A COMPARISON OF EARLY SHOOT DEVELOPMENT OF SEEDLINGS OF SOME TREES COMMONLY RAISED IN THE NORTHEAST OF NORTH AMERICA

by

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Abstract - The shoot system is described for first-season and second-season development of spruces and pines, and for first-season development of birches and oaks, when growing under non-forced and forced conditions. In spruces, pines, and birches, which germinate epigeously, epicotyledonary shoot extension in the first season is achieved by neoformed growth, which under forced conditions may include syllepsis. In oaks, which germinate hypogeously, one surge of extension growth is achieved by neoformed growth, but subsequent growth surges occur as performed stem sections in successive terminal buds extend. Second-season extension in spruces results from preformed growth from rested buds, and from some neoformed growth. In pines, second-season extension results entirely from extension of preformed stem sections. The stem sections are preformed in resting rosettes of primary leaves (the most common form in non-forced conditions), in resting long-shoot buds, or in different proportions of both of these.

INTRODUCTION

Those who grow tree seedlings in nurseries strive to produce uniform crops of seedlings, which meet acceptable standards of size, health and vigor, as quickly and as efficiently as possible. They are concerned, therefore, with rapidity of growth, with general appearance, and with achievement of readily measured criteria of seedling size, balance and vigor. In different regions or jurisdictions, standards have been, or are being developed. Except in general terms, there has been little account taken of the developmental processes or patterns which result in the achievement by the seedling of a certain size, appearance, or condition. Indeed, it is hard to find detailed descriptions of first-year and second-year development of common tree species - for most, they do not exist.

When tree seedlings are forced to develop quickly, as in today's greenhouse, containerized, culture systems, or in accelerated-growth conditions or even in highly fertilized nursery beds, some species develop very differently from when grown in non-forced conditions. Others simply produce more of the same kind of growth. It is important that the grower understands the manner of development of the different species so that what is occurring can be properly interpreted.

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In this paper, four contrasting styles of seedling shoot development are described. For simplicity, development is described by genus, - spruces (Picea), pines (Pinus), birches (Betula), and oaks (Quercus) - but is based on observations or information available from elsewhere for only a few species within each genus (Table 1). The diagrams presented are stylized to display the general modes of development. The descriptions are restricted to the first or first two seasons of active growth and are generalized. Thus, while general features and structures of development are described, specific detail is not.

GERMINATION AND EARLY SHOOT DEVELOPMENT

Spruce and pine seeds are usually sown devoid of any seed attachments (wings), but seeds of birches and oaks are sown while they are still inside the fruits in which they were produced. Thus, in the latter, the young seedling has to penetrate not only the seed coat, but also the fruit wall, as germination occurs. In spruces and pines the embryo is surrounded, in the seed, by megagametophyte tissue which provides nutriment for germination. In seeds of birch and oak there is no endosperm: instead, the cotyledons occupy most of the space in the seed, and they provide nutriment for the germination process. Germination in spruces, pines and birches is epigeous, whereas in oaks it is hypogeous.

As epigeous germination begins, the embryo expands and the radicle begins to elongate. The seed coat (and fruit wall in birch) is split and the radicle grows out, turns downwards and grows further into the soil, thus anchoring the young seedling. Concomitantly, the hypocotyl begins to elongate slowly, then at an increasing rate. It arches upwards out of the soil. As it does so, it either pulls the cotyledons and shoot apex out of the seed coat (and fruit in birch), leaving the seed coat in the soil, and then straightnes up as the cotyledons spread apart, assume a more-or-less horizontal and grow rapidly to full size, or it carries the seed coat (and fruit in birch) up out of the soil as the hypocotyl straightens up and the cotyledons then pull their way out of the covering seed coat, spread apart, and assume a more-or-less horizontal position as they grow rapidly to full size. Both forms of cotyledon emergence occur in seedlings of each genus, but the former is more common in birches, and the latter more common in spruce and pines.

While these clearly evident processes have been occurring, the shoot apex, situated between the whorled (spruces and pines) or paired (birches) bases of the cotyledons, has also become active. The shoot apex first expands, and then begins to initiate leaves around its lower flanks. In spruces and pines, several leaves are produced in succession, and later more-or-less synchronously in spirals around the apex; whereas, in birches leaves are produced one at a time. The leaves grow rapidly to overarch the apex, thus protecting it as the cotyledons spread apart. So, as the cotyledons are pulled out from the seed coat and spread out, the developing shoot system (plumule, or primoridal bud - Jablanczy 1964) is revealed above the tip of the hypocotyl at their bases. As growth continues, the older leaves exapnd and diverge from the shoot axis as new leaves are formed by the apex, and, in turn, protect it.

In spruces, the first-formed leaves are similar in general form to those produced by the tree **in** later life (in some speices, some details differ - Jablanczy 1964), but in pines, the first-formed leaves differ distinctly from those produced later in life. They are borne singly, in spirals around a shoot that ultimately becomes a long shoot. In later life, leaves of different morphology are borne in twos, threes, or fives (depending on pine species), on lateral short shoots, which are themselves borne on long shoots. In pines, therefore, the first-formed, or primary leaves, are morphologically and morphogenetically different from the secondary leaves. In birches, there is a gradual transition in form of leaf from the tiny trilobed, first-formed one, to larger, later leaves which are doubly serrate and similarly morphology to neoformed leaves on long shoots on mature trees.

The hypogeous germination of oaks starts similarly to epigeous germination, but after radicle extension and ensuing rapid downward penetration into the soil, there is virtually no hypocotyl elongation, but the shoot apex is promoted into vigorous growth. The basal portions of the cotyledons extend sufficiently to push the shoot apex (atop a short epicotyl) out of the seed coat and fruit wall. The epicotyl then turns upwards and vigorous extension growth occurs below the apex as the apex produces lateral appendages around its lower flanks. These protect the apex as it is pushed out of the soil. Vigorous upward growth of the shoot so formed continues to produce a much larger initial structure above ground than is the case for spruces, pines or birches. Below ground, the cotyledons, which supply nutriment for the massive early development, shrivel and degenerate as their usefulness passes.

SUBSEQUENT SHOOT DEVELOPMENT

Subsequent shoot development varies with genera, and with conditions of growth. Thus each genus will be dealt with separately, and, for each genus development will be described under poor or normal, or non-forced conditions, and under forced conditions (which usually mean extended photoperiod, relatively high temperature and high fertilizer levels).

SPRUCES

First-Season and Second-Season Development under Normal Conditions

Newly produced leaves cluster loosely above the cotyledons and around the shoot apex which produced them. As more leaves are produced, the stem sections [1] associated with the older leaves elongate, and thus height growth of the shoot above the cotyledons begins. This process of progressive production of leaves by the apex, and of their elongation and spreading apart to lengthen the shoot continues until some environmental stimulus (or a combination of stimuli) causes a change in the differentiation process. When this occurs, the rate of initiation of new lateral structures by the apex lessens, and the structures differentiate as bud scales rather than as leaves. So, instead of becoming green,

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[1] Doak (1935) defined the term "stem unit" for pines to include an internode and the node and its nodal appendages at its extremity. That usage is maintained in this paper. The term "stem section" is used here to define the internode as used by Doak - the portion of stem associated with a primary lateral appendage such as a scale or a leaf.

remaining narrow, and elongating considerably, they become yellow and brown and broaden, but elongate little. This signifies initiation of the terminal bud.

If growth has been relatively vigorous, lateral buds may also be initiated in the axils of a few of the leaves along the shoot. When this occurs, a lateral shoot apex is first initiated, and then, as it enlarges, it begins to initiate its own bud scales around its flanks, and the lateral bud becomes evident.

After a period of about a month during which bud-scale initiation continues, and the bud scales grow, the terminal shoot apex within the new terminal bud reverts to leaf production, and the lateral shoot apices in lateral buds (if there are any), commence their first period of leaf production. But the new leaves are initiated within the confines of the surrounding bud scales, and they remain as leaf primordia. That is, they remain rudimentary, packed closely together in multiple spirals around the shoot axis, which extends only enough to accommodate the leaf primordia. Meanwhile, the buds expand to accommodate the shoot primordia. After a period of rapid leaf-primorida formation, the apex in each bud slows its activities and then becomes dormant, and the seedling has completed its first period of active shoot development. The lateral buds situated higher up the shoot tend to produce more preformed content and become larger than those lower down, but the terminal bud is always the largest on the seedling. The process, as described, produces a single-stemmed, one-season old, unbranched seedlings (Fig. 1A).

The extension growth up to and including the cotyledons was performed in the embryo in the seed. That is, the different elements were laid down, and thus apparent in a state of dormancy (rest and quiescence - Romberger 1963) in the embryo: when growth occurred, the preformed elements elongated by means of cell division and cell expansion. The extension growth above the cotyledons is the result of free growth (Jablanczy 1971), or neoformed growth (Halle et al. 1978). In such growth, the organ involved expands to its mature state immediately following its initiation - it does not experience a period of rest. On the other hand, the bud (or buds)contains elements (the leaf and stem-section primordia) which are preformed for the next growing season, and which experience a period of rest when in the bud.

In the second season, the shoot primordia begin to expand within the buds, and then the buds burst. The preformed stem sections and their accompanying preformed leaves elongate, and the preformed shoots extend. As this process begins, the shoot apices once again become active and initiate more lateral structures around their flanks. These differentiate as leaves and grow out immediately below the terminal shoot apex, but such neoformed growth is unlikely on the lateral shoots where the new lateral structures differentiate as bud scales. Transition to bud-scale initiation occurs on the terminal apex after a short period of neoformed growth. Thus, on the terminal shoot at least, some of the second-season leaves are preformed, and some are neoformed (Fig. 1B). Because bud formation starts earlier in the second season than it did in the first, the preformed content for the third season is greater than it was for the second season.

First-Season and Second-Season Development under Forced Conditions

Both the amount of growth, and to some extent the mode of development of spruce seedlings is different when forced. In the first season, neoformed growth occurs more rapidly, and thus, greater shoot elongation occurs and many more leaves are formed (Fig. 2A). New lateral-shoot apices are formed in the axils of some of the leaves progressively and acropetally. These lateral-shoot apices, however, instead of initiating bud scales and forming buds, initiate structures which differentiate immediately as leaves and then elongate to full size. At the same time, the stem sections at the bases of these new leaves elongate, so the new lateral shoots grow out immediately without having first rested in buds: their growth is neoformed and the shoot is a sylleptic shoot (sensu Halle et al. 1978).

Because these sylleptic shoots are produced acropetally, the lowest ones grow to greater lengths than those formed later. If conditions continue to support vigorous growth, side shoots may form sylleptically along the first-order lateral shoots. If conditions for growth become poorer (forcing is reduced or removed), then new lateral axes in the axils of leaves differentiate bud scales instead of leaves, and thus lateral buds are formed. Similarly, terminal buds are formed at the ends of all the lateral shoots and at the summit of the main stem (Fig. 2B). Within each of these buds, shoot primordia with preformed leaves for the next growing season are then formed.

In the second season, neoformed growth will occur on the terminal shoot as the preformed elements are expanding. It may also occur, but is less likely, on the more vigorous of the lateral shoots. The duration of neoformed growth will be less than in the first season, even under continued forced conditions. Sylleptic growth may again occur along the neoformed portion of the main stem, but is less likely than in the first season. Along the preformed portions of the shoots, lateral-bud initiation will occur concurrently with shoot elongation. Nevertheless, buds will tend to become larger and to have more preformed content if they are close to the terminal bud. The terminal bud of the seedling will be the largest (Fig. 2B).

PINES

First-Season and Second-Season Development under Normal Conditions

After the pine seed coat is shed and the cotyledons spread out, the primary leaves formed in succession by the apex form a rosette. That is, the primary leaves develop in a compact cluster, with always the latest-formed overarching the shoot apex. It is not until the rosette has reached a considerable size that elongation of some of the associated stem sections occurs. This elongation starts between the earliest-formed primary leaves and spreads upwards along the stem, but a rosette with no stem elongation is maintained in the upper portion of the stem. Thus, this form of growth has the effect of raising the terminal rosette of primary leaves. Once the basal stem elongation occurs, it becomes evident that lengths of successive primary leaves below the rosette increase with distance up the stem, while those remaining in the rosette decrease in length to the centre of the rosette (Fig. 3A). Lateral buds may form in the axils of some of the lowest of the primary leaves, and lateral buds may also become apparent in the axils of a few primary leaves at the base of the rosette (Lester 1968; Farrar 1976). Close examination of the axils of other primary leaves in the rosette will reveal other lateral-bud primordia. It is in this state that the seedling grown under poor to normal conditions becomes dormant. Thus, no terminal bud is formed: the shoot apex overwinters in the centre of the terminal rosette of primary leaves, protected by the overarching of the last-formed primary leaves (Fig. 3A).

Extension growth of the second season occurs only from elongation of the stem sections associated with the primary leaves that rested in the terminal rosette. As the second growing season starts, the primary leaves in the first-season rosette begin to spread apart acropetally. At the same time, the shoot apex resumes production of lateral structures, but they differentiate into scales and start to form a terminal bud. As extension growth continues, the lateral buds in the axils of the primary leaves which had formed the rosette, produce short shoots, each bearing secondary leaves. These secondary leaves usually elongate much more than do comparable leaves on short shoots on an older tree. Also, more secondary leaves per short shoot may be produced than is common on older trees (e.g., three secondary leaves on a short shoot instead of the usual two in Pinus banksiana or P. sylvestris). The primary leaves do not elongate in their second season. They are simply spread apart in the spiral order of their formation in the first-season rosette; therefore, there is an acropetal decrease in the lengths of successive primary leaves up the second-season portion of the extended long shoot (Fig. 3B).

Within the new terminal bud, development progresses throughout the second season. The apex continued to produce scales until conditions cause it, once again, to become dormant. The earlier-formed scales grow long enough to become part of the externally visible scales of the bud, but the later-formed ones remain inside the bud, as they elongate little. Short-shoot buds form in the axils of all scales except a few at the base of the bud, a few around the apex at the summit of the long-shoot primordium, and a few immediately below these latter, in the axils of which lateral long-shoot-bud primordia form. The short-shoot buds form their own scales and their apices may initiate secondary-leaf primordia before entering dormancy. Thus, the growth elements for extension of the main seedling axis for the third growing season are preformed in the second-season terminal bud. Lateral long-shoot buds may also be developed in a similar manner, below the terminal bud.

In such a two-season-old seedling, the position of the summit of the first season's growth cannot be detected externally (Farrar 1976). The position may be suggested by presence of short shoots with secondary leaves above it, but there is no ring of bud-scale scars or other marking to delineate the position (Fig. 3B). Internally, the summit of the first sheath of xylem increment marks the position (Farrar 1976).

Depending on relative conditions for growth, seed source, or species, some elements of development as described in what follows for forced growing conditions may be visible in pine seedlings grown in what are deemed to be non-forced, or normal conditions. The amount of variation in seedling development in pines, even in those of northern regions, is large. This may account for some of the apparent reluctance (cf. Farrar 1976) to describe seedling development of pines.

First-Season and Second-Season Development under Forced Conditions

When pines are well grown in their early stages, or are forced by long photoperiods, high temperatures or high nutrition, first-season growth is substantially greater than that described for poor or normal (non-forced) conditions. In addition, development is variable. Farrar (1976) briefly described three forms of first-season development, and Thompson (1981) labelled forms Type 1 and Type 2, and described a third variant (which he grouped with Type 2). Thompson (1981) also indicated presence of a terminal "bud" of varible size in his Type 1 seedlings. When these variations in development are grouped, at least four variants are apparent in northern pines and between-species differences may account for others. Also **in** the whole genus, other patterns occur (Lanner 1976), but Lanner (1976) included only one of the variants described in this paper.

Stylized (and generalized) diagrams of the four variants are shown in Figs. 4 to 7. The first (Fig. 4) is similar to the development already described for non-forced pines, but the number of primary leaves produced is greater, and a few lateral buds initiated in the axils of primary leaves differentiate and grow into mature structures in the first season (Fig. 4A). Commonly, one or more differentiate into basal, sylleptic long shoots, lacking their own basal bud scales, and bearing primary leaves. This feature is common to all forced variants, whether or not it is depicted in the figures. A few lateral buds differentiate scales and then short shoots with elongated secondary leaves of variable length. Second-season extension is entirely from the rosettes of primary leaves (on the main stem and on basal long shoots), and secondary leaves are borne on short shoots in the axils of virtually all the primary leaves that had rested in the rosettes (Fig. 4B). In the second season, terminal and lateral long-shoot buds are formed, and these develop preformed elements for third-season growth.

In the second variant (Fig. 5), a small terminal long-shoot bud (and possibly lateral long-shoot buds) is developed in the centre of the rosette. The rosette, itself, is in consequence, comprised of fewer primary leaves (Fig. 5A). Elongation in the second season is the result first of expansion of the stem section subtending the primary leaves of the rosette, and second, of expansion of the stem section subtending the scales that made up the terminal bud. Thus, the preformed growth of the terminal long shoot of the second season has two origins (Fig. 5B). Short shoots with secondary leaves are borne in the axils of most of the primary leaves that had rested in the rosette and of all except, perhaps, the first and last scales which had occurred in the terminal bud. If one or more small lateral long-shoot buds had been formed below the terminal bud at the centre of the rosette, then lateral long shoots would have elongated above the points of attachment of the last primary leaves. As extension growth occurs, the new terminal long-shoot bud (buds if more than one long shoot elongated), and new lateral long-shoot buds develop their content for the next season.

In the third variant (Fig. 6), the shoot apex, in the first season, changes from production of primary leaves to production of scales at a relative early stage (Thompson 1981) and all stem sections associated with primary leaves undergo full extension (Fig. 6A). Thus relatively few primary leaves are produced and first-season height growth ceases earlier than in the variants described earlier. Lateral long-shoot buds are likely to form below the terminal long-shoot bud, which becomes relatively large. Short shoots with secondary leaves develop in the axils of most of the primary leaves (Fig. 6A). The second-season growth results entirely from expansion of the stem sections associated with the scales of the long-shoot buds (Fig. 6B), as is the case in older northern pines. For P. banksiana, Farrar (1976) observed production of an intermediate whorl Tnot a basal whorl from separate lateral long-shoot buds) of lateral long shoots on some specimens. These lateral long shoots were preformed as lateral long-shoot primordia part way along the main shoots axis within the terminal long-shoot bud.

In the fourth variant (Fig. 7), primary-leaf production occurs for longer, and thus is greater, than that of the third variant. A terminal bud, but normally no lateral long-shoot buds (Thompson 1981), is formed and then the stem sections associated with the primary leaves in the rosette elongate within the first growth season. Short shoots also develop in the axils of these primary leaves, but extension of the secondary leaves is limited and results in a acropetal decrease of lengths achieved by secondary leaves of these short shoots (Fig. 7A). The second season's growth occurs solely by expansion of the stem sections associated with the scales of the small terminal bud (Fig. 7B). As in the other variants, terminal and lateral long-shoot buds are formed during the second season: they contain the preformed elements of growth for the third season.

BIRCHES

First-Season Development under Normal Conditions

The shoot apex between the bases of the two oppositely arranged cotyledons produces single leaves in turn, their number being dependent on the conditions of growth. Under a stand of trees only one or two leaves are produced, but under open conditions, several leaves will form. Each leaf, in turn, covers the apex while the next is being formed. Then, when the apex is adequately protected by the next leaf and its stipules, the first expands its lamina and extends its petiole and then the associated stem section elongates. This manner of growth follows a zig-zag pattern in the vertical sense, and also a spiral pattern in the horizontal sense with each new leaf developing in a position about 137° away from the previous one. The first-formed leaf is usually small and three-lobed; later leaves are progressively larger (Fig. 8A) and the number of indentations around the margins are gradually increased through coarsely serrate to serrate, to evenly doubly serrated (if enough leaves are produced to cover the full range). The first-season leaves are usually densely pubescent. Lateral buds are initiated in the axils of the cotyledons and the leaves, but their development is slow until height growth ceases. Then they develop more fully, and the later-produced buds become larger than the earlier-produced ones and usually produce two preformed leaves. The shoot apex, however, usually aborts along with some its latest products or possibly remains as a "loose" bud of stipule pairs and primordial laminae (Downs and Borthwick 1956). If the apex is aborted, height growth of the second season is derived from a lateral bud, and the mode of growth is sympodial by substitution (Halle et al. 1978).

First-Season Development under Forced Conditions

In birches, the differences between first-season development of seedlings under normal and forced conditions are similar to those of spruces. When forced, birch seedlings produce much more of the same kind of growth as normally grown seedlings, but also tend to produce sylleptic shoots (Fig. 8B), though the capacity for sylleptic growth varies with species. When sylleptic shoots are formed, they form acropetally from leaf axils in the middle region of the main stem, and therefore are shorter towards the tip of the main stem, where, when conditions change, normal lateral buds are formed. As in the case of non-forced conditions, when lateral buds are produced, their content inside the bud scales is restricted to usually two differentiated leaves and their accompanying stipules, and possibly one or more undifferentiated primordia around the apex. Thus, growth of vigorously elongating shoots of the second season, which bear several leaves, is only partially preformed in the buds.

OAKS

First-Season Development under Normal Conditions

As the shoot developed by the hypogeously germinating oak seed extends above ground, its apex is already forming lateral appendages. The first two to four of these are normally scale-like, but at times may become small, rudimentary leaves (Olsen and Boyce 1971). They are usually arranged spirally up the stem, but sometimes two are produced opposite each other. Later lateral appendages develop into the first set of true leaves. These can be described as a set because little elongation of their associated stem sections occurs between them, so they develop at the summit of the new shoot as it reaches the end of its rather brief period of elongation. The leaves tend to be scarcely lobed, or to have sinuate, undulate or scarcely dentate margins, the lobes or teeth may or may not be equipped with short spinose tips, depending on species. Above this set of leaves, the shoot apex forms more scales (stipules) and then a terminal bud. Lateral buds may form in the axils of the lower of these scales, as well as in the axils of the leaves, the scales or rudimentary leaves situated lower on the stem (Fig. 9A), and the cotyledons (Kurmes and Boyce 1964).

Sometimes, depending on conditions and species, a second surge of elongation occurs under normal conditions. However, because such a surge of growth is a constant feature of forced growth, it will be described under the next heading.

First-Season Development under Forced Conditions

When forced, the height growth achieved by the first surge of growth is greater than that under non-forced conditions (Fig. 9B). After that surge of growth, during which a terminal (and lateral) bud was formed, the seedling "rests" for about 16 days. Then the shoot primordium which has been formed within the terminal bud expands, the bud bursts, and the shoot elongates rapidly. As it does so, preformed scales and leaves expand. The scales occupy positions along the lower part of the elongated shoot while most of the leaves are again clustered in a set at the summit (Fig. 9B). As this second surge of shoot elongation comes to an end, the apex will already have started to form another terminal bud, and, again, lateral buds are formed. The second set of leaves are generally larger, and more deeply and definitely lobed than the first set - they are more similar to the "adult" leaves associated with the species concerned.

If conditions remain good, after another break of about 16 days, a third surge of growth may occur. The result is another segment of shoot with scales and a set of leaves which are more "adult-like" still, and another cluster of buds at the terminal point (Fig. 9B). A fourth, or even a fifth surge of height growth may occur in the first season if conditions remain good. Each surge of growth after the first is essentially preformed in the terminal bud at the summit of the previous surge of growth. Normally, all of the lateral buds remain inhibited and thus do not form shoots in the first season.

CONCLUSIONS

Seedlings of spruce and birch respond to forced conditions in their first season by producing continuous neoformed growth above the preformed cotyledons. This growth can include sylleptic shoots which increase crown volume substantially. Seedlings of pine can also produce neoformed growth continuously in their first season, but in many instances, subjection of the seedling to forced-growth conditions results in terminal-bud formation and hence less ultimate height growth and crown volume. First-season seedlings of oak produce one limited surge of neoformed growth following hypogeal germination. If forced, they will subsequently produce more surges of growth derived from preformed elements in successive terminal buds, thus exhibiting several cycles of rhythmic growth.

In the second season, after a period of rest, spruces and birches extend many and few preformed elements, respectively, while initiating more stem units which grow out immediately (neoformed growth) before bud formation. This second-season growth is derived from a terminal bud in spruce, but more probably from a lateral (pseudoterminal) bud in birch. In (northern) pines, all second-season extension growth is preformed and produced in one surge of growth (even in multiwhorled

P. *banksiana* and P. *contorta*). This growth is derived from elongation of stem sections between first-season rosette-borne primary leaves, between scales of terminal buds, or between both primary leaves and scales of terminal buds. In the second season, the shoot apex of pine produces only elements for the new terminal bud. In oaks, second-season extension growth is preformed in the last terminal bud of the previous year, and in subsequent buds produced **in** rhythmic sequence in the second season.

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Table 1. The spruce, pine, birch and oak species which have been the subjects of repeated observations, and additional sources of information used in developing generalized descriptions of early shoot development on seedlings.

Genera	Species	Sources of additional information
Spruce	*Picea abies* (L.) Karst	Dormling et al. 1968; Gregory and Romberger 1972.
	Picea glauca (Moench) Voss	Jablanczy 1964, 1971; Pollard 1974; Pollard and Logan 1977, 1979.
	Picea mariana (Mill.) B.S.P.	Jablanczy 1964, 1971; Pollard and Logan 1977; 1979.
	Picea pungens Engelm.	USDA 1948; Young and Hanover 1976. 1977, 1978.
	Picea rubens Sarg.	Jablanczy 1964, 1971.
Pine	*Pinus banksiana* Lamb.	Lester 1967, 1968; Riding and Lester 1968; Farrar 1974, 1976.
	Pinus contorta Dougl.	Thompson 1976; Wheeler 1979.
	Pinus nigra Arn.	Lester 1968.
	Pinus resinosa Ait.	USDA 1948; Lester 1967, 1968; Riding and Lester 1968; Sasaki and Kozlowski 1969; Farrar 1974, 1976.
	Pinus strobus L.	Fowler 1961; Lester 1968.
	Pinus sylvestris L.	Wareing 1950a, b; Denne 1971; Thompson 1981.
Birch	*Betula alleghaniensis* Britton	Winget and Kozlowski 1965.
	Betula papyrifera Marsh.	Yeatman and Voigt 1958; Grant and Thompson 1975.
	Betula populifolia Marsh.	USDA 1948; Grant and Thompson 1975.
Oak	*Quercus macrocarpa* Michx.	USDA 1948; Kurmes and Boyce 1964.
	Quercus rubra L.	Farmer 1975; Immel et al. 1978.

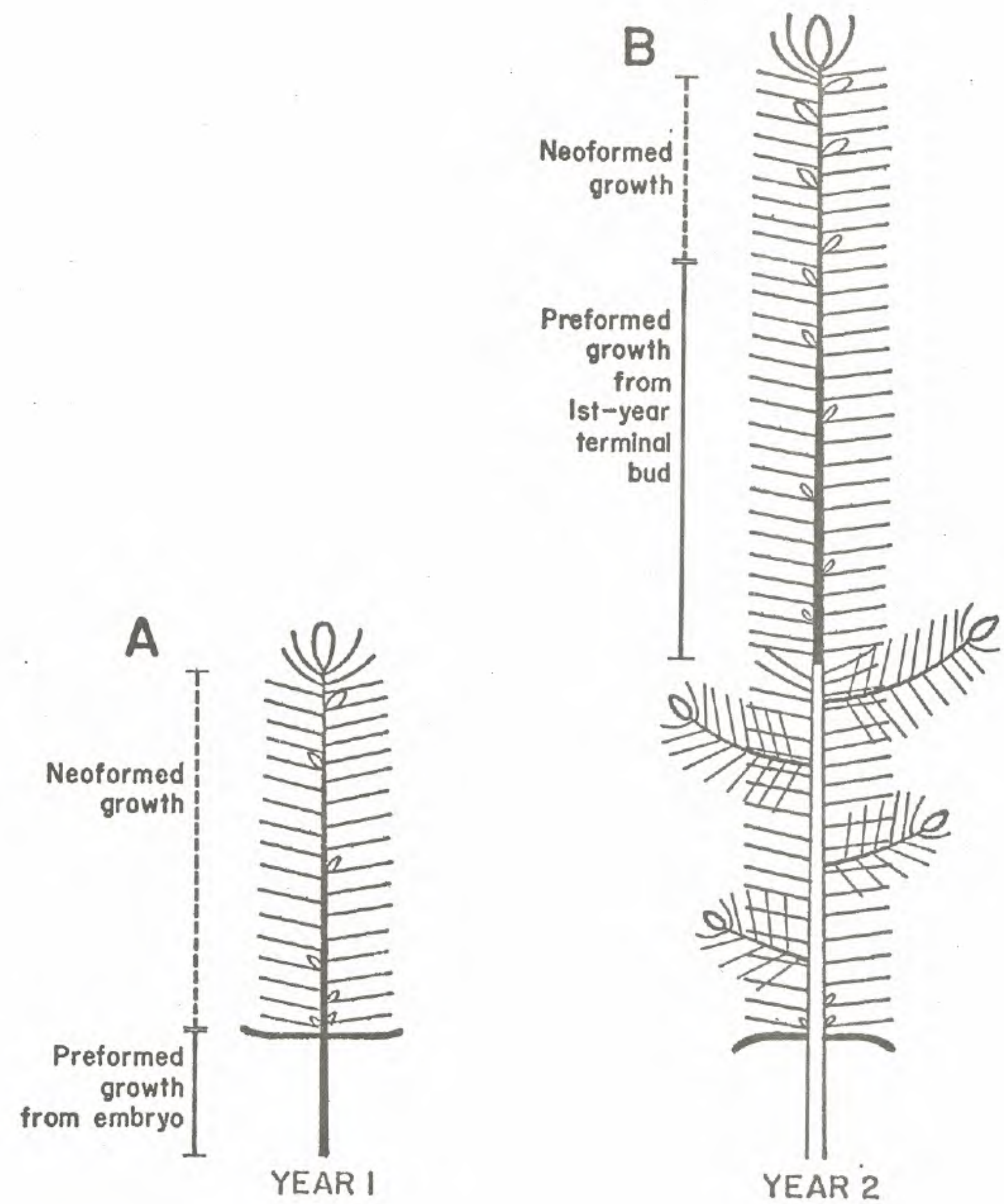

Figure 1. The shoot system of a spruce seedling grown under normal growth conditions: A. after one growing season, B. after two growing season. Leader growth in the second year is partially preformed in the first-season terminal bud and partially neoformed. In this and subsequent figures, the buds depicted can be assumed to contain preformed stem units roughly proportional in number to the bud sizes shown.

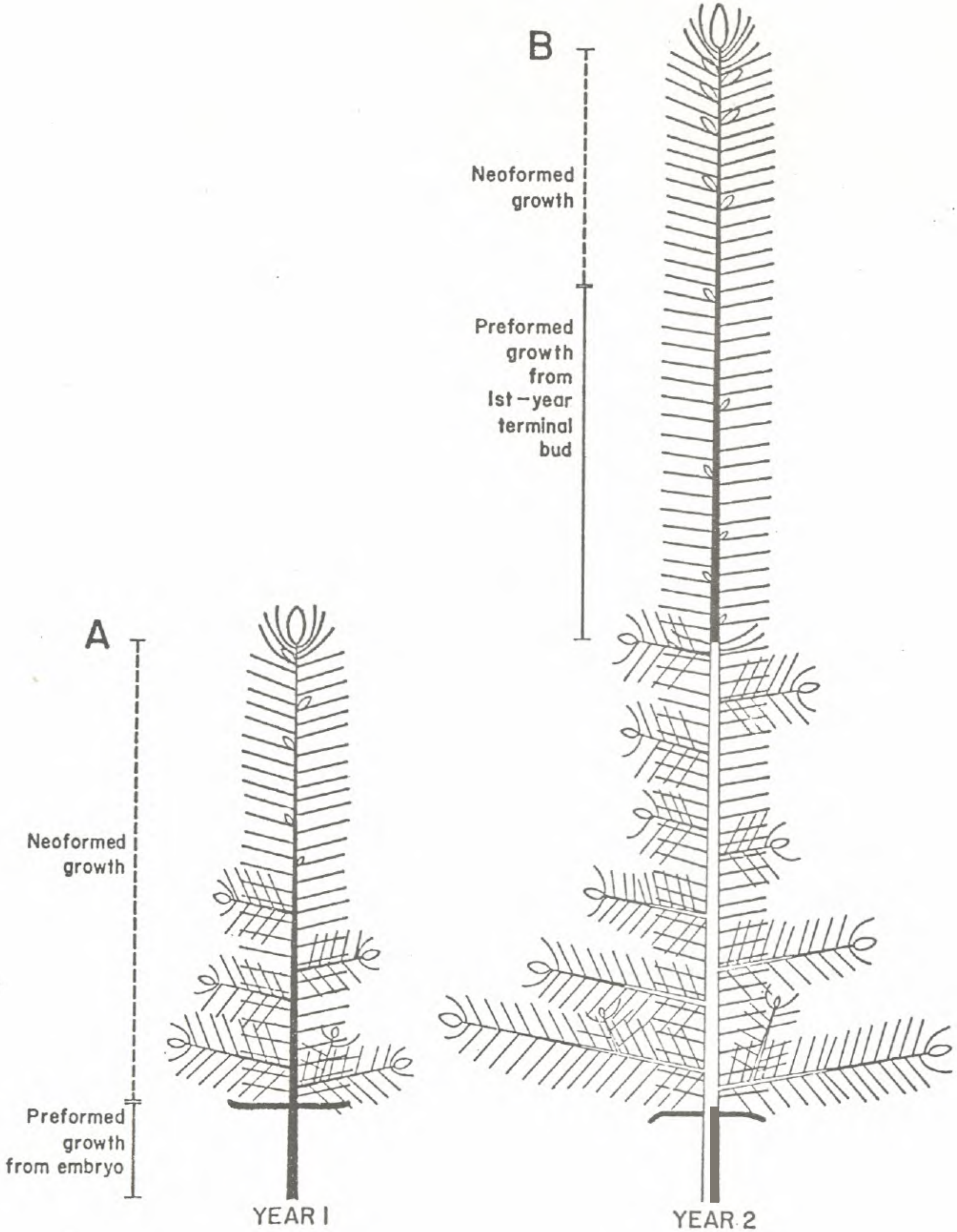

Figure 2. The shoot system of a spruce seedling grown under forced growth conditions: A. after one growing season, B. after two growing seasons. Sylleptic shoots, which are common in the first season, are shown without remnants of bud scales at their bases (because they have none); whereas shoots derived at least partially from scaly resting buds are shown with remnants of their bud scales at their bases.

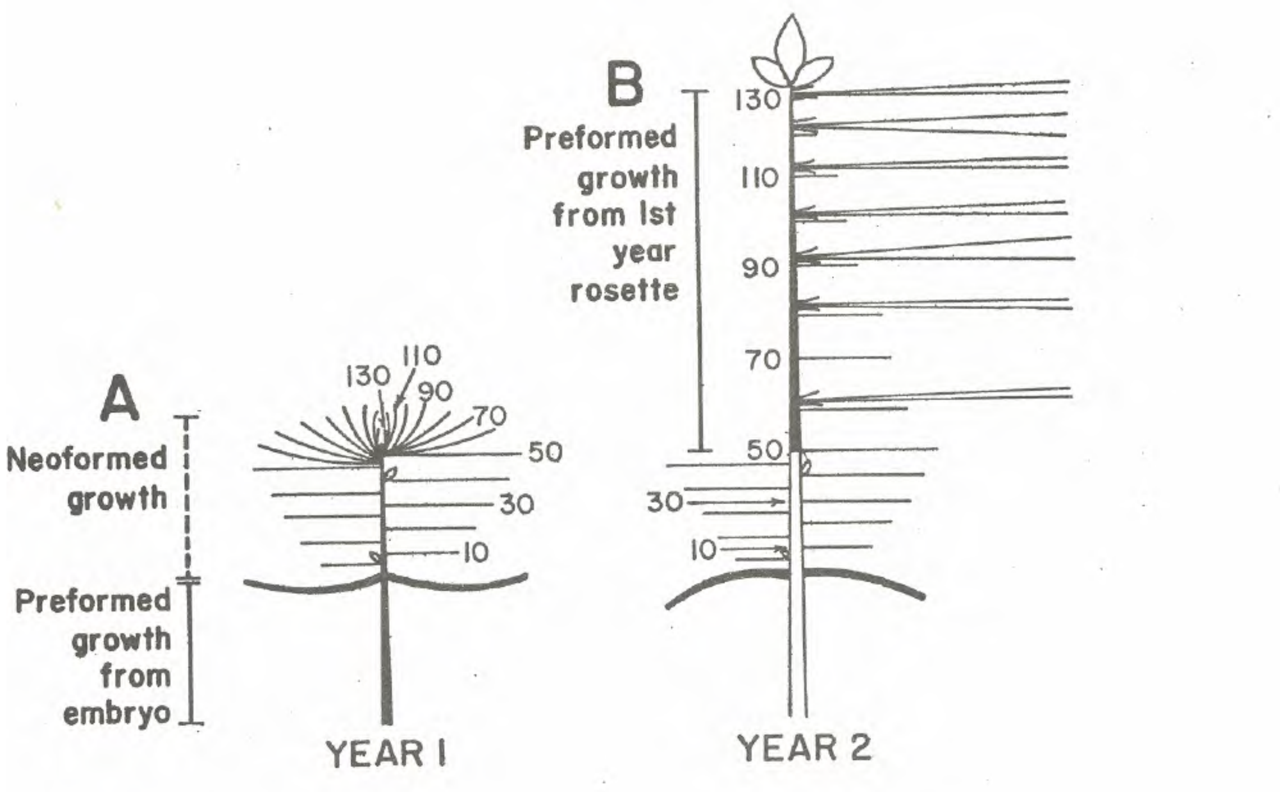

Figure 3. The shoot system of a pine seedling grown under normal growth conditions: A. after one growing season, B. after two growing seasons. The numbers of primary leaves indicated are as given by Farrar (1976) for Pinus banksiana, and are used as a basis for hypothetical comparison with the variants of development shown in Figs. 4 to 7. In the second season short shoots bearing long secondary leaves grow in the axils of the primary leaves (numbered 50 to 130) which had formed the resting rosette of primary leaves.

Figure 4. Variant 1 of the shoot system of a pine seedling grown under forced growth conditions: A. after one growing season, B. after two growing seasons. All second-season growth is preformed in the first-season terminal rosette of primary leaves numbered 120 to 240 (see Fig. 3 for explanation of the numbers.

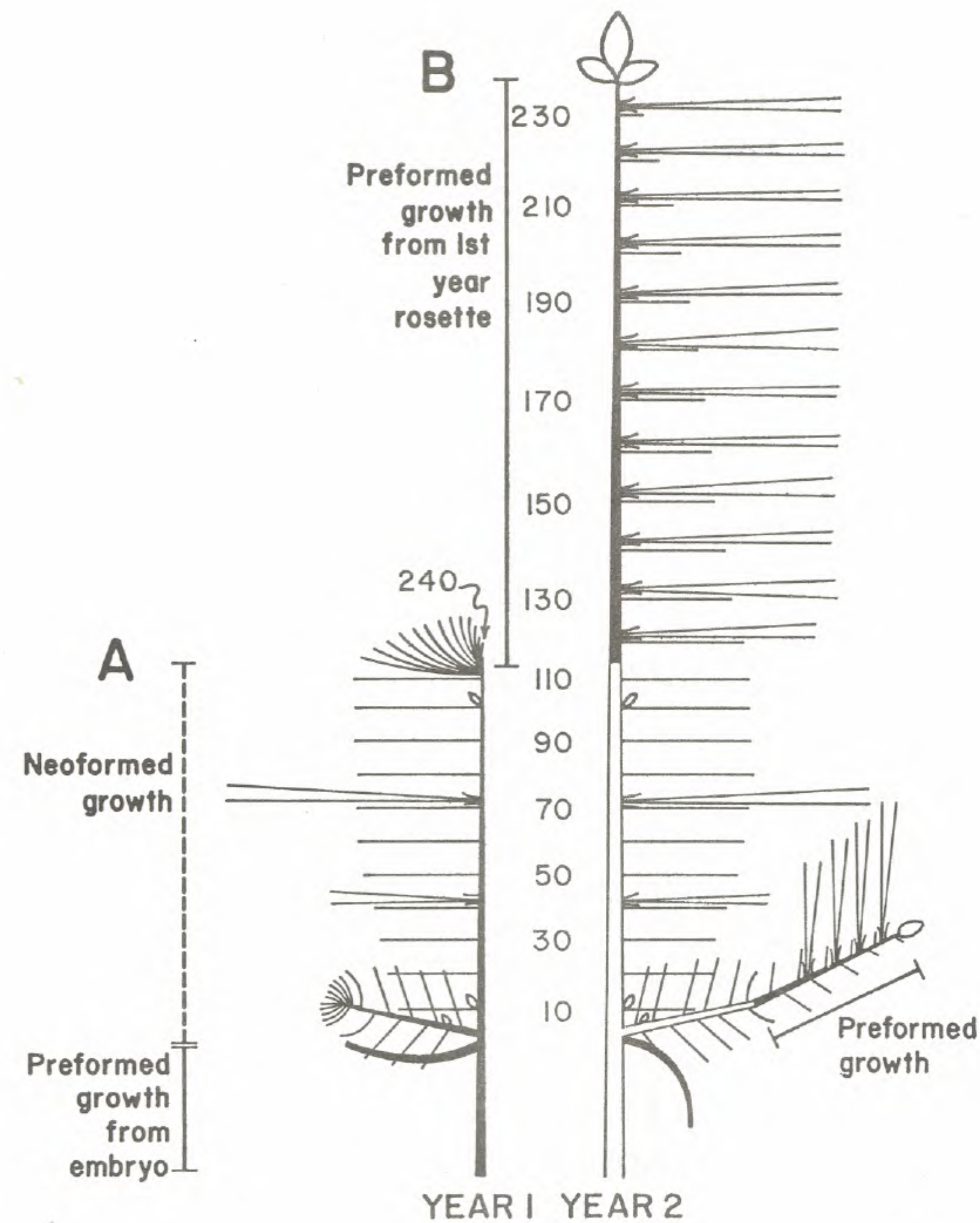

Figure 5. Variant 2 of the shoot system of a pine seedling grown under forced growth conditions: A. after one growing season, B. after two growing seasons. The second-season growth is partially preformed in the first-season rosette of primary leaves (numbered 120 to 170) and partially preformed in the first-season terminal bud (scales from the bud are shown as wedge-shapes numbered 180 to 230 - see Fig. 3 for explanation of the numbers).

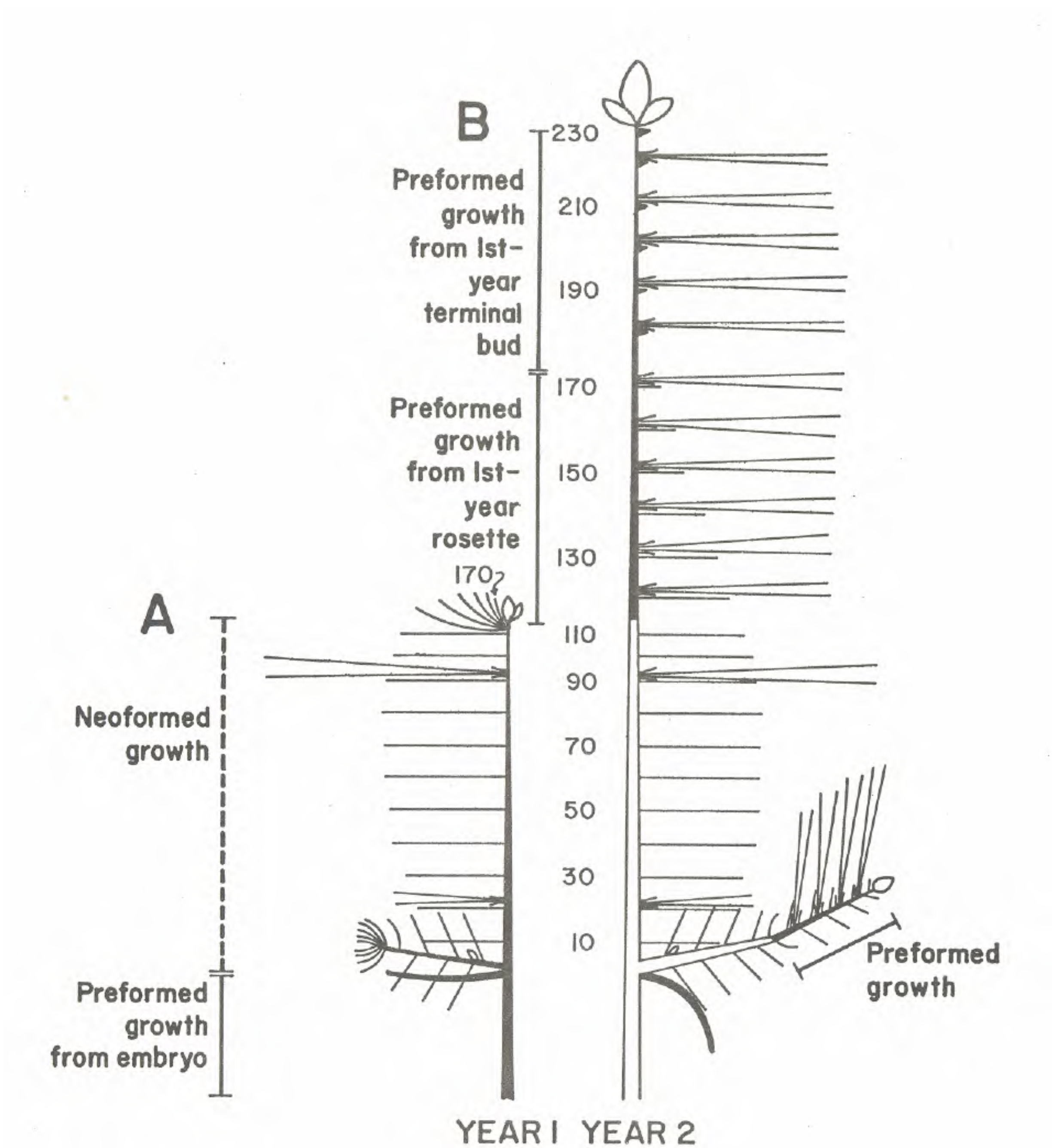

Figure 6. Variant 3 of the shoot system of a pine seedling grown under forced growth conditions: A. after one growing season, B. after two growing seasons. The second-season growth is preformed in the first-season terminal bud (scales from the bud are shown as wedge-shapes numbered 90 to 180) and all first-season stem sections are elongated early in the first season (see Fig. 3 for explanation of the numbers).

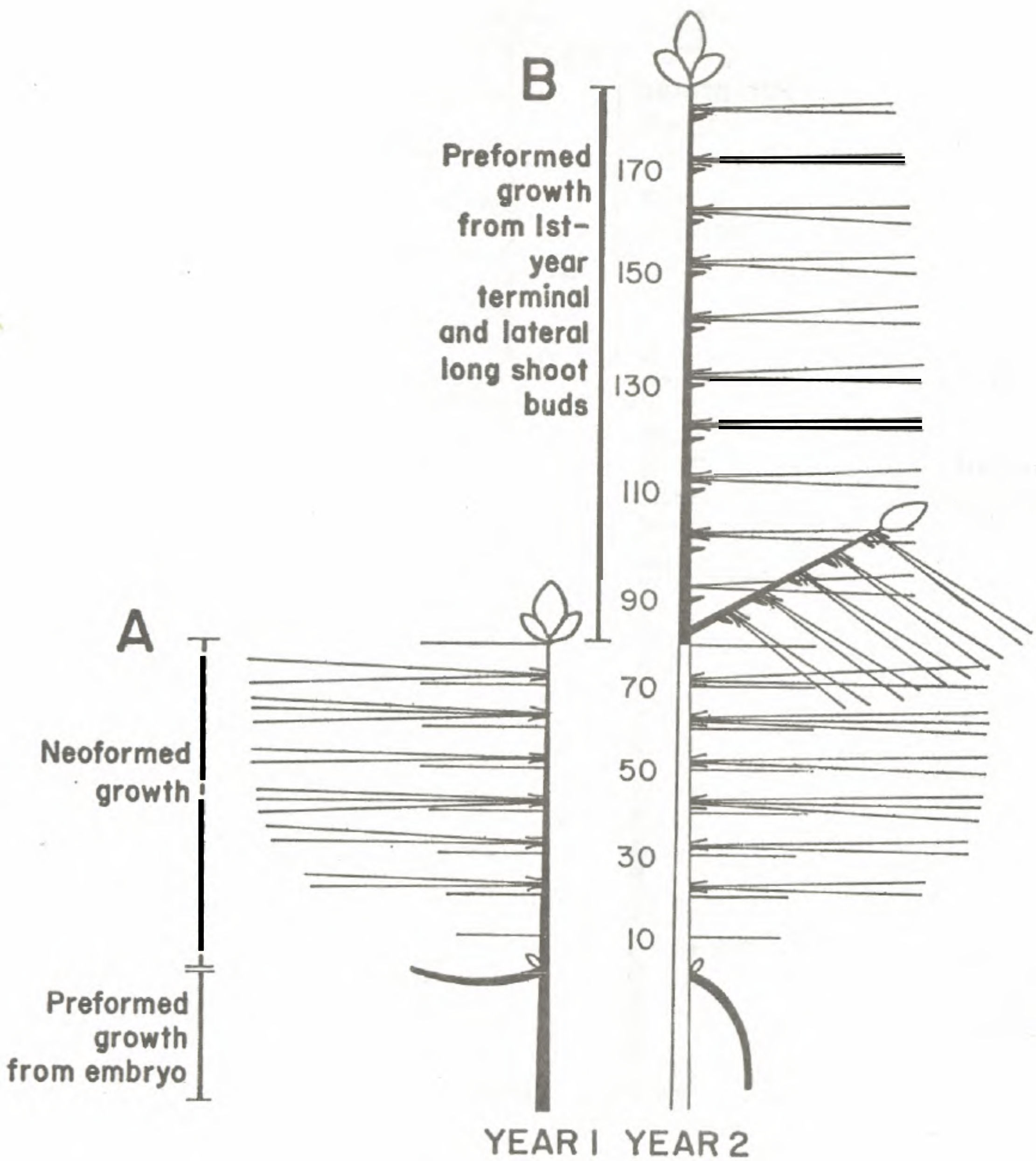

Figure 7. Variant 4 of the shoot system of a pine seeding grown under forced growth conditions: A. after one growing season, B. after two growing seasons. The second-season growth is preformed in the first-season terminal bud (scales from the bud are shown as wedge-shapes numbered 180 to 230) which forms before the stem sections of the first-season rosette of primary leaves (numbered 100 to 180) and the short secondary leaves on short shoots in their axils are elongated late in the first season (see Fig. 3 for explanation of the numbers).

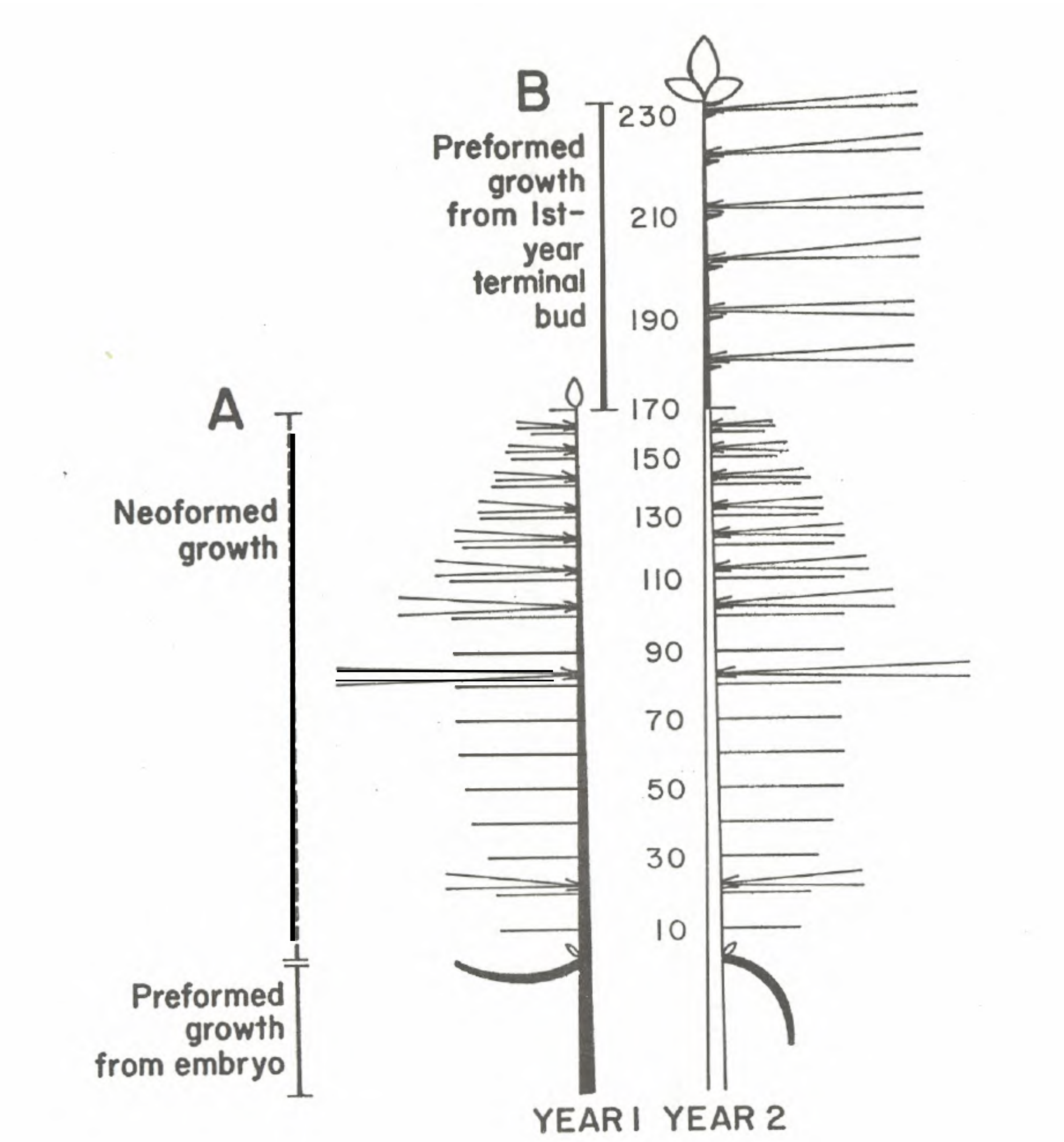

Figure 8. The first-season shoot system of a birch seedling: A. grown under normal conditions, and B. grown under forced conditions. The pair of stipules which occurs at the base of each leaf is represented by a single short line: an axillary bud develops and is shown in the axil of each leaf and of each cotyledon.

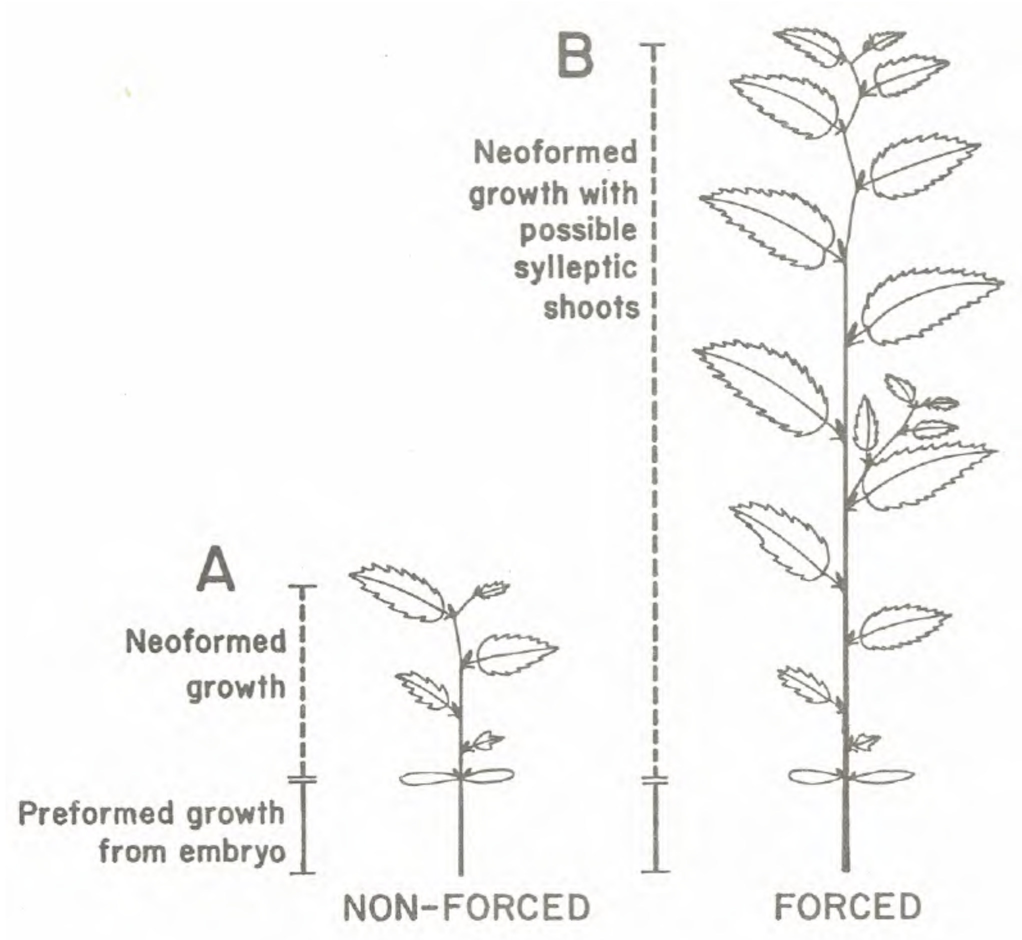

Figure 9. The first-season shoot system of an oak seedling: A. grown under normal conditions, and B. grown under forced conditions which permit several successive surges of essentially preformed growth from terminal buds after the initial surge of neoformed growth subsequent to hypogeal germination. Scales are shown as single lines subtending lateral (axillary) buds, pairs of stipules are represented by single lines subtending leaves.