'Wichita', in an orchard in Texas, increased the incidence of premature germination, with vivipary occurring in direct proportion to fruiting stress (Figure 7), which was also associated with delayed shuck opening. During years with heavy crop loads, premature germination has even been observed to occur before the kernel matures (Sparks et al., 1995). Wood (2015) demonstrated that combining moist soil, with plenty of N

triggered considerable vivipary in 'Cheyenne'. Any process which delays shuck ripening or splitting does seem to result in an increased incidence of vivipary, as this prevents the drying of the nut when the shuck opens, which is required to prevent the seed from germinating. The maintenance of high moisture within the nut could therefore be a contributing factor to premature germination, provided temperatures are high enough. Dimalla and Van Staden (1978) demonstrated that the pecan shell is freely permeable to water and gases, but places a mechanical restriction on radicle growth. This mechanical effect can be overcome by germinating nuts at high temperature (30-35 ºC). The high temperature requirement for vivipary in pecan may therefore be linked to overcoming the mechanical restraint placed on the seed by the shell. Early crop maturity and a hot, dry March could therefore potentially cause an increase in the incidence of vivipary. Early crop maturity generally results from early budbreak due to high chilling units below 4 ºC in winter and high heat units in spring, which advances shoot elongation and flower development (https://site.extension.uga.edu/pecan/2019/10/green-shucks-sticktights-and-poor-kernel-development/), and as a result the crop matures earlier, over a hotter time of year. Tracking chill unit accumulation, spring heat and temperatures in March may be important for predicting the possible occurrence of vivipary and may require an earlier harvest.

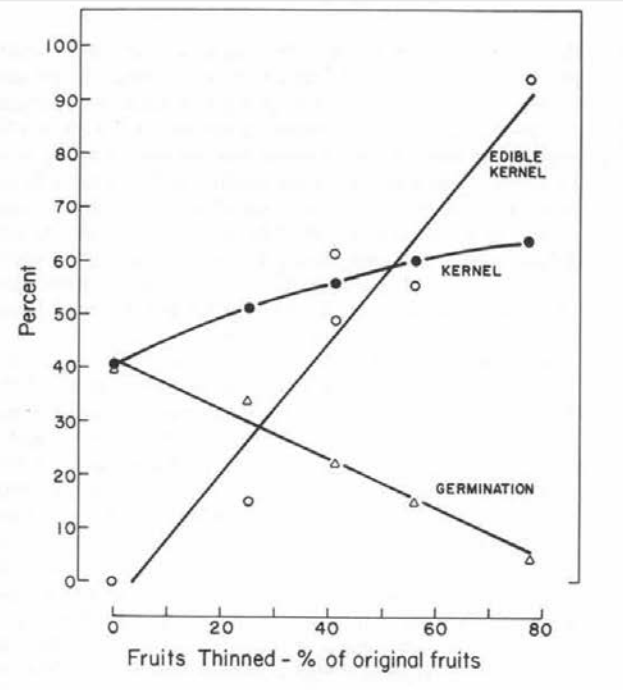

Figure 7 Percent kernel, edible kernel and germination of 'Wichita' nuts, as influenced by fruit thinning during the water or liquid endosperm stage of fruit development (Sparks et al., 1995)

Abscisic acid is proposed to play an important role in seed maturation and seed dormancy, with ABA deficient or ABA insensitive species exhibiting vivipary (Farnsworth, 2000). Although the mechanism is not completely understood, vivipary occurs when ABA is not produced or translocated to the developing embryo by the mother plant, or the embryo itself does not produce ABA or the receptor to the hormone is absent (Farnsworth, 2000; Wood, 2015). In such cases the embryo does not complete its development to the desiccation stage, instead germinating as soon as it becomes viable. Under normal conditions, ABA induces a regulatory cascade that causes maturation and desiccation of the seed, so that it is able to survive in a dormant/semi-dormant state when unattached to the mother plant. This process includes dehydrin proteins and particular carbohydrates that stabilise the drying seed and most likely also includes other plant hormones (Díaz, 2013; Farnsworth, 2000). The importance of ABA in vivipary or pre-harvest sprouting is illustrated by findings in soybean (Ackerson, 1984), wheat and rice (Fang and Chu, 2008), where low ABA was associated with pre-harvest germination. The importance of ABA for preventing vivipary in pecan was demonstrated by Wood (2015), who found that applications of fluridone, an inhibitor of ABA biosynthesis, was able to increase the incidence of vivipary in 'Oconee'. In addition, effects of fluridone could be reversed by a timely exogenous application of ABA and the normal incidence of vivipary, relative to a control, could be reduced through exogenous applications of ABA (Wood, 2015). Wood (2015) therefore suggested that ABA is a key regulator of vivipary in pecan; and therefore, environmental factors that directly or indirectly influence either ABA concentration, or possibly receptor sensitivity to ABA, will most likely increase the incidence of vivipary. In addition, factors which impact nitrate metabolism will also likely influence the occurrence of vivipary. Bearing this in mind, Wood (2015) speculated that micronutrient deficiencies, including Fe, Mo and Cu, could have an impact on the incidence of vivipary, as these elements play a role in ABA biosynthesis and nitrate metabolism.

The impact of high nitrates on vivipary is most probably due to the fact that nitrate acts as a modulator of several metabolic and developmental processes in plants, one of which is the breaking of seed dormancy (Miller et al., 2007). Alboresi et al. (2005) demonstrated in Arabidopsis that high NO_3^- prevented the maintenance of dormancy and stimulated germination, which may have involved interaction with both the ABA or gibberellin pathways. Nitrate seems to regulate ABA levels by activating enzymes responsible for ABA catabolism, thereby reducing ABA concentration in tissues (Duermeyer et al., 2018). As a result, ABA is unable to accumulate in seeds and germination can be initiated under favourable conditions. However, links between NO_3^-, GA biosynthesis and vivipary are not clear. This work has only been done in Arabidopsis and needs to be expanded to other plants and more information is required on the exact mechanisms. In terms of other macronutrients, high ABA was associated

with low incidence of vivipary and high potassium content in bell peppers, with low potassium leading to an increased incidence of vivipary (Marrush et al., 1998).

A molybdenum deficiency has been linked to pre-harvest sprouting in maize (Farwell et al., 1991) and wheat (Modi and Cairns, 1995). Farwell et al. (1991) suggested that Mo deficiency was a primary causal factor in pre-harvest germination in maize, but that an undetermined environmental factor was the actual trigger. Foliar applications of Mo were able to reduce pre-harvest sprouting and yield loss in wheat, together with a decline in grain nitrate concentration (Modi and Cairns, 1995) and rice subjected to simulated flooding (Tejakhod et al., 2018). In addition, a molybdenum cofactor biosynthesis mutant in rice was characterised by pre-harvest sprouting (Liu et al., 2019). A Mo deficiency is typically associated with a reduction in activity of molybdenum cofactor (MoCo) requiring enzymes, required for nitrate metabolism and ABA biosynthesis (Bittner, 2014). The last step in ABA biosynthesis, the conversion of ABA aldehyde to ABA requires a MoCo enzyme, ABA aldehyde oxidase (Mendel and Hänsch, 2002), whilst, the conversion of nitrate to nitrite is catalysed by a MoCo-containing enzyme, nitrate reductase. Thus, a Mo deficiency could lead to high NO_3^- and low ABA, both of which are linked to vivipary in pecans. Low plant Mo is often associated with acidic soils and is the only micronutrient whose availability increases with an increase in soil pH. Low plant Mo could also be associated with soil sulphate concentrations, as low sulphate concentrations in the soil promote molybdate uptake (Shinmachi et al., 2010) and high levels of sulphates inhibit the uptake of Mo because sulphate act as a potent inhibitor of Mo uptake. These factors should be considered in years where vivipary is an issue, in order to make corrections in the following season.

Whilst a role for Mo in vivipary is relatively straight forward, proposing roles for Fe and Cu, as suggested by Wood (2015), is not as simple. A tight connection between molybdenum and iron metabolism is proposed, with Fe acting as a crucial regulator of Mo metabolism (Bittner, 2014). As a result, iron deficiencies may also lead to a reduction Mo uptake and as many molybdoenzymes also require iron-containing prosthetic groups, activity of MoCo-containing enzymes may be impeded in iron deficient plants. Once again this could lead to a reduction in ABA biosynthesis and nitrate to nitrite conversion, thereby creating favourable conditions for vivipary. Copper has also been found to supress ABA catabolism in rice, resulting in an inhibition of seed germination (Ye et al., 2014). Copper deficiencies may therefore encourage ABA catabolism and favour vivipary, but there is no evidence to support this hypothesis at present.

Abscisic acid is, however, not the only hormone involved in seed dormancy and germination. There may be a role for gibberellins in promoting vivipary, as a timely application of prohexadine-calcium (gibberellin (GA) inhibitor) could slightly reduce the incidence of vivipary (Wood, 2015). Gibberellins play a role in promoting germination of many seeds and an increase in gibberellin levels during germination were reported in pecan seeds by Dimalla and Van Staden (1978). Under favourable conditions (light, temperature and moisture) GA biosynthesis and associated pathways are activated in seeds, which results in the release from the inhibitory effect of ABA (Vishal and Kumar, 2018) and as a result germination is able to proceed. In fact, GAs have been proposed to play an important role in temperature sensing in seeds (Urbanova and Leubner-Metzger, 2018). Crosstalk between these ABA and GA pathways may therefore be important for initiation of germination whilst nuts are still on the tree.

Ethylene may have an indirect impact on vivipary by inducing shuck opening and thus allowing dehydration which prevents the germination of pecan seeds (Díaz, 2013). Exogenous applications of ethephon in some instances may therefore help avoid vivipary, but this needs to be done with caution, as ethephon applications can also induce leaf abscission. Shuck dehiscence is, however, more sensitive to exogenous ethephon applications, than leaf or fruit abscission (Kays et al., 1975) and trunk injections of ethylene have been shown to be effective for inducing shuck dehiscence with limited leaf abscission (Stein et al., 1986). Importantly, ABA and ethylene seem to both have important roles in inducing abscission in some plants, with ABA possibly controlling ethylene production (Wilmowicz et al., 2016) and thus a lack of ABA in the embryo may also impact ethylene and therefore opening of the shuck. This could offer a possible explanation as to why some shucks fail to open when the kernel is mature and why these nuts often exhibit vivipary. This interaction in pecans, however, still needs to be investigated, as the control of abscission can be species-specific (Botton and Ruperti, 2019).

5 POSSIBLE REMEDIAL ACTIONS

The factors contributing to the incidence of stick-tights are very similar to those contributing to vivipary and thus remedial actions or management practices to address these disorders will in many instances be discussed together. However, measures specific to each disorder will also be outlined. Many management practices that reduce stick-tights are focussed on reducing tree stress that leads to kernel abortion or poorly filled nuts during the nut filling and shuck dehiscence stages and ensuring good sunlight distribution throughout the canopy. Practices to reduce vivipary focus on optimising crop load and ensuring good fertilizer and

irrigation management, but if environmental conditions are favourable for the incidence of vivipary, then an earlier harvest is recommended.

Good decisions at planting, and when the orchards are young, can reduce the incidence of stick-tights and vivipary. The choice of compatible cultivars to achieve successful cross-pollination throughout the life of the orchard is very important. Based on findings from the USA, it would also seem that a mixture of southern and northern cultivars, that cross pollinate each other, will be important in some of the hotter production regions in order to reduce vivipary. This is, however, dependent on the adaptability of both genotypes to the hotter regions. Good pruning strategies are also important for ensuring that sunlight penetrates throughout the canopy. This is important for preventing shuck decline in shaded parts of the canopy, for ensuring good airflow and as a way of avoiding an overload of nuts. Overcrowding of orchards should also be avoided and therefore a good pruning and training strategy should be employed, starting when the orchards are still young. This includes choosing an appropriate planting density for the chosen training and pruning system. Part of maximising photosynthesis is also ensuring a healthy canopy through judicious insect and disease control throughout the season.

Good water management throughout pecan nut development, but especially during kernel filling and shuck dehiscence, is critical for reducing the number of stick-tights and the possibility of vivipary. This includes ensuring there are no prolonged water deficits during this time and that there is no over-irrigation, which causes waterlogging in the orchard. Some quantitative means should be used to schedule irrigation, such as soil water content measurements, pre-dawn or midday leaf water potentials, or through or a water use model approach, such as crop coefficients. The value of leaf water potential measurements is that it integrates the entire root system with available soil water and is therefore not a point measurement, as is the case for soil water monitoring equipment. Pre-dawn and midday leaf water potentials are recognised as one of the best ways of scheduling irrigation based on plant stress. Othman et al. (2014) established midday leaf water potential thresholds for pecans in New Mexico, with values between –0.40 and –0.85 MPa indicating well-watered conditions, –0.90 to –1.45 MPa moderately stressed and –1.5 and –2.0 MPa severely stressed. These can be used as a valuable reference; however, work is currently being conducted to evaluate these thresholds under South African conditions. Work on the impact of mild water stress at different phenological stages on yield and quality in South Africa have demonstrated that mild water stress does impact the incidence of stick-tights. In the shuck dehiscence stage, if midday leaf water potential was maintained close to-0.7 MPa (pre-dawn water potential of -0.3 MPa), there

was very little stress in the orchard. However, as midday leaf water potential approached -1.0 MPa (pre-dawn water potential of -0.5 MPa), the incidence of stick-tights increased.

Linked to good water management is appropriate fertilization. The canopy should mature with sufficient nitrogen and zinc for optimal photosynthesis and normal kernel development. However, excessive nitrogen (especially nitrates) should be avoided late in the season, as this contributes to both poor shuck opening and vivipary. Micronutrients, including Fe, Cu and Mo, should also probably not be limiting. As Mo deficiencies have been linked to pre-harvest germination in a few cereal crops, this may be of particular importance, especially in acidic soils. This, however, still needs to be confirmed in pecan orchards.

As both stick-tights and vivipary are associated with heavy crop loads, appropriate thinning practices should be carried out in heavy “on” years to ensure an even crop from year to year, that is of good quality. Thinning should ideally be done when the ovule is 50-100% expanded and before the kernel enters the dough stage. Thinning at 50% ovule development should be done for cultivars with big nuts, whilst thinning when the embryo is fully expanded can be done for cultivars with smaller nuts. Thinning can be done mechanically using a tree shaker, but some experience and knowledge of the actual crop load is required to achieve the desired thinning level. This ensures that remaining nuts are filled evenly and should reduce the incidence of pops or poorly filled kernels that often leads to stick-tights and will also increase marketable yield.

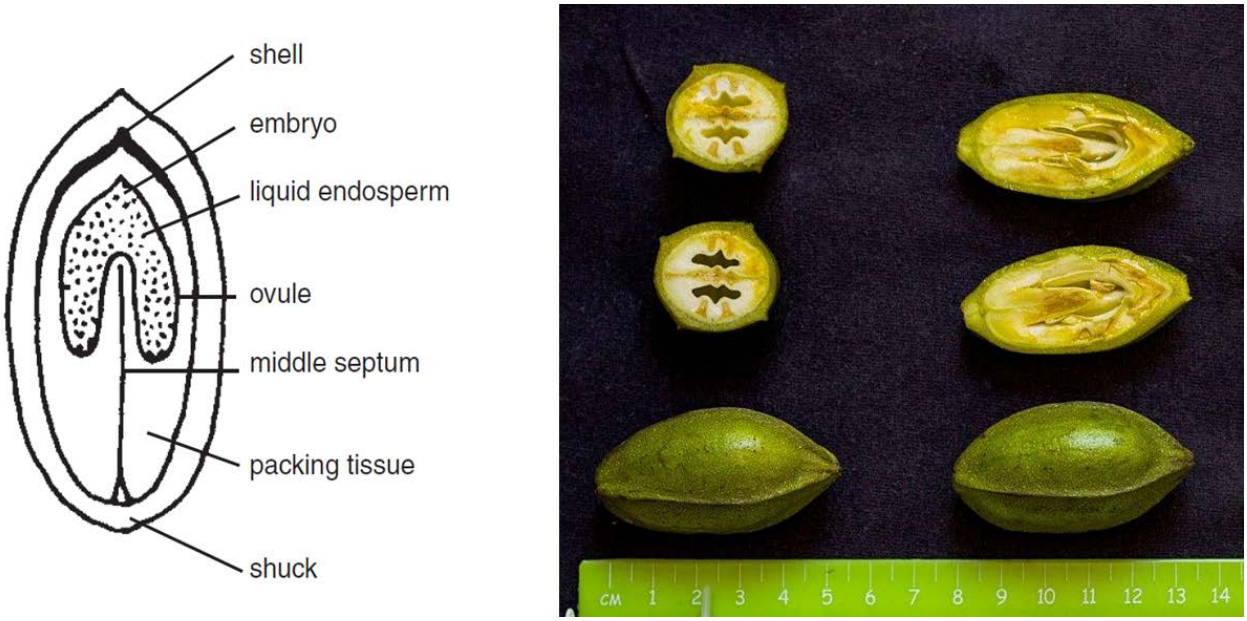

Figure 8 Stage at which to thin fruit to reduce vivipary and stick-tights caused by poor kernel filling

According to Wood (2015) practices to reduce vivipary include a) ensuring that soil moisture levels are near field capacity during kernel filling (i.e., usually March and April for most cultivars; but ensuring that soils do not become waterlogged, this is important as water use will decline as a result of the drop in temperatures); b) using Temik (Aldicarb; 2-methyl-2-(methylthio)-proprionaldehyde-0-(methylcarbamoyl)-oxime) to advance early-ripening; c) avoiding excessive crop-loads by either timely mechanical thinning or by indirect fruit thinning via hedge pruning; and d) early harvesting using mechanical shakers. If chill accumulation was sufficient to meet the chill requirements of the trees and the spring was warm, resulting in fast canopy development at the start of the season, then nuts are likely to mature during a warmer period (temperatures regularly approaching or exceeding 30 ºC) and the growing season is likely to be longer than usual. Under these circumstances, an earlier “green” harvest might be necessary, as is practiced in many of the warmer pecan producing areas in the USA. “Green harvest” creates additional processing expenses because, unlike the traditional pecan harvest, it requires mechanical removal of the unsplit pecan shucks and drying of the nuts. Growers should also be aware of conditions that are conductive to vivipary, as environmental factors, in many instances, seem to trigger this disorder.

6 CONCLUSIONS

The factors contributing to the occurrence of stick-tights and vivipary are fairly well defined for pecans and in many instances these disorders can be minimised through good management of water, nutrients and pests and diseases, which reduce tree stress. However, there are instances where environmental conditions are such that tree stress is mostly unavoidable and the occurrence of these phenomena can only be slightly lessened through management practices. These conditions usually include unusual dry and hot conditions during nut filling and shuck dehiscence or unusually wet and cloudy conditions during nut filling.

There are still a number of areas where more research could allow for better understanding of these phenomena. Firstly, the reasons why shucks with mature kernels fail to open need to be determined. Whilst, it is postulated that this possibly is a result of poor ethylene production as a result of low ABA in these nuts, this is unproven in pecans and the reasons for low ABA are also not clear, but could be linked to high nitrates and/or micronutrient deficiencies. The role of micronutrients also needs to be clarified in pecans, especially the role of molybdenum. The occurrence of vivpary should also be better documented under South African conditions to better define what is meant by “warm conditions” during shuck dehiscence and to better

understand causal factors. By determining threshold temperatures, a basic model for the occurrence of vivipary could be developed which could allow for predictive capabilities, thereby facilitating earlier harvesting in some years. In this regard the work by Dimalla and Van Staden (1978) should be referred to, as these authors suggest a temperature requirement of 30-35 ºC to overcome the mechanical restriction placed on radicle protrusion by the hard shell. This could be achieved by documenting the occurrence of vivipary and stick-tights in different seasons and different regions and correlating with temperature data.

Finally, the compatibility of different cultivars for cross pollination needs to be documented under South African conditions and for the different growing regions, which differ substantially in terms of climate. The interactive effect of chilling and heating on flowering characteristics of the different cultivars needs to be understood in order to achieve reliable cross pollination in orchards, throughout the life time of the orchard. Once again, industry wide surveys could potentially assist in the improved understanding of pollen shed and female flower receptivity in different pecn producing regions.

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