The Pistillate Inflorescence of Sweetgum (Liquidambar styraciflua L.)

By DAN SCHMITT[1])

(Received for publication July 15, 1965)

In 1905 SHOEMAKER reported on the morpholgy and anatomy of the sweetgum *(Liquidambar styraciflua* L.) inflorescence in relation to a more exhaustive study of floral development in witch-hazel *(Hamamelis virginiana* L.); more recently FLINT (1959) wrote a detailed account of megasporogenesis in sweetgum. Because of the significance of floral structure and anatomy for phylogenetic studies and for practical breeding purposes some additional morphologic and anatomic details may be of interest.

The information reported here was obtained incidental to an attempt to follow pollen tube growth during an investigation of self-sterility in sweetgum. The pistillate inflorescences (heads) were sectioned at varying time intervals after pollination, thus affording an opportunity to observe the morphologic structure and anatomy of the heads in some detail as well as to locate the pollen tubes.

Methods

Two sweetgum trees, each in North Carolina forest populations separated by 40 miles, were used as seed parents for post-pollination analysis. Sixty heads from each tree were collected over a period of eight weeks following controlled pollination, and immediately after harvest the heads were quartered and dropped in a modifiod FAA solution (FLINT, 1959). They subsequently were embedded in Tissuemat according to the TBA method of JOHANSEN (1940) and sectioned at either 15 or 20 μ. The sections were stained with hematein (SASS, 1958) followed by lacmoid (CHEADLE *et al.*, 1953).

Figure 1. — Cross section of the pistillate inflorescence of sweetgum four days after pollination. Arrow marked *(A)* indicates position of the interfascicular cambium delimiting axis of the inflorescence. (B) is a stamen (×15).

[1]) Research Forester, U. S. Forest Service, Institute of Forest Genetics, Gulfport, Miss.

Results

Figure 1 shows the axile nature of the pistillate inflorescence. Its growth is determinate only in a qualified sense, since the interfascicular cambium which is confluent with that of the peduncle continues to function for several weeks after fertilization. It does so, however, as a secondary or marginal meristem, thus contributing to the globular shape of the head.

The bicarpellate capsules are appendicular. Three main bundles enter each carpel resulting in tri-lacunar gaps in the marginal meristem of the head. The bundles become ramiform in the receptacle. The initial peripheral branches develop acropetally to form the staminate traces, usually three — four per carpel. Subsequent branching produces a prominent dorsal bundle and several ventral bundles in each carpel. As the inflorescence grows in size, papillae form on the surface of the capsules. Within each papilla a vascular trace is initiated which differentiates basipetally towards the existing vascular net.

Before pollen release from the staminate inflorescence the bicarpellate capsules are nearly distinct, i. e. united only at the base. The sides of the capsules are covered by transversely oriented epidermal hairs. As the inflorescence continues growth the hairs of the adjacent capsules interlock *(Fig. 2),* thus firmly uniting the capsules almost to their summits.

The stamens arise from the sunken capsule edges, usually at a corner. The filaments are short and traversed by a vascular trace which extends into the connective supporting the two anthers. The germinal tissue of each anther, located in two initially discrete patches, develops normally producing plasmodial tapetum and microsporocytes. The latter develop into polyporate pollen grains. In the two trees investigated some of the stamens from the nominally pistillate inflorescences produced functional pollen in the sense

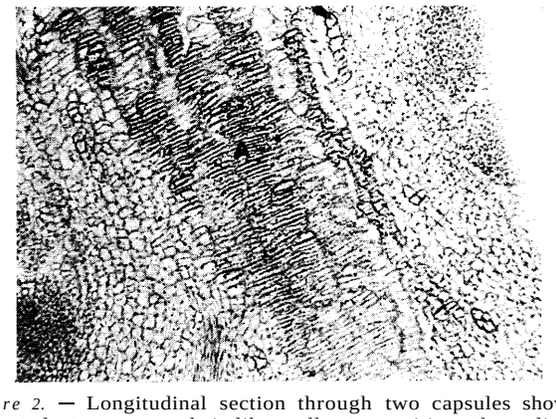

Figure 2. — Longitudinal section through two capsules showing elongated, transverse, hair-like cells *(A)* uniting the adjacent capsules (×80).

Figure 3. — Pollen germinating in anther locule of the female inflorescence. Arrow indicates pollen tube; *(B)* shows well developed endothecium (×138).

that it was capable of germination *(Fig. 3)*. Much of the pollen produced by these stamens, however, is small, wrinkled and probably abortive.

Pollen from the primarily female inflorescence is released by the rupture of a well developed endothecium *(Fig. 3)*. However the maturation of the stamen and its pollen is not synchronized with the development of the rest of the pistillate inflorescence whereas pollen release from the staminate inflorescence coincides with stylar receptivity.

Discussion

The literature clearly indicates that both staminate and pistillate flowers lack corollas; the staminate flowers also definitely do not have calyces. On the other hand statements concerning the presence or absence of a calyx on the flowers of the pistillate inflorescence vary. The evidence advanced to support the presence of a calyx consists of a more or less convolute rim constituting the capsule edges. This rim was held to be a rudimentary calyx (SARGENT, 1921). Other authors were noncommittal (e. g. HARMS, 1930). The absence of a calyx was affirmed by SAMORODOVA-BIANKI (cited in ERNST, 1963) because of the marginal origin of the stamens. In my material there was no evidence of a distinct capsule rim, and, as previously noted, the peripheral vascular traces were all associated with the stamens. These observations tend to confirm the opinion that the pistillate flowers lack calyces as well as corollas.

The stamens on the female inflorescence are neither rudimentary nor, from the standpoint of pollen production, nonfunctional. Although it is possible that the two North Carolina trees were unique in this respect, this does not seem likely because SHOEMAKER (1905) reported and illustrated pollen in the locules of anthers of a pistillate inflorescence from a sweetgum tree in New York (however in his judgement the pollen was abortive, and the stamens functioned as nectaries).

It is rather striking that in sweetgum neither pollen from the staminate inflorescence nor from the stamens of the pistillate inflorescence can effect prompt fertilization of the ovules. In the case of the pollen from the staminate inflorescence, the ovules lack egg apparatus during and for some time after pollen release. However the growth of the pollen tube is arrested in the chalaza until the ovule forms an egg apparatus, usually one to three weeks after pollination.

Asynchrony of pollen from the primarily pistillate inflorescence is of a different type. This pollen is released three to four weeks after the pollen from the staminate inflorescence has been released. By this time the stylar tissue, particularly the stigmatic tissue and the extra-xylary fibrous sheath in the styles, and the internal parenchymatous tissues of the ovaries, have become sclerified. More important, the ovules have already been fertilized or else they have aborted (SCHMITT and PERRY, 1964).

Chalazogamy, delayed fertilization, and the production by both types of inflorescence of functional pollen whose release is not synchronous with ovule development, are perhaps adaptations reflecting the as yet imperfect transition to monoecy in *L. styraciflua*. Because sweetgum achieves its optimum development in the southern region of the mixed mesophytic forest with which it has long been associated and whose climatic requirements are presumed to have changed little since Tertiary times (BRAUN, 1950), it is possible that structurally more primitive floral types (more nearly perfect) could be found in such populations. In this connection it is worth noting that investigations on the floral structure of sweetgum (including this one) were based on trees located in the northern part of its range or from trees of unknown origin in European botanic gardens.

Actually the pistillate flower of sweetgum has a number of features usually considered primitive, *viz.* several archemegaspores, polygonum type embryo sacs, bitegmic anatropous ovules with a prominent nucellus, free nuclear endosperm, and an obviously phyllocarpous ovary. Thus, apart from the reduction in floral parts and the tend towards monoecy, neither of which is complete, the floral structure of sweetgum is relatively primitive. The wood anatomy is also primitive (TIPPO, 1938). The evidence from wood anatomy and floral structure and anatomy lend support to MAKAROVA's (1957) opinion, based on paleobotanic studies of leaf variation in the genus, that *Liquidambar,* is an ancient angiosperm genus in the *Hamamelidaceae,* and that *L. styraciflua* was probably the stem species in this small genus.

Acknowledgements

The research was partly financed by National Science Foundation, Grant No. 10680 to Dr. BRUCE ZOBEL, N. C. State University, to whom my thanks are also due for stimulating questions during the course of the investigations. I should also like to acknowledge the assistance and advice of Dr. T. O. Perry and Dr. ERNEST BALL, N. C. State University, Raleigh; and to thank Drs. E. BAYNE SNYDER and J. R. WILCOX of the Institute of Forest Genetics, U. S. Forest Service, Gulfport, Miss. for reading the manuscript.

Summary

Examination of the pistillate inflorescence of sweetgum at varying intervals after pollination showed that the stamens on the capsules produced pollen capable of germination. But by the time this pollen was released, the tissuses of the gynoecium had sclerified. Such pollen could conceivably function only in cross-pollination.

A previous Russian report, based on botanic garden material, that the pistillate flower of sweetgum lacked a calyx was confirmed.

Despite the reduction in floral parts, the sweetgum pistillate flower is relatively primitive.

Literature Cited

BRAUN, E. L.: Deciduous forests of eastern North America. Blakiston, Philadelphia, 596 pp. (1950). — CHEADLE, V., GIFFORD, E., Jr., and ESSAU, K.: A staining combination for phloem and contiguous tissues. Stain Technol. 28: 49—53 (1953). — ERNST, W.: The genera of the *Hamamelidaceae* and *Platanaceae* in the Southeastern United States. J. Arnold Arbor. 44: 193—210 (1963). — FLINT, F.: Development of the megagametophyte in *Liquidambar styraciflua* L. Madroño 15: 25—29 (1959). — HARMS, H.: *Hamamelidaceae*. Natürl. Pflanzenfamilien 2nd ed., 18 a: 303—345 (1930). — JOHANSEN, D.: Plant microtechnique. 1st ed. McGraw Hill Book Co., New York, 523 pp. (1940). — MAKAROVA, Z. I.: The history of the genus *Liquidambar*. Bot. Zurnal 1182—1195 (1957) *(In Russian)*. — SARGENT, C. S.: Manual of the trees of North America. 2 volumes, 2nd ed.. Dover Publications Inc., New York, 910 pp. (1961). — SASS, J. E.: Botanical microtechnique. 3rd ed., Iowa State University Press, Ames, 228 pp. (1958). — SCHMITT, D., and PERRY, T. O.: Self-sterility in sweetgum. Forest Sci. 10: 302—305 (1964). — SHOEMAKER, D.: On the development of *Hamamelis virginiana*. Bot. Gaz. 39: 248—266 (1905). — TIPPO, O.: Comparative anatomy of the *Moraceae* and their presumed allies. Bot. Gaz. 100: 1—99 (1938).

Anatomische Beobachtungen zur Bewurzelung der Kurztriebe von Pinus radiata

Von ALICIA HOFFMANN DE C. und JOCHEN KUMMEROW

Pflanzenphysiologisches Laboratorium der Universidad de Chile, Santiago

(Eingegangen am 30. 6. 1965)

Einleitung

Es ist in jüngster Zeit wiederholt versucht worden, Kurztriebe von Kiefern zu bewurzeln, um diese als Stecklinge zum Aufbau von Klonen zu benutzen (THIMANN und DELISLE 1942, TODA 1948 und 1952, JECKALEJS 1956, ZAK und MCALPINE 1957, REINES und MCALPINE 1959, ISIKAWA und KUSAKA 1959, RUDOLPH und NIENSTAEDT 1964, MERGEN und SIMPSON 1964).

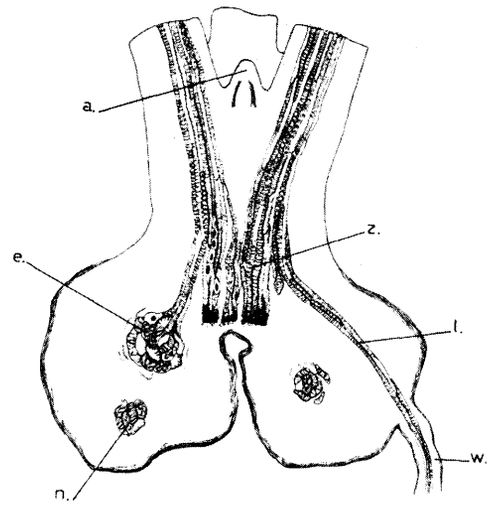

Abb. 1: Schematische Darstellung des medianen Längsschnittes durch die Basis eines Nadelbündels 4 Wochen nach dem Pflanzen im Bewurzelungskasten. Vorbehandlung: 50 ppm IBS, 24 h. Der an seiner Basis unterbrochene Zentralzylinder *(z)* zeigt die Position der ursprünglichen Schnittstelle, an welcher der Kurztrieb vom Stamme abgetrennt worden war. Innerhalb von 4 Wochen hat sich der hier längsgeschnittene, kräftige Kalluswulst gebildet. *a:* Apikalmeristen der Kurztriebsknospe. *l:* Kontinuierlicher Strang von Leitgewebe, der den Zentralzylinder des Kurztriebs mit einer neuangelegten Wurzel *(w)* verbindet. *e:* Blindes Ende eines Leitstranges im Kallus. *n:* Nest von spiralig angeordneten Tracheidalzellen. (Vergr. 25×.)

Vorstehende Arbeit wurde durch den Forschungsauftrag Nr. FG-Ch-100-1 des US-Landwirtschaftsministeriums finanziert (PL 480). Die verwendeten optischen Hilfsmittel stellte die deutsche Forschungsgemeinschaft zur Verfügung. Herrn Dr. BERT LEXEN, Washington, danken wir für sein stetiges Fördern unserer Untersuchungen.

Aus den Resultaten dieser Arbeiten können wir entnehmen, daß zumindest bei einigen Arten die Bewurzelung der Kurztriebe möglich ist, so bei *P. strobus, P. densi-thunbergii, P. densiflora, P. elliottii, P. echinata* und *P. banksiana*. Zu ähnlichem Ergebnis sind auch die Autoren dieser Arbeit bei *P. radiata* gekommen, worüber in Kürze an anderer Stelle berichtet werden soll. Die Bewurzelung ist nur der Anfang der Schwierigkeiten, welche sich einer Benutzung der Kurztriebe als Stecklinge in den Weg stellen. Nach (oder vor) der Bewurzelung muß die oft äußerst reduzierte Kurztriebknospe zum Austrieb angeregt werden, eine Knospe, die unter normalen Umständen kaum zum Austrieb gelangt, es sei denn durch das Restitutionswachstum (COOPERRIDER 1938) nach Beschädigung des Langtriebes.

In unseren Versuchen hatte sich wiederholt gezeigt, daß kräftig bewurzelte Kurztriebe, deren Knospen sich in 2—5 cm hohe Langtriebe verwandelt hatten *(Abb. 3)*, sehr leicht vertrockneten, wenn sie aus der feuchtigkeitsgesättigten Atmosphäre der Anzuchtkästen in das Freiland verpflanzt wurden, wo sie recht häufig Bedingungen ausgesetzt waren, die eine hohe Transpiration erforderten. Wir vermuteten, daß anatomische Ursachen die ausreichende Wasserversorgung der jungen Triebe in Frage stellten. Im folgenden sollen die wichtigsten Resultate unserer diesbezüglichen Studien mitgeteilt werden.

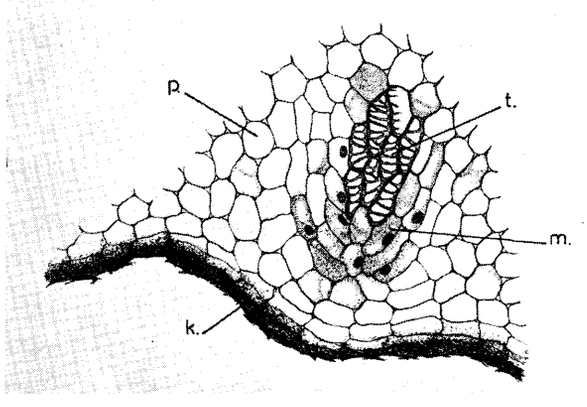

Abb. 2: Graphische Darstellung einer im peripheren Kalluspar-enchym entstehenden Wurzel. *p:* Kalluspar-enchym. *t:* Tracheiden. *m:* Meristematische Zellen, welche sich zum Wurzelspitzenmeristem herausdifferenzieren. *k:* Den Kallus umhüllendes Korkgewebe. (Vergr. 60×.)