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GROWTH RELATIONSHIPS OF LEAVES AND INTERNODES IN VINY ANGIOSPERMS WITH DIFFERENT MODES OF ATTACHMENT[1]

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ABSTRACT

The timing of leaf expansion in relation to the elongation of adjacent internodes was compared in 37 species of vines which climb by means of twining stems, tendrils, or roots. Interspecific comparisons were made with a growth index, L, defined as the fraction of the final length of a leaf when an adjacent internode reached 75% of its final length. The index was calculated for both of the leaf positions adjacent to an internode: L_a for the leaf above the internode, L_b for the leaf below the internode. The value of L was low in many twiners and tendril climbers (L_a, $L_b < 0.33$ in 15 of 29 species). Four twiners formed scale leaves (L_a and $L_b = 1.0$) and in two climbers with leaf tip tendrills (*Pisum*, *Gloriosa*) the maturation of leaves was not delayed ($L_a = 0.73$, 0.94 respectively). In all five species (5/5) of monocotyledonous root climbers a leaf completed elongation together with, or before, one of the adjacent internodes. In 2/3 species of dicotyledonous root climbers the elongation of leaves was delayed in relation to both adjacent internodes, but the value of L_a was greater than in most twiners. The timing of adjacent internode elongation was evaluated using a second index, T, defined as the fraction of final length of an internode when the subjacent internode reached 75% of its final length. Wide-ranging extremes were found among various species, from 0.70 in *Asparagus* to 0.05 in *Anthurium*. Root climbers exhibited generally lower T values than twiners or tendril climbers. These results are in agreement with the concept of earlier qualitative studies that the pattern of leaf and internode development in vines is related to their mode of attachment. Delayed leaf expansion has been considered important in the biology of twining and tendril climbing vines because large foliage leaves are thought to decrease the effectiveness of shoots "searching" for a support. The present study provides the first quantitative, comparative description of the timing of leaf growth in vines. The leaves of non-vines commonly mature together with, or before, the adjacent internodes.

VARIOUS AUTHORS have described the expansion of foliage leaves in the shoots of twining and tendril-climbing vines as delayed behind the elongation of internodes (Schenck, 1892; Raciborski, 1900; Gradmann, 1929; Troll, 1937; Baillaud, 1962). The timing of leaf expansion in root climbers has not received much attention. One goal of this study is to describe in detail the growth relationships between leaves and internodes of vines, according to their mode of attachment. Previous accounts have dealt only with the relative size of leaves along the shoot. A developmental index of leaf expansion will be selected to make quantitative comparisons among vines, as well as comparisons with the literature on leaf expansion in non-vines.

Shoot extension is pronounced in many vines, and for this reason they are especially suitable for studies of internode development. Very little information is available about the timing of the elongation of successive internodes (Wetmore and Garrison, 1966). A second goal of the study is to describe this aspect of internode development using a quantitative index, and to integrate the results with previous descriptions of the growth of individual internodes of vines (Fisher and French, 1976; French and Fisher, 1977).

Both monocotyledonous and dicotyledonous vines have been included in this study so that taxonomic comparisons of leaf and internode development can be made. Recent comparisons of viny shoot growth in angiosperms, which have been published without supporting documentation, (Stebbins, 1974) may now be appraised.

MATERIALS AND METHODS—Plants under cultivation in greenhouses or in outdoor plantings at Fairchild Tropical Garden, or the USDA's Subtropical Horticulture Research Unit, Miami, Florida, were measured during the periods given for each species (Table 1). Both the maximum and minimum temperatures during the study period, and the average daily temperature at Miami International Airport, approximately 7 km to the north, are also included in Table 1. Temperature data were obtained from the National Oceanic and

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TABLE 1. *List of species and growing conditions*

Species	Family	Temperature (C)			Dates of Measurements
		High	Avg.	Low	
Aganosma acuminata G. Don	Apocynaceae	33	28	21	9/11/75–10/20/75
Anthurium polyschistum R. E. Schult.	Araceae	Greenhouse			10/ 6/75– 1/10/76
Antigonon leptopus Hook. & Arn.	Polygonaceae	30	26	19	10/10/75–11/ 7/75
Aristolochia veraguensis Duch.	Aristolochiaceae	33	28	23	9/11/75–10/10/75
Asparagus falcatus L.	Liliaceae	28	22	8	1/ 8/75– 1/14/75
Bauhinia fassoglensis Kotschy ex Schweinf.	Fabaceae	33	28	23	9/11/75–10/ 1/75
Beaumontia grandiflora (Roxb.) Wall.	Apocynaceae	33	28	19	9/11/75–11/ 7/75
Bomarea rosea Herb.	Alstroemeriaceae	Greenhouse			10/ 8/75–11/17/75
Bowiea volubilis Harv.	Liliaceae	Greenhouse			10/10/75–11/15/75
Cayratia trifolia (L.) Domin.	Vitidaceae	33	28	23	9/15/75–10/13/75
Combretum paniculatum Vent.	Combretaceae	29	21	8	12/ 1/74– 1/ 6/75
Dioscorea bulbifera L.	Dioscoreaceae	Greenhouse			1/10/75– 2/ 1/75
Ficus pumila L. var. *minima* Bailey	Moraceae	29	23	8	10/29/74–11/22/74
Gloriosa superba L.	Liliaceae	33	28	23	5/10/75– 6/14/75
Ipomoea purpurea (L.) Roth. cv. Heavenly Blue	Convolvulaceae	Greenhouse			10/30/74–11/20/74
Jasminum volubile Jacq.	Oleaceae	30	26	19	10/10/75–11/ 7/75
Lagenaria siceraria (Molina) Standley	Cucurbitaceae	Greenhouse			12/ 9/75– 1/15/75
Luzuriaga latifolia (R. Br.) Poir.	Philesiaceae	29	24	14	10/29/74–11/20/74
Momordica charantica L.	Cucurbitaceae	Greenhouse			11/25/75– 1/ 5/76
Mucuna sloanei Fawe. & Rendle	Fabaceae	Greenhouse			10/30/74–11/20/74
Passiflora laurifolia L. cv. Jamaica 6	Passifloraceae	29	24	14	10/25/74–11/20/74
Peixotoa glabra A. Juss.	Malpighiaceae	33	28	21	9/11/75–10/20/75
Philodendron oxycardium Schott.	Araceae	33	28	21	9/11/75–10/20/75
Pisum sativum L. cv. Melting Sugar	Fabaceae	Greenhouse			10/30/75–11/17/75
Porana paniculata (Sweet) Roxb.	Convolvulaceae	33	28	21	9/11/75–10/20/75
Ludovia sp.	Cyclanthaceae	Greenhouse			10/ 3/75– 1/14/76
Pyrostegia ignea (Vell.) Presl.	Bignoniaceae	30	26	19	10/10/75–11/ 7/75
Rhaphidophora aurea (Lind. and André) M. R. Birdsey	Araceae	29	23	11	11/22/74– 2/ 3/75
Schlegelia parasitica (Sw.) Miers ex Griseb.	Bignoniaceae	29	22	8	10/29/74–12/ 1/74
Smilax bona-nox L.	Smilacaceae	29	23	12	1/27/75– 2/20/75
Stigmaphyllon sp.	Malpighiaceae	33	26	23	9/11/75– 9/29/75
Tecomanthe venusta S. Moore	Bignoniaceae	30	26	19	10/10/75–11/ 7/75
Tetrastigma voinierianum Pierre	Vitidaceae	33	28	19	9/11/75–11/ 7/75
Thunbergia alata Bojer	Acanthaceae	Greenhouse			5/15/75– 6/ 9/75
Thunbergia grandiflora Roxb.	Acanthaceae	29	22	9	10/21/75–12/ 9/75
Toxicodendron radicans (L.) Kuntze ssp. radicans	Anacardiaceae	30	25	19	10/17/75–11/12/75
Vanilla sp.	Orchidaceae	33	27	29	4/30/75– 6/17/75

Atmospheric Administration. Greenhouse temperatures ranged between 16 and 35 C. The elongation of leaves and internodes was measured at intervals of 1–5 days, depending upon the rate of growth for each species, until growth stopped. To establish the final length, leaves were measured at intervals of several weeks after internode elongation was completed. Values for opposite leaves were averaged and treated as one leaf. All measured shoots were actively growing leaders and were provided with supports unless specifically mentioned. Surface marking studies were conducted to measure the localization of growth within internodes, by using previously described methods (French and Fisher, 1977). Young internodes were marked into three equal segments with ink and measured until elongation ended. In *Ludovia* a fine needle was used to mark young internodes which were enclosed within a sheathing leaf. Voucher specimens have been deposited in the herbarium of Fairchild Tropical Garden (FTG). The data were taken from two or more shoots for 31 of the 37 species examined (31/37).

RESULTS—Species were grouped into three categories: 1) twiners, 2) tendril climbers, and 3) root climbers, depending on their mode of attachment to a support. In order to define the quantitative indices, two species which exhibit large differences in their pattern of leaf and internode growth were selected for detailed comparison. Later, these indices will be used to compare growth patterns in twiners, tendril climbers, and root climbers.

Thunbergia grandiflora is a rapidly growing twiner with perennial shoots bearing simple, opposite leaves. The unsupported searcher shoots are long and whiplike (see illustration in French and Fisher, 1977). Some lateral buds grow out after the adjacent internodes have completed elongation, forming additional searcher shoots. A

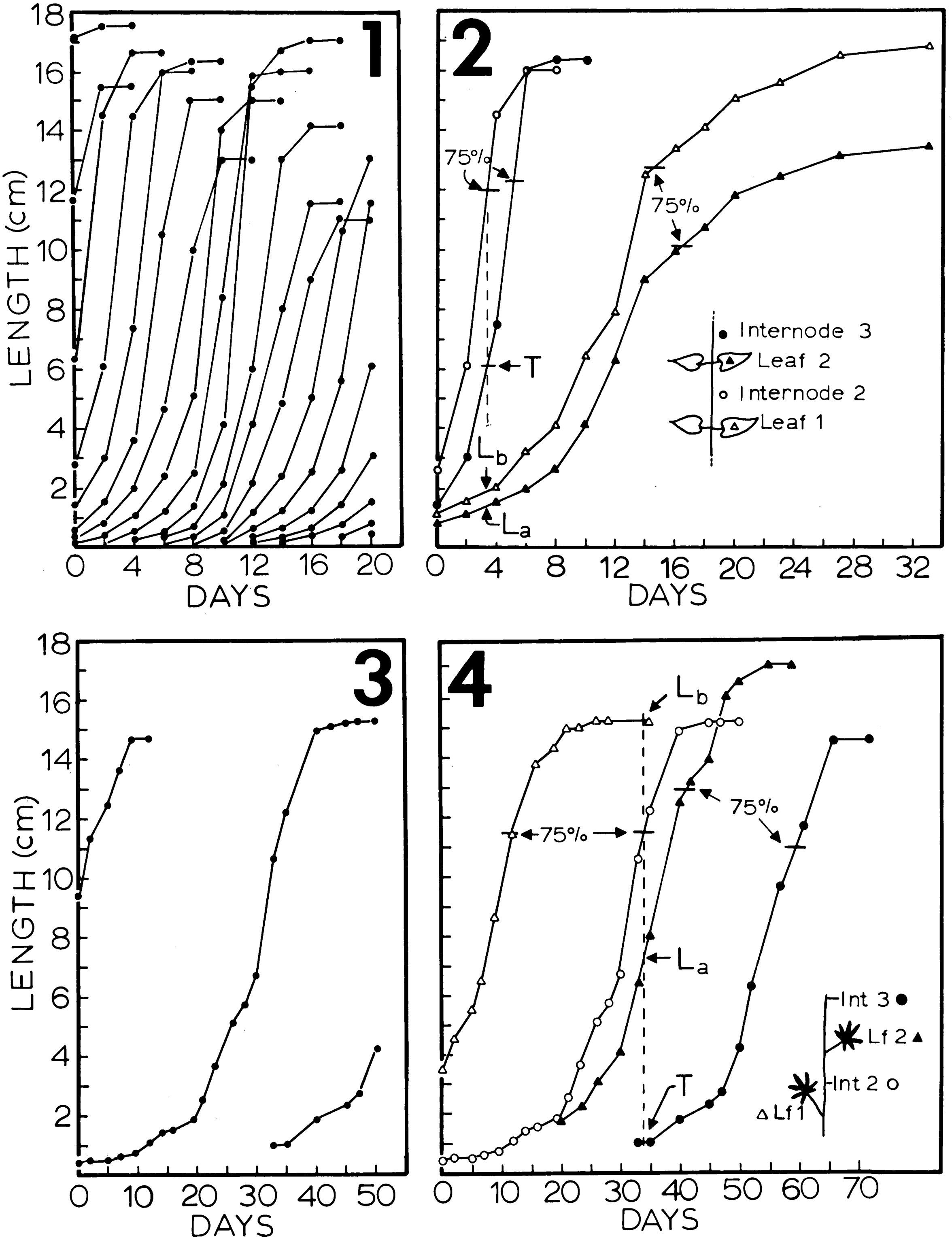

Fig. 1–4. **1.** Elongation curves of internodes on an actively growing shoot of *Thunbergia grandiflora*. **2.** Elongation curves of two successive internodes and adjacent leaves in *T. grandiflora*, on the same shoot as in Fig. 1, annotated to define the indices L_a, L_b, and T, explained in Results; circles, internodes; triangles, leaves. **3.** Elongation curves of internodes on a growing shoot of *Anthurium polyschistum*. **4.** Elongation curves of successive internodes and adjacent leaves in *Anthurium*, on the same shoot as in Fig. 3, annotated to define the indices L_a, L_b, and T; circles, internodes; triangles, leaves.

tangled shoot system develops under favorable conditions, shrouding neighboring trees and shrubs.

Anthurium polyschistum is a relatively slow-growing root climber with a sympodial main axis, i.e., some internodes of the main axis arise from axillary buds at the base of terminal inflorescences, which may remain dormant; roots grow out from each node to attach the stem to a support and leaves are palmately compound.

The growth curves for successive visible leaves and internodes of *Thunbergia* and *Anthurium* are presented in Fig. 1–4. It is readily apparent that *Thunbergia* differs from *Anthurium* in producing a larger number of internodes/unit time, and that the internodes complete elongation in a shorter period. Also, the leaves of *Thunbergia* lag behind the elongation of internodes adjacent to them, while the leaves of *Anthurium* grow more closely with subjacent internodes. In order to quantitatively compare the timing of the growth of leaves and internodes during elongation, an index was calculated based on the relative length of a leaf and an adjacent internode at a fixed fraction of final length. The index, L, equals the fraction of the final length of a leaf when an adjacent internode reaches 75% of its final length.

This length was selected for reference because the phase of most rapid growth of internodes is ending. It is at a time when the differences between the length of leaves and adjacent internodes are pronounced in many species with delayed leaf expansion.

The growth of a leaf is usually considered only in relation to the growth of the internode below it (e.g., Hancock and Barlow, 1960). This is presumably based on the assumption that an internode and the leaf terminating it form a more natural unit than an internode and the subjacent leaf. However, the growth curve of a leaf may be more nearly coincident with the suprajacent internode than the subjacent internode, as will be described later for *Philodendron.* In order to provide a more complete description of leaf-internode growth, L was calculated for both the leaf above the internode (L_a) and below the internode (L_b) (Fig. 2, 4). In species with strongly delayed leaf expansion, both L_a and L_b are frequently low, i.e., less than 0.33. When L_a and L_b = 1.0, leaves mature before adjacent internodes.

The time difference between an internode reaching 0.75 final length and the subjacent leaf reaching 0.75 final length was also calculated, and is represented by D. Unlike L, the value of D is influenced by the growth rate of the leaf after the internode reaches 0.75 final length. In two species having identical values for L, D would be lower in one species if a more rapid expansion took place after L was measured. Examples of species with similar values for L and different values for D are discussed later with the data on twiners.

In *Thunbergia* the expansion of leaves is grossly delayed in relation to the expansion of internodes, $L_a = 0.06$ and $L_b = 0.14$. A leaf is only several cm in length (vs. 18.9 cm final length) when the adjacent internodes reach a final length of 14.5 cm. Leaves reach 0.75 final length 10.6 days after their suprajacent internodes.

In *Anthurium* a leaf reaches 0.75 final length 17 days before the suprajacent internode, and about one week behind the subjacent internode; $L_a = 0.45$, $L_b = 1.0$. The curve representing leaf elongation is more nearly coincident with the subjacent than the suprajacent internode.

One consequence of both the delay in expansion of leaves in *Thunbergia* and its rapid production of internodes is the presence of an average of 15.6 mature internodes above the most recent leaf to mature (combined length = 1.7 m). In *Anthurium* there are no mature internodes above the most recent leaf to mature.

Growth curves for successive internodes of *Thunbergia* and *Anthurium* are presented in Fig. 1, 3. In order to quantitatively express the timing of the elongation of adjacent internodes, an index was selected based on the relative lengths of adjacent internodes. This index, T, represents the fraction of final length of an internode at the time the subjacent internode reaches 75% of its final length. The lengths of internodes are calculated by interpolation from time-length graphs, Fig. 2, 4. In *Anthurium* the timing of adjacent internode elongation is markedly stepwise, T = 0.05. In *Thunbergia* the growth curves of adjacent internodes are more nearly coincident and T = 0.47. The growth rate of whole shoots of *Thunbergia* is 13.6 times greater than in *Anthurium* (9.5 cm/day vs. 0.7 cm/day). Internodes reach approximately the same length in both species, but the average growth rate of an exposed internode is greater in *Thunbergia* (1.3 cm/day vs. 0.5 cm/day) and the plastochron interval (time between 75% point of successive internodes) is shorter in *Thunbergia* (1.4 days vs. 23.5 days).

The results of surface marking studies show that the pattern of differential growth in internodes also differs markedly between *Thunbergia* and *Anthurium.* In *T. grandiflora* the distribution of growth throughout the internode is relatively uniform, while in *Anthurium* growth is extremely localized in the upper part of the internode. These differences are revealed in the ratio of the length of the upper to lower segment at maturity: 1.0 vs. 5.4 for *Thunbergia* and *Anthurium* respectively (Table 2). A region of residual growth is found in the base of internodes of *Thunbergia*, which acts like a pulvinus (French and Fisher, 1977).

TABLE 2. *Leaf and internode growth in vines*

Taxon	T^a	$L_a{}^b$	$L_b{}^c$	D^d	p^e	$F_I{}^f$	$F_L{}^g$	U/L^h	F^i	cm/d^j
TWINERS										
Monocotyledons										
Asparagus	0.70 ± 0.02	1.00 ± 0.00	1.00 ± 0.00	—	0.2 ± 0.1	2.3	1.1	1.0	0.27	14.3
Bomarea	0.42 ± 0.03	0.66 ± 0.02	0.77 ± 0.02	- .03	1.7 ± 0.2	3.3	4.2	1.9	0.27	1.5
Bowiea	0.60 ± 0.04	1.00 ± 0.00	1.00 ± 0.00	—	0.9 ± 0.2	2.2	0.3	1.3	0.49	2.2
Dioscorea	0.48 ± 0.01	0.18 ± 0.01	0.24 ± 0.01	6.0	1.7 ± 0.1	13.1	21.4	1.8	0.08	8.6
Luzuriaga	0.21 ± 0.01	1.00 ± 0.00	1.00 ± 0.00	—	3.3 ± 0.1	23.8	2.6	2.3	0.05	9.5
Dicotyledons										
Aganosma	0.48 ± 0.02	0.39 ± 0.01	0.45 ± 0.01	5.7	1.3 ± 0.1	8.2	9.5	1.3	0.14	6.2
Aristolochia	0.56 ± 0.01	0.23 ± 0.01	0.30 ± 0.01	5.5	0.9 ± 0.1	8.7	26.3	1.5	0.13	11.3
Beaumontia	0.28 ± 0.02	0.10 ± 0.02	0.14 ± 0.02	—	4.4 ± 0.3	25.9	21.4	2.1	0.06	5.6
Combretum	0.60 ± 0.01	0.18 ± 0.01	0.21 ± 0.01	12.6	1.2 ± 0.2	3.6	7.1	1.5	0.14	3.9
Ipomoea	0.27 ± 0.03	0.13 ± 0.01	0.30 ± 0.01	3.9	1.7 ± 0.1	23.3	19.2	3.4	0.03	14.2
Jasminum	0.46 ± 0.01	0.37 ± 0.01	0.47 ± 0.01	—	1.9 ± 0.1	10.5	8.3	1.8	0.12	5.8
Mucuna	0.31 ± 0.02	0.09 ± 0.02	0.19 ± 0.03	3.5	1.7 ± 0.1	21.0	23.4	2.0	0.04	11.3
Peixotoa	0.36 ± 0.03	0.15 ± 0.01	0.21 ± 0.01	7.1	1.6 ± 0.2	14.7	11.8	1.8	0.10	9.9
Porana	0.57 ± 0.03	0.15 ± 0.01	0.19 ± 0.01	10.2	1.0 ± 0.1	4.6	11.7	1.5	0.21	4.3
Stigmaphyllon	0.54 ± 0.02	1.00 ± 0.00	1.00 ± 0.00	—	0.9 ± 0.1	9.0	0.9	2.0	0.26	8.3
Tecomanthe	0.26 ± 0.01	0.10 ± 0.01	0.19 ± 0.01	—	3.7 ± 0.2	20.7	20.6	1.7	0.10	6.1
Thunbergia alata	0.22 ± 0.03	0.29 ± 0.02	0.63 ± 0.03	1.1	3.2 ± 0.2	14.9	5.0	3.1	0.07	4.0
Thunbergia grandiflora	0.46 ± 0.01	0.06 ± 0.00	0.14 ± 0.01	10.6	1.9 ± 0.1	14.5	18.9	1.0	0.08	9.5
TENDRIL CLIMBERS										
Monocotyledons										
Gloriosa	0.52 ± 0.03	0.94 ± 0.03	0.98 ± 0.01	- 4.6	1.4 ± 0.2	4.4	19.7	1.4	0.23	3.5
Smilax	0.44 ± 0.03	0.33 ± 0.01	0.44 ± 0.02	4.2	1.8 ± 0.1	11.2	10.2	1.6	0.08	5.9
Dicotyledons										
Antigonon	0.54 ± 0.02	0.22 ± 0.01	0.31 ± 0.02	4.7	0.8 ± 0.2	6.7	8.9	1.5	0.16	7.8
Bauhinia	0.57 ± 0.02	0.23 ± 0.01	0.30 ± 0.01	3.0	0.8 ± 0.1	7.0	9.0	1.4	0.19	8.0
Cayratia	0.50 ± 0.01	0.12 ± 0.03	0.18 ± 0.01	9.3	1.1 ± 0.2	4.9	14.7	0.8	0.27	5.5

TABLE 2. *Continued*

Taxon	T^a	$L_a{}^b$	$L_b{}^c$	D^d	p^e	$F_I{}^f$	$F_L{}^g$	U/L^h	F^i	cm/d^j
Lagenaria	0.14 ± 0.01	0.29 ± 0.02	0.53 ± 0.02	1.2	2.1 ± 0.3	24.4	17.4	2.4	0.10	11.0
Momordica	0.37 ± 0.03	0.33 ± 0.02	0.51 ± 0.02	—	1.5 ± 0.2	3.9	6.5	2.1	0.21	2.5
Passiflora	0.39 ± 0.01	0.30 ± 0.01	0.44 ± 0.01	3.9	2.0 ± 0.2	6.9	12.4	1.8	0.08	2.9
Pisum	0.14 ± 0.01	0.73 ± 0.02	0.96 ± 0.01	- 2.7	2.8 ± 0.1	7.6	3.7	3.2	0.14	3.1
Pyrostegia	0.27 ± 0.01	0.10 ± 0.01	0.21 ± 0.01	—	3.2 ± 0.4	7.9	9.6	1.6	0.19	2.6
Tetrastigma	0.43 ± 0.02	0.18 ± 0.01	0.23 ± 0.01	13.6	2.2 ± 0.2	12.0	28.7	1.0	0.20	5.5
ROOT CLIMBERS										
Monocotyledons										
Anthurium	0.05 ± 0.006	0.47 ± 0.03	1.00 ± 0.00	-17.0	23.0 ± 2.5	15.7	21.3	5.5	0.15	0.7
Philodendron	0.19 ± 0.004	0.37 ± 0.02	0.92 ± 0.02	- 8.4	9.8 ± 0.2	14.6	31.7	1.5	0.36	2.2
Ludovia	0.13 ± 0.01	1.00 ± 0.00	1.00 ± 0.00	—	26.5 ± 3.3	9.4	24.1	0.5	0.30	0.3
Rhaphidophora	0.18 ± 0.01	0.72 ± 0.03	0.97 ± 0.02	-10.4	9.1 ± 0.9	18.8	13.8	2.4	0.10	2.2
Vanilla	0.43 ± 0.01	0.75 ± 0.01	0.89 ± 0.01	- 5.4	5.6 ± 0.4	8.2	17.9	2.2	0.15	1.1
Dicotyledons										
Ficus	0.31 ± 0.03	0.48 ± 0.03	0.74 ± 0.02	0.1	2.6 ± 0.2	1.9	1.4	2.7	0.28	0.8
Toxicodendron	0.26 ± 0.02	0.24 ± 0.02	0.49 ± 0.03	1.8	2.6 ± 0.1	5.2	10.6	2.3	0.26	1.6
Schlegelia	0.24 ± 0.01	0.32 ± 0.02	0.49 ± 0.02	5.7	4.8 ± 0.3	8.8	7.2	2.9	0.11	1.6

[a] T = the fraction of final length of an internode when the subjacent internode reaches 75% of its final length, ± standard error.

[b] L_a = the fraction of final length of a leaf when the subjacent internode reaches 75% of final length, ± standard error.

[c] L_b = the fraction of final length of a leaf when the suprajacent internode reaches 75% of final length, ± standard error.

[d] D = the number of days that an internode leads or lags (–) behind the subjacent leaf in reaching 75% final length.

[e] p = plastochron, days between successive internodes reaching 75% of final length.

[f] F_I = final length of internode (cm).

[g] F_L = final length of leaf (cm).

[h] U/L = length of upper/lower segment of marked internode at maturity.

[i] F = fraction of final length when internode marked into three equal segments.

[j] cm/d = rate (per day) of shoot growth.

Twiners—Monocotyledons: *Asparagus*, *Bomarea*, *Bowiea*, *Dioscorea*, *Luzuriaga*.

In all five monocotyledonous twiners the elongation of aerial shoots is limited to a part of one year, although shoots may persist for several years (*Luzuriaga*, *Asparagus*) or die back to a perenniating organ (*Dioscorea*, *Bowiea*, *Bomarea*). In *Luzuriaga*, *Asparagus*, and *Bowiea*, small scale leaves are produced on the main axis. The bases of *Asparagus* leaves are modified as recurved thorns. Foliage leaves are formed in *Dioscorea* and *Bomarea*. Lateral branches are normally absent from lower regions of shoots of *Luzuriaga* and *Asparagus*. Lateral branches bear leaves (*Luzuriaga*) or phylloclades (*Asparagus*). Lateral branch outgrowth is relatively uninhibited in *Bowiea*; in addition, the branches also twine. In the shoots of *Bomarea* and *Dioscorea*, the outgrowth of lateral branches is inhibited.

Dicotyledons: *Aganosma*, *Aristolochia*, *Beaumontia*, *Combretum*, *Ipomoea*, *Jasminum*, *Mucuna*, *Peixotoa*, *Porana*, *Stigmaphyllon*, *Tecomanthe*, *Thunbergia alata*, *Thunbergia grandiflora*.

Ipomoea is an annual; *Thunbergia alata* tends to be small and herbaceous; *Jasminum* is a climbing shrub; the other species are high-climbing lianas. Simple alternate leaves are formed in *Aristolochia*, *Combretum*, *Ipomoea*, *Mucuna*, and *Porana*. Simple, opposite leaves are formed in *Aganosma*, *Beaumontia*, *Jasminum*, *Peixotoa*, *Stigmaphyllon* (whorl of three scale or foliage leaves), and *T. alata*. Opposite compound leaves are found in *Tecomanthe*. Both twining and nontwining axes are formed on *Aganosma*, *Beaumontia*, *Stigmaphyllon*. Twining axes of *Stigmaphyllon* may form only scale leaves, which abscise early, or foliage leaves. The outgrowth of axillary branches is inhibited in all species during elongation of the main axis.

In 10/14 species of twiners with foliage leaves, their expansion lags markedly behind internode elongation, and L_a, L_b equals 0.33 or less (Table 2). Leaf expansion is relatively less delayed in *Aganosma* ($L_a = 0.39$, $L_b = 0.45$) and *Jasminum* ($L_a = 0.37$, $L_b = 0.47$). In *T. alata* the leaf terminating an internode is much delayed in expansion compared with the leaf at the base ($L_a = 0.29$ vs. $L_b = 0.63$). Leaf expansion is essentially coincident with internode elongation in *Bomarea* ($L_a = 0.66$, $L_b = 0.77$). In species with scale leaves the leaf maturation is precocious, and L_a, $L_b = 1.0$ in *Asparagus*, *Bowiea*, *Luzuriaga*, and *Stigmaphyllon*.

The value of D in *Mucuna* (3.5 days) is unexpected, considering the low value of L_b for *Mucuna*. The low D reflects a relatively rapid leaf expansion after the suprajacent internode reached 0.75 final length. Species with similar values of L_b (*Porana*, *Peixotoa*, *Combretum*) have much higher values for D (10.2, 7.1, 12.6). *Combretum* exhibits an especially long lag in leaf expansion.

With respect to the index of timing of internode elongation (T), a wide range of values is found in the twiners, from 0.7 (*Asparagus*) to 0.21 (*Luzuriaga*) in monocotyledons, and from 0.60 (*Combretum*) to 0.22 (*T. alata*) in dicotyledons (Table 2). With decreasing T a smaller number of internodes contribute to the daily increase in shoot length, so that each individual internode contributes a higher percentage of the total daily shoot growth, e.g., 4% in *Asparagus* vs. 86% in *Luzuriaga*.

Tendril climbers—Monocotyledons: *Smilax* and *Gloriosa*.

Smilax forms high-climbing shoots with alternate, simple foliage leaves, each bearing two tendrils from near the base, whose homology has been debated. Thorns are present on the stem, but were not observed to be of direct aid in climbing. *Gloriosa* forms annual herbaceous shoots from a perennial rhizome axis and bears opposite to alternate leaves. The tip of the leaf develops a long flattened tendril which attaches the climbing shoots to a support.

Dicotyledons: *Antigonon*, *Bauhinia*, *Cayratia*, *Lagenaria*, *Momordica*, *Passiflora*, *Pisum*, *Pyrostegia*, and *Tetrastigma*.

Only *Lagenaria*, *Momordica*, and *Pisum* are annuals. Branch tendrils are formed in *Antigonon*, *Bauhinia*, *Cayratia*, *Lagenaria*, *Momordica*, *Passiflora*, and *Tetrastigma*. Leaves are compound in *Pisum* and *Pyrostegia*, and in these species some leaflets are modified as tendrils. Leaves are simple and alternate in *Antigonon*, *Bauhinia*, *Lagenaria*, *Momordica*, and *Passiflora*. Compound alternate leaves are formed in *Pisum*, *Cayratia*, and *Tetrastigma* and compound opposite leaves in *Pyrostegia*. In *Cayratia* every third node lacks a tendril.

In *Smilax*, *Pyrostegia*, and in all seven of the species with branch tendrils, leaf expansion lags behind elongation of adjacent internodes (Table 2). The value of L_b ranges from 0.18 in *Cayratia* to 0.53 in *Lagenaria*. In *Gloriosa* and *Pisum*, in which the distal part of each leaf acts as a tendril, leaf elongation is not delayed. In *Gloriosa* the elongation of a leaf is nearly complete before either adjacent internode ($L_b = 0.98$, $L_a = 0.94$). In *Pisum* an internode and the suprajacent leaf elongate together ($L_a = 0.73$) while the subjacent leaf is nearly mature ($L_b = 0.96$).

The value of L_b in *Bauhinia* is equal to L_b in *Antigonon*, and lower than L_b in *Smilax* and *Passiflora*; yet D is lower in *Bauhinia* than in all 3 species. Like *Mucuna*, *Bauhinia* exhibits a relatively rapid leaf expansion after 0.75 final length is reached by the suprajacent internode.

The tendril climbers show a wide range in the timing of internode elongation. The value of T varies from 0.57 in *Bauhinia* to 0.14 in *Pisum* and *Lagenaria.*

Root climbers—Monocotyledons: *Anthurium, Philodendron, Ludovia, Rhaphidophora, Vanilla.*

Shoots of all species attach by adventitious roots arising either at or near the node (*Anthurium, Philodendron, Ludovia, Vanilla*) and from the entire length of the internode, also (*Rhaphidophora*). Shoots of *Vanilla* and *Rhaphidophora* are monopodial, while those of *Anthurium* and *Philodendron* are sympodial. The pattern of branching in *Ludovia* is not known. Leaves are alternate in all species, and simple, except for palmately compound leaves in *Anthurium*. *Rhaphidophora* exhibits a variety of shoot morphology depending on the growing conditions, as has been partly described by Raciborski (1900). Data are presented for the pendant shoots of *Rhaphidophora* and *Philodendron* that develop when climbing shoots lose their support.

Dicotyledons: *Ficus, Schlegelia, Toxicodendron.*

In *Ficus* roots arise in a tight cluster at and near the node on the ventral surface of the stem, in *Schlegelia* roots arise over contact surface of the internode, in *Toxicodendron* roots arise from the entire surface of the distal part of the internode. Leaves are alternate in *Ficus* and *Toxicodendron*, opposite in *Schlegelia*, simple in *Ficus* and *Schlegelia*, and compound in *Toxicodendron*.

In all of the monocotyledonous root climbers that were examined, the elongation of leaves either precedes or is nearly coincident with the elongation of one of the adjacent internodes (Table 2). The foliage leaves of *Ludovia* mature precociously (L_a, $L_b = 1.0$), so that several elongating internodes are proximal to the most recent leaf to mature. A foliage leaf of a pendant shoot of *Rhaphidophora* matures together with a subjacent internode ($L_b = 0.92$ vs. $L_a = 0.72$). In many pendant shoots of *Rhaphidophora* the laminae are reduced strongly and leaves mature sooner ($L_a = 1.0, L_b = 0.92$).

In *Philodendron* a leaf and suprajacent internode are covered by a cataphyll (see Troll, 1937, p. 630) until the elongation of the next internode below is nearly completed. The young internode that is exposed by the opening of the cataphyll grows together with the leaf at its base, rather than with the still cataphyll-sheathed leaf which terminates the internode. In this respect *Philodendron* differs from the other two aroids, *Rhaphidophora* and *Anthurium*, which have the closest growth relationship with the leaf terminating the internode. Although L_b is 0.92 in *Philodendron*, the leaf and internode complete growth at approximately the same time. In *Vanilla* leaf growth is closely related to both adjacent internodes. An internode and leaf at its upper end complete elongation at about the same time, but at 75 % of final internode length the leaf at its base is also 75 % of final length. The slope of internode and leaf growth curves is rather low in *Vanilla*, so that more leaves and internodes are elongating at a time than in other species with a similar plastochron. The value of T is rather high in *Vanilla* (Fig. 6), considering the value of P, in relation to other species.

In both *Toxicodendron* and *Schlegelia* the value of L_b is 0.49, while D is lower in *Toxicodendron*, indicating a relatively more rapid expansion of leaves in *Toxicodendron* than *Schlegelia* after 0.75 final internode length.

In all three aroids (*Anthurium, Philodendron,* and *Rhaphidophora*), the value of T in Table 2 is low (0.05–0.18). Only one elongating internode is exposed, except when an internode is completing elongation and the next youngest internode is first exposed. The young internode and its suprajacent leaf emerge from a sheathing petiole in *Rhaphidophora* and *Anthurium*.

In the dicotyledonous root climbers leaf expansion is somewhat delayed in two of three species, although the values of L_a are above those of most twiners and tendril climbers. The value of T is also low in dicotyledonous root climbers.

Distribution of growth in internodes—The young internodes of 23 species were marked into three equal segments and measured at regular intervals until mature. The ratios of final lengths are presented in Table 1, together with results from 14 species marked in the previous study (French and Fisher, 1977). The amount and duration of growth in the upper of the three segments is greater than the lower segment in nearly all of the species. In some species with high T values and short internodes (e.g., *Asparagus, Bowiea, Combretum*), the growth differences between upper and lower segments are small. Growth is more localized in the upper segments of internodes of *Anthurium* and *Pisum* ($U/L = 5.4, 3.2$). In both of these species the value of T is low (0.05, 0.14). The average length of the lower segment exceeds the length of the upper segment in all of the marked internodes of *Cayratia* (Vitidaceae) $U/L = 0.8$ and *Ludovia* (Cyclanthaceae) $U/L = 0.5$. In *Cayratia* a swollen region of residual growth is located at the base of the internode. In *Ludovia* there is no clear-cut evidence of residual growth in the base of the internode despite the consistently greater amount of growth ($n = 9$, range in $U/L = 0.36$–0.74). In the other member of the Vitidaceae, *Tetrastigma*, $U/L = 1.0$ ($n = 8$, range 0.74–1.38).

Relationship between T and U/L, P, and internode length—In Fig. 5–7 the data from Table 2 for T and differential growth (U/L), plastochron

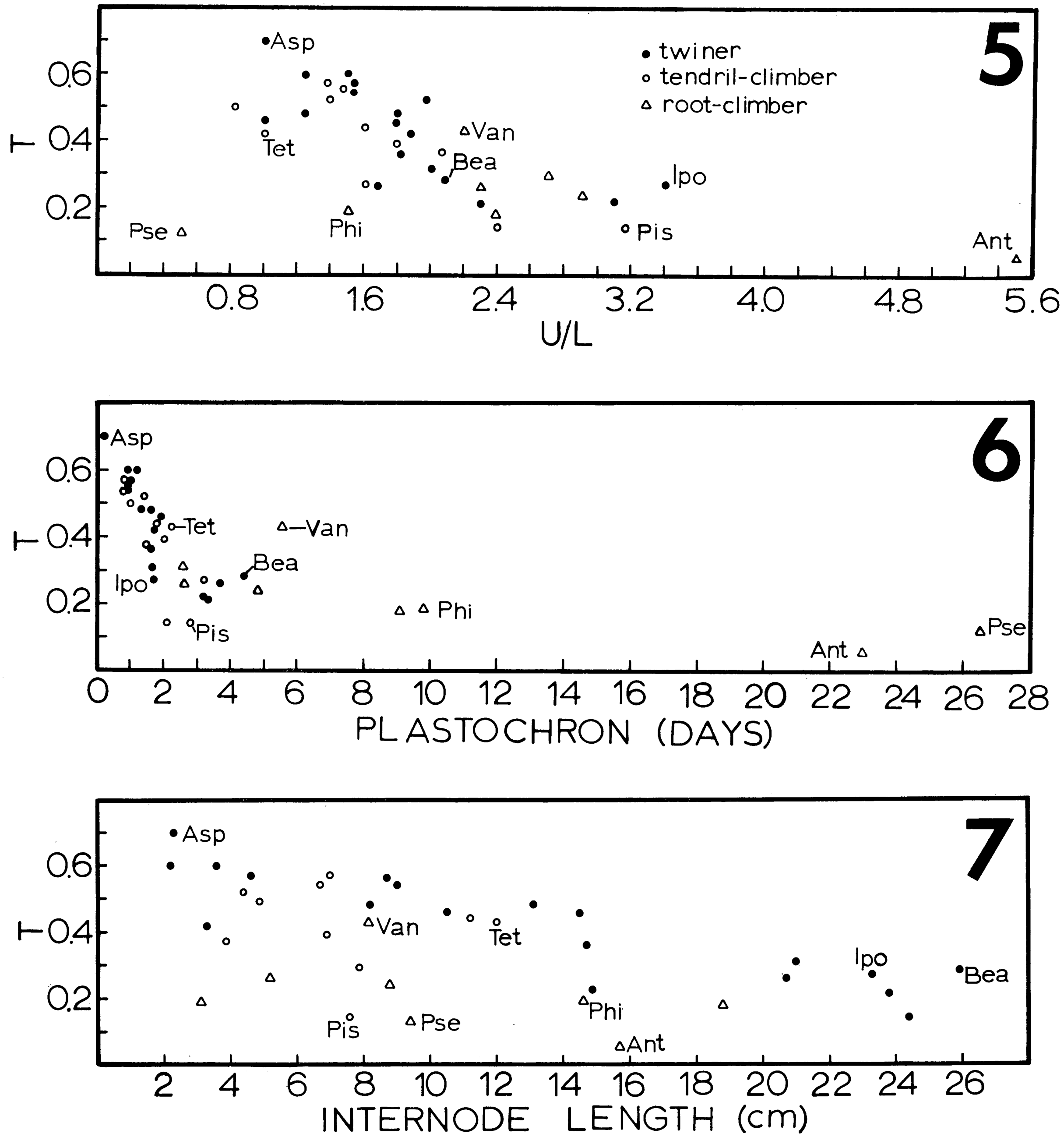

Fig. 5–7. **5.** Plot of T vs. U/L in 37 species of vines. T represents the overlap in successively elongating internodes (see Fig. 2 and Results), and U/L represents the ratio of final length of upper to lower segments of marked internodes. **6.** Plot of T vs. P (plastochron). P represents the interval between 75% points of successive internodes. **7.** Plot of T vs. average final length of internodes. *Anthurium* (Ant); *Asparagus* (Asp); *Beaumontia* (Bea); *Ipomoea* (Ipo); *Philodendron* (Phi); *Pisum* (Pis); *Ludovia* (Pse); *Tetrastigma* (Tet); *Vanilla* (Van).

(P), and internode length are plotted. Of the 9 species with $T < 0.25$, the value of U/L is > 2.3 in 7 species. In *Ludovia* and *Philodendron* the value of U/L is low (0.5, 1.5). In the 9 species with higher T (> 0.5), the value of U/L is 1.6 or less in 8 species. Thus, in the sample examined here, no species are found to exhibit both a high T and a high U/L, approaching for example, $T = 0.5$ and $U/L = 3.0$.

With decreasing P the value of T tends to increase in the species examined here. Of the 20 species in which $P < 2.0$ days, the value of $T >$

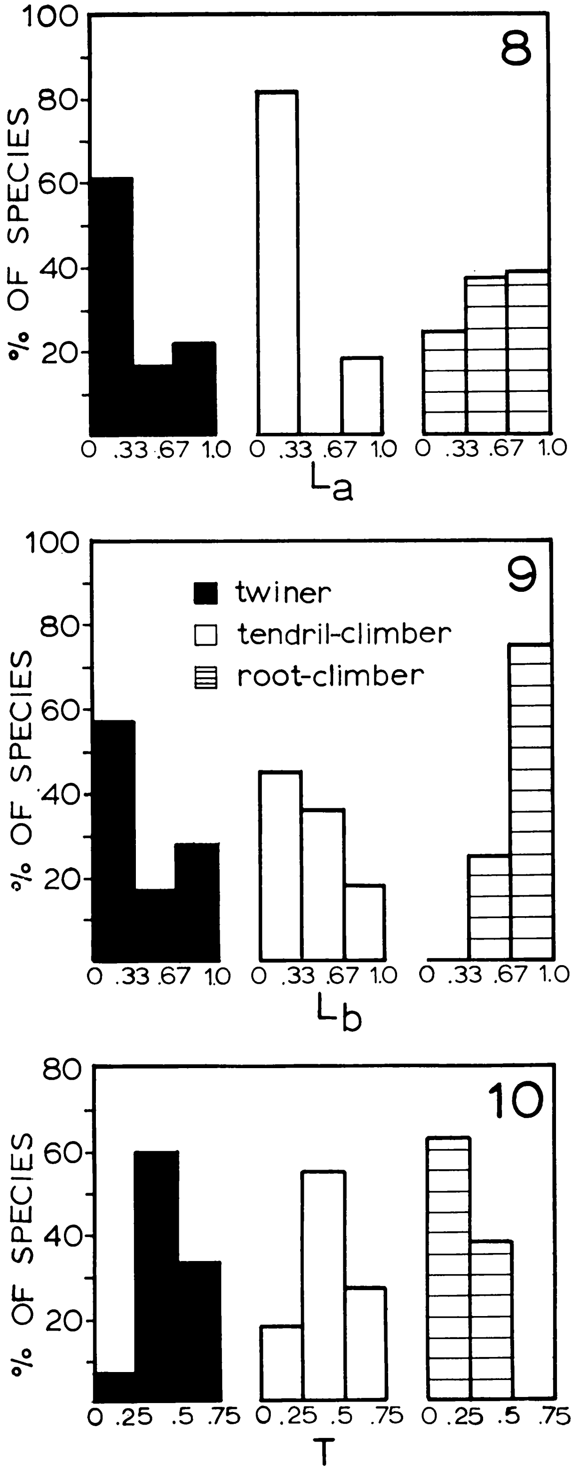

Fig. 8–10. **8.** Summary histogram for data on L_a in 37 species (Table 2). **9.** Summary histogram for data on L_b in 37 species (Table 2). **10.** Summary histogram for data on T in 37 species (Table 2).

0.4 in 16 species. In 10/11 species in which $P > 3.0$ days the value of $T < 0.3$. *Vanilla* stands out as possessing a high T for the value of P, in relation to other species (Fig. 6).

In twiners increasing final internode length is correlated with decreasing T (Fig. 7). In tendril and root climbers there is no clear trend in the relationship between T and final length. No tendril climber with an internode length greater than 12 cm was examined.

Summary distribution of L_a, L_b, and T in vines—Figures 8, 9 summarize the percent of twiners, tendril climbers, and root climbers with $L = 0.0$–0.33, 0.34–0.66, 0.67–1.0, respectively. A majority of twiners and tendril climbers have values of L_a of 0.33 or less, while a majority of root climbers exceed 0.33. The values for L_b are shifted to higher percentage values, especially in tendril climbers and root climbers. A majority of root climbers exceeds $L_b = 0.66$, while the distribution of twiners remains approximately the same as for L_a.

The value of T is widely varied in twiners and tendril climbers but the majority of species fall into the 0.26–0.50 class. T is lower in root climbers, with no species in the 0.51–0.75 class.

Growth rates—The highest rates are found in twiners (*Asparagus, Ipomoea, Mucuna,* and *Aristolochia* grew 11–14 cm/day) and the lowest rates are in root climbers (Table 2). All species of root climbers are actively growing, but even those under the most uniform high temperatures (*Philodendron, Vanilla, Pseudoludovia, Anthurium, Toxicodendron*) grow more slowly than any of the dicotyledonous twiners, most of the monocotyledonous twiners, and the tendril climbers.

DISCUSSION—The results of the present study support the qualitative generalizations of Schenck (1892), Raciborski (1900), and other authors concerning the timing of leaf and internode elongation in twiners. Foliage leaf expansion in twiners tends to be either markedly delayed behind internode elongation, or else precociously maturing scale leaves are produced. Together with the suppression of lateral branch outgrowth, either of these extreme patterns of leaf development maintain a whiplike shoot morphology.

This structural convergence has been interpreted as an evolutionary response to the physical influences on a twining shoot as it circumnutates in search of a support (Schenck, 1892; Raciborski, 1900; Gradmann, 1929; Baillaud, 1962). The presence of young, relatively unexpanded leaves, or small scale leaves is thought to increase the effectiveness of a searcher shoot by lightening the load on the shoot and removing the potential hindrance of large leaves. Raciborski demontrated that contact with a support promotes the greater expansion of leaves of some twining shoots, and in some species was necessary for continued shoot elongation. In many of the twiners examined here the expansion of foliage leaves was strongly delayed, even though the shoots twined up supports, thus contact clearly does not abolish the delay in leaf expansion.

In climbers with lateral branch tendrils the expansion of leaves also lagged behind the elongation of internodes (i.e., L is small). In monocotyledonous root climbers a variety of leaf-internode growth relationships was described, but none of them resembled the marked delay in leaf expansion found in twiners. In two of three dicotyledonous root climbers the expansion of leaves lagged behind both adjacent internodes; however, the values of L were greater than in most twiners with foliage leaves.

Raciborski proposed that the absence of a support inhibited leaf expansion less in tendril climbers than twiners, and had little or no effect on expansion in root climbers, with the notable exception of some aroids, e.g., *Rhaphidophora.* Raciborski was largely concerned with relative size rather than timing of expansion. In order to test his proposal for the species described here, growth measurements on unsupported shoots are necessary. In the case of *Philodendron* the timing of leaf expansion in climbing and pendant shoots is similar.

In order to gain a balanced perspective of the timing of leaf-internode growth in vines, some comparisons with non-vines are in order. Families of growth curves for both leaves and internodes are not frequently encountered in the literature, but they have been provided for apple (Hancock and Barlow, 1960) *Populus*, *Ginkgo* (Critchfield, 1960, 1970b), and *Betula* (Kozlowski and Clausen, 1966), from which the values of L_a and L_b have been calculated. In apple the final lengths of internodes and leaves were relatively constant during the period of measurement. The leaves and adjacent internodes (curves 5–9 in Fig. 1 from Hancock and Barlow, 1960) exhibited a close and relatively constant growth relationship, $L_a = 0.68$ (range 0.67–0.70) and $L_b = 0.79$ (range 0.77–0.80). In *Ginkgo*, *Populus*, and *Betula*, the early leaves elongate in near synchrony with little accompanying elongation of internodes. In later leaves of *Ginkgo* and *Populus*, there is a close growth relationship between an internode and an adjacent leaf. For *Ginkgo* $L_a = 0.78$ (range 0.73–0.82 for leaves 9–13). In *Populus* $L_a =$ 0.59–0.7 for leaves 7–10. In *Betula* (Kozlowski and Clausen, 1966), leaves and adjacent internodes grow together, but with a relationship that changes with the vigor of shoot growth and with the decreasing final length of leaves and internodes at the end of growth. In the tendril-climbing vine *Parthenocissus*, leaf expansion is delayed, although growth curves were not supplied (Critchfield, 1970a).

Previous studies of leaf and internode growth in monocotyledons have concerned grasses exclusively. In wheat, corn, blue grama, and *Agropyron* (Stubbendieck and Burzlaff, 1971; Sharman, 1942; Heimsch and Stafford, 1952; Etter, 1952; Smith and Rogan, 1975) the blade and sheath of a leaf complete elongation before the internode below, except in some of the upper internodes of corn (Heimsch and Stafford, 1952); therefore L_a, $L_b = 1.0$. A description of the close relationship between leaves and internodes in grasses has recently been provided for *Agropyron* (Rogan and Smith, 1975; Smith and Rogan, 1975). The establishment of internodes in *Agropyron* was correlated with the end of apical growth in the suprajacent leaf, and with the establishment of a basal intercalary meristem in that leaf. An internode and suprajacent leaf have been considered as a biological unit in grasses, the phytomer (Stubbendieck and Burzlaff, 1971). The inapplicability of the phytomer concept to monocotyledons in general was discussed previously from the histological standpoint (Fisher and French, 1976). It has also proved to be of limited value for describing the range of growth relationships between leaves and internodes in monoctoyledons.

The present report provides an opportunity to compare the timing of leaf expansion in monocotyledons and dicotyledons, although only limited information is available. In dicotyledons there are no documented examples of precocious maturation of foliage leaves like that described for *Pseudoludovia* (Cyclanthaceae). Also, in the palm, *Chamaedorea*, the foliage leaves mature before the adjacent internodes have begun their final, rapid phase of elongation (unpublished observations). The strongly delayed leaf expansion in twining and tendril climbing vines appears to be exceptional in non-viny dicotyledons and in monocotyledons. A closer growth relationship between leaves and internodes like that described for trees, discussed previously, and for monocotyledonous root climbers appears to be more typical of non-viny dicotyledons. In ferns delayed expansion of leaves is exhibited by some rhizomatous species (e.g., *Pteridium*) and by the root-climbing fern *Microgramma* (Hirsch and Kaplan, 1974).

Very few studies have been concerned with a combined descriptive and experimental account of leaf-internode growth relationships. In *Helianthus* the suprajacent leaf has the closest growth relationship with an internode and it is also the leaf whose removal has the most inhibitory effect on internode elongation (Wetmore and Garrison, 1965; Garrison, 1973). Also, the young leaves of *Helianthus* have been shown to be a source of gibberellin, which promotes internode elongation

(Jones and Phillips, 1966). In apple both leaves adjacent to the internode have a close growth relationship with the internode ($L_a = 0.68$, $L_b = 0.79$). The removal of a leaf has the most inhibitory effect on the suprajacent internode (Hancock and Barlow, 1960; Barlow and Hancock, 1956). In *Vicia* (Millet, 1970) the removal of a single young leaf inhibited elongation of the suprajacent internode, while in *Coleus* (Jacobs and Bullwinkel, 1953) the growth of the subjacent internode was inhibited. Information is not available concerning the growth relationships of leaves and internodes in these latter 2 species. Tammes (1903) removed young leaves from the vines *Vitis* and *Humulus* without inhibition of internode elongation. Tammes noted, however, that adjacent internodes were several cm long at the time of leaf removal. Leaf and internode development need to be examined from both a descriptive and experimental standpoint in additional species, including those with divergent patterns of development, e.g., twining vines with delayed leaf expansion or scale leaves.

Troll (1937) proposed that a characteristic feature of shoot development in vines was the abrupt increase in internode length immediately below the shoot apex, which he referred to as precocious internode elongation. There is no indication that a broad quantitative survey was conducted to document this conclusion. Other aspects of shoot growth need to be considered in evaluating the significance, if any, of precocious internode elongation to the presence of the viny habit. For example, the length of the plastochron may be more strongly correlated with precocious internode elongation than the viny habit. There is considerable diversity in the abruptness of internode length increase below the apex within vines. In a species with a long plastochron, e.g., *Philodendron*, the total number of elongating internodes present is small. When internode length behind the apex is plotted against internode number, the resulting curve exhibits a steep rise (unpublished observations, similar to those presented in Fisher and French, 1976). In comparison, a similar plot of the twiner *Dioscorea bulbifera*, which has short plastochrons and many elongating internodes, shows a gradual slope. Clearly, more species must be examined, and also the concept of precocious internode elongation needs to be more carefully defined. Troll described the entire duration of internode elongation in twiners as accelerated, and leaf maturation as delayed. This is clearly not the case in *Thunbergia grandiflora*, for example, in which the first visible leaves are longer than the adjacent internodes.

No previous attempts have been made in the literature to describe various parameters of internode growth (T, U/L, P, final internode length) in a comparative way. Wetmore and Garrison (1966) described the timing of successive internode elongation in *Helianthus* and *Syringa* as stepwise, and overlapping, respectively. Calculations from the representative growth data supplied for *Helianthus* (Garrison, 1973) show that $T = 0.1$, which approaches the low value of T in *Anthurium* (0.05). In *Helianthus* differential growth is pronounced in the upper part of the internode ($U/L = ca\ 3.5$) and the plastochron appears to be relatively long (8–12 days). In *Ginkgo*, *Populus* (Critchfield, 1960, 1970b) and apple (Hancock and Barlow, 1960), $T = 0.5$, 0.34 and 0.51, respectively. Data on patterns of differential growth are not available. Burkom (1913) conducted marking studies on a variety of species, but his data can only be compared in a limited way with that presented here. Burkom recognized that the growth relationships between internodes varied, but he did not attempt to compare species by using quantitative indices. He distinguished between shoots with 1) individualized growth of internodes, i.e., each internode exhibits a peak in relative growth rate that is separated from the peaks of other internodes by regions with lower rates, and 2) shoots with a single peak of maximum growth rate, which declines proximally and distally. The latter category seems to correspond to apices with high T. The changes in relative growth rate of internodes are probably quite complex (Williams, 1975, p. 71, for flax) and Burkom's analysis of growth rates in successive internodes needs to be reinvestigated.

In nearly all of the species examined here a wave of maturation proceeds from the base to the top of an internode, and into the base of the next internode above. The differential growth at the top of an internode does not result because it is a region of isolated, residual growth which persists after the base of the internode above has matured. In viny shoots the successive internodes show the same pattern of differential growth. In *Anthurium*, for example, the marked differential growth of the upper region is charcteristically followed by a region of little differential growth at the next internode above.

The amount of localized growth in an internode (U/L) and the timing of successive internode elongation (T) are measures of growth within the shoot. Figure 5 shows that in shoots from various species with a wide range in U/L and T, these two parameters tend to increase and decrease in a correlated manner. As the elongation of adjacent internodes becomes more overlapping (higher T) the differential growth within a single internode (U/L) decreases. Species with low T usually have relatively high U/L, but in some U/L is low. No species were found to exhibit both high T and high U/L. This correlation between T and U/L represents only the typical relationship between these parameters. Theoretically, through an unusual combination of growth differences between the upper and lower regions, the association of high T and high U/L could be accomplished. A region of residual growth at the top of the internode, i.e., an apical intercalary meristem, could generate high T and high U/L. Apical intercalary meristems are unusual in vegetative axes, compared with the frequency of basal intercalary meristems (Troll, 1937).

Unusual patterns of differential growth in internodes have been described for several dicotyledonous families (Acanthaceae, Polygonaceae, Caryophyllaceae; see French and Fisher, 1977, for references). Several references concerning internode growth in the Vitidaceae suggest that it also does not follow the typical pattern for dicotyledons. In *Vitis* the internodes are reported to mature first in the middle, and last at the base (Fournioux, 1972, cited in Pratt, 1974). Also in *Parthenocissus* Critchfield (1970a) reported that prolonged growth took place in the internode between the two tendril nodes. Residual growth is also present in the base of internodes of *Cayratia*.

Stebbins (1974, p. 332) briefly remarks that as a consequence of the lack of a cambium in monocotyledonous stems they were able to elongate more rapidly than stems of most dicotyledons. This favored evolution in the direction of herbaceous climbers, as in the Araceae and Commelinaceae (both root climbers), rattan palms, and climbing bamboos (both hook climbers). However, in the present study shoot growth was measured in several climbing species in the Araceae, *Philodendron, Rhaphidophora*, and *Anthurium* (Table 2). In these species shoot growth was relatively slow (2.2 cm/day, 2.2 cm/day, and 0.7 cm/day), compared with dicotyledonous twiners.

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