Topophysis in Relation to Periderm Development and Incidence of Cankering in Eastern Cottonwood

by
J. J. JOKELA and L. E. GRAY

Departments of Forestry and Plant Pathology
University of Illinois
Urbana, Illinois

INTRODUCTION

Cloning is a practical means for multiplying desirable genotypes in many forest tree species. It is of greatest utility in breeding and genetic studies when members of the same clone behave similarly and clonal and seedling data are comparable. There is increasing evidence, however, that these conditions do not always prevail.

Aside from quantitative differences attributable to varying size and handling of the propagules, phenotypic expression may vary because of the tendency of vegetatively propagated material to retain morphological and physiological characteristics of the portion of the plant from which it was taken. Molisch (9) proposed the term "topophysis" for such tendencies. Although the term has not gained universal acceptance, it has been widely used in forestry literature. These tendencies are generally regarded as expressions of varying degrees of "juvenility" which result from the progressive aging of the apical meristems.

The studies of Schaffalitsky de Muckadell (10) in European beech are illustrative. Delayed leaf abscission is a juvenile trait in this species. Schaffalitsky de Muckadell found that grafts made from lower leaf-retaining epicormics retained their withered leaves throughout the winter and those made from upper leaf-shedding epicormics of the same tree did not. To explain this apparent reversal in maturity, he hypothesized that the youngest meristems are those left at the base of the tree which have retained the stage of juvenility existing in the apical meristem from which they are descended. Although plausible, the hypothesis is inadequate. As pointed out by Leopold (5), it does not aid in understanding why a juvenile form of growth follows pruning or why growth from mature buds grafted onto juvenile stock reverts to juvenile form.

Many additional examples of topophysis in forest trees, only a few of which are cited here, appear in the literature. Chase (1), for example, found that cuttings taken from thornless branches on thorny trees of honey locust were still thornless at 8 years of age. An example of particular interest to foresters is the reported failure of lateral branch cuttings to attain an upright growth form, as terminal cuttings do. This has been observed in China-fir by Mirov (8) and in other tree species with a marked horizontal branching habit.

Topophytic alterations of the phenotype can cause greater or lesser similarities between and within clones and hence between and within genetic subgroupings than would result from the degree of genetic relationship alone. Such nonrandom environmental variations can influence selection and impinge on the validity of estimates of genetics components of variance and their interpretation. The variance associated with cloning has been studied in yellow monkey flower by Libby and Jund (6). To the extent that so-called topophytic effects are unrecognized or improperly taken into account, they can lower the efficiency of selection and lead to erroneous inferences about breeding behavior.

This paper reports on differences between clonal and seedling plantations encountered in the courses of a study of heritability in eastern cottonwood, *Populus deltoides* Bartr.

PLANTATION ESTABLISHMENT

The observations were made in a plantation of 95 unrelated clones and a plantation of 92 unrelated single-parent progenies of eastern cottonwood on adjacent and comparable bottomland sites in the Sangamon Forest Plantations in Piatt County, Illinois. Three native Illinois populations (southern, west-central, and east-central) are represented in each plantation. The clonal plantation was established in the fall of 1959 with potted cuttings rooted under intermittent mist. The cuttings had been obtained the previous spring from trees 4 to 11 inches in diameter.

To minimize possible topophytic variance, all cuttings were restricted to the current season's growth on branch tips in the upper crown. The seedling plantation was established in the spring of 1960 with 1-year-old seedlings.

A split-plot design, with populations as main plots and 'four replications, was used in both plantations. Subplots consisted of two trees of the same clone and four trees of the same progeny group in the clonal and seedling plantations, respectively.

OBSERVATIONS AND RESULTS

In a previous report on heritable variation in several traits observed during the first 4 years, the senior author (3) reported that population differences were more marked in the seedling than in the clonal plantation. He also observed that (in the case of height growth and branch angle) broad-sense estimates of heritability, based on clonal data, were unexpectedly lower than narrow-sense estimates, based on seedling data. Subsequently, differences between the clonal and seedling plantations have been observed with respect to bark characteristics and incidence of cankering.

Difference in Bark

Roughening of the bark on the lower stems of trees in the seedling plantation was first noted during the 3rd year following planting. This roughening of the bark or rhytidome development has extended progressively upward into the lower crowns of all trees in the seedling plantation. In contrast, only 10 percent of the trees in the clonal plantation were rough barked at 8 years of age. Two-thirds of these occurred in the 16 clones in which the trait occurred repeatedly.

There was a slight tendency for the rough-bark trait to occur on trees originating from cuttings from the smallest trees from which cuttings were taken. The bark difference was so consistent and striking (Fig. 1) that if its origin were unknown, one might suspect that it was a genetic or varietal difference.

Fig. 1.—The light-colored, smooth bark of the tree at right is characteristic of trees originating from cuttings taken from the upper crowns of adult trees. The rough-barked tree at left is of seedling origin.

TABLE 1.—Incidence of Bark Cankers on Eastern Cottonwood, Sangamon Forest Plantations, Piatt County, Illinois.

Tree Rating (Canker Score)	Plantation Age							
	6 Years				7 Years			
	Clonal		Seedling		Clonal		Seedling*	
	No.	%	No.	%	No.	%	No.	%
0	88	18.8	5	0.4	261	55.3	257	30.3
1	226	48.4	107	8.4	147	31.1	325	38.4
2	90	19.3	536	42.2	15	3.2	103	12.2
3	46	9.9	302	23.8	25	5.3	61	7.2
4	11	2.4	196	15.4	15	3.2	64	7.6
5	5	1.1	90	7.1	7	1.5	27	3.2
6	1	0.1	35	2.7	2	0.4	10	1.1
Total	467	100.0	1,271	100.0	472	100.0	847	100.0
Mean Score	1.3		2.8		0.8		1.4	

*The third block of the seedling plantation was not included in the second rating.

Difference in Cankering

A preliminary survey made in the fall of the 5th growing season gave indications that cankering was more severe in the seedling than in the clonal plantation. During June of the following year, all trees were rated for canker in three blocks of each of the three populations in both plantations. Trees were rated on an ordinal scale, based on the following criteria:

0—no visible signs of cankering anywhere on tree
1—very few cankers, usually one or two, occurring on smaller branches
2—moderate amount of cankering on smaller branches, possibly one or two on larger branches
3—small cankers on trunk or a large number on small and large branches
4—numerous large cankers on trunk and larger branches
5—heavy cankering on trunk, death or dieback imminent
6—dead with visible signs that cankering was causal factor

Because of the possibility that the greater severity of cankering in the seedling plantation resulted from the subjective nature of the scoring, a second rating was made in June of the following year. The same criteria were used but greater emphasis was placed on active cankers. Small, healed-over cankers were ignored.

The results of the canker ratings are summarized in Table 1.

DISCUSSION

Difference in Bark

The smooth-bark characteristic of trees in the clonal plantation is obviously traceable to their origin from cuttings taken from the upper parts of adult trees. A similar occurrence of smooth-barked trees in poplar clones 1-214 and 1-245 was reported by May (7). The consistent occurrences of the smooth-bark trait in the clonal plantation indicates that it is characteristic of eastern cottonwood propagated from cuttings taken from the upper parts of pole-size and larger trees.

The rough-barked trees have several sequent periderms. In contrast, the smooth-barked trees have a single persistent periderm which is interrupted only at the juncture of a limb with the stem and at lenticels and wounds. A smooth, persistent periderm, characteristic of trees in the clonal plantation, was considered normal by Kaufert (4) in the closely related species of aspen; rough bark, characteristic of trees in the seedling plantation, was attributed to disease and other external factors related to site and injury. Regardless of the factors influencing periderm formation in eastern cottonwood, only the trees in the clonal plantation have had the ability to maintain for more than a few years an essentially unbroken original periderm over the entire length of the stem. As a consequence, the outer bark is only one-third to one-fourth as thick as that of rough-barked seedlings of comparable diameter.

Difference in Cankering

The incidence of cankering shown in Table 1 is greater than is generally recognized as occurring in native eastern cottonwood. The lower incidence shown by the second rating is probably due mainly to the greater emphasis placed on *active* cankers in this rating. It may also account for the smaller differences between seedlings and clones shown by the second rating, since active cankers were more readily detected on the smooth-barked trees in the clonal plantation.

The mean scores of 1.3 and 2.8 for clonal and seedling plantations, respectively, for the first rating

and 0.8 and 1.4 for the clonal and seedling plantations, respectively, for the second rating should be regarded only as a relative index of the greater susceptibility of the seedlings to cankering, primarily because of the ordinal scale of rating. The proportionately greater number of lower scores assigned to trees in the clonal plantations is indicative of the greater severity of cankering in the seedling plantations. This difference was significant ($P(x^2) < .01$) in all three populations for both years that ratings were made.

In spite of their statistical significance, these results are considered suggestive rather than conclusive evidence that smooth 'barked trees are less susceptible to cankering than the rough-barked trees because of the limitations and subjective nature of the data. Additional observations should be made elsewhere, especially at younger ages. If the rough-barked seedlings are in fact more susceptible, the explanation may lie in the more favorable conditions provided by the rough-fissured bark for the germination and development of spores of fungi.

The common canker producing species of *Cytospora, Dothichiza,* and *Fusicoccum* were isolated from active cankers by Gray, Jokela, and Wycoff (2). However, no attempt has been made to evaluate their relative importance.

A possible disadvantage of a thin, smooth bark is less resistance to freezing and sunscald. Such injuries have not been observed in either plantation. On the other hand, the quantitative and qualitative differences in the outer bark between trees in the clonal and seedling plantations may be of economic value to the pulp and paper industry.

SUMMARY

The utility of cloning in breeding and genetic studies is lessened by associated variation related to the physical and physiological differences among vegetative propagules. This is illustrated by the differences reported between clonal and seedling plantations of three native Illinois populations of eastern cottonwood of comparable age, size, and genetic constitution.

Roughening of the bark on the lower stems began within a few years after planting in the plantation of seedling origin. Trees originating from cuttings taken from the upper crown of adult trees still had a light-colored, smooth bark at 8 years of age. This difference reflects the greater ability of the trees of cutting origin to maintain a single, superficial periderm. Possibly related to this bark difference is the greater incidence and severity of cankering observed in the seedling plantation.

It has been reported previously that population differences were more marked in the seedling than in the clonal plantation and that broad-sense heritabilities estimated from clonal data were unexpectedly smaller than narrow-sense estimates based on seedling data in the case of early height growth and branch angle. The single periderm of the clones as opposed to the thick multilayered periderm of the seedlings may be of interest to the pulp and paper industry.

LITERATURE CITED

1. Chase, S. B. 1947. Propagation of thornless honeylocust. J. For. 45 : 715-722.
2. Gray, L. E., J. J. Jokela, and H. B. Wycoff. 1965. Blackstem of cottonwood. Plant Dis. Reptr. 49: 867-868.
3. Jokela, J. J. 1963. Heritable variation in natural populations of *Populus deltoides* Bartr. in Illinois. Ph.D. thesis, Univ. of Ill.
4. Kaufert, F. H. 1937. Factors influencing the formation of periderm in aspen. Amer. J. Bot. 24:24-30.
5. Leopold, A. C. 1964. Plant growth and development. McGraw-Hill, New York.
6. Libby, W. J. and E. Jund. 1962. Variance associated with cloning. Heredity 17: 533-540.
7. May, S. 1963. L' "ingentilimento" apparente de cloni di pioppo a corteccia grigia e rugosa per effecto di topofisi. Cellulosa e Carta 14 (10) : 5-8.
8. Mirov, N. T. 1937. Applications of plant physiology to problems of forest genetics. J. For. 35 : 840-844.
9. Molisch, H. 1920. Pflanzenphysiologie als Theorie der Garntnerei. 3rd ed. Gustav Fischer, Jena.
10. Schaffalitsky de Muckadell, M. 1954. Juvenile stages in woody plants. Physiol. Planta. 7: 782-796.