ALLOMETRIC GROWTH OF *XANTHIUM* (COMPOSITAE) LEAVES

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ABSTRACT

When *Xanthium* lamina width is plotted versus leaf length during the entire period of growth, a straight line is obtained representing an allometric relationship with a regression correlation coefficient of 0.9973 a lamina width to length ratio of 0.502 ± 0.01 and chordate morphology. On the other hand, gibberellic acid treated plants yield a correlation coefficient of 0.9871 a lamina width to length ratio of 0.372 ± 0.0074 and lanceolate leaves. The fraction of leaf width to leaf length is a measure of lamina width reduction. Gibberellic acid alters the mechanism which controls the balance between the leaf length and the leaf width.

KEY WORDS: *Xanthium*, leaf growth, allometry, gibberellic acid.

Allometry is the relative growth of a part of an organ, in relation to an entire plant organ. In the present investigation the width of the lamina was compared with leaf length of *Xanthium pensylvanicum* during the entire period of growth in control and gibberellic acid (GA_3) treated plants. Data display hormonally controlled mechanisms involved in determining leaf shape during development.

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 leaf plastochron index (LPI) developed by Erickson and Michelini (1957), Erickson (1960).

To obtain data for the allometric relationship between leaf length and width, (Fig. 3) the dimensions were measured with a vernier caliper for small leaves and a ruler for longer leaves, respectively. Rates of elongation (dX/dt) were calculated by a 3-point derivative formula (Milne 1949). Straight lines in Figs 3 and 4 were fitted by the least squares method.

Randomly selected plants of approximately uniform age were used. One group served as controls, whereas the other group was treated with 0.7 mg of GA_3 per plant. The hormone was applied in lanolin paste to young internodes 8-12 mm in length (Maksymowych, Cordero and Erickson 1976).

RESULTS

Figure 1 represents a plot of leaf length (leaf No. 9) vs LPI. This sigmoid curve represents the "grand period of growth" with an acceleration phase up to approximately LPI +1.0, an exponential phase between +1.0 and +4.0 LPI, and a deceleration

phase between LPI +4.0 and +7.0. After LPI +7.0 the leaf has mature anatomy (Maksymowych 1990) and does not elongate. An equation can be fitted to this sigmoid curve $X = X_0 e^{rt}$, where X is the mature leaf length, X_0 is any initial leaf length, e is the base of a natural logarithm, r is the relative rate and t is the time in days. When the same plot is presented as a semilogarithmic plot (Fig. 2), the exponential phase of growth is now represented by a straight line between LPIs +1.0 and +4.0. The equation now becomes $\log X = \log X_0 + rt$. This is known as logarithmic transformation of an exponential equation and serves as a mathematical proof of the exponential phase. The derived absolute rates (dX/dt /day) indicate a maximum rate of elongation of about 18 mm per day at LPI +3.5. Then the rate curve decreases precipitously and becomes 0 after LPI +8.0.

Figure 3 represents an allometric relationship between leaf length and leaf width obtained from measurements of intact leaves (Table 1). The correlation coefficient of the fitted line was 0.9797. The ratio between leaf width and leaf length was 0.510 ± 0.01 and was obtained from measurements of 36 *Xanthium* plants.

Figure 4 represents a plot of leaf length vs leaf width of 15 plants treated with gibberellic acid (GA_3). Such plants produced morphogenetically altered leaves, from chordate in control plants to lanceolate in treated plants (Fig. 5). The correlation coefficient of the fitted line was 0.9870 and a width to length average ratio of 0.37 ± 0.074 .

Students t test of the significance between slopes of the control and GA_3 treated plants revealed a highly significant difference between the two slopes ($t=5.2$; d.f. = 47; $P < 0.01$).

DISCUSSION

Allometric relationship makes it possible for us to compare the growth of lamina width with respect to the elongation of

Figs 1-4.

Fig. 1. Leaf Length of *Xanthium pensylvanicum* plotted against leaf plastochron index (LPI) representing grand period of growth.

Fig. 2. Logarithm leaf length and absolute rate of elongation plotted against LPI. The exponential phase of growth is represented by the straight line in the log length plot. The peak of leaf elongation was 18 mm per day at LPI 3.5.

Fig. 3. Leaf length of *Xanthium pensylvanicum* plotted against leaf width representing allometric relationship of growth.

Fig. 4. Leaf length from gibberellic acid (GA_3) treated plants plotted against leaf width. The lamina width to length ratio was 0.37, whereas in control plants it was 0.5, representing the degree of reduction of lamina width. Gibberellic acid treatment caused morphogenetic changes from chordate in control plants to lanceolate in treated plants.

the whole leaf. It was observed that the leaf maintains a strict relationship of width to length which for *Xanthium* was 0.5 with apparently very small variability of ± 0.01 . One is tempted to speculate on the possible mechanism which controls lamina width. Marginal and plate meristems are involved in leaf development (Maksymowych 1990). The marginal meristem initiates lamina and the plate meristem brings about the extension of the blade in area. The marginal meristem in *Xanthium* forms six basic layers of cells by anticlinal, periclinal and oblique divisions in the activity of the meristem (Maksymowych 1990). The preponderance of cell division in the plate meristem is anticlinal. From the basic six layers of cells a mature lamina is established with a total 8-10 cell layers of the upper and lower epidermis, palisade and middle mesophyll layers. It appears that the activity of the plate meristem was altered by GA_3 treatment, for lanceolate instead of chordate leaves were produced. The significantly reduced area of the lamina may

have resulted from inhibition of cell division and/or cell enlargement of the plate meristem during lamina development. In addition to a reduction in the blade area of GA_3 treated plants, leaf length and the length of petioles were both reduced. In control plants the ratio of leaf width to leaf length was 0.5, in GA_3 treated plants the ratio was 0.37. This ratio is the measure of the degree of lamina width reduction.

Since leaf development appears to be under genetic control, transcription and translation processes must be involved producing enzymes which control cell division and enlargement in the plate meristem. Huxley (1972) postulated that "genes controlling relative rates will have to exert their action by influencing the rates of processes and so fall in line with other numerous rate-factors" of lamina expansion in area and processes controlling leaf elongation. The differential rates of lamina width and leaf length are precisely coordinated to yield a ratio of 0.5.

TABLE 1. ALLOMETRIC relationship between *Xanthium* leaf length and leaf width a.

LEAF LENGTH (mm)	LEAF WIDTH (mm)	LEAF LENGTH (mm)	LEAF WIDTH (mm)	LEAF LENGTH (mm)	LEAF WIDTH (mm)
0.170	0.65	23.000	11.500	124.000	61.000
0.260	0.130	32.000	15.000	134.000	64.000
0.390	0.190	34.000	17.000	135.000	77.000
0.580	0.290	48.000	24.000	140.000	70.000
0.880	0.440	51.000	31.000	153.000	82.000
1.300	0.650	62.000	31.000	158.000	76.000
2.000	1.000	76.000	38.000	183.000	85.000
2.900	1.450	79.000	45.000	188.000	90.000
4.300	2.150	90.000	45.000	214.000	113.000
6.500	3.250	102.000	43.000	234.000	120.000
10.000	5.000	105.000	55.000	265.000	132.000
15.000	7.500	118.000	60.000	275.000	141.000

a. $\bar{X}$ of ratio of leaf width/leaf length = 0.502 ± 0.01

Fig. 5. Lanceolate mature leaf from GA₃ treated plant at left and the control leaf on the right side.

To paraphrase Thompson (1942) the form of an organism (or an organ) is determined by its rates of growth in various directions.

Huxley (1972) suggested the formula for allometric growth $y=bX^k$, where y is the length of the leaf, X is the breadth, b is a constant (the value of y when X is unity), and k is the ratio between the growth rates of X and y. The value of k indicates whether the leaf is becoming large ($k > 1.0$) or its lamina is becoming narrower ($k < 0.1$).

Hammond (1941) investigated allometric growth of 24 dicotyledenous plants. Eight plants had a k value greater than 1.0, with the relative rate in length higher than the relative rate of growth in width. Thirteen plants had k value smaller than 1.0 in which the relative rate of growth in width exceeded that of length. Four plants displayed a range of k between 0.73 and 1.3 indicating variable relative rates of growth.

In addition, Hammond (1941) presented a graph of allometric growth of 12 plants where leaf length is plotted against leaf width. The presented lines are similar to ours presented in Figs 3 and 4.

In some plants heteroblastic leaf development may be affected by light intensity which may affect carbohydrate metabolism and mineral nutrition (Ashby 1948). Allsopp (1953) investigated the effects of various sugars on the development and morphology of aseptic cultures of *Marsilea* sporelings. He concluded that the heteroblastic development was determined by the effects of nutrition, obtaining best growth with sucrose and glucose.

McCallum (1902) succeeded in producing areal leaves on submerged shoots of *Proserpinaca palustris* by immersing the latter in nutrient solutions of a concentration insufficient enough to plasmolyze the cells. Leaf morphology was changed from linear shape to leaves with broader bases. Thus, allometry was changed by an experimental method.

Our results obtained from treatment of *Xanthium* leaves with GA₃ produced a striking morphogenetic change where chordate leaves were transformed into lanceolate. Since the ratio of leaf width to leaf length changed from 0.5 to 0.37 the leaves became narrower as a result of treatment.

Allometry is not a broadly investigated subject. We know very little about the mechanism controlling leaf shape. Unravelling the mechanisms involved in determination of final leaf shape remains an experimental challenge for the future.

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ALLOMETRYCZNY WZROST LIŚCI *XANTHIUM* (COMPOSITAE/)

STRESZCZENIE

Porównując szerokość blaszki *Xanthium* z długością liścia w czasie całego okresu wzrostu, uzyskujemy linię prostą obrazującą związek allometryczny z współczynnikiem korelacji regresji 0,9973, stosunek szerokości do długości blaszki 0.502 ± 0.01 oraz kształt sercowaty. Natomiast rośliny traktowane kwasem giberelinowym wykazują współczynnik korelacji 0.372 ± 0.0074 oraz liście lancetowate. Stosunek szerokości do długości liścia stanowi miarę redukcji szerokości blaszki. Kwas giberelinowy zmienia mechanizm kontrolujący równowagę między długością a szerokością liścia.

SŁOWA KLUCZOWE: *Xanthium*, allometria, wzrost liści, stosunek szerokości do długości, kwas giberelinowy.