

**Asymmetric development of Cotyledons of Tomato Embryo:
Testing the prediction of Self-Organization**

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Abstract

Developmental biologists have long strived to understand how organisms acquire shape and form. The architecture of the mature plant is established during embryogenesis. They have learned much about how gene expression controls the specification of cell type and about how cells interact with one another to coordinate such specific decisions. Far less is known about autocatalytic feedback flow of resource molecules regulating a plant and its parts, shape and form. Indeed, it has even been proposed that the development of shape is not under genetic control but rather is determined by physical forces. Asymmetric development of sinks that depend on common resource pool has been viewed as a consequence of autocatalytic feedback process of flow of resource units into them. The feedback process implies that the stronger a sink is relative to its competitors, the greater is its probability of getting further resources as a non-linear function of its resource drawing ability and sink size. We have shown that this model contrasts with that of sink strength dependent model in its prediction of the subsequent development of the initial asymmetry of growing cotyledons of the tomato embryo (*Lycopersicon esculentum* L.), when their resource drawing ability is enhanced by exogenous application of the growth regulators (NAA, GA and BA), we test these prediction and show that the results are in conformity with the autocatalytic model proposed by Ganeshiah and Uma Shaanker.

Key words: Autocatalytic feedback, Growth Regulators, Resources Molecules, Sink Strength, *Lycopersicon esculentum*

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Introduction:

Asymmetric development of branches, of leaves in the branches, of fruits in inflorescences, and of seeds in fruits, is a common feature in plants. These asymmetries are mostly non-genetic and are viewed to be a consequence of competition among growing sinks for limited resources. The explanations are however, highly system specific and are inadequate in offering a general explanation for the observed patterns associated with the asymmetric growth and development of organs. Recently, a process of self-organized movement of resources has been forwarded as basic underlying model for the origin of asymmetry among growing sinks. The model suggests that asymmetry can be generated even under resource abundant condition. The process involves a feedback aggravation of differences in the growth rates among the developing organs that arise due to an initial random drift of the resources molecules into these sinks.

Basically self-organization is the process wherein a certain order or pattern emerges as a result of stochastic interaction among the components of an otherwise random system (Arthur et al. 1987). Self-organization as a mechanism has been used to explain several physical and chemical processes such as laminar flow of water, arrangement of sand furrows, and cyclic chemical reactions (Prigogine and Stengers 1984; Nicolis and Prigogine 1977), *de nova* emergence of township (Arthur et al. 1987) etc.

The process of self-organization is also extended to explain a range of phenomenon in plants. For example, differential development of seeds and fruits, asymmetric feature such as varying number of flowers among inflorescence, differential growth of tillers, leaves and branches and irregular plant architecture, could be viewed as a consequence of the autocatalytic feedback during the development of these organs.

In this article, we show that certain predictions of this model are upheld in the pattern of development of cotyledons of tomato during embryo development. By altering the resource drawing ability of cotyledons that depend on common resource pool during their early growth and by examining the their growth pattern kickoff size asymmetry among them. The results conform with the prediction of the autocatalytic growth model proposed by Ganeshiah and Uma Shaanker, (1992, 1994) and Ganeshiah et al., (1995).

The model and the prediction

The process of self-organization was proposed by Ganeshiah and Uma Shaanker (1992, 1994) and Uma Shaanker et al., (1995) to explain the emergence of dominance hierarchy among the developing seeds and the consequent abortion of seeds. They showed that differential development could arise among them otherwise identical seeds purely by two simple processes: a) random drift of resources, resulting in an initial asymmetry in the resources status of the developing seeds and b) amplification of this initial asymmetry due to an autocatalytic feedback process.

The rate, at which dominance hierarchy or asymmetry occurring in developing seeds, is a function their Sink Drawing Ability (SDA) of the growing cotyledons of the embryo. A major prediction of their model is that everything else being constant, if SDA of ovules is more then asymmetry is enhanced. They demonstrated this in 3 – 4 species and suggesting that the model can be extended to any system where simultaneously growing sinks are drawing resources from a common resource pool.

MATERIAL AND METHODS

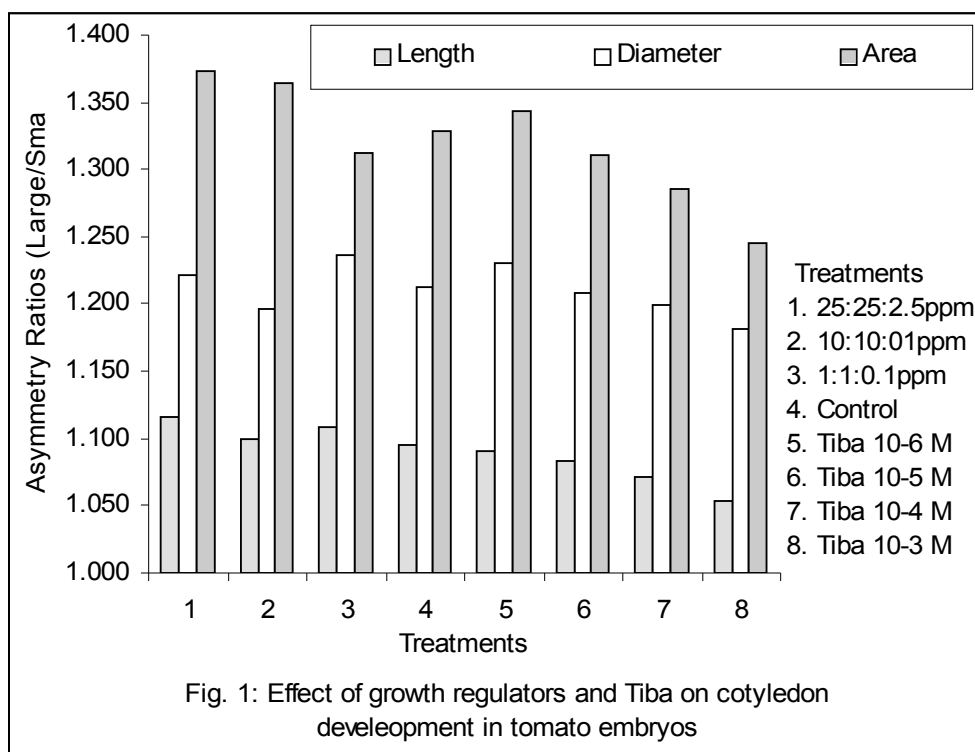
System – Ten accessions of tomato (*Lycopersicon esculentum* L.) were used in the present and grown at Botany Garden, University of Agricultural Sciences, Hebbal, with all package of practices. The developing ovaries immediately following fertilization were treated with growth regulators solution 25: 25: 2.5 ppm, 10:10:1 ppm and 1: 1: 0.1 ppm (NAA: GA: BA) and 10^{-3} M, 10^{-4} M, 10^{-5} M and 10^{-6} M (Triiodobenzoic acid - TIBA) every morning for 10 days and a control was maintained without spraying. Hormones thus applied would diffuse into young developing ovaries such that the sink strength of ovules is simultaneously enhanced. Three fruits from 10 days treated were randomly harvested from each treatment, they were dissected and 10 embryos were examined for the their pattern of development under microscope and images of the embryo were captured in computer. The length and diameter of both cotyledons were measured using the Aequitas Program, size of the each cotyledon was calculated as product of length x diameter. From this data we computed the asymmetry ratios as follows: a. **cotyledon length asymmetry ratio**: ratio of the length of the long cotyledon to short cotyledon of the embryo, b. **cotyledon diameter asymmetry ratio**: ratio of the diameter of the long cotyledon to short

cotyledon of the embryo, and c. **cotyledon area asymmetry ratio**: ratio of the area of the long cotyledon to short cotyledon area of the embryo.

Observations

Effect of exogenous application of TIBA and growth regulator on embryo development pattern

Application of growth regulators enhanced the initial differences between two cotyledons (Long and Short) of the embryo and such enhanced differences are used to calculate asymmetry between the growing cotyledons. Asymmetry ratio for the growing cotyledon length, diameter and also for area decreased in fruits treated with TIBA compared to control and while the growth regulators enhanced their asymmetry between the two cotyledons of the embryo (Fig. 1 and Plate 1).



Further, the extent of asymmetry was also found to be a function of concentration used. For instance the asymmetry ratio for length of the cotyledon was 1.095 in control and was reduced to 1.053 in the fruits treated with 10⁻³ M TIBA but increased to 1.116 in 25:25:2.5 ppm (NAA: GA: BA) figure 1. Similarly, the asymmetry ratio for the area was 1.328 in control was reduced to 1.245 in the fruits treated with 10⁻³ M TIBA but increased to 1.373 in 25:25:2.5 ppm (NAA: GA: BA). In general, there appears to be increase in symmetry

with high concentration of TIBA and decrease in symmetry with higher concentrations of growth regulators (NAA: GA: BA). The effect of growth regulators on enhancing the difference between the cotyledons of the embryo was more prominent at higher concentration. Asymmetry with respect to number of cotyledons was also observed in ovaries treated with growth regulators, that it is resulted in induction of tricotyledons per embryo compare to control and TIBA treatments (Fig. 1).

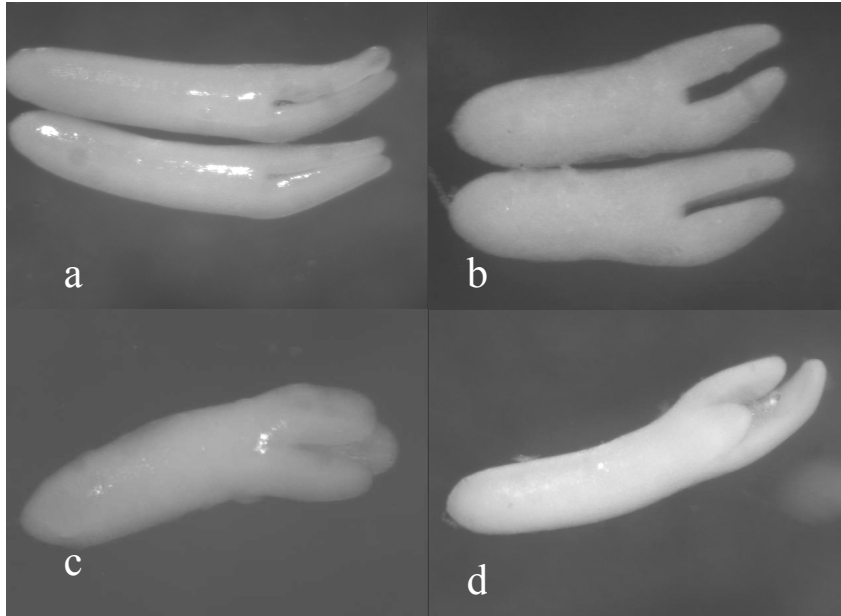


Plate. 1: Tomato embryos: a) Symmetry with respect to length and number of cotyledons per embryo b) Asymmetry with respect to length of the cotyledons of the embryo, c) and d) Asymmetry with respect to number of cotyledons per embryo.

Discussion

The present problems with hormonal signals transferring dominance effects are reviewed and as a new hypothesis, it is stated that the sequence of sink development (cotyledons of the tomato embryo) may establish the dominance effect. An individual unable to buffer random accidents of developmental processes, whether genetic or environmental in origin, may exhibit slight deviations from perfect symmetry. Such deviations are termed as asymmetry because they are nondirectional and random. Generation of asymmetry in the developing cotyledons of the developing embryo can be explained assuming strong dominance hierarchy among developing cotyledons generated at high levels of SDA due to exogenous application of growth regulator. Under high SDA, the random drift in the resource flow to one of the cotyledon offers a greater dominance advantage to that leading

to their complete development and suppression of the other. The dominance can be observed very early in the ontogeny of cotyledons of the embryo wherein many cases competition for limiting assimilated is less likely, because of the low demand of these small sinks for assimilates (Bohner & Bangerth 1988).

The results show that when the metabolic activity of the cotyledons of the developing embryo was enhanced, the asymmetry in their size becomes aggravated. This is the conformity of the model proposed by Ganeshaiyah & Uma Shaanker (1994) for the movement of resources into developing sinks (cotyledons). Their model suggests that the fate of any developing sink depend upon its history; among the competing sinks, those that have already received more resources dominate over the others and hence derive further resources and so aggravating the dominance hierarchy. Such an autocatalytic feedback process of resources flow is in fact supported by the observations made by Peel and Ho (1970) who used aphid colonies drawing plant sap as sinks, Ganeshaiyah et al. (1995) in Mestha, and Thyagaraju (1997) in Chick pea. In short, self-organized movement of resource molecules combined together with the specific SDA of the growing tissue seems capable of explaining the emergence of any design of the plants at all levels of growth and development of plants could be viewed as a manifestation of such epigenetic process of movement of resource molecules to spatially and temporally interacting sinks.

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