NATIVE POPLARS OF SOUTHERN ALBERTA AND THEIR HYBRIDS

by T. C. BRAYSHAW

Résumé en français

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ABSTRACT

A hybrid swarm involving all the species of poplars native to southern Alberta was observed and sampled. The samples were analyzed using Anderson's methods: the scatter diagram and the hybrid index; and some of the stands were analyzed using a three-way modification of the hybrid index.

Since no cultural methods were employed, the results of the analyses are considered to be tentative. The combinations postulated for the hybrids found are the simplest combinations that are thought to be capable of producing the observed effects.

There are indications that crossing between the species of this region has been proceeding for many generations in natural alluvial habitats whose instability favours the establishment of hybrids.

Direct hybrids between most of the species were observed. No direct hybrids between *P. tremuloides* and the section *Tacamahaca* were found, but other possible combinations were. Several individuals showing admixtures of characteristics of three species were found.

Populus X *Andrewsii* appears to be a product of crossing between *P. deltoides* var. *occidentalis* and *P. tremuloides*.

RÉSUMÉ

L'auteur a prélevé des échantillons en vue d'étudier la progression d'hybrides provenant du croisement de toutes les espèces de peupliers de l'Alberta méridional. Les échantillons ont été étudiés d'après les méthodes d'Anderson: le graphique de dissémination et l'indice d'hybridation; tandis que certains peuplements ont été étudiés à l'aide d'une triple modification de l'indice d'hybridation.

Aucun procédé sylvicultural n'ayant été mis à l'essai, les données recueillies au cours de l'étude n'ont pu être confirmées. Les combinaisons présumées pour les individus hybrides étudiés sont les plus simples qui puissent produire les effets observés.

Les données recueillies semblent indiquer que les croisements entre les essences de peupliers de la région se sont produits au cours de plusieurs générations dans les milieux alluviaux naturels, dont la nature instable favorise l'établissement des hybrides.

Des hybrides provenant du croisement direct de la plupart des espèces de peupliers ont pu être observés. L'on n'a trouvé aucun hybride provenant du croisement direct de l'espèce *P. tremuloides* avec la section *Tacamahaca*, mais on a observé des hybrides qui provenaient probablement de recroisements où ces espèces intervenaient. Plusieurs sujets possédaient les caractéristiques de trois espèces différentes.

Apparemment, l'espèce *Populus* X *Andrewsii* provient du croisement de *P. deltoides* var. *occidentalis* avec *P. tremuloides*.

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Native Poplars of Southern Alberta and their Hybrids

by

T. C. BRAYSHAW [1]

INTRODUCTION

During the summer of 1959, while investigating the native tree species of Alberta, the author found that the population of hybrid poplars there was much more extensive and complex than had been suspected. Consequently, a number of poplar stands in the region was visited and specimens collected. The area was revisited briefly for further sampling in 1963.

Moss (1959) lists six species of *Populus* as occurring in Alberta. These are:

P. angustifolia James	narrowleaf cottonwood
P. balsamifera L.	balsam poplar
P. trichocarpa T. & G.	black cottonwood
[=*P. balsamifera* L. subsp. *trichocarpa* (T. & G.) Brayshaw]	
P. Sargentii Dode	plains cottonwood
[=*P. deltoides* Bartr. ex Marsh. var. *occidentalis* Rydb.]	
P. tremuloides Michx.	trembling aspen
P. acuminata Rydb.	lanceleaf cottonwood

Sudworth (1934) indicates in his range maps the presence of all these species in Alberta except *P. trichocarpa.*

Of the species listed above, *P. angustifolia, P. deltoides* var. *occidentalis,* and *P. acuminata* are confined to the southern plains of the province; while the other species are more widespread, especially north and northwestward.

In describing the vegetation of the province, Moss (1944) mentions the occurrence of hybrid poplars at Lethbridge and other points along the rivers.

GEOGRAPHY OF THE AREA

The principal area of hybridization, which involves the overlapping ranges of these species, is confined to the plains region of southern Alberta from the Red Deer River southward. Hybrids between *P. balsamifera* subsp. *balsamifera* and subsp. *trichocarpa* have been found far to the northwest of this area — north at least to the Peace River, and west into central British Columbia. However, that complex has been dealt with in a separate report. Only the southern part of this region, as described above, is dealt with in detail in this report.

Topography

The southern prairies of Alberta consist of a sloping plain, rising from an elevation of around 2,000 feet in the east to 4,000 feet or more in the west where it abuts against the foothills of the Rocky Mountains.

On debouching from the mountains, the rivers cross the plain in a series of coulees of varying depth. In these coulees erosion and deposition by streams re-

[1] Research Officer, Department of Forestry of Canada, Petawawa Forest Experiment Station, Chalk River, Ontario.

sult in the formation of narrow flood plains and constantly shifting channels with bars of gravel or sand. The coulees carrying the rivers are usually separated by broad, level, almost treeless uplands, broken in places by dry coulees, depressions containing ponds, marshes or lakes, and sandhill areas. The depressions and sandhills may support scattered clumps of poplars.

Apart from the Rocky Mountain foothills, the only hills of considerable height to break the level of the plain are the Cypress Hills of southeastern Alberta and adjacent Saskatchewan. This isolated range rises to 4,800 feet and supports forest, at least on its northern slopes.

Climate

The climate is typically continental and cool, with warm summers and cold winters. Precipitation is low on the plains, but increases with altitude as one enters the foothills of the mountains (see Table 1). The heaviest precipitation occurs from June to August. Exposure to dry winds, especially the chinook winds in winter when the ground is frozen, is thought to be another important factor limiting tree growth.

TABLE 1: ANNUAL PRECIPITATION IN INCHES AT VARIOUS STATIONS IN SOUTHERN ALBERTA (ANON.).

Banff	19.16
Bassano	13.57
Calgary	16.65
Lethbridge	15.01
Medicine Hat	12.81
Pincher Creek	20.01

Vegetation

Most of the area is covered by grassland; which is generally treeless in the south but bears clumps of aspen, usually associated with moist depressions, with increasing frequency northward.

Bordering the prairie in the north and northwest is the B-19 Section of the Boreal Forest (Rowe, 1959), with an outlier in the Cypress Hills. Intermingling with the Boreal Forest and bordering the prairie to the west and southwest in the foothills of the Rocky Mountains, is an eastward extension of the Montane Forest (Section M-5). The margin of both these forest types is a belt of aspen with scattered occurrences of other trees.

Along most of the rivers, ribbon-like gallery forests extend across the plain from the wooded foothills. Exceptions are those streams that flow in very shallow or open coulees (for example the Little Bow River) where lack of shelter from the wind appears to be the main factor preventing tree growth. These gallery forests are dominated by various species of poplar, accompanied by willows (*Salix* spp.), black or water birch (*Betula occidentalis*), and occasional conifers from the foothill forests. The species of poplar making up these stands are derived partly from the adjacent forest regions, and partly from the gallery forests to the south and east. Thus, *Populus balsamifera*, subsp. *balsamifera*, a boreal forest species, follows the rivers from the Bow River northward, making contact in this region with its close relative subsp. *trichocarpa*, a western cordilleran variant that follows the streams emerging from the foothills. *P. deltoides* var. *occidentalis* has entered the region by following up the rivers from the Mississippi and Red River basins; and *P. angustifolia* seems to have spread from stream to stream along the edge of the foothill zone from the south, apparently accompanied by *P. acuminata*.

Habitat and Hybridization

As a result of constant erosion, deposition, and channel-shifting by the rivers, stability of the adjacent habitats is seldom attained for long. Thus, these riverbank stands may be considered to be in a perpetually seral condition. This instability is most pronounced at the western edge of the area, where the rivers emerging from the foothills have steep gradients and are correspondingly active in erosion. Fresh bars of material sorted into various textures and of varying depths are constantly becoming available for colonization while older deposits are being removed or stripped of their vegetation. This process is most favourable for hybrids, giving them opportunities for establishment on a variety of soils free from competition by established parent populations.

Apart from the ubiquitous *Populus tremuloides*, all the poplar species discussed here reach geographical limits of their ranges within this region. Of these limits, those of *P. deltoides* and *P. angustifolia* are probably determined by a combination of cold climate and competition with the hardier *P. balsamifera*; while the latter species is apparently restrained more by drought and wind exposure than temperature, with competition between it and *P. deltoides* also playing its part. The capacity for growth and reproduction of *P. angustifolia* and *P. deltoides* are probably lower here than further to the south and southeast, so that hybrids may enjoy a relatively better chance of survival in competition with them.

METHODS

During the field seasons as many poplar stands were visited as time permitted. Their locations are listed in Appendix I and shown in Figure 1. Specimens covering the range of variation in each stand were collected and pressed.

Owing to the variability in foliage with age of the tree and position on the tree, specimens were taken whenever possible from branches having both terminal long shoots (turions) and lateral slowly growing branchlets (brachyblasts), six feet or higher above the ground, adventitious shoots arising from the basal parts of the trunk being avoided. The incidence of flowering in 1959, when the bulk of the collection was made, was disappointingly low, so most of the specimens obtained were purely vegetative; however, a number of specimens with pistillate catkins was obtained in 1963.

The pressed material was augmented by specimens obtained through exchange with the Plant Research Institute of the Department of Agriculture, in Ottawa. Other specimens were examined in the Plant Research Institute itself, and in the National Museum in Ottawa. In this way material was studied from stands not visited by the author. Some material was also examined in the herbarium of the University of Alberta in Edmonton during the field seasons.

After each specimen was catalogued, measurements were made of its leaf and petiole form, and other discernible features were recorded (e.g. the colour of the twig and of the dorsal, or abaxial, leaf surface; and the characteristics of the bud scales and catkins when available). Comparisons were made with samples of species drawn from areas where they are not in contact with each other, partly from material in the National Museum and the Plant Research Institute. The opportunity was also taken to examine the type specimens of some taxa while they were on loan to the latter herbarium.

From the data obtained, scatter diagrams were drawn up, using the method employed by Anderson (1949). All the trees in one stand were included in one graph, so that the composition of the stand could most readily be observed. The scatter diagrams use as co-ordinates the ratio of width/length (w/L) of the leaf, and the position of its greatest width (expressed by the ratio of the distance from the base to the widest point/length (b/L) as shown in Figure 2. Testing with pure

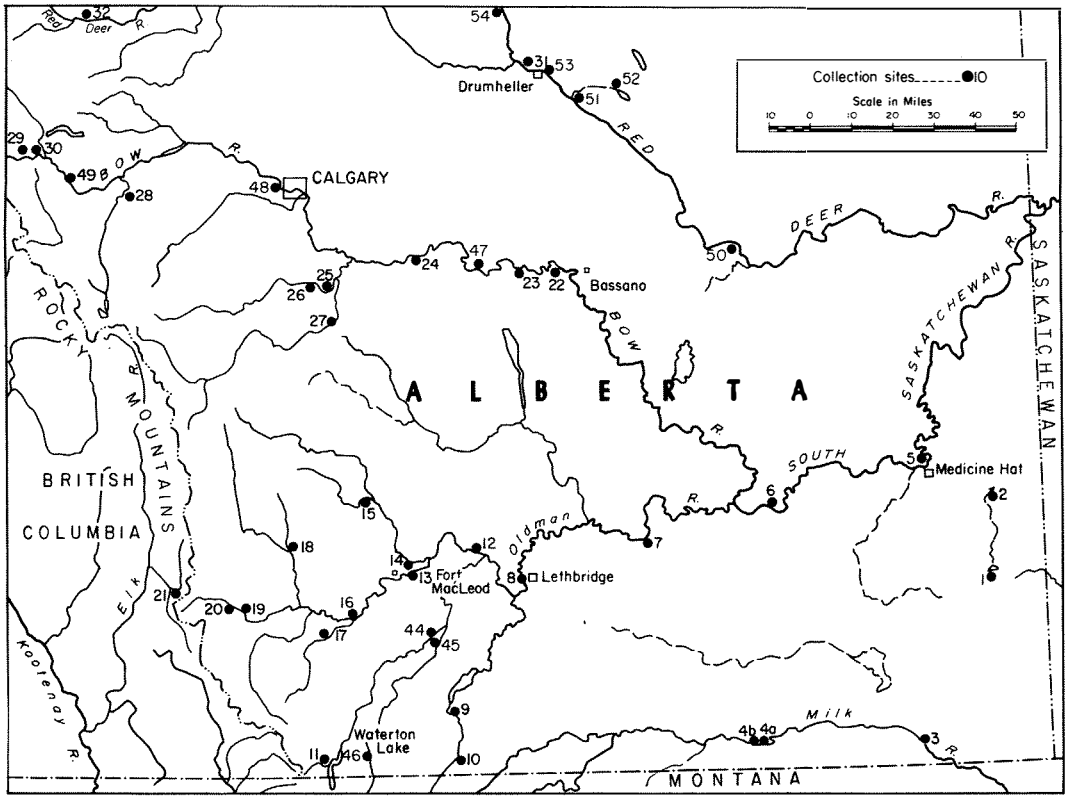

FIGURE 1. Map of southern Alberta showing the sites of collections of poplars in 1959 and 1963. Numbers correspond to those in Appendix I.

species showed that most of them are well separated on these characters since they differ radically in leaf form (Figure 3).

Eleven other characters were plotted by modifying the spot representing each specimen on the scatter diagrams. Nine of these, as indicated in Figure 2, are used in the scattergrams reproduced here as Figures 4 and 5.

Hybrid indices (Anderson, 1949), which give a linear measure of the degree of introgression of one species by another, were, in their original form, applicable only to those stands in which not more than two hybridizing species were involved. In many of the stands, however, three or more species contributed to the hybrid swarm.

It has been found possible to adapt the hybrid index to swarms involving three parent taxa, provided that characters can be found whose expressions in the three taxa are distinct and mutually exclusive. This ensures that there is no doubt as to which species is to be assigned points for any given character expression in a specimen. It also results in a constant total score for all specimens tallied in a given hybrid index study.

In assigning points for each character expressed in a specimen, the choice is made between three species instead of only two, as in the linear hybrid index, and the points are distributed according to the relative degrees of expression contributed by each. Thus the total score for each individual is divided among the contributing species according to their representations in the individual. The index value for each individual in a stand can be stated as a series of three num-

bers; provided that the order in which the contributing species are quoted has first been laid down. Hypothetically, it should be possible to extend this method to swarms involving larger numbers of parent species, but in this study, the problem of finding enough characters with mutually exclusive expressions then became magnified to a prohibitive degree. It is possible to show graphically the composition of a stand that has been analyzed in this way by plotting the values for the individuals on triangular co-ordinate paper. If this is done, additional characters, such as can serve to distinguish one species from the other two, can be indicated by appendages to the spots representing the individuals, each appendage indicating the species expressed by its direction (pointing toward the appropriate corner of the graph), and the number of characters so expressed by its length. In contrast to the rectangular scattergrams described above, the hybrid

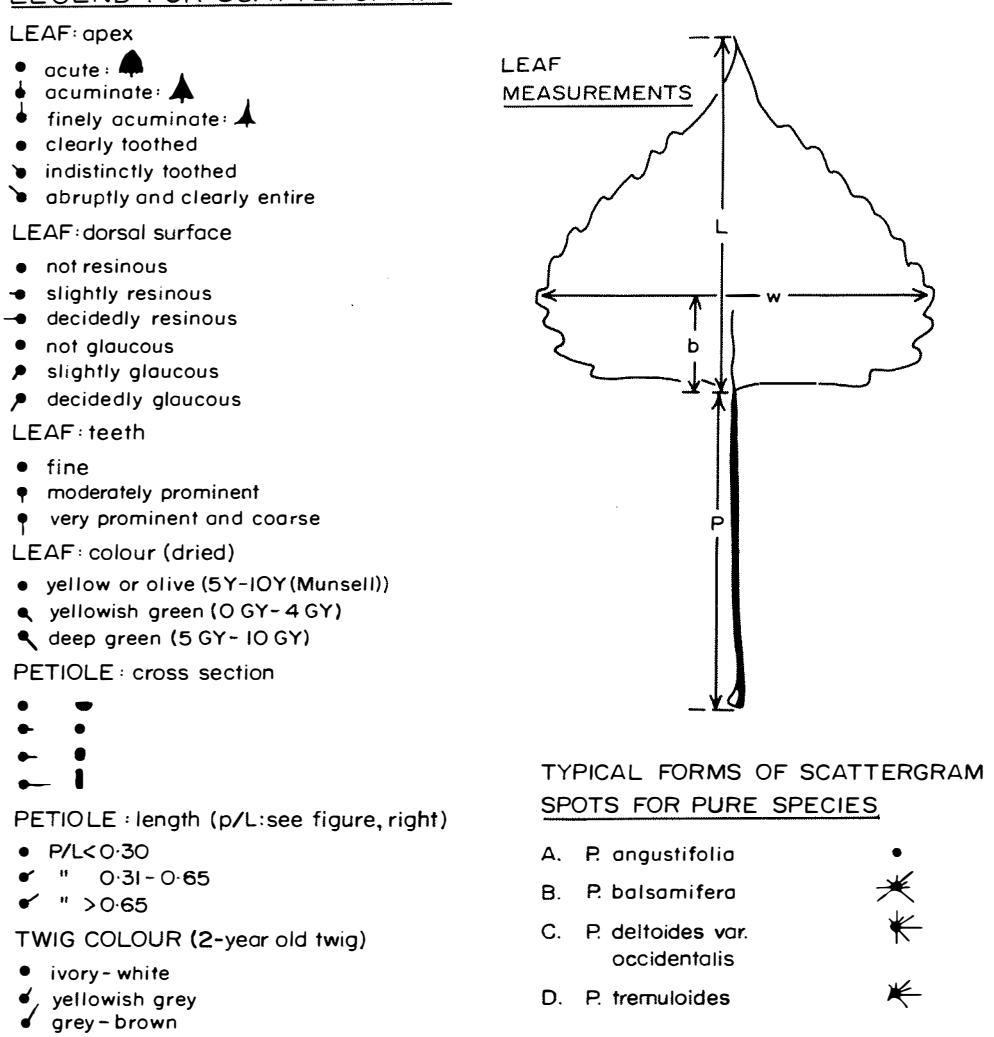

FIGURE 2. Legend for the rectangular scattergrams showing the characters used and the method of plotting them.

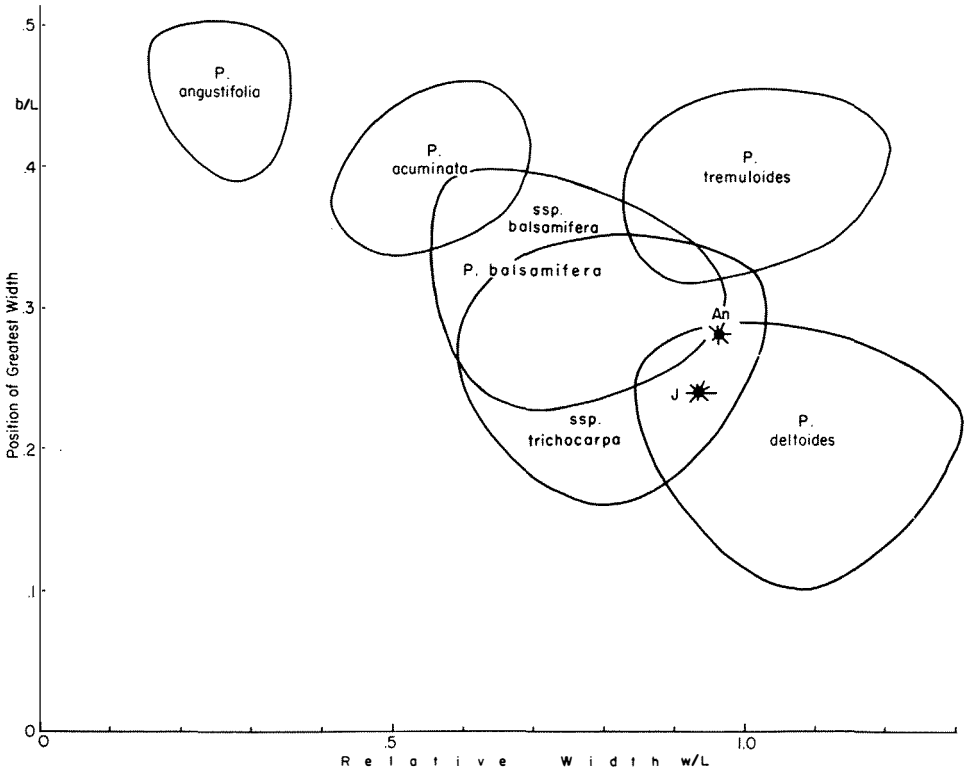

FIGURE 3. The ranges of leaf shape in the taxa of poplar in Alberta. The two spots are scattergram points for the type specimens of *P.* X *Andrewsii* (An) and *P.* X *Jackii* (J).

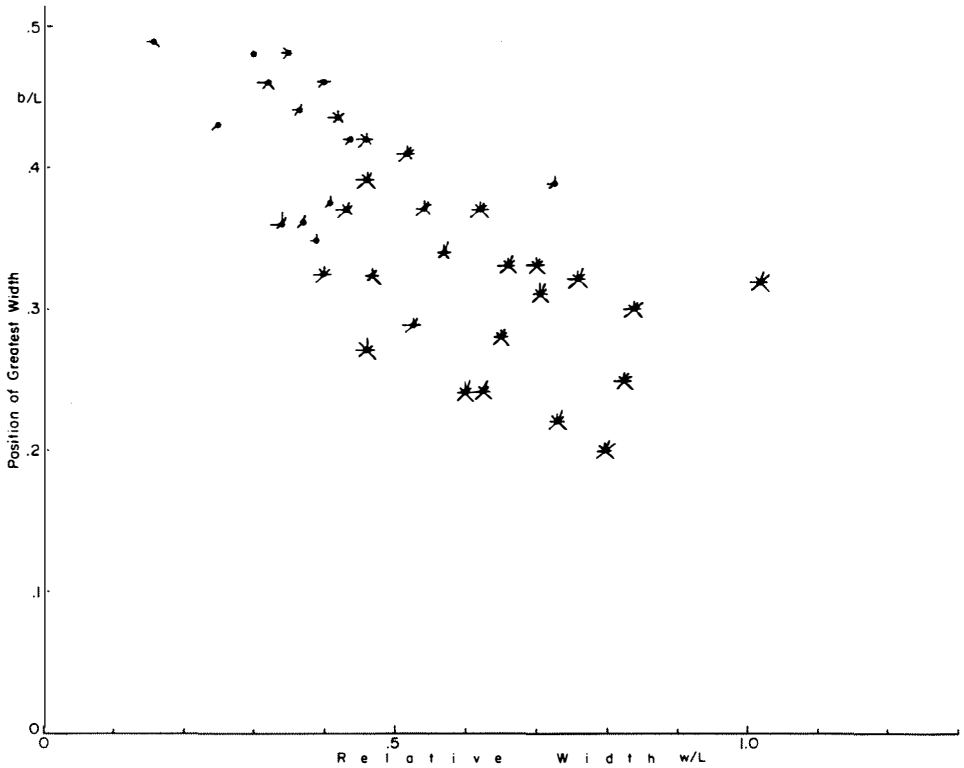

FIGURE 4. Scattergram of population of *P. balsamifera* X *angustifolia* series, including data from stands at Fort MacLeod and Cardston.

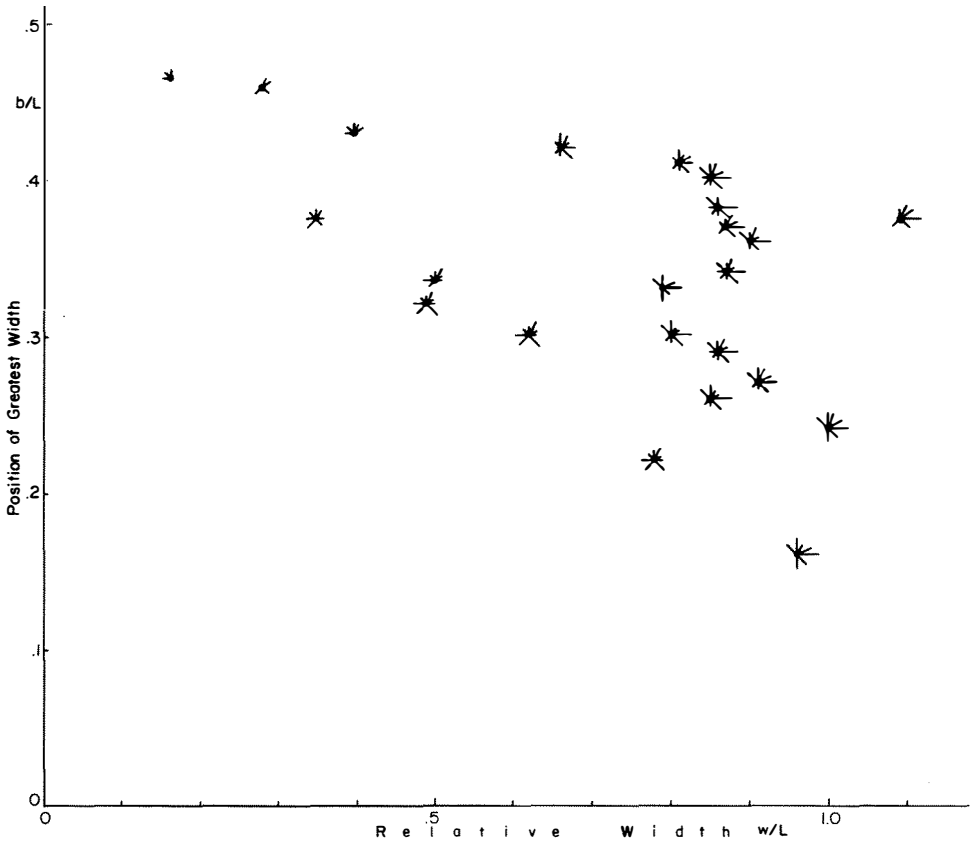

FIGURE 5. Scattergram for the stand at Crowfoot.

index scattergrams do not identify the specific characters scored. Figure 6 shows the type of graph used, and some examples from the stands examined in this study.

In referring to herbarium specimens in the text of this report, and in the list of specimens in Appendix II, the collector's name is followed by the collector's number (if given) and the code letters for the herbarium in which each specimen is located. A second herbarium quoted for the same specimen indicates the location of a duplicate. At the Petawawa Forest Experiment Station herbarium, the numbers are given by the herbarium rather than by a particular collector, and so these numbers follow the code for the herbarium. This procedure is followed in other cases where the collector's number is unknown or uncertain.

The herbaria are referred to by their codes as quoted in the Index Herbariorum (Lanjouw and Stafleu, 1959), as follows:

CAN National Museum of Canada, Ottawa.
DAO Plant Research Institute, Department of Agriculture, Ottawa.
PFES[2] Petawawa Forest Experiment Station, Chalk River, Ontario.

[2] Removal of the collection of native Canadian tree material from the Petawawa Forest Experiment Station is intended. Persons wishing to examine specimens coded under PFES in this report should enquire of the Department of Forestry of Canada, Ottawa, as to their new location.

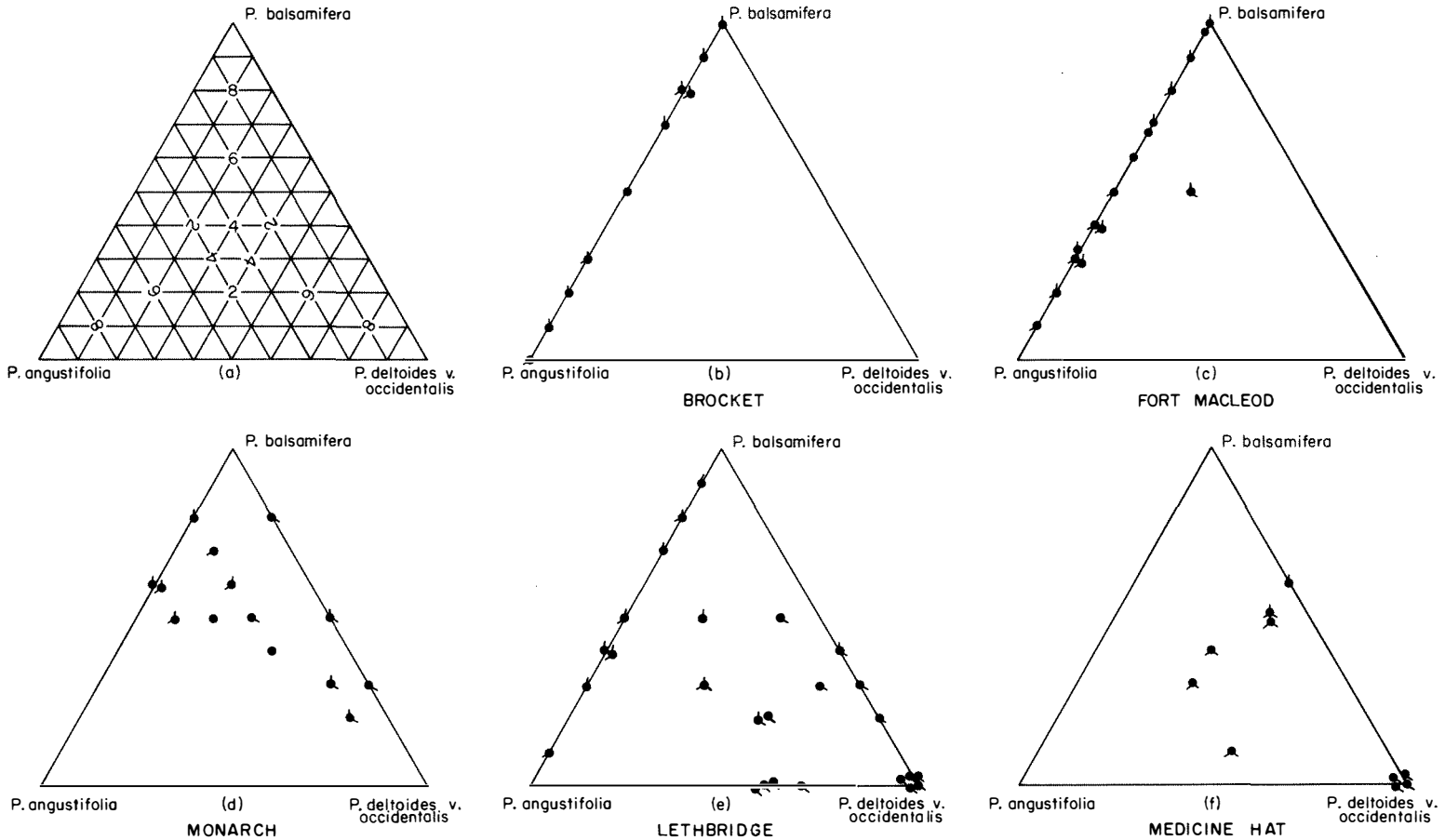

FIGURE 6. The three-way hybrid index, and its application to stands on the Oldman and South Saskatchewan Rivers. Fig. 6(a) shows the three directional scales of the index in relation to the species. Figs. 6(b) to (f) show the compositions of stands at five places, running from west to east, along the rivers.

THE SPECIES

The genus *Populus* is divided into a number of sections, the assignment of the western Canadian species to their sections being as follows (Smith, 1943):

Section:	*Leuce*	*P. tremuloides*
	Tacamahaca	*P. balsamifera*
		P. trichocarpa
		P. angustifolia
		P. acuminata
		P. X *Jackii*
	Ageiros	*P. deltoides*
		P. Sargentii
		P. X *Andrewsii*

Hybridization appears to be possible between sections as well as between species within a section. It is interesting to note that all the species of this area have the same chromosome number (2n=38) (Smith, 1943).

The ranges of the species and subspecies of *Populus* in southern Alberta are outlined in the range map (Figure 22).

Some details of the following descriptions of the species in Alberta are based on observations on local material; otherwise, published descriptions are followed.

Trembling Aspen

***Populus tremuloides* Michx.**

Extensively suckering and colonial tree, with white *bark* becoming dark grey and shallowly furrowed in age. *Branches* moderately short, somewhat ascending. *Young twigs* brown, turning a neutral grey after a year or two. *Buds* non-resinous, with glabrous eciliate scales. *Leaves* very broadly ovate to orbicular, with a brief acuminate apex, finely serrate throughout; the margin sometimes with a slight flexure near the base. *Leaf colour* deep yellowish green above; paler, rather glaucous beneath, the glaucous epidermis often partly concealing the veins. Leaf proportions range as follows: w/L=0.8 — 1.2; b/L=0.3 — 0.45. *Petiole* nearly as long as leaf blade, slender and flexible, laterally compressed above, glabrous, and seldom bearing glands. *Leaf attitude* variable; the leaves nearly always oscillating. *Staminate flowers* with eight stamens, *pistillate flowers* with an ovate to lanceolate, bicarpellate ovary. *Fruit* a 2-valved, lanceolate glabrous capsule.

While some of the specimens collected with catkins are typical of the species, a few belong to var. *aurea* (Tidestrom) Daniels, which is distinguished from var. *tremuloides* by its shorter calyces and larger anthers. The deeper autumn leaf colouring which is also said to mark this variety was not observed during the field season. Figure 7 shows a specimen of *P. tremuloides* var. *aurea*, photographed, as are all those illustrated, against a square-centimetre grid.

This, the most widely ranging of the species, commonly occurs around ponds and depressions in the grassy uplands, but is relatively uncommon in the river-bank stands.

Balsam Poplar

***P. balsamifera* L.**

Tall tree with light grey *bark* darkening and furrowing with age. *Branches* ascending and the crown columnar. *Twigs* pale brown, becoming grey or grey-brown. *Vegetative buds* with 5 - 7 very resinous, pubescent and ciliate bud scales; fragrant. *Leaves* on turions ovate to lanceolate; on brachyblasts ovate, acuminate, rounded to cordate at base; crenate-serrate, the flattish teeth becoming in-

distinct toward the apex of the leaf. *Leaf colour* deep green above, tending to darken on drying; the dorsal surface strongly glaucous, and often stained brownish with secreted resin, but the veins not concealed. *Petiole* terete, channeled above, 1/3 to 2/3 as long as the blade, glabrous or puberulent, often with a pair of glands at the junction with the blade. *Leaf attitude* generally declining, with the transverse axis horizontal. *Peduncle* and axis of the pistillate catkin pubescent.

In the following treatment of the two subspecies, only characters in which they differ are described.

P. balsamifera L. subsp. *balsamifera*

Twigs always terete. *Leaf* proportions on brachyblasts range as follows: w/L=0.5 — 0.95, b/L=0.2 — 0.4. *Staminate flowers* with 12 to 20 stamens. *Fruit* a narrowly ovate to lanceolate capsule, glabrous, and usually 2-valved (Figure 8).

This subspecies typically has glabrous leaves and petioles, and rounded leaf bases, at least in eastern Canada. Specimens with subcordate to cordate leaf bases, leaves and petioles puberulent, are distinguished as variety *subcordata* Hylander. This variety is found more commonly than the typical one in Alberta. Intermediate forms with rounded leaf bases and puberulent petioles, have also been found. Although this puberulence is considered to be diagnostic for var. *subcordata*, which is also known in eastern Canada, in Alberta it appears to be at least in part a characteristic of the intergradation between *balsamifera* and *trichocarpa*.

This subspecies ranges throughout the Boreal Forest, and southward in Alberta at least as far as the Bow River. Though frequently an upland tree in the Boreal Forest, in southern Alberta it grows mainly on the river banks. The geographic range limits of this and other species are shown on the range map (Figure 22).

Black Cottonwood

***P. balsamifera* L. subsp. *trichocarpa* (T. & G. ex Hook.) Brayshaw**
(*P. trichocarpa* T. & G. ex Hook.)
(*P. balsamifera* L. var. *californica* S. Watson)

Vigorously growing *twigs* and *shoots* sometimes angled, especially on saplings. *Leaves* relatively broader, but the range of proportions broadly overlapping: w/L=0.6 — 1.0, b/L=0.15 — 0.35 on brachyblasts: frequently cordate at base, especially on old trees. Veins beneath usually sparsely puberulent. *Petioles* pubescent. *Staminate flowers* with 40 to 60 stamens. *Fruit* a subglobose to broadly ovate capsule, 3-valved, and usually pubescent, but none of these characteristics quite constant (Figure 9).

Specimens with more acuminate leaves than the average for *trichocarpa*, and glabrescent capsules, have been described as *P. hastata* Dode (*P. trichocarpa* var. *hastata* (Dode) Henry). This variant falls within the range of individual variation in leaf form; and the glabrescent capsule suggests that it is one of the forms that can be assumed by intermediates between the two subspecies. It has been dealt with taxonomically in another report. It occurs scattered through the range of subsp. *trichocarpa*, with increasing frequency north and northeastward, as the range of subsp. *balsamifera* is approached.

A tree characteristically of riverbanks and alluvial flats, subsp. *trichocarpa* ranges into this area from the Montane Forest region to the west and south. In the plains of Alberta it occurs regularly along the rivers from the Bow southward, and has been found on the Red Deer and Peace Rivers.

An example of an intermediate form between the two subspecies, is shown in Figure 10, in which both two- and three-valved capsules can be discerned.

Narrowleaf Cottonwood

***P. angustifolia* James.**

A smaller tree than the other species considered here, this species has a somewhat willow-like aspect with a slender trunk, light yellowish grey *bark*, and a narrowly pyramidal crown; the ascending *branches* sometimes drooping at the ends. *Twigs* slender, at first yellowish brown, becoming bright white to ivory coloured by the second or third year. *Bud* scales glabrous, eciliate, and moderately resinous. *Leaves* small: usually 50 to 60 mm. long on brachyblasts, and up to 75 mm. long on turions; acute to obtuse on brachyblasts, or acuminate on turions; cuneate at base, narrow: w/L=0.15 — 0.3, b/L=0.4 — 0.5; margin finely but sharply glandular-serrate to apex. *Leaf colour* light yellowish green above, slightly if at all paler beneath; turning olivaceous or yellowish, but not darkening, on drying; a further yellowish cast often produced by the sulphur-yellow resin secreted by the marginal glands. *Petiole* usually less than 1/3 length of blade, semi-circular in section and flattened above, rather stiff, glabrous and eglandular. *Leaf attitude* stiffly ascending or diverging from the twig. *Fruit* an ovate, glabrous, 2-valved capsule on a pedicel 4 - 5 mm. long (Figure 11).

In its typical pure form, this species is rare in Alberta. An isolated small population on the Bow River differs slightly from the pure form: the twigs are not so white nor the leaves so yellow as in the species, and the leaves tend to be more acuminate and rather glaucous and veiny beneath. An example (*Brayshaw & Doan*, PFES *2594*) is illustrated in Figure 12. Its catkins agree with Sargent's (1922) description. The original description by James (1823) was not available. It appears to be slightly introgressed, but in this form is maintaining itself in a pioneering role on the riverbank.

Although Sudworth (1934) indicates *P. angustifolia* as occurring west of the Rocky Mountains in British Columbia and Montana, it is not now known in that part of Montana (White, 1951), nor was it found in British Columbia in this survey. However, some unusually narrow-leafed *P. balsamifera* subsp. *trichocarpa* specimens found along Alexander Creek near the Crowsnest Pass in British Columbia (*Brayshaw & Doan*, PFES *2431*) and in the Flathead Valley in Montana suggest that introgressant genes from *P. angustifolia* may have crossed the height of land via the *P. balsamifera* subsp. *trichocarpa* population.

In Alberta, *P. angustifolia* normally occurs with at least one other species with which it can cross, and appears almost lost in the swarm of hybrids and introgressants that more or less resemble it. It is the one species reviewed here whose characters were largely predicted from analysis of the hybrid swarm.

Within its range, this is the pioneer species of the riverbank poplar communities. Colonizing newly exposed bars, it is apparently unable to compete with the other species when the canopy closes over it. This ecological characteristic is no doubt one of the factors contributing to the relative success of its taller hybrid offspring. This species has entered the area from the south, along the zone where fast rivers emerge from the mountains to follow rapidly shifting channels. The known range for this species in Alberta is shown in Figure 22. In addition, one specimen (*Macoun*, CAN *40748*), somewhat introgressed by *P. balsamifera*, has been found at Frenchman's Creek, Cypress Hills, in Saskatchewan.

Plains Cottonwood

***P. deltoides* Bartram ex. Marshall var. *occidentalis* Rydb.**
(*P. Sargentii* Dode)

A rather broad-crowned tree, with long, massive, spreading and ascending branches. *Bark* becoming very thick (to 8 cm.), deeply furrowed into coarse flat-topped ridges, light brownish grey. *Twigs* light yellowish brown, becoming

paler and yellowish grey; often angled on vigorously growing shoots and saplings. *Bud scales* somewhat resinous, pubescent, and ciliate. *Leaves* broadly deltoid, truncate at base, and finely and abruptly acuminate or attenuate at apex: w/L= 0.85 — 1.3, b/L=0.1 — 0.3. *Leaf margin* variable; from finely glandular-serrate to coarsely sinuate, the prominent teeth often slightly hooked and glandular at apex; the serrate portion of the margin ending abruptly at some distance below the attenuate apex of the leaf. The number of teeth on a side changes progressively through the season; the first leaves of spring on turions with 12 - 14 teeth per side, dropping to 7 - 11 teeth on later leaves, then rising to 20 - 24 teeth per side on the last leaves produced during the growing season; on brachyblasts the leaves more uniform, with 7 - 16 prominent teeth per side (Figure 13).

The *leaf colour* is a deep yellowish green above and beneath, tending to darken on drying; the dorsal surface not glaucous except when first expanding, occasionally slightly resinous in a pair of oblique bands converging on the apex, the veins usually inconspicuous. *Petiole* 2/3 as long to fully as long as the blade, slender and flexible, laterally compressed in the upper part, as in *P. tremuloides*; slightly puberulent when expanding, becoming glabrous, often with a pair of glands at its junction with the blade. *Leaf attitude* more or less pendulous, with the surfaces vertical or nearly so; oscillates in a breeze. *Fruit* a narrowly ovate capsule, tapering to both ends; 3-valved, smooth and glabrous, 9 - 14 mm. long, on a pedicel 5 - 7 mm. long, in a long open catkin.

This variety is distinguished from the eastern *P. deltoides* (var. *deltoides*) by its pubescent and ciliate bud scales, the usually more coarsely toothed leaves, and slightly puberulent young petioles. These varieties appear to merge via a form, intermediate in leaf characters and still with ciliate bud scales, found in southern Manitoba.

In Alberta, this species is almost confined to riverbanks, and appears to have entered the region from the Mississippi and Red River basins via the Missouri and Saskatchewan River systems.

Lanceleaf Cottonwood

***P.* X *acuminata* Rydb.**

"Leaves more or less rhomboidal, abruptly acuminate, with cuneate base and long petioles (1′-2′ long,[3] or more), semi-pendant, thinner than in the preceding [*P. angustifolia*], drying green; denticulation scarcely any at base and near top; at the middle regular and larger than in the preceding; lateral nerves seldom more than 8 on each side; crown broadly pyramidal with spreading branches" (Rydberg, 1893).

In describing this species, Rydberg rejected the idea that it might be a hybrid between *P. monilifera* [=*P. deltoides*] and *P. angustifolia* on the grounds that the latter species was absent from the two stands in which he had found *P. acuminata*. White (1951) quotes Blankinship (1905) as believing this to be a hybrid, agrees with him, and suggests that it may be a *P. angustifolia* X *trichocarpa hastata* hybrid. Little (1950, 1953) treats it as a *P. angustifolia* X *Sargentii* hybrid.

THE HYBRIDS

Owing to the low incidence of flowering in 1959, and the dioicous nature of poplars generally, it was found necessary to use vegetative features in most cases to distinguish the species and their hybrids. This proved satisfactory, since the species are clearly defined in their vegetative characteristics. The more abundant fruiting material found in 1963 was of value in analyzing the *P. balsamifera* complex, which was then treated as a member of the total population, identifiable by its vegetative characters.

[3]In this, and other publications of the period, the symbol ′ was used to denote inches.

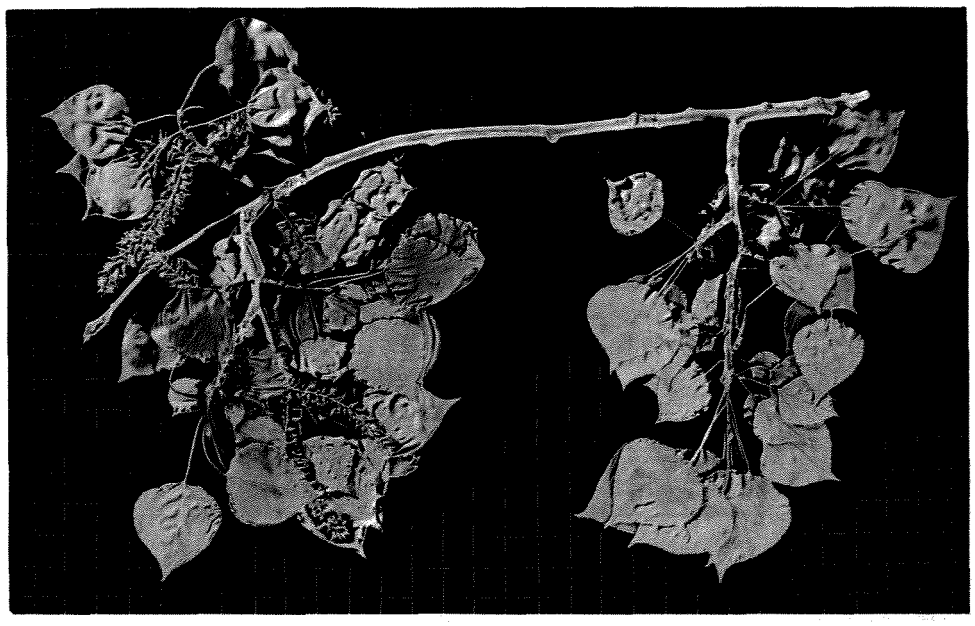

FIGURE 7. *Populus tremuloides* var. *aurea*: specimen from Kananaskis (*Brayshaw & Doan*, PFES *2619*, All specimens illustrated have been photographed against a square-centimetre grid.

FIGURE 8. *P. balsamifera* subsp. *balsamifera*, approaching var. *subcordata* (*Brayshaw & Doan*, PFES *2651*).

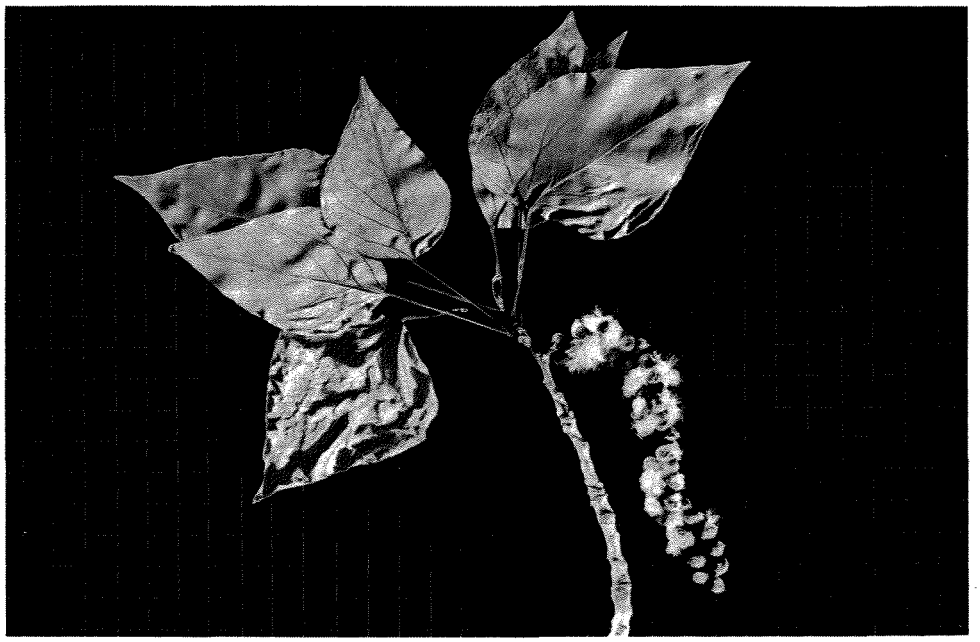

FIGURE 9. *P. balsamifera* subsp. *trichocarpa* (*Brayshaw & Doan*, PFES *2498*).

FIGURE 10. *P. balsamifera:* intermediate between subsp. *balsamifera* and subsp. *trichocarpa* (*Brayshaw & Doan*, PFES *2645*).

FIGURE 11. *P. angustifolia* (*Brayshaw & Doan*, PFES *2551*).

FIGURE 12. Fertile specimen of *P. angustifolia* from Cluny (*Brayshaw & Doan*, PFES *2594*).

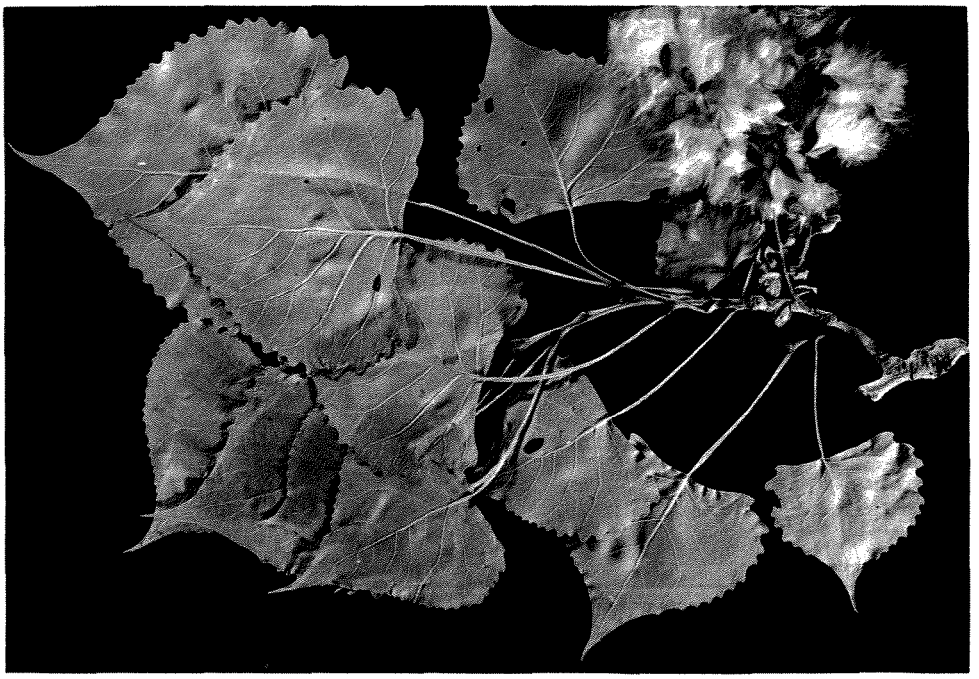

FIGURE 13. *Populus deltoides* var. *occidentalis* (*Boivin 9435*, PFES).

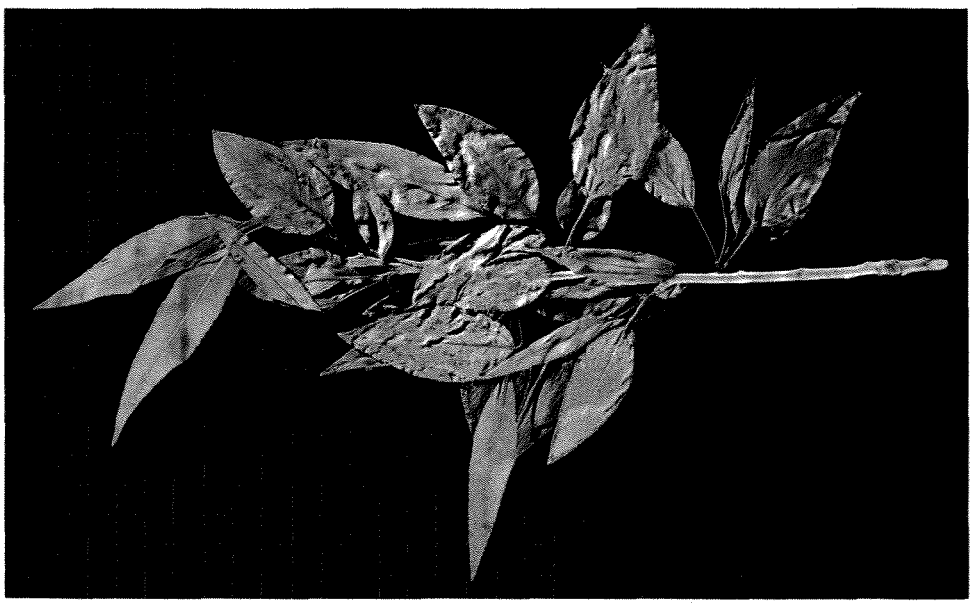

FIGURE 14. Example of an intermediate between *P. balsamifera* and *P. angustifolia* (*Brayshaw & Doan*, PFES *2497*).

FIGURE 15. *P. balsamifera* X *deltoides* var. *occidentalis* specimen resembling *P.* X *Jackii* (*Brayshaw & Doan*, PFES *2516*).

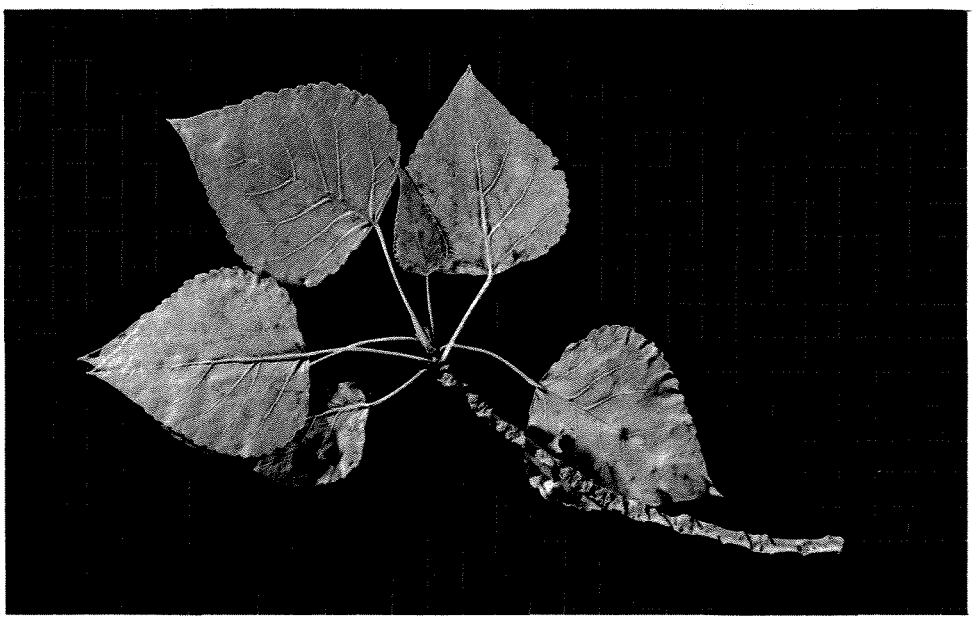

FIGURE 16. *P. deltoides* var. *occidentalis* X *tremuloides* hybrid similar to *P.* X *Andrewsii* (*Brayshaw & Doan*, PFES *2579*).

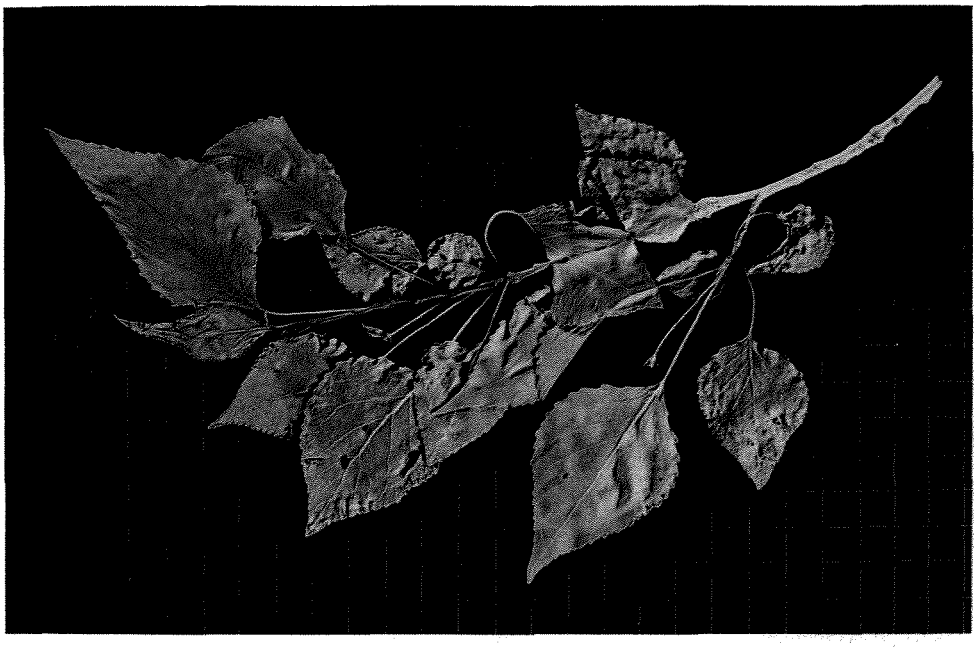

FIGURE 17. *P. angustifolia* X *deltoides* var. *occidentalis* hybrid (*Brayshaw & Doan*, PFES *2480*).

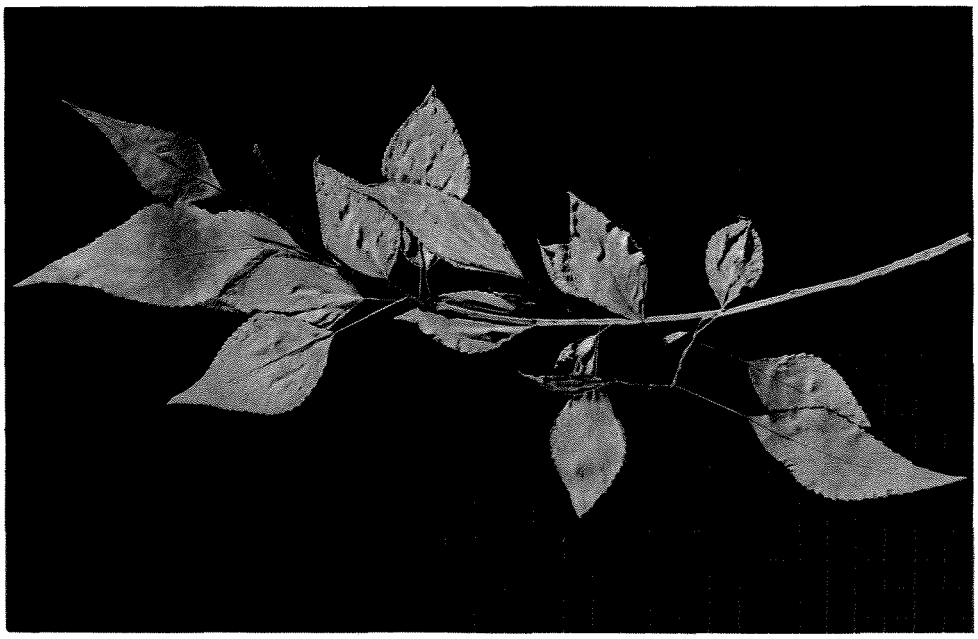

FIGURE 18. Specimen resembling *P.* X *acuminata* as described and figured by Rydberg (1893) (*Brayshaw & Doan*, PFES *2457*).

FIGURE 19. *P. tremuloides* X (*balsamifera* X *deltoides* var. *occidentalis*) (*Brayshaw & Doan*, PFES *2631 A*).

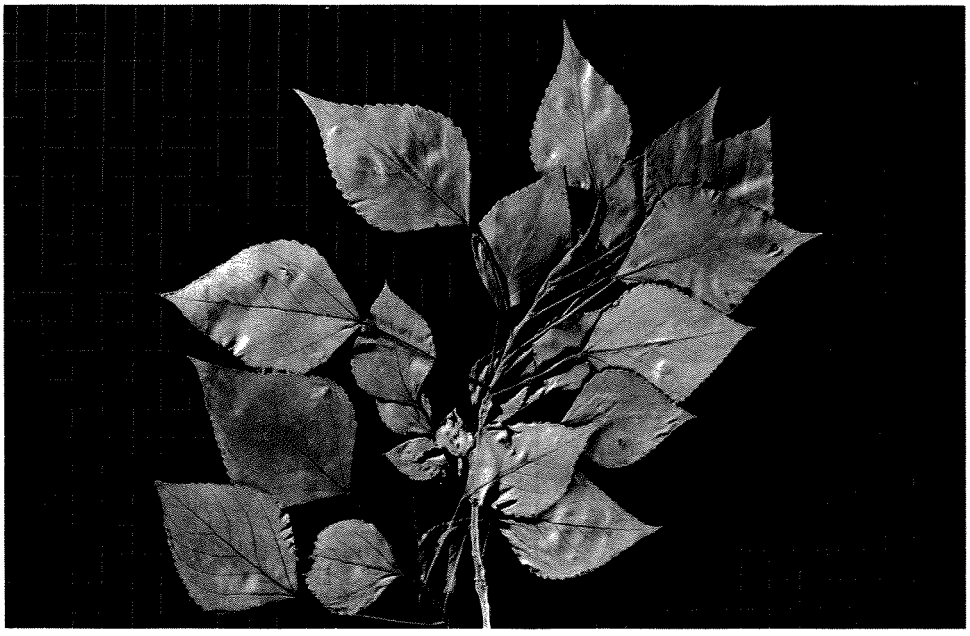

FIGURE 20. *P. balsamifera* — *deltoides* — *angustifolia* hybrid (*Brayshaw & Doan*, PFES *2459*).

The *Populus angustifolia — balsamifera* population

Associated with *P. balsamifera* in many stands in southern Alberta is a wealth of poplars having narrow leaves and short petioles, but varying widely among themselves in other features. The initial problem was to decide which of this material constitutes the true *P. angustifolia.*

The characteristics of *P. balsamifera* are well known. When scatter diagrams were plotted of the characters of the various specimens from stands where only these two species had been found, a spindle-shaped distribution pattern was obtained (Figure 4). Normal *P. balsamifera* specimens occurred at one end of the spindle, and characteristics at variance with this species occurred with increasing frequency toward the other end. By combining these latter characteristics, it was possible to arrive at a description of the vegetative characteristics of *P. angustifolia*, which permitted its selection from the population of introgressants (see above).

TABLE 2. HYBRID INDEX VALUES ASSIGNED TO THE *POPULUS ANGUSTIFOLIA – BALSAMIFERA* POPULATION.

Character	Expression	Points assigned
TWIG (2 yr. old) colour	white - ivory	0
	ivory - grey	1
	dull grey	2
PETIOLE		
surface	glabrous	0
	puberulent	1
length (p/L)	under 0.2	0
	0.2 - 0.35	1
	over 0.35	2
cross section	flattened above	0
	terete	1
LEAF		
blade: width (w/L)	under 0.4	0
	0.4 - 0.6	1
	over 0.6	2
" b/L	over 0.4	0
	0.33 - 0.4	1
	under 0.33	2
basal angle (between margin & midrib)	under 40°	0
	40° - 60°	1
	over 60°	2
basal curvature	straight	0
	convex	1
apex	acute or rounded	0
	acuminate	1
"	serrate	0
	entire	1
colour (dried)	yellow - olive	0
	olive - green	1
	green (often darkening)	2
dorsal surface	not glaucous	0
	slightly glaucous	1
	strongly glaucous	2
" "	not brown resinous	0
	slightly brown resinous	1
	decidedly brown resinous	2
Maximum value (=*P. balsamifera*): (Ideal *P. angustifolia*=0).		21

A linear hybrid index based on the vegetative characters was made up and applied to the nothocline involving these two species (see Table 2). This produced a series of values running from 0 for the predicted pure form of *P. angustifolia* to 21 for ideal *P. balsamifera.*

Some characteristics of *P. balsamifera* (e.g. glaucous, brown-resinous dorsal leaf surface, and puberulent petiole) appear with great frequency in the hybrid offspring. This may be a true case of dominance, or it may be an effect of natural selection on the hybrid population. The spindle-shaped distribution pattern in Figure 4 is an expression of linkage, which strongly reduces the chances of certain combinations of characteristics occurring. For instance the narrow leaves of *P. angustifolia* are not found combined with the long petioles of *P. balsamifera,* nor is the opposite combination seen. Variation in one character is correlated directly with variation in the other.

The specimens that were most nearly intermediate in hybrid index values between these species (index values 10 - 13) varied widely among themselves, indicating that crossing has been going on for several generations. In these intermediate specimens, the average leaf length was 65 mm., w/L=0.3 — 0.6, b/L= 0.33 — 0.4. Leaf base rounded or cuneate, apex acute or acuminate, indistinctly serrate. Leaf colour yellowish green, slightly tending to darken on drying; the dorsal surface glaucous, brown-resinous. Petiole about 1/3 length of blade, more or less terete or lunate in section, glabrous or sparsely puberulent, occasionally bearing glands. Twigs pale ivory-grey. Bud scales ciliate or eciliate. Figure 14 shows an example of an intermediate form from Cardston.

Populus deltoides var. *occidentalis* and its hybrids

This tree is notable for its ability to cross with other species in the area. That part of the hybrid swarm involving *P. deltoides* was made more difficult to analyze by the fact that few stands were found in which *P. deltoides* was mixed with only one other species. Along the South Saskatchewan and Oldman Rivers, it is introgressed to varying degrees by *P. balsamifera* and *P. angustifolia,* even where these species, as such, are not found. On the Bow River, *P. tremuloides* crosses with it in addition to the other species; and on the Red Deer, *P. tremuloides* introgression is again evident, but *P. angustifolia* is absent, and appears never to have been there, since no character expressions distinctive for it are found in the local population.

The extreme readiness with which this species crosses with the others in this region suggests that, in view of the apparent absence of its hybrid offspring at Calgary and Cardston, the trees of *P. deltoides* recorded from these localities (see Appendix II) have been recently introduced into those areas and are not naturally occurring specimens. With one exception, all stands that included other species mixed with *P. deltoides* also contained hybrids between them. The one exception, at Steveville ferry, contained only one young and moribund tree of *P. balsamifera,* which though apparently of natural occurrence, probably represents a recent arrival of this species into that area, which is well downstream of the normal limit of *P. balsamifera.*

One specimen found at Monarch (*Brayshaw & Doan,* PFES 2516; Figure 15) appears almost identical with the type specimen of *P.* X *Jackii* Sarg. (*J. G. Jack*; Aug. 11, 1909; in the Arnold Arboretum herbarium), which is a hybrid between the eastern form of *P. deltoides* and *P. balsamifera,* described originally from Nun's Island, Chateauguay, Quebec. The former differs only in that its leaves are slightly less cordate at base, and slightly more prominently acuminate at apex, than in the type specimen. Neither specimen includes catkins. Forms intermediate between this hybrid and all the species (including both parents) have been found.

Direct hybrids between *deltoides* and *angustifolia*, showing no other species characteristics, were not common. They tended to resemble *deltoides* more than *angustifolia*. This may be due to dominance of '*deltoides*' genes over their alleles, or may be the result of natural selection operating on a potentially completely intergrading population. *P.* X *acuminata* Rydb. is a nothomorph of this nothocline, and, on the basis of Rydberg's (1893) description and figure, resembles *angustifolia* more than do most of the hybrids found in this survey. A further indication of its hybrid origin is the fact that its pollen has been found to have a sterility of 45 percent, compared with 7 percent for *P. deltoides* var. *occidentalis* (Smith, 1943). Figure 17 shows a typical specimen from this hybrid series, and Figure 18, one that closely resembles *P.* X *acuminata*.

P. tremuloides is usually ecologically separated from the other species, and is not often found with them. When it does appear in the riverbank stands, as at Crowfoot, it shows little tendency to cross with them. No hybrids were found between *tremuloides* and members of the section *Tacamahaca*; but this species apparently can cross with *deltoides* and with hybrids between *deltoides* and other species. *P.* X *Andrewsii* Sargent appears to be a nothomorph of the *deltoides* - *tremuloides* series, rather than *P. deltoides* var. *occidentalis* X *acuminata*, as indicated by Sargent (1913). The specimen in the collection (*Brayshaw*, PFES *2579*; Figure 16) most nearly resembling the type of *P.* X *Andrewsii* differs from it in having rather smaller and stiffer leaves.

Apart from *P. tremuloides*, all the species in this region appear to cross with each other freely wherever they meet.

It is interesting to note that *P. deltoides* var. *occidentalis* seems to be a constant component of hybrids involving more than two parent species. An example of such a hybrid, which appears to have been formed by crossing between *P. tremuloides* and a hybrid of *deltoides* X *balsamifera* origin, is illustrated in Figure 19. Figure 20 shows a specimen from Medicine Hat (*Brayshaw & Doan*, PFES *2459*) in which characteristics of *P. balsamifera*, *P. deltoides*, and *P. angustifolia* are all discernible. This specimen, scored in the three-way hybrid index, rated 5,4,1, for the above species, respectively, and the non-exclusive characters were expressed for all three (see Table 3).

The range map of the poplars (Figure 22) shows the locations and putative composition of some of the more interesting hybrids; in particular those involving *P. tremuloides*, those occurring beyond the range limits of one or more of their parents and hybrids showing combinations of characteristics from more than two parents.

Those hybrid combinations found in Alberta are shown in Figure 21 where examples of typical leaf forms of the various species and their hybrids are shown in the margin. The leaf outlines do not show significant differences for all comparisons.

HYBRID STANDS

In most of the stands examined, only two species are involved in the hybrid population. Figure 4 is a scattergram illustrating such a hybrid population in two stands combined, at Cardston and Fort MacLeod. It can be seen that the spots that represent the individuals form a spindle connecting the positions corresponding to the leaf proportions of *P. balsamifera* and *P. angustifolia* (Figure 3), and that changes in the expressions of characters indicated by the appendages follow a definite trend along the spindle. Specimens with the characteristics typical of *P. balsamifera* appear at the appropriate end of the spindle. Characteristics by which *P. angustifolia* differs from *P. balsamifera* appear with increasing frequency with progress along the spindle, until a complete or almost

complete replacement has taken place at the other end. When the population was plotted in this way it became possible to see which of all the narrow-leafed specimens was true *P. angustifolia.*

Five stands along the Oldman and South Saskatchewan Rivers, where *P. angustifolia, balsamifera* and *deltoides* are involved, have been analyzed using the three-way hybrid index. The five 'exclusive' characters and three additional, non-exclusive, characters used are given in Table 3.

For each exclusive character two points were allotted, both points being assigned to one species when the expression of the character was fully typical of that species, or one point only when the expression was only partially developed; the other point was then assigned to the other species that was indicated in the partial expression. Occasionally expressions of all three species could be seen. In these cases, the two species that appeared to be most distinctly expressed were given the two points. The total score for each specimen was thus 10 points, divided among the three species according to their relative degrees of expression. The three non-exclusive characters were used to distinguish in each case one species from the other two, the species in question being indicated by italicizing the corresponding expression in Table 3. The hybrid index scores were plotted on triangular co-ordinate graphs, the score for each species increasing toward its respective apex of the triangle (Figure 6 (a)). The non-exclusive characters were shown as appendages on the spots, indicating by their direction the species they distinguished.

TABLE 3. EXPRESSIONS IN THREE SPECIES OF THE EIGHT CHARACTERS USED IN MAKING UP THE THREE-WAY HYBRID INDEX.

Character	*P. angustifolia*	*P. balsamifera*	*P. deltoides* v. *occidentalis*
Mutually exclusive characters			
Leaf teeth form	fine, sharp	low, rounded, crenate	prominent, sinuate
Leaf teeth at apex	teeth to apex	progressively flatten and fade out	cease abruptly below apex
Leaf base	cuneate	rounded to cordate, convex.	truncate
Leaf colour (dorsal surface)	yellowish to olive	whitened	green
Upper petiole cross-section	semicircular, flat above	terete, channelled above	compressed laterally
Non-exclusive characters			
Twig colour (2-yr.-old)	*white to ivory*	grey-brown	grey-brown
Petiole pubescence (at maturity)	absent	*present*	absent
Leaf apex form	acute	acuminate	*attenuate*

The five stands shown in Figure 6 (b-f) form a series running from west to east (and also downstream) from Brocket to Medicine Hat.

Comparisons among these graphs reveal a number of interesting facts. Where only two parent taxa are contributing to the population of the stand, as at Brocket, the spots for the individual trees are all lined up along the axis joining the parents. The appearance of a spot lying off this axis, (as at Fort MacLeod (Figure 6)), and the directions of its appendages, immediately reveals the presence of genes from the third species, *P. deltoides*, although the locality is well beyond the range limit of that species. At Monarch, the next stand sampled to the east-

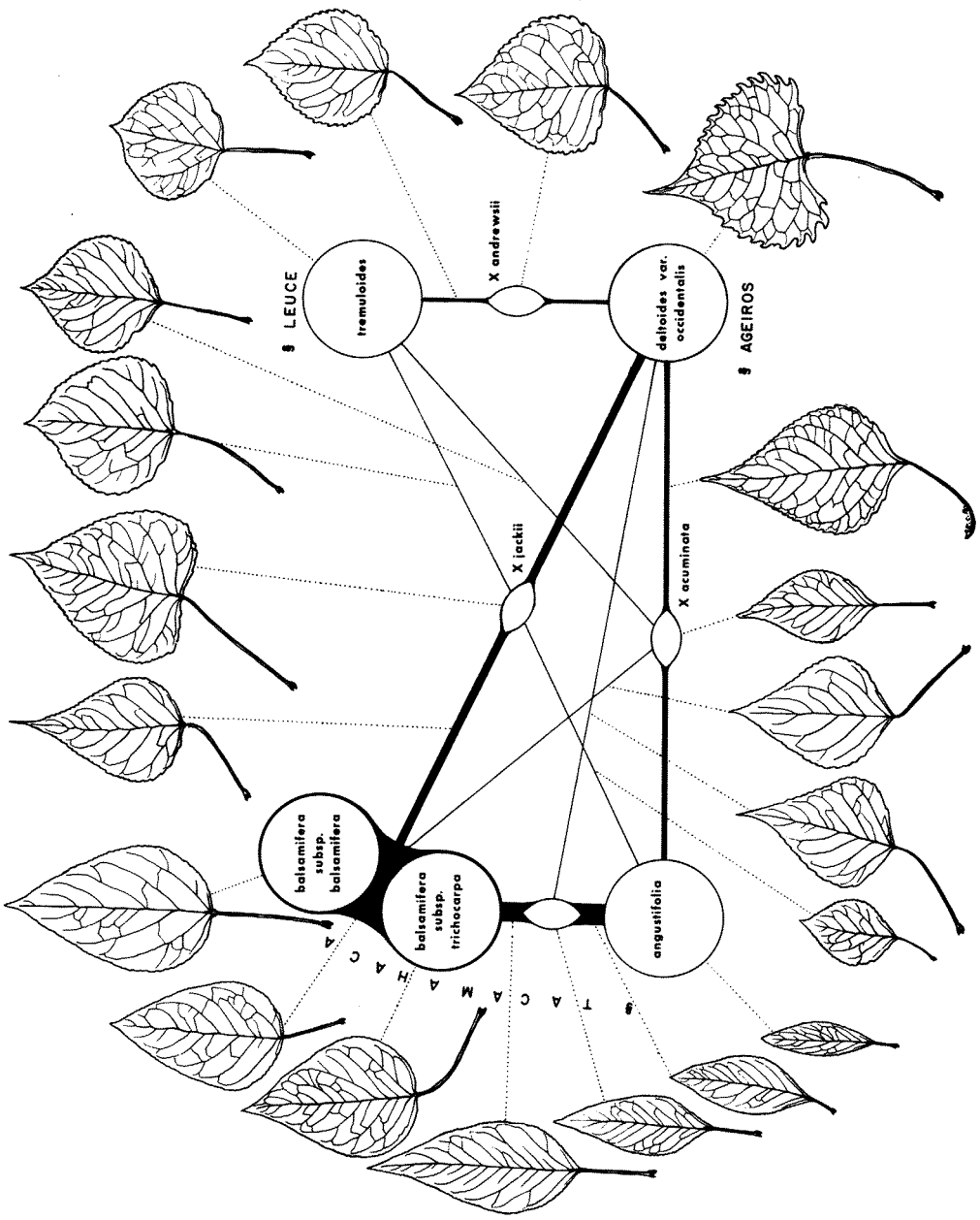

FIGURE 21. Diagram of the putative crosses found, showing leaf outlines of typical specimens of the species and hybrids.

ward, both *angustifolia* and *balsamifera* have dropped out, but *deltoides* has not yet appeared. The stand therefore consists of nothing but trees of mixed origin, whose exact pedigrees are now often impossible to determine. The increasing influence of *P. deltoides* with progress eastward is very apparent, though that species does not appear in the stands until Lethbridge is reached. Further downstream, the hybrid population which has dominated the scene thins out, and *P. deltoides* var. *occidentalis* becomes the dominant tree. This trend is indicated by the composition of the stand at Medicine Hat.

At Crowfoot, on the Bow River above Bassano, a stand was found that for its size is more complex than those found anywhere else. *P. tremuloides* occurs as an adjacent fringe on the landward side of the gallery forest and contributes genes to the population growing along the riverbank. The specimen that most nearly resembles *P.* X *Andrewsii* was found in this stand. One effect of the influence of *P. tremuloides* in this stand is the triangular form of the "spindle" in the scattergram for this stand (Figure 5). *P. angustifolia* occurs here as a slightly introgressed form, as described earlier, in which it grows as a pioneer fringe on recently deposited sediment on the riverbank. Trees of this species growing in mixture with other species are somewhat suppressed, and this species is more often represented by hybrids where it is in mixture with the larger tree species.

Though *P. angustifolia* in its local form was found only at Crowfoot and Cluny on the Bow River, hybrids between it and *P. balsamifera* were found as far upstream as Carseland. It was noticed there, that where *P. balsamifera* dominated the stands, the first visible indication of the presence of *angustifolia* genes in a tree was shown by the leaf attitude. Trees with leaves of the size typical of *balsamifera* but slightly narrower than normal for that species betrayed their *angustifolia* ancestry by the stiffly ascending and divergent attitude of the leaves, this giving a distinctly 'spiky' silhouette to the branches, in contrast to the smoother silhouette of typical *balsamifera.*

On the Red Deer River, upstream from Drumheller, a few hybrids of apparent *tremuloides* ancestry occur, although pure *P. tremuloides* itself is scarce or absent from the riverbank for the first several miles. Further up the river, at the crossing of Highway 21, near Alix, trees of *P. tremuloides* and *P. balsamifera* were found that showed traces of *'deltoides'* characteristics in them.

DISCUSSION

Reliability of Results

Since no cultural methods have been employed to check the conclusions made here, these must be regarded as hypotheses. Undoubtedly, the genetic background of this hybrid swarm is actually much more complex than is described here. Interbreeding between the local species of poplar has evidently been proceeding for many generations. Complete information on the genetic behaviour of these species is lacking, but it may be expected that after many generations of more or less free interbreeding between them a nearly continuous intergradation of specific characteristics can be produced, subject to limitations imposed by linkage and natural selection. Consequently, the best that can be done here is to give the simplest combination that is thought capable of producing the observed array of characteristics in each case.

The putative makeup of the hybrid swarm in this region is shown in Figure 21. Leaf outlines at half natural size are shown for each species and putative hybrid combination. Differences in leaf outline alone are not significant in every case, but are visible in those cases where they are thought to be significant.

Ranges of Species and Hybrids

A point worth drawing attention to is that hybrids are often found in areas where not all, possibly none, of their parent species occur. Several such cases are shown in Figure 22. This effect has been seen in connection with all the species discussed in this paper. An outstanding example of it is the purely hybrid stand at Monarch. It is evident that a collector finding a hybrid at a given location need not assume that both or all its parent species must be found in the immediate vicinity.

Two possible explanations for this apparently eccentric distribution of hybrids suggest themselves. One of these requires no assumptions regarding changes in the range of the species in prehistoric times; while the other assumes a pattern of change that is understood to have been followed by many species during post-Pleistocene times.

In the process of introgression, genes from one parent species in contact with another, at the limit of range of either species, can be passed through a few intervening hybrid generations and repeated backcrosses to the other species. Once this has been accomplished, these genes may be transmitted after many generations to individuals growing far from the locality where the original gene-exchange took place, and far beyond the limits of the range of the species that originally contributed them. Such gene-flow, involving species that occupy different though contiguous geographic ranges, is termed 'allopatric introgression' by Anderson (1953). By this means, many varieties and forms differing from the typical ones may appear in the introgressed species, and hybrids may be found in unexpected places.

An alternative explanation is based on the understanding (now well established from work in other fields) that the climate in the immediate post-Pleistocene period was warmer than it is now and that many species then extended their ranges into areas from which they were subsequently compelled by changing conditions to retreat. If this happened with the interfertile poplars in this region, the retreat from an area could take the form of a gradual elimination of the more tender species by natural selection and competition in the mixed population. Those hybrids inheriting the adaptive characteristics from their hardier parents, being relatively favoured ecologically, would regenerate effectively, and would eventually form, with the hardier species, the entire population of the area.

The actual history of this hybrid population may well involve a combination of both of these processes, but it is not well enough understood to permit an estimation of their relative importance.

Factors Affecting Hybridization

Internal Barriers

The fact that all the poplar species represented in the region have the same chromosome number (2N=38) suggests ease of crossing on at least one basis. However this gives no information on the degree of homology between the corresponding chromosomes of heterogenetic origin. The high degree of pollen sterility that has been found in *P.* X *acuminata* indicates that here at least a partial barrier exists and that hybrids are likely to be less fertile than unintrogressed species. Smith (1943) lists the degree of pollen sterility of *P.* X *acuminata* as 45 percent, while that of *P. Sargentii* is 7 percent and that of *P. tremuloides*, 2 percent. If this situation prevails in the other hybrids, one would expect it to reduce greatly the frequency of hybridization in the second and subsequent generations. However, the abundance and diversity of the hybrids, many of which obviously must be more than one generation removed from the original interspecific crosses whence they are descended, indicates that though the partial

internal barriers that exist may be in some degree effective at the individual level, they have been of negligible effect at the population level. The ecological conditions favouring crossing more than compensate for the restrictions imposed by the genetic barriers.

Disparity in flowering period is another barrier to crossing. All the species considered here flower in early spring. Unfortunately the field schedule did not permit observations to be made through the flowering season. However, the relative development of the abundant fruiting catkins found in June 1963, indicated that the order of flowering had probably been: *P. tremuloides - balsamifera - angustifolia - deltoides.* Although the flowering periods differ, overlapping is almost certain to occur between so many flowering periods compressed into such a short spring season, especially when unseasonal fluctuations in weather may delay the flowering of the earlier species. Once hybridization has been initiated, the hybrids might be expected to be intermediate in their flowering periods and overlap in time with their parents, thus forming a phenological 'bridge' between the flowering periods. Thus in this way also, the internal barriers to crossing would be very incomplete in their effectiveness and easily overcome.

Influence of Habitat

The favourable situation for the establishment of hybrids is probably a function of both climatic and edaphic conditions, acting in combination to influence the relative competitive abilities of the various taxa making up the stands.

The cool, dry and windy climate of this region, generally unfavourable to tree growth, tends to eliminate most tree species from competition with the poplars, and to confine most of the poplars to the banks of the rivers. The fact that three of the species of poplar here reach their geographical limits suggests that they have also, at least when they are in competition with each other, reached the limit of their tolerance for the combination of climatic and edaphic conditions.

On leaving the mountains, the rivers, running in shifting, often braided channels in the beds of their coulees, naturally maintain complete sequences of disturbed habitats; and the ecological barriers that would exist between stable habitats are broken down. Such seral habitats are well suited to continuous or repeated colonization by pioneer species such as the poplars. Further, there are always sites open for occupation by any hybrids produced. This is a natural process analogous to man's 'hybridization of the habitat' as described by Anderson (1949).

The habitats of the parents, or approximations to them, naturally favour those backcrosses or recombinations most nearly approaching the parent species, at least in their adaptive characteristics. However, the continuous range of habitats available here permits the establishment of combinations that often bear little resemblance to any one parental species. As a result, after a number of generations of interbreeding, a hybrid swarm is generated that includes many individuals whose pedigree is difficult if not impossible to reconstruct.

Influence of the Relative Abundance of Species

The scarcity of *Populus angustifolia,* in comparison with the numbers of hybrids derived from it and with the representatives of other species, draws attention to the effect of a great disparity in the relative abundances of two or more interbreeding species. With more or less concurrently blooming species of a wind-pollinated dioicous genus such as *Populus,* a pistillate tree of a rare species is more likely to receive pollen from another species or from a hybrid than from a staminate tree of its own kind, unless one happens by chance to be close at hand.

From this premise it is inferred that a great disparity in abundance between interfertile species, where their ranges overlap, enhances the chance of hybridization. The outcrossing of the rarer species may be so strongly favoured as to compensate, or even overcompensate, for the effects of genetic or phenologic barriers that are only partially effective. Consequently, barring the intervention of ecological influences that are discriminatingly favourable to the species in its pure form, successive generations would witness a progressive reduction in its abundance. This process would be self-perpetuating until the species in its pure form is lost. All that will then be found is a hybrid swarm in which the species is represented by forms that only approximately resemble it. It may be postulated that chance recombination may occasionally reproduce phenotypes indistinguishable from the 'lost' species; but without the intervention of rigorous natural selective forces, the probability of this event is almost infinitesimal if that species differs from its more abundant relatives by more than a very few characteristics.

Populus angustifolia appears to be an example of a species that is thus breeding itself out of existence in its pure form, in Alberta at least.

Evolutionary Aspects

Since the species have discernibly different ecological requirements, their complete or almost complete gene complements must have corresponding adaptive significance. Nevertheless, the great diversity among the hybrids that can be found together making up a stand suggests that many of the genes, taken individually, have little or no adaptive value. In such a situation, where the effect of natural selection is insignificant among them, these genes may be transmitted to offspring at random (subject to linkage effects); so that their frequency and apparent prominence in the population may vary unpredictably in time, new combinations continually being produced, while others may disappear.

Here is seen a mechanism of evolution in action. Highly diversified populations have been generated in partial isolation on the rivers of this region. A host of strange combinations is being perpetuated, using the genic material at hand, without the necessity, or apparently the occurrence, of new mutations. One might expect this population to be a potential source from which new varieties and species could in time become differentiated. However, the most important single requirement for the evolution of new taxa is isolation. Since the several species that have entered this region are still in contact with each other and with their own continuous ranges, and are therefore still contributing genes to the population here, it is evident that the present isolation is not complete enough for stabilization of distinct varieties or forms. Thus the actual emergence of new forms is hindered. Changes of evolutionary significance are taking place, but are not in general leading in the direction of differentiation or stabilization of new varieties, but rather in the opposite direction, towards diversification of the population. The one possible exception to this is the local form of *P. angustifolia* on the Bow River, described above, whose intolerance to competition from other species and whose pioneering tendency tend to maintain it, through an ecological enhancement of its incomplete geographical isolation. In its present form, it varies appreciably from individual to individual, and can hardly be said to be stabilized in its total gene complement.

Utilization

Among the wealth of diverse forms of poplars found along the rivers of southern Alberta, there are many that appear to have ornamental possibilities. The examination of these riverbank stands to select material for cultivation should be well worth while. It could result in the introduction into cultivation

of a wider range of poplar varieties than is currently utilized. These varieties could be not only ornamental, but also adapted to the climatic conditions of the prairie provinces at least as well as, if not better than, the imported species and hybrids derived from them, that are being widely planted in the region at the present time.

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APPENDIX I

Collection Sites

Sites of Collections by Brayshaw, Doan and Merilees, in 1959 and 1963

All places named are in Alberta unless otherwise indicated. Most of the collection sites are shown in Figure 1. Species and putative combinations found at each site are indicated by letters as shown below:

A *P. angustifolia*
B *P. balsamifera*
C *P. deltoides* var. *occidentalis*
D *P. tremuloides*

Sites sampled in 1959

1. Elkwater, bridge W of village. B
2. Irvine, 1 mile SW: bridge on Highway 1. C
3. N bank of Milk R: ca. 4 miles SE of Comrey (49°05'N, 110°43'W). C
4a Writing-on-stone Park: N bank of Milk R. C
4b Writing-on-stone Park, 1 mile W: N bank of Milk R. C, CXA
5. Medicine Hat: left bank of South Saskatchewan R., E of Golf Course. C, AXC, BXC, & trispecific hybrids.
6. Burdett Ferry: N bank of South Saskatchewan. C, CXD.
7. Taber, 2 miles NW: camp ground on S bank of Oldman R. AXB, BXC.
8. Lethbridge: both banks of Oldman R. opposite town. C, AXC, AXB, BXC, & trispecific hybrids.
9. Cardston, 3 miles NE; on E bank of St Mary R., S of H'way 5. A, B, AXB.
10. Cardston, 6 miles S: on E bank of St. Mary R., N of Highway 40. A, B, AXB.
11. Waterton Lake: Cameron Creek valley. B.
12. Monarch: N bank of Oldman R. at crossing of Highway 3. AXB, BXC, & trispecific hybrids; no pure species.
13. Fort MacLeod, one mile W: on S bank of Oldman R. at crossing of Highway 2. A, B, AXB.
14. Fort MacLeod, 5 miles NW: S bank of Willow Creek, one mile N of Highway 2. A, B, AXB.
15. Claresholme, ca. 6 miles SW: S bank of Trout Creek (49°58'N 113°43'W). A, B, AXB.
16. Brocket, 2 miles NW: at bridge over Oldman R., both sides of river and road. A, B, AXB.
17. Pincher Creek: N bank of creek W of Highway 6. B, AXB.
18. Lundbreck, ca. 17 miles N: bank of Oldman R. at crossing of Porcupine Ranger Station road. B.
19. Frank: on the slide, S of Highway 3. B, AXB.
20. Blairmore: S bank of Crowsnest R. B, AXB.
21. Between Crownest & Michel, B.C.: S bank of Alexander Creek. B, BXA.
22. Crowfoot,: S bank of Bow River at ferry. A, B, C, D, AXB, CXD, & trispecific hybrids involving all these.
23. Cluny: S bank of Bow R. at bridge. A, B, AXB.
24. Carseland, 2 miles SE: N bank of Bow R. at bridge. B, BXA.
25. Okotoks: S bank of Sheep R. at crossing of Highway 2. B.

26. Okotoks: S bank of Sheep R. at crossing of Highway 7. B, AXB.
27. High River: N bank of Highwood R. at N edge of town. B.
28. Kananaskis Forest Experiment Station: 3 miles SW of Headquarters. B, D.
29. Banff: N shore of Vermillion Lake. B
30. Banff: N slope of Tunnel Mtn. B.
31. Drumheller, ca. 3 miles NW: E bank of Red Deer R. adjacent to gravel yard. B, C, BXC, DX(BXC).
32. N bank of Red Deer R. at crossing of Cochrane—Nordegg road. B.
33. Nordegg, ca. 25 miles SW: left bank of North Saskatchewan R. B.
34. Edgewater, B.C., one mile S: on E bank of Columbia R. B.
35. Yellowhead, B.C.: one mile SW. B.
36. Geikie, (W of Jasper). B.
37. Jasper, 6 miles N: on Highway 16. B.
38. Kinuso, one mile SW: N bank of Swan R., S of Highway 2. B.
39. Peace River: W bank of river, opposite town. B.
40. Bluesky, 2 miles E: W bank of Leith R., N of Highway 2. B.
41. Dunvegan: N bank of Peace R. E of ferry landing. B.
42. Grande Prairie, 6 miles S: S bank of Wapiti R. at campsite W of bridge. B.
43. Maple Creek, Sask.: ca. 19 miles S, on road to Cypress Park. B.

Additional sites sampled in 1963.

44. Standoff, Alta.: S bank of Waterton R. at Highway 2. A, B, AXB.
45. Standoff: N bank of Belly R., W of Highway 2. B, AXB.
46. Mountain View, ca. 5 miles W: banks of Belly R., S of Highway 5. A, B, AXB.
47. Gleichen, ca. 9 miles SW: banks of Bow R. on road to Arrowwood. B, AXB.
48. Bowness: right bank of Bow R. at crossing of Highway 1. B.
49. Canmore: 3 miles E on road to Exshaw. B.
50. Steveville ferry: W bank of Red Deer R. B, C.
51. East Coulee: E bank of Red Deer R. B, C.
52. Little Fish Lake, Hand Hills. C, D, BXC.
53. Drumheller: right bank of Red Deer R. adjacent to town. B, C, BXC.
54. Morrin bridge: left bank of Red Deer R. B, C, BXC.
55. Alix, ca. 9 miles SE: crossing of Red Deer R. at Highway 21. B, D, BXC, DXC.

APPENDIX II

Representative Herbarium Specimens of Species and Hybrids

In the following list, the collection localities are given first, all being in Alberta unless otherwise stated. Since this report is based primarily on the collections made by G. E. Doan and the author in 1959, these collectors' names are omitted in this series of specimens for the sake of brevity. But in other collections, the collector's name is given after the locality. Since *Populus tremuloides* is generally clearly defined over a range that includes all the area dealt with here, no specimen list is included for this species. In other cases, specimens are selected so as to give an indication of the range limits of the taxa of this region.

Populus balsamifera subsp. *balsamifera*

Banff (Tunnel Mt.), PFES *2621*. Nordegg, ca. 25 miles SW, PFES *2634* (DAO). Geikie station (near Jasper), PFES *2640*. Faust, *Rowe*, PFES *2307*. Peace River, PFES *2649*. Bluesky, 2 miles E, PFES *2651* (DAO). Grande Prairie, 6 miles S, PFES *2653*. Standoff (Belly River), *Brayshaw & Merilees*, PFES *4638*.

P. balsamifera subsp. *trichocarpa*

Cardston, 6 miles S, PFES *2498* (DAO). Crowfoot, *Brayshaw*, PFES *2572A*. High River, PFES *2612*. Gleichen, *Braysahw & Merilees*, PFES *4644*. Peace River, PFES *2646*. Grande Prairie, 6 miles S, PFES *2654*. Edgewater, B.C., one mile S, PFES *2432* (DAO).

P. balsamifera: indeterminate examples.

A, intermediate
Elkwater, PFES *2441* (DAO). Carseland, PFES *2600.B*. Okotoks, PFES *2613*. Jasper, PFES *2636*. Kinuso, PFES *2645*. Red Deer River, at crossing of Cochrane — Nordegg road, PFES *2632*.
B, approaching subsp. *balsamifera*
Kananaskis Forest Experiment Station, *Brayshaw & Ogilvie*, PFES *2616*. Banff (Tunnel Mtn.), PFES *2622*. Jasper, PFES, *2642*. Maple Creek, Sask., ca. 19 miles S, PFES *2440*.
C, approaching subsp. *trichocarpa*.
Elkwater, PFES *2442*. Cluny, PFES *2587*. Jasper, PFES *2638*. Peace River, PFES *2647*.

Populus angustifolia

Cardston, 3 miles NE, PFES *2495.B*. Fort MacLeod, one mile W, PFES *2524*. Brocket, 2 miles NW, PFES *2551*. Pincher Creek, 5 miles NW (on Castle River), *Dore & Breitung 12417* (DAO, PFES). Claresholme, 6 miles SW (on Trout Cr.), PFES *2537*. Cluny, PFES *2594* (DAO). Standoff, *Moss 414* (CAN). Lethbridge, *Boivin & Perron 12154* (DAO, PFES). Frenchman R., Cypress Hills, Sask., *Macoun* CAN *40748*. Crowfoot, *Brayshaw*, PFES *4645*. (The above specimens, from PFES *2594* onward, all show indications of slight introgression by *P. balsamifera*).

P. deltoides var. *occidentalis*

Irvine, one mile SW, PFES *2444*. Comrey, 4 miles SE, (on Milk R.), PFES *2445*. Writing-on-stone Park, *Brayshaw*, PFES *2449*. Medicine Hat, *Boivin 9435* (DAO, PFES). Belly River, *Dawson 10508* (CAN). Lethbridge, PFES *2470*. Crowfoot, *Brayshaw* PFES *2570*. Cardston, *Dore & Breitung 12116* (DAO), (planted?). L. Pakowki, *Boivin & Perron 12347* (DAO, PFES). Calgary, *Breitung 1837* (DAO), (planted?). Both at Calgary and at Cardston, this species is unrecorded except for those cited specimens collected from adjacent to the towns.

Populus angustifolia - balsamifera series.

A, Intermediates (hybrid index=8/21 - 13/21).
Cardston, 3 miles NE, PFES *2497*. Frank, PFES *2563* (DAO). Blairmore, PFES *2569*. Cluny, PFES *2598.A*. Lethbridge, *Boivin, Perron & Harper, 12194* (DAO, PFES).
B, Approaching *P. angustifolia* (hybrid index=6/21).
Lethbridge, PFES *2478* (DAO). Cardston, 6 miles S, PFES *2503*. Milk River below Pend Oreille, *Macoun* CAN *40747* (as *P. angustifolia*). Gleichen, *Brayshaw & Merilees* PFES *4642*.
C, Approaching *P. balsamifera* (hybrid index=16/21 - 17/21).
Cardston, 3 miles NE, PFES *2496*. Alexander Creek W of Crowsnest, B.C., PFES *2431*. Carseland, *Brayshaw & Merilees*, PFES *4643*.

P. angustifolia - deltoides var. *occidentalis* series

A, intermediate.
Lethbridge, PFES *2480*.
B, approaching *P. angustifolia* (resembling *P.* X *acuminata*)
Lethbridge, *Boivin, Perron & Harper 12191* (DAO, PFES). Medicine Hat, PFES *2457* (DAO).
C, approaching *P. deltoides* var. *occidentalis*
Lethbridge, PFES *2479*. Lethbridge, *Dore & Breitung 11741* (DAO, PFES). Lethbridge, *Moss 1245* (DAO); (the last specimen was used to illustrate *P.* X *acuminata* in Native Trees of Canada, ed. 5, (1956) p. 105, upper photograph).

Populus balsamifera - deltoides var. *occidentalis* series.

A, intermediate (resembling *P.* X *Jackii*).
Monarch, PFES *2516*.
B, approaching *P. deltoides* var. *occidentalis*.
Lethbridge, PFES *2483*.
C, approaching *P. balsamifera*.
Drumheller, PFES *2630* (DAO). Monarch, PFES *2509*.

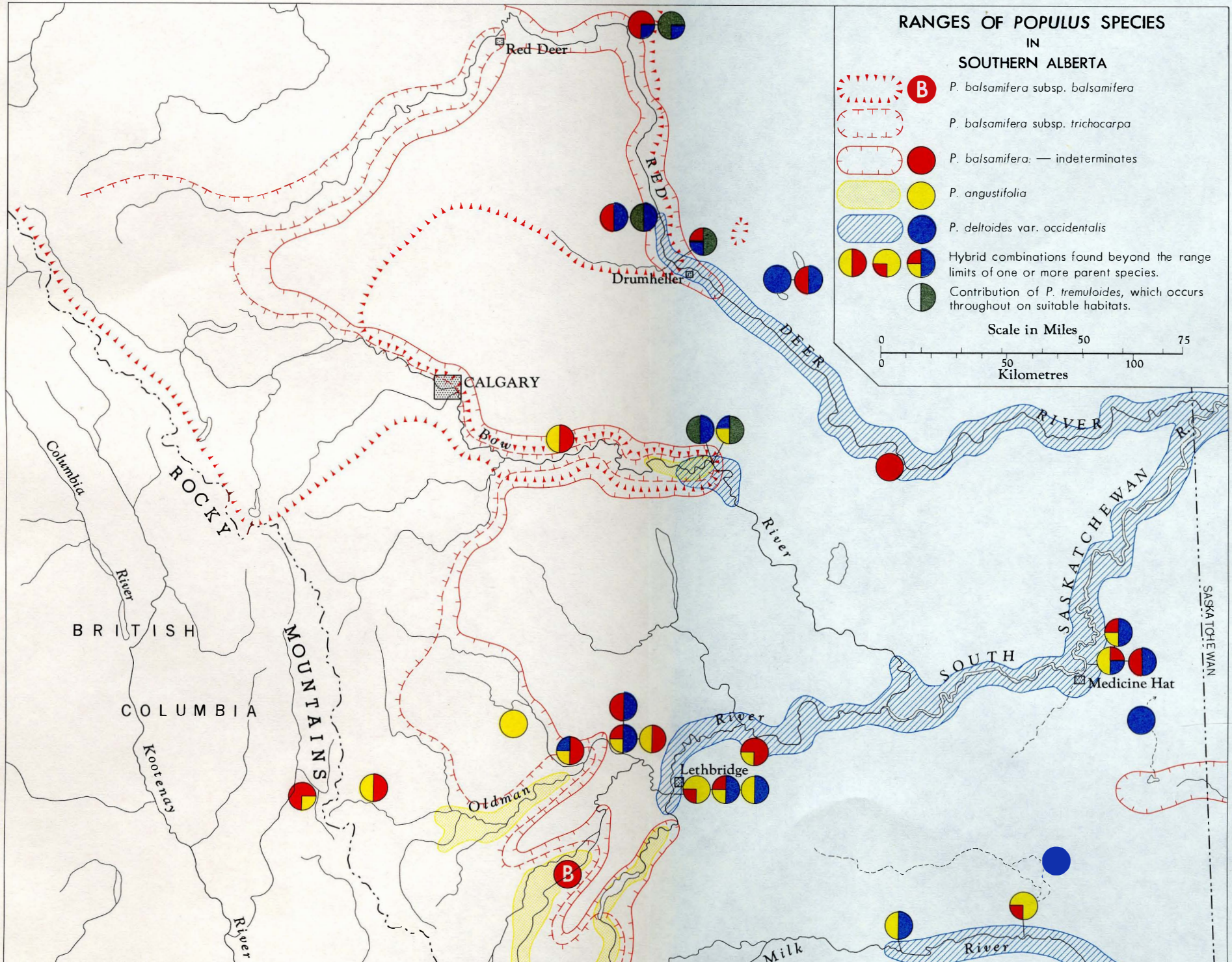
Populus deltoides var. *occidentalis - tremuloides* series.

A, intermediate.
Crowfoot, *Brayshaw*, PFES *2579*. Drumheller, 8 miles SE, *Boivin & Perron 12350* (DAO, PFES).
B, approaching *P. deltoides* var. *occidentalis*.
Crowfoot, *Brayshaw*, PFES *2580*.
C, approaching *P. tremuloides*.
Crowfoot, *Brayshaw*, PFES *2581.A*. (DAO). Drumheller, 8 miles SE, *Boivin & Perron 12349* (DAO, PFES).

Specimens that appear to be trispecific hybrids, all involving *P. deltoides* var. *occidentalis* in their parentage.

P. deltoides X (*angustifolia* X *balsamifera*)
Monarch, PFES *2519* (DAO). Lethbridge, PFES *2485*.
P. angustifolia X (*deltoides* var. *occidentalis* X *balsamifera*)
Lethbridge, PFES *2481*. Medicine Hat, PFES *2458*.
P. balsamifera X (*angustifolia* X *deltoides* var. *occidentalis*)
Monarch, PFES *2512*. Lethbridge, PFES *2482*. Medicine Hat, PFES *2459*.
P. tremuloides X (*balsamifera* X *deltoides* var. *occidentalis*)
Drumheller, 3 miles NW, PFES, *2631* (DAO). Crowfoot, PFES *2575* & *2577*.
P. tremuloides X (*angustifolia* X *deltoides* var. *occidentalis*)
Crowfoot, *Brayshaw* PFES *2584*.

FIGURE 22. Range map of the species of poplar in southern Alberta showing the locations and compositions of some of the hybrids. The occurrence of *P. tremuloides* in the hybrids is indicated by dark brown tint.


RANGES OF POPULUS SPECIES
IN
SOUTHERN ALBERTA
B
P. balsamifera subsp. balsamifera
P. balsamifera subsp. trichocarpa
P. balsamifera: — indeterminates
P. angustifolia
P. deltoides var. occidentalis
Hybrid combinations found beyond the range limits of one or more parent species.
Contribution of P. tremuloides, which occurs throughout on suitable habitats.
Scale in Miles
0
50
75
0
50
100
Kilometres
Red Deer
Drumheller
CALGARY
Bow
River
RED DEER
RIVER
SASKATCHEWAN
R.
SASKATCHEWAN
Columbia
River
ROCKY
MOUNTAINS
BRITISH
COLUMBIA
Kootenay
River
Oldman
River
Lethbridge
SOUTH
Medicine Hat
Milk
River
B