Leader growth and the architecture of three North American hemlocks

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Height growth in hemlock (*Tsuga canadensis* (L.) Carr., *T. heterophylla* (Raf.) Sarg., *T. mertensiana* (Bong.) Carr.) is by rhythmic growth of a monopodial axis with continuous branch production throughout the growing season. Leader growth is plagiotropic and leader erection is a process lasting several years. Two types of events disrupt the basically monopodial nature of the axis. (1) Frequent (43%) apical meristem death shifts dominance to a nearby lateral branch in *T. canadensis*. (2) Weak apical control allows occasional shifts in dominance from the leader to a branch without meristem death (13 and 24% in *T. heterophylla* and *T. canadensis*, respectively, but none in *T. mertensiana*). These growth patterns contain elements of several tree architectural models but fit none well.

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La croissance en hauteur de la pruche (*Tsuga canadensis* (L.) Carr., *T. heterophylla* (Raf.) Sarg., *T. mertensiana* (Bong.) Carr.) se produit par la croissance rythmique d'un axe monopodial, avec production continue de rameaux durant toute la saison de croissance. La croissance de la pousse terminale est plagiotrope et son redressement est un processus qui se poursuit durant plusieurs années. Deux types d'événements pertubent la nature fondamentalement monopodiale de l'axe. (1) La mortalité fréquente (43%) du méristème apical amène le transfert de la dominance vers un rameau latéral avoisinant chez *T. canadensis*. (2) Un contrôle apical faible permet occasionnellement le transfert de la dominance de la pousse terminale vers un rameau sans que le méristème meure (13 et 24% chez *T. heterophylla* et *T. canadensis* respectivement, maix aucun chez *T. mertensiana*). Ces modes de croissance contiennent des éléments de plusieurs modèles architecturaux des arbres, mais ne correspondent précisément à aucun d'entre eux.

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As early as 1915, Frothingham commented on the nonerect or drooping leading shoots of eastern hemlock *Tsuga canadensis* (L.) Carr. More recently, Mergen (1958) described the process of leader extension and straightening in eastern hemlock. He showed that continual production of reaction wood in the current season's leader led to the gradual erection of the leader from a near horizontal position in July to near vertical in October.

Most recently, several authors have discussed hemlock in terms of tree architecture and placed it within two distinctly different models. Edelin (1977) placed eastern and western (*T. heterophylla* (Raf.) Sarg.) hemlock in Mangenot's model in which the season's growth is initially vertical, and later, with an abrupt transition, horizontal. Height growth is by a superposition of these annual units, and the main axis is therefore sympodial. This pattern is commonly seen in *Vaccinium corybosum* L. and is illustrated in Fig. 1A. Hallé *et al.* (1978) have placed eastern hemlock in Troll's model in which all axes are plagiotropic, and height growth is by superposition of the axes. The main axis is therefore also sympodial (Fig. 1B). A third model, Champagnat's, has some similarities with the above two. Vertical axes become pendulous under their own weight, and height growth is then by superposition of these units to form a sympodial main axis. This growth pattern is seen in *Sambucus nigra* L. and is illustrated in Fig. 1C.

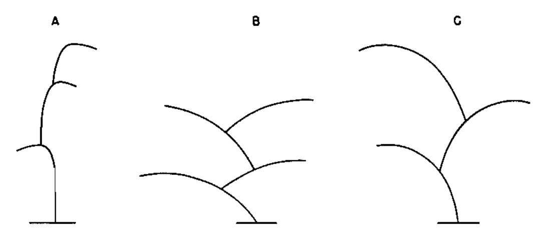

FIG. 1. (A) Mangenot's model. (B) Troll's model. (C) Champagnat's model.

In light of this apparent confusion about growth habits in hemlock, the object of this study was to follow the processes of (*i*) leader growth and straightening and (*ii*) injury and leader replacement, and then to relate the findings in terms of the models and definitions of tree architecture (Hallé *et al.* 1978). Emphasis is placed on eastern hemlock but information on western and mountain (*T. mertensiana* (Bong.) Carr.) hemlock is included.

Materials and methods

Eastern hemlock

During the 1979 growing season and again in April 1980, the growth and incidence of apical meristem injury or death and subsequent leader replacement was followed in a population of 42 hemlock trees, 1.5–6 m tall, growing under an open canopy of red pine (*Pinus resinosa* Ait.) at the Harvard Forest, Petersham, Massachusetts. Damage to the 1978 growth

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(damage that had occurred in 1978) and subsequent leader replacement were also noted.

In this same population, the deviation from vertical of the 1978 and 1979 growth was measured in October 1979, and the deviation of the 1977, 1978, and 1979 growth was measured in April 1980. Measurements were made with a weighted protractor suspended from a string. The actual angle measured was the deviation from vertical of a line drawn between the beginning and end of a given season's growth.

Fourteen eastern hemlock stems, 2–5 m tall, were dissected to determine which of the present live branches had at one time been the main leader of the tree. Eight of these trees (11 to 16 years old) came from the area of the above population of 42 trees and 6 were the top 10 to 17 years of growth from 14–15 m overstory trees in a nearby mixed hemlock–hardwood forest.

The pith was exposed to determine whether a particular portion of the tree axis maintained the continuity of the pith from the previous portion or arose as a branching from it. A leader was defined by linear continuity of the pith; a branch was defined by branching of the pith (Fig. 2). When it was determined that an axis arose as a branch, the age at which dominance changed from the old leader (now branch) to the replacement leader was considered to be when the diameter of the replacement leader was greater than that of the old leader. This age is expressed as the number of years since initiation of the branch and leader, as determined by ring counts.

Western and mountain hemlock

In July 1980, near Elbe, Washington, at about 1000 m altitude, deviation from vertical of 1978, 1979, and 1980 growth was measured and the incidence of leader replacement in the last 6–10 years growth was determined on fifteen 1–2 m tall open-grown western hemlock trees. Similar measurement was made at 1300 m on sixteen 1–2 m tall open-grown mountain hemlock trees.

Results

Eastern hemlock

The main axis of an eastern hemlock tree is vertical although at least the top 3 years of growth often show a pronounced curvature (Table 1). The most distal portions may approach horizontal while older portions of stems are more erect. Presumably because most hemlock leaders are initiated in a near horizontal position, leaf arrangement is planar, although the phylotaxy is spiral. There was a slight increase in leader angle between fall and spring.

Changes in leader dominance (a former branch becoming the main leader of the tree) were found to be of two types. In the first type, death of the apical meristem causes shifts during the current growing season or between this season and the next growing season. This shift involves fine twigs and external evidence of a changeover disappears in 3–4 years. In 1978, 31% of the apical meristems were injured or killed and replaced by a lateral. In 1979, 55% were similarly replaced. The cause of meristem injury or death is not clear; sometimes they appeared eaten and sometimes simply deformed. Damage occurred during the growing season, rarely during winter.

The second type of leader shift was not directly attributable to meristem death. Here, apparently normal and healthy leaders lost dominance, became plagiotropic, and were replaced by former branches. Many years after the leader had become a branch, it would be growing and functioning as a normal branch. This type of shift appears to be common (Table 2). These shifts tended to take place in the first 3 years after leader initiation but could take place up to 6 years later.

Western and mountain hemlock

The pattern of height growth in western hemlock is nearly identical to that of eastern hemlock. Leaders drooped (Table 1), had a planar needle arrangement, and showed frequent leader replacement in dominance by a branch (Table 2). The leader of western hemlock hung considerably lower than that of eastern hemlock, presumably related to the greater annual leader growth in the former (more pendulous in July).

Annual leader growth in mountain hemlock was only 3–5 cm. Needle arrangement was not planar, and leader replacement was infrequent (Table 2). In spite of these differences with eastern and western hemlocks, leaders in mountain hemlock were plagiotropic and gradually erected over 3 or more years (Table 2).

Western or mountain hemlocks exhibited little apical meristem injury or death and subsequent leader replacement.

Discussion

Height growth of eastern hemlock

The process of height growth in eastern hemlock is more complex than previously described. Mergen (1958) showed that leaders do become more erect over their first growing season and the following fall. The results reported here indicate that the straightening process may take several years. It is not clear whether the initial drooping condition is the result of simple plagiotropy or an inability to support the weight of twig and needles. Mergen's observation that the distal few centimetres of the leader tend to point upward is evidence for the latter, which would indicate the secondary plagiotropy described in Champagnat's model.

Mergen's trees had nearly vertical leaders at the end of the growing season, compared with 50–60° found in this study. The cause of this difference is not clear but may be related to the unusual amount of growth of his trees (50 cm versus 25 cm in this study) under nursery conditions.

TABLE 1. The angle of deviation in a given year's growth from the vertical. Mean ± SE

	Measurement time			
	Eastern hemlock		Western hemlock	Mountain hemlock
Year	October 1979	April 1980	July 1980	July 1980
ϕ1980[a]	—	—	−61.33±3.76[b]	52.81±6.55
ϕ1979	50.5±2.4	57.5±2.5	60.00±5.34	49.37±4.49
ϕ1978	20.7±1.9	29.5±2.1	32.33±4.61	20.00±2.74
ϕ1977	—	12.7±1.6	—	—

[a]Angle of departure from vertical of a line drawn from proximal to distal end of growth of a given year.
[b]Minus sign indictes distal end of 1980 growth was below proximal end.

TABLE 2. Mean (± SE) number of shifts in dominance from leader to branch without apical meristem death

Species	N^a	No. of shifts per 10 years
Eastern hemlock, understory	110	2.73±0.43
Eastern hemlock, overstory	82	2.05±0.45
Western hemlock	116	1.29±0.31
Mountain hemlock	80	0.38±0.21

[a]Total number of years of growth examined.

There is frequent meristem injury or death resulting in leader replacement by a branch. In the 2 years of observation, an annual average of 43% of the leaders were so replaced. Because eastern hemlock produces laterals on the current season's growth, this replacement is usually by the lateral meristem closest to the lost apical meristem. The process is rapid, and diameter growth in subsequent years obscures the event.

Shifts in leader dominance also occur without associated leader death, the immediate cause of this shift being unclear. About 24% of the leaders were replaced in this way. The drooping behavior of hemlock leaders and the growth of laterals on the current year's leader may both be taken as indications of a weak or otherwise unusual process of apical dominance and control. The frequent shifts in dominance between branches and the leader may also be part of the same syndrome.

There are several points to be made in summarizing the method of height growth of eastern hemlock. (1) Leader growth is probably secondarily plagiotropic and axis erection is a process lasting several years. (2) As is found in most other conifers, height growth in hemlock is at least potentially monopodial. (3) Height growth is in practice sympodial because of frequent meristem death or later shifts in leader dominance. These changes, however, might be considered unpredictable events resulting from accident (meristem death) or poor apical control (later shifts). (4) The initial plagiotropy of the leader produces a planar leaf arrangement. This planar arrangement is repeated in branch arrangement and is apparent years after the leader has become erect. The branch plane shifts from year to year because of shifts in the direction that the leader droops.

Western and mountain hemlock

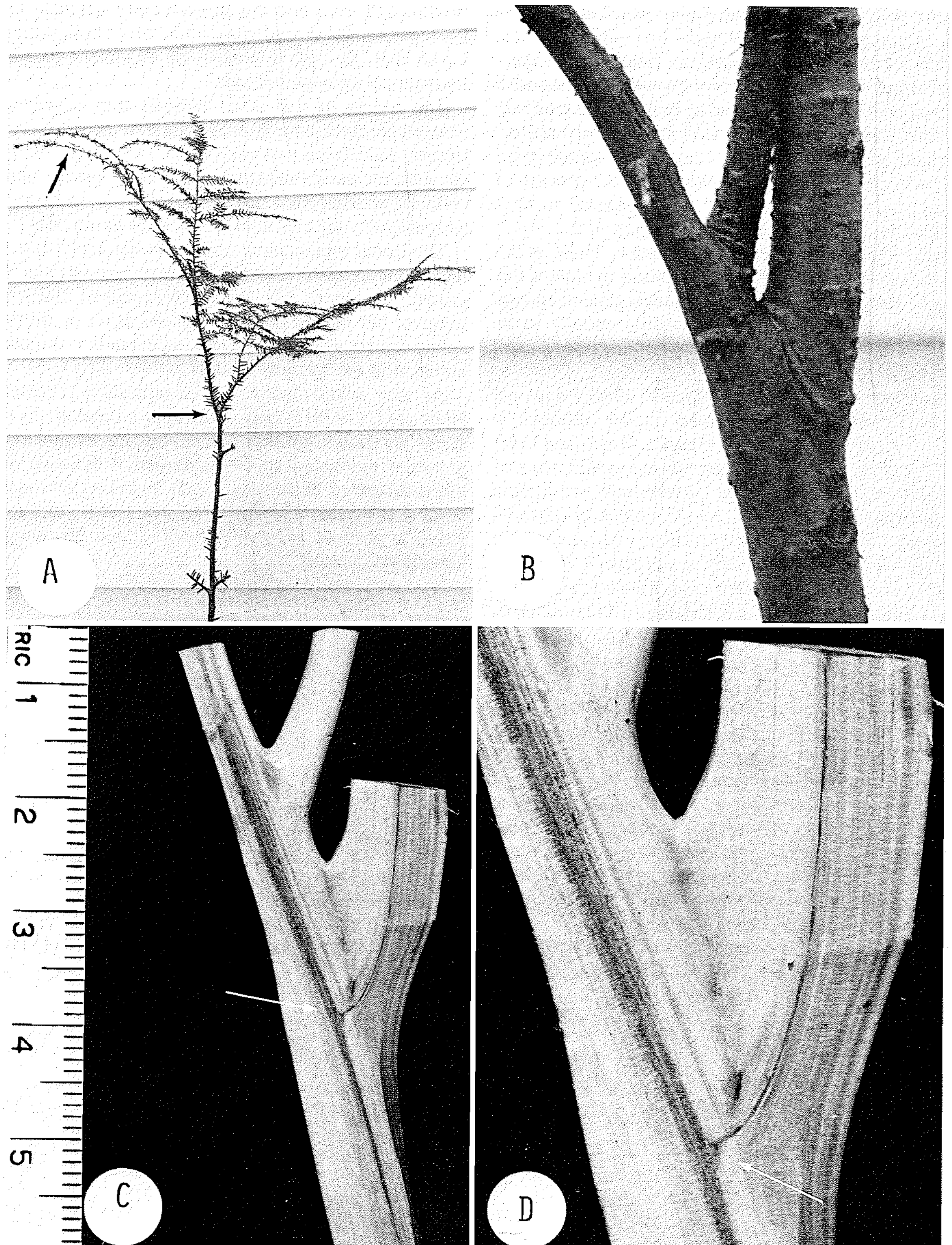
It appears that most of the conclusions about height growth in eastern hemlock apply to western hemlock (points 1–4 above). Frequent meristem death is lacking and it is not clear from this study whether leader plagiotropy is primary or secondary. A study like that of Mergen (1958) following an annual growth cycle would clarify this point.

Leaders of western hemlock appear to exhibit primary plagiotropy but do gradually become erect. There is little leader replacement in this species.

Tree architecture

Tree architecture is a system of classification of tree species based on patterns of growth. Specific models are

FIG. 2. (A) Upper arrow, plagiotropic hemlock leader. Lower arrow, site of shift in dominance from leader to branch. (B) Branching before dissection. B, C, and D are same specimen. (C) Dissected branching, showing that present leader arose as a branch. Arrow identifies branching pith. (D) Enlargement of Fig. 2C showing branching of pith. Arrow identifies branching. ×2.


A
B
C
D

best exemplified by younger, healthy, undamaged specimens, and in models where flower position is important, in specimens initiating their first inflorescences. Models are based on structural, not functional, characteristics and utilize such facets of growth as monopodial and sympodial axes, presence of branches, periodicity of growth and branching, differentiation between orthotropic and plagiotropic shoots, inflorescence position, and modular growth. Reiteration, the process of leader injury and replacement, is considered to be a duplication of a species model, not a part of it.

Using these and other characteristics, Hallé *et al.* (1978) have described 23 general types or models of tree growth. They tried to make these models general enough to include some variation yet specific enough to be useful. As seen below, however, the system still requires some refinement.

The mode of growth of all three hemlocks does not strictly fit into any architectural model although it contains elements of those of Massart, Roux, and Troll (Hallé *et al.* 1978). Hemlock growth is a modification of a model including rhythmic growth and orthotropic monopodial axes with continuous branch production throughout the growing season. The modification is the plagiotropic leader, most likely an adaptation to the low light levels found in eastern and western hemlock's usual understory environment (Mergen 1958) and associated with a weakening of apical control that allows frequent later shifts in leader dominance.

These three hemlocks do have a mixed axis but, because height growth is basically monopodial, have little else in common with those models in which mixed axes occur (Mangenot, Champagnat, and Troll). I have chosen to emphasize a model to which hemlock is closely allied and from which it is perhaps even derived: rhythmic growth, orothotropic monopodial axis, and continuous branching. The plagiotropy of hemlock leaders, whatever the direct cause, is perhaps best viewed as a secondary modification of the model, an adaptation by hemlock to shady habitats.

Hallé *et al.* (1978) state that there is a continuum between two closely allied models. Hemlock, however, seems to draw characteristics from several very different models and does not fall conveniently between two. Perhaps a model is needed which involves a plagiotropic leader that, through a process of secondary erection, maintains a monopodial axis.

The results of this study indicate that eastern and western hemlock have been assigned to incorrect architectural models on two occasions. This then calls into question the assignments of other *Tsuga* species and is certainly an indication that careful study is necessary in assigning any species with mixed axes to a model.

The leader replacement process in hemlock raises an interesting question about architectural models and tree growth in general. Is leader replacement following frequent but unpredictable meristem death or shifts in apical control a "normal" event, an event that should be included in the species' model?

As they acknowledge, the classification scheme of Hallé *et al.* (1978) is only a first approximation. As this study has shown, models will continue to evolve as the growth of more plant species is studied. A dynamic view of models must be adopted, each including reasonable variation. Further discussions of tree architecture must strive to produce adaptable, flexible, and functionally significant models.

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