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The Elongation of the Leaf of *Cyclamen persicum* Mill. (Cultivars)

MARSHALL D. SUNDBERG*

ABSTRACT - The leaves of three cultivars of *Cyclamen persicum* were examined at several stages of development in order to determine the pattern of elongation in both the lamina and petiole. Although there is a considerable literature on lamina elongation, relatively little is known about the growth of the petiole. In the latter structure it is usually assumed that an intercalary meristem is involved. Elongation of the young leaf is initially due to activity distributed throughout the developing organ. Maturation of the leaf progresses acropetally from the base of the petiole and basipetally from the tip of the lamina. As the leaf matures elongation in both the lamina and petiole becomes restricted to their region of common attachment.

Morphologists are generally agreed that the angiosperm leaf consists of three parts; the leaf base, the petiole, and the lamina (Foster and Gifford, 1974). The growth and development of the lamina, especially of the dicots, has been extensively studied and the general features may be found in any textbook of plant anatomy (Esau, 1965; Cutter, 1971; Fahn, 1974). Troll (1939) presents a comprehensive survey of the morphology of the leaf, including the leaf base, and recently a considerable amount of work has been done by Kaplan on the development of the leaf base (1975). Relatively little is known, however, about the growth of the petiole.

Maksymowych (1959) has included the petiole in his study of leaf development in *Xanthium*. He showed that elongation of the petiole is at first acceleratory and that its rate of increase peaks after that of the corresponding lamina. In addition, growth of the petiole continues for a number of plastochrons after the lamina matures and the period of acceleratory growth appears to be associated with cell division. Maturation of the lamina in *Xanthium* is said to be basipetal, that is, the cells near the tip of the lamina mature first and the area of maturation proceeds towards the base of the blade. This is the case in most, if not all, species in which leaf elongation has been examined. The direction of maturation of the petiole, however, was not described.

Hagemann has included a brief description of petiole growth in his morphological monograph on *Cyclamen* (1959). He attributed the hyponastic curvature of the young petiole of *Cyclamen* to a sublaminar intercalary meristem. He states that this meristem is also responsible for the further growth of the petiole. In light of the paucity of information on petiole growth, and because the stems of many species that were assumed to contain intercalary meristems have been demonstrated to lack them (Fisher and French, 1976), it was decided to reexamine the elongation of both the lamina and petiole of several *Cyclamen* cultivars with particular attention being given to the direction of maturation of these organs.

Measuring Growth Increments.

Young seedlings of *Cyclamen* cultivars were used in this study. These consisted of c.v. Cardinal (6 plants), c.v. Rosa von Zeldendorf (5 plants) and second generation crosses of the F-1 hybrid Rosemunde (10 plants). The plants were

grown in nutrient enriched moss peat according to the schedule of Widmer *et al.* (1972). Prior to the beginning of schedule of Widmer *et al.* (1972). Prior to the beginning of the study, the seedlings were transplanted into individual 4-inch pots and these were set out in the greenhouse under natural illumination and a day-night temperature regime of 22 C - 18 C. The plants were watered daily and no additional fertilizer was required over the duration of the investigation.

Five typical individuals were selected for the marking study. The petiole and lamina of one to several leaves on each of these plants were marked with india ink at either

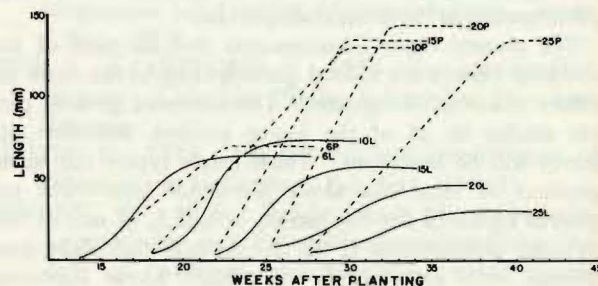


FIGURE 1 — Diagrammatic representation of the average lengths of leaf lamina (L) and petiole (P) at successive weeks after planting. Only 5 of approximately 30 leaves along the main shoot are represented.

2mm or 5mm intervals. A 000 Castel TG lettering pen and mm rule were used to mark the plants. At one week intervals the size of each segment was measured with a vernier caliper. As the tissues expanded the leaves had to be remarked. The new mark was placed approximately in the center of the band which resulted from expansion of the original mark. At first three independent measurements were made of each segment and the average value calculated, however, once a segment became about 4mm long it was found that the error in measurement was less than 5 percent and only single measurements were recorded thereafter. The study was concluded when most of the leaves being measured appeared to have reached their maximum size.

Growth Patterns Described.

The relative elongation of the lamina and petiole of successive leaves of *Cyclamen persicum* F-1 Rosemunde was intensively studied in a previous, unpublished investigation. A brief summary of the salient features of that investigation

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will provide the background necessary for the present study. In the former work several plants were harvested from a large population at weekly intervals over the course of an entire growing season. The dimensions of the leaf parts were scored and the average size recorded for each collection. From these data it was concluded that the lengths of both lamina and petiole, when plotted arithmetically against time, exhibit a sigmoid growth pattern. The growth curves of successive leaves overlap so that adjacent leaves were in sequential phases of acceleratory or deceleratory growth. In addition, there was a stepwise gradient in the maximum length achieved such that through leaf 10, each mature leaf was slightly larger than its predecessor. The mature petiole length of later leaves remained approximately constant at this maximum while the mature lamina length of later leaves began to steadily decrease (fig. 1). The mature lengths of selected leaves along the axis were as follows: leaf 5, $62.24 + 0.72\text{mm}$ (lamina), $89.33 + 3.55\text{ mm}$ (petiole); leaf 7, $69.20 + 1.14\text{mm}$ (lamina), $111.21 + 3.81\text{mm}$ (petiole); leaf 11, $62.01 + 0.90$ (lamina), $143.11 + 2.14\text{mm}$ (petiole).

A sigmoid growth curve suggests that the early phase of elongation is positively exponential. Semilogarithmic plots of the data confirmed that this was true and also demonstrated that the inflection point occurred at approximately $\frac{1}{2}$ the total length in both the lamina and petiole. Thus, the acceleratory phase of elongation was responsible for approximately half the final length achieved. A prolonged period of acceleratory growth such as this implied that the entire developing organ, rather than a single intercalary area, was participating in the elongation process.

The present study demonstrates that all parts of the developing organs are indeed participating in the early acceleratory phase of elongation. The observed growth patterns are similar in all of the leaves studied, therefore only 3 leaves will be described. These leaves typify the increasing gradient of final size along the shoot axis. The growth pattern observed for the lamina of leaf 5, of one of the F-1 hybrids, is illustrated in fig. 2. Initially this blade was subdivided into four, 2mm segments. These segments are lettered sequentially from the tip of the blade to the point of insertion on the petiole (fig. 2a). The cumulative growth of the lamina on successive weeks after marking is shown in fig. 2 b. Each of the segments is contributing to the increase in total lamina length. In addition, a new segment is measurable at week 7. This segment, e, occurs at the base of the blade just above its union with the petiole. During the first 5 weeks each segment is contributing approximately equally to the total length, fig. 2c, however, the 2 distal segments (a,b) appear to mature at about week 5 while the 2 proximal segments continue to elongate. This is the characteristic pattern of lamina elongation as described in the literature, therefore data obtained from laminae of additional leaves will not be presented here.

The trends observed for elongation of the petiole are unlike those described for the lamina. The data represented in fig. 3a, bare from the petiole of the same leaf used in fig. 2. The petiole was originally divided into five, 2mm segments. At this point the petiole had attained nearly half its final length (fig. 3a). The elongation of the 2 proximal segments has already stopped and elongation is limited to the more distal segments. During week 3 a new segment appears adjacent to the insertion of the lamina. The early cessation of growth by the proximal segments along with the addition of a distal segment during the course of the observations

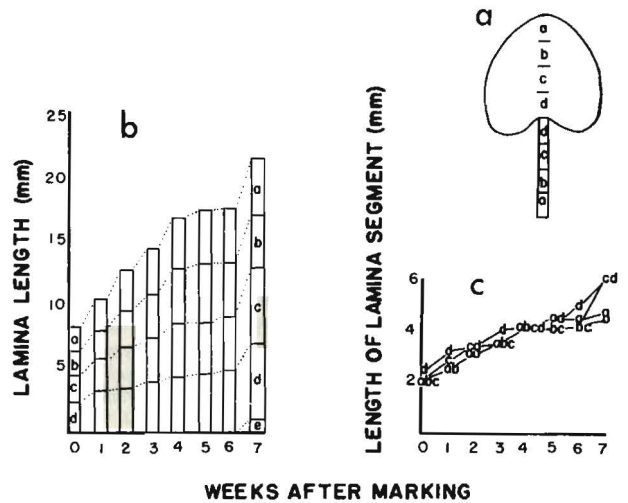


FIGURE 2 — Lamina elongation during the period of study. Manner of designating leaf segments of both the lamina and petiole (a): contribution of individual lamina segments to the total lamina elongation of leaf 5 (b): length of the individual segments of leaf 5 (c).

suggests that maturation in the petiole is acropetal.

Additional data from petioles 7 and 11 of 2 different plants are used to verify the trend observed in petiole 5 and to provide information on the growth of a younger petiole. These data are illustrated in figs. 2cd and ef respectively. The petiole of leaf 7 was initially subdivided into three, 2mm segments (fig. 3a). At this time the organ was approximately $\frac{1}{5}$ its final size and still in the period of acceleratory growth. Similar to the observation for early lamina growth, each segment contributes approximately equally to the early acceleratory growth of the petiole. The direction of maturation in the petiole, however, again appears to be acropetal. The rate of elongation of the proximal segment begins to drop at about week 4 while the rates of the more distal segments continue to increase (fig. 3d). By comparing figures 3 a and 3c it can be seen that the proximal segment at week 3 in the latter case is approximately equivalent to both segments a and b at time 0 in the former example. It is not unexpected, then, that the elongation of this segment should begin to drop off after 3 weeks. On the other hand, the proximal segment of petiole 7 does continue to grow for a longer time than would be expected based on petiole 5. This is probably attributable in part to the greater final size achieved by the leaf higher along the axis (22 vs 27 mm). However, it may also be due to additional elongation of the distal portion of segment 'a' which is equivalent to the base of segment c in petiole 5 at time 0. Further evidence for the acropetal pattern of maturation is the appearance and subsequent elongation of segment 'd' at the distal end of the petiole. Before considering leaf 11, it should be noted that petiole 7 is the only one in which growth was studied during the interval of time where the sigmoid pattern of petiole elongation is apparent (fig. 3c).

The trends observed in petiole 11 (fig. 3 e,f) are similar to those already described for leaves 5 and 7. The total length of the petiole at the time of marking is about $\frac{1}{3}$ its final length. Although this study was terminated prior to the attainment of maximum size, subsequent examination revealed that the maximum petiole length for this plant is between 45 and 50 mm. In terms of the overall growth curve, this petiole is near the inflection point at the time of marking. As a result, the pattern described for this petiole is similar to that

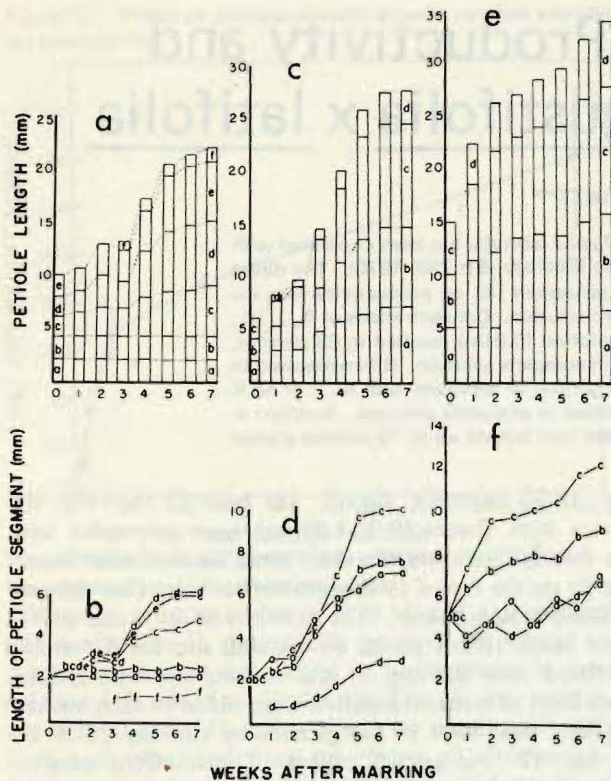


FIGURE 3 — Petiole elongation during the period of study. Data is presented for leaves 5, 7, and 11 (a, b, c, d, e, f respectively). Contribution of individual petiole segments to the total petiole elongation (a, c, e): length of the individual segments for the respective leaves (b, d, f).

described for petiole 5. The proximal segment has already nearly terminated growth at the time of marking. The slight increase in length observed, like that observed in the proximal segment of petiole 7, is probably due to the more distal cells of that initial segment which would have been included in segment c of petiole 5. Likewise, a new segment, d, appears at the distal end of the petiole during the study. It is likely that most of the additional 10mm of growth required to achieve the maximum size is due to elongation of this segment. A comparison of figs. 3c and 3e suggests that again the growth pattern observed for the more distal, potentially longer petiole is simply a continuation of the basic pattern observed in the lower petiole.

Two trends emerge.

The pattern of lamina elongation in *Cyclamen* is similar to that described in other genera. Growth occurs in all regions of the young developing blade. This phase corresponds to the early phase of acceleratory elongation. Maturation of the lamina appears to be basipetal as elongation becomes restricted to the segments adjacent to the petiole and an

additional segment may arise in this region. The early pattern of elongation in the petiole is similar to that of the blade, that is, all regions of the petiole are active and growing at approximately the same rates. This phase, like the corresponding phase of the blade occurs during the period of acceleratory petiole elongation. Maturation of the petiole, however, appears to be acropetal as elongation of the petiole gradually becomes localized adjacent to the lamina. The proximal segments mature first as a new segment arises adjacent to the point of lamina insertion. This pattern is similar to that described by Garrison (1973) for the internodes of *Helianthus*, and the pattern of peduncle elongation in *Cyclamen* (Zinsmeister, 1960). An acropetal pattern of internode maturation has also been described by Fisher and French (1976) for the internodes of many angiosperms. An analysis of cell division and cell elongation in the various regions of the petiole is needed to determine the role of each of these processes in the activity of the meristem.

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