THE PHENOLOGY OF SWEETGUM LIQUIDAMBAR STYRACIFLUA L.)[1]

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INTRODUCTION

Sweetgum (Liquidambar styraciflua L.) is a valuable forest tree species charac terized by fast growth and good form. It has wide ecological amplitude, occurring on a variety of sites over a large geographical range. Maximum growth is attained on the moist alluvial soils of river bottoms in the Atlantic and Gulf castal Plains. Sweetgum has long been recognized for its commercial importance and recently has attracted the attention of forest geneticists who sec the opportunity for exploiting its productive potential. Many basic studies are relevant to tree breeding programs; among these, the vegetative and reproductive phenology is of particular importance. This knowledge will aid in the execution of programs requiring that the developmental stages of the tree be synchronized with such practices as controlled pollination, fertilization, grafting and planting.

METHODS

Thirty sweetgum trees located on the University of Georgia Whitehall Forest were selected for study. The trees, all over 15 years old, occupied sites ranging from a moist river bottom to a dry west-facing slope. Field study began February 8, 1965, and continued through the growing seasons of 1965 and 1966. Observations of the developmental state of buds, shoots, leaves, and cambium were made weekly from February 8 to March 1, three times per week until March 30, and weekly thereafter until November. Vegetative buds, mixed buds and specimens including phloem, cambium and xylem were collected on each visit and fixed in FAA for microscopic study. These were embedded in paraffin, sectioned, stained with safranin 0-analin blue, and mounted on glass slides using standard techniques. The prepared slides were then studied in chronological order to determine the sequential development of the struc-tures under consideration.

RESULTS AND DISCUSSION

Development of Reproductive Structures

Mixed buds were formed by mid-September and remained dormant over the following winter. The staminate inflorescence elongated rapidly and emerged from the bud scales in late March or early April. This will be referred to as the "floral flush."

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The staminate inflorescenses consist of many 2-lobed stamens born on short filaments and arranged in conical clusters; twelve to fourteen clusters are connected by short stalks to a central rachis. In September, the primordial staminate in florescenses were macroscopically visible upon removal of the bud scales and sporogenous tissue was differentiated in the anthers by early February. Meiosis in the archesporium took place from March 15 to April 5 in the 30 trees studied over the two years observed. The terminal stamens turned a red color prior to pollen release as also observed by Schmitt (1961). Pollen dispersal in the study area occurred from April 10 to April 22.

The pistillate inflorescence is a head composed of from 30 to 50 bi-locular ovaries. It is attached to the bud below the base of the staminate rachis by a slender peduncle and is subtended by 4 bracts. The 12 to 14 hemianatropous ovules are aligned in 2 to 4 longitudinal rows on the placental wall which separates the 2 locales of the ovary. The multiple fruit may contain from 30 to 50 viable seeds but will have as few as 7 in average years (Fowells 1965).

The pistillate inflorescences were small and undifferentiated until the beginning of floral flushing, at which time they began to grow and differentiate rapidly. The megaspore mother cells were apparent in basal ovules by April 15 and most megasporocytes had undergone meiosis by May 4. Megasporogenesis was found to be the "polygonum type" as described by Maheshwari (1950) and is in agreement with the observations of Flint (1959). Fertilization took place from April 30 to May 12 and embryos and endosperm developed rapidly. Seed matured in early September until mid-October after which they were shed intermittently over the ensuing fall and winter. Figure 1 shows the range of time for the previously described reproductive phenomena during the two years observed.

FIGURE 1

FIGURE 2

FIGURES 1 AND 2 ILLUSTRATE THE RANGE OF INITIATION DATES FOR REPRODUCTIVE AND VEGETATIVE EVENTS RESPECTIVELY FOR THE 30 TREES STUDIED OVER 2 SEASONS.

Development of Vegetative Structures

The "vegetative flush," or rapid elongation of leaves from vegetative buds, began from April 4 to April 26 on the 30 trees studied. All leaves arising from uoth vegetative and mixed buds were mature by May 15. Buds with scales were formed on short shoots by June 1 but long shoots continued to elongate and develop new leaf primordia throughout the growing season. Longitudinal growth of long shoots ceased by August 15 and bud scales formed over the apical region.

The cambium was hydrated and produced new phloem elements about March 30, however, in agreement with the observations of Jackson (1952) new xylem was not differentiated until May 15 after the leaves were mature. This suggests that in sweetgum xylem formation is not triggered by basipetal auxin movement as intimated by Reines (1959) in black cherry and many authors in other species but rather by the production of photosynthates in the foliar organs. Time of occurence of the above vegetative phenomena are shown in Figure 2.

Floral flush occurred 3 to 8 days later in 1966 than in 1965 and the vegetative flush was 2 to 6 days later in 1966. Meterological data obtained from the U. S. Weather Bureau in Athens show that the mean temperature for the winter months was 2.6 degrees cooler in 1966 than in 1965. The delay in floral and vegetative flushes in 1966 may have been caused by the cooler temperatures.

The vegetative and reproductive phenology of sweetgum in a local area has been investigated. Further studies on the influence of climate and geographic distribution on these phenomena are needed.

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DISCUSSION[1]

MORGENSTERN - I have a question for Dr. Clausen regarding the random pattern of fruit characteristics in yellow birch. I was wondering whether you had looked at the distribution of the fruit characters from the point of view of natural selection from an optimum area progressing north and south. Is there any indication that you get a decline in size as you go north as well as a decline, a smaller size, as you go south, that perhaps might lead you to some different conclusions?

CLAUSEN - I really haven't looked at it from that point of view. Just recollecting from the data, I doubt whether it would be true, but it might well be worth checking that particular aspect, but I really couldn't tell you on the basis of the information I have now.

SQUILLACE - I have a similar question for Dr. Clausen. Have you plotted the seed source data on a map at the respective locations and looked for patterns? Very often you can get a pattern that is not related to latitude or longitude; in other words, you can get a pattern such as was mentioned by Dr. Morgenstern in which there is a gradient from the interior portion of the species range outwards toward the limits, or some similar pattern that is not related to latitude, longitude or climatic factors in a simple manner.

CLAUSEN - I did attempt a little plotting; I think the only thing I plotted was against latitude. I did not plot it on the distribution map simply because I didn't have time. I must confess our Station is not very efficient in statistical procedures; and consequently, I only got my last analysis a week and a half ago, and I wrote the paper last week, so there wasn't that much time to follow up some of these things. I think your suggestion is a good one, Tony, and I will look at them when I get back.

JOHNSON - I'd like to ask Bob Kellison to clarify for me the growth information after two years' outplanting for the various provenances of yellow poplar he worked with.

KELLISON - There were no differences in height growth, Bill. This was true for the various seed sources when grown at one location and also when they were compared across locations. I believe that differences in height growth will be found but they were not evident at this time because all plants had been reduced to a common level by freeze and rabbit damage. A third cause for the lack of differences probably lies in the method of analysis. The data obtained so far have been analyzed only for source within location and location differences. When they are analyzed for trees within source and within plot differences, I imagine significant differences will be found. I will remeasure the plots this fall and, hopefully, they will have recovered from the external influences of rabbits and cold to make the data more meaningful.

GABRIEL - My question is directed to Mr. Hicks. Do you recall how many days before fertilization that you first noted megasporogenesis?

HICKS: The interval is about 15 days.

[1] Transcripts of the discussion were sent to each of the participants for editing with the specific request not to change the contents of their remarks.

FECHNER - I'd like to ask Jerry Stairs a question. I think you said that while the southerly ecotypes were surviving, that they were growing better, faster, taller than the northerly ecotypes; is this correct, and if so, is this simply because they grew longer in time (maybe did not shut off growth soon enough), and consequently were then killed back, or why?

STAIRS - I'm not sure if I can give you a quantitative answer, the southern seedling, are injured by freezing during each winter, and thus the next year's growth is by sprouting. A comparison of sprout growth increment with normal growth is not a valid comparison. We haven't compared elongation times or other factors because of this problem. As a general observation I would say that annual elongation of the southern seedlings was greater in the first year or two after planting. The final answer will have to be found by planting the two races where they can both survive.

KRIEBEL - Bob, I just wondered where your nursery is. You had a chart showing your variation height growth in the nursery. If you mentioned where the nursery was, I missed it. This could make a considerable difference.

KELLISON - The North Carolina Forest Service Nursery at Clayton, about 15 miles south of Raleigh, right on the edge of the Piedmont-Coastal Plain.

HUNT - I've a comment regarding the seedling growth data as you observed them in the nursery, Bob. Perhaps you would offer an opinion also. Your southern coastal and central coast sources apparently grew best. You stated, however, that this was probably not anything extraordinary since the bed density was so low. I feel your results are even more exceptional because of this reduced density. We have some practicing nurserymen here today that might back me up. High density hardwood seedbeds often exhibit early stagnation and mortality with a reduction in both height and caliper growth. Medium bed densities tend to increase seedling height at the expense of stem diameter growth. This is especially noticeable in the center of the bed where the density is the greatest. Low density beds often produce seedlings of larger stem caliper. They may have more leaves, but I note a slight reduction in height growth. If this were the case in your nursery, I would want to follow up why the seedlings in the less dense beds still grew taller. Perhaps stem caliper would prove a bit more meaningful in this case.

KELLISON - Possibly, that's true. However, the seedlings in the real sparse beds were always considerably taller and larger in diameter than those in the more densely graving beds. Since the seedlings from all other seed lots were growing at comparable density and these weren't, it was my observation that they had been unduly influenced by spacing. Possibly the conclusion I reached was premature since it was based only on height growth; diameter growth was judged only on observations.

McNABB - I haven't observed it real closely but probably what he said is true; the ones that were denser had more vegetative growth on the perimeter than the ones where the beds were sparse.

KLEIN - In a nursery where the seed is likely to be good, a pine nursery for example, a sparse bed indicates some difficulty with bed conditions; and these same conditions are likely to inhibit growth. But in this case, the sparseness may have been due to few seeds, rather than seedbed conditions acting to inhibit germination. For a species such as tulip-poplar, in which seed is likely to be limiting, a correlation between germination and growth is not necessarily to be expected. Where the seedlings were dense, then the density itself may have been reducing the growth.

STAIRS - I believe that Mr. Hunt's suggestion was that height growth in some seedling beds could be positively correlated with density. I think John Barber could comment on this question.

BARBER - I made a feeble attempt to do some nursery bed selection in yellow poplar in Georgia nurseries and we found that it was hopeless. The main problem was that as we went to lower bed densities, we got larger seedlings with more variation between seedlings. Where the beds were very dense, the seedlings tended to be short and of very small stem diameter.

GENYS - In an experiment with 25 strains of tulip tree in Maryland, I have also observed that seedlings in denser portions of the nursery beds were smaller than those at the edges or at lower densities.

TAFT - It's been said that the greater the distance between parent trees the higher the seed set. Did you find this in your crosses between the Mississippi and New York trees?

STAIRS - I really can't say right now because we have only germinated seed from our first series of trials. In this first experiment the distant crosses were certainly as successful as the local ones. We do have a cooperative study with tulip poplar in progress with the U. S. Forest Service at Gulfport; perhaps we will be able to further quantify this answer at a later date. We presently have seed.in storage from the latter study, but as you have pointed out previously this species is very parthenocarpic and apparent seed yield may not be meaningful.

GABRIEL - Jerry, weren't you in the least bit curious about variation in height-growth, or other characters, that might have shown up in your parental stock and in your hybrids? It seems rather odd to me that you wouldn't have at least measured them once.

STAIRS - We have made measurements in the greenhouse prior to transplanting to the nursery. At that time the hybrids were growing faster than the parent species. However, after transplanting the differences are less clear and are made difficult to evaluate because of cold damage. I would suggest that the evidence is encouraging and that we are conducting further studies. The situation is a common one, as you pointed out in your work on Shumard Oak, southern strains often grow faster but are less cold-hardy. We hope that intra-specific hybridization will allow a positive synthesis of these factors.

CECH - I'd like to address a question to Dr. Stairs. Do you think that short-term studies on cold-hardiness are adequate for species with a long life cycle? Will the range in cold stress in the short-term study be nearly as broad as that in a long-term study?

STAIRS - No, short-term studies only give us tentative answers. In such studies, we ignore the question of the unusually cold winter or varying times of late and early frosts. I would only say that present results are encouraging but they will require long-term field trials for final answers.

JOHNSON - I have a question for Ray Hicks. Did I understand you to say that sweetgum seed matured about mid-September?

HICKS - They mature somewhat earlier than that, but you have to crack the head open to get them out. They're not dispersed until October, or thereabouts.

JOHNSON - Might they not mature earlier than September, but this earlier maturity not be detectable by the techniques you used?

HICKS - This is possible. I didn't delve into that very deeply at all; I just took the seeds out and germinated a few. This was when I started getting germination.

LARSSON - I have a question for Dr. Stairs. Planting hardwoods has generally been a failure in Ontario. Our preliminary studies using tulip poplar from Indiana or Maryland have indicated that good success can be assured on the proper soils if the trees are planted under protected conditions in openings in woodlots. I would like to have Dr. Stairs' opinion on this matter.

STAIRS - Yes, I think this a general observation that is often made. Tulip poplar in our region also does best in protected coves or among existing trees. We will look at this problem of genotype-environment interaction in future studies. One cannot always assume that southern sources are without a considerable measure of cold resistance. We have 30-year-old bald cypress growing very well in Syracuse. Don Fowler reported several years ago that white pine seed from Tennessee required more stratification than did seed from Canada. This requirement apparently help protect the southern seed from too early germination during alternating winter temperatures.

CONKIE - I have a question for Ray Hicks. I understood you to say that your sample trees varied from river bottom to drier hilltop situations. Would you cc went on differences of phenology with reference to the location of parent trees?

HICKS - Well, I didn't attempt to make a statistical analysis since I only had 30 trees, and 10 per site, I divided it up into three different categories, more or less a hillside site, intermediate site, and a river-bottom site. But just from observation alone I can say with a fair degree of confidence that there seems to be very little difference in site. I had one tree in the river bottom that was very far ahead of all the rest, but then the rest of the trees in the river bottom area were behind some of the trees that were up on the slope. So I think this was Just an odd tree.

FERET - I'd like to direct a question to Bob Kellison. I've observed yellow poplars along the Delaware River with leaf characteristics similar to those of your acid soil ecotype. I'd like to know if you've made any correlations between soil moisture content and the leaf characteristics of this particular ecotype.

KELLISON - I have not correlated the "acid soil ecotype" with moisture content Many questions have arisen since this distinct type of yellow-poplar has been observed and I hope to answer some of them through further studies. Last fall a number of collections were made from areas up and down the East Coast where the water table is near the surface of the ground, as it was at the south coastal location. These sources are now being grown in the nursery and some of them are exhibiting the same leaf pattern as those from the "acid soil ecotype." I would like to see you later about getting a seed source from the area you mention.

DORN - I'd like to direct a question to Bob Kellison. You mentioned branch angle in tulip-poplar, but I didn't catch whether you measured it on all these trees; and if you have, how did you determine branch angle in view of the fact that different branches on the same tree would have different angles.

KELLISON - First, I did a preliminary study to determine if I could measure a limited number of branch angles within one tree and get an acceptable approximation of the angle of branching for the whole tree. Bayne Snyder at Gulfport had done this for longleaf pine and found that by measuring a limited number (six, 1 think) of angles within the central portion of the crown he could determine the branching angle of the whole tree. Following Snyder's approach, I found that by measuring six angles within the central portion of the crown the branching angle of the tree could be characterized quite well. To answer your second question, I climbed every tree and measured the angle of the six branches with a plastic gauge which I had constructed.

GENYS - Mr. Kellison, you mentioned that you were able to distinguish a particular ecotype of tulip tree on the basis of the leaves. Are these characteristics phenotypic or genotypic?

KELLISON - The results are included in the paper but because of time I didn't elaborate on it in the presentation. Regardless where the progenies are growing, I can identify that particular seed source. For example, 12 trees were selected from the south coastal location and progenies from each of these trees can be identified as originating in that location, just by the shape of the leaf. Of course, I can't distinguish between trees within the location but there is no problem in identifying the seedlings as originating in the south coastal location. This leaf characteristic was evident in the nursery bed and it is evident in the two-year-old plantations, regardless of whether it is planted in the mountains, Piedmont or Coastal Plains.

CONNOLA - I'd like to ask Dr. Clausen did you take elevation into consideration?

CLAUSEN - Yes. I hope you can make it out on the first table. There are elevational differences there, but I did not have the time to try to correlate any of the fruiting characteristics with elevation; and of course you do get some confounding with elevation. I might just go a little outside of the subject of the paper to give an indication of the effect of elevation. We were talking about cold-hardiness of hardwoods in general, and this spring, I checked the progenies that came from these collections. Actually I have 55 collections, but some of them are stand collections so they are not included in this paper. My southern-most source which is from Union County, northern Georgia, had surprisingly little winter damage, but it is from about 4700 feet as I remember. The two Tennessee sources which are from about 1400' and 1700' elevation are the two most severely damaged sources in the whole study, so elevation is very important, I'm sure of that, but whether it affects the fruiting characteristics, I really don't know. Certainly it affects the cold-hardiness; this is pretty obvious, and very likely it has some influence on other characteristics too; I would be very surprised if it didn't. I can't give you any specifics as far as the fruiting characteristics are concerned. Certainly latitude doesn't explain everything. You have a confounding with the elevation.