Growth Patterns of Gemmlings of
Lycopodium lucidulum

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Knowledge of branching patterns in *Lycopodium* is often based on herbarium specimens of mature plants or parts of plants. Comparative studies of the architecture and chronological events have received little attention. Most information concerns the mode of dichotomy or stelar structure in plant parts of different age (Ogura, 1972). Primack (1973) compared shoot growth patterns in five species of *Lycopodium*.

Investigations of the ontogeny of young plants and their changes as they reach maturity are limited by the difficulties in collecting gametophytes and young sporophytes of different age. There are few references to the growth pattern of vegetatively propagated plantlets and their chronological development (Bruchmann, 1898; Troll, 1937, for *L. selago*).

The present study of *Lycopodium lucidulum* Michaux is concerned with the method of elaboration of a mature plant from a single gemma. As *L. lucidulum* grows and branches very slowly in time, plants of different age had to be compared to analyze ontogenetic changes.

MATERIALS AND METHODS

Lycopodium lucidulum populations were studied in the understory of mixed hardwoods at Harvard Forest, Petersham, Massachusetts. These occur in old forests dominated by white pine and red maple and particularly in wet undisturbed forests close to small streams.

Measurements and drawings of old individual plants were done in the field; whole smaller clumps were removed and studied in the laboratory. To analyze the growth in length within a definite period, eight erect axes were marked with ribbons at a measured distance from the apex. From this fixed point the additional growth of the apices was noted at weekly intervals over a period of 5 months (19 April to 13 September, 1986) (Fig. 1). An additional estimate of the yearly growth was provided by a single axis (marked in 1978 by K. Esseichick) which showed a similar average to that of the 8 more recently marked axes.

RESULTS

Deterministic shoot dynamics.—*Lycopodium lucidulum* has erect axes that duplicate themselves through equal dichotomy (isotomy) of the apices. Mature shoots of *L. lucidulum* lack definite strobili but have alternating vegetative and fertile zones along the stem (Fig. 2). Microphylls or vegetative leaves are longer
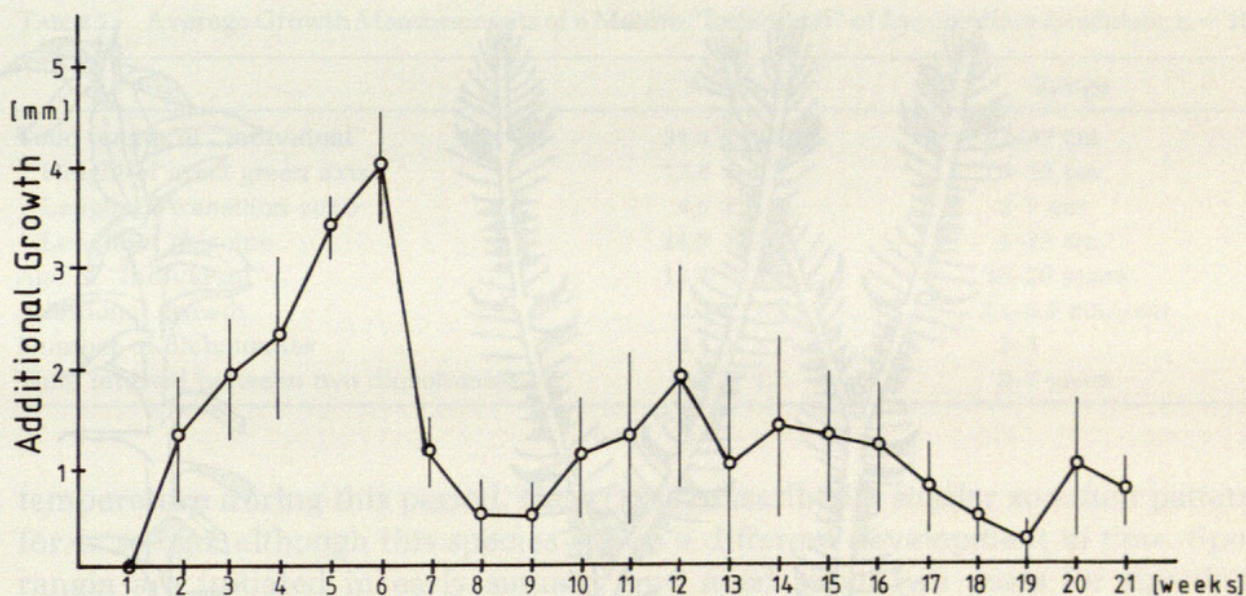
FIG. 1.   Shoot extension in *Lycopodium lucidulum* (additional growth in length per week) during one growth period (19 Apr 1986 to 31 Sept 1986). Bars represent standard deviation (n = 8).

(12 mm) and wider (2 mm) than the sporophylls (fertile leaves), which are 5 mm long and less than 1 mm wide. There is an abrupt transition between these different types with only 1–2 whorls of an intermediate size.

The shoot complexes have a certain "individual" size because of simultaneous additional growth at the distal green end and rotting at the rhizomatous creeping end (Table 1). Erect distal axes retain a uniform height because older parts recline to a prostrate position with yellowing microphylls indicating loss of chlorophyll ("transition zone") (Table 1).

The lower portion of older, now rhizomatous axes becomes covered by accumulated leaf litter within which root develpment is pronounced. Rhizome length may be arbitrarily measured from the point of the youngest visible root that is just penetrating the stem cortex to the oldest persistent part of the axis.

Roots are initiated endogenously. Some root primordia can be found near the apex, associated either with two branches of a dichotomy or within the zone of the main yearly growth increment, indicated externally by larger vegetative microphylls. Root initials are much delayed in their further development. Additional, possibly adventitious, root primordia can be found in older parts of the shoot. The region where root extension is most pronounced seems to be the transition zone. Here the root meristems develop and grow about 1–2 cm inside the cortex in proximal direction. They break through the cortex at irregular distances from their origin and fix the now horizontal part of the axis to the ground.

Field observations, growth measurements, and dissection of winter buds suggest that the small sporophylls are preformed late in the vegetative period of the previous growing season but remain enclosed in the apical bud during the winter. Dissection of a bud in early spring shows the sporophylls bearing immature sporangia. The large vegetative microphylls appear later during the main growth period in April to June, i.e., they are newly formed.
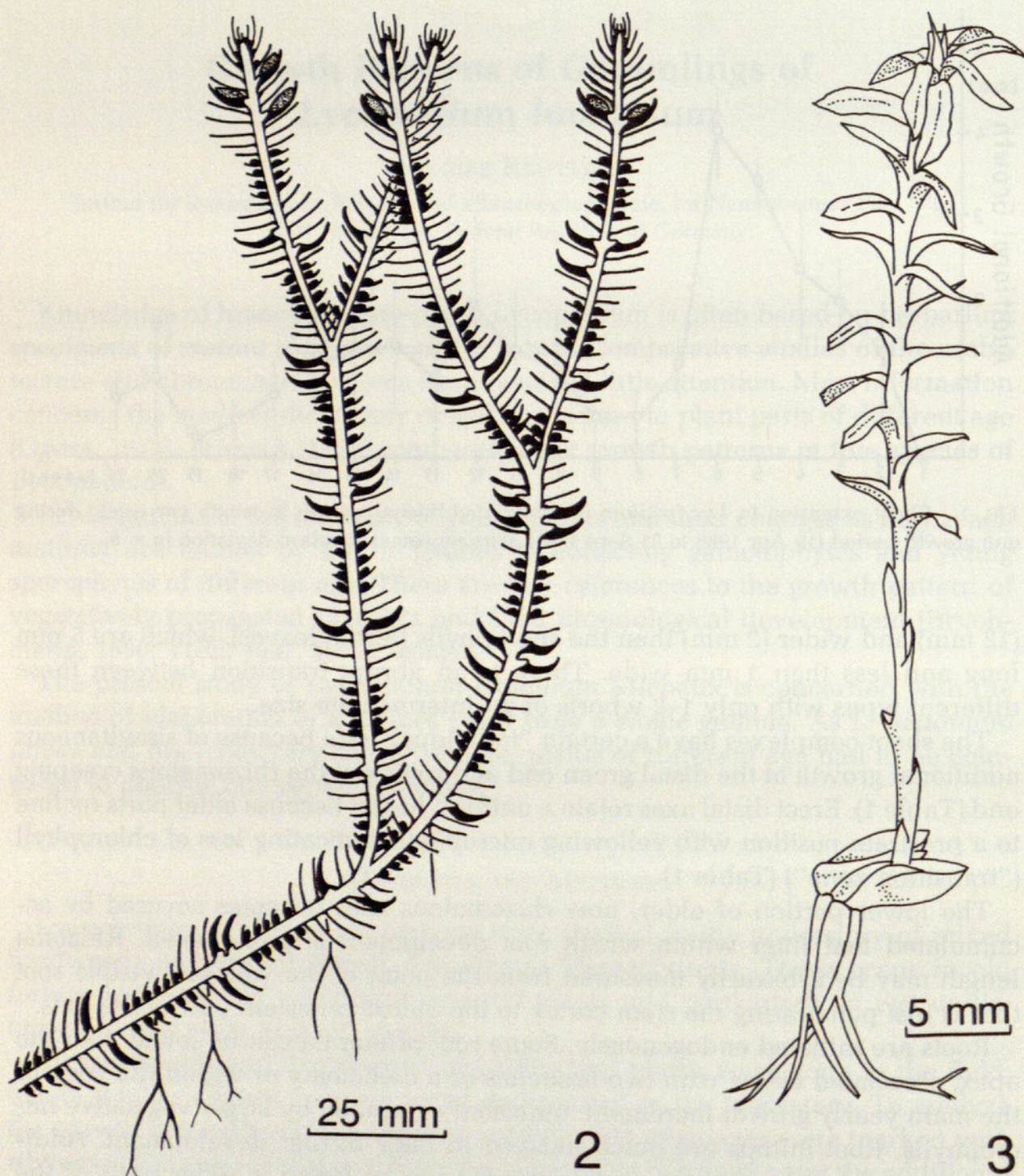
FIGS. 2, 3. *Lycopodium lucidulum*. 2. Mature shoot (fragment) with alternating zones of sporophylls and larger microphylls. Gemmaphores of the recent growth period with gemmae. 3. Gemmling with gemma still attached.

In this period of vegetative growth, the plant also produces gemmae. Axes that are to branch also will undergo isotomy at this time. The age of a shoot can be estimated from fluctuation in leaf size since a single vegetative and fertile zone develops each year. Growth measurement of some shoots during the 5 month monitoring period confirmed the seasonal cycle (Fig. 1). The decrease of the growth rate in June is probably related to the unusually high rainfall and low

TABLE 1. Average Growth Measurements of a Mature "Individual" of *Lycopodium lucidulum*; n = 15.

	Mean	Range
Total length of "individual"	31.9 ± 6.5	21–47 cm
Height of erect green axis	12.8 ± 2.5	9–19 cm
Length of transition zone	4.6 ± 1.4	2–7 cm
Length of rhizome	14.5 ± 7.2	4–33 cm
Age of "individual"	13.4 ± 2.8	10–20 years
Additional growth	2.4 ± 1.7	2.1–2.7 cm/year
Number of dichotomies	3.1 ± 1.1	2–5
Time interval between two dichotomies	4.3 ± 1.7	2–7 years

temperature during this period. Case (1943) described a similar zonation pattern for *L. selago*, although this species shows a different development in time. Sporangia are initiated in early summer and need about two years for ripening; gemmae are laid down in mid-summer and are shed in fall of the following year.

Equal branching of the apical meristem occurs only in the green, erect shoots. The number of terminal axes (x) follows the simple relationship

$$x = 2^n$$

where n is the number of previous dichotomies. This regular pattern can be found in many gemmlings (i.e., young plants derived from gemmae; Stevenson, 1976). In older plants the regular system is often disturbed by damage and consequent loss of one or more shoots. No deterministic mechanism for the development of additional branches as a response to damage was observed, so that a lost branch is irreplaceable. The total number of branches (x) on the plant therefore diminishes from the ideal number according to the relation

$$x = 2^n - 2^{n-a}$$

(for an injury at the a-th dichotomy) or

$$x = 2^n - 2^{n-a} - 2^{n-b} \ldots$$

(for an injury at the a-th and b-th and ... dichotomy). There is no evident change in growth form, rate of extension, or branching frequency of one axis of a dichotomy, compared to undamaged shoot pairs, if the corresponding one is damaged. Very occasionally lateral gemmae that fail to become detached can replace a lost main axis, but this is not a deterministic feature of growth.

Gemmae development.—No plants were observed developing from gametophytes. The following information therefore relates only to plants developed from gemmae.

Gemmae are produced on older shoots by structures ("gemmaphores") that have the position of a microphyll but show all features of a shoot (Stevenson, 1976). Typically, the gemmaphore initiates 3 pairs of microphylls that remain on the old stem after gemma separation. The distal part of this gemmaphore develops another 3 pairs of microphylls, one pair of them large and fleshy. This fleshy pair forms a heart-shaped structure (the gemma sensu stricto) that separates from the

gemmaphore by means of an abscission layer. A root primordium develops on the proximal end of the gemma before abscission occurs.

Gemmae are shed in fall and become buried with leaf litter. In the following spring the gemmae develop an axis and microphylls that differ in shape from those of the adult plant (Fig. 3). The length of these first axes depends mostly on the thickness of the covering litter. The covered parts bear few scalelike microphylls. On average the exposed axis of the gemmling in the first season reaches a length of 1.5–3.0 cm with green leaflike structures, which are rounder and about half the size of the adult microphylls (5 × 3 mm). They are arranged in an increasing phyllotactic spiral. Often there are one or two endogenous roots in addition to the first developed gemma root. Usually the two fleshy microphylls become lignified and persistent so that they can be recognized on plants up to 18 years old. This allows the reconstruction of the development and branching pattern of the plant from its first dichotomy.

The gemmling undergoes its first dichotomy at the beginning of the second year (Fig. 4). Subsequent dichotomies occur either in the next vegetative period or in later years. Usually the two daughter branches of a dichotomy show the same branching pattern, so that young plants with few branches have a very symmetrical shape (Fig. 5). In comparison with the adult stages there is a measurable tendency in older plants to prolong shoot growth and reduce branching frequency, expressed in the increasing distance between two successive dichotomies (Fig. 6A). The delay of branching can be recognized by the seasonal change in leaf size, which is first shown by the plant in its second or third year. Although no sporangia are produced on plants of this age, one can distinguish larger from smaller microphylls, the latter equivalent in shape and size to sporophylls. Annual growth periodicity is the same as in the adult plant; little variation results from different climatic or nutritional circumstances (Fig. 6B).

The internal angle between two daughter branches of one dichotomy decreases from a range of 90°–180° in the first dichotomy to 20°–30° in the dichotomies of the mature shoot (Fig. 6B). The planes of the first and second dichotomy, independent of the angle between the daughter shoots, regularly are arranged in an interplanar angle of 90°, described as "cruciate" by Troll (1937) for *Lycopodium selago*. Subsequent inclinate orientation of dichotomy planes (Øllgaard, 1979) shows interplanar angles with less than 30°, which means that all descendants of each branch resulting from the first dichotomy are arranged with their apices in a half circle. This variation of the branching angles, together with the increasing shoot growth increments results in the arrangement of the erect shoots in "growth-rings" or "fairy-rings" (Fig. 5). The largest diameter of a plant observed with an attached basal gemma was about 50–60 cm. In older stages, the original orientation towards a center of origin is less easily recognizable.

Gemmlings bear the first sporangia at an age of 6–7 years. Daughter gemmae appear about 2 years later. This change to fertility seems independent of the frequency of previous dichotomies. With increasing age and diameter the oldest parts of the plant decay and the distal shoots become separated. The persistent fragments, consisting usually of 2–8 connected shoots resulting from the most recent 1–3 dichotomies, have several functional apical meristems at their distal
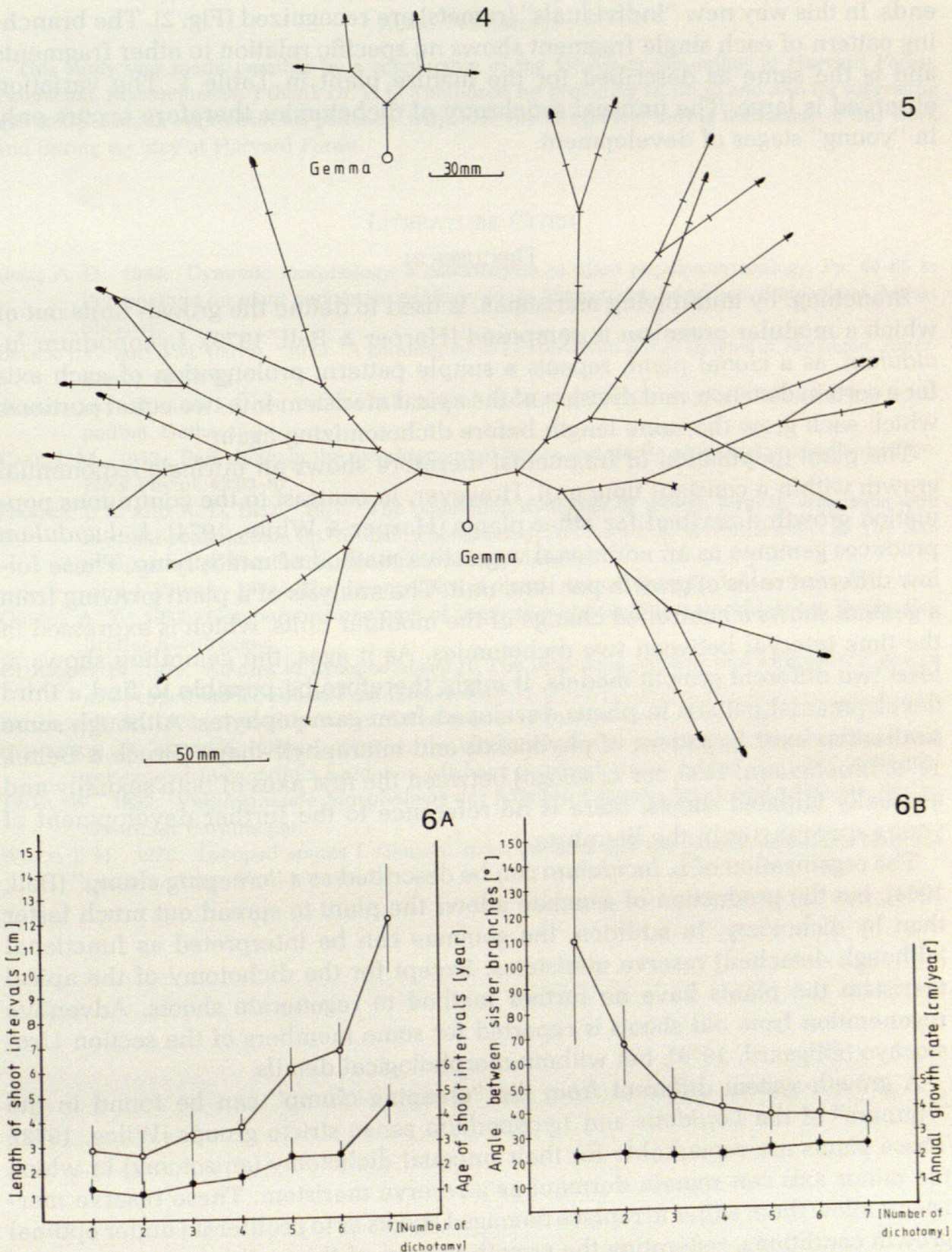
FIGS. 4–6. Branching pattern in *Lycopodium lucidulum*. 4. Young plant with attached gemma. Intervals represent growth of one year. Angle between shoots and length of intervals as in nature. 5. Nine year old plant. X-marked shoots are damaged. Angle between shoots and length of intervals as in nature. 6A. Length of shoot intervals between dichotomies of different rank (open circles). Corresponding age of shoot intervals between dichotomies (closed circles). Bars represent standard deviation (n = 10). 6B. Annual growth rate of shoot intervals of different age and length (closed circles). Angle between the sister branches of dichotomies of increasing grade (open circles). Bars represent standard deviation (n = 10).

ends. In this way new "individuals" (ramets) are recognized (Fig. 2). The branching pattern of each single fragment shows no specific relation to other fragments and is the same as described for the mature plant in Table 1. The variation observed is large. The unusual synchrony of dichotomies therefore occurs only in "young" stages of development.

DISCUSSION

Branching, by multiplying meristems, is used to define the growth units out of which a modular organism is composed (Harper & Bell, 1979). *Lycopodium lucidulum*, as a clonal plant, repeats a simple pattern: prolongation of each axis for a certain distance, and division of the apical meristem into two equal portions, which each grow the same length before dichotomizing again.

The plant (population of fragments) therefore shows an intrinsic exponential growth within a constant time unit. However, in contrast to the continuous population growth described for other plants (Harper & White, 1974), *L. lucidulum* produces gemmae as an additional vegetative method of multiplying. These follow different rules of growth per time unit. The analysis of a plant growing from a gemma shows a controlled change of the modular units, which is expressed in the time interval between two dichotomies. As it ages, the gemmling shows at least two different growth models. It might therefore be possible to find a third developmental pattern in plants developed from gametophytes. Although some similarities exist in pattern of phyllotaxis and microphyll shape (Bruce & Beitel, 1979; Bruchmann, 1899, for *L. selago*) between the first axes of both sexually and asexually initiated shoots, there is no reference to the further development of young sporophytes in the literature.

The organization of *L. lucidulum* can be described as a "creeping clump" (Bell, 1984), but the production of gemmae allows the plant to spread out much faster than by dichotomy. In addition, the gemmae can be interpreted as functional (although detached) reserve meristems. Except for the dichotomy of the apical meristem the plants have no further method to regenerate shoots. Adventive regeneration from old shoots is reported for some members of the section *Urostachya* (Øllgaard, 1979), but without morphological details.

A growth-system different from the "creeping clump" can be found in the "runners" of the *Lepidotis* and *Lycopodium* sensu stricto groups (Wilce, 1972). These plants are remarkable for their unequal dichotomy (anisotomy) in which the minor axis can remain dormant as a reserve meristem. These reserve meristems allow them either to replace damaged shoots or to proliferate under optimal growth conditions, reiterating the growth pattern of the mother axis.

It seems that the growth pattern involving runners is environmentally much more flexible than the rather fixed *L. lucidulum* system. Because of its isotomy the architecture of *L. lucidulum* is restricted in its ability to repair damage, but compensates for this disadvantage by the development of gemmae. This could be interpreted as a derived pattern imposed on an ancestral determinism.

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