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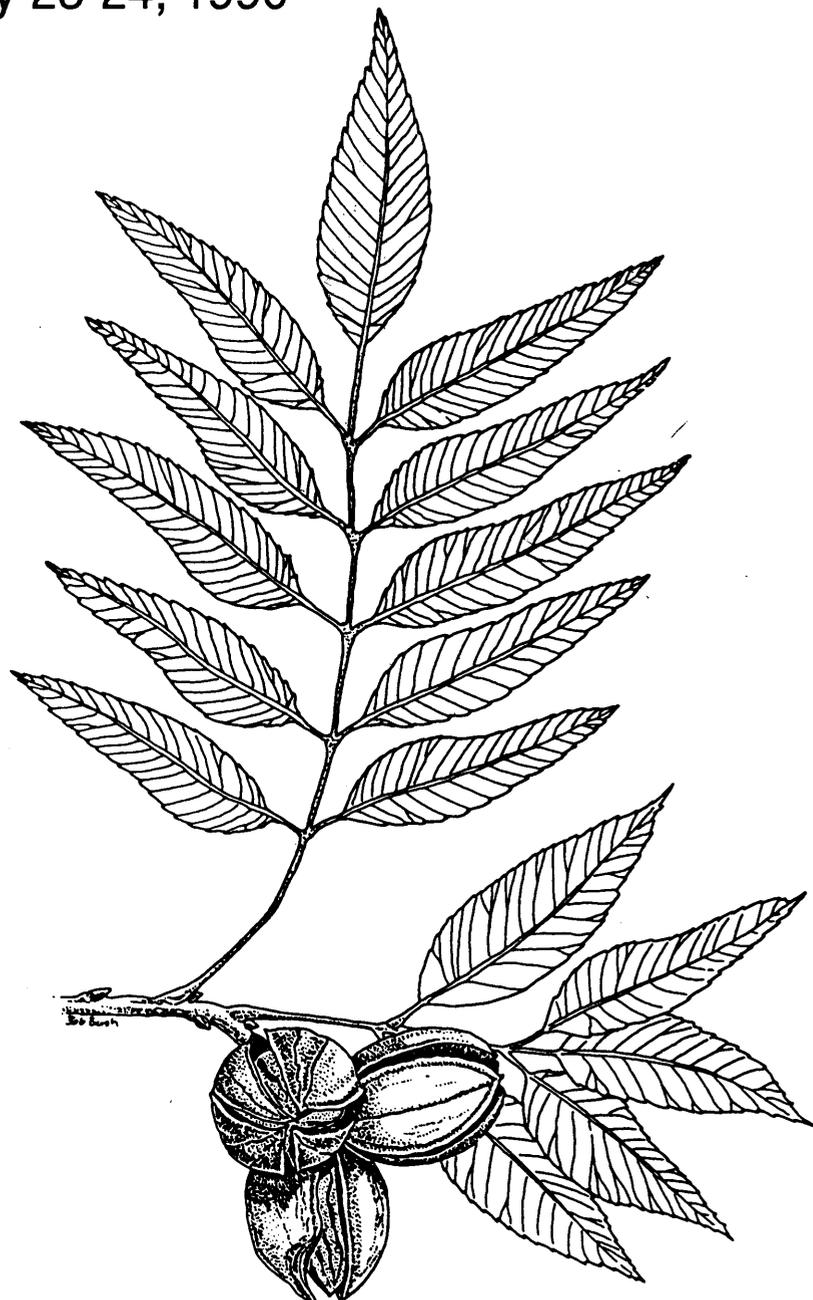
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EFFECT OF THE POLLEN PARENT ON FERTILIZATION SUCCESS

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ABSTRACT

Examples of pollen competition and selective fruitlet abortion were presented from the literature. Preliminary data demonstrates similar events likely occur in pecan. That is, pollen germination and tube growth is temperature dependent and a genotype by environment interaction may exist. A northern pollen source tended to germinate and grow slightly better than a southern pollen source at lower temperatures. Some pollen types appear to grow more vigorously *in vivo* than others which may impart some selective advantage in fertilization success. A disequilibrium was found in the rate of fertilization success when a mixture of four pollen parents was used to pollinate 'Cheyenne'.

INTRODUCTION

Pecan pollination occurs in the spring and little thought is given to the phenomena beyond the requirement that pollen must be present during stigma receptivity. If stigma receptivity overlaps with pollen shed, pollination is effective, fertilization occurs, and a successful pecan crop likely will be produced. One common criterion to select a pollenizer cultivar is that it has a complimentary dichogamy pattern to the main crop cultivar. However, fertilization success of different pollen types and eventual fruit maturity are not necessarily random events. Several examples with other plants illustrate this point.

Avocados have extremely high rates of fecundity and an individual tree may produce 10⁶ perfect flowers. However, only several hundred fruit typically reach maturity. Are there mechanisms that selectively influence which fruit mature? Degani and co-workers (1986) presented clear

evidence that fruitlet abortion in avocado is linked to a scorable biochemical marker and therefore has a genetic component. Maturing and aborted avocado fruit were genotyped for one gene controlling leucine aminopeptidase (*lap-2*). The 'ss' genotype of *lap-2* was detectable in both immature and aborted fruit but never was found among mature fruit.

Secondly, the degree of competition among pollen can effect plant performance in future generations. For example, the size of the pollen dose used in controlled pollinations (either a large or small dose of pollen applied to the stigma) can influence plant performance. Davis and co-workers (1987) demonstrated a high pollen dose resulted in "superior" squash seed. Characteristics used to determine seed superiority were plant performance for fruit weight, seed per plant, days to first flower, and initial germination rate.

Mulcahy and Mulcahy (1975) showed carnation seedlings, resulting from pollinations made more distal to the ovary, germinated more quickly and grew faster than seed derived from pollinations made more proximal to the ovary. The more distal pollinations created greater competition among pollen by forcing pollen tubes to grow a longer distance to reach the micropyle. Furthermore, some attributes of vigor (originating in the gametophytic pollen) were conferred to the sporophytic seedling! Expression of genes in the gametophyte that overlap is the sporophyte has been estimated to be about 60% (Tanksley et al., 1981).

EXAMPLES OF POLLEN COMPETITION IN PECAN

Pollen competition and selective abortion of pecan fruit does occur. An extreme example of selective abortion involves interspecific hybridization. Early *in vivo* growth of some hickory pollen (i.e., *C. myristiformis* and *aquatica*) on pecan stigmas is not inferior to pollen tube growth after conspecific pollination of pecan (Figure 1). However, seed set is generally low after interspecific crosses of *Carya* are made (personal obs.). Therefore, some mechanism reduces the frequency of hybridization among *Carya* species.

Normal fruitlet abortion in pecan is moderate and is estimated to range from 20 to 50 percent (Sparks and Madden, 1985). A more subtle example of selective abortion involves selfed pecan fruit. Self-pollination is responsible for a

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small but real fruitlet drop (e.g., the third drop) (Sparks and Madden, 1985). In addition, selfed fruit that do mature typically have less volume and kernel weight than cross-pollinated fruit (Romberg and Smith, 1946; Marquard, 1988a). Perhaps, the maternal parent "recognizes" the genetic liability of selfed fruit and aborts a greater percentage and/or allocates less resources (i.e., carbohydrates) to those developing fruit. Temme (1986) suggests many factors can explain variability in seed weight and that "detectable genetic variation (should) be added to the list of (possible) factors...".

Supplemental pollination of pecan could be considered under at least two conditions. First, if pollen production in a given orchard is expected to be relatively low, additional pollen could enhance effective pollination and nut set. Secondly, if an orchard is composed of a single cultivar, selfing may predominate, and fruit quality may be reduced. Supplemental pollination in the second case likely will be ineffective for three reasons. First, peak receptivity is not easily determined and only a portion of the female flowers will be receptive at any one time. Second, time of pollen deposition can significantly influence fertilization success. Pollen that first impacts the stigma has a decided disadvantage over later arriving pollen.

Bagged flower clusters were pollinated twice with two different pollen parents. Pollinations were separated temporarily to evaluate the influence of timing of pollen deposition. Pecan pollen that arrived 4 and 24 hours after initial pollen impaction had about a 40 and 3% chance, respectively, for fertilization success (Figure 2). Because of temporal differences in pollen deposition, one pollen type is given a competitive advantage. However, these data demonstrate that fertilization success strongly favors the first pollen to arrive on the receptive stigma.

Thirdly, a supplemental release of pollen may be greatly diluted by a high background of native pollen in the orchard thereby reducing the probability of success. As a first approximation, 50 grams of pollen per acre has been recommended as a suitable dose of pollen (McClure, 1986). That quantity can be extracted from 2.5 gallons of properly collected catkins which can easily be gathered from a single tree.

Supplemental pollination by fixed wing aircraft over a solid block of 'Western' resulted in fertilization success of 10-17% (Marquard, 1988b). Twenty-eight grams of pollen were applied

per tree and equates to about 1,300 grams of pollen per acre (at 10m x 10m spacing) which is likely uneconomical in most situations.

I have also evaluated pollen competition among four types used simultaneously in a pollen mixture. A mixture of pollen was prepared and used in controlled pollinations with 'Cheyenne' as the maternal parent. Four pollen parents were chosen so that each could be uniquely identified as the paternal parent in mature fruit using two heritable biochemical markers (Marquard, 1987). Each pollen source in the mixture was equally represented by weight. 'Cheyenne' pollen and three cross-pollen types were used in the mixture and paternity was identified in each mature fruit. Assuming percent germinability of each pollen parent was equal and fertilization success is random, then the fertilization success of each pollen parent should be about 25 percent. The logic and biochemical markers used to evaluate paternity is shown in Table 1. Progeny showed a skewed distribution in the success rate of each paternal parent. Apparently, self-pollen failed to effectively compete with cross-pollen types whereas two cross-pollen parents showed high fertilization success (Table 1). Pollen used in this work was collected the same day and treated identically. Unfortunately, percent germination of each pollen parent could not be reliably determined at the time of the experiment. However, these data suggest fertilization success may not be a random event if more than one pollen parent simultaneously impacts the stigma. Also noteworthy, the most successful cross-pollen parent produced the double heterozygous condition for the two scorable biochemical markers that were used (Table 1).

Differences in pollen tube growth rate among pollen parents also could skew fertilization success. All possible combinations of crosses were made among 'Western', 'Cape Fear', and 'Cheyenne' cultivars and *in vivo* growth of pollen tubes was evaluated four hours post-pollination. From one years date, 'Cape Fear' pollen grew more quickly than the others (Figure 3). These faster growing types may have an early competitive advantage that results in a higher rate of fertilization success. In addition, self-pollen did not appear to be disadvantaged within the time frame of this study (Figure 3).

Finally, the rate of vivipary (i.e., preharvest germination) in pecans can be influenced by the pollen source. Ou et al., (1990) made various controlled crosses and demonstrated that a more

northern pollen source (i.e., 'Johnson') yielded fruit that were slower to germinate than fruit with a more southern paternal parent (i.e., 'Cherokee'). Pollen tube growth is temperature dependent and I have rarely observed *in vitro* pollen germination below 17°C or above 32°C. Optimum germination and tube growth occurs at about 23-29°C (Figure 4). The ability of 'Gibson' and 'Cape-Fear' pollen to germinate and grow was simultaneously evaluated on a solid media at various temperatures. Preliminary data suggests northern 'Gibson' pollen performs slightly better at lower temperatures and has a lower temperature optimum for tube growth than 'Cape-Fear' pollen. If there is a genotype by environment interaction, southern pollen may have a selective advantage at higher ambient temperatures where vivipary is more likely to occur.

CONCLUSION

Selective abortion of fruit and pollen competition exists in other plant species and this paper demonstrates that similar mechanisms likely exist in pecan. Since the pollen parent can influence nut quality in pecan, selection of pollenizer cultivars to maximize production may be more complex than simply selecting cultivars with complimentary dichogamy patterns.

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Table 1. Equal portions of four pollen parents were mixed and used in controlled pollinations of 'Cheyenne' to evaluate competition among pollen types. Each pollen parent was selected for its unique genotype using two biochemical markers [malate dehydrogenase - 1 (*Mdh-1*) and phosphoglucose isomerase - 2 (*Pgi-2*)]. Pollen parent of each mature fruit could thereby be determined. Genotypes of possible parents and progeny given.

Possible Pollen Parent	<i>Mdh-1</i>		<i>Pgi-2</i>		Percent fertilization success
	Cheyenne (bb)		(bb)		
	<i>Mdh-1</i>	<i>Pgi-2</i>	<i>Mdh-1</i>	<i>Pgi-2</i>	
Self	(bb)	(bb)	(bb)	(bb)	1
Cross ₁	(bb)	(aa)	(bb)	(ab)	14
Cross ₂	(aa)	(bb)	(ab)	(bb)	34
Cross ₃	(aa)	(aa)	(ab)	(ab)	51

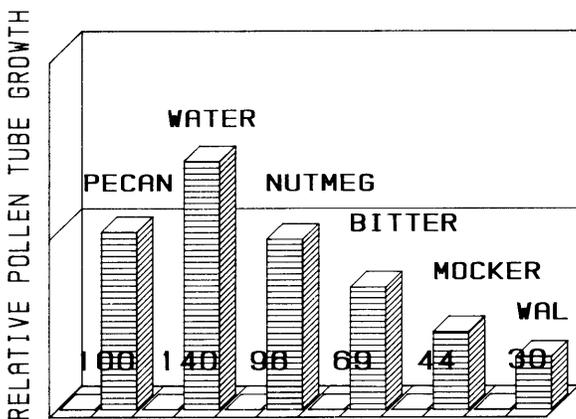


Figure 1. Relative growth rate of various pollen sources on pecan stigmas. Pollen sources included: pecan (*Carya illinoensis*), waterhickory (*C. aquatica*), nutmeghickory (*C. myristiformis*), bitternut hickory (*C. cordiformis*), mockernut hickory (*C. tomentosa*) and one walnut species (*Juglans macrocarpa*).

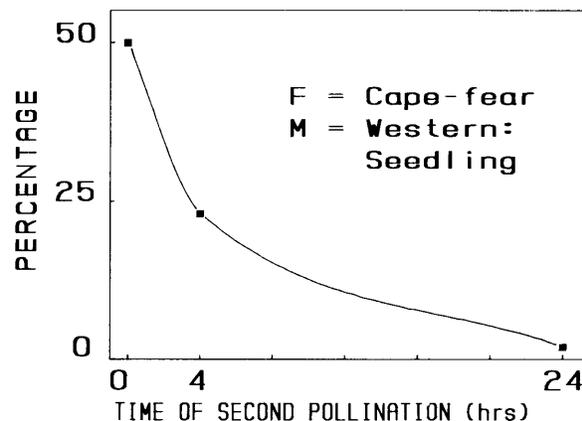


Figure 2. Percentage of mature fruit with 'Western' as a paternal parent. At time zero, 'Western' and a seedling pollen were applied simultaneously to receptive female flowers of 'Cheyenne'. All remaining female clusters were initially pollinated with the seedling pollen followed four or 24 hours with 'Western' pollen. Paternity in mature fruit was determined by genetic markers.

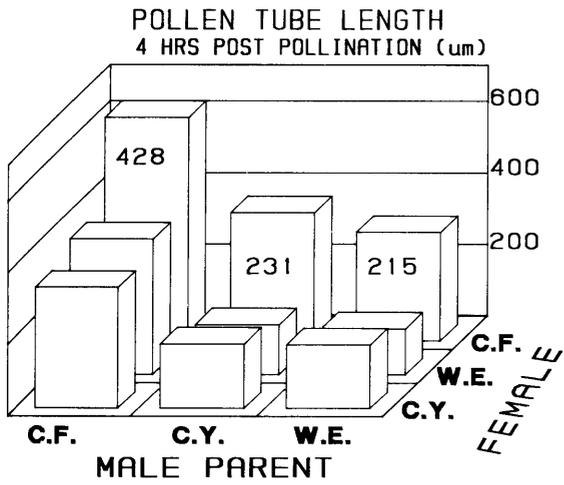


Figure 3. All possible combinations of controlled pollinations were made between 'Western', 'Cape Fear' and 'Cheyenne'. Stigmas were harvested four hours post-pollination and pollen tube length was determined by UV microscopy.

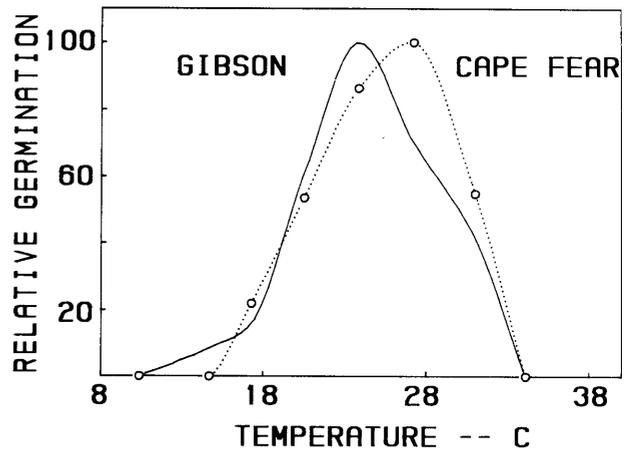


Figure 4. Relative rate of pollen germination of 'Gibson' and 'Cape Fear' pollen at various temperatures.