Growth Patterns of Five Species of Lycopodium[1]

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Descriptions of the type and rates of growth of the lycopods have not been included in several recent studies of *Lycopodium* (Cardillo, 1970; Kukkonen, 1967; Bierhorst, 1971; Wilce, 1965). Wilce seems to have given the most attention to periodicity, for she says, "In arborescent and usually tufted species, determination of the age of the main upright axis is a simple matter of counting the number of seasonal 'leaf rings.' These leaf rings mark the retardation or cessation of growth at the end of each season; with their small, crowded leaves, they might be compared to an angiosperm bud, but with the difference that the leaves of the lycopodiaceous 'bud' are persistent." (However, she did not report observing annual "leaf rings" on the rhizome of *L. flabelliforme.*)

Colonies of five species of *Lycopodium* (*L. lucidulum* Michx., *L. annotinum* L., *L. flabelliforme* (Fern.) Blanch., *L. clavatum* L., and *L. obscurum* L.) growing at the Harvard Forest, Petersham, in central Massachusetts, were examined to determine their growth patterns and growth rates. Descriptions of the arrangement of the aerial shoots and rhizomes were made in the field. Measurements of annual growth of the aerial shoots and rhizomes were made in the laboratory on fresh specimens brought in from the field. The annual growth of the rhizomes of *L. flabelliforme, L. clavatum,* and *L. annotinum* was determined by locating the distinct microphyll compressions on the rhizome where the rhizome tip slowed down and then ceased growing in the fall and winter. Annual growth of aerial shoots can be determined in all species by noting the microphyll compressions on the shoot and branchlet axes.

My observation that there are annual, externally visible microphyll compressions on the rhizomes of *L. annotinum, L. clavatum,* and *L. flabelliforme,* seems to be an original one. In *L. annotinum* the actively growing rhizome has straight microphylls, which are 5 mm long and 0.8 mm wide, spaced 13 mm apart. In late fall, the curved microphylls, which are about 7 mm long and 0.7 mm wide, are spaced 5 mm apart. In *L. clavatum* the actively growing rhizome has microphylls which are about 4 mm long and 0.8 mm wide at the base, spaced about 8 mm apart. In late fall the microphylls, which become longer and narrower (to 8 mm long and 0.5 mm wide), are spaced about 1.5 mm apart. In *L. flabelliforme* the shape of the microphylls does not change, but during active growth the rhizome microphylls are about 16 mm apart, whereas they are only 2 mm apart toward the end of the season.

Lycopodium annotinum, L. clavatum, and *L. flabelliforme* have well-differentiated strobili and grow by a superficial rhizome just below the leaf litter. *Lycopodium annotinum* has a sessile strobilus and leaves with aristate tips. *Lycopodium*

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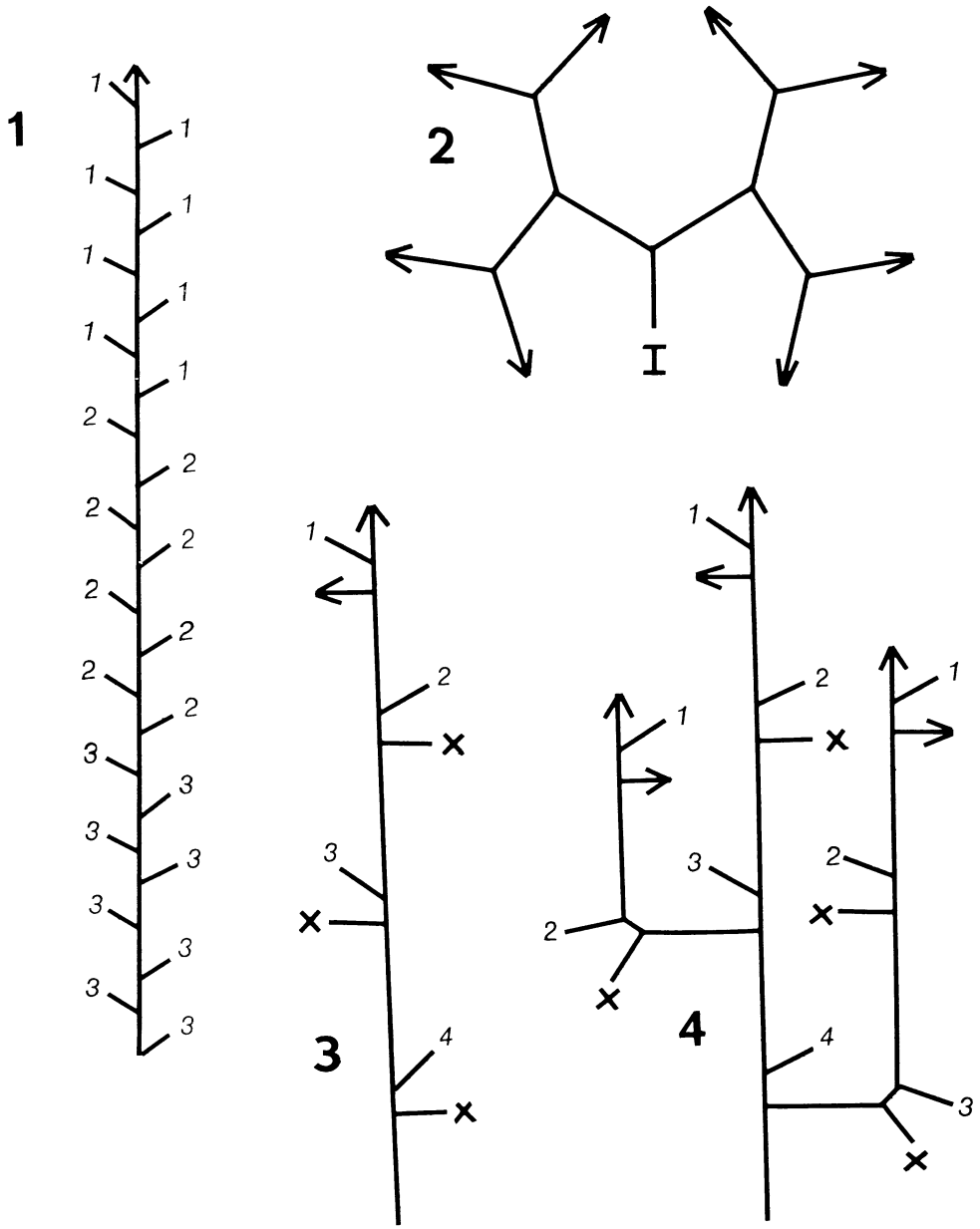
clavatum has peduncled strobili and leaves with long, hair-like tips. *Lycopodium flabelliforme* has dark green, flattened, fan-like branchlets. For ease of reference in the account that follows, the year in which an annual rhizome segment is laid down and the aerial shoots first initiated will be termed Year 1, the following year of growth of that segment will be Year 2, and so on. The rhizome of each species initiates aerial shoots during the same season the rhizome is growing. The average annual growth of the rhizome and the number of aerial shoots initiated for each species can be seen in *Table 1*. The aerial shoots arise by dichotomous, pseudomonopodial branching of the actively growing rhizome tip along a plane parallel to the surface of the ground, alternately to either side. This has the effect of creating two parallel lines of aerial shoots, one on either side of

TABLE 1. SUMMARY OF GROWTH DATA FOR FOUR SPECIES OF *LYCOPODIUM*.

	flabelliforme	*clavatum*	*annotinum*	*obscurum*
Microphyll compressions on rhizome	yes	yes	yes	no
Average and range of annual rhizome growth (cm)	38 (26–50)	70 (48–103)	32 (22–45)	17 (13–21)
Average number and range of aerial shoots per year	9.3 (7–13)	12.8 (12–14)	7.9 (7–9)	1
Average distance between aerial shoots (cm)	4.0	5.6	4.0	17.4
Average length of aerial shoot at end of Year 1 (cm)	1.3	5	6.3	17.4
Range in length of mature aerial shoot without strobilus (cm)	12–18	4–9	11–22	18–23
Sample size for each measurement	20	20	20	15

the rhizome (*Fig. 1*). At the end of Year 1, the aerial shoots closest to the rhizome tip are just tiny nubs that are barely discernible from the rhizome and are still below the leaf litter; the oldest shoots on the segment, which were initiated in the spring, may be as long as 7 cm. In Years 2, 3, 4, and 5 additional growth occurs on the aerial shoots, with the shoots finally attaining a length of 10–20 cm.

In all three species, strobili are generally produced in Year 4 or 5. The life span of most aerial shoots is four or five years, although some were observed to have died earlier. Occasionally a vigorous shoot will have a sixth year of growth. An aerial shoot may bend over and develop into a side rhizome, rather than continuing as an aerial shoot. In subsequent years the rhizome decays, with the result that the main rhizome and the side rhizomes become separate plants. This method of vegetative reproduction is the only means of reproduction I observed for these three species. No young sporophytes or gametophytes were found in the area where these species were observed.



Schematic branching patterns in *Lycopodium*. FIG. 1. *L. annotinum*, three year pattern. FIG. 2. *L. lucidulum*. FIG. 3. *L. obscurum*, four year pattern. FIG. 4. Same, vigorous plant. Arrow = rhizome apices; I = initiation point; x = dead side rhizome; 1, 2, 3, and 4 = first, second, third, and fourth year aerial shoots.

Lycopodium lucidulum is distinct from the other local Clubmosses in that it has no differentiated creeping rhizome. Furthermore, it lacks a definite strobilus, having instead alternating vegetative and fertile zones along the stem. *Lycopodium lucidulum* forms "fairy rings" up to two meters across.

New individuals of *L. lucidulum* may be produced vegetatively from gemmae that form in the upper leaf-axils of a large individual. All of the young plants observed were sprouting from these gemmae, never from gametophytes. The gemmae seem to be shed in the late summer or fall. In the spring of Year 1 a gemma sends a stem up above the leaf litter which has atypical, short, rounded microphylls. In all subsequent years the microphylls are elongated and sharp-pointed. After Year 1, the stem grows from 1.5 to 2.2 cm per year, with the apex dividing dichotomously every few years. This stem tip division seems to be synchronized in some way throughout the plant, since all the stem tips on a plant divide at approximately the same time. A twelve-year-old plant will commonly have eight or sixteen stem tips, which represent three or four stem divisions.

When the plant is about six years old, sporangia and their associated, large sporophylls are produced for the first time. The large sporophylls are produced early in the growing season, whereas the increasingly small vegetative microphylls are produced later in the season.

Every year the leaf litter that falls on the plant presses the stem toward the ground, decreasing the height. The 2 cm yearly growth of the stem compensates for this decrease in height and keeps the stem tips always about 8 cm above the leaf litter, and the divisions of the stem serve to spread the stem tips around in a circle (*Fig. 2*).

Lycopodium obscurum is readily distinguishable from the other local *Lycopodium* species by its truly underground rhizome that is buried an average of 6 cm and by its relatively tall, aerial shoots with arborescent branching.

The growth pattern of *Lycopodium obscurum* is not easily determined, since this species lacks microphyll compressions on the rhizome (*Table 1*). Many rhizomes were examined in May, 1971, and the most recently produced aerial shoot on each was always in the same stage of development. The aerial shoot was usually several centimeters long and directed upwards, although still below the surface of the ground, with the rhizome having continued horizontally about 6 cm beyond it. The second aerial shoot on each rhizome was two years old, as determined by its microphyll compressions, and the third aerial shoot was three years old. This is strong evidence that the rhizome only produces one aerial shoot per year. Since the average distance between aerial shoots on a rhizome is 17.4 cm, the average annual growth of the rhizome must be the same.

After the main rhizome of *L. obscurum* has grown several centimeters during the growing season, it sends off a weak side rhizome to one side by unequal dichotomous branching. The main rhizome continues for about 2 cm and again branches dichotomously in a plane parallel to the ground; the branch on the same side as the side rhizome develops upward into an aerial shoot, whereas the branch on the opposite side continues as the main rhizome (*Fig. 3*). This pat-

tern is repeated the following year with the side rhizome and the aerial shoot being produced on the other side of the main rhizome.

The weak side rhizome usually dies in Year 2, but occasionally in vigorous plants or plants with an injured main rhizome tip, it develops with its own side rhizomes and aerial shoots. A side rhizome initially grows at right angles to the main rhizome, but while initiating its first lateral rhizome and aerial shoot, the side rhizome turns 90 degrees and continues its growth parallel to the main rhizome (*Fig. 4*).

The growth patterns of the aerial shoots of *L. obscurum* can be determined easily by the prominent microphyll compressions along their length. In Year 1, the shoots arise by dichotomous branching of the rhizome. The shoots overwinter just below the surface of the forest floor. In Year 2, a rapid growth of up to 18 cm brings the shoots above the leaf litter. The branchlets of the shoots are held sharply upwards. In Year 3, the branchlets expand, with the shoots taking on their arborescent appearance. The branchlets may show slight additional growth, and the aerial shoots may develop sessile strobili during this year. In Year 4, the aerial shoots begin to wither and die.

The five species of *Lycopodium* examined showed different patterns of growth and different rates of growth. These differences may be important characters in distinguishing between species, as well as in understanding the relationships of each species to its environment.

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REVIEW

"THE FERNS AND OTHER PTERIDOPHYTES OF MONTANA, WYOMING, AND THE BLACK HILLS OF SOUTH DAKOTA," by Robert and Jane L. Dorn. 94 pp. 1972. Available from the authors, Department of Botany, University of Wyoming 82070. $1.00.—According to the introduction, "the primary purpose of this treatment is to provide an easy means for identifying the pteridophytes of Montana, Wyoming, and the Black Hills of South Dakota." The authors provide the kind of keys, descriptions, and limited synonymy that one expects to find in a manual. For each species they also provide a full page illustration showing habit, technical details, and known range within the area covered. In general they take a broad view of specific limits (e.g., *Polypodium vulgare*), and they do not pretend to provide any new insight into difficult groups. They have done a good job of what they set out to do.—*Arthur Cronquist, New York Botanical Garden, Bronx Park, Bronx, NY 10458.*