

## Variability in Pecan Flowering

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### Abstract

Efficient pecan orchard design requires accurate information concerning flowering patterns of cultivars. Methods of evaluating pecan flowering vary widely in the literature, and may influence reported patterns. Critical aspects of pecan flowering are reviewed, especially, as they relate to monitoring bloom. Dichogamy patterns are reported for 13 pecan cultivars observed over four years at Shreveport, LA. Patterns of flowering varied between years, with dates of inner scale split, pollen shed, and stigma receptivity being related to seasonal growing degree day accumulations. Cultivars did not flower in identical sequence in all years, but did consistently exhibit either protogyny or protandry. Data from 12 cultivars collected at Brownwood, TX in 1992 are evaluated in relation to previous reports of flowering for those cultivars in the 1972 and 1974 seasons. Dichogamy data for three consecutive years from New Mexico are also evaluated for patterns due to season. At all locations, date of first bloom varied by year. Pollen shed and pistil receptivity for a cultivar varied in relation to bloom dates of other cultivars in different years. Two cultivars may have altered patterns of bloom overlap in different seasons. When designing orchard configurations, planners should rely on observations made over several seasons, and from trees as close as possible to the proposed orchard location. Rather than attempting to pick two cultivars that closely overlap bloom, or choosing a certain number of protandrous and protogynous cultivars, it may be preferable to select multiple cultivars to provide early, mid-, and late-season pollen, with the pistillate receptivity period of key cultivars in the orchard being heavily targeted.

### Monitoring Flowering in Pecan

Monitoring pecan flowering requires an understanding of the flowering system. Mature pecan trees bear male and female flowers at different locations on the same tree. Pecan flowers develop from the compound buds, which are composed of two lateral floral or catkin buds and a central mixed bud (Fig. 1). As growth resumes in spring, the central mixed bud elongates to form the vegetative shoot,

which may terminate in the female (pistillate) inflorescence. The two lateral floral buds each produce a three stalked catkin group, the male (staminate) inflorescence (Fig. 2).

A pecan tree has **dichogamous** flowering (dicho = 'two part'; gamy =

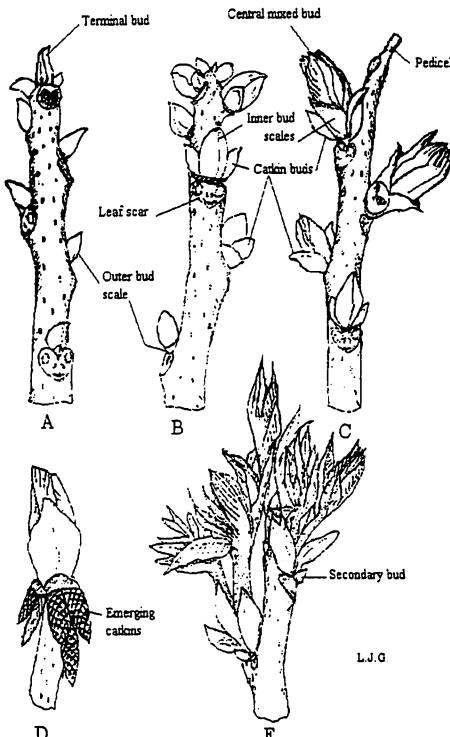


Figure 1. Stages of pecan bud growth. A) Dormant winter buds covered with single outer scale. B) Bud swell. As buds begin growth, outer scale is shed, revealing inner scales of shoot bud and separate inner scales around lateral catkin groups. C) Inner scale split, revealing leaves (protogynous cv). D) Inner scale split with catkins (protandrous cv). E) Leaf burst, with leaves reflexing from axis and leaflets visible (protogynous cv).

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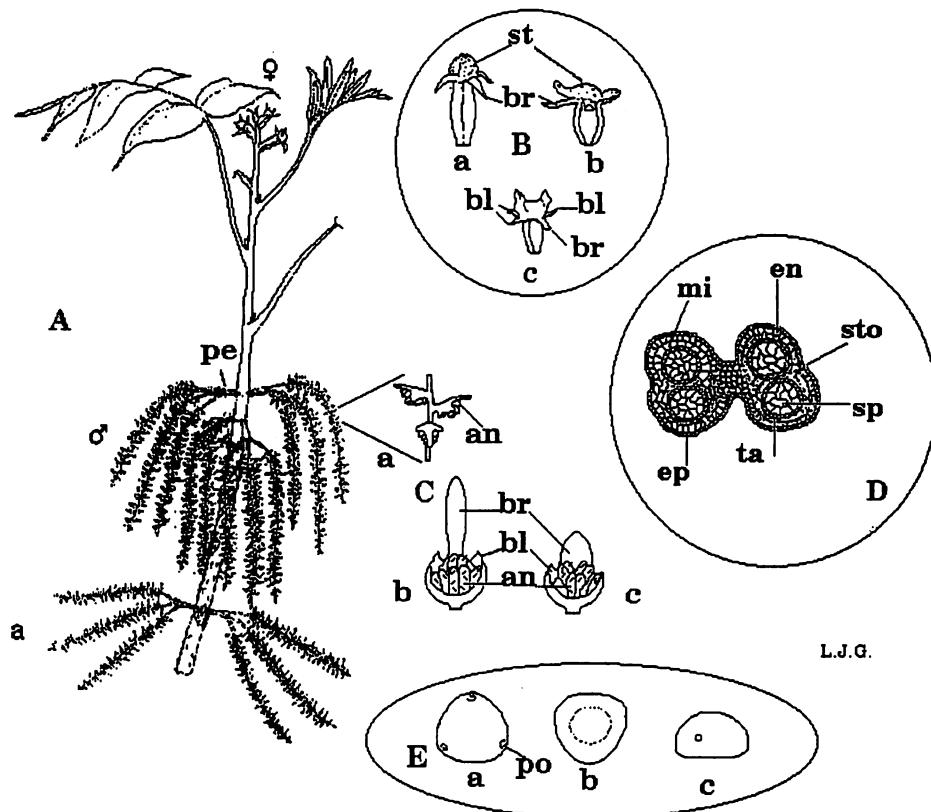


Figure 2. Flowers of pecan. A) shoot with pistillate flowers borne in spike at end of current season's growth; staminate flowers borne in pairs of 3-stalked catkin groups at base of current season's growth, or, a, from lateral buds in which the vegetative shoot aborts; pe = peduncle; B) Stigma variation in pistillate flowers of pecan; a, 'Pawnee'; b, 74-10-43; c, 74-10-42; br = bract; bl = bracteole; st = stigma; C) Variation in staminate flowers of pecan; a, individual flowers in alternate phyllotaxy on stalk of catkin; b, staminate flower of protogynous cultivar with elongated bract; c, staminate flower of protandrous cultivar, with shortened bract; an = anther, with acicular hairs; D) Section of anther, showing 4 circular pollen sacs or thecae; ep = epidermis; en = endothecium; mi = middle layers; ta = tapetum; sp = sporogenous tissue (pollen); sto = position of stomium; E) Pollen grains of pecan; a, distal view of triporate pollen grain; po = pore; b, proximal view, showing enfolding; c, equatorial view, showing sub oblate shape.

'sexual union'), since male and female flowers on a tree mature at different times. If male flowers dehisce pollen before pistillate flowers are receptive, the tree is **protandrous** (*protos* = first; *andro* = male) and is classified as **type I**; if female flowers are receptive before pollen is shed from catkins, the tree is **protogynous** (*protos* = first; *gyne* = female), and is classified as **type II**. Since different trees have different bloom patterns or dicho-

gamies, groups of trees are termed **heterodichogamous** (*hetero* = different; *dichogamy* = two part bloom). This type of flowering encourages genetic diversity by maximizing outcrossing (17).

The separation of male and female bloom periods for an individual tree may be **complete**, or the timing of pollen shed may overlap stigma receptivity (**incomplete dichogamy**). When a tree has complete separation of male

and female bloom, it must be cross pollinated by another tree. Without pollination, female flowers dehisce, and no crop is set. If the tree has incomplete dichogamy, it may be partially self-pollinated, allowing for some nut set. Self pollination is undesirable, however, since it has been shown to reduce nut quality (9, 13).

#### Staminate inflorescence

##### Differentiation

The staminate inflorescence (catkin group) is initiated during the previous spring prior to pollen shed. Two catkin groups are differentiated on opposite sides of the shoot bud, and are enclosed in separate inner scales. Sometimes, another pair of catkin groups are formed inside the inner scales of the central bud, opposite to each other and at right angles to the first two catkin groups. Each catkin group is enclosed by its own inner bud scales, and the entire compound bud, including lateral catkin groups and the shoot bud, is enclosed by the outer bud scale (Fig. 1).

Catkin development progresses to different stages in protandrous and protogynous cultivars: protandrous cultivars initiate anthers on catkins in the buds of the staminate inflorescence during the summer prior to pollen shed; protogynous cultivars initiate anthers on catkins during the spring that pollen is shed (3, 20). Luza and Polito (5) found that when walnut trees resumed growth in the spring, staminate flower differentiation resumed in protandrous clones prior to resumption of differentiation in protogynous clones. Comparable studies have not been performed for pecan.

#### Structure and development

The staminate inflorescence, or catkin group, is composed of three aments or catkins, joined to a common stalk, or peduncle (Fig. 2). Protogynous cultivars typically have long, thin catkins, while protandrous cultivars typically have catkins which are shorter and of greater diameter (25). Regardless of

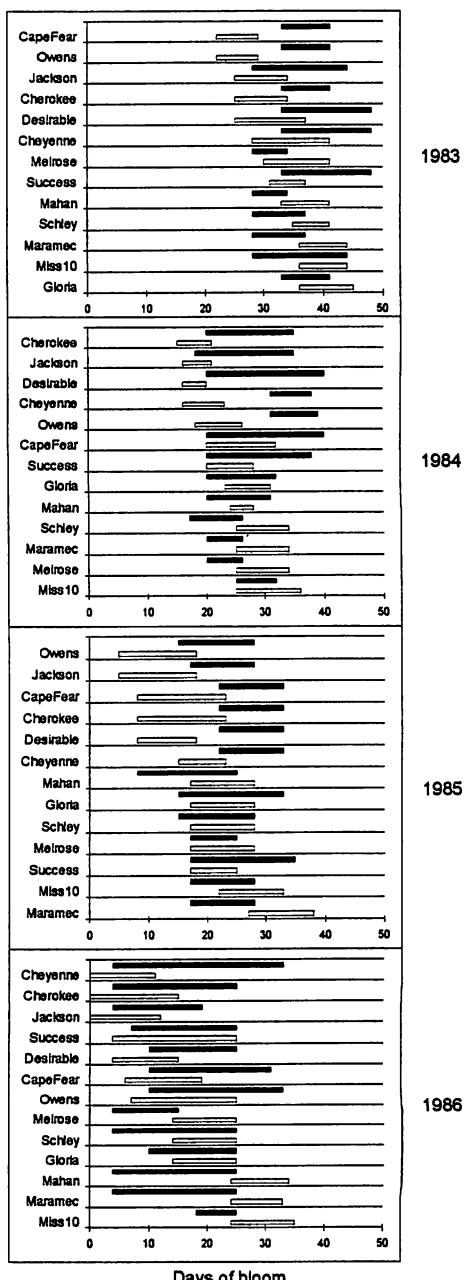


Figure 3. Patterns of dichogamy in 13 pecan cultivars grown at Shreveport, LA, 1983-1986, in order of pollen shed by year, shown as days of bloom relative to the earliest year (1986). Pollen shed □, Pistil receptivity ■.

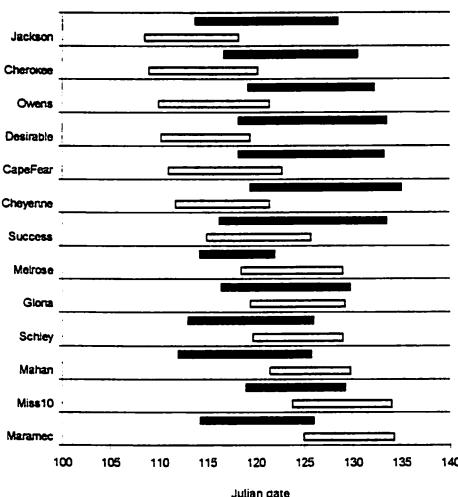


Figure 4. Patterns of dichogamy in 13 pecan cultivars at Shreveport, LA, averaged over 4 years (1983-1986). Julian date 110 = April 20. Pollen shed □, Pistil receptivity ■.

dichogamy class, the central catkin of a catkin group is usually the longest.

Cultivars vary in the quantity of catkins produced. Some cultivars, such as 'Desirable' and 'Cape Fear,' are known as heavy catkin producers, while others typically produce fewer catkins. Catkin production for a cultivar should be assessed at the beginning of anther dehiscence for that cultivar to insure maximum catkin presence. Assessments made over entire orchards on a single date may be inaccurate due to variation in catkin emergence between cultivars.

Each catkin is composed of many individual staminate flowers: ~72/catkin in protandrous cultivars; ~123/catkin in protogynous cultivars (from data in 22). Each individual staminate flower is composed of a central bract and two lateral bracteoles. Protogynous cultivars typically have male flowers with long, thin bracts, while protandrous cultivars typically have male flowers with short, broad bracts (22) (Fig. 2).

From three to seven stamens develop in each staminate flower. The stamen is composed of the anther, where the

pollen develops, and the filament, or stalk, which attaches it to the flower. In pecan, the filament is so short that it is inconspicuous. When mature, each anther will have four pollen sacs, or thecae (Fig. 2).

Pollen is developed in the pollen sacs. Pollen grains are free within the pollen sac 15 to 20 days before pollen

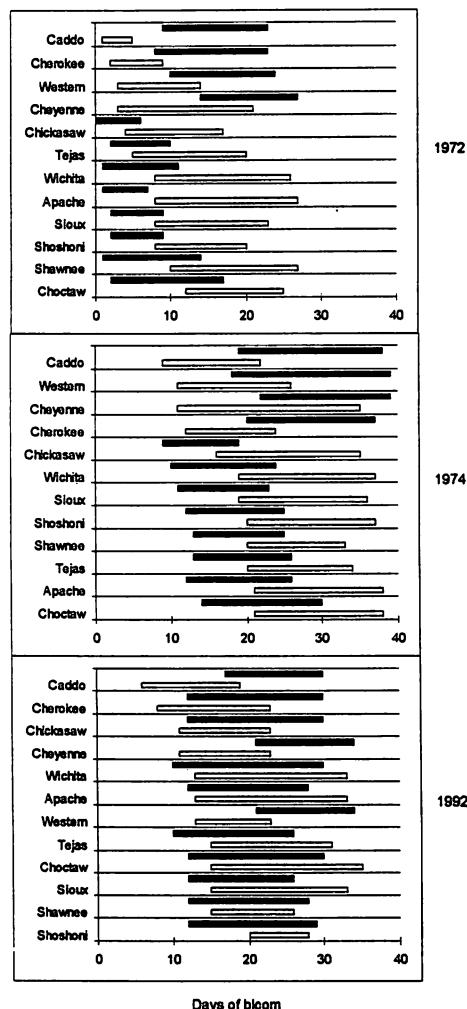


Figure 5. Patterns of dichogamy in 12 pecan cultivars grown at Brownwood, TX, in order of pollen shed by year, shown as days of bloom relative to the earliest year (1972). Pollen shed □, Pistil receptivity ■.

**Table 1. Summary of methods used in monitoring pecan dichogamy in separate tests.**

Location	Years	Trees/cv	Interval	Events	Criteria
LSU Pecan Station Robson, LA	'83-'86	2	1-2 per wk	Pollen shed Receptivity	first to last reflectance
Pecan Field Station Brownwood, TX	'72	2	variable	Pollen shed Receptivity	first to last pol. adherence
	'74	2-9	variable	Pollen shed Receptivity	first to last pol. adherence
	'92	4	2 per wk	Pollen shed Receptivity	first to last pol. adherence
N. Mex. State Univ. Las Cruces, NM	'62-'64	unknown	unknown	Pollen shed Receptivity	first to last unknown

is shed (23). Shortly before dehiscence, the four pollen sacs fuse to form two chambers by the dissolution of the separating wall. The anther wall is two cell layers thick, with an outer epidermis and an inner endothecium. Pollen is shed when the pollen sac splits open along a longitudinal slit (stomium). The opening of the anther is caused by drying and contraction of the outer layer in relation to the inner layer. When moistened, the anther has the ability to re-close (23).

Anther dehiscence is hastened under dry conditions, but is delayed under moist, cool conditions (27). Woodroof and Woodroof (25) reported that pecan pollen continued maturation but did not dehisce if relative humidity exceeded 85%, with subsequent dry conditions resulting in periods of very heavy shed. Sustained high winds coupled with low humidity tend to shorten the period of effective pollination both by speeding pollen dehiscence and by reducing the period of pistillate receptivity (25). Conversely, high humidity delays pollen dehiscence and extends the period of pistil receptivity.

Given typical diurnal fluctuations in temperature and relative humidity, the best time to monitor catkin development and collect catkins is in early morning before pollen shed begins.

For routine monitoring of pollen shed, observations should begin in mid-morning when decreasing relative humidity allows pollen dehiscence.

Cultivars may vary in the duration of pollen shed, with some cultivars, such as 'Caddo' having the reputation for a short period of shed, while cultivars such as 'Wichita' usually shed pollen longer. The duration of pollen dehiscence for a cultivar may vary greatly in different seasons, as a function of variable weather, and has the potential for extreme variability in different locations across the range of climates where pecan is grown.

#### *Pistillate inflorescence Differentiation*

Female flowers are differentiated during early stages of bud growth in the spring. Wetzstein and Sparks (19) found that flowers were differentiated at bud swell, after outer scales were split, but prior to inner scale split. There were no apparent differences in time of differentiation of pistillate flowers by protogynous and protandrous cultivars. In walnut, pistillate flowers are differentiated in the season prior to blooms and proceed to different stages in protogynous and protandrous individuals (12).

Although all compound buds on the previous seasons shoot could potential-

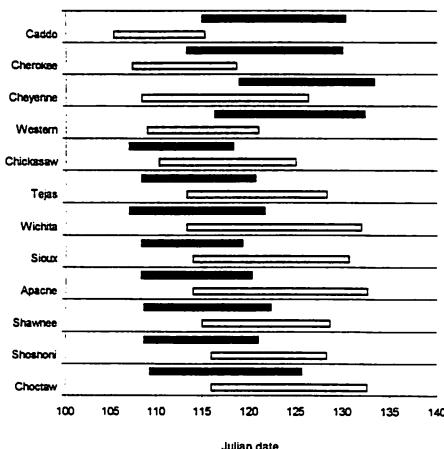


Figure 6. Patterns of dichogamy in 12 pecan cultivars grown at Brownwood, TX, averaged over 3 years (1972, 1974, 1992). Julian date 110 = April 20. Pollen shed □, Pistil receptivity ■.

ly form new shoots in the spring, strong apical dominance in pecan usually limits growth (and therefore fruiting) to only two or three compound buds near the terminal portion of the shoot. Lateral buds in basal positions often initiate growth, but abort the shoot tip, forming only catkin groups. When terminal shoots are damaged by early spring freezes, secondary or tertiary buds may break which still have the potential to differentiate female flowers.

#### Structure and development

Pistillate flowers are borne in a spike at the end of the current season's shoot. The basal flowers are the oldest, while the very youngest flowers at the apex are often underdeveloped and abort in the first drop. The number of flowers produced on a single inflorescence varies with shoot length, cultivar, and season (4).

Pistillate flowers consist of a bilobed stigma on a stigmatic disk surrounded by 3 bracteoles and a bract. The bracteoles and bract are fused at the base to form the involucre or shuck (8) (Fig. 2).

As pistillate flowers mature, stigmatic surfaces often change shape, color, and reflectivity, making assessment of receptivity a subject of debate. The color of stigmas is a trait which cannot be accurately relied upon as an index to receptivity, since color varies between cultivars from deep red (as in 'Success' and 'Pawnee') to vivid green (as in 'Stuart'). Variation in shape and size of pistillate flowers and stigmatic surfaces at the time of receptivity further complicates the problem (Fig. 2). In general, pistillate flowers of protogynous cultivars become receptive at a smaller size than those of protandrous cultivars. Receptivity has been judged by the presence of a "viscous fluid" on the stigmatic surface (1, 10, 24). Wetzstein and Sparks (20) noted that receptive stigmas appeared "moist and fleshy." They described the stigmatic surface of pecan as "dry," despite the presence of an "electron-dense" "noncopious surface exudate." The occurrence of the exudate in relation to stigmatic maturation has not been studied. However, receptivity has been related to adherence of applied pollen to the stigmatic surface, which is possibly associated with production of the exudate. Smith and Romberg (14) reported that stigmas become receptive slightly before the date on which pollen "adheres to them in sufficient quantity to be seen with the naked eye." We consider that criterion to be the best available for judging receptivity, and recommend its use by researchers evaluating receptivity in pecan.

In the absence of pollination (as in damp, cloudy, weather or when pistillate flowers are protected in casings) stigmatic surfaces may remain receptive for a week. If the stigma receives pollen, the stigmatic cells collapse and dry within 24 hours after pollen hydration and germination (21), causing the stigma to appear brown and dried. Calculations based on dates of stigma drying have also been used to estimate receptivity in pecan (2, 16).

### Dichogamy Patterns of Pecan Cultivars at Different Locations Over Several Years

Dichogamy records are available from several years at several locations. Nakayama (11) reported dichogamy patterns observed at Las Cruces, NM for 1962-1964. Madden and Brown (6, 7) reported patterns observed at Brownwood, TX in 1972 and 1974, which is supplemented in this paper with observations made in 1992. Data were collected in Shreveport, LA from 1983-1986, and will be reported here. Although these data may be suitable for preliminary analysis of variation in dichogamy patterns over years and at different locations, problems are associated with interpretation of the data. Methods of evaluation were different at different locations, with possibly important differences arising due to different criteria for considering stigmas receptive, different intervals of observation, and different numbers of trees being observed (Table 1).

#### Shreveport, LA

Results of the Shreveport test are shown in Fig. 3. Patterns of dichogamy are arranged in order of pollen shed and pistillate receptivity, by year. Seasons show variability in the inception of bloom, with 1983 being the latest season and 1986 being the earliest (Fig. 3, Table 2). The seasonal timing of pollen shed and pistil receptivity is controlled largely by temperature (Table 3). The correlation between the first occurrence of pollen shed or pistil receptivity for a cultivar and monthly growing degree days (base 50) was analyzed using data collected at Shreveport (1983-1986). For pollen shed, the correlation was highly significant ( $P > |R| = .0001$ ) for each month from January to April, with the correlation increasing as the event approached. For all months, the correlation was negative, indicating that as temperature increased, the Julian date of pollen shed decreased: warmer seasons resulted in earlier growth. The

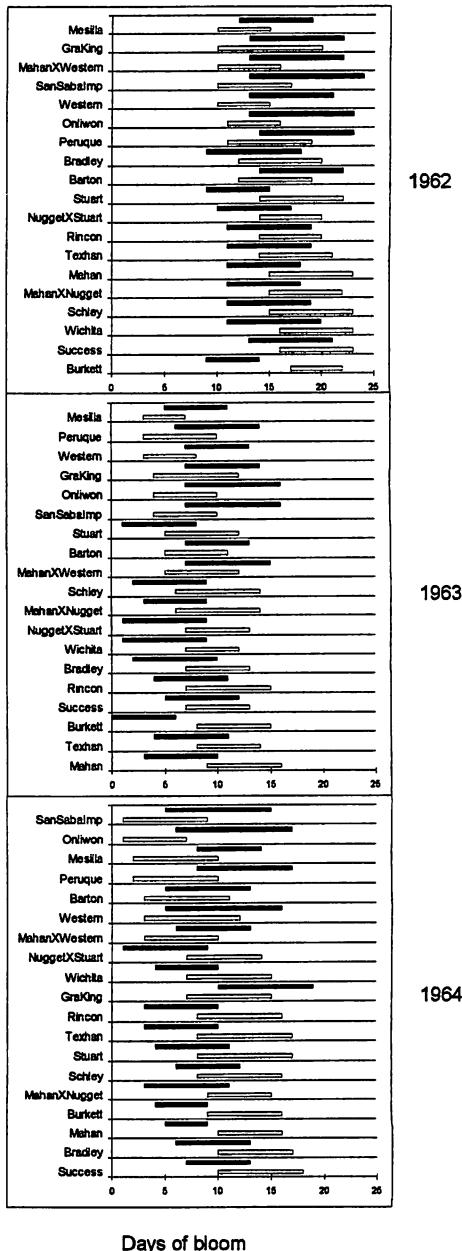


Figure 7. Patterns of dichogamy in 19 pecan cultivars grown at Las Cruces, NM (1962-1964) in order of pollen shed by year, shown as days of bloom relative to the earliest year (1963). Pollen shed □, Pistil receptivity ■.

**Table 2. The effect of season on mean Julian date of inner scale split (ISS), pollen shed (PS), and stigma receptivity (SR) for 13 pecan cultivars at Shreveport, LA.**

Year	ISS	first PS	last PS	first SR	last SR
1983	94.5 a <sup>2</sup>	126.5 a	134.2 a	127.7 a	137.4 a
1984	90.7 b	117.6 b	124.3 b	118.7 b	129.7 b
1985	88.6 b	111.1 c	121.5 bc	114.4 c	126.0 c
1986	83.8 c	107.4 d	119.0 c	104.2 d	121.4 d

<sup>2</sup>Means in a column followed by the same letter are not significantly different at the 0.05 level using paired t tests.

data for stigma receptivity were generally similar, with significant negative correlations for each month from January to April. February temperatures were more closely correlated to female flower bloom than other months; the warmer the February temperatures, the earlier the female bloom. These patterns may not be the same in other locations or with different cultivars.

The duration of the bloom season varied between years, with 1983 and 1984 being the shortest seasons (26 days), and 1986 being the longest (35 days).

From year to year, the flowering period of a cultivar varied in relation to the flowering periods of other cultivars. For instance, 'Cape Fear' was the first protandrous cultivar to shed pollen in 1983, but the last to shed in 1984 (Fig. 3). 'Gloria Grande' was among the last of the protogynous cultivars to shed pollen or have receptive stigmas in 1983, and among the earliest of the protogynous cultivars for both events in 1984. As a result of the seasonal variability, 'Cape Fear' pollen did not overlap 'Gloria Grande' receptivity in 1983, but was an excellent match in 1984.

Cultivar dichogamy patterns were averaged over the four years of observations (Fig. 4). The value of this figure is in providing a generalized ranking of the progression of cultivar flowering from early to late season. According to these data, very early pollen shed typically precedes pistillate receptivity. Furthermore, several protogynous cultivars which shed pollen during the mid-season (e.g. 'Melrose',

'Gloria Grande,' and 'Schley') are as effective as protandrous cultivars in pollinating other protogynous cultivars with late receptivity (e.g. 'Gloria Grande,' 'Mississippi 10,' and 'Maramec'). Several protandrous cultivars have periods of stigma receptivity which extend past the pollen shedding period of most protogynous cultivars. Late season pollen shed, as is provided by 'Mississippi 10' and 'Maramec' may be very beneficial under those conditions.

Within cultivar overlap of pollen shed and pistil receptivity will vary by year and cultivar. Over the years of observations at Shreveport, protogynous cultivars had greater overlap of pollen shed and pistil receptivity than protandrous cultivars. Sparks (15) reviewed dichogamy reports from several locations and concluded that "substantial fruit set from selfing is unlikely when the main cultivar is protogynous because protogynous cultivars tend to have complete dichogamy." Further observations would be needed, using standardized methods at multiple locations over multiple years, to validate any generalization.

#### Brownwood, TX

Results of the Brownwood tests are shown in Fig. 5. Seasons vary in the inception of flowering, with 1972 being the earliest season. The 1974 and 1992 seasons were comparable in date of inception. The duration of the bloom season varied from 27 days in 1972 to 30 days in 1974.

The protogynous cultivar 'Chickasaw' began to shed small amounts of

pollen on some trees prior to first stigmatic receptivity in 1992, a protandrous pattern. When data are averaged over years (Fig. 6), 'Chickasaw' is accurately shown as a protogynous cultivar with early to mid-season pollen shed. As noted in Shreveport data, the flowering of a cultivar relative to other cultivars also varies in different years, with the variability potentially influencing pollination efficiency (e.g. 'Western Schley' pollen shed in relation to 'Chickasaw' receptivity).

#### *Las Cruces, NM*

Data from New Mexico (Fig. 7) show the same general patterns of variability as seen in other data: years vary in the inception of bloom, and cultivars vary in relation to each other in different years (e.g. 'GraKing' and 'Wichita'). An unusual aspect of these data is the consistent protogynous pattern of 'Success', which is protandrous in other locations (18). 'Success' has a bright red stigma which often appears receptive prior to pollen adherence. Nakayama (11) did not report the criteria used to judge receptivity. Stigma color may have been misinterpreted, resulting in the aberrant pattern reported. Other cultivars have dichogamy patterns consistent with other reports.

The duration of bloom is apparently much shorter in New Mexico than in either Shreveport or Brownwood, lasting only 15 to 18 days in any year. This would be expected, based on the arid conditions of the location, which should hasten pollen dehiscence and shorten stigma receptivity. Even within the condensed bloom period, cultivars can be separated into early-, mid-, or late-season pollen shedding or receptive classes. Only 'Burkett' consistently showed complete dichogamy.

#### *Variation between locations*

Since the same cultivars occur in two locations, the timing of pollen shed and pistil receptivity at different

locations can be compared. 'Cheyenne' typically began shedding pollen about April 18 in Brownwood, TX but began about April 22 in Shreveport, LA. 'Cherokee' began shedding about April 17 in TX and about April 19 in Shreveport. The greater apparent duration of pollen shed by 'Cheyenne' at Brownwood is probably due to the increased number of trees being monitored (9 vs. 2, Table 1). The bloom of the two cultivars relative to each other is consistent at the different locations.

Bloom began about April 22 and extended to May 15 for 'Success', 'Schley' and 'Mahan' in Shreveport. Bloom began about May 3 and extended to May 15 for those same cultivars at Las Cruces, indicating about a 10 day difference in both the inception and duration of bloom. Furthermore, the bloom patterns of the cultivars relative to each other are greatly different: 'Success' is protan-

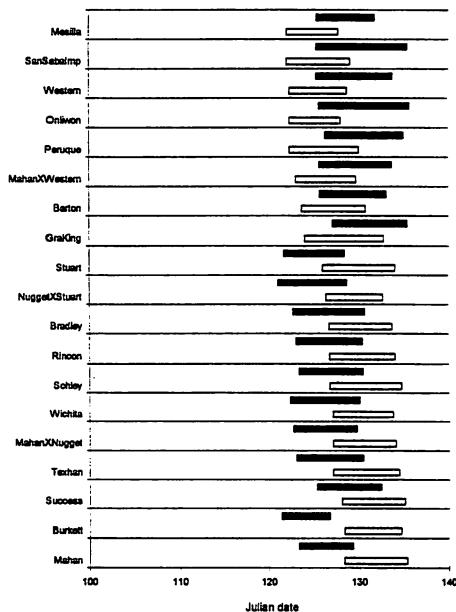


Figure 8. Patterns of dichogamy for 19 pecan cultivars grown at Las Cruces, averaged over 3 years (1962-1964). Julian date 110 = April 20. Pollen shed □, Pistil receptivity ■.

drous, and efficiently pollinizes 'Schley' and 'Mahan' in Shreveport, but is reported as protogynous and inefficient in pollinating those cultivars at Las Cruces.

Differences in bloom patterns between Brownwood and Las Cruces are much less pronounced, both in timing and in pattern, although duration of bloom at Las Cruces was shorter by almost 2 weeks.

### Conclusions

The heterodichogamous flowering system of pecan increases cross pollination between trees, which helps maintain heterozygosity in the population. The system is enhanced by seasonal variability in timing of bloom which results in altered patterns of bloom overlap between the same cultivars in different seasons. In management conditions which include abundant native trees, adequate overlap of pollen shed with pistil receptivity can be assumed due to the inherent variability of the species. In areas where abundant native trees surround an improved orchard site, some attention should be paid to patterns of flowering. This becomes more critical as the acreage of the improved orchard increases, or as proximity and abundance of native trees decreases.

This analysis suggests that it would be a mistake to place much credence in reports of dichogamy patterns for pecan cultivars based on only one year of data. Summaries of dichogamy data, such as that offered by Worley et al. (26), are more reliable for estimating the general season during which a cultivar will either shed pollen or have receptive stigmas. It should be understood that individual seasons may vary greatly, reducing the pollination efficiency of any two cultivars. As a result, multiple cultivars should be included in orchards to insure adequate pollination over variable seasons. Rather than attempting to pick two cultivars which closely overlap based on previous re-

**Table 3. Correlation between Julian date of first pollen shed (FPS) or first stigman receptivity (FSR) and monthly accumulated growing degree days (GDD) above a base of 50F, Shreveport, LA.**

Event	January GGD50	February GGD50	March GGD50	April GGD50
FPS	-0.428 <sup>z</sup>	-0.597	-0.699	-0.709
FSR	-0.691	-0.845	-0.736	-0.775

<sup>z</sup>Pearson Correlation Coefficients, N = 52. All values significant at 0.0001.

ports, or choosing a certain number of protandrous and protogynous cultivars, it may be preferable to choose multiple cultivars which can be relied upon to provide early, mid-, and late season pollen, with the pistillate receptivity period of the key cultivars of the orchard being heavily targeted. Tables of dichogamy patterns provide general, rather than detailed, information concerning the season of bloom for cultivars and should be studied with that in mind.

Given the variability of cultivar performance in different locations, it is obvious that the most reliable information will be obtained closest to the orchard site in question. In order to accurately compare cultivar performance at different locations, it is important that consistent methods of evaluation be used. Researchers monitoring bloom in pecan cultivars should standardize procedures to insure uniformity of methods.

The efficient design of orchards requires attention to pollination patterns. This necessitates having adequate numbers of cultivars with variable dichogamy patterns, adequate numbers of trees of those cultivars to do the job (with tree numbers being justified by nut production), and configuration of all cultivars to insure both pollination and management efficiency. It is appropriate that a good deal of time be spent planning an orchard, since the trees will offer testimony to the planning for many years to come.

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**Announcement**

A symposium on “Technological Advancement in Banana Production and Processing—India, International” is being organized under the sponsorship of Indian Council of Agricultural Research and Kerala Agricultural University during 21-23 August 1996.

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