Virus-resistant transgenic papaya helps save Hawaiian industry

Dennis Gonsalves

The pivotal year in the history of Hawaii's papaya industry was 1992. In May 1992, papaya ringspot virus (PRSV) was discovered in Puna on Hawaii Island, where 95% of Hawaii's papaya was being grown. Just one month earlier, a small field trial to test the resistance of a transgenic papaya line had been started on Oahu Island, where papaya production had previously been devastated by PRSV. The timely commercialization of PRSV-resistant transgenic papaya trees has revived Hawaii's papaya industry and provides an example of the challenges and opportunities for horticultural biotechnology.

In 1945, D.D. Jensen made the first report in Hawaii of PRSV, a potyvirus that is transmitted nonpersistently by aphids (Gonsalves 1998). PRSV was first discovered on Oahu and caused such severe damage that the papaya industry was relocated to Puna in the late 1950s and early 1960s. The papaya industry expanded and prospered in Puna, primarily because PRSV was absent. However, by the 1970s PRSV was found only about 19 miles away in Hilo, and the Hawaii Department of Agriculture (HDOA) took rouging (the removal of infected trees) and quarantine actions to prevent its spread to Puna. In 1986, efforts were initiated to develop a virus-resistant transgenic papaya by transforming commercial lines of Hawaiian papaya with the coat protein gene of PRSV from Hawaii.

By 1991, the team of Maureen Fitch, Jerry Slightom, Richard Manshardt and Dennis Gonsalves identified a transgenic line (55-1) that showed resistance under greenhouse inoculations. These plants were micropagated and established in a field trial in Waimanalo on Oahu in April 1992. By December 1992, it was evident that line 55-1 was resistant under field conditions. From the 1992 field trial, two cultivars were developed and designated 'SunUp' and 'Rainbow'. 'SunUp' is homozygous for the coat protein gene while 'Rainbow' is an Fl hybrid of 'SunUp' and the nontransgenic 'Kapoho'. Unfortunately, by October 1994, PRSV had spread throughout much of Puna, causing HDOA to abandon rouging efforts to slow the spread of PRSV. The race was on to move the transgenic papaya line to commercialization. A 1995 field trial in Puna conclusively showed that 'SunUp' and 'Rainbow' were resistant under prolonged and heavy disease pressure.

Courtesy of R. Manshardt

Two varieties of papaya resistant to papaya ringspot virus have been developed using biotechnology: SunUp, *left*, and Rainbow, *right*. They have performed well for Hawaiian growers, even under prolonged and heavy disease pressure.

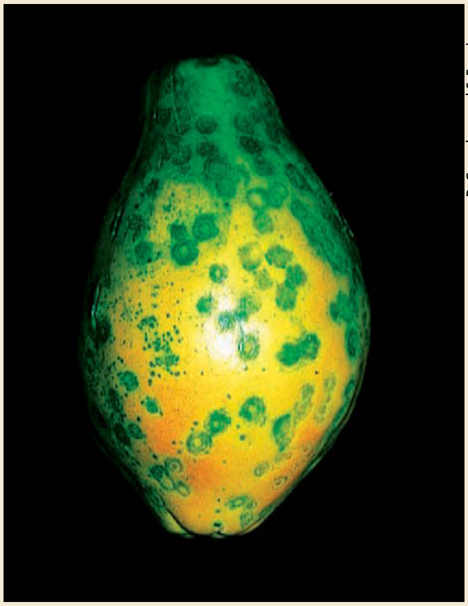
The experience in Hawaii shows that transgenic virus resistance is an excellent approach for controlling viral diseases in horticultural crops.

The U.S. Department of Agriculture's Animal Plant Health Inspection Service (APHIS) deregulated transgenic line 55-1 in November 1996, and the U.S. Environmental Protection Agency deregulated it in August 1997. The consultation process with the U.S. Food and Drug Administration was completed in September 1997. Licenses to commercialize the transgenic papaya were obtained by the Papaya Administrative Committee in Hawaii by April 1998. A celebration was held to mark the debut of the transgenic papaya on May 1, 6 years after PRSV was discovered in Puna and after the first field trial of line 55-1 was initiated. The transgenic fruit is currently sold throughout the United States.

In 1992, Puna produced 53 million pounds of papaya, but by 1998 production had dropped to only 26 million pounds as PRSV spread throughout the region. Since then, the transgenic varieties have enabled farmers to reclaim infected areas and in 2001, Puna produced 40 million pounds of papaya. The resistance has held up remarkably well and remains stable after 5 years of extensive plantings.

Hawaii also exports papaya to Canada and Japan. The transgenic papaya was recently deregulated in Canada, which is a relatively small market for Hawaii. The main challenge is deregulation of transgenic papaya in Japan, where Hawaii sells about 30% of its papaya. Presently, nontransgenic papaya must also be produced in Hawaii to satisfy the Japanese market, but this is increasingly difficult due to the disease pressure. Exporters face added expenses to guard against the accidental shipment of transgenic papaya to Japan. In December 2000, Japan's Ministry of Agriculture, Forestry and Fisheries approved line 55-1, and the Ministry of Health, Labor and Welfare is reviewing a recently submitted petition for deregulation. Anticipated approval of transgenic papaya in Japan will allow Hawai-

Simply the diversity of crops utilized in horticulture slows the adoption of new technologies. For example, as many as 60 distinct cultivars of iceberg lettuce alone may be grown throughout the year.



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Papaya ringspot virus causes small, darkened rings on the surface of fruit, as well as foliar damage.

ian growers to expand their transgenic papaya markets and will eliminate excessive costs associated with segregating trans-genic and nontransgenic fruits.

The experience in Hawaii shows that transgenic virus resistance is an excellent approach for controlling viral diseases in horticultural crops. This industry was fortunate to have a potential product already under development when PRSV was discovered in the main growing area of Puna. There are many reports that virus-resistant transgenic plants are being developed in diverse crops, but few have been commercialized. The papaya story shows that this approach can provide a stable and safe option for virus protection that can be essential for the success of specific horticultural crops.

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Reference

Gonsalves D. 1998. Control of papaya ringspot virus in papaya: A case study. Annu Rev Phytopathol 36:415–37.

ies (see sidebar, page 96). The latter approach avoids the task of transforming many varieties of a particular tree crop and in the future may be used to regulate quality and productivity traits.

Nutrients, consumer qualities. Although more difficult technically and therefore not close to market, there are many potential opportunities for enhancing the nutritional value or consumer appeal of horticultural products through biotechnology. In addition to modification of ripening, projects to increase the content of vitamins, minerals or nutraceuticals in horticultural products are in progress (Grusak and Della Penna 1999). The development of Golden Rice with enhanced beta-carotene (pro-vitamin A) in the grain (Ye et al. 2000) demonstrated the potential for biotechnology to increase nutritional value. Whether such products will have sufficient consumer appeal in fully developed markets to drive their commercialization remains to be seen.

Floriculture, ornamental plants

Since floricultural and ornamental plants are grown for aesthetic or other nonedible purposes, there may be less potential for public concern about GE varieties than there has been with biotech food crops.

Flower color. Several ornamental plants, including carnation, rose and gerbera, have been engineered for modified flower color. Research has focused on the manipulation of either anthocyanins (red and blue colors) or carotenoids (yellow and orange colors), with the intent of creating a wider range of flower colors than occurs naturally, as well as to produce natural dyes for industrial purposes (Lu et al. 2003). Florigene is selling Transgenic Moon series carnations engineered for dark violet-purple color around the world. The varieties are developed in Australia and flowers are produced primarily in South America for marketing in the United States and Japan.

Floral scent. Putting the scent back into flowers that have "lost" this trait over years of traditional hybridization and selection, or creating new fragrances in plants, has considerable potential and appeal. Research on genes controlling the different biochemical pathways for various floral fragrances is being conducted on wild plants and on crops such as snapdragon, petunia and rose (Vainstein et al. 2001).

Plant size. Currently, growth-regulating chemicals are applied to ornamental plants to inhibit gibberellic acid (GA) synthesis and reduce plant height during crop production. Many newly introduced ornamental species are receiving particular attention via conventional breeding for dwarf plants because their natural habits do not fit into marketing systems requiring compact plants. The manipulation of GA metabolism via biotechnology has the potential to produce ornamental and flowering plants with reduced-height phenotypes (Clark et al. 2003). The development of lawn grasses that require significantly less frequent mowing is another obvious application. Early experiments suggest that expression of genes controlling height can be applied to many plant species.

Leaf life. Engineering of plants to delay leaf senescence (yellowing) is also being pursued in ornamental crops. For years, ornamental breeders have selected new cultivars of plants with more attractive "stay green" phenotypes. Cytokinins are plant hormones well known to delay the loss of chlorophyll in leaves; using biotechnology, targeted expression of genes involved in cytokinin synthesis is now possible. When a gene promoting cytokinin biosynthesis is inserted into plants in conjunction with a regulator (promoter) that turns the gene on only when the leaf starts to senesce, leaf life is extended in transgenic plants exposed to drought, nutrition and pathogen stress (Gan and Amasino 1995; Clark et al. 2004).

Ethylene sensitivity. As in fruit ripening, manipulation of ethylene synthesis or sensitivity has applications in the ornamental plant industry. Ethylene accelerates floral and foliar senescence, and chemical methods have been developed to miti-