STICK-TIGHTS AND VIVIPARY IN PECANS

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1 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 or 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 for 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). In December there is typically a second nut drop period, which is associated with incomplete fertilization or in other words poor fruit set. Nuts are shed because either the egg is not fertilized or the endosperm fails to develop. 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.

Following normal fertilization, the nut starts to increase in size and after approximately 80-90 days final fruit size is reached (January/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. 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.

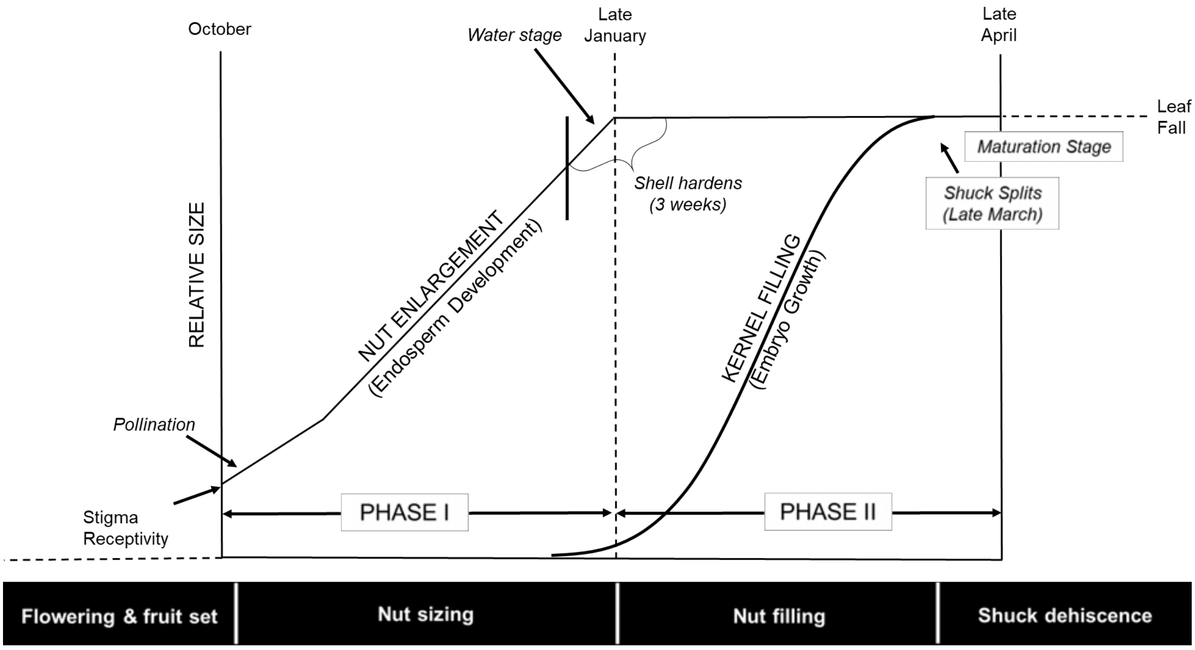

Figure 1 Pecan nut development (adapted from Herrera, 1990)

Stage I is also the stage of rapid endosperm development and from December to February the endosperm is rich in growth substances and sugars. This is often referred to as the water stage. 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 on the tree, 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 and cause nuts to fall in 3 or 4 days. 5) Physical damage (e.g. hail) that results in a disturbance of the ovary wall or shell of the nut (Byford and Herrera, 2005).

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. Kernel filling 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. 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 to be retained more in the shuck.

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 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 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. 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. 5) The prevailing weather conditions can also impact nut filling. Prolonged dry spells or drought or prolonged cloudy conditions will reduce kernel filling, mostly through a reduction in photosynthesis and therefore the supply of photoassimilates. 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 is a particular problem in trees which 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). 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. Importantly, 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, Van Staden and Dimalla (1976) and Dimalla and Van Staden (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. 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.

2 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.

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)

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) and can be cultivar specific. 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. Late watering of pecan (without causing waterlogging), up until the leaf drop stage, reduces stick-tights and increases a clean nut drop. Nutrition is also important as 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) also demonstrated that shuck dehiscence was delayed and the rate of dehiscence was drastically reduced as Zn deficiency increased. 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.

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). 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. However, in the 2018/2019 season significant water stress was achieved during shuck dehiscence and the % stick-tights significantly increased. 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.

3 CAUSES OF VIVIPARY IN PECANS

Vivipary refers to the germination of seeds while still attached to the mother plant (Figure 3). 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. 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 (Farnsworth, 2000; Sparks et al., 1995; Wood, 2015). In some cases vivipary related crop loss can be >70% in parts of the USA (Wood, 2015). In South Africa vivipary seems much more prevalent in the hotter pecan production regions, located in the west of the country (Personal communication Hardus du Toit).

Figure 3 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 an especially powerful triggers for vivipary in plants. In addition, vivipary in pecan is favoured by a high crop load, long growing season, self-pollination 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). 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, as the mechanical effect of the hard shell is overcome at temperature between 30 and 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 can therefore create conditions that are conducive for the occurrence of vivipary,

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 application 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. Importantly, high NO_3^- (Duermeyer et al., 2018) and low potassium (Marrush et al., 1998) have been shown to alter ABA levels in seeds and as a result vivipary. Micronutrients, including Fe, Mo and Cu, also have roles to play in ABA biosynthesis and nitrate metabolism and therefore deficiencies of these elements may also play a role in increasing the incidence of vivipary.

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 of 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, grain nitrate concentration and yield loss in wheat (Modi and Cairns, 1995) and rice subjected to simulated flooding (Tejakhod et al., 2018). 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). 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. Importantly, this needs to be investigated further in pecans.

4 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. 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. It would also seem that a mixture of southern and northern cultivars could be important in some of the hotter production regions in order to reduce vivipary, depending 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 from when the orchards are still young, together with a sensible planting density. 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 the kernel filling and shuck dehiscence stages 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 or pre-dawn or midday leaf water potentials. Pre-dawn and midday leaf water potentials are recognised as one of the best ways of scheduling irrigation based on plant stress. There are some basic threshold values developed in the USA (Othman et al., 2014), which are currently being refined for South African conditions.

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, Mo and Cu should also not be limiting. Molybdenum deficiencies may be particularly important in the occurrence of vivipary and attention should be paid to this micronutrient in areas where vivipary is fairly common.

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 can be done mechanically using a tree shaker, but some experience and knowledge of the actual crop load is required to achieve the desired level of thinning. Thinning should be done before the nut enters the dough stage (Figure 4) 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 the marketable yield.

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. A “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.

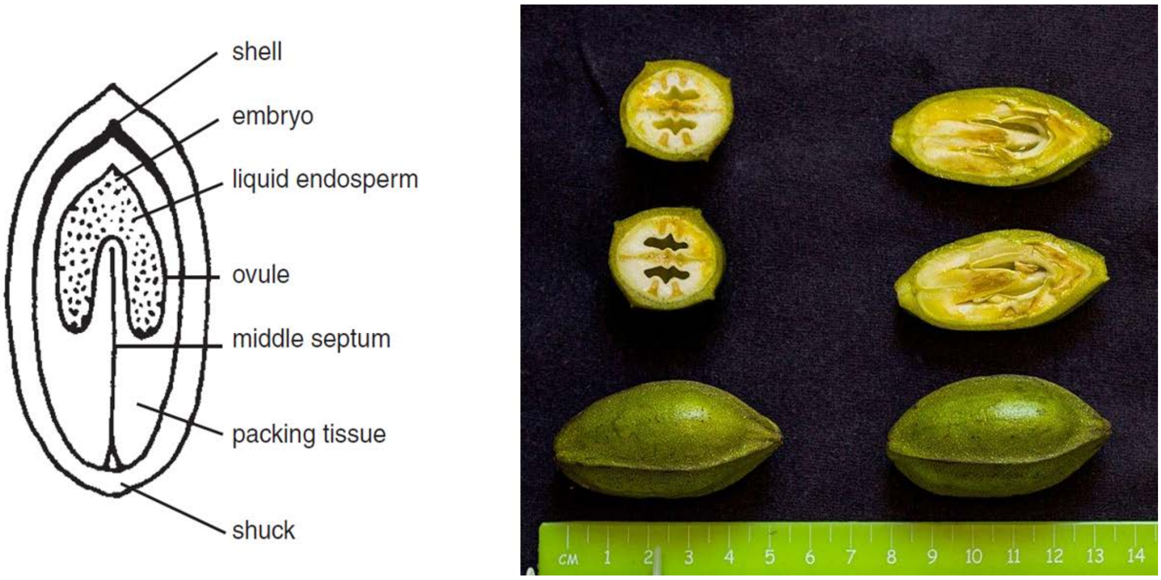

Figure 4 Stage at which to thin fruit to reduce vivipary and stick-tights caused by poor kernel filling

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