MORPHOLOGY AND DEVELOPMENT OF WHITE SPRUCE AND BALSAM FIR SEEDLINGS IN FEATHER MOSS

by

A. Jablanczy and G. L. Baskerville

FOREST RESEARCH LABORATORY

FREDERICTON, NEW BRUNSWICK

INFORMATION REPORT M-X-19

Canadian Forestry Service
August 1969

INTRODUCTION

Information on the growth of white spruce, Picea glauca (Moench) Voss, and balsam fir, Abies balsamea (L.) Mill. seedlings in natural conditions is scarce, most studies being restricted to seedlings in nurseries or semi-natural conditions. Little attention has been paid to the differences between the development of wildlings and nursery-grown seedlings.

The dense carpet of feather mosses which commonly forms under white spruce stands in Nova Scotia provides a difficult environment for seedlings and has a profound influence on their development. The spruces and balsam fir are adapted to this habitat because they develop both horizontal and vertical components to their root systems (heterorhizy).

Morphological changes in natural seedlings during juvenile growth in feather moss has prompted the definition of three developmental phases. Although recognition of phases in the development of seedlings has been suggested by many workers (Pessin, 1934; Toumey and Korstian, 1947; Morris, 1948; Baker, 1950; Crossley, 1953; Quaite, 1956; Robbins, 1959), the phases have not been considered in relation to environmental conditions. As the survival and development of a seedling depends on its ability to adapt to changing conditions, particularly in the rhizosphere, an understanding of these adaptations should be useful in the development of practical measures for regenerating stands of old-field white spruce.

THE WHITE SPRUCE HABITAT

Almost pure stands of white spruce commonly develop on abandoned fields in the Maritimes. These stands may contain up to 20% balsam fir and 5% each of black spruce, Picea mariana (Mill.) BSP., and red spruce Picea rubens Sarg. They usually occupy southern and western slopes, adjacent level areas and hill tops, and sometimes extend to northern slopes. Mature trees, about 80 years old are 60 to 80 ft high (18 - 20 m) and 8 to 12 in. diameter at breast height (20 - 30 cm). Stands contain 20 to 40 cords/acre (120 - 240 m^3/ha) on a basal area of 150 to 200 ft^2/acre (35 - 45 m^2/ha).

In dense stands the forest floor is usually devoid of vegetation and consists of fresh litter over some 2 in. of mor humus. Where the insolation of the forest floor reaches about 20% of full diffuse light the ground is covered with a dense carpet of feather moss. The main component of the feather moss community is Calliergonella schreberi (BSG.) Grout which may be replaced by Rhytidiadelphus triquetrus (Hedw.) Warnst. on moist areas or by Hylocomium splendens (Hedw.) BSG., Ptilium crista-castrensis (Hedw.) de Not., Climacium dendroides (Hedw.) Web. & Mohr, Thuidium delicatulum (Hedw.) Mitt., Dicranum scoparium Hedw. and other mosses accompany the main species. Sphagnum spp. occupy wet depressions. On fresh localities where the insolation exceeds 50% of full light, haircap moss, Polytrichum commune Hedw., displaces the feather mosses. The moss carpet is usually interspersed with Lycopodium spp. and such herbaceous plants as Viola spp., Cornus canadensis L., Coptis groenlandica (Oeder) Fern., Maianthemum canadense Desf., Linnaea borealis L., Pyrola spp., Trientalis borealis Raf., and Vaccinium spp. The occurrence of most of these plants increases with increasing insolation. In openings wider than about one-quarter of the tree height, ferns, broad-leaved plants and grasses develop.

METHODS

In this study it was convenient to subdivide the moss-litter layer into two layers, the second of which includes the L layer above the traditional F and H layers (Fig. 1). These two layers are:

M_1 - The living moss leaves and stalks of the last 2 years growth forming a ½- to 2-in. thick, loose, brownish-green carpet, whose green tint increases with moisture.

M_2 - A spongy layer about 1 in. thick consisting of litter, dead and slowly decomposing moss stalks and leaves, more than 2 years old, mixed with other organic debris. This layer has fairly good water-holding capacity.

In the period 1961-63, some 1000 white spruce and balsam fir seedlings evenly distributed across an age range of 1 to 10 years were lifted from feather moss sites in Nova Scotia. One hundred white spruce and fir seedlings from the Acadia Forest Experiment Station nursery were used for comparison.

The seedlings were mounted as herbarium specimens and examined (microscopically where necessary) to determine the length of root and of annual internodes of the stem, the number of adventitious routlets, the maximum extended length of root (potential penetration), and morphological characteristics used for species identification (Jablanczy, 1964).

To gain some indication of the influence of environmental variables on seedling development, soil temperature (by thermistor), pH (by portable meter), and moisture content (by gravimetric methods) were recorded near the source of the sample seedlings. The measurements were made in 1962 and 1963 at the beginning of the growing season and in mid-summer in the following three layers: 0 to 1 in., 1 to 2 in., and 2 to 4 in. below the surface of the mor. At each sample location, an ocular estimate of canopy density was made and the intensity of diffuse light was determined with a light meter.

Seedling age was determined by counting the annual internodes from the base of the epicotyl. The two bud scars marking its top and bottom are convenient reference points which, combined with the absence of lammas growth in spruce and fir, makes the method satisfactory. Counts of annual rings proved unreliable because suppressed seedlings often did not lay down a recognizable annual ring and arcs of compression wood were misleading.

PHASES OF SEEDLING DEVELOPMENT

This study revealed three distinct stages in spruce and fir seedling development: a "plumulous" stage following germination, a "soft-seedling" stage beginning with the growth of the epicotyl, and a well-established vigorously growing "hard-seedling" stage. In general the size, branching, vestiture, bud structure and rooting habit of wild seedlings were more closely related to the phase of seedling development than to age. For instance, a suppressed 5-year-old white spruce seedling may be 3 cm tall and have immature "soft" buds, whereas an open-grown seedling of the same age may be over 20 cm tall with "hard" buds.

Plumulous Stage

The germinant consisted of a radicle, hypocotyl, a few cotyledons, and a naked apex with plumules. The plumules were pale-colored, primordial scales or needles. At this stage both spruce and fir developed a tap root about 25 mm long. The hypocotyl length (in mm) of 170 white spruce and 45 balsam fir wildlings varied as follows:

Species	Range	Mean
White spruce	14-42	26.9
Balsam fir	20-46	31.6

White spruce may have 5 to 8 cotyledons but 80% of the seedlings examined had either 6 or 7. Balsam fir had 4 cotyledons, occasionally 5. The length of cotyledons averaged 11 mm on white spruce and 13 mm on balsam fir. The cotyledons usually survived for 2 years and then withered gradually whithout the formation of a separation layer. The plumulous stage in both species commonly lasted about 3 weeks. No seedlings were found in this stage in the autumn following germination.

Soft-seedling Stage

About 3 weeks after germination, the soft-seedling stage began with the emergence from the apex of the epicotyl and the primary needles. The epicotyl length (in mm) of 170 white spruce and 45 balsam fir soft-stage wild seedlings measured from point of cotyledon attachment to the bud base, varied as follows:

Species	Range	Mean
White spruce	0.1-4.5	1.3
Balsam fir	0.2-4.0	1.2

The epicotyl length of white spruce from the nursery averaged about 5 mm. Stem diameter was about 1 mm in spruce and 1.5 mm in fir and virtually no change occurred until the seedling passed into the hard stage. The stem of a white spruce seedling became pubescent in the second year and retained this characteristic during the soft-seedling stage. This contrasts with seedlings of red spruce and black spruce, which have glabrous stems (Jablanczy, 1964).

Wild seedlings of spruce and fir usually had no branches in the first 2 or 3 years. Small soft-seedlings with branches were usually much older than would be suspected. About 25% of the seedlings examined had developed branches during their third year and by their fifth year about 50% had 2 to 6 branches in 1 or 2 whorls. The branches of a soft-seedling were often as long as the leader thus producing a bushy top (Fig. 1).

The leaf margins of white spruce soft-seedlings were ciliate at first, but became smooth within a few years. The needles of red spruce and black spruce are never ciliate. During the first year about 20 needles (4 to 40) formed on the epicotyl of white spruce; balsam fir had about 5 needles (4 to 8). On white spruce these first needles were 5 to 6 mm long but each successive year produced produced progressively larger needles to a maximum of 12 mm in the fifth year. The primary needles, like the subsequent foliage, generally persisted for 4 years.

The first winter bud developed 4 to 6 weeks after epicotyl sprouting which usually occurred by the end of July. This bud is not predetermined in the embryo, but is formed de novo in the germinant (Romberger, 1963). No seedling was found to survive winter without a dormant terminal bud although Armson (1960) reported that in a southern Ontario nursery many white spruce seedlings did not form buds in the first year.

The morphology of the first bud was typical for all buds formed in the soft-seedling stage of white spruce (Fig. 2). The spherical to ovate, often flat-topped juvenile bud was more loosely joined to the tip of the leader shoot than the embedded buds of older specimens. The rudimentary shoot in the bud chamber was enveloped by scale tissue of about 20 layers and covered with 2 to 4 green, rounded caudate, outer bud scales with bullate surfaces. The bulging, dorsal ribs of the two outer scales extended beyond the bud tip forming recurved, blunt beaks which were often serrate or ciliate on the basal section; these scales often bore irregular purplish spots on both sides. The bud was surrounded by a dense cluster of slightly incurved needles. Buds formed in subsequent years were similar to first year buds but the recurved beaks on the outer bud scales became straight with acuminate bristles which surpassed the bud tips. Lateral buds were always smaller than the terminal buds.

The soft terminal buds gradually matured to hard buds marking the end of the soft-seedling stage.

In balsam fir, no distinctive features of bud formation were observed although the embedded resinous buds on soft seedlings were much smaller than those on hard seedlings.

Seedlings of both species extended taproots down about 25 to 40 mm in the first year and developed a few short laterals (Figs. 3 and 4). In the second and third year the taproot, usually with many branching tips, penetrated to a depth of about 40 to 50 mm and one or two upper horizontal branches developed humus runners from 50 to 100 mm long (Fig. 1). In succeeding years most taproot endings died and disintegrated but some persisted when located along the decayed material in old root channels. In older white spruce seedlings, rarely less than 4 years old, the first pair of adventitious roots developed from dormant accessory buds of the epicotyl. Subsequent roots of this type emerged from dormant axillary buds or from the vicinity of internodal bud scars (Figs. 1 and 4). Bannan (1942) found the source of the adventitious spruce roots located in the parenchymatous gaps above the medullary crowns in the dormant bud. Balsam fir roots arose irregularly from any section of the stem (Fig. 4). Usually these fast-growing, adventitious roots did not have root hairs or detectable mycorrhizae.

The soft-seedling stage of white spruce lasted 2 to 3 years in a nursery site on mineral soil, 4 to 5 years in a grass community, and 10 years or longer in a moss carpet under mature forest. Balsam fir had a less distinct range of time in the soft-seedling stage which may be more prolonged than in spruce. Rapid shoot growth marked the end of this growth period.

Hard-seedling Stage

Within 3 years of receiving increased insolation, the seedlings developed the full characteristics of the hard-seedling stage: accelerated growth of the leader, apical dominance, and regular annual rings. Stem and needle hairs diminished on the white spruce, hard buds replaced the soft ones, and the lateral root system extended sinkers into the mineral soil. No recovery of the taproot occurred. The pubescense on white spruce stems disappeared first from the terminal leader and finally from the lateral leaders, but inferior twigs remained pubescent. Fast growing spruce seedlings in the nursery sometimes lost the pubescense on the leaders during the second or third year. Balsam fir stems were permanently pubescent.

The hard-seedling bud in spruce resembled the mature terminal bud of an adult tree (Fig. 5). This bud was pointed ovate, its primordial shoot chamber surrounded by more than 20 layers of scales, and the outer surface formed of 6 to 10 parchment-like scales with stiff bristles extending just beyond the bud tip. The bud was embedded for about half its length in the cork tissue of the shoot tip.

ROOT DEVELOPMENT

In the feather moss carpet of a mature white spruce stand, only the organic layers appear to be associated with juvenile seedling growth since the roots of spruce and fir seedlings usually do not penetrate permanently into the mineral soil in the first 2 or 3 years. Tamm (1953) studied the nutritional capacity of feather moss seedbeds in Scandinavia and stated that the decomposing moss creates a situation resembling a hydroponic environment for seedling roots. Tamm found that the moss layer contained fair amounts of available nitrogen, calcium and phosphorous which originated from the air and the leachates of trees. The pH values of the moss layer and the concentration of potassium in it were higher than those in the under-lying layers.

In white spruce stands in Nova Scotia, the spongy semi-decomposed moss litter mixed with other organic debris (M_2) proved to be a most stimulating medium for root growth. Although the taproot seldom penetrated beyond the humus layer in the first year, roots usually reached the boundary between the moss mor and the mineral soil in the second year. Early in the third spring, humus runners developed near the upper surface of the moss mor presumably because conditions such as aeration and temperature were more conducive to root growth there than in the mineral soil. In subsequent years in a vigorously growing, fresh moss carpet, the central root tips, which had penetrated into the humic (A_h) or eluviated (A_e) mineral layers, discontinued their extension and deteriorated (Fig. 1). Thus the high mortality which commonly occurs in dry summer periods after the second year may result from an incapacity of the mor and surface mineral soil to satisfy the needs of the seedling for water. In any event once the root form changes, seedlings appeared to be more dependent on their new horizontal root structures, as was found also by Wagg (1964).

No general mechanical reason was found for the discontinuation of vertical root growth. The only natural force which would tear or extract the lowest portion of taproot is strong wind. On some exposed localities, the shallow lateral roots of swaying mature trees can transmit an undulating movement to the organic carpet, lifting and separating it from the mineral soil. The senior author measured surface movements with a vertical amplitude of 8 cm during a gale in Guysborough, N. S.

The few measurements of soil temperature and moisture taken in 1962 and 1963 indicate much lower temperatures and more nearly saturated conditions at the beginning of the growing season in the uppermost mineral horizon than in the moss mor. In late July, moisture content was lower in the surface mineral soil than in the organic part of the forest floor although this should be offset, at least in part, by a difference in availability. Values of pH were not consistent but tended to be lower at the top of the mineral horizon than in the organic material, especially the moss litter (M_2).

In openings where haircap moss replaced the feather mosses, the chances of seedling survival appeared to be greater. Haircap moss has permanent rhizoids and water-conducting central strands which weave through the mor and link it to the M_2 layer. In these conditions, seedlings developed multi-layered adventitious roots with branches as long as 20 cm and, as there is no discontinuity at the moss mor/mineral soil interface, the taproot persisted. In mineral soil without an organic accumulation, the central root system continued growth and, in the third or fourth year, reached a depth of about 15 cm where, presumably, the soil moisture content seldom drops below wilting point.

SUMMARY AND CONCLUSIONS

Field and laboratory studies were undertaken to observe the early development of seedlings of white spruce and balsam fir in feather moss white spruce stands. The morphology of seedlings showed distinct phases of development: plumulous-, soft-, and hard-seedling stages.

In the Maritimes, white spruce and balsam fir seedlings pass out of the plumulous phase 2 or 3 weeks after germination. The soft-seedling stage is a period of slow growth which may last from 2 to 10 years, depending on conditions of insolation. Morphological characteristics are: slow growth; lack of branching or sparse branching with suppressed apical dominance; intermittent cambial dormancy; ciliate needle margin; pubescent stem and in white spruce, specific bud features; discontinued growth of central root tips, except those protected by buried old stems or roots; and formation of epicormic adventitious roots from dormant buds.

In the hard-seedling stage, seedlings change into relatively vigorous plants resembling adult trees. Morphological characteristics are: relatively fast growing terminal shoot with apical dominance; ample branching; normal cambial activity; mature bud structures and in white spruce, glabrous needle margins and terminal leader; and root sinkers penetrating deep into the mineral soil.

REFERENCES

Armson, K. A. 1960. White spruce seedlings: the growth and seasonal absorption of nitrogen, phosphorus and potassium. Univ. Toronto Press, Forest. Bull. 6.

Baker, F. S. 1950. Principles of silviculture. McGraw-Hill, New York.

Bannan, M. W. 1942. Notes on the origin of adventitious roots in the native Ontario conifers. Amer. J. Bot. 29: 593-598.

Crossley, D. I. 1953. Seed maturity in white spruce. Can. Dep. Resources Develop., Silvicult. Res. Note 104.

Jablanczy, A. 1964. Identification of black, red and white spruce seedlings. Can. Dep. Forest., Publ. 1039.

Morris, R. F. 1948. How old is a balsam tree. Forest. Chron. 24: 106-110.

Pessin, L. J. 1934. Annual ring formation in Pinus palustris seedlings. Amer. J. Bot. 21: 599-604.

Quaite, J. 1956. Survival of white spruce seedlings resulting from scarification in a partially cut mixedwood stand. Can. Dep. N. Aff. Natur. Resources, Forest Res. Br., Tech. Note 44.

Robbins, W. J. 1959. Juvenility in trees and shrubs. Proc., Int. Bot. Congr. Montreal, 1959.

Romberger, J. A. 1963. Meristems, growth, and development in woody plants. U. S. Dep. Agr., Forest Serv., Tech. Bull. 1293.

Tamm, C. O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). Meddelanden, Statens. Skogaforstkningsinstitut, Band 43, Centraltryckeriet, Esselte, Stockholm 1954. pp. 1-140.

Toumey, J. W. and C. F. Korstian. 1947. Foundations of silviculture. John Wiley and Sons, Inc., New York.

Wagg, J. W. B. 1964. White spruce regeneration on the Peace River and Slave River lowlands. Can. Dep. Forest., Publ. 1069.

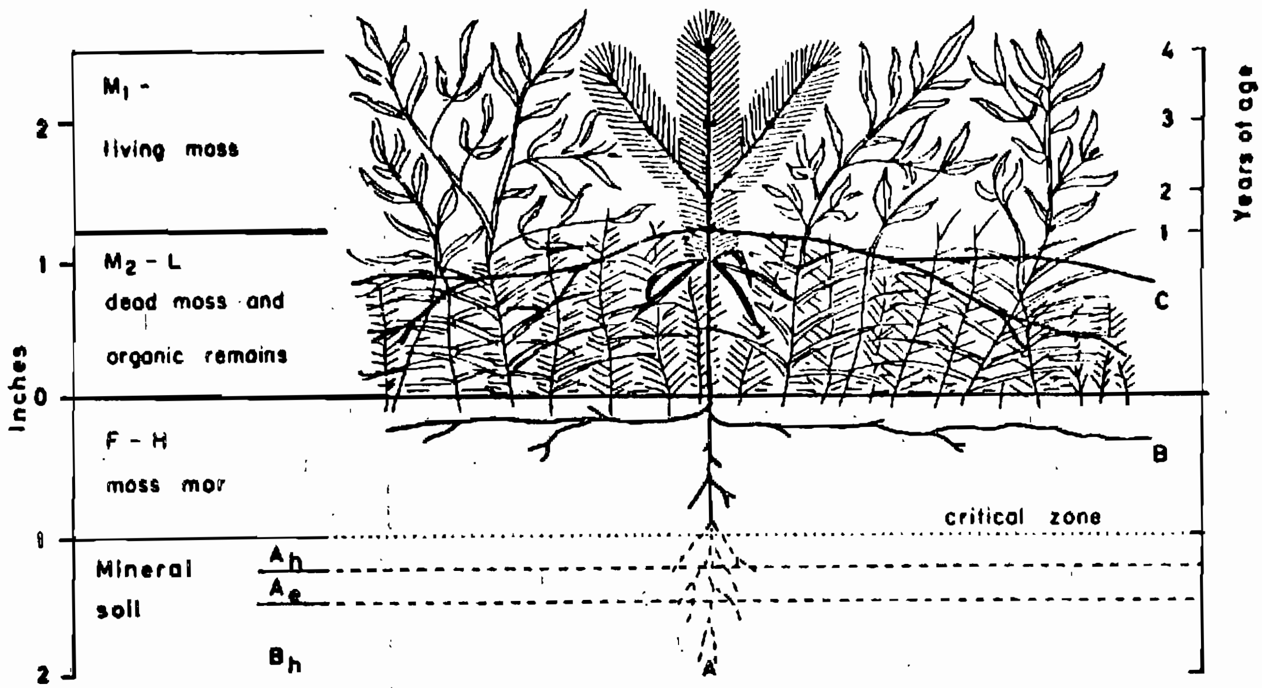


Figure 1. Diagram showing the vertical structure of the feather moss seedbed. The seedling shows three root phases: A - tap root, B - humus runner, and C - adventitious root.

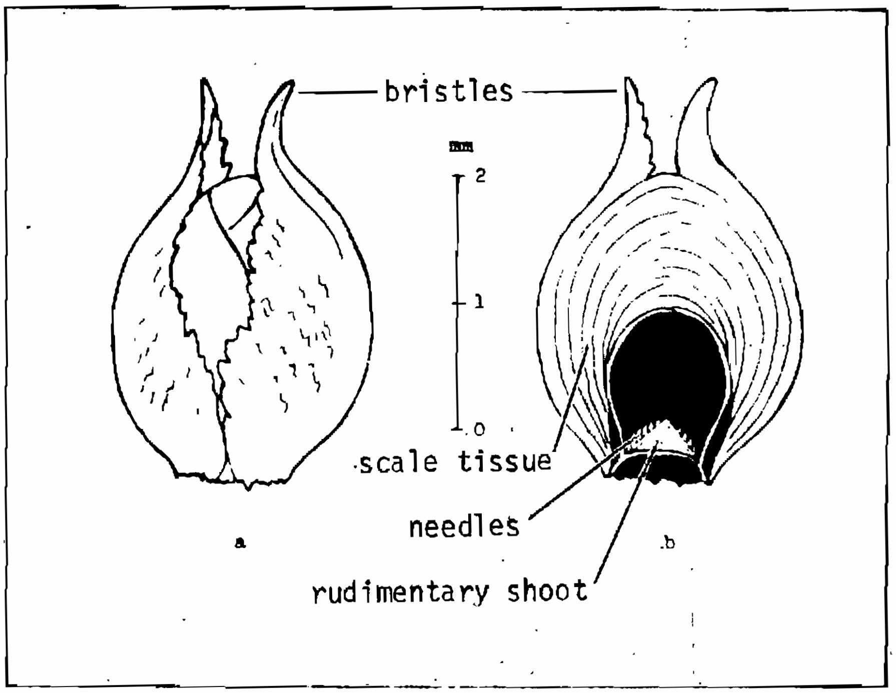


Figure 2. Terminal leader bud of white spruce seedling at its soft seedling stage: a - view; b - median section.

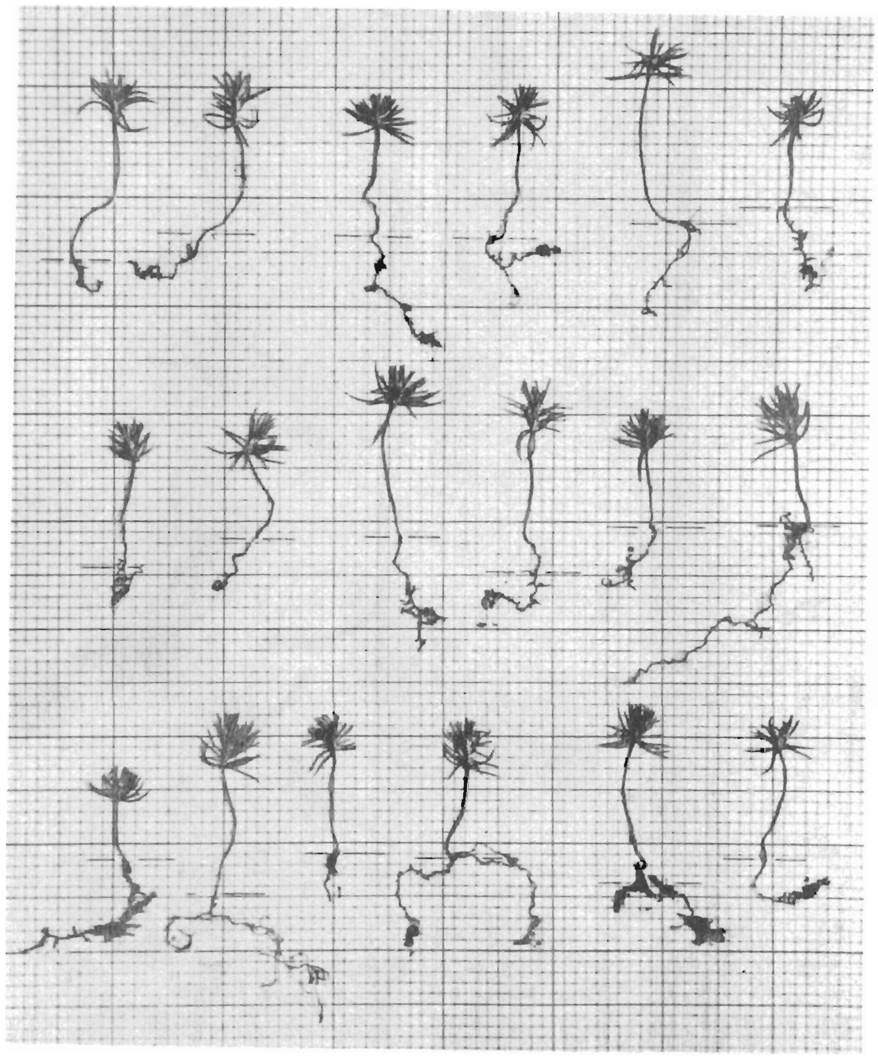
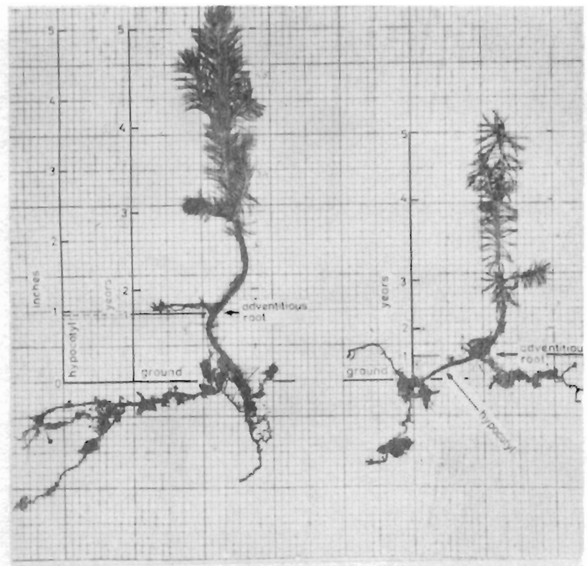


Figure 3. One-season-old white spruce seedlings from a feather moss site (1-inch cross-section paper).

A



B

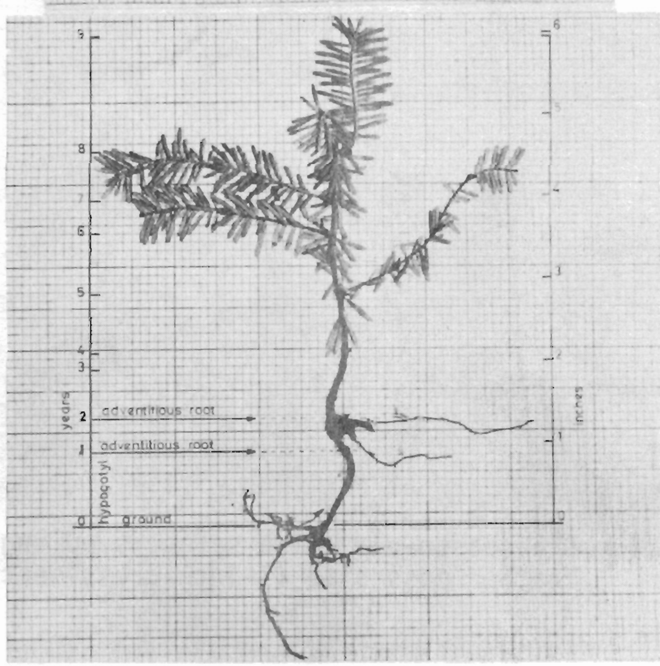


Figure 4. Adventitious roots on white spruce and balsam fir seedlings from a feather moss site.

A. 5-year-old white spruce seedlings with adventitious rootlets. Left - From open north edge of a cleared strip. Right - From a closed stand.

B. 9-year-old balsam fir seedling with two sets of adventitious rootlets. Only rudiments of lower whorl are detectable.

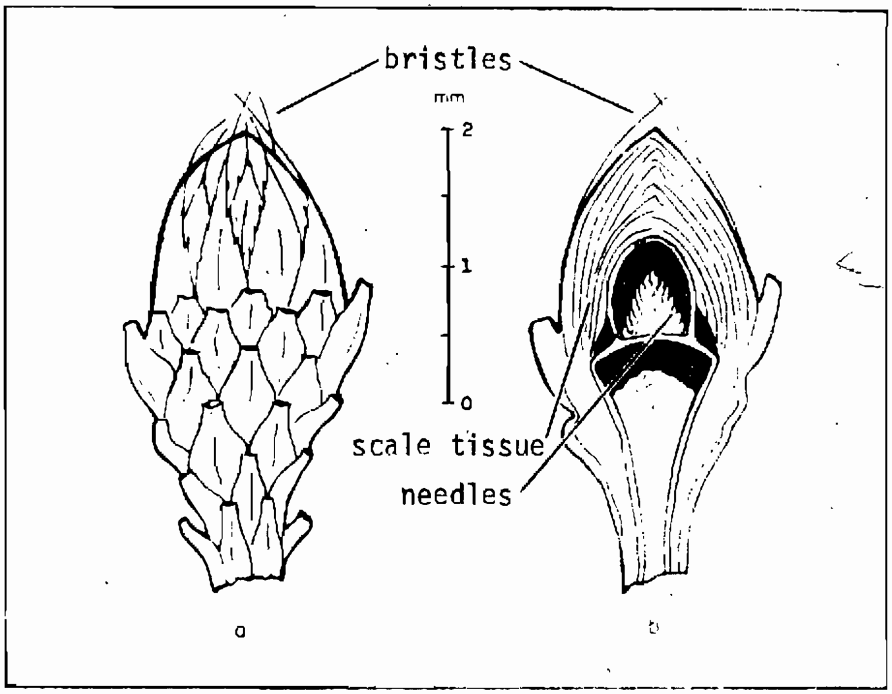


Figure 5. Terminal leader bud of white spruce seedling at its hard seedling stage: a - view; b - median section.