A Morphological Comparison of Blue and Engelmann Spruce in the Scotch Creek Drainage, Colorado[1])

By P. R. Schaefer and J. W. Hanover[2])

(Received 10th October 1984)

Summary

This paper concerns the morphological analysis of 38 blue and 24 Engelmann spruce from opposite ends (low and high elevations, respectively) of the Scotch Creek drainage in southwestern Colorado. The objective was to determine the suitability of these two groups for use as reference populations in future studies of natural hybridization between blue and Engelmann spruce within the drainage. Forty-three morphological traits were analyzed. A morphological index including seven qualitative traits (twig pubescence, bark texture, branching habit, epicormic branching, scale apex margin, twig color, scale apex shape) and a discriminant function based on three quantitative traits (# stomatal lines, free scale length, needle sharpness) were able to differentiate the blue and Engelmann spruce in the study. The blue and Engelmann spruce groups explained 95% of the variance present in the discriminant function. The probability of misclassification was zero. From a morphological standpoint the reference populations appear appropriate for future investigations of natural hybridization between blue and Engelmann spruce in the study area.

Key words: natural hybridization, discriminant analysis, speciation.

Zusammenfassung

Die Arbeit enthält die Analyse morphologischer Merkmale von 38 *Picea pungens* und 24 *Picea engelmannii* Herkünften aus den höchsten und niedrigsten Lagen des Scotch Creek Drainage im südwestlichen Colorado. Ziel der Untersuchung war, zu prüfen, of diese zwei Gruppen als Bezugspopulationen für zukünftige Studien zur natürlichen Hybridisierung zwischen *Picea pungens* und *Picea engelmannii* im Scotch Creek Drainage geeignet sind. Es wurden 43 morphologische Merkmale analysiert. Ein morphologischer Index, der 7 Qualitätsmerkmale enthält, (Zweigbehaarung, Rindentextur, Zweighabitus, äußere Beastung, Knospenschuppenhülle, Zweigfarbe, Knospenschuppenform,) und eine Diskriminanzfunktion, die auf 3 quantitativen Merkmalen beruht, (Stomata-Reihen, freie Schuppenlänge, Nadelspitze), waren geeignet zwischen *Picea pungens* und *Picea engelmannii* in dieser Studie zu differenzieren. Die *Picea pungens* und *Picea engelmannii*-Gruppen erklärten 95% der in der Diskriminanz-Funktion vorhandenen Varianz. Die Wahrscheinlichkeit einer Fehlklassifizierung war gleich Null. Aus morphologischer Sicht erschien die Bezugspopulation für zukünftige Untersuchungen zur natürlichen Hybridisierung zwischen *Picea pungens* und *Picea engelmannii* in dem untersuchten Gebiet geeignet.

Introduction

Blue *(Picea pungens* Engelm.) and Engelmann *(Picea engelmannii* Parry) spruce are thought to be closely related species. Within the geographic area covered by blue spruce the ranges of both species are nearly identical, although the species are generally separated altitudinally. Very few spruce species in Wright's (1955) study exhibited closer affinities for one another than blue and Engelmann spruce. Daubenmire (1972) found no absolute differences between these species in any morphological traits, using samples collected from throughout the range of both species. Jones and Bernard (1977) suggested that the overlap of certain morphological traits of blue and Engelmann spruce was probably responsible for several reports of natural hybridization between these species. The authors concluded, however, that consideration of several traits will lead the experienced observer to the correct identification of blue and Engelmann spruces.

The most useful morphological traits for taxonomic studies in *Picea* appear to be those associated with female cones (Horton, 1959; Taylor, 1959; Weaver, 1965; Daubenmire, 1968, 1972, 1974; Taylor *et al.*, 1975; Strong, 1978). A wide array of other traits have also been used successfully in taxonomic studies of spruce, however their diagnostic ability varies with the species under consideration.

The observation of an area of extensive range overlap in the Scotch Creek Drainage of southwestern Colorado encouraged the present authors to investigate the possibility of natural hybridization between blue and Engelmann spruce. Previous investigations of this nature were hampered by an inability to completely distinguish between reference individuals of each species (Daubenmire, 1972; Taylor *et al.*, 1975; Mitton and Andalora, 1981). It is clear that traits must be found which can be used to unequivocally distinguish between blue and Engelmann spruce before investigations concerning natural hybridization between the species can be undertaken. The purpose of the present study was to analyze and evaluate a wide array of morphological traits for their use in differentiating between blue and Engelmann spruce found at extreme ends (low and high elevation, respectively) of the Scotch Creek Drainage. This information will provide the basis for future studies of natural hybridization between these two species in the study area.

The Study Area

The Scotch Creek Drainage is part of the Dolores River watershed in southwestern Colorado, located in Dolores County about five kilometers south of Rico *(Figure 1a)*. Elevation of the drainage is 2590 m at the lower end and rises to over 3050 m at the upper end. The valley floor is narrow with steep (up to 110%) adjacent slopes. The drainage has an east-west orientation, with many smaller tributaries joining it from the north and south *(Figure 1b)*.

Scotch Creek joins the Dolores River in a wide, low, flat area separated from the rest of the drainage by state highway 145. The spruce in this area are not large (max. ht. 16 m, diam. 36 cm), and probably became established naturally after construction of the original highway through the area. The spruce within the lower end of the drainage itself tend to be much larger (often > 51 cm DBH, > 25 m tall), although smaller trees are also present. The slopes to

[1]) Michigan Agricultural Experiment Station Paper No. 11033

[2]) Assistant Professor, Department of Horticulture-Forestry, South Dakota State University, Brookings, S. D., USA and Professor, Department of Forestry, Michigan State University, East Lansing, Michigan, USA, respectively.

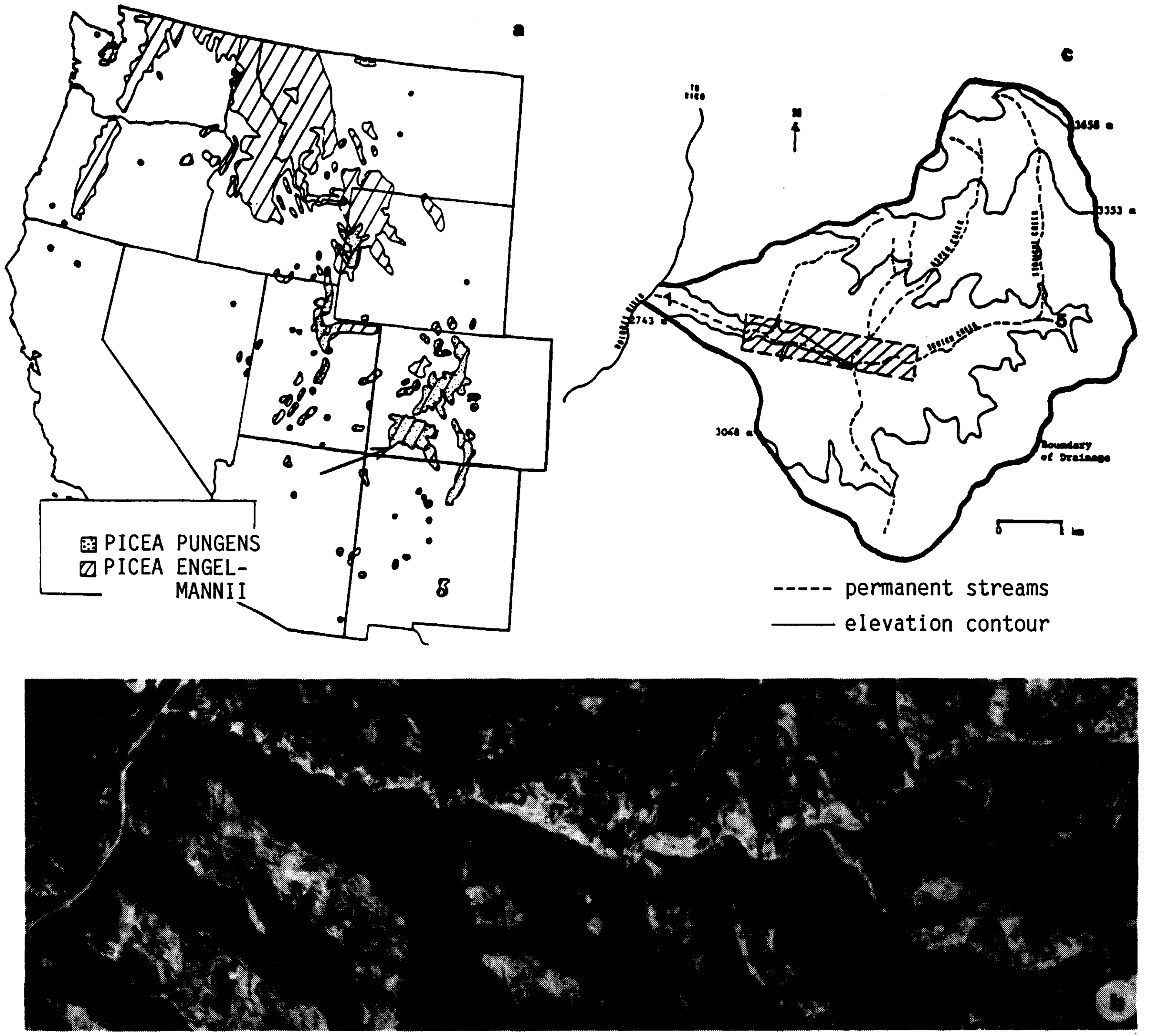


Figure 1. — a) Location of the Scotch Creek drainage, b) topography of the drainage, c) diagram of the study area indicating collection zones 1 and 5 and the area of range overlap (shaded rectangle).

either side of the creek are rugged, with large rock outcrops and steep talus slopes. The occurrence of spruce is limited to single trees or very small groups on the rocky side-slopes, with greater numbers found in small stands along the valley floor.

The upper end of the study area terminates at an elevation of 2970 m, as the areas to the east of this have been clearcut. At this point the road is well above he valley floor along the southern (north-facing) slope. The slope is very steep (90 + %) and littered with many fallen trees (by natural causes). The area is cool and moist and supports a fairly dense, mixed stand of Engelmann spruce and subalpine fir *(Abies lasiocarpa* (Hook.) Nutt.). Aspen is also present, especially on more open, west-facing, gentler slopes.

Materials and Methods

The trees for this study were sampled in the fall of 1981. The only requirement was that they bear a crop of at least 30 current year's cones to provide adequate seed for a progeny test. Trees were located at the extreme lower (blue spruce) and extreme upper (Engelmann spruce) ends of the study area *(Figure 1c* zones 1 and 5, respectively). Trees were identified as either blue or Engelmann spruce using a standard dendrology text (Harlow and Harrar, 1969), descriptions published by Jones and Bernard (1977) for the Southwest and the authors' experience gained from working with these species for several years.

The reference populations were selected based on initial observations that indicated that each reference population did not contain any member of the alternative species. It was anticipated that cones from the first 50 trees meeting the fecundity requirement would be collected in each area. Due to a relatively poor seed year this goal was not achieved. Cones were collected from 38 blue spruce at the lower end and from 24 Engelmann spruce at the upper end of the drainage. Since some of the cones would be used for measurement purposes it was important that the collections be unbiased. Sampling bias was reduced by collecting all of the cones from each branch removed from a tree. Sampling bias was further reduced by selecting four cones at random, which were then set aside for measurement purposes prior to seed extraction. These cones were soaked in water until they closed before measurements were made. One scale was removed from the center of each cone. A total of 17 cone and cone scale traits were measured (*Table 1*). The average value of the four cones or cone scales for each tree was used in all analyses.

Seed data included the number of seeds per cone, 100 seed weight, percent germination and germination rapidity. For the germination study 15 seeds from each tree were placed on water-saturated filter paper in a separate petri dish for each tree. Each dish was randomly placed on a growth frame under flourescent lights at a temperature of 25° C. The experiment was replicated twice. The study was terminated after 20 days. At that time no seeds had germinated for three days. Percent germination was determined for each tree in each replication and the average value was then calculated. A seed was considered to have germinated when its radicle was as long as the seed itself. Germination rapidity for each tree was calculated as:

$$\text{Rapidity (days)} = \frac{\Sigma \text{ seedlots (days to germ. x \# of germ. seed)}}{\text{Total \# of germinated seed}}$$

(HANOVER and WILKINSON, 1969).

Seeds were sown in the greenhouse in a randomized complete block design, with six seedlings per sample tree plot and four replications. The seedlings were grown under accelerated-optimal-growth conditions (HANOVER *et al.*, 1976). These conditions were maintained for six months, at which time the seedlings were allowed to enter their dormant stage. After one month in the greenhouse the seedlings were scored for hypocotyl color (1 = green, 2 = intermediate, 3 = red), and the number of cotyledons for each seedling was determined. When seedling growth had ceased, height measurements were made to the nearest centimeter.

Five morphological traits were recorded in the field, with each scored on a subjective scale (*Table 2*). Foliage was collected in the field from each parental selection, and fourteen foliar traits were analyzed (*Table 3*). Four foliage samples were lost between collection and measurement. Except for bud scale orientation all measurements were made on two-year-old twigs and needles. All needle measurements were based on four needles per tree from which an average value was determined.

A device was developed to quantify needle sharpness and stiffness (*Figure 2*). Needle sharpness was determined by continuously adding weight (sand) to the balance arm until

Table 1. — Description of cone and cone scale characters. All were based on 4 randomly selected cones/tree.

Character	Description
Cone length	(cm)
Cone width	Measured at the middle of the cone (cm)
Cone size	(length x width)/10 (Taylor et al, 1975)
Cone ratio	length/width (Taylor et al, 1975)
Cone scale length	(mm)
Cone scale width	(mm)
Cone scale size	(length x width)/10 (Daubenmire, 1972; Taylor et al, 1975)
Cone scale ratio	length/width (Daubenmire, 1972; Taylor et al, 1975)
Seed length	Measured from the imprint left in the cone scale (mm)
Seed width	"
Seed wing length	"
Seed wing width	"
Seed + wing length	"
Free scale length	Distance from the tip of the seed wing imprint to the tip of the cone scale (mm) (Daubenmire, 1972; Taylor et al, 1975)
Percentage of free scale	(Free scale length/cone scale length) x 100 (Daubenmire, 1972; Taylor et al, 1975)
Scale apex shape	1 (rounded), 2 (intermediate), 3 (truncate)
Scale apex margin	1 (entire), 2 (intermediate), 3 (erose)

Table 2. — Description of the morphological characters scored in the field.

Character	Description
Bark texture	Scored from 1 (smooth (young tree) or scaley (mature tree)) to 5 (scaley (young tree) or rough-ridged (mature tree))
Bark color	Scored from 1 (red or red-brown) to 5 (gray or gray-brown)
Foliage color	Scored from 1 (yellow-green) to 5 (steel blue)
Epicormic branching	Scored from 1 (none) to 5 (extensive)
Branching habit	Scored from 1 (non-planar) to 3 (distinctly planar)

Table 3. — Description of foliage characters. All needle characters were based on 4 randomly selected needles from 2 year old twigs.

Character	Description
# of stomatal lines	Maximum # of stomatal lines summed over all 4 sides of the needle
Needle length	(mm)
Needle width	Measured at the middle of the needle, perpendicular to the axis between the dorsal and ventral needle surfaces (mm)
Needle thickness	Measured at the middle of the needle along the axis between the dorsal and ventral needle surfaces (mm)
Needle length/width	----
Needle width/thickness	----
Needle angle	Angle of departure of the needle from the twig (degrees)
Needle curvature	Needles were shortened to 15 mm by trimming each end equally. The distance from the bottom edge (at the center of the needle) to the line connecting the ends of the needle was recorded (mm)
Needle sharpness	Amount (gm) of sand required to force needle through plastic wrap membrane. (see text)
Needle stiffness	Amount (gm) of sand required to deflect needle 1 mm from the starting position (see text)
Needle sharpness index	Needle stiffness/sharpness
Twig color	Scored from 1 (tan or pale yellow) to 5 (orange)
Twig pubescence	Scored from 1 (densely pubescent) to 3 (glabrous)
Bud scale orientation	Scored from 1 (appressed) to 3 (reflexed) on terminal buds.

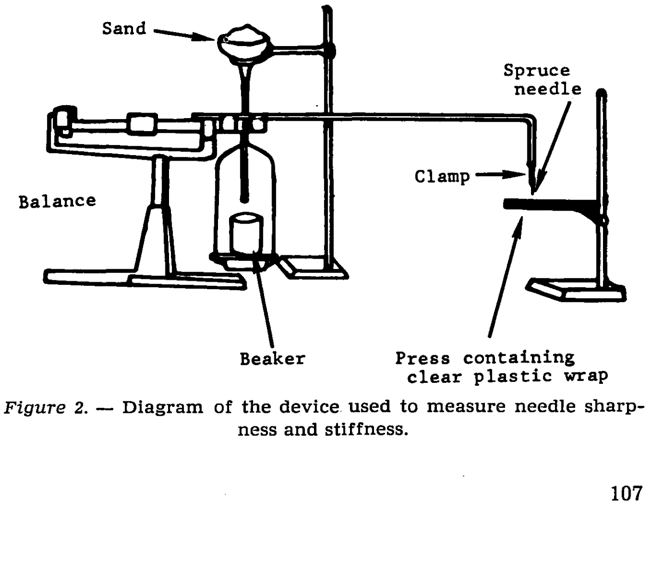


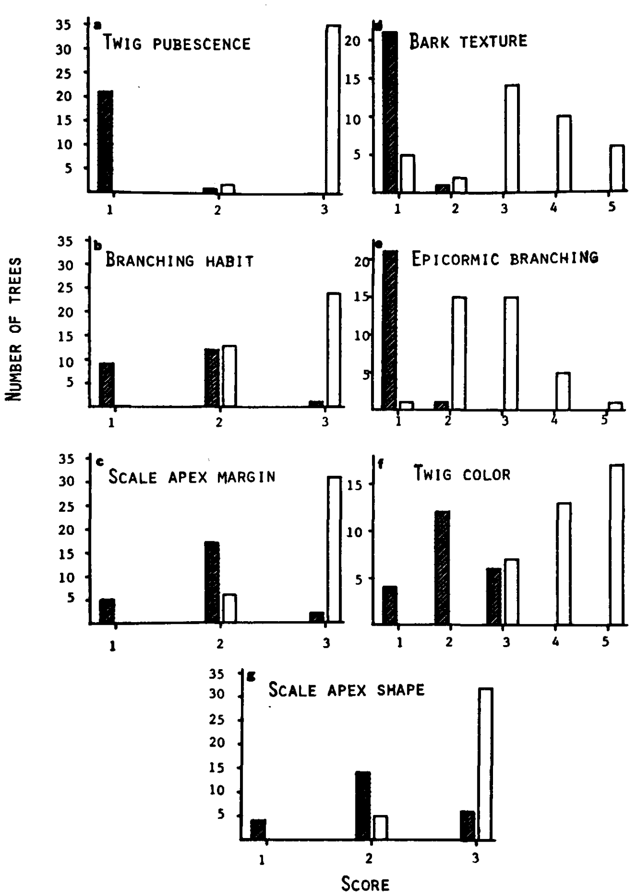
Figure 2. — Diagram of the device used to measure needle sharpness and stiffness.

the needle punctured the clear plastic wrap membrane (.052 mil.). Relative needle sharpness was estimated by the weight of sand (grams) required to puncture the membrane. Needle stiffness was measured using the same device except that the needle was placed horizontally between two supports (spaced 1 cm apart), and the back (rounded) edge of a single edged razor blade was attached to the balance arm to apply pressure across the center of the needle. Needle stiffness was recorded as the weight of sand required to deflect the center of the needle 1 mm from the starting position.

Statistical Approach

An approach similar to that of PARK and McLACHLAN (1978) was used to screen morphological traits for potential diagnostic value in the present study. The qualitative characters were plotted in frequency histograms to determine how well species might be distinguished by each character. The means, standard deviations, and ranges of the quantitative characters were also plotted for each species. Differences between species for those quantitative traits that appeared to be diagnostic were tested for statistical significance by Analysis of Variance procedures.

Discriminant analysis (FISHER, 1936) and ANDERSON's (1949) hybrid index technique were used to test the combined diagnostic ability of the selected variables. Only qualitative traits were used with the hybrid (or morphological) index, while only quantitative traits were included in the discriminant analysis. Although there is evidence that the



Figures 3 a—g. — Frequency histograms of qualitative morphological characters of blue and Engelmann spruce that were considered diagonistic. Open bars = blue spruce, lined bars = Engelmann spruce.

linear discriminant function is fairly robust when its underlying assumptions are violated (LACHENBRUCH and GOLDSTEIN, 1979; KNOKE, 1982), the authors felt that they would have greater confidence in their results if qualitative variables were excluded from the discriminant analysis. All quantitative variables were standardized before calculation of the discriminant function. Discriminant analysis has proved to be a useful tool in studies of species relationships among forest trees (Clifford and Binet, 1954; MERGEN *et al.*, 1965; NAMKOONG, 1966; LEDIG *et al.*, 1969; DANCIK and BARNES, 1975; FLAKE *et al.*, 1978; KUDRAY and HANOVER, 1980). A stepwise selection form of discriminant analysis was used in the present study. This method selects the subset of variables which best discriminates between the groups under consideration. The procedure is described by KLECKA (1976). The probability of misclassification was calculated using the leaving-one-out or jacknife method (LACHENBRUCH and GOLDSTEIN, 1979).

Results and Discussion

The initial step of graphing the distributions of the morphological traits revealed that seven of 12 qualitative characters appear to be of diagnostic value in distinguishing blue from Engelmann spruce *(Figure 3a—g)*. JONES and BERNARD (1977) considered bark texture and color, degree of epicormic branching, branching habit, and twig color to be diagnostic in comparisons of blue and Engelmann spruce. The results presented here agree with their conclusions, with the exception of bark color. Foliage color, bud scale orientation, seedling hypocotyl color, number of cotyledons and seedling height were also found to have little diagnostic ability in the present study. Measures of twig pubescence were used in the studies of DAUBENMIRE (1972), TAYLOR et *al.* (1975) and MITTON and ANDALORA (1981). Twig pubescence density would appear to be a useful trait in the present study as well.

PARKER and McLACHLAN (1978) proposed four categories for determining the diagnostic ability of quantitative traits. In the present study only two categories were considered, diagnostic and non-diagnostic. A character was considered to have diagnostic value if the overlap of its range between the two species was not greater than 30% of the total range of both species combined. This cutoff value was chosen because there was a clear break in the range overlap values at this point. On this basis 12 of the 31 quantitative morphological characters were determined to be of value in differentiating the species *(Figures 4a—l)*. Species differences for all of the diagnostic traits were highly significant *(Table 4)*.

DAUBENMIRE (1972) suggested that certain measurements of the ovuliferous scale were most useful in separating the species. He proposed a taxonomic guide to distinguish between blue and Engelmann spruce based on these observations and the nature and density of twig pubescence. The study of TAYLOR *et al.* (1975) generally agreed with that of DAUBENMIRE. They determined that the percentage of free scale (see *Table 1* for description) and the nature and density of twig pubescence separated the species. There was still some slight overlap in these two traits, however. It is apparent from their data that the length of the median cone, cone size, cone scale length and free scale length may also have diagnostic ability (see *Table 1* for description).

The results of the present study are generally in agreement with those of DAUBENMIRE (1972) and TAYLOR *et al.* (1975) regarding the usefulness of cone scale and twig

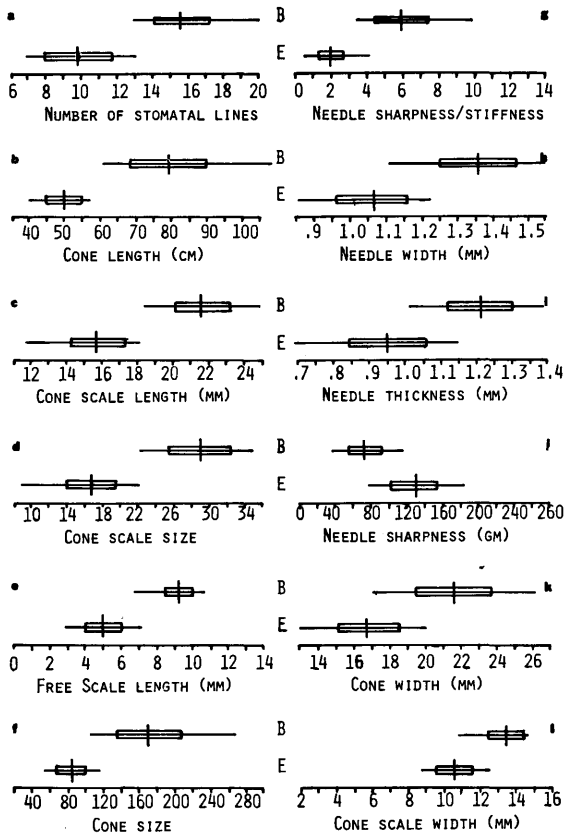


Figure 4 a—l. — Means (vertical lines), ranges (horizontal lines) and standard deviations (horizontal bars) for 12 quantitative morphological characters of potential diagnostic value. B = blue spruce, E = Engelmann spruce.

pubescence measurements in comparisons of blue and Engelmann spruce. However, several other measures also appear to distinguish the species. DAUBENMIRE (1972) noted that 60 mm is often designated as a critical cone length separating the shorter Engelmann spruce cones from the longer blue spruce cones. Individual trees in almost all of his Engelmann spruce populations had cones exceeding this length. He also found individual blue spruce with cones less than 60 mm long. In the present study the use of average tree values for cone lengths has resulted in a complete separation of the species. The average length of Engelmann spruce cones was always less than 60 mm and the average length of blue spruce cones was always greater (Figure 4b).

It is important to note that all of the spruce analyzed in the present study occur at the same latitude, within a narrow geographic area. Previous studies have generally involved trees from a rather wide range of latitudes. This fundamental difference between the present study and earlier investigations may account in part for the apparent increase in diagnostic value for many of the traits evaluated in the present study when compared to evaluations based on a broad range of latitudes.

Absolute free scale length, cone width and cone size also have diagnostic potential, as do the five needle traits, number of stomatal lines, needle width, thickness and sharpness and needle stiffness/sharpness (see *Table 2* for description). Needle sharpness was used by MITTON and ANDALORA (1981), however, this trait was measured on a qualitative scale. They found that the variation between blue and Englemann spruce was significant with blue having the sharper needles. The quantitative measure of needle sharpness in the present study indicates that blue spruce needles are indeed sharper than those of Engelmann spruce and that this difference is highly significant.

The Potential for Species Differentiation Using Discriminant Analysis and the Morphological Index Technique

The results of the morphological index exemplify the importance of determining the diagnostic ability of traits before including them in the analysis *(Figure 5).* The scores assigned to each trait in the index have been described in *Table 1, 2,* and 3. The morphological index was based on a simple summation of the assigned character values for each individual in the population. The frequency of individuals at each score on the index was then plotted in bar chart form. A tree exhibiting purely Engelmann spruce characters would receive a score of seven on the index, while a tree exhibiting purely blue traits would receive a score of 27. The characters included in the morphological index exhibit strong diagnostic ability when taken as a group and should be of use in future studies of natural hybridization between blue and Engelmann spruce in the Scotch Creek study area.

The discriminant analysis was also effective in separating the blue and Engelmann spruce populations *(Figure 6).* The stepwise procedure used in the analysis was very effective in simplifying the discriminant function, as only three of the original 12 variables remained in the function. These variables were the number of stomatal lines, free scale length and needle sharpness. The blue and Engelmann spruce groups explained 95% of the variance in the discriminant function. The probability of misclassification for the function was zero. The inclusion of any of the remaining variables provided little, if any, improvement in differentiating the species.

Various measures of the number of stomatal rows have been used in comparions of several spruce species. MORGENSTERN and FARRAR (1964) and GORDON (1976) found such measures to be of little use in their studies of red and black spruce. GARMAN (1957) and DAUBENMIRE (1968) felt that such measures were useful in comparisons of Engelmann and white spruce, and Sitka and white spruce, respectively. DAUBENMIRE'S (1975) measure of dorsiventrality was not useful in studies of Engelmann and white spruce, however. DAUBENMIRE (1972) also used a measure of dorsiventrality for

Table 4. — Degrees of freedom and mean squares showing the significance of the variation between blue and Engelmann spruce for 12 quantitative characters of potential diagnostic value.

Character	DF Between groups	DF Error	Mean Square Between groups	Mean Square Error
# stomatal lines	1	56	422**	2.65
Needle sharpess index	1	56	206**	1.61
Needle sharpess	1	56	39784**	457
Needle width	1	56	1.109**	.0112
Needle thickness	1	56	.8855**	.0093
Cone length	1	60	13000**	85
Cone scale length	1	60	520**	2.28
Cone scale size	1	60	2212**	10.87
Free scale length	1	60	242**	.9075
Cone size	1	60	114135**	886
Cone width	1	60	320**	4
Cone scale width	1	60	111**	.9463

** Significant at the .01 level of probability.

the number of stomatal rows in blue and Engelmann spruce, but he apparently did not include this value in his analysis. Three measures of the number of stomatal rows were included in the study of MITTON and ANDALORA (1981). The discriminant function including these and several other morphological variables was unable to completely separate blue and Engelmann spruce populations. The present study suggests that a single measure of the number of stomatal rows is of potential use in distinguishing between these species. This measure also has the advantage of being relatively easy to make, because no determination of the needle surface being examined is required.

DAUBENMIRE (1972) and TAYLOR *et al.* (1975) both considered the percentage of free scale a diagnostic character. The results of the present study indicate that free scale length is more useful than the percentage of free scale in differentiating blue and Engelmann spruce. Free scale length has the advantage of being easier to determine than the alternative measurement.

To our knowledge this is the first study in spruce to make use of a quantitative measure of needle sharpness. The importance of this character in distinguishing between blue and Engelmann spruce is underscored by its inclusion in the discriminant function.

The results of this study indicate that the discriminant function defined using quantitative morphological traits may be useful in detecting possible hybridization between blue and Engelmann spruce in the study area. LEDIG *et al.* (1969) and NAMKOONG (1966) used discriminant analysis in a similar manner. LEDIG et al. based their discriminant function on two parental populations and then used this function to classify a hybrid population resulting from controlled crosses of the parental species. The distribution of the hybrid population was intermediate to those of the parental populations on the discriminant function. NAMKOONG also found that discriminant functions were useful in studies of introgression. However, NAMKOONG (1966) and ADAMS (1982) have cautioned that discriminant functions based on two taxa may not be reliable in correctly classifying individuals from a third taxon. If the third taxon consists of hybrids of the first two taxa and inheritance is additive, this may not be a problem, as evidenced by the results of LEDIG *et al.* (1969). If the hybrids exhibit transgressive values on some traits, their classification would be unpredictable (ADAMS, 1982).

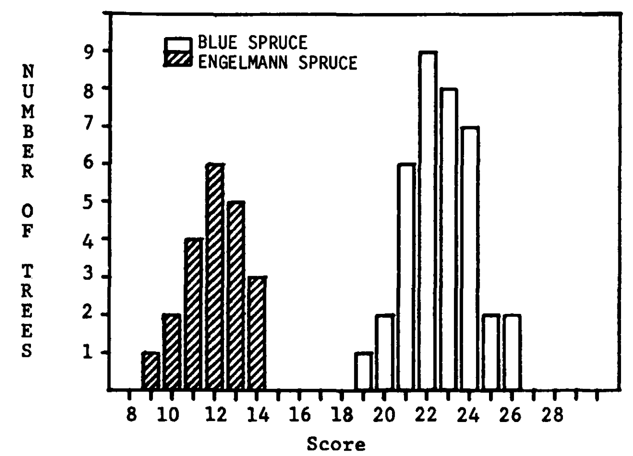


Figure 5. — Morphological index of blue and Engelmann spruce based on 7 qualitative characters.

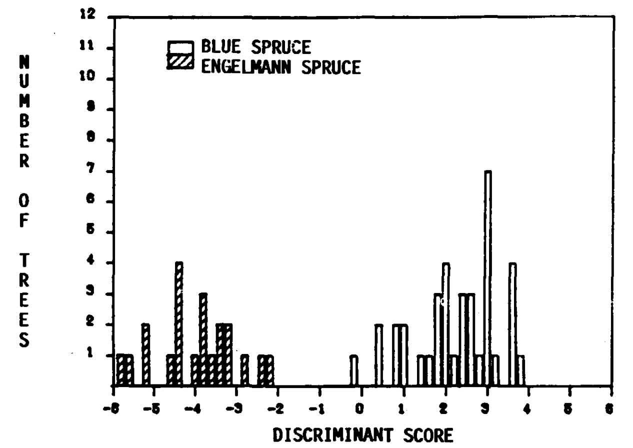


Figure 6. — Discriminant analysis of blue and Engelmann spruce based on three quantitative morphological characters.

The discriminant function developed in this paper will be used in a future investigation of natural hybridization between blue and Engelmann spruce in the Scotch Creek drainage. The above arguments indicate that it will be necessary to verify any results based on this function using another multivariate technique. An F-weighted principal coordinates analysis (ADAMS, 1982) or cluster analysis will be used for this purpose.

The ability of the morphological index and the discriminant analysis to differentiate between blue and Engelmann spruce is somewhat at odds with the results of previous studies of these species (DAUBENMIRE, 1972; TAYLOR *et al.*, 1975; MITTON and ANDALORA, 1981). Three possible reasons for this present themselves when comparing the present study with those previouus. The first possibility is that the present study included only traits with potential diagnostic value in the analyses. MITTON and ANDALORA (1981) apparently did not critically evaluate the morphological characters in their study for diagnostic ability before including them in a discriminant analysis. TAYLOR *et al.* (1975) accounted for characters with little diagnostic value by assigning smaller weights to these than to diagnostic characters. It may have been more useful to simply eliminate the non-diagnostic traits from further analysis.

The second reason concerns the reference populations used in the various studies. ADAMS (1982) noted two problems associated with obtaining samples of reference individuals. He suggested that individuals from sympatric populations may be introgressed and yet, individuals from allopatric (possibly quite distant) populations may be quite differentiated from the actual parents involved in hybridizations. Selection of reference populations largely depends on the scope of the research and the inferences one wishes to make. The present study attempted to use populations just beyond (about 1.5 kilometers) the range of overlap of the two species, although four trees tentatively identified as Engelmann spruce were found in the vicinity of the blue spruce collections. As indicated by the results these populations proved to be distinctly different from one another, and they should provide a better reference for each taxa within the remainder of the study area than would more distant populations. The studies of DAUBENMIRE (1972) and TAYLOR *et al.* (1975) involved collections from populations covering a broad geographic range. Their attempts to detect natural hybridization may have been hampered using as reference groups allopatric populations that were generally a great distance from the areas of suspected hybridization. Perhaps too little is known regarding the genetic variation within each of the species for such broad-based studies to be successful.

A third possible reason for the greater apparent differences between the reference populations in the present study compared to those of previous studies may be the existence of an elevational component of environmental variation in the present study. One interpretation of the greenhouse seedling study would be that genetic differences between the species were not nearly as large as indicated by the analysis of the parent trees, suggesting that elevational differences were relatively large. Although this may in part be true, two potential drawbacks of the seedling study need clarification. First, relatively few seedling traits were measured, so it is quite possible that more diagnostic traits were overlooked. For example, the three most diagnostic traits of mature trees were not examined in the seedlings. Second, it is also possible that juvenile morphological traits in blue and Engelmann spruce do not differ as greatly as mature traits, as the results of the seedling analysis could be interpreted to indicate. For these reasons a great deal of weight cannot be placed on the results of the seedling analysis.

One further note is that the elevational differences within the study area (~ 380 m) were relatively small compared to the elevational range of the combined species in this part of Colorado (~ 1500 m). Associated with this is that the blue spruce reference population was very near its altitudinal limit in this area, while the Engelmann spruce reference population occurred at a fairly low elevation for this species in this area. Again, this suggests that the differences exhibited by the species in this study were probably largely genetic. On this basis a poor separation of species within the area of range overlap in the drainage would suggest possible hybridization between blue and Engelmann spruce. A forthcoming paper will address this possibility.

References

ADAMS, R. P.: A comparison of multivariate methods for the detection of hybridization. Taxon **31**: 646—661 (1982). — ANDERSON, E. G.: Introgressive hybridization. 2nd ed. (1968). Hafner Publishing Co., New York and London (1949). — CLIFFORD, H. T. and F. E. BINET: A quantitative study of a presumed hybrid swarm between *Eucalyptus elaeophora* and *E. goniocalyx*. Aust. J. Bot. **2**: 325—336 (1954). — DANCIK, B. P. and B. V. BARNES: Multivariate analysis of hybrid populations. Naturaliste Can. **102**: 835—843 (1979). — DAUBENMIRE, R.: Some geographic variation in *Picea sitchensis* and their ecologic interpretation. Can. J. Bot. **46**: 787—798 (1968). — DAUBENMIRE, R.: On the relation between *Picea pungens* and *Picea engelmannii* in the Rocky Mountains. Can. J. Bot. **50**: 733—742 (1972). — DAUBENMIRE, R.: Taxonomic and ecologic relationships between *Picea glauca* and *Picea engelmannii*. Can. J. Bot. **52**: 1545—1560 (1974). — FISHER, R. A.: The use of multiple measurements in taxonomic problems. Ann. Eugenics **7**: 179—188 (1936). — FLAKE, R. H., L. URBATSCH and B. L. TURNER: Chemical documentation of allopatric introgression in *Juniperus*. Syst. Bot. **3**: 129—144 (1978). — GARMAN, E. H.: The occurrence of spruce in the interior of British Columbia. Can. Dept. Lands and Forest, Tech. Publ. T49. 31 p. (1957). — GORDON, A. O.: The taxonomy and genetics of *Picea rubens* and its relationship to *Picea mariana*. Can. J. Bot. **9**: 781—813 (1976). — HANOVER, J. W. and R. C. WILKINSON: A new hybrid between blue spruce and white spruce. Can. J. Bot. **47**: 1693—1700 (1969). — HANOVER, J. W., E. YOUNG, W. A. LEMMIEN and M. VAN SLOOTEN: Accelerated-Optimal-Growth: A new concept in tree production. Mich. State Univ. Agric. Exper. Sta. Res. Rep. No. 317. 16 p. (1976). — HARLOW, W. M. and E. S. HARRAR: Textbook of Dendrology. 5th ed. McGraw-Hill, Inc. New York (1969). — HORTON, K. W.: Characteristics of subalpine spruce in Alberta. Forestry Branch, Canada Dept. Northern Affairs and National Resources. For. Res. Div. Tech. Note. No. 76. 20 p. (1959). — JONES, J. R. and N. T. BERNARD: How to tell Engelmann from blue spruce in the Southwest. USDA For. Serv. Gen. Tech. Rep. RM-34 11 p. (1977). — KLECKA, W. R.: Discriminant Analysis, pp. 434—467. In: N. H. NIE, C. H. HULL, J. G. JENKINS, K. STEINBRENNER and H. H. BENT (eds.). Statistical Package for the Social Sciences. McGraw-Hill, N. Y. (1976). — KNOKE, J. D.: Discriminant Analysis with discrete and continuous variables. Biometrics **38**: 191—200 (1982). — KUDRAY, G. M. and J. W. HANOVER: A preliminary evaluation of the spartan spruce (*Picea glauca* × *P. pungens*). Res. Pap. NO. 405. Mich. State Univ. Agric. Exp. Sta., East Lansing, MI. (1980). — LACHENBRUCH, P. A. and M. GOLDSTEIN: Discriminant Analysis. Biometrics **35**: 69—85 (1979). — LEDIG, F. T., R. W. WILSON, J. W. DUFFIELD and G. MAXWELL: A discriminant analysis of introgression between *Quercus prinus* L. and *Quercus alba* L. Bull. Torrey Botan. Clubs. **96**: 156—163 (1969). — MERGEN, F., D. T. LESTER, G. M. FURNIVAL and J. BURLEY: Discriminant analysis of *Eucalyptus cineria* × *Eucalyptus maculosa* hybrids. Silvae Genet. **15**: 148—154 (1965). — MITTON, J. B. and R. ANDALORA: Genetic and morphological relationships between blue spruce, *Picea pungens* ENGELM. and Engelmann spruce, *Picea engelmannii* PARRY in the Colorado Front Range. Can. J. Bot. **59**: 2088—2094 (1981). — MORGENSTERN, E. K. and J. L. FARRAR: Introgressive hybridization in red spruce and black spruce. Univ. of Toronto, Fac. of Forestry Tech. Rept. N0. 4. 46 p. (1964). — NAMKOONG, G.: Statistical analysis of introgression. Biometrics **22**: 488—502 (1966). — PARKER, W. H. and D. G. MCLACHLAN: Morphological variation in white and black spruce: Investigation of natural hybridization between *Picea glauca* and *P. mariana*. Can. J. Bot. **56**: 2512—2520 (1978). — STRONG, W. L.: Evidence for *Picea pungens* in north-central Montana and its significance. Can. J. Bot. **56**: 1118—1121 (1978). — TAYLOR, R. J., S. WILLIAMS and R. DAUBENMIRE: Interspecific relationships and the question of introgression between *Picea engelmannii* and *Picea pungens*. Can. J. Bot. **53**: 2547—2555 (1975). — TAYLOR, T. M. C.: The taxonomic relationship between *Picea glauca* (MOENCH.) Voss and *P. engelmannii* PARRY. Madrono **15**: 111—115 (1959). — WEAVER, T. W. III.: Variation in the spruce complex of the northern Rocky Mountains, *Picea glauca, Picea pungens, Picea engelmannii*. Masters thesis, Univ. of Montana (1965). — WRIGHT, J. W.: Species crossability in spruce in relation to distribution and taxonomy. For. Sci. **1**: 319—349 (1955).

Short Note: Increased Growth Rate of Uapaca kirkiana Muell. – Arg. by X-Rays and Gamma Rays

By A. S. HANS and E. S. LINGUMBWANGA

Tree Improvement Research Centre, P.O. Box 21210,
Kitwe, Zambia

(Received 16th March 1984)

Summary

The preliminary experiments have revealed significant increased growth rate of *Uapaca kirkiana* seedlings exposed to x-rays and gamma rays. This has given fillip to the application of radiation-induced mutations on the slow growing indigenous, multipurpose fruit trees with possible large scale assistance and cooperation of the International Atomic Energy Agency.

Key words: X-rays, gamma rays, Roentgen, *Uapaca kirkiana*.