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The Hybrid Pinus peuce Griseb. x Pinus strobus L.

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The white pine (Pinus strobus L.) breeding project at the Southern Research Station of the Ontario Department of Lands and Forests, Maple, Ontario was initiated in 1946 and is a direct continuation of similar work at the Petawawa Forest Experiment Station of the Dominion Forest Service, Chalk River, Ontario. The breeding of white pine types showing a high degree of resistance to blister rust (Cronartium ribicola FISCHER) and to damage caused by attacks of the white pine weevil (Pissodes strobi PECK) are the chief aims of the present work. Pinus peuce GRISEB. is well known for its resistance to blister rust in Europe (TUBEUF, 1924; 1927) and in North America (SPAULDING, 1925; HIRT, 1940). In the earlier part of this century P. strobus was severely damaged by blister rust in western Europe. At this time, P. peuce was advocated as a possible replacement as a forest tree (TUBEUF, 1927). The much slower growth rate of P. peuce in comparison with P. strobus and other undesirable silvicultural characteristics, notably the more restricted ecological amplitude (DIMITROV, 1926; GEYR, 1932) make it a poor substitute at best. However, the high degree of resistance of P. peuce to blister rust warranted its early inclusion in the white pine breeding project and, therefore, a collection of all available origins of this species in the form of grafts and seedlings has been in progress during the last ten years.

In 1950, Mr A. G. JOHNSON, then working at the Arnold Arboretum, pointed out (in personal correspondence) the resistance of one P. peuce tree in their collection to damage from weevil attack. The tree is surrounded by three P. peuce trees grown from the same seed lot and by several native white pine, all with severely damaged leaders caused by weevil attack. The leader of the tree in question had been repeatedly punctured by the weevil but had withstood the attacks apparently by means of heavy resin flow and subsequent healing of the puncture wounds. A similar situation was found in the fall of 1955 in some planted P. peuce along Ontario highway # 7 to the east of Havelock, Ontario. The trees had been planted by the Ontario Department of Highways as a windbreak and are at present about 8 feet tall. Several of the trees show signs of previous heavy weevil attacks and subsequent healing without leader mortality. A similar reaction to light weevil attack is occasionally found in native white pine. Although a detailed study of this situation has as yet not been carried out, it seems probable that young P. peuce can withstand much heavier weevil attacks without leader mortality than P. strobus and thus, also from this standpoint, P. peuce may be of value in a white pine breeding program.

The hybridization of P. strobus with P. peuce was attempted during the early phases of breeding work with the white pines in Canada. The cross was seemingly successful and a number of seedlings were raised (JOHNSON and HEIMBURGER, 1946). Unfortunately, these supposed hybrids were lost at an early date. A natural hybrid P. peuce X P. strobus has been reported growing in Denmark by C. SYRACH LARSEN (DUFFIELD and STOCKWELL, 1949). Scions of this tree were obtained and grafted at Maple. The glabrous twigs of this clone indicate that this character of P. peuce was dominant over the sparingly pubescent twigs of P. strobus (HEIMBURGER, 1953). Numberous seedlings have been obtained during recent years resulting from artificial hybridization of P. peuce with P. strobus. In the rate of growth and growth form they resemble P. peuce more than P. strobus. The hybrids have also been reported elsewhere (WRIGHT, 1953) but with no detailed description. Our own results and other available information seem to indicate that the cross of P. peuce 'with P. strobus is easy to make in both directions. The pollen of the Danish hybrid has been used in Placerville, Calif. (DUFFIELD and STOCKWELL, 1949) and at Maple, and was found to be fertile.

In the fall of 1938 cones were collected from a single P. peuce (4158; 95-134-9) growing at the Dominion Arboretum in Ottawa, Ontario. At that time this was the only P. peuce of flowering age in the Arboretum. Several native white pine had been planted nearby when the Arboretum was established, at about the end of the last century. An abundant crop of cones was produced by both species in 1938 and the possibility of natural hybridization was at hand. The seeds from the P. peuce cones yielded seedlings that first could not be distinguished from seedlings of P. peuce of Macedonian origin while the seeds from the P. strobus cones yielded seedlings and indistinguishable from ordinary P. strobus. In 1940 some of the P. peuce-like seedlings of Ottawa origin were sent to the Montreal Botanical Garden in exchange for other plant materials.

In the fall of 1955 the recently established Morgan Arboretum of Macdonald College near Montreal was visited and a group of 10 young P. peuce-like trees, some bearing P. strobus-like cones attracted attention. It was established that the trees in question had been received in 1951 from the Montreal Botanical Garden which in turn could trace their origin to the P. peuce-like plants sent there from the Petawawa Station in 1940. The possible hybridity of one tree could then be postulated by its cones. In the spring of 1956, seven of these trees flowered and Dr. W. H. BRITTAIN, curator of the Morgan Arboretum, kindly collected pollens. The pollens showed over 90% germination in distilled water and were used in current white pine breeding work at Maple. In the fall of 1956, branch materials from all the ten trees in question as well as all available newly ripened cones were collected. The possible hybridity of seven additional trees could then be postulated by their cone characters.

In the meantime, scion materials of 13 sister seedlings of the P. peuce in Ottawa have been collected at the Petawawa Forest Experiment Station and elsewhere, and the grafts successfully established at Maple.

Materials and methods

Branch and cone materials of the putative hybrids from the Morgan Arboretum as well as from grafts and seedlings of P. peuce and P. strobus of a wide range of origins

in the Maple collection were used in the present study. In addition, *P. strobus* × *peuce* obtained from artificial hybridization and grafts of *P. peuce*-like seedlings of Ottawa origin, contributed branch and needle samples. The Forest Botanical Garden at Charlottenlund, Denmark, kindly supplied branch and cone materials of their supposed *P. peuce* × *strobus* hybrid and other trees of their collection, for comparison. Branches and cones from the *P. peuce* windbreak plantings near Havelock, Ontario were also utilized.

The method of analysis used in the study of the putative hybrids and their parent species was similar to the method developed by ANDERSON (1936) for describing introgression and hybridization in natural populations (See also RILEY, 1938). A hybrid index was established by which materials intermediate between the putative parent species could be evaluated. It is possible, by utilizing such a hybrid index to distinguish the F_1 hybrids and various hybrid derivatives from their parent species. This method has previously been used successfully with forest trees, (DANSEREAU and LAFOND, 1941; DANSEREAU and DESMARAIS, 1947; ZOBEL, 1951). The materials available permitted a detailed study of foliage and branches. Cones and seeds were available from only a limited number of sources and had not been subjected to uniform drying conditions prior to the time of the study. Because of this inadequate sample the analysis of cone data is incomplete, though mention is made of some of the more important characters. A hybrid index scoring system was used whereby *P. peuce*-like characters were given a value of 0 and most *P. strobus*-like characters a value of 4. As certain characters proved to be more valuable in distinguishing the supposed hybrids from the parents, it was found desirable to weight these characters. Quantitative characters were scored so that they had values of 0, 1, 2, 3, or 4 while qualitative characters received values of 0, 2 or 4. The number of serrulations on the innner edge of the needle tip was found to have more taxonomic value than the other characters in making the desired distinction, when using adult materials, and was therefore weighted by two, giving index values of 0, 2, 4, 6 or 8 rather than the values of 0, 1, 2, 3 or 4 used for the other characters. The results of the study are reproduced graphically in Figure 1 in respect to the selected characters.

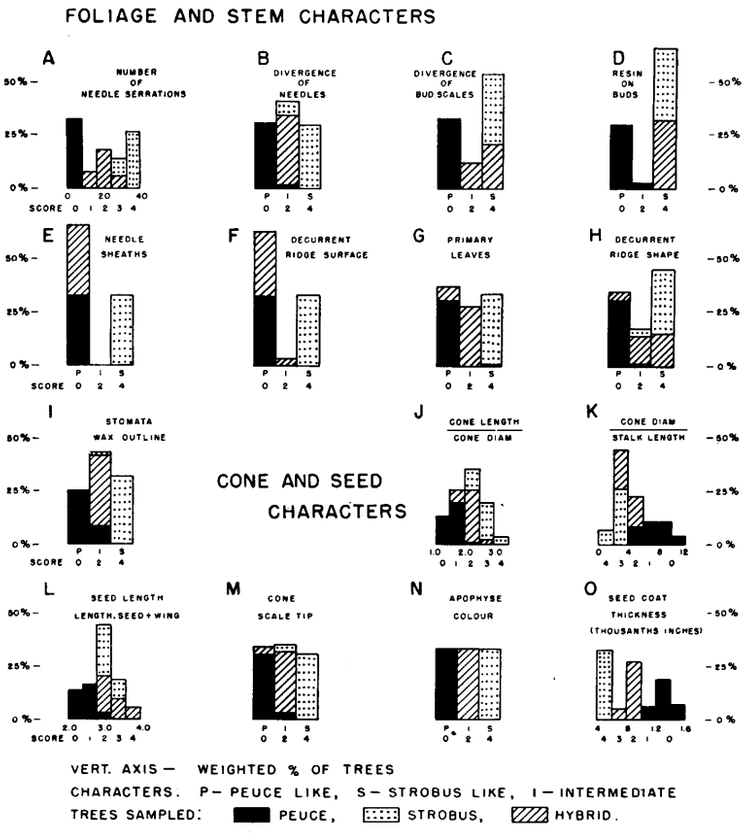

Fig. 1. — Distribution of trees scored for single characters. The numbers of trees of the three different classes are unequal (33 *P. peuce*, 22 *P. strobus*, 17 intermediate). They were therefore given unequal weights in the graphs so that all the trees of each class add up to 33.3% and all trees sampled make up the 100%.

Foliage and stem characters

A. Number of serrulations on the inner edge of fully developed needle tips. The cross section of a white pine needle is approximately a triangle. The two outer edges of the needle are sharply serrulate from the tip to near the base. In *P. strobus* the inner needle edge is strongly serrulate, while the inner edge of the *P. peuce* needle is entire or has only a few serrulations. The serrulations were counted along the inner needle edge for the first two centimeters of the needle tip. The needles of *P. peuce* were found to have an average number of serrulations (average of ten needles per sample) varying from 0 to 6.9; the number ranged from 31.0 to over 50 for *P. strobus* and from 8.4 to 29.0 in the supposed hybrids. This character is not very dependable when used with juvenile material. The number of serrulations for two centimeters of fully developed needle tip was found to be higher in seedlings (2-0, 3-0) than in older plants (8 yrs. or greater). In this young material the range for *P. peuce* was found to correspond to the putative hybrid, and the range for the putative hybrid corresponded to older *P. strobus*. Young *P. strobus* materials had over 50 serrulations for the two centimeters of needle tip.

In respect to this quantitative character the materials were given index values as follows:

Index score	*Serrulations*
0	0 — 7.9
2	8 — 15.9
4	16 — 28.9
6	24 — 31.9
8	32 — 40 or more

The two species show no "overlap" in this character and there is but slight "overlap" between *P. strobus* and the intermediate form. It is thus a very good character to separate *P. strobus* from *P. peuce* and the supposed hybrid (See Figures 1 and 3).

B. Divergence of fully developed needles from the stem. The needles of *P. peuce* are appressed to the stem giving the new growth a broom — or brush-like — appearance so that the terminal branch buds are not visible from the side and only slightly visible from the end. The needles of *P. strobus* diverge rather widely from the stem so that the terminal bud is readily visible from the end and from the side. The needles of *P. peuce* are usually more stiff and straight than

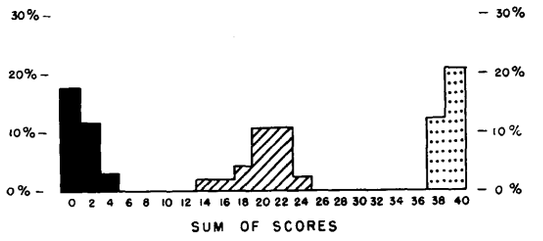

Fig. 2. — The distribution of trees scored on foliage and stem characters.

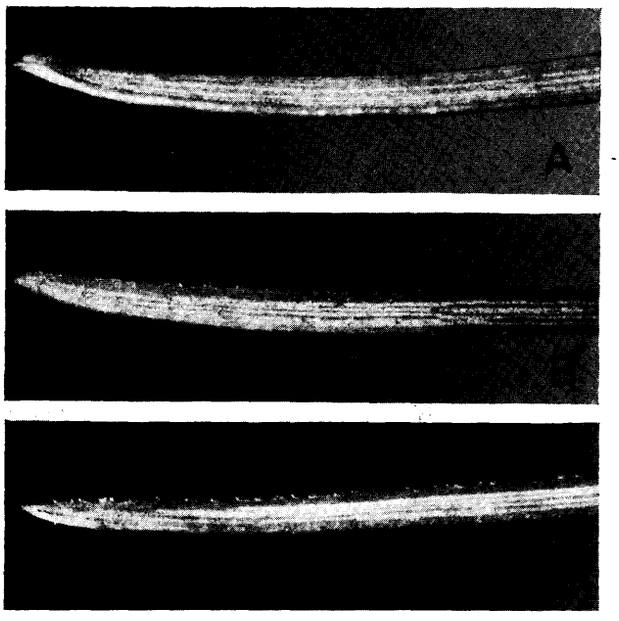

Fig. 3. — Fully developed needle tips, showing the degree of serrulation on the inner edge. — (A) *P. peuce*, — (B) intermediate, — (C) *P. strobus*.

those of *P. strobus*. This also tends to give the branches of *P. peuce* and the intermediate form a more brush-like appearance than *P. strobus*. In the supposed hybrid the needles show an intermediate degree of divergence from the stem. Both *P. strobus* and *P. peuce* show some overlap for this character with the intermediate form (See Figures 1 and 4). Young seedlings and grafts can be readily classified in respect to this character.

C. Divergence of bud scales. The buds of *P. strobus* have appressed scales while in *P. peuce* the bud scales are divergent. In the intermediate form the expression of this character may be between the species but is often similar to *P. strobus* (See Figures 1 and 5).

D. Amount of resin covering the buds. The lower bud scales of *P. peuce* have a thin coat of resin along their edges. In *P. strobus* and the intermediate form the lower bud scales are almost completely covered with resin (See Figures 1 and 5).

E. Persistence of needle sheaths. The secondary leaves of pines develop from the axes of reduced (small scarious bracts) primary leaves (Rehder, 1940). In white pines they are in fascicles of five surrounded at the base with a sheath of thin, chaff-like bud scales. This sheath remains attached to the stem into the first winter in *P. peuce* and

Fig. 4. — Stems, showing the divergence of fully developed needles. — (A) *P. peuce*, — (B) intermediate, — (C) *P. strobus*.

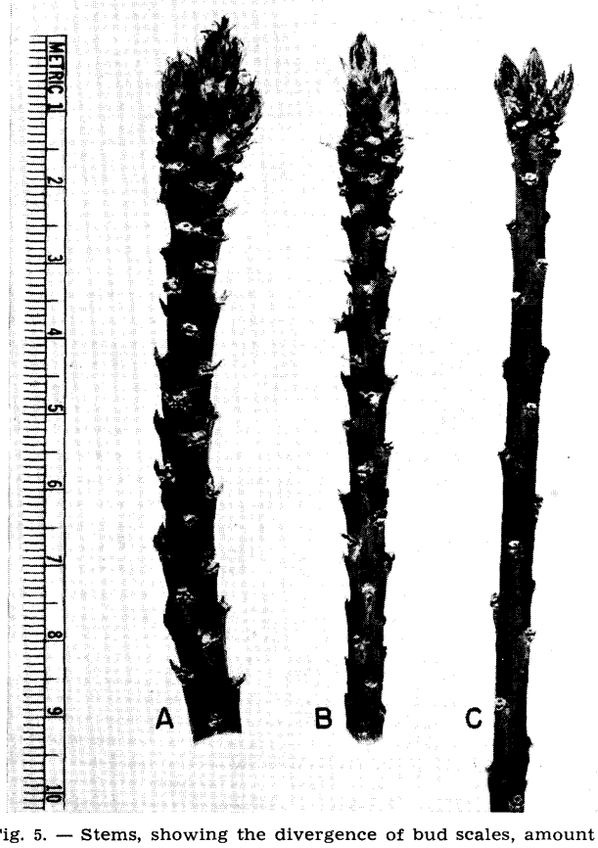

Fig. 5. — Stems, showing the divergence of bud scales, amount of resin covering the buds and the surface of the decurrent ridge. — (A) *P. peuce*, — (B) intermediate, — (C) *P. strobus*.

the intermediate form. In *P. strobus* the sheath is shed during the first summer (See Figure 1).

F. Surface of the decurrent ridge. In white pines the needle fascicles are attached to low decurrent ridges on the stem. In *P. peuce* and most of the intermediate forms these ridges are glabrous while in *P. strobus* they are pubescent. Some of the intermediate forms have a slight pubescence along the decurrent ridge during the early part of the first summer, but later in the season they lose this pubescence. In the later part of the season the stems of *P. strobus* are quite glabrous, but evidence of pubescence remains visible along the decurrent ridges. This character is valuable in distinguishing *P. strobus* from *P. peuce* and the intermediate forms (See Figures 1 and 5).

G. The primary leaves. As stated under E, the primary leaves in pines are reduced to small, scarious bracts on non-juvenile shoots. In *P. peuce* these primary leaves are difficult to remove during their first year, and when removed leave an uneven scar covering much of the decurrent ridge supporting the fascicle. In *P. strobus* these leaves are easily removed during the first summer and leave a smooth, even scar covering only the top of the decurrent ridge. The putative hybrids are usually intermediate in respect to this character having primary leaves that are more or less difficult to remove during the first summer. There is an overlap between the intermediate form and *P. peuce* in respect to this character and a slight overlap between *P. peuce* and *P. strobus* (See Figure 1). This character is of little value in itself, but when used in combination with the other characters it facilitates identification.

H. Shape of decurrent ridge supporting the needle fascicle. The ridge supporting the needle fascicle in most *P. peuce* is bulbous and broadly u-shaped in cross-section; in *P. strobus* it is usually straight and narrowly v-shaped. The expression of this character is variable in that the putative hybrid may be intermediate or similar to the species in this respect. Some *P. peuce* and *P. strobus* are intermediate for this character (See Figure 1).

I. Outline of stomata wax cover. In most *P. peuce* and *P. strobus* the needles have rows of stomata on their inner two flat surfaces, facing the other needles. One *P. peuce* clone received from Philadelphia has rows of stomata on all three surfaces, as have *P. albicaulis* ENGELM. and *P. flexilis* JAMES. DALLIMORE and JACKSON (1948) suggest this as a characteristic feature of *P. peuce* but the authors found the Philadelphia clone to be the only one exhibiting this character. In most *P. peuce* the majority of stomata have square or rectangular wax covers while in most *P. strobus* these are rounded or oval. The putative hybrid is intermediate in this respect having both rounded and rectangular stomata wax covers, in almost equal numbers. There is overlap of both *P. strobus* and *P. peuce* with the intermediate forms in this character (See Figure 1).

Cone and seed characters

J. Ratio of cone length to cone diameter. The cones of *P. peuce* are short and sub-cylindric in comparison to the long, narrow cylindric cones of *P. strobus*. The cones of the intermediate form are often as long as those of *P. strobus* but have a relatively larger diameter when dry. The ratio of cone length to cone diameter was found to vary from 1.3 to 2.1 in *P. peuce*, from 2.3 to 3.3 in *P. strobus* and from 1.6 to 2.6 in the putative hybrids (See Figures 1 and 6). This character is scored as follows:

Index score	*Ratio*
0	1.0 — 1.49
1	1.5 — 1.99
2	2.0 — 2.49
3	2.5 — 2.99
4	3.0 — 3.49

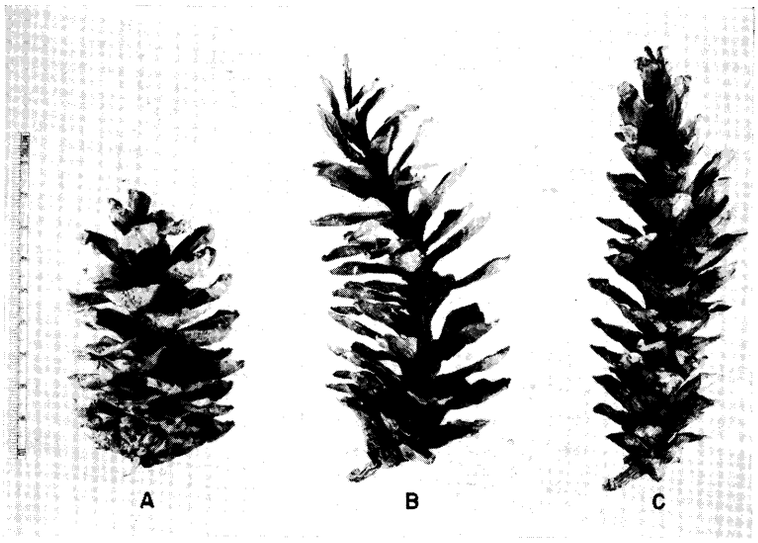

Fig. 6. — Cones, showing several of the characters enumerated in the text. — (A) *P. peuce*, — (B) intermediate, — (C) *P. strobus*.

K. Ratio of cone diameter to length of cone stalk. The thick cones of *P. peuce* are supported by short stalks while the more slender cones of *P. strobus* have relatively long stalks. The ratio of cone diameter to stalk varies from 4.4 to 10.0 in *P. peuce* and from 1.6 to 3.2 in *P. strobus*. The corresponding variation in the intermediate form is from 2.6 to 5.0, indicating overlap for this character (See Figures 1 and 6). The scoring is as follows:

Index score	*Ratio*
4	1.0 — 1.99
3	2.0 — 3.99
2	4.0 — 5.99
1	6.0 — 7.99
0	8.0

L. Ratio of seed length to length of seed plus wing. P. peuce usually has larger seeds with shorter wings than *P. strobus*. The ratio of seed length to length of seed plus wing ranges from 2.1 to 3.0 in *P. peuce* and from 2.9 to 3.5 in *P. strobus*. The seeds of the intermediate form are generally intermediate in length, but have a combined length of seed and wing as great or greater than that of *P. strobus*, yielding a ratio ranging from 2.9 to 3.8, i. e., in part extending beyond the range of *P. strobus* (See Figure 1). This character has been scored as follows:

Index score	*Ratio*
0	2.0 — 2.39
1	2.4 — 2.79
2	2.8 — 3.19
3	3.2 — 3.59
4	3.6 — 3.99

M. Cross section of cone scale tip. The scale tips of most *P. peuce* cones are sharply concave upwards while those of *P. strobus* are flat or slightly convex. The cones of most of the putative hybrids have scale tips that are intermediate between these extremes. There is some overlap between the intermediate form and *P. peuce*. There is also a slight overlap between the species and the intermediate form (See Figures 1 and 6).

N. Colour of cone scale apophyses. Because the drying conditions for the cones were not uniform, the colour of cone scale apophyses could not be determined as accurately as the other characters. In general, the apophyses of cone scales of *P. peuce* are tawny yellow, those of *P. strobus* are brown and the intermediate types range in between.

O. Seed coat thickness. The thickness of the seed coat was found to be a "good" distinguishing character for both species and the intermediate forms. It ranged from 0.0011 inches to 0.0016 inches in *P. peuce* and from 0.0004 inches to 0.0005 inches in *P. strobus*. The intermediate forms had seed coats ranging from 0.0007 inches to 0.0009 inches in thickness, i. e., they were clearly intermediate between the pure species and showed no overlap (See Figure 1).

This quantitative character was scored as follows:

Index score	*Thickness (thousandths inches)*
4	0.4 — 0.59
3	0.6 — 0.79
2	0.8 — 0.99
1	1.0 — 1.19
0	1.2

Results and discussion

In order to determine the validity of the hybrid index approach to distinguish the putative parent species from intermediate forms, 33 *P. peuce*, 22 *P. strobus* and 17 of the available intermediate forms were examined. Total index values were arrived at for each single plant examined by utilizing the foliage and stem characters described above and adding up the scores. These are summarized in a frequency distribution shown in Figure 2. It is seen that all the *P. peuce* examined had index values ranging from 1 to 5; *P. strobus* ranged from 37 to 40 in this respect and the intermediate forms from 13 to 25. The mean index value for *P. peuce* is 1.3 with a standard deviation of plus or minus 1.4; the mean for *P. strobus* is 39.4 with a standard deviation of plus or minus 1.1. The intermediate forms have a mean index value of 19.7 with a standard deviation of plus or minus 2.6. The possibility of a *P. peuce* having an index value as high as 8 or an intermediate form having an index value as low as 8 was determined to be approximately 2 and 3 chances per million respectively. The possibility of a *P. strobus* having an index value as low as 32 or an intermediate form having one as high as 32 was determined to be approximately 1 and 2 in a million respectively. It is thus very highly probable that the intermediate forms are indeed hybrids of *P. peuce* and *P. strobus* with index values definitely in between those of their putative parent species and significantly separate from these. No individuals combining the characters of both *P. peuce* and *P. strobus* were found among the numerous samples in our collection, with the exception of the intermediate forms examined in this study. Cone and seed characters have not been analysed in the same manner because of lack of materials available for this study. It can be pointed out, however, that a total index based on these characters would be valuable where only cones and seeds are available. In this respect the thickness of the seed coat appears to be of high diagnostic value.

It is a remarkable fact that the *P. peuce* in the Dominion Arboretum yielded exclusively hybrid seedlings after open pollination in 1937. The pollen of this tree has been used in both present and former breeding work (Johnson and Heimburger, 1946) and has been found fertile. Further studies will be necessary to determine the cause of self-incompatibility of this tree. In 1957 the flowering of this tree was slightly protandrous with good possibility for self-pollination.

The *P. strobus* in the vicinity also had protandrous but somewhat later flowering. There were thus good possibilities for the *P. peuce* to be pollinated by *P. strobus*. Seeds from several open-pollination *P. griffithii* McClelland in Rochester, N. Y. and Toronto, Ont., growing singly among or near native white pine, have yielded only about 10% hybrids among their offspring. The F_1 hybrid *P. peuce* × *P. strobus* is of doubtful value to forestry even if found sufficiently resistant to blister rust and weevil attack in further tests. In rate of growth it is intermediate between the parent species and does not show hybrid vigor, at least not under our growing conditions. The high pollen fertility and early flowering make it of value for further breeding work. Backcrossing to *P. strobus* then suggests itself as the most promising breeding procedure, having the aim of introducing resistance to blister rust and damage from weevil attack into various strains of *P. strobus* showing promise in other respects. It is believed that at least some of the characters studied will be found useful in determining the hybrid index of individual plants derived from these hybrids in succeeding generations. Such a hybrid index may also be helpful in separating the derived hybrids from the other two known hybrids of *P. strobus* with old-world related species. The hybrid *P. griffithii* × *P. strobus* has been described by Fitschen (Beissner-Fitschen, 1930) who named it *P. Schwerinii*. The hybrid *P. parviflora* Sieb. & Zucc. × *P. strobus* has been found and described by Johnson (1952) who named it *P. Hunnewellii*. A formal description or name to the hybrid *P. peuce* × *P. strobus* has been omitted in order not to clutter the botanical literature with unnecessary hybrid names. If in succeeding generations a more or less true breeding form having a reasonable wide distribution is derived from this hybrid, it may warrant a separate designation, just as is the case with *Populus canescens* Sm. It is worthy of note that both *P. Schwerinii* and *P. Hunnewellii* resemble their old-world parent species in habit of growth while the cones are more like those of *P. strobus*. The same is the case with the hybrid *P. peuce* × *P. strobus*.

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Summary

In 1955 some pines intermediate between *P. peuce* Griseb. and *P. strobus* L. were found growing in the Morgan Arboretum, Macdonald College, P. Q., Canada. An investigation of their origin showed that they were progeny of a single *P. peuce* growing with some *P. strobus* in the Dominion Arboretum, Ottawa. A detailed analysis of the foliage and stem characters separating *P. peuce, P. strobus* and the intermediate form, using the hybrid index method of Edgar Anderson was then carried out. Needle serrulation, divergence of needles from the stem, divergence of bud scales, resin on buds, persistence of needle sheaths, decurrent ridge shape and surface, primary leaves, and stomata wax cover were the stem and foliage characters studied. Cone and seed characters found useful in separating *P. peuce, P. strobus* and the intermediate form were cone shape, seed and wing length, shape of cone scales and seed coat thickness. Seed coat thickness was found to have great diagnostic value. The study made the hybrid origin of the intermediate form very highly probable. The value of this hybrid in forestry and in breeding work with white pines is discussed.

Résumé

Titre de l'article: *l'hybride Pinus peuce Griseb* × *Pinus strobus L.* —

En 1955, on a remarqué dans le Morgan Arboretum, Macdonald College, P. Q., Canada, quelques arbres intermédiaires entre *P. peuce* et *P. strobus* L. L'étude de leur origine a montré qu'il s'agissait des descendants d'un *P. peuce* unique poussant avec quelques *P. strobus* dans le Dominion Arboretum, Ottawa. Une analyse détaillée des caractères des aiguilles et du rameau distinctifs de *P. peuce, P. strobus* et de la forme intermédiaire, faite d'après la méthode de l'»index d'hybridation« d'Edgar Anderson fut alors enterprise. Les caractères suivants furent étudiés pour les aiguilles et les rameaux: la denticulation des aiguilles, la divergence des aiguilles par rapport au rameau, la divergence des écailles des bourgeons, le caractère résineux ou non des bourgeons, la persistance des gaines de la base des aiguilles, la forme et la surface de l'arête des aiguilles, les feuilles primaires et la cuticule cireuse des stomates. Pour les cônes et les graines, les meilleurs caractères distinctifs furent: forme du cône, longueur de la graine et de son aile, forme des écailles du cône et épaisseur de l'enveloppe de la graine. Ce dernier caractère a une excellente valeur de diagnostic. D'après cette étude, le caractère hybride de la forme intermédiaire et très probable. La valeur de cet hybride en foresterie et pour l'amélioration des pins à cinq feuilles est étudiée.

Zusammenfassung

Titel der Arbeit: *Der Bastard Pinus peuce Griseb.* × *Pinus strobus L.* —

Im Morgan Arboretum, Macdonald College, P. Q., Canada, fand man 1955 intermediäre Typen zwischen *P. peuce* und *P. strobus*. Nachforschungen ergaben, daß sie Nachkommen eines *P. peuce*-Einzelbaumes sind, der neben einigen Stroben im Dominion Arboretum, Ottawa, steht. Verff. führten an der Strobus, der Peuce und der Intermediärform eingehende Analysen der Nadel- und Stammmerkmale nach der Hybrid-Index-Methode von Anderson durch. Im einzelnen wurden untersucht: Nadelzähnung, Stellung der Nadel zum Zweig, Divergenz der Knospenschuppen, Verharzung der Knospen, Lebensdauer der Nadelscheide, Form und Oberfläche der Nadelansatzstelle, Primärnadeln und Wachsdecke der Stomata. Im gleichen Sinne erwiesen sich Zapfenform, Samen- und Flügellänge, Form der Zapfenschuppen und Stärke der Samenschale als brauchbare Zapfen- und Samenmerkmale. Vor allem die Dicke der Samenschale war von großem diagnostischem Wert. Die Untersuchungen machten die Bastardnatur der Intermediärform sehr wahrscheinlich. Der forstliche Wert und die züchterischen Möglichkeiten werden diskutiert.

Literature

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