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Lagenaria leucantha: New Model Plant for Studying Fruit Development

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ABSTRACT

Lagenaria leucantha, belonging to the Cucurbitaceae family, is an important vegetable crop widely grown in greenhouses throughout Asia. It lacks the ability of natural parthenocarpy and pollination is essential for successful fruiting. Fruit growth of *L. leucantha*, after anthesis, starts by cell division and is followed by cell expansions that make the greatest contribution to the final fruit size that is characteristic of the growth and development of most fruits. As an important cucurbita crop, *L. leucantha* is distinct from the model plant *Arabidopsis*, which belongs to the mustard family, in many aspects of development. CPPU, a synthetic cytokinin, can effectively promote cell division and induce parthenocarpy in *L. leucantha*. This not only provides an effective solution to ovary abortion, but also provides an experimental system for studying fruit development, in particular, the mechanism of chemical-induced parthenocarpy.

Keywords: acid invertase, cell division, cell enlargement, CPPU, CycD3, parthenocarpy
Abbreviations: AI, acid invertase; **BA**, benzyladenine; **CPPU**, *N*-(2-chloro-4-pyridyl)-*N*'-phenylurea; **DAA**, days after anthesisb; **GAs**, gibberellins; **IAA**, indole-3-acetic acid; **NAA**, α-naphthaleneacetic acid

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INTRODUCTION

Fruit development involves a complex interaction of molecular, biochemical and structural changes that transforms a group of fertilized ovules into a mature fruit. In recent years, studies on the mechanism of fruit development have dramatically increased because of its physiological and horticultural importance. Mature fruits can be categorized generally as either fleshy or dry. Arabidopsis has become a model plant for research in plant biology, while its fruit belongs to the dry fruit category. For fleshy fruit, tomato has emerged as the model plant to date, but it is more used for fruit ripening. Belonging to the Cucurbitaceae, *Lagenaria leucantha* (**Fig. 1**) is also a fleshy fruit, and its edible fruit is immature. This paper will review fruit development in *L. leucantha*, highlighting our previous studies.

LAGENARIA LEUCANTHA

L. leucantha, also known as white-flowered gourd, or bottle gourd, belongs to the Cucurbitaceae family, and the monoploid chromosome number is 11 (Ng 1993). Its fruit is nutritious, and whose young fruits are used as a cooked vegetable similar to zucchini; the flesh is white, firm, and has an excellent texture and a mild taste.

Native to areas south of equatorial Africa, *L. leucantha* has been cultivated for many centuries, and is one of the oldest vegetables in China (Zhu and Zheng 2001). It is a monoecious annual vine, which can climb up to a height of 3 meters. The separate flowers are axillary and white. Pistilate flowers have an inferior ovary. Recently, cultivation of *L. leucantha* in greenhouses has greatly expanded due to its strong tolerance to pests and its good taste.

NO NATURAL PARTHENOCARPY IN *LAGENARIA LEUCANTHA*

For most cucurbitaceous crops, pollination is essential for successful fruiting since natural parthenocarpy occurs only in some cucumber cultivars. As observed in watermelon and melon (Gotou *et al.* 1989; Hayata *et al.* 1995), *L. leucantha* also lacks the ability of natural parthenocarpy since all of the unpollinated ovaries abort (Yu 1999).

As a result, the female flowers rarely fruit in the early part of the growth stage, since the plant produces almost entirely female flowers with a few male flowers during the

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Invited Mini-Review

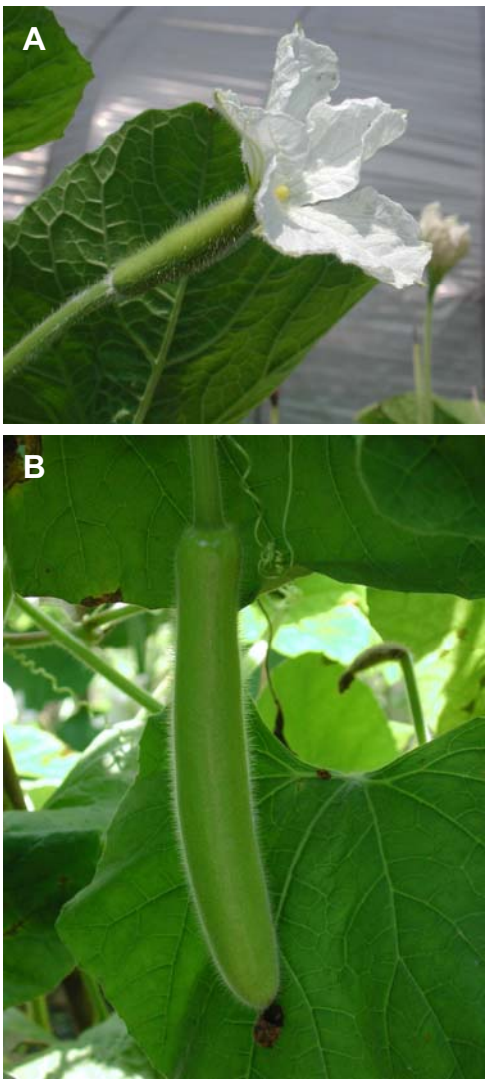

Fig.1 Pistilate flower (A) and fruit (B) of *L. leucantha*.

fall and spring. In addition, a low fruit set has also been a serious problem during the rainy season because of the sluggish activity of pollinating insects such as honey bees (www.uga.edu/vegetable/cucumber.html). Artificial hand pollination is used to improve fruit set under unfavorable conditions, in spite of its inconvenience, since both male and female flowers open in the evening. However, poor fruiting still occurs in commercial production, since fruit set percentages for natural pollination and hand pollination were only 2.5% and 12.5%, respectively, and all of the set fruits failed to normal size (Yu 1999).

FRUIT GROWTH OF *L. LEUCANTHA*

The process of fruit development occurs in three distinct phases: fruit set, fruit growth and ripening. Fruit growth comprises two major cellular activities: cell division and cell enlargement. Cell division activity is usually restricted to an initial period of a few days after anthesis, followed by cell expansions that make the greatest contribution to the final fruit size (Coombe 1976). Fruit development of *L. leucantha* is typically as that which occurs in cucumber (Marcelis and Baan Hofman-Eijer 1993). Our previous result in *L. leucantha* showed that cell division practically ceased after anthesis in unpollinated fruit. The cell number of pollinated fruit increased after anthesis and cell division occurred mainly in the first 4 days after anthesis (DAA; Yu *et al*. 2001a). In contrast to cell division, cell enlargement, another important process responsible for fruit growth, occurred mainly after 4DAA in pollinated fruit, while there was only a slight increase in cell area for the unpollinated fruit after anthesis (Yu *et al*. 2001a). While in tomato fruit, the cell division phase ends within 10 DAA, and the initial period of cell expansion is thought to occur at around 15 DAA (Gillaspy *et al*. 1993).

As an important cucurbit crop, *L. leucantha* is distinct from the model plant *Arabidopsis*, which belongs to the mustard family, in many aspects of development. Belonging to the dry fruit category, fruit of *Arabidopsis* matures in a process more akin to senescence and disperses its seeds via abscission-like programs, including dehiscence or shattering (Adams-Phillips *et al*. 2004). But the molecular regulation of early steps in fruit formation and development defined primarily in *Arabidopsis* (Pinyopich *et al*. 2003) have proven extremely useful in advancing fruit development research in fleshy fruit species such as tomato and also in *L. leucantha*. Although they are both fleshy fruits, tomato has been used more for analysis of fleshy fruit ripening (Tanksley 2004), while for *L. leucantha*, fruit growth and not ripening, is more important, because the edible fruit of *L. leucantha* is immature. Therefore, *L. leucantha* can be used as a model plant in studies of fleshy fruit development, especially for fruit growth.

FRUIT DEVELOPMENT AND EXOGENOUS HORMONES

Generally, ovary growth and cell division are temporarily reduced during the period of anthesis, until pollination and fertilization occur. This process is associated with the production of growth substances (Coombe1976; Hedden and Hoad 1985). Application of plant growth regulators can substitute for pollination and induce parthenocarpic fruit development in many plant species (Ozga 2002). Many studies have showed that plant hormones such as GAs, auxins and cytokinins have a key role during fruit set and development.

Auxins and gibberellins (GAs) are possible limiting factors controlling fruit set and development, and have been successfully used to improve fruit set in many plants (Hedden and Hoad 1985; Talon *et al.* 1990; Gillaspy *et al.* 1993). Cytokinins are another hormone that affect cell division, assimilate transport and protein synthesis (Shishido *et al.* 1990). There are also an increasing number of studies on the influence of cytokinin on fruit set and development in fruit crops and vegetable crops (Gotou *et al.* 1989; Hayata *et al.* 1995; Ohara *et al.* 1997).

However, the key hormone controlling early fruit development varies from plant to plant. In pea, GA_3 is the key regulatory signal for induction of fruit set and development (Ozga 2002). In improving fruit set and fruit growth of persimmon, however, *N*-(2-chloro-4-pyridyl)-*N*'-phenylurea (CPPU) was much more effective than GA_3 (Hasegawa *et al*. 1991). The non-parthenocarpic nature of cucumber cv. 'Chojitsu-Ochiai No. 2' was probably not due to low auxin level, but perhaps due to the low level of endogenous cytokinins (Takeno *et al*. 1992).

NAA and BA have been found to be effective in inducing parthenocarpy in some cucumber cultivars with small fruit size, such as applying NAA or BA at 100 mg l^{-1} to the ovary of cucumber cvs. 'Pandex' (parthenocarpic) and 'Khira' (non-parthenocarpic) (Kim et al. 1992), and applying NAA or BA at 0.1, 1.0 or 10 μg/fruit to the ovary of cucumber cultivars of cucumber cvs. 'Chojitsu-Ochiai No. 2' (parthenocarpic) and 'Mogami' (non-parthenocarpic) (Takeno et al. 1992), but ineffective in melon (NAA at 100 mg l^{-1}) (Masuda *et al.* 1990) and watermelon (BA at 500 ppm) (Hayata *et al*. 1995). In agreement with the results in watermelon and melon, our results (Yu 1999) showed that only CPPU was effective in inducing parthenocarpy in *L. leucantha*. CPPU showed great effectiveness on pollinated ovaries by increasing fruit set percentage and fruit size and both effects were greater than those by NAA and GA_3.

As described in our reports (Yu 1999; Yu *et al*. 2001a, 2001b; Li *et al*. 2003), unpollinated ovaries did not develop further and the cell size remained almost unchanged. Pollinated- or CPPU-treated unpollinated ovaries grew to the normal size. Significantly, the growth of the CPPU-induced fruit was much faster than the pollinated fruit. And signifi-

cant increase in cell size was observed both in the pollinated ovaries and CPPU-treated ovaries. CPPU was first dissolved in ethanol at a concentration of 2000 mg l^{-1} in the presence of 0.2% Tween 80, and then diluted with water. The solution was sprayed onto ovaries of previously bagged female flowers at anthesis. The parthenocapy percentage induced by CPPU was as high as 100% within the tested concentration (10-100 mg l^{-1}) (Yu 1999; Li *et al.* 2003). Our study showed that not only could CPPU be used to prevent flower abortion in *L. leucantha* by induction of parthenocarpy in the absence of male flower or under unfavorable weather conditions, but also it is commercially feasible to eliminate hand pollination or to improve pollinated fruit by CPPU application.

GENE EXPRESSION OF CPPU-INDUCED PARCENOCARPIC FRUIT IN *L. LEUCANTHA*

Cell division and cell enlargement are two important processes responsible for fruit final size. However, most previous efforts to study gene expression during fruit development have focused on fruit ripening such as in tomatoes (Moore *et al*. 2002), peaches (Trainotti *et al.* 2003), pears (Itai *et al* 2000; Fonseca *et al.* 2004), melons (Hadfield *et al.* 2000), bananas (Liu *et al*. 1999; Gupta *et al*. 2006), strawberries (Aharoni and O'Connell 2002) and peppers (Kim *et al.* 2002). In comparison, information is lacking on genes that are specifically expressed at the early developmental stage of fruits, even there are some (Narita and Gruissem 1989; Salts *et al*. 1991; Tieman and Handa 1996; Ohta *et al*. 2005), mainly derived from fruit development in tomato. Somewhat like *L. leucantha* in fruit growth, cell division in tomato fruit occurred mainly in the first 10 DAA and cell enlargement occurred mainly after 15 DAA (Gillaspy *et al*. 1993). Mature tomatoes are red, juicy, tasty and eaten. For *L. leucantha*, however, the pulp of mature fruit will become dried and pulpy. Since it is the immature fruit that is edible in *L. leucantha*, the early developmental stage of fruit that includes cell division and cell enlargement seems more important in fruit development of *L. leucantha*. Gene expression in fruit development of *L. leucantha* has mainly been related to cell division and cell development until now.

LlCycD3

Cell cycle progression in eukaryotes is regulated by cyclins. D-type cyclins are thought to link environmental and developmental cues to the cell cycle. Cytokinins were shown to activate *Arabidopsis* cell division through the induction of CycD3 in whole plants, as well as in tissue culture (Riou-Khamlichi *et al.* 1999). Over-expression of D-type cyclins not only reduced the length of the G_1 phase, but also partially overrode the need of dividing cells for mitogens (Zwijssen *et al*. 1996). By contrast, CycD3 of alfalfa was not induced by cytokinins and the overproduction of CycD3 in alfalfa had no obvious effect (Jeleñska *et al.* 2000). In *L. leucantha*, it there is a direct action of cytokinins on CycD3 expression. Two *LlCycD3* genes isolated from the fruit of *L. leucantha* showed different expression patterns during fruit development (Li *et al*. 2003). *LlCycD3;1* showed the highest expression at anthesis whereas *LlCycD3;2* showed higher expression levels at an early stage after anthesis in CPPU-induced fruits and pollinated fruits. Different expression patterns have been detected for two D3 cyclins in *Antirrhinum* and tobacco (Doonan 1998; Sorrell *et al.* 1999). Accordingly, the specific function for two D3 cyclins in *L. leucantha* remains to be further determined. Whatever the case, CPPU promoted the expression of CycD3 in parthenocarpic fruit growth and the regulation of expression of the *CycD3* gene appears to be a key mechanism by which cytokinins influence cell proliferation and fruit development.

A few other genes related to cell division have been found to be induced in growing pear fruit, such as genes encoding MAP-kinase-like protein and Cyclin a2 (Fonseca *et al*. 2004).

LlAI

The growth of a fruit, including cell division and cell enlargement actually, is characterized by high metabolic activity, a characteristic of utilization sinks. The increase in sink strength is provided by the activation of carbohydrate import and metabolism in fruits. In tomato, the expression of *LeODD* and *LeGLO2* played a role in the biosynthesis of some metabolites required for the cell expansion phase of fruit development (Ohta *et al*. 2005). In strawberry, *cel2* involved in cell wall expansion was showed to play a pivotal role in fruit development prior to ripening (Palomer *et al*. 2006). And some cell wall-modifying enzymes, such as expansin and xyloglucan endotransglycosylase, involved in cell enlargement were associated with vigorous fruit growth in peach (Hayama *et al*. 2001). Very little, however, has been studied in cucurbita on the mechanism of cell enlargement.

Sucrose and the galactosyl-sucrose oligosaccharides, stachyose and raffinose, have been shown to be the major carbohydrates translocated in cucurbits (Chrost and Schmitz 1997). The galactosyl-sucrose oligosaccharides are catabolized to sucrose and galactose by α-galactosidase in the fruit tissue, which then are assimilated via acid invertase and sucrose synthase into the mesocarp tissue, respectively. Acid invertase (AI; EC. 3.2.1.26) is responsible for the hydrolysis of sucrose to glucose and fructose and is thought to play a central role in determining sink strength of developing plant organs (Ho 1984) and is commonly related to cell elongation (Morris and Arthur 1984). Most of the growth of *L. leucantha* fruit after 4 days after anthesis is the result of cell enlargement (Yu *et al*. 2001a).

AIs are divided into vacuolar (or soluble) and extracellular (or insoluble) forms, with acid and basic pIs, respectively. LlAI, based on the predicted amino acid sequence for AI from fruit tissue of *L. leucantha*, was most similar to vacuolar AI by sequence comparison. In unpollinated ovaries, the expression of the LlAI gene decreased together with ovary abortion. Pollination/fertilization induced active fruit growth and cell enlargement accompanied by substantial increases in the activity of AI in the first 4 days after anthesis and high increases in the transcript levels of LlAI in young fruits. And those were similar in CPPU-induced parthenocarpic fruits (Li *et al.* 2004).

The changes of the transcript of LlAI also showed the significant role of CPPU and pollination/fertilization in fruit development (Li *et al.* 2004). They both stimulated the expression of LlAI. Accordingly, they have similar roles in regulating AI such that CPPU treatment or pollination/fertilization stimulated the activities of soluble AI in *L. leucantha*. This not only indicates that cytokinins, produced by pollination/fertilization, could increase the expression of LlAI and the enzyme activity, but also concluded that CPPU has intrinsic cytokinin properties and it contributes to fruit enlargement processes by strengthening the fruit's sink activity through stimulating the expression and increasing the activity of LlAI.

CONCLUSION

Fruit growth is a complex process involving cell division, cell enlargement and major changes in fruit metabolism. Actually cell division and cell enlargement involves many other physiology actives such as cell wall loosening. It is well known that the plant cell wall is a complex network of cellulose, hemicelluloses, pectins and structural proteins (Kaku *et al*. 2004; Lu *et al*. 2006). So apart from these genes mentioned above, fruit growth should involve the up- and down-regulation of hundreds of other genes, most of which are yet to be identified, and it is still a long way to elucidate the mechanism of fruit development of *L. leucantha.* However, we can with confidence say that CPPU, a synthetic cytokinin, can effectively promote cell division

and induce parthenocarpy in *L. leucantha*. This not only provides an effective solution to ovary abortion, but also provides an experimental system for studying fruit development, in particular, the mechanism of chemical-induced parthenocarpy.

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