ENVIRONMENTAL CONTROL OF NEEDLE CHARACTERISTICS IN SUBALPINE BLACK SPRUCE

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Two distinct forms of *Picea mariana,* one upright and the other more or less prostrate, exist in the vicinity of treeline on several New England mountains. Characters distinguishing the two types were discussed by Teeri (1969) in establishing the varietal status of *Picea mariana* (Mill.) BSP. var. *semiprostrata* (Peck) Teeri. Individuals of this taxon are recognized by their prostrate growth form, lack of a dominant upright axis, and short, glaucous needles that are slightly adaxially curved. The most prominent character other than the growth form is the needle length. Needles average 4 mm. (2.2 to 5.5 mm.) in length in the prostrate form as compared with upright individuals that have needles averaging 7.5 to 8.5 mm. The study reported here indicates that needle characteristics and, perhaps, other features of the prostrate variety are subject to considerable modification by the environment.

Plants were collected during late August and September 1972 from Lion's Head (1450 m.) and Cape Horn (1280 m.) on Mt. Washington, N.H., and in Bear Swamp, Wolcott, Vt. (340 m.). Both upright and prostrate forms were collected at the treeline sites on Mt. Washington. Only the typical form was obtained from Wolcott. Individual plants from all populations were transferred to a commercial potting mixture (Jiffy Mix) and grown in a cool greenhouse (10 to 20°C). All individuals were watered daily and fertilized weekly with a 20-20-20 nutrient solution (Universal Chem-

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ical Co.). Buds expanded during April, and both the new needles and the previous year's needles produced under natural conditions were analyzed in early July. Fifty needles were selected from each indicated age class on three separate individuals from each of the populations studied. The samples were pooled according to age class and source population. A final sample of 100 needles was taken from each pooled sample for actual measurement. Length measurements were taken to the nearest 0.1 mm. Photographs of sample individuals were also taken.

New growth needles of the short needle var. *semiprostrata* contrasted dramatically in length compared with growth which had occurred under natural conditions (Fig. 1). The new growth needles were not only longer by about 5 mm. (Table 1), but they were darker green in color and had no pronounced curvature. New needles of the other populations of *Picea mariana* also had a healthier appearance than the naturally produced needles, but, otherwise, differences in needle length were not at all pronounced (Fig. 1, Table 1).

Average needle lengths along with standard deviations are presented in Table 1. Tests for significance were applied using the analysis of variance technique. The natural needle length (short form) of var. *semiprostrata* was significantly different (5% level) from the other sample lengths including the needles produced in this variety under cultivation. The needle lengths resulting from cultivation of all three populations were not significantly different.

Table 1. Average needle length and standard deviation for three populations of *Picea mariana.*

Source Elevation (m.)	Needle Length (mm.)	
	Natural	Cultivated
A) 1450 (var. *semiprostrata*)	4.5 ± 0.54	9.4 ± 1.2
B) 1450 and 1280 (var. *mariana*)	8.5 ± 0.97	8.1 ± 1.2
C) 340 (var. *mariana*)	6.4 ± 0.73	8.5 ± 1.3

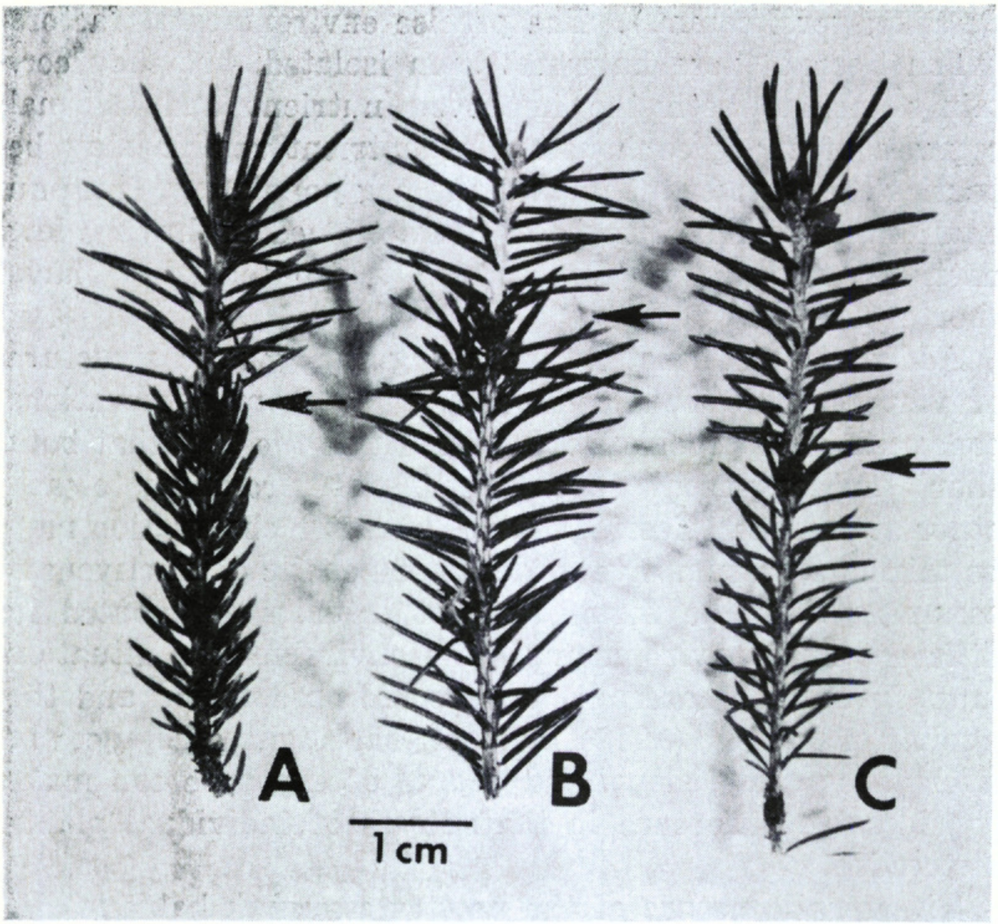

Figure 1. Branches of *Picea mariana* with needles produced naturally (below arrow) and under cultivation (above arrow). Sources of the original populations are: A) 1450 m., Mt. Washington, var. *semiprostrata*; B) 1450 m., Mt. Washington, long-needle form; and C) 340 m., Bear Swamp.

The results indicate that needle length in var. *semiprostrata* is under some degree of environmental control. Needle curvature is also capable of being modified. Curvature appears to be related to needle length in that the shorter needles (less than 5 mm.) of all populations had varying degrees of adaxial bending, while the longest needles were most frequently straight. Modified needle growth in black spruce under cultivation has previously been observed, but not fully reported (Kozlowski, 1971;

R. Pike, pers. comm.). The precise environmental factors which operate here have not been isolated, but they certainly include both the improved nutrient and thermal regimes of the greenhouse. The nutrient regime may be particularly important in that the bog population, from an environment which has been characterized as having low nutrient availability (Small, 1972), also tended to have shorter needles.

Additional information regarding the genetic structure of var. *semiprostrata* can be obtained from observations concerning the prostrate form itself and the fact that both short- and long-needle types exist in close proximity to each other at treeline (Teeri, 1969). The latter observation may be taken as presumptive evidence of genetic distinctiveness assuming that the forms are not actually distributed in different microenvironments. The environmental situation must be studied carefully as personal observation and the studies of Tiffney (1972) indicate that slight differences in microtopography, slope, and degree of exposure can make considerable difference in the success of individual plants at treeline.

The genetic nature of the prostrate growth habit is difficult to demonstrate experimentally because of the long period of time necessary to develop this form. There is a tendency for new twigs on the uppermost branches to occur vertically. Frequently the preceding year's needles on these protruding branches have been removed on the windward side. Thus we may be witnessing an example of wind trimming as has been observed in other climates (Thomas, 1973). Additionally, the work of Jaffe (1973) suggests that the stunting of individuals could be an aspect of thigmomorphogenesis resulting from the mechanical action of wind.

The contiguous natural distribution of characteristic forms of both varieties as well as character variation which is essentially clinal in nature (Teeri, 1968) perhaps has resulted from disruptive selection similar to processes described by Antonovics and Bradshaw (1970) and Snaydon (1970). Phenotypic variation which has little importance in other parts of the range of *Picea mariana* may assume considerable significance at alpine treeline. Several morphological features of var. *semiprostrata* make it particularly well adapted to the alpine environment (Teeri, 1969). Additionally, it has frequently been observed that growth rates, such as needle elongation, and cold-hardiness are inversely related (Alden and Hermann, 1971). Thus, at the distributional limit for a species, a uniquely adapted genotype could exist sympatrically with the more common genotype even in a homogeneous environment. Some degree of reproductive isolation exists between the varieties due to the infrequency of cone production at treeline (Teeri, 1968).

It is not the intention of this study to reorganize the taxonomy of black spruce. The variety *semiprostrata* as defined from natural specimens is sufficiently unique to merit distinction. However, it should be recognized that the genetic basis for this taxon lies not in a narrowly specified phenotype, but in its plasticity and the sensitivity of the genotype to interaction with the environment.

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