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FLORAL PHENOLOGY AND MORPHOLOGY OF BLACK COTTONWOOD, *POPULUS TRICHOCARPA* (*SALICACEAE*)¹

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Seasonal changes in the development of reproductive structures are documented for *Populus trichocarpa* Torr. and Gray. Buds were collected and studied from several trees for a 2-yr period, but to maintain a congruous phenology, representative structures from only one male and one female tree are presented. Collected tissues were fixed, dehydrated, embedded in wax, sectioned, and differentially stained. The development of reproductive meristems begins early in the spring, before leaves emerge. However, the anatomy of male and female flowers is virtually indistinguishable until late spring. The structures of the gynoeceum develop in about 2 wk, then continue to enlarge through the summer and autumn until the trees become dormant. The unilocular ovary consists of usually three, but sometimes four carpels. Stamen development begins in the center of a disk-shaped meristematic region and proceeds centrifugally. Megasporogenesis and microsporogenesis take place late in the winter, approximately 2 wk before anthesis. Dissection of mature flowers revealed 30–50 seeds per capsule on female trees and 40–60 stamens on male trees. When compared to most other *Populus* species, *P. trichocarpa* has a relatively large number of reproductive structures.

The genus *Populus* consists of about 30 species divided into six sections, which together comprise about 10% of the family Salicaceae (Schreiner, 1974; Eckenwalder, 1977; Dickmann and Stuart, 1983). Evidence of *Salix* is found earlier in the fossil records than are those of *Populus*, but both species are among some of the earliest flowering plants. Despite considerable evolutionary history, structural diversity in the family is limited and has been documented in several reviews of morphology, anatomy, and systematics (e.g., Penhallow, 1905; Holden, 1912; Berry, 1917; Fisher, 1928a, b; Nagaraj, 1952; Sattler, 1973; Dickmann and Stuart, 1983).

Populus flowers occur as unisexual, pedunculate, pendulous catkins that appear early in the spring before the foliage develops. Three to 4 wk after anthesis, buds containing next year's developing inflorescences appear in the axils of leaves on extension shoots of flowering branches. Results from this study show that conspicuous morphological changes have already occurred at this point, indicating that the molecular events associated with the initiation of the next year's inflorescences likely begin in conjunction with or shortly after anthesis.

The structural development of male and female inflorescences has been described for *P. alba* L., *P. candicans* Aiton, *P. grandidentata* Michx., *P. tremuloides* Michx. (Fisher, 1928b), *P. deltoides* Bartr. ex. Marsh. (Fisher, 1928b; Nagaraj, 1952), and *P. tremula* Michx. (Graf, 1921; Nagaraj, 1952; Lester, 1963; Sattler, 1973). *Populus* flowers are considered highly evolved, with their apparent simplicity due to extreme reduction rather than an expression of archaic features (Fisher, 1928b). Although *P. trichocarpa* Torr. and Gray has been the subject of several studies of variation in productivity and population genetics (e.g., Gabriel, 1956; Brayshaw, 1965; Stettler, 1971; Heilman and Peabody, 1981; Eckenwalder, 1984a, b, c;

Heilman and Stettler, 1985; Weber, Stettler, and Heilman, 1985; Stettler et al., 1988; Rogers, Stettler, and Heilman, 1989; Heilman and Stettler, 1990; English, Greenaway, and Whatley, 1991; Müller-Starck, 1992), the development of reproductive structures in this species has not been described in detail.

The goal of this study was to document structural development in reproductive buds of *P. trichocarpa*. This work is part of an ongoing effort to study floral homeotic gene expression in *P. trichocarpa* and its hybrids. The information obtained is to serve as a baseline from which to interpret effects of genetically disrupted reproductive development.

MATERIALS AND METHODS

Observation of native *P. trichocarpa* trees in the Willamette River drainage in the vicinity of Corvallis, Oregon (44.34° N, 123.16° W) revealed considerable variation in the timing of anthesis from tree to tree, but early flowering and late flowering trees remained so from year to year. To avoid confusion caused by different timing, tissue for the study of inflorescence development was collected from only one male and one female tree throughout the year.

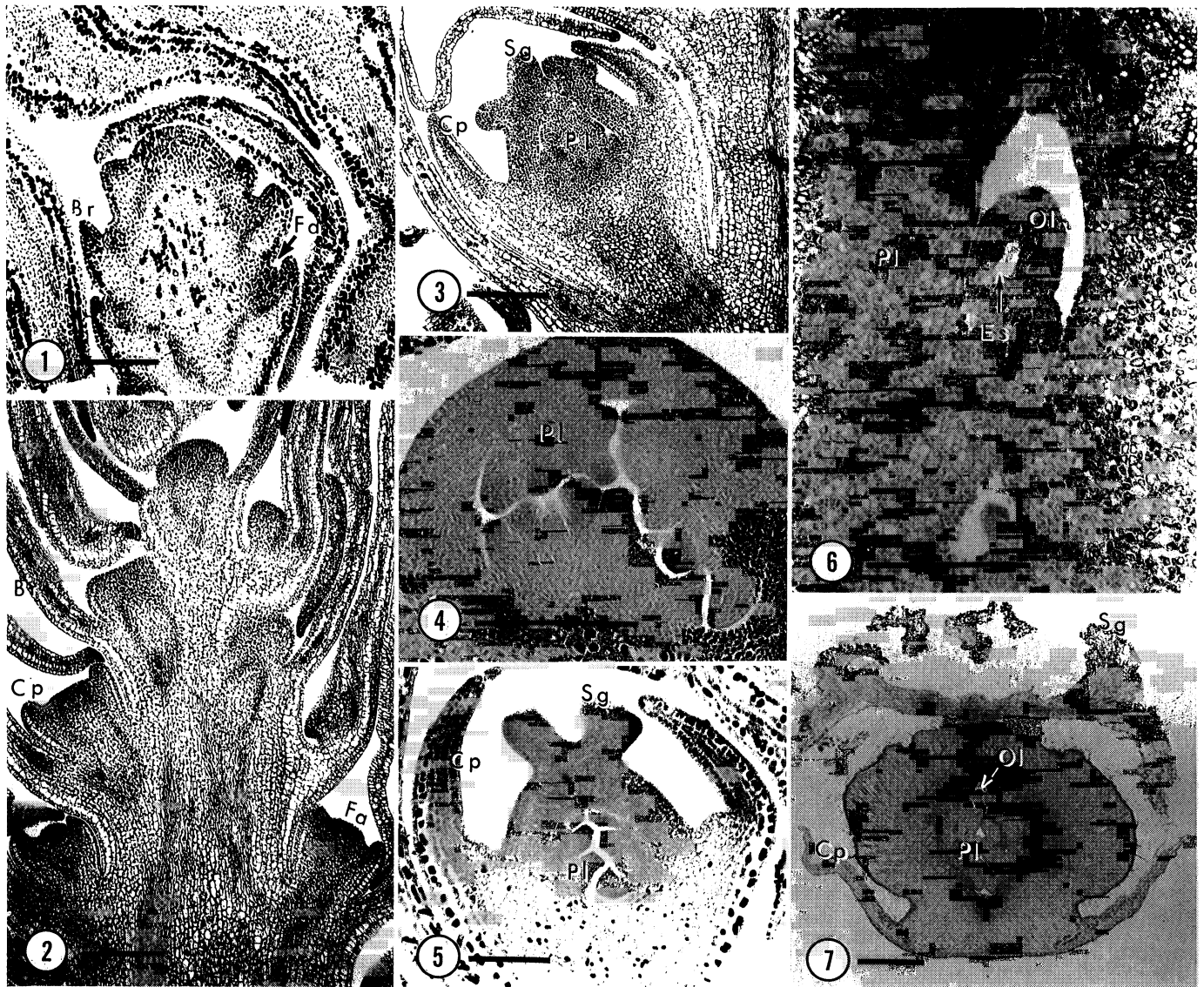
Buds were collected on a weekly basis from April through October, and on a monthly basis from November through March. At the time of collection, excised buds were fixed in an ice-cold 1% glutaraldehyde, 4% paraformaldehyde phosphate buffered saline solution (pH 7.4). To ensure complete penetration of the tissue, buds were left in the fixing solution for 24 hr. Beginning approximately 8 wk after anthesis, when the developing buds were large enough to dissect in the field, bud scales were removed in order to improve penetration of the fixing solution. After fixing, the buds were dehydrated in an ethanol series and cleared in tertiary butyl alcohol before embedding in Paraplast® (Fisher). Serial sections were cut 10 µm thick, mounted on glass slides coated with poly-L-lysine, and differentially stained with safranin and fast green.

To determine the number of stamens and the number of seeds produced, inflorescences were collected and individual flowers dissected. Male inflorescences were col-

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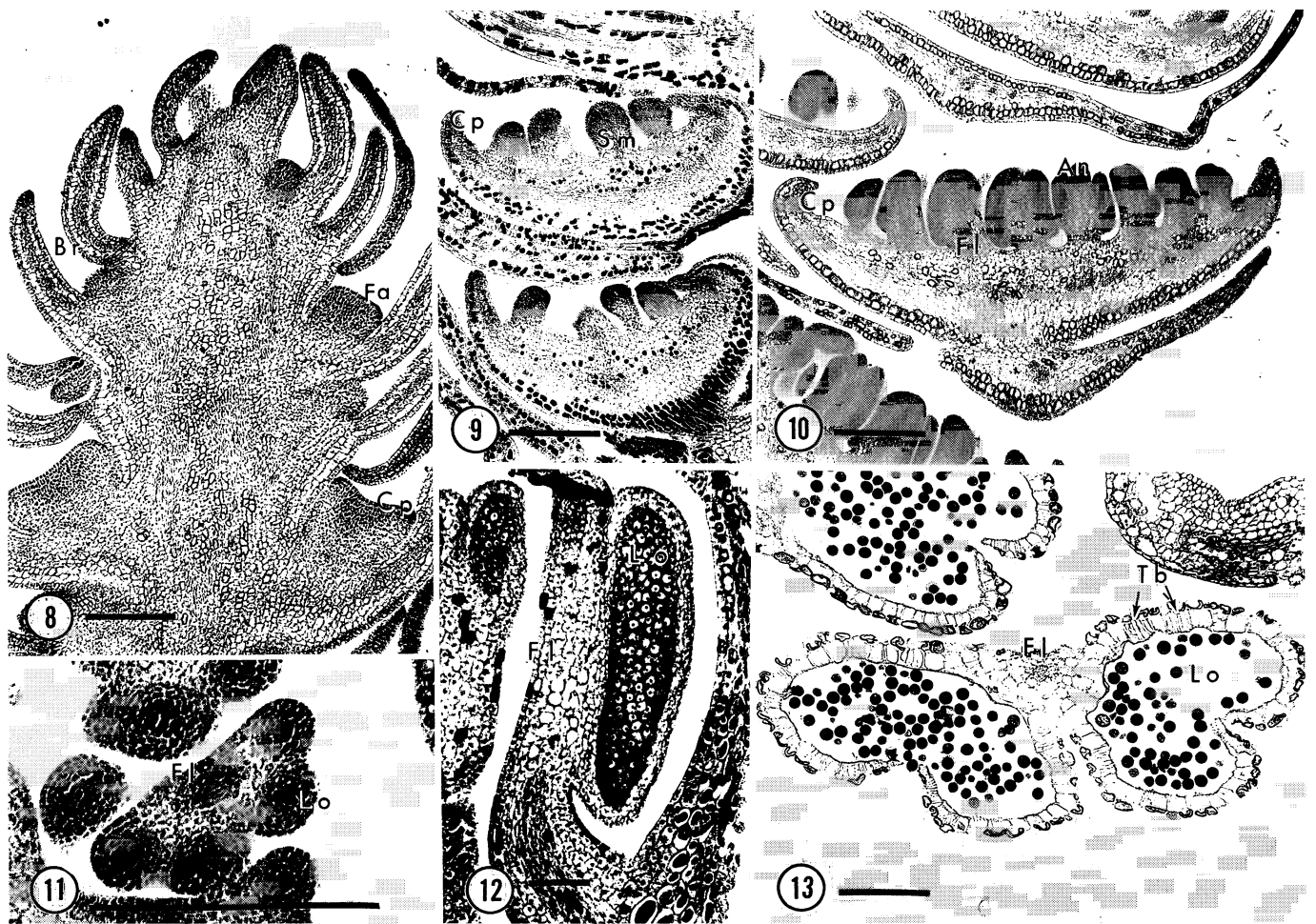
Figs. 1-7. Developmental series for female inflorescences of *Populus trichocarpa*. 1. Longitudinal section of an inflorescence collected in early May showing the initiation of floral apices (Fa) in the axils of each bract (Br). Bar = 100 μ m. 2. Longitudinal section of an inflorescence collected in mid-June showing the acropetal development of the cuplike, reduced perianth (Cp) around flattened (top of the inflorescence), then rounded (bottom of the inflorescence) floral apex (Fa). Bracts (Br) have extended to completely enclose the inflorescence. Bar = 100 μ m. 3. Longitudinal section of one flower collected in early July. The perianth cup (Cp) now completely surrounds the gynoecium. Semicircular stigmas (Sg) have developed atop the unilocular ovary, which contains the developing placentae. Bar = 100 μ m. 4. Transverse section of a pistil collected in mid-September showing the parietal placentation (Pl). Bar = 100 μ m. 5. Longitudinal section of a flower collected in late October showing the change in shape of placenta (Pl) margins, which is an indication of archespore development. Bar = 100 μ m. 6. Longitudinal section of the ovary collected in early April showing the developing embryo sac (Es) within the anatropous ovule (Ol). Bar = 100 μ m. 7. Longitudinal section of a nearly mature capsule collected in early April. Bar = 1 mm.

lected in March, before pollen shed, and female inflorescences were collected in May, before seed dispersal.

RESULTS

In the spring, after anthesis, the first conspicuous morphological evidence of the transition from vegetative to reproductive development in an axillary meristem of a *Populus* bud is rapid elongation and the appearance of lateral appendages along the meristem flanks (Fig. 1). Each inflorescence differentiates acropetally, and a single inflo-

rescence may contain well-differentiated and undifferentiated tissues simultaneously. The lateral appendages become bracts, and in the axil of each bract, increased mitotic activity defines a zone of cells destined to take part in floral organogenesis (Fig. 1). As the bracts elongate, the cells in the axil become organized into a flattened, disk-shaped structure (Figs. 2, 8). Continued development at the edge of each flower primordium forms a raised ring of tissue. Until late May or early June, structural development in a male inflorescence is virtually indistinguishable from development in a female inflorescence.



Figs. 8–13. Developmental series for male inflorescences of *Populus trichocarpa*. 8. Longitudinal section collected in mid-May showing floral apices (Fa) surrounded by the cuplike, reduced perianth (Cp) developing in the axils of the bracts (Br) of the inflorescence. Development proceeds acropetally from a round apex (top of the inflorescence) to a flattened, then an indented apex (bottom of the inflorescence). Bar = 100 μ m. 9. Longitudinal section collected in mid-June showing emerging, rounded stamen (Sm) primordia surrounded by the perianth cup (Cp). Bar = 100 μ m. 10. Longitudinal section collected in late June showing the differentiation of the stamen into a short filament (Fl) and a tetrasporangiate anther (An). Bar = 100 μ m. 11. Transverse section of an anther collected in early July showing the initiation of microsporocytes in each of four locules (Lo). Bar = 100 μ m. 12. Longitudinal section of one stamen collected in early February showing the compactly arranged microsporocytes within the locule (Lo). Bar = 10 μ m. 13. Transverse section of an anther collected in late March, after microsporogenesis, showing the loosely arranged, mature pollen grains (PO) and thickened bands (Tb) in the cell walls. Bar = 100 μ m.

Female organogenesis—At the same time the raised tissue ring is forming, the center of each floral apex in a female flower expands and becomes a rounded, convex structure (Fig. 2). The tissue ring continues to increase in size to form a cup around the floral apex. Increased growth at the margin of the floral apex, inside the tissue ring, becomes a girdling gynoecial primordium. The primordium develops into three or four carpels that unite to form a unilocular ovary, the style, and stigmas (Fig. 3). Development of a convex floral apex (as in the lower portion of Fig. 2) into structures of the gynoecium (Fig. 3) is completed in about 2 wk. Parietal placentae develop (Fig. 4), and the entire structure continues to enlarge throughout the summer. In the fall, the rounded margins of the placentae become more angular (Fig. 5), a change that coincides with the origin of archesporial cells in the nucellus.

In the spring the archesporial cells increase in size and

undergo meiosis and embryo sac formation (Fig. 6). The mature gynoecium consists of a subglobose ovary covered with trichomes, topped by deeply lobed stigmas, and containing anatropous ovules (Fig. 7). The membranous, cup-shaped tissue ring is persistent under the gynoecium. Each *P. trichocarpa* inflorescence develops 20–40 capsules, with each capsule containing 30–50 seeds. When the capsules mature and release the seeds, each seed is accompanied by a portion of the placenta bearing several unicellular hairs. Although not directly observed in *P. trichocarpa*, practically every epidermal cell in *P. deltoides* and *P. tremuloides* gives rise to a hair (Nagaraj, 1952).

Male organogenesis—In contrast to female flowers, organ development in a male flower is not concentrated in the center of the floral apex. Continued expansion of the raised ring of tissue at the edge of the disk-shaped pri-

TABLE 1. Comparison of the number of carpels, seeds, and stamens found in individual flowers of various *Populus* species.

Section Species	# Carpels	# Seeds	# Stamens	References
<i>Tacamahaca</i> Spach.				
<i>P. trichocarpa</i> Torr. and Gray	3–4	30–50	40–60	Sargent, 1896; Rehder, 1940; FAO, 1980; This study
<i>P. angustifolia</i> James	2		12–30	Sargent, 1896; Rehder, 1940
<i>P. balsamifera</i> L.	2	15–20	12–30	Sargent, 1896; Brayshaw, 1965; Eckenwalder, 1984c; FAO, 1980
<i>P. cathayana</i> Rehd.	(2–)3–4			Rehder, 1940
<i>P. koreana</i> Rehd.	2–4		10–30	Rehder, 1940
<i>P. laurifolia</i> Ledeb.	2–3		20–30(–60)	Rehder, 1940
<i>P. maximowiczii</i> Henry	3–4		30–40	Rehder, 1940
<i>P. simonii</i> Carr.	2–3		8	Rehder, 1940
<i>P. szechuanica</i> Schneid.	3–4			Rehder, 1940
<i>P. yunnanensis</i> Dode	3–4			Rehder, 1940
<i>Aigeiros</i> Duby				
<i>P. deltoides</i> Bartr. ex Marsh.	3–4	4–32	40–60	Sargent, 1896; Fisher, 1928b; Rehder, 1940; Nagaraj, 1952; Hejnowicz, 1973; Schreiner, 1974; FAO, 1980; Eckenwalder, 1984c
<i>P. fremontii</i> Wats.	3–4	10–25	30–40(–60)	Sargent, 1896; Eckenwalder, 1984c
<i>P. nigra</i> L.	2		6–30	Rehder, 1940; Bugała, 1973; FAO, 1980
<i>Leucoides</i> Spach.				
<i>P. heterophylla</i> L.	2–3		12–20	Sargent, 1896; Rehder, 1940; FAO, 1980
<i>P. lasiocarpa</i> Oliv.	2–3		3–6, 30–40 ^a	Rehder, 1940; FAO, 1980
<i>Populus</i> Ecken. (= <i>Leuce</i> Duby)				
<i>P. alba</i> L.	2–4	3–4	5–10	Graf, 1921; Fisher, 1928b; Rehder, 1940; Nagaraj, 1952; Bugała, 1973
<i>P. grandidentata</i> Michx.	2–4		6–12	Fisher, 1928b; Rehder, 1940
<i>P. tremula</i> L.	2	10–20	8–15	Graf, 1921; Rehder, 1940; Bugała, 1973
<i>P. tremuloides</i> Michx.	4	4–10	5–12	Sargent, 1896; Graf, 1921; Fisher, 1928b; Nagaraj, 1952; Lester, 1963; Hejnowicz, 1973; Sattler, 1973
<i>Turanga</i> Bge.				
<i>P. euphratica</i> Oliv.	3		8–25	FAO, 1980; Eckenwalder, 1984c
<i>Abaso</i> Ecken.				
<i>P. mexicana</i> Wesm.	2(–3)			Eckenwalder, 1984c

^a *P. lasiocarpa* is generally monoecious, but sometimes also has perfect flowers. Unisexual flowers have more stamens than bisexual flowers.

mordium, and slower cell differentiation in the middle, results in a concave meristematic region (Fig. 8). Stamen primordia emerge from the meristem as rounded protrusions (Fig. 9), with organogenesis proceeding centrifugally. Extrorse anthers form on the 40–50 stamen primordia on each disk (Fig. 10), with each anther consisting of two pollen sacs divided into two locules (Fig. 11). Each locule is a microsporangium and develops numerous microspore mother cells, at which stage the staminate buds pass the winter (Fig. 12).

In the spring, the inner wall layer of the microsporangium matures as a tapetum and the microspore mother cells divide meiotically to form tetrads of microspores. As the microspores mature, tapetal cells disintegrate and the tetrads separate into individual pollen grains. The endothecium walls develop secondary thickening that appears as bands extending perpendicular to the long axis of the anther (Fig. 13). The bands are not found in cells between the two anther halves, or in the area of dehiscence.

As the anther nears maturity, the partitions between the locules break down so that the tetrasporangiate anther appears bilocular. The thickened bands in the anther walls cause differential shrinkage during drying, which promotes the rupture of the stomium. When released, the mature pollen grains measure about 29 μm in diameter.

DISCUSSION

The timing of seasonal events in the development of flowers of *P. trichocarpa* are diagrammed in Fig. 14. Early differentiation events in the transition from vegetative to reproductive growth in late April and early May are common for the development of a catkin type of inflorescence. The buds of flowering branches develop lateral appendages with broad apices, then prolific cell division in each apex results in a ground tissue which ultimately generates the reproductive structures.

In *Populus* the floral apices form a wide, flat, disk-

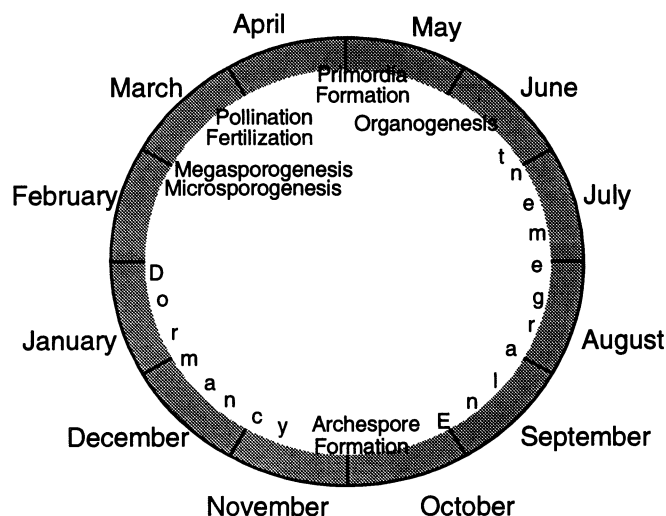


Fig. 14. Diagram of typical reproductive phenology for *Populus trichocarpa* in the area of Corvallis, OR.

shaped receptacle. The raised ring of tissue that organizes at the edges of the disks in both male and female flowers becomes a membranous cup surrounding the lower portion of the androecium and gynoecium. The number of vascular traces to the tissue ring indicate that at one time it was made up of several parts, possibly arranged as two whorls (Fisher, 1928b). This evidence of a perianth that is now extremely reduced suggests that the apparently simple, unisexual *Populus* flowers are a result of evolution toward fewer floral parts (Fisher, 1928b).

The relatively large numbers of stamens, carpels, and seeds found in *P. deltoides* (Table 1) led Fisher (1928b) to conclude that this species has lagged behind other *Populus* species in the stabilization and reduction of floral parts. *P. trichocarpa* has similar numbers of stamens, carpels, and seeds (Table 1), which would indicate that it too has lagged behind the evolutionary trends of other *Populus* species. *P. trichocarpa* and *P. deltoides* may appear closely related by their floral morphology, but they are native to geographically separate areas (Sargent, 1896; Schreiner, 1974; FAO, 1980; Eckenwalder, 1984b) and, based on a variety of identifying characteristics, have been classified into different sectional subdivisions of the genus (Table 1). When 18 synapomorphies including vegetative and floral characteristics are used to generate a cladogram, the phylogenetic relationship between *P. trichocarpa* and *P. deltoides* is more distant than between *P. trichocarpa* and *P. balsamifera*, both of section *Tacamahaca*, or between *P. deltoides* and *P. fremontii*, both of section *Aigeiros* (Eckenwalder, 1984c). Species of these two sections share many floral characteristics (Table 1), and are more closely related to each other than to species of other *Populus* sections (Zsuffa, 1973; Eckenwalder, 1977, 1984b).

Floral morphology appears to be less stable in some *Populus* species than in others (Fisher, 1928b). Unisexual *Populus* flowers are believed to be an early evolutionary development because of the lack of vestigial traces to a third (staminate) whorl in female flowers and to a fourth (carpellate) whorl in male flowers (Fisher, 1928b). The only known bisexual *Populus* species is *P. lasiocarpa*, which

is described as monoecious, even though catkins often contain a few perfect flowers (Rehder, 1940; Schreiner, 1974; FAO, 1980). Several of the normally dioecious *Populus* species occasionally produce perfect flowers. Perfect flowers have been noted in *P. grandidentata* (Hastings, 1918), *P. tremula* (Klaehn, 1957), *P. tremuloides* (Nagaraj, 1952; Santamour, 1956; Pauley and Mennel, 1957; Lester, 1963), and *P. trichocarpa* (Stettler, 1971). One bisexual flower has also been observed in a haploid, anther-derived plant of *P. maximowiczii* (Stoehr, Zsuffa, and Eckenwalder, 1988).

The addition of structures in a perfect flower ranges from apparently normal, viable organs, to recognizable, but deformed, sterile organs (Hastings, 1918; Lester, 1963; Stettler, 1971). There is evidence that the perfect condition is heritable, and that the complex mechanisms of inheritance are regulated to some extent by auxin levels (Santamour, 1956; Stettler, 1971). Whatever the mechanisms regulating sex expression in *Populus*, predominately female trees more often have perfect flowers than predominately male trees (Pauley and Mennel, 1957).

The sporadic appearance of perfect flowers in a predominately unisexual genus hints at the complexity of the molecular regulation of floral structure development. Our continuing studies will address when and where genes controlling various aspects of reproductive development are active.

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