GROWTH OF *XANTHIUM* (COMPOSITAE) INTERNODES AT DIFFERENT POSITIONS ON THE STEM

JOSEPH A.J. ORKWISZEWSKI AND ROMAN MAKSYMOWYCH

Biology Department, Villanova University,
Villanova, PA 19085

(Received: June 23, 1997. Accepted: August 26, 1997)

ABSTRACT

Internode growth of vegetative *Xanthium* plants was studied at various levels on the stem with application of the plastochron index. The bottom internodes were of small size and they displayed small rates of growth. Both, the size of the internodes and their growth rates increased proceeding in the acropetal direction. Rates of cortical cell elongation followed a bell shaped curve, starting with a rate of 7 μm per day, reaching a peak of 15 μm per day and stopping after leaf plastochron index 14. Young internodes, smaller than 25 mm, grew at a constant relative elemental rate of 0.2 day^{-1} throughout. Internodes larger than 30 mm displayed an acropetal pattern of elongation.

KEY WORDS: *Xanthium pensylvanicum*, internode, relative elemental rates.

INTRODUCTION

Marking experiments were performed first by Julius Sachs (1873) in his classical experiments on root growth of *Vicia faba*. By placing series of marks on a root he was able to differentiate between growing and non-growing regions of this organ. From the displacement of marks and mitotic counts Sachs formulated a concept of zones of cell division, elongation and maturation of the primary root. A similar, but more refined method was used by Erickson and Sax (1956a, b) in corn root studies. Erickson and Sax introduced the term relative elemental growth rates of cell division and cell elongation in their growth study of *Zea mays*. Root growth was represented by two bell shaped curves. One represented relative elemental rates of cell division with a peak of 1.5 mm distance from the tip and the other showed relative elemental rates of cell elongation, with the peak at 3.5 mm distance from the tip. Erickson and Sax (1956a, b) concluded that between 0-3 mm root growth involved two processes, cell division and cell elongation. After 3 mm from the tip development involved cell elongation alone. Growth of *Zea mays* roots stopped after 8 mm distance from the tip.

In comparison to that of roots, the growth of stems has not been investigated as extensively. This paper is an attempt to study the growth of internodes of *Xanthium* plants and to determine their growth rates at various levels on the stem.

MATERIALS AND METHODS

Burs of *Xanthium pensylvanicum* (Walr.) were germinated and the plants were grown as described by Maksymowych, Maksymowych and Orkwiszewski (1985). Morphological ages of plants were determined by the use the plastochron index (PI) developed by Erickson and Michelini (1957).

Internode length on the primary shoot starting at the base were measured with a vernier caliper twice a week. From each curve, the rates of internode elongation ($dX/dt \text{ d}^{-1}$) were calculated by a 3-point derivative formula (Milne 1949, Table 1).

Preliminary experiments were performed to ascertain whether or not the cell length pattern of internodes excised from plants of similar indices differed significantly. Two plants of close PI were selected. One had a PI of 11.52, the other 11.55. A 3 mm segment was excised from the internode at the midpoint between two nodal regions and the tissue was fixed in 3:1 95% ethyl alcohol:glacial acetic acid. Tissues were processed and sectioned at 10 μm thickness, and slides were prepared according to standard cytological techniques (Jensen, 1962). Cortical cell lengths were measured under 430X magnification by means of a calibrated Whippel ocular micrometer from the initial and final cell lengths for each internode (Fig. 1). Cell lengths of the two internodes did not differ significantly.

To obtain data for relative elemental rates of elongation, the internodes were marked with India ink at approximately 1 mm intervals and photographed on 3 successive days. It was

TABLE 1. Relationship between internode length, its position on the stem and the rates of internode elongation and cell elongation.

INTERNODE No.	AVERAGE ABSOLUTE RATE dX/dT mm day ⁻¹	AVERAGE RELATIVE RATE $1/X(dX/dT)$ day ⁻¹	AVERAGE MATURE LENGTH (mm)	AVERAGE RATE OF CELL ELONGATION (μ m/day)	AVERAGE CELL LENGTH (μ m)	STANDARD DEVIATION
1	0.49	0.10	5.5	2.8	27.4	7.63
2	2.26	0.10	34.1	4.0	32.5	8.91
3	3.08	0.17	20.7	6.0	41.2	11.98
4	6.21	0.32	55.1	7.0	65.4	22.40
5	7.46	0.29	55.1	7.8	67.5	25.18
6	8.48	0.28	63.1	9.0	67.8	23.19
7	8.43	0.29	68.5	9.8	87.2	19.72
8	6.37	0.29	61.9	11.7	88.5	21.66
9	3.61	0.14	58.5	14.0	109.8	16.74
10	5.88	0.24	64.5	15.4	112.7	23.29
11	9.84	0.32	60.1	12.5	114.6	8.7
12	7.78	0.26	59.3	7.5

Fig. 1. Longitudinal section of a mature *Xanthium* internode. The spherical bodies in epidermis (ep), collenchyma (col) and cortex (cor) are chloroplasts.

assumed that during the 3-d interval the marks would separate from each other, thus establishing a growth pattern of internode elongation. For a more detailed method of analysis the reader is referred to Maksymowych, Maksymowych and Orkwiszewski (1985).

RESULTS

Figure 1 represents a photomicrograph of a longitudinal section through a mature *Xanthium* internode. Proceeding from the left the tissues are: epidermis (ep) collenchyma (col) and cortex (cor). The emphasis in this study is on the rates of elongation of cortical cells. The spherical bodies in all three tissues are chloroplasts as revealed by transmission electron microscopy (TEM) (Maksymowych et al., 1993). On the average the epidermis had 9.8, collenchyma 29.7 and cortex 31 chloroplasts per cell.

Figure 2 represents log values of serial internode lengths starting with No. 1 the basal internode and finishing with No. 12 the apical internode. The early stages of growth are exponential as evident by straight lines obtained from the log length plot against days. The internodes were initiated at equally spaced time intervals.

Rates of cortical cell elongation plotted against the leaf plastochron index (LPI) in Fig. 3 started with a small rate of 7 μ m/d at LPI 4. The maximum rate of 15 μ m/d was reached at about 10 LPI. After 14 LPI all cells reached maturity.

Absolute rates of internode elongation are given in Table 1. Basal internodes display small rates of elongation. Internode No. 1 elongated with 0.49 mm/d and No. 22.26 mm/d. Rates of growth increased in the acropetal direction with internode No. 11 growing at 9.84 mm/d. The trend is apparent. The most basal internodes with small sizes displayed small rates of elongation. The sizes and the rates of growth increased up to the 11th internode and leveled off thereafter. A similar trend

Fig. 2. Log internode length of *Xanthium* plotted against days.

Fig. 3. Rate of cortical cells elongation plotted against the leaf plastochron index (LPI). The peak of elongation was at LPI 10.0. Elongation stopped after LPI 14.

Fig. 4. Relative elemental rate of *Xanthium* internode elongation plotted vs. distance from the apex. The rates of this young internode were constant (0.25 day^{-1}) throughout.

Fig. 5. Relative elemental rates of *Xanthium* internode 37 mm long plotted vs. distance from the internode apex. The pattern of this older internode was acropetal.

is also apparent considering the size and the rates of elongation of the cortical cells (Table 1). Internode No. 2 had cells $27.4 \mu\text{m}$ long, internode No. 3 $32.5 \mu\text{m}$; the size increased to $114.6 \mu\text{m}$ in internode No. 12. The absolute rates of cell elongation were small in the basal internodes; internode No. 2 had a rate of $4 \mu\text{m/d}$ and No. 10, $15 \mu\text{m/d}$.

Table 1 represents absolute rates of elongation which are increments of growth of the whole internode. It would be of interest to examine the distribution of growth along the vertical axis of an internode. Relative elemental rates of growth [$d(dX/dt)/dX \text{ d}^{-1}$] represent growth of a minute segment of an internode relative to the segment size at any distance from the apex. The segment at the apical node is defined here as the internode apex.

Figure 4 represents the relative elemental rate of a young internode, 25 mm long plotted against distance from the apex. The elemental rates of this internode were constant throughout at 0.25 d^{-1} , representing 25% increment of each segment.

Older internodes displayed an acropetal pattern of growth. In an acropetal pattern of growth the basal segments stop growing first and the apical ones, last. As evident from Fig. 5, an internode 40 mm long displayed an acropetal pattern of growth. The apical segment elongated at about 25% and after 10 mm distance from the apex the growth rate decrease precipitously, reaching 0 at 37.5 mm distance from the apex.

DISCUSSION

The spherical bodies in Fig. 1 were identified by TEM as chloroplasts. Chloroplasts were present in epidermis, collenchyma and cortex tissues of *Xanthium* stem. They also have been found in the same tissues of *Ambrosia*, *Cucurbita*, *Galinsoga*, *Lycopersicon*, *Mentha*, *Physostegia*, *Rubus*, *Saponaria* and *Solidago* in addition to *Xanthium* (Maksymowych et al., 1993). The presence of chloroplasts in stem

tissues enhances survival of herbaceous seedlings, Nilsen and Bao (1990).

Erickson and Michelini's (1957) graph of *Xanthium* leaf length is strikingly similar to our set of curves on internode length as presented in Fig. 2. Criteria for developing the PI: exponential early growth, equally spaced initiation of leaves and a set of parallel lines, were met in our data on internode length (Fig. 2). However, we felt that there is no need to derive a new internode PI, since LPI (Erickson and Michelini, 1957) can be used to stage internode development. Leaf growth mimics internode growth, and a leaf subtending a particular internode can accurately designate the internode developmental stage, as evidenced in these studies.

Development of internodes and nodes positioned in the proximity of the stem apex is based on the activity of apical and subapical meristems. Each initiated internode is separated by meristematic tissue that will develop into a node. Internodes and nodes at the apical region are closely packed together, so much so, that their size is too small for marking experiments. However, based upon marking experiments of young internodes, one could hypothesize that the apical shoot grows as a unit with a relative elemental rate of 0.2 d^{-1} throughout, since in the apical shoot there is no sharp separation between internodal and nodal tissues. The authors are not aware of any analysis that covers the entire portion of the apical shoot. Similar studies, however, have been made with individual internodes of some dicotyledons. Wetmore and Garrison (1961) and Garrison (1973) reported that internodes of *Syringa vulgaris* and *Helianthus annuus* have meristems progressively confined to upper regions of the internode, displaying an acropetal pattern of elongation. Enright and Cumbie (1973) investigated internodal development of *Phaseolus vulgaris*. They determined that early growth of internodes takes place throughout the internode and that later growth was limited to successively higher regions. This also can be interpreted as an acropetal pattern of growth similar to older *Xanthium* internodes.

Table 1 represents the relationship between *Xanthium* internode position on the stem, the growth rate of internodes and their rates of cell elongation.

Young internodes at the base of the stem grew at low rates and displayed low rates of cortical cell elongation. For instance the third internode, counting from the bottom, was 20.7 mm long; it elongated 3.08 mm/d and displayed $6 \mu\text{m/d}$ cell elongation. Whereas the tenth internode was 64.5 mm long; it

elongated 5.88 mm/d and demonstrated $15.4 \mu\text{m/d}$ cell elongation. This was the maximum rate of cell elongation of all internodes on the stem. With increasing age the rate of internode elongation and the rate of cell elongation both declined.

Data were presented for absolute rates and relative elemental rates of internode growth of *Xanthium*. Internode growth represents an organized system which is most assuredly under complex genetic control. The process of development must be under the influence of a "genetic conductor," one that regulates developmental processes, e.g., indicating when cell division has to stop, when cell elongation and differentiation should start and at what distance from the internode apex. These events may occur by means of repressing and derepressing genes in the space of internode length and developmental time.

LITERATURE CITED

- ENRIGHT A.M., CUMBIE B.C., 1973. Stem anatomy and internodal development in *Phaseolus vulgaris*. American Journal of Botany. 60: 915-922.
- ERICKSON R.O., SAX K.B., 1956a. Elemental growth rate of the primary root of *Zea mays*. Proceedings American Philosophical Society 100: 487-498.
- ERICKSON R.O., SAX K.B., 1956b. Rates of cell division and cell elongation in the growth of the primary root of *Zea mays*. Proceedings American Philosophical Society 100: 499-512.
- ERICKSON R.O., MICHELINI F.J., 1957. The plastochron index. American Journal of Botany 44: 297-305.
- GARRISON R., 1973. The growth and development of internodes in *Helianthus*. Botanical Gazette. 134: 246-255.
- JENSEN W.A., 1962. Botanical histochemistry. W.H. Freeman. San Francisco, CA.
- MAKSYMOWYCH R., MAKSYMOWYCH A.B., ORKWISZEWSKI J.A.J., 1985. Stem elongation of *Xanthium* plants presented in terms of relative elemental rates. American Journal of Botany 72: 1114-1119.
- MAKSYMOWYCH R., DOLLAHON N., DI COLA L.P., ORKWISZEWSKI J.A.J., 1993. Chloroplasts in tissues of some herbaceous stems. Acta. Societatis Botanicorum Poloniae 62: 123-126.
- NILSEN E.T., BAO Y., 1990. The influence of water stress on leaf photosynthesis in *Glycine max* and *Spartium junceum* (Leguminosae). American Journal of Botany 45: 383-387.
- SACHS J., 1873. Über das Wachstum der Haupt- und Nebenwurzeln. Arbeiten des Botanischen Institut Würzburg 1: 385-474.
- WETMORE R.H., GARRISON R., 1961. The growth and organization of internodes. Recent advances in botany. University of Toronto Press.

WZROST MIĘDZYWIEŻLI U *XANTHIUM* (COMPOSITAE) W RÓŻNYCH MIEJSCACH ŁODYGI

STRESZCZENIE

Badano wzrastanie międzywieżli u wegetatywnych roślin *Xanthium* na różnych wysokościach łodygi, stosując wskaźnik plastochronowy. Dolne międzywieżla były małe i wykazywały niskie tempo wzrostu. Tak wielkość międzywieżli, jak i ich tempo wzrastania zwiększało się w kierunku akropetalnym. Tempo wydłużania się komórek kory wykazywało kształt krzywej dzwonowatej, począwszy od tempa 7 m na dzień, osiągnęła szczyt przy 15 m/dzień i zatrzymując się po osiągnięciu wskaźnika plastochronowego = 14. Młode międzywieżla, mniejsze niż 25 mm rosły przez cały czas w stałym względnym tempie = $0,2 \text{ dzień}^{-1}$. Międzywieżla większe niż 30 mm wykazywały akropetalny wzór wydłużania się.

SŁOWA KLUCZOWE: *Xanthium pensylvanicum*, międzywieżla, relatywne tempo wzrostu.