Shoot elongation, leaf demography and bud formation in relation to branch position on *Larix laricina* saplings

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Summary. Shoot development was investigated on branches of *Larix laricina* (Du Roi) K. Koch trees growing in their 8th year in two plantations and in a natural stand approximately 12 years old. Expansion of throughout-crown series of short and long shoots was measured weekly, and later colour change and natural fall of leaves were assessed. Similar shoots were collected at intervals and dissected, the long shoots by 25-leaf segments. Leaf area and weight, as well as time of bud formation, were determined. Increasing acropetal trends were evident in time to bud burst: duration of short-shoot leaf-cluster expansion; size of leaf clusters and number, area and weight of leaves per cluster; duration and rate of long-shoot elongation; number, area and weight of leaves on long shoots; time to terminal-bud formation on long shoots. Along each long shoot, stem and leaf elongation and lateral-axis formation progressed acropetally. Lateral axes were most numerous on second to fourth 25-leaf segments. On longer shoots, some axes in middle segments developed as sylleptic short shoots rather than as lateral buds. Leaves of short shoots and basal leaves on long shoots turned yellow and abscissed sooner than axial leaves on long shoots. Colour change and loss among axial leaves were acropetal along shoots and up the crown. Thus, last-formed leaves, in axils of some of which last-formed lateral buds occurred, were held longest.

Key words: Crown development and structure — Long shoots — Patterns of vigour — Short shoots — Within-crown phenology

Introduction

Development of the crown of saplings of *Larix laricina* (Du Roi) K. Koch, tamarack or eastern larch, has been the subject of recent investigation. Remphrey and Powell (1984a, 1985, 1987) described and simulated the structural result of several successive years of growth. They also showed (1988) how projected leaf surface area was deployed after first early leaf expansion and then late leaf expansion had been completed in any of 5 successive years. There is a basipetal pattern of decreasing lengths of comparably ordered and of increasingly ordered proleptic (*sensu* Hallé et al. 1978) long shoots (Remphrey and Powell 1984a, 1987). A reverse pattern exists among sylleptic long shoots on the main axis (Remphrey and Powell 1985; Powell and Vescio 1986) but not among long shoots produced monopodially from those sylleptic long shoots (McCurdy and Powell 1987). The patterns among the proleptic long shoots are associated with patterns in relative amounts of both preformed and neoformed foliage (Remphrey and Powell 1984b).

The terminal buds of *L. laricina* trees growing in northeastern North America burst in May before those of many associated species, but rapid elongation of the new leaders does not start until relatively late (e.g. Cook 1941). Rapid and stable elongation then lasts for about 2 months and declining elongation may continue well into September (Cook 1941; Kienholz 1941; Baldwin 1955; Mitchell 1965; Powell and Vescio 1986). The slow start to elongation occurs as preformed basal leaves extend in a cluster (Clausen and Kozlowski 1967). Expansion first of preformed axial leaves (Owens and Molder 1979) and then of neoformed axial leaves accompanies the period of
rapid leader elongation. Lateral (axillary) axes with different propensities for development are associated with different positions along the tree leader and hence with different initiation times and periods for development (Powell 1987). The extended period of expansion of successive leaves may also be involved because lateral axes initiated early in the season will be supported by a different leaf population from those initiated later. Lateral axes initiated early in the season appear to have the least potential for development, as they typically form proleptic short shoots the following season. Mid-season lateral axes have the greatest chance of current-season expansion as sylleptic short or long shoots (Powell and Vescio 1986; Powell 1987). Late-season lateral axes have the greatest potential for proleptic long-shot extension the next season (Powell 1987; and see Frampton 1960; Fujimoto 1978; Owens and Molder 1979 for other Larix species). The chances for differentiation as lateral or terminal reproductive structures are also positionally related (Powell et al. 1984; Tosh and Powell 1986).

There are major inconsistencies in the literature on Larix concerning the time when lateral axes are initiated on branches (cf. Frampton 1960; Fujimoto 1978; Owens and Molder 1979). They appear to relate to differences in vigour of the subject matter used in the various investigations. Vigour (e.g., shoot length) can be readily expressed in terms of position in the crown (Remphrey and Powell 1984a, b, 1987), so examination of growth associated with vigour may provide a key to understanding differences in bud-initiation.

Knowledge of among-branch patterns of shoot elongation and of leaf expansion and longevity will therefore provide a basis for enhancing understanding of processes affecting lateral-axis production, differentiation, and propensity for subsequent development. Information on leaf demography will also be useful in assessing potential contributions to the tree's resources by leaves of different types and produced in different crown locations. These aspects are addressed in this paper.

Materials and methods

The L. laricina used in this study grew in one of three areas defined by Powell et al. (1984) as stands, A, C and D. Stands A and C were 7-year-old plantations (at the start of the year of study) situated 2 km apart on previously cultivated land at the Provincial Forest Nursery at Kingsclear, New Brunswick (Latitude 45º 57' N, Longitude 66º 47' W). They were established from seed from a single source situated 40 km east of the nursery. Stand D was naturally established on land cleared of forest 12 years previously and situated in Fredericton, New Bruns-wick, 8 km southsoutheast of stands A and C. Stand A grew on a well-drained loam on a gentle northeast-facing slope (altitude 40 m), stand C on a moderately well-drained sandy loam on level ground (altitude 65 m), and stand D on a poorly drained, level, peaty, more upland site (altitude 135 m).

The two plantations (A and C) were row-thinned in March 1985 (Powell 1987). The remaining trees ranged in height at that time from 5 to 8 m and had leaders (of 1984) that averaged about 1 m in length. Trees used in the natural stand (D) were reasonably open-grown and ranged in height from 3 to 6 m. The study was conducted throughout the growing season (April – November) of 1985, and comprised three components as follows.

Measurements in situ. Eight trees were selected for measurement of shoot expansion. In order to ensure that these trees represented a broad range of developmental types, four were essentially non-syleptic (with no sylleptic long shoots on the 1984 leader and no, or only one or two sylleptically originated branches in earlier years), and four were moderately to heavily syleptic (bore many sylleptic long shoots on the 1984 and previous leaders, see Remphrey and Powell 1985, 1988; Powell and Vescio 1986; McCurdy and Powell 1987; Powell 1987). Three of these trees were in stand A and five in stand C.

On all trees, two short-shoot buds were marked at each of 16 locations covering 6 years of crown development (Fig. 1). On sylleptic trees two short-shoot buds were marked at each of an additional seven locations (Fig. 1). When one or two 2- or 4-year-old syleptically originated branches occurred on trees designated as non-syleptic, pairs of short-shoot buds were also marked on them. On all trees, two buds in potentially long-shoot locations were marked at each of six locations, and on syleptic trees two similar buds were marked at each of an additional three locations (Fig. 1). In each pair except that on the tree leader (where both buds were distal laterals), one bud was a terminal bud and the other a distal lateral bud. Some of these buds developed short shoots rather than long shoots (Fig. 1). On syleptic trees two short-shoot buds were marked at each of an additional seven locations (Fig. 1). When one or two 2- or 4-year-old syleptically originated branches occurred on trees designated as non-syleptic, pairs of short-shoot buds were also marked on them. On all trees, two buds in potentially long-shoot locations were marked at each of six locations, and on syleptic trees two similar buds were marked at each of an additional three locations (Fig. 1). In each pair except that on the tree leader (where both buds were distal laterals), one bud was a terminal bud and the other a distal lateral bud. Some of these buds developed short shoots rather than long shoots (Fig. 1). All bud locations were restricted to one side of the tree's crown. The buds were marked by loosely twisting a colour-coded, fine plastic-coated wire around the parent shoot immediately below the bud. To simplify analysis, the short-shoot buds were grouped into seven crown regions (1–7 in Fig. 1).

Starting on 11 April 1985 (day 101), all marked buds and the shoots that grew from them were measured weekly. Measurements of short shoots continued until 15 August (day 227) and of long shoots until 19 September (day 262). Length of the bud or the structure emerging from the bud was measured from the base of the bud to the tip of the projecting structure, which was usually the tip of the most distal leaves. Width of the bud or of the cluster of leaves (of a short shoot or of basal leaves of a long shoot) was measured perpendicularly to the principal axis of the parent long shoot. All measurements were made with vernier calipers and measurement locations were reached from tripod ladders.

Dissection of collected shoots. Shoots were collected from four trees each week from 10 May (day 130) to 23 July (day 204) and then from two trees each week until 20 August 1985 (day 232). Of the four trees, two were from plantations (A or C) and two were from the natural stand (D). When collection was reduced to two trees per week, collections alternated between plantations and the natural stand. A tree was used for no more than four successive collections. This was so that shoot populations in given locations were not unduly reduced as that would have affected random selection in later collections from within the population. Also, use of trees was staggered. For example, in the natural stand, of the two initial trees, one pro-