Seed Maturation, Flower Receptivity, and Selfing in Sweetgum *(Liquidambar styraciflua* L.)

Pamela K. Tauer and C.G. Tauer

Research Specialist, The Holden Arboretum, Kirtland, OH
Professor of Forestry, Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK

Abstract

We evaluated sweetgum trees at two Oklahoma locations to determine when their seed matured, when female flower receptivity peaked, and if they would self-pollinate. Sweetgum seed reached full maturity by the second week of November, female flowers were receptive within 7 days following emergence from the buds, and receptivity peaked within 2 to 3 weeks. A green dulling to slight yellowing of the seed balls can be indicative of mature seed. Calendar date (e.g., second week of November, depending on latitude) is a better measure of maturity, however, because the color changes can be very subtle. Seed balls may be harvested as early as mid-September with a minimal loss in seed germination. Sweetgum does not easily self-pollinate, if at all.

Introduction

Sweetgum (*Liquidambar styraciflua* L.) ranges in location from Connecticut to northern Florida and westward to Missouri, Oklahoma, Arkansas, and northeast Texas. Sweetgum also occurs in scattered locations in central Mexico, Guatemala, El Salvador, Honduras, and Nicaragua (Kormanik 1990). Sweetgum is a common bottom-land hardwood of the Southeast United States. The largest trees of this species occur in the lower Mississippi River Valley (Kormanik 1990), reaching mature heights of 45 m (148 ft) and diameters of 1.2 m (3.9 ft) (Brown and Kirkman 1990). The wood of sweetgum is used for pulp, lumber, and veneer. The seeds are excellent food for birds, squirrels, and chipmunks (Kormanik 1990; Bonner 1974).

Sweetgum shows little variation in seed germination rates, seedling growth, and morphology across its wide geographic range (Bonner 1974). Sweetgum is monoecious; that is, male and female flowers are separate, but on the same tree. Across sweetgum's natural range, the male and female flowers develop from March until May. The pistillate flowers produce spherical fruiting heads that later form 22 to 35 mm diameter seed balls, which are a multiple of two-celled woody capsules (Bonner 1974).

Sweetgum trees produce viable seed crops when they reach 20 to 30 years of age (Bonner 1974). Sweetgum trees can continue seed production every season until they are at least 150 years of age (Kormanik 1990). During seed maturation, the moisture content inside the seed ball drops dramatically, the capsules open, and winged seeds disperse. For seed collection purposes, Bonner (1974, 1987) and Dirr and Heuser (2006) suggest sweetgum seed will be mature when the seed balls begin to change color from bright green to a dull yellow or light brown from September to November. Following collection, the seed balls should be dried completely to ensure the seeds will fall out or can be easily extracted. The seed balls may be dried indoors in 7 to 10 days or outdoors in about 3 to 5 days (Bonner 1987). Under normal conditions, 35 liters (1 bushel) of seed balls yield approximately 365 g (0.8 lb) of clean seed. The number of seeds in 454 g (1 lb) of seeds averages around 82,000 (Schopmeyer 1974). Seed soundness, suggesting seed quality and viability (Hartmann and Kester 2002), is usually around 80 to 90 percent in a good seed year (Kormanik 1990).

Under favorable climatic conditions, sweetgum disseminates an average of 56 viable seeds per seed ball, but only 7 or 8 seeds under the poorest conditions (Kormanik 1990). Seed dispersal is quite variable for sweetgum. The maximum dispersal distance is approximately 183 m (600 feet), but sweetgum seeds move an average of 61 m (200 feet) from the point of release (Fowells 1965).

Sweetgum seed has a shallow dormancy (Nikolaeva 1967), meaning the seed may germinate after it has been in cool, dry storage for some extended period of time (Evans and Blazich 1999). Simple pregermination treatments will enhance the percent and uniformity of sweetgum seed germination, however. One such treatment is stratification in moist media at 3 to 5 °C (30 to 41 °F) for 2 to 4 weeks (Bonner 1987). The seed can also be placed in an aerated water bath for 14 to 20 days at a constant 3 to 5 °C (38 to 41 °F). If seed have been in storage for an extended time, the stratification period can be lessened.

An optimum sweetgum seed germination testing protocol is night temperatures of 20 °C (68 °F) for 8 hours and day temperatures of 30 °C (86 °F) for 16 hours (AOSA 1993). Light is not necessary for germinating stratified seeds (Bonner and Gammage 1967). Tetrazolium staining (Bonner and Gammage 1967), radiography (Belcher and Vozzo 1979), and the excised embryo method (Bonner and Gammage 1967; Flemion 1948) are all good tests to determine seed viability. The germination of sweetgum seed is epigeal, meaning the cotyledons emerge above the surface of the soil after germination (Schopmeyer 1974; Hartmann and Kester 2002).

In spite of the amount of information available regarding sweetgum seed, we were unable to find any information describing the identification of or the timing associated with peak receptivity of the female flowers. In addition, in relying on Bonner's (1987) suggestion of collecting the seed balls when they change color from bright green to a dull yellow or brown, we lost seed in the fall waiting for the seed balls to start to show a color change. We thought we needed clarification of, or a better description of, this color change. We also wondered if sweetgum would self-pollinate. Consequently, we initiated a study with three objectives: to determine (1) when sweetgum seed matures within the seed balls and how this point of maturity can be visually observed, (2) when sweetgum female flowers are receptive for pollination in the spring, and (3) if sweetgum can self-pollinate.

Materials and Methods

We selected sweetgum trees at two locations in Oklahoma for this study. The Stillwater location (central Oklahoma) is outside the natural range of sweetgum but has a considerable number of relatively young sweetgum trees planted as ornamentals. The Idabel location (southeast Oklahoma) is within the natural range of sweetgum with many mature trees present. At each location, we selected four trees as the research trees where seed balls would be bagged and collected. The only criteria for tree selection were accessibility and sexual maturity.

The Maturation Question

To address our first objective, we collected two seed balls from each tree at the Stillwater location on August 11 and August 21, and at Idabel on August 13 and 28, and then every Monday from September 1 through November 24, 2008 (collection day occasionally varied by a day due to weather). Seed balls were observed and photographed weekly on the selected trees to look for color changes and to watch for natural capsule opening. We placed the two seed balls collected weekly from each tree in a prelabeled bag and returned them to the laboratory. The seed balls were then transferred to glass beakers, allowed to air dry for 2 weeks, returned to plastic bags, and placed in a 4 °C (40 °F) walk-in cooler (Percival Modutrol Controlled Systems, Boone, IA) for storage until the end of November 2008. When collection was completed, the seeds were counted, soaked overnight in water, and stratified by placing the moist seeds inside pre-labeled plastic bags in the walk-in cooler at 3 to 5 °C (30 to 41 °F) for 4 weeks. We then removed the seeds from stratification and germinated them on moist filter paper in Petri dishes in growth chambers, for 8 hours in the dark at 20 °C (68 °F) and for 16 hours of light at 30 °C (86 °F). We counted seeds and recorded them as germinated when the emerging radicle was at least 5 mm long.

The Receptivity Question

To answer our second objective, we placed 20 pollen exclusion bags on branches of each of the four trees at each location as soon as the female flowers were visually distinguishable. We placed the pollen bags on the trees on March 24, 2008, at the Idabel location and on April 4, 2008, at the Stillwater location. In addition, we labeled two branches with seed balls but did not bag them until 3 days later. Each pollen bag had one or more female flowers; we removed any male flowers before the branch was placed in the bag. Pollen flight after bagging was noted by day 3 at Idabel and day 4 in Stillwater. All eight trees were shedding pollen by day 8. Pollen flight lasted 14 days or less for any individual tree.

The selected trees were visited every third day (occasionally plus or minus 1 day because of weather). At each visit, we removed two bags and placed bags on branches that had bags removed 3 days earlier (except for the first revisit when the two labeled but unbagged branches were bagged). Thus, only two branches were exposed to potential pollination during each 3-day period. Each day that bags were removed, pictures were taken of the female flowers. Three days after the last sets of bags were removed for pollination, we removed all bags from all branches on April 28, 2008, at Idabel and May 6, 2008, at Stillwater. On October 23, we collected all seed balls from bagged branches of all four trees at both locations and noted any missing or aborted seed balls. Collected seed balls were placed in prelabeled plastic bags and brought to the laboratory to dry, extract, and count the seeds. We used the same stratification, germination, and counting protocols described above.

The Selfing Question

For our third objective, we placed two bags on each tree on March 24, 2008, for Idabel and April 4, 2008, for Stillwater. These bags contained both female and male flowers and remained on the trees for the entire pollen flight period. We removed these bags on April 28 at Idabel and May 6 at Stillwater. The self-pollinated seed balls were collected on October 23, placed in prelabeled plastic bags, returned to the laboratory, and subjected to the same extraction, stratification, and germination protocols previously described.

Results and Discussion

Objective 1: The Maturation Question

Figure 1 presents the average number of seeds per seed ball. Tree number 2 from the Stillwater location was removed because this tree was discovered to be dying and many of the seed balls aborted. Only the first two data points were available from the Idabel location because seed balls were mistakenly collected only for the two August dates. For these dates at the Idabel location, however, 68 and 60 seeds per seed ball were found from the first and second collection dates, respectively. The average seed yield for the Stillwater trees was less than 20 seeds per seed ball for the two August collection dates. Clearly, seed yield is set by August. The lower seed yield at the Stillwater location likely reflects the limited number of trees and thus a limited pollen cloud on the Stillwater landscape, where the only sweetgum trees are planted as ornamentals.

Percent germination across collection dates at the Stillwater location showed zero germination for the mid-August collection, and then a variable, but generally increasing germination percent through November (figure 2). At Idabel, percent germination for the August 13 and 28 collection dates was 35 percent and 71 percent, respectively. These limited data from Idabel trees suggest that seed maturation was occurring, and was ahead of seeds collected at the Stillwater location, but not complete during August. The data also support Kormanik's (1990) estimate that sweetgum can average about 56 viable seeds per seed ball under favorable conditions.

Although seed yield is set by August, the seed is not yet fully mature until mid-November. Seed balls may be harvested as early as mid-September, however, when seed is at an early maturation stage and germination will be high. These results support Michael Cunningham's (personal communication with ArborGen, LLC, in 2008) suggestion of collecting seed balls about the same time seed orchard loblolly pine cones are collected, which is early October in Oklahoma. Collection timing will, of course, vary by location.

In mid- to late September, when seed balls were in the early maturation stage, the seed balls were still fairly bright green, with little sign of color change (figure 3). For early collections, the date rather than the color might be a better indicator of the optimum time to collect. By early to mid-November, when the seed were fully mature, the bright green of the seed balls faded to shades of dull green to yellow-brown (figure 3), such that seed ball color may be an indicator of seed maturity at this stage. These results agree with Bonner (1974) and Dirr and Heuser's (2006) results that color change to shades of light green to brown is an indicator of full maturity. The color change can be quite subtle (figure 3), however, particularly in the absence of photos of earlier observations for comparison. This subtle change explains why we lost seed in the past while waiting for an obvious color change. The documented maturity date may be the more reliable indicator of the optimum time to collect sweetgum seed.

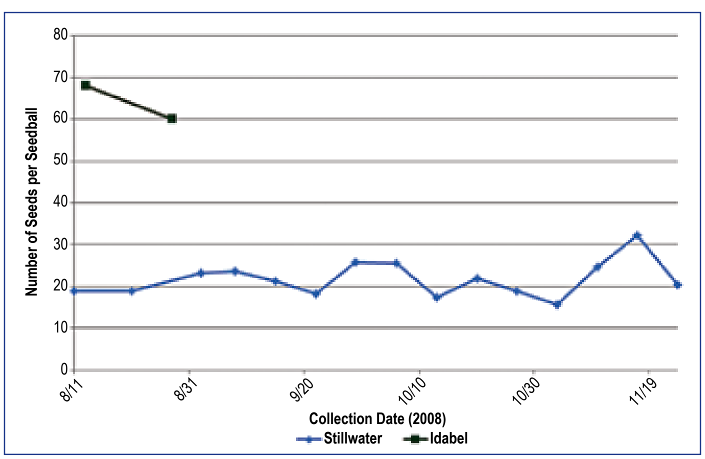

Figure 1. The average number of seeds per seed ball by collection date for all trees at Stillwater, OK, and the first two collection dates for all trees at Idabel, OK.

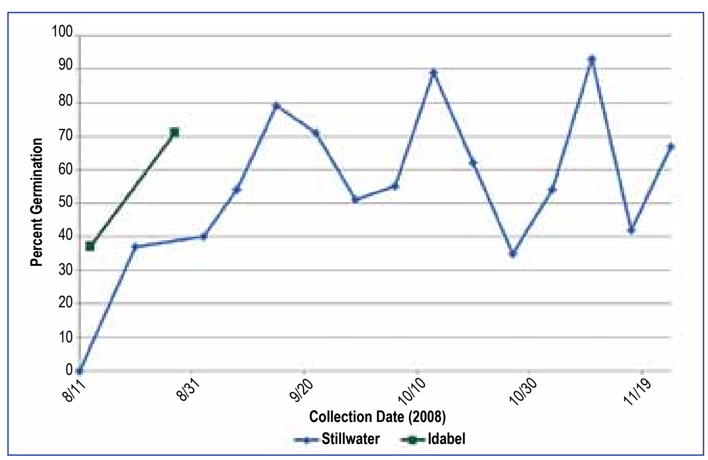

Figure 2. Germination percent by collection date for all trees at Stillwater, OK, and the first two collection dates for all trees at Idabel, OK, to assess maturation.

Figure 3. Photos of a seed ball from Tree 1 (Stillwater, OK) at early maturity, **upper left**, and at full maturity, **upper right**; and a seed ball from Tree 4 (Stillwater, OK) at early maturity, **lower left**, and at full maturity, **lower right**.

Objective 2: The Receptivity Question

The average number of seeds per seed ball across receptivity times (bag removal date) for individual trees varied greatly at each location, ranging from zero to greater than 80 seeds, depending on the tree, collection date, and location (data not shown). On average, however, the Idabel trees had considerably greater seed production than the Stillwater trees (figure 4). As suggested earlier, lower seed set and yield at Stillwater probably reflects a limited pollen cloud on the landscape.

The receptivity seed set count was much lower than the maturation seed set count observed for objective 1. This difference likely reflects the effects of having the seed balls bagged for much of the pollination period. More than 3 days may be required for full seed set, but the simple presence of the bags may have also limited seed set or had other negative effects. Germination data indicate that sweetgum female flowers were most receptive to pollination on the third week of April in Stillwater and approximately 1 week earlier farther south in Idabel (figure 5). As expected, latitude influences flower receptivity timing. Female flowers were receptive almost as soon as they emerged and maximum receptivity was reached in 2 to 3 weeks.

Although the highest numbers of seeds per seed ball at the Idabel location were from a receptivity time in late March, germination percentages were low at that time. High germination percentages did not occur until the second week of April receptivity time. For the Stillwater location, the highest numbers of seeds per seed ball and the highest germination percentages occurred from a receptivity time during the third week of April. This timing difference between the sites is probably attributable to climatic differences due to the 260-mile, north-to-south geographic separation.

Figures 6 and 7 show the physical characteristics over time of seed balls from two of the Stillwater trees. As soon as receptivity was reduced, the stigma showed signs of drying and browning. Most of the trees had green or yellow-green flowers, but some had flowers and fruit with a reddish hue, as seen in figure 7 (lower left). This red coloration persisted until maturity and could disallow the use of color changes to accurately determine maturity. This observation, along with the subtle color changes noted previously (figure 3, upper pictures), further suggests that date may be the most reliable indication of maturity.

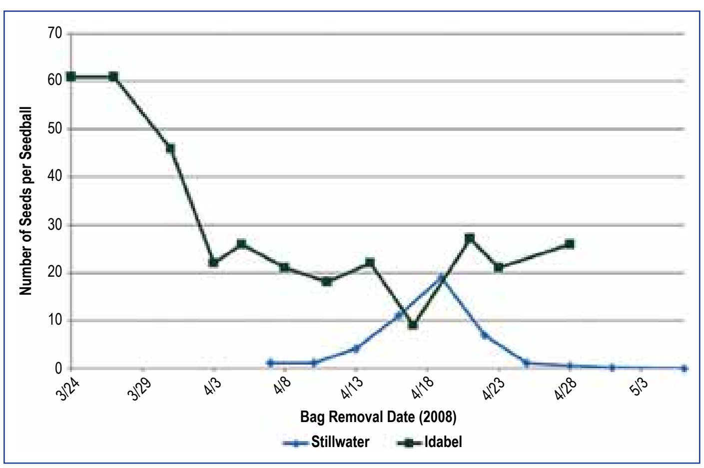

Figure 4. The average number of seeds per seed ball at each receptivity date for all trees at Idabel and Stillwater, OK.

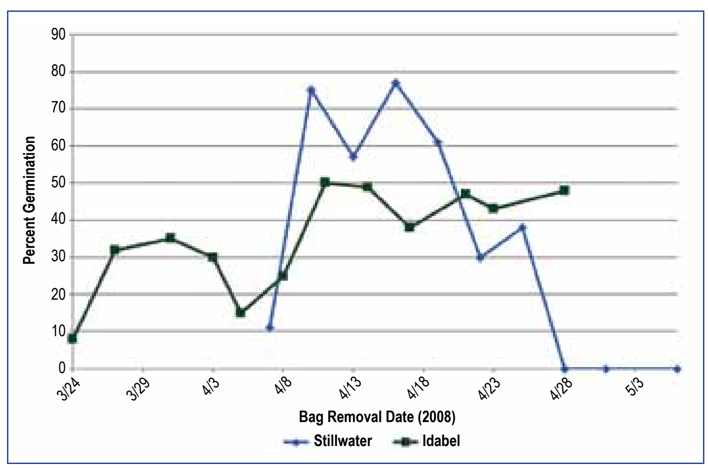

Figure 5. Germination percent by receptivity date for all trees at Idabel and Stillwater, OK.

Figure 6. Photos of Tree 1, Stillwater, OK. **Upper left,** a female flower on the first day of the study; **upper right,** a female flower on day 7; **lower left,** a female flower at peak receptivity; **lower right,** a female flower at the termination of bagging, past receptivity.

Figure 7. Photos of Tree 4, Stillwater, OK. **Upper left,** a female flower on the first day of the study; **upper right,** a female flower on day 7; **lower left,** a female flower at peak receptivity; **lower right,** a female flower at the termination of bagging, past receptivity.

Objective 3: The Selfing Question

Of approximately 40 selfed seed balls from seven trees, only two trees at the Idabel location produced four mature seed balls (three from one bag and one from a second bag). These mature seed balls were the only selfing seed balls harvested from both locations. A total of 25 seeds were extracted from these seed balls and only 8 germinated after stratification. The selfed seed balls may have been pollinated because of self-pollination, may have been pollinated because of contamination resulting from a ripped bag (likely for the single bag with three seed balls), or may have been pollinated before the bags were placed on the female flowers (doubtful). Clearly, these results suggest that sweetgum does not easily self-pollinate.

Conclusions

Seed of sweetgum reaches full maturity by the second week of November in Oklahoma. Seed maturity across the range will no doubt vary by latitude, but a slight yellowing to browning of the seed balls can be indicative of mature seed. Seed balls may be harvested as early as mid September, however, with a minimal loss in germination percent. Since the color changes can be very subtle, we suggest collection based on date and not color.

As expected, female flower pollen receptivity at the southern location occurred earlier. Sweetgum flowers become receptive within 7 days following emergence from the buds and receptivity peaks within 2 to 3 weeks following emergence. If someone's goal is controlled crossing of sweetgum, the flowers should be bagged as soon as they can be recognized following bud break. The bagged flowers should then be pollinated for 14 to 21 days after bagging.

Finally, sweetgum does not easily self-pollinate, if at all.

Address correspondence to: Chuck Tauer, Room 008C, Agriculture Hall, Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078; e-mail: chuck.tauer@okstate.edu.

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