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Plant Tumor Development on Tomato Derived from *Lycopersicon hirsutum*

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Nonpathogenic tumor ("Intumescence" or "Oedema") is a physiological disorder that may develop on tomato (*Lycospericon esculentum*) leaves. Although genotype and water congestion resulting from the imbalance between plant water use and uptake have been considered as the primary cause of the blister-like symptoms, initiation and process of the tumorous growth remains unclear. A wild tomato species *Lycopersicon hirsutum* is known for its susceptibility to intumescence formation, particularly in greenhouse. In a recent greenhouse study of grafted tomatoes, the rootstock 'Maxifort' (a hybrid derived from *L. hirsutum)* showed marked symptom of foliar oedema, indicating the possibility of genetic inheritance of intumescences. Tomato 'Florida-47' did not exhibit any tumorous growth in either non-grafted treatment or grafted treatment with 'Maxifort' as rootstock. The incidence of oedema on 'Maxifort' was further evaluated when it was grafted onto the unsusceptible 'Florida-47'. Replacing the roots of 'Maxifort' with that from an unsusceptible tomato variety did not alter the overall susceptibility of 'Maxifort' to intumescences as the injury was present in all the grafted 'Maxifort' plants. Internal morphology of oedema-afflicted leaves of 'Maxifort' revealed evident cell enlargement, while the involvement of cell division in intumescence development needs to be further determined.

Nonpathogenic tumorous growth, also known as oedema or intumesence injury, has been observed on horticultural crops such as potato (*Solanum tuberosum*) (Petitte and Ormrod, 1986), eggplant (*Solanum melongena*) (Eisa and Dobrenz, 1971), tomato (*L. esculentum* and *L. hirsutum*) (Lang et al., 1983), and ivy geranium (*Pelargonium peltatum*) (Rangarajan and Tibbitts, 1994), particularly under protected cultivation. Susceptibility to eodema varies considerably among cultivars (Eisa and Dobrenz, 1971; Petitte and Ormrod, 1986). Meanwhile, an array of abiotic factors is suggested to contribute to intumescences on plant vegetative shoots, e.g., humidity, temperature, light quality and intensity, and air quality (Pinkard et al., 2006). Plant tumors, however, may also develop in response to infection by bacteria, fungi, viruses, or insects (Mani, 1964). Traditionally plant-water relation is believed to play a key role in the intumescence injury, whereas new evidence has indicated the involvement of phytochrome and phytohormones in regulations of tumor development in plants (Morrow and Tibbitts, 1988).

Intumescences could be induced on both cultivated (*L. esculentum*) and wild tomato (*L. hirsutum*) plants. Although the symptoms differed substantially with the callus-like tissue mainly on petioles, midribs, and stems of *L. esculentum* while the gall-like protrusions primarily on leaves of *L. hirsutum*, hypertrophy of epidermis, palisade, and spongy parenchyma cells was seen in both species (Lang and Tibbitts, 1983; Lang et al., 1983; Morrow and Tibbitts, 1988). *Lycopersicon hirsutum* has been used as a model crop to study factors that trigger intumescence because of its high susceptibility. However, underlying mechanisms of intumescence initiation still remains poorly understood.

In our recent greenhouse experiment on grafted tomato production, the rootstock 'Maxifort' (De Ruiter Seeds, Lakewood, CO) demonstrated intumesence injury on leaves starting at 7–9 leaf stage. The blister-like symptom resulted in necrosis, wilting, and abscission of older leaves. However, 'Florida 47' tomato grown under the same conditions did not show any plant tumors and 'Florida 47' grafted onto 'Maxifort' (a *L. esculentum* x *L. hirsutum* hybrid) never showed any intumesence development. This suggests the possibility of genetic inheritance of intumescences.

Can unsusceptible tomato as the rootstock affect the tumor development on the susceptible tomato scion? Hence, the objectives of this experiment were to examine the internal morphology of

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tumorous growth on leaves of 'Maxifort' tomato and investigate the rootstock effect on intumescence development on 'Maxifort' tomato as the scion.

Materials and Methods

Tomato grafting and planting. Seeds of 'Maxifort' and 'Florida 47' tomato were sowed into the 128-cell Speedling flats (Speedling Incorporated, Sun City, FL) in the greenhouse on 18 and 21 Dec. 2007, respectively. Grafting was performed on 31 Jan., 2008 when 5–6 true leaves were present, using the cleft method (Oda, 1999). Grafted treatments (rootstock/scion) were 'Maxifort'/'FL-47', 'Maxifort'/'Maxifort', 'Florida-47'/'Maxifort', and 'Florida-47'/'Florida-47' tomatoes. Non-grafted 'Maxifort' and 'Florida-47' tomatoes were used as the controls. Completely healed grafts and non-grafted control plants were transplanted into 6-inch pots filled with growing medium (Metro-Mix 200; Sun Gro Horticulture, Bellevue, WA) on 15 Feb. 2008. The experiment was arranged as a completely randomized design with eight single-pot replications in each treatment. Plants in each pot were supplied with approximately 250 mL of 200 mg/L N nutrient solution (using Scotts General Purpose 20N–8.8P–16.6K) at 2-d intervals. In the greenhouse, air temperature ranged from 15 °C (night minimum) to 29 °C (day maximum) and relative humidity was kept below 70% throughout the growing season. The onset of intumescence development was recorded. Incidence of intumescences on tomato plants was assessed on 12 Mar. 2008.

Histology of intumescences. Leaves from non-grafted 'Maxifort' tomatoes showing typical tumorous growth represented by the small blisters on the surface were sampled on 12 Mar. 2008. Intumescences on both adaxial and abaxial leaf surfaces were examined. The blisters (with a small portion of adjacent unaffected areas) from tomato leaf tissues were excised and fixed with 4% glutaldehyde in phosphate buffered saline under vacuum for 2 h. Samples were then post-fixed with 2% (w/v) osmium tetroxide in 0.05 mM sodium cacodylate buffer overnight at 4 °C, followed by buffer rinsing and dehydration through a graded acetone series. Samples were then embedded in Spurr's resin, and polymerized at 65 °C (Spurr, 1969). Sections 500 nm in length were cut with Leica Ultracut R (Bannockburn, IL), affixed to glass slides by heating at 130 °C, and stained with toluidine blue-O. The stained sections were examined with an Olympus BH compound microscope equipped with Retica 200R digital camera (Qimaging, British Columbia, Canada).

Results and Discussion

The onset of intumesence injury on the leaves of 'Maxifort' tomato was related to plant growth stage. The symptom did not appear until the 8–9 leaf stage. The light-green to whitish blisters, 1–4 mm in diameter, formed primarily on the older leaves along the veins as plants continued to grow. No symptoms were observed on petioles, stems, or flowers of 'Maxifort' tomatoes. The tumorous growth developed on both lower and upper surfaces of laminae in 'Maxifort' tomato, resulting in either upward (Fig. 1A) or downward curling of leaves (Fig. 1B). Previous studies on *L. hirsutum* also found hypertrophied surface cells on both adaxial and abaxial leaf surfaces (Lang et al., 1983). To our knowledge, this is the first report of intumescence injury on the leaves of a *L. esculentum* x *L. hirsutum* hybrid.

Examination of the histology of intumescences on 'Maxifort' tomato indicated hypertrophy of lower epidermis and spongy parenchyma (Fig. 2A) as well as upper epidermis and palisade cells (Fig. 2B). It was uncertain if cell proliferation was involved in the tumorous growth on 'Maxifort' tomato leaves. Analysis of DNA levels is needed to determine if cell division plays a role in the development of intumescences.

All the plants in the treatments of non-grafted 'Maxifort', 'Florida-47/'Maxifort', and 'Maxifort'/'Maxifort' tomatoes demonstrated intumescences on the leaves, while the symptom was absent in the treatments of non-grafted 'Florida-47', 'Florida-47'/'Florida-47', and 'Maxifort'/'Florida-47' (Table 1). Although grafting tended to delay the appearance of intumescences by 3-4 d, using an unsusceptible tomato variety as the rootstock did not affect the overall susceptibility of 'Maxifort' tomato to intumescence injury (Fig. 1C). Very likely, certain regulatory mechanisms existed in the shoots to control tumorous growth on 'Maxifort' tomato under the greenhouse conditions.

Despite the genetic factors, the specific environmental effects on intumescence development on 'Maxifort' tomato deserve further research. Plant oedema is often ascribed to water congestion as a result of the imbalance between plant water uptake and water use or transpiration. Warm moist soil and cool nights with high relative humidity were suggested as the major cause of oedema

A B C

Fig. 1. Nonpathogenic tumorous growth on (**A**) lower surface of leaves from non-grafted 'Maxifort' (*L. esculentum* x *L. hirsutum*) causing upward curling; (**B**) upper surface of leaves from non-grafted 'Maxifort' causing downward curling; and (**C**) upper surface of leaves from 'Maxifort' grafted onto 'Florida-47'.

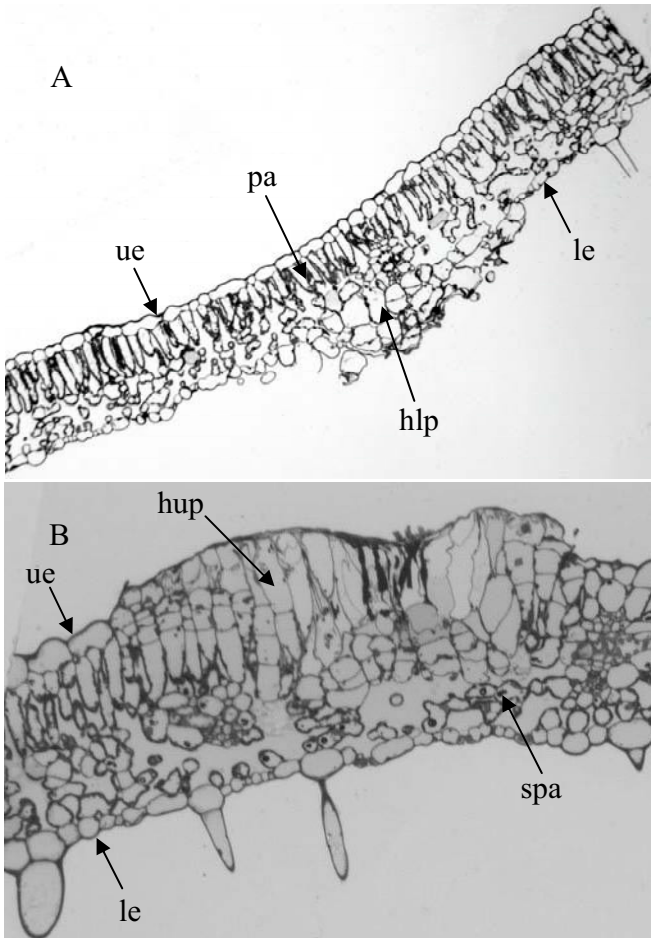

Fig. 2. Transverse sections of tomato leaves with tumorous growth: (**A**) a leaf of 'Maxifort' (*L. esculentum* x *L. hirsutum*) showing intumescence on the lower surface; and (**B**) a leaf of 'Maxifort' showing intumescence on the upper surface. hlp = hypertrophied lower epidermis and spongy parenchyma; hup = hypertrophied upper epidermis and palisade cells; le = lower epidermis; pa = palisade cells; spa = spongy parenchyma; ue = upper epidermis.

on susceptible eggplant cultivars (Eisa and Dobrenz, 1971). In fact, recommended strategies to prevent or reduce occurrence of oedeama on the greenhouse crops have been focused on water management and control of humidity and ventilation. However, studies of factors controlling intumescences in tomato indicated that water congestion associated with high humidity and reduced transpiration did not trigger the onset of symptoms but only made them more pronounced (Lang and Tibbitts, 1983). The effect of transpiration-reducing chemicals on plant oedema development has been found to be highly inconsistent according to another study in which 21 plant species were tested (Abbas et al., 1999). It was postulated that the lack of UV radiation in the greenhouse might be conducive to intumesences on tomato plants since exposure of plants to UV-B radiation helped prevent tumorous growth in tomato (Lang and Tibbitts, 1983). Thus it would be interesting to examine the incidence of intumenscences on 'Maxifort' tomato plants grown outdoors.

Table 1. Incidence of intumescences on tomato plants grown in the greenhouse (assessed 26 d after transplanting).

Treatment[y]	Incidence of intumescences[z]
'Florida-47'/'Maxifort'	8 out of 8 plants
'Florida-47'/'Florida-47'	0 out of 8 plants
'Maxifort'/'Florida-47'	0 out of 8 plants
'Maxifort'/'Maxifort'	8 out of 8 plants
Non-grafted 'Florida-47'	0 out of 8 plants
Non-grafted 'Maxifort'	8 out of 8 plants

[z]It was based on the number of tomato plants showing intumescences out of the 8 plants in each treatment.
[y]Grafted treatments were denoted by rootstock/scion.

'Maxifort' tomato is currently considered as one of the most vigorous rootstocks for greenhouse production of grafted tomatoes. It is unclear whether the observed susceptibility of 'Maxifort' tomato to intumescence injury under greenhouse production has any relation with its function as a vigorous tomato rootstock.

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