

- Gardner, F.E., P.C. Marth, and L.P. Batjer. 1939. Spraying with plant growth substances to prevent apple fruit dropping. *Science* 90:208–209.
- Gardner, F.E., P.C. Marth, and L.P. Batjer. 1940. Spraying with plant growth substances for control of the preharvest drop of apples. *Proc. Amer. Soc. Hort. Sci.* 37:415–428.
- Guiltnan, M.J. and J. Deikman. 1994. Molecular and genetic approaches to the study of plant hormone action. *Hort. Rev.* 16:1–32.
- Gustafson, F.G. 1936. Inducement of fruit development by growth-promoting chemicals. *Proc. Natl. Acad. Sci.* 22:628–636.
- Howlett, F.S. 1940. Experiments concerning the practicability of certain chemicals as a means of inducing fruit setting in the tomato. *Proc. Amer. Soc. Hort. Sci.* 37:886–890.
- Huxley, J.S. 1935. Chemical regulation and the hormone concept. *Biol. Rev. Cambridge Philos. Soc.* 10:427–441.
- LaRue, C.D. 1936. Effect of auxin on abscission of petioles. *Proc. Natl. Acad. Sci.* 22:254–259.
- Letham, D.S. 1967. Chemistry and physiology of kinetin-like compounds. *Annu. Rev. Plant Physiol.* 18:349–364.
- Libbenga, K.R. and A.M. Mennes. 1995. Hormone binding and signal transduction, p. 272–297. In: P.J. Davies (ed.). *Plant hormones*. Kluwer Academic Publ., Dordrecht.
- Miller, C.O., F. Skoog, M.H. Von Saltza, and F.M. Strong. 1955. Kinetin, a cell division factor from deoxyribonucleic acid. *J. Amer. Chem. Soc.* 77:1392.
- Nickell, L.G. 1958. Gibberellin and the growth of plant tissue cultures. *Nature* 181:499–500.
- Ohkuma, K., J.L. Lyon, F.T. Addicot, and O.E. Smith. 1963. Abscisin II, an abscission-accelerating substance from young cotton fruit. *Science* 142:1592–1593.
- Owens, L.D., M. Leiberman, and A. Kunishi. 1971. Inhibition of ethylene production by rhizobitoxine. *Plant Physiol.* 48:1–4.
- Pratt, H.K. and J.D. Goeschl. 1969. Physiological roles of ethylene in plants. *Annu. Rev. Plant Physiol.* 20:541–584.
- Sachs, J. 1880. *Stoff und Form der Pflanzenorgani*. I. Arb. Bot. Inst. Würzburg 2:452–488.
- Schneider, G.W. and J.V. Enzie. 1944. Further studies on the effect of certain chemicals on the fruit set of apple. *Proc. Amer. Soc. Hort. Sci.* 45:63–68.
- Skoog, F. and D.J. Armstrong. 1970. Cytokinins. *Annu. Rev. Plant Physiol.* 21:359–384.
- Steward, F.C. and N.W. Simmonds. 1954. Growth-promoting substances in the ovary and immature fruit of the banana. *Nature* 173:1083–1084.
- Stowe, B.B. and T. Yamaki. 1957. The history and the physiological action of the gibberellins. *Annu. Rev. Plant Physiol.* 8:181–216.
- Went, F.W. 1928. *Wuchstoff und Wachstum*. Rec. Trav. Botan. Neerland. 25:1–116.
- Went, F.W. 1940. Plant hormones. In: F.R. Moulton (ed.). *The cell and protoplasm*. AAAS Publ. 14:147–158.
- Zimmerman, P.W. and F. Wilcoxon. 1935. Several chemical growth substances which cause initiation of roots and other responses in plants. *Contr. Boyce Thompson Inst.* 7:209–229.
- Zimmerman, P.W. and A.E. Hitchcock. 1942. Substituted phenoxy and benzoic acid growth substances and the relation of structure to physiological activity. *Contr. Boyce Thompson Inst.* 12: 321–343.

## Hydroponics

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Hydroponics is a technology for growing plants in nutrient solutions (water containing fertilizers) with or without the use of an artificial medium (sand, gravel, vermiculite, rockwool, perlite, peatmoss, coir, or sawdust) to provide mechanical support. *Liquid* hydroponic systems have no other supporting medium for the plant roots; *aggregate* systems have a solid medium of support. Hydroponic systems are further categorized as *open* (i.e., once the nutrient solution is delivered to the plant roots, it is not reused) or *closed* (i.e., surplus solution is recovered, replenished, and recycled).

In combination with greenhouses, it is high-technology and capital-intensive. It is also highly productive, conservative of water and land, and protective of the environment. Yet for most of its employees, hydroponic culture requires only basic agriculture skills. Since regulating the aerial and root environment is a major concern in such agricultural systems, production takes place inside enclosures designed to control air and root temperatures, light, water, plant nutrition, and adverse climate.

There are many types of controlled environment/hydroponic systems. Each component of controlled-environment agriculture (CEA) is of equal importance, whether it be the structural design, the environmental control, or the growing system. Not every system is cost-effective in every location. All too often, importance is given to only one or two of the key components, but the system fails due to lack of attention to any one of the components. If improper attention is given to the greenhouse structure and its environment, no hydroponic system will prove economically viable. While hydroponic and CEA are not synonymous, CEA usually accompanies hydroponics. Their potentials and problems are inextricable.

### HISTORICAL REVIEW

The development of hydroponics has not been rapid. Although the first use of CEA was the growing of off-season cucumbers under "transparent stone" (mica) for the Roman Emperor Tiberius during the 1st century, the technology is believed to have been used little, if at all, for the following 1500 years.

Greenhouses (and experimental hydroponics) appeared in France and England during the 17th century; Woodward grew mint plants without soil in England in the year 1699. The basic laboratory techniques of nutrient solution culture were developed (independently) by Sachs and Knap in Germany about 1860 (Hoagland and Arnon, 1938).

In the United States, interest began to develop in the possible use of complete nutrient solutions for large-scale crop production about 1925. Greenhouse soils had to be replaced at frequent intervals or else be maintained in good condition from year to year by adding large quantities of commercial fertilizers. As a result of these difficulties, research workers in certain U.S. agricultural experiment stations turned to nutrient solution culture methods as a means of replacing the natural soil system with either an aerated nutrient solution or an artificial soil composed of chemically inert aggregates moistened with nutrient solutions (Withrow and Withrow, 1948).

Between 1925 and 1935, extensive development took place in modifying the methods of the plant physiologists to large-scale crop production. Workers at the New Jersey Agricultural Experiment Station improved the sand culture method (Shive and Robbins, 1937). The water and sand culture methods were used for large-scale production by investigators at the California Agricultural Experiment Station (Hoagland and Arnon, 1938). Each of these two methods involved certain fundamental limitations for commercial crop production, which partially were overcome with the introduction of the subirrigation system initiated in 1934 at the New Jersey and Indiana Agricultural Experiment Stations (Withrow and Withrow, 1948). Gericke (1940) published a description of a quasi-commercial use of the liquid technique and apparently coined the word *hydroponics* in passing. The

technology was used in a few limited applications on Pacific islands during World War II. After the war, Purdue Univ. popularized hydroponics (called *nutriculture*) in a classic series of extension service bulletins (Withrow and Withrow, 1948) describing the precise delivery of nutrient solution to plant roots in either liquid or aggregate systems. While there was commercial interest in the use of such systems, hydroponics or *nutriculture* was not widely accepted because of the high cost in construction of the concrete growing beds.

After a period of  $\approx 20$  years, interest in hydroponics was renewed with the advent of plastics. Plastics were used not only in the glazing of greenhouses, but also in place of concrete in lining the growing beds. Plastics were also important in the introduction of drip irrigation. Numerous promotional schemes involving hydroponics became common with huge investments made in growing systems.

Greenhouse areas began to expand significantly in Europe and Asia during the 1950s and 1960s, and large hydroponic systems were developed in the deserts of California, Arizona, Abu Dhabi, and Iran about 1970 (Fontes, 1973; Jensen and Teran, 1971). In these desert locations, the advantages of the technology were augmented by the duration and interest of the solar radiation, which maximized photosynthetic production.

Unfortunately, escalating oil prices, starting in 1973, substantially increased the costs of CEA heating and cooling by one or two orders of magnitude. This, along with fewer chemicals registered for pest control, caused many bankruptcies and a decreasing interest in hydroponics, especially in the United States.

Since the inception of hydroponics, research to refine the methodology has continued. In the late 1960s researchers at the Glasshouse Crops Research Institute (GCRI), Littlehampton, England, developed the nutrient film technique along with a number of subsequent refinements (Graves, 1983). This research gave rise to the hydroponic systems used today. Jensen and Collins (1985) published a complete review of hydroponics highlighting many new cultural systems developed in Europe and the United States.

Almost 20 years have passed since the last real commercial interest in hydroponics, but today there is renewed interest among growers establishing CEA/hydroponic systems. This is especially true in regions where there is concern about controlling pollution of groundwater with nutrient wastes or soil sterilants. Today growers appear to be much more critical in regard to site selection, structures, the growing system, pest control, and markets.

## CONTROLLED ENVIRONMENT AGRICULTURE

### Site selection

Prior to 1970, the greenhouse vegetable industry was located near the high-population centers, mainly in the states of Ohio, Michigan, and Massachusetts. In 1867, a committee of the Massachusetts Horticultural Society noted the rapid growth of vegetables under glass and suggested that prizes be offered to encourage the practice (Massachusetts Horticultural Society, 1880). All commercial production was in soil.

In 1965, Ohio was the major greenhouse vegetable region in the United States, with more than 240 ha. After 1970, with the rapid rise in energy cost to heat greenhouses, along with the construction of superhighways to transport fresh produce from southern regions, Ohio became an importer of tomatoes. Today, the greenhouse vegetable industry in these eastern states has collapsed and is insignificant.

With the superhighways in America, the energy required to transport fresh vegetables from the southern region of the United States and from Mexico is less than that required to heat a greenhouse. For example, in conventional greenhouses in Ohio, nearly 40,000 kcal of energy are required to grow 1 kg of tomatoes vs. only 4000 kcal in the open field. Shipping 1 kg of tomatoes 5000 km north by semi-truck expends only 1865 kcal of energy.

Today with superhighways and high energy costs, light is considered the most important factor for greenhouse vegetable production, rather than locating close to a population center. In the United States, the highest light levels are in the southwestern desert regions of the

Table 1. Solar photosynthetically active radiation (PAR) by location in the United States.

Location	PAR (mol·m <sup>-2</sup> )		
	December	June	October–March
Tucson, Ariz.	23	63	195
Miami, Fla.	25	44	187
San Diego, Calif.	21	48	172
Denver, Colo.	17	58	153
Philadelphia, Pa.	10	46	100
Cleveland, Ohio	8	48	92
New York, N.Y.	6	44	78

country. This is especially important to know if a grower is to grow greenhouse vegetables during the winter, when tomato and cucumber prices are at their highest (Table 1). Generally, a 1% decrease in light reduces yield 1%. A greenhouse in a high light region can produce more than 500 t of winter tomatoes per ha per year. Producing such yields in northern latitudes is only possible if the crops are grown through the summer period, when market prices are at their lowest.

Along with the light factor are temperature considerations, especially in the southwest desert. For example, if tomatoes are selected as the crop to be grown year-round, low elevations must be avoided, due to the difficulty in maintaining desirable temperatures in the greenhouse during late spring and early fall, even with fan and pad cooling. In the late 1960s, hydroponic installations were installed in low-elevation regions in Texas and Arizona. In most regions of Texas, evaporative cooling is ineffective due to high ambient humidity. Escalating energy costs in the 1970s added to the costs of cooling in the summer, as well as heating during the winter months. This, coupled with insect and disease problems and high amortization costs, especially when growers were purchasing turnkey greenhouse systems rather than building their own growing system, caused most hydroponic installations to fail financially. This was true not only in Texas and Arizona, but throughout the United States.

Given the high cost of fan and pad equipment, future hydroponic growers will be selecting sites at specific elevations that have summer temperatures that do not require evaporative cooling, therefore sparing the costs of such cooling equipment. At the same time, an elevation should be selected that is not too high in order to avoid high heating costs in winter. In southern Arizona, such an elevation for tomato production would range from 1250 to 1675 m and for cucumber production, 600 to 1250 m.

Proposed as an alternative to fan and pad cooling are high-pressure fog systems. Recent experiences have proven this method of cooling desirable if the feed water is absolutely free of any undissolved or dissolved solids. It is important for the greenhouse structure to have ridge vents to accommodate ample air exchange for prescribed temperature and humidity control. Any time a grower deviates from the prescribed growing temperatures for a given crop, yields will be lowered. The more a grower has to cool or heat a greenhouse in order to maintain recommended temperatures, the greater the cost to operate the facility, therefore lessening financial return. If evaporative cooling systems are used, locating the greenhouse in a region of low outdoor humidity is important.

Especially important is selection of a site free of insects that might be vectors for severe virus diseases. Early hydroponic ventures did not consider this. In the United States and Mexico, sites were selected where white flies existed. These can be a vector of gemini viruses, which are extremely lethal to most solanaceous and cucurbit crops. Screens on air intakes do not always work, as the white fly almost always gains entry into the growing area. Growing in regions where there are mild winters normally increases the incidence of insects and diseases due to the continued life cycle of the pest. Selecting a site that isn't already a major producer of vegetable crops is also advisable.

### Energy and water

There are many choices of energy sources, such as natural gas, propane, fuel oil and electricity. Many early hydroponic growers did not consider cost differences between the types of energy. Many used propane, which proved to be very expensive. The only economical



choices are natural gas and fuel oil. Coal was once used but air pollution standards and regulations make the use of this fuel prohibitively expensive.

There is new interest today in lighting greenhouses with high-intensity-discharge lamps. Both the capital and operating cost of such systems are extremely high and will not, in the foreseeable future, permit competition with winter greenhouse vegetables grown in high-light regions. An exception may be in Quebec, Canada, where the electrical rates are extremely low.

Water quality has become a major concern of greenhouse growers, especially where large amounts of water are applied to a restricted volume of growing medium. Plant growth is affected by the interaction of the dissolved chemical elements in the water supply, the chemical properties of the growing medium to which the water is applied, and the fertility program employed.

In selecting a greenhouse site, a grower must be aware of several chemical properties that might cause problems for greenhouse growers: pH, alkalinity, soluble salts, calcium, magnesium, boron, fluoride, chloride, sulfates, sodium, carbonate, and iron. The cleaner the water, the greater the opportunity to achieve maximum yields. The water designated for use in a greenhouse must be analyzed for agricultural suitability during greenhouse site selection.

### Structures and environmental control

The European glass structures that today are commonly being built for vegetable production in the southwestern part of the United States are very different from the polyethylene/fiberglass houses used in hydroponic production between 1965 and 1990. The European structures are much higher.

To achieve a more uniform growing environment, without rapid temperature fluctuations, more total volume of space is being allotted within a greenhouse; today the gutters of greenhouse structures are commonly more than 5 m above ground level.

The types of polyethylene sheet films are much the same except those introduced over a decade ago that retard the loss of infrared heat. These films are reported to reduce 20% of the heat loss from a greenhouse and have become common in today's industry, especially in Europe. Other glazing materials, such as fiberglass, polyvinyl chloride, Mylar and Tedlar, have proven either less appropriate, inconvenient, or in most cases, much more expensive than polyethylene, even though the latter may have to be replaced more frequently. Newer materials, such as polycarbonates and acrylics have become much more common, but their popularity has been offset by high costs.

Greenhouses are expensive, however, and controlling the environment within a greenhouse requires considerable energy. Starting 20 years ago, there was major research emphasis on the use of solar energy and reject heat from large industrial units. Although solar energy as a greenhouse heat source is technically feasible, it has not proven economical because of collection and storage costs. The economics of using waste heat from generating plants favors incorporating the heat-use system into the overall plans for new plants, rather than modifying existing ones.

In the last 10 years, there has been interest in the development of cogeneration plants; small electrical plants receive government assistance if designed to use the waste heat from the electrical generators. Several such facilities have been established that use the waste heat either to heat greenhouse vegetables or water for fish production. While such opportunities are inviting, excess government regulation and red tape have discouraged many investors from taking advantage of such opportunities.

Whatever the source of energy, it should be conserved once it is in the greenhouse. In regions of cold winter weather, thermal curtains of porous polyester or an aluminum foil fabric are installed to reduce night heat loss by as much as 57%. In the deserts of the southwest, winter temperatures are not severe enough to warrant curtains. While curtains will provide energy savings, they are not sufficiently effective to warrant their high cost. Furthermore, the shade from the curtains, even when rolled up and stored during the day, can reduce yields.

Computers can operate hundreds of devices within a greenhouse (vents, heaters, fans, hot water mixing valves, irrigation valves,

curtains, lights, etc.) by utilizing dozens of input parameters, such as outside and inside temperatures, humidity, outside wind direction and velocity, carbon dioxide levels and even the time of day or night. Unlike early control systems, computers are used today to collect and log data provided by greenhouse production managers. A computer can keep track of all relevant information, such as temperature, humidity, CO<sub>2</sub>, and light levels. It dates and time tags the information and stores it for current or later use. Such a data acquisition system enables the grower to gain a comprehensive understanding of all factors affecting the quality and timeliness of the product.

### Hydroponic/soilless culture

While there are many types of growing systems, the two most popular growing media today are rockwool and perlite. Due to the high cost of rockwool, root volume is being reduced. Growers in Arizona are growing six tomato plants from a rockwool slab no bigger than 7.5 × 130 × 15 cm. Each plant has a root volume no greater than 2438 cm<sup>3</sup>. (A gallon contains 3608 cm<sup>3</sup>.) The irrigation system may be activated more than 30 times per day. At the University of Arizona, excellent tomato crops have been grown in a container no larger than 956 cm<sup>3</sup>. In this case, the irrigation system was left on continuously to optimize root aeration, pH, and nutrition. Maximum yields were 12.8 kg of tomatoes per plant over a 6-month period.

In the future, growers will provide little root volume in order not only to reduce media cost but to maximize control over mineral nutrition, pH, aeration and root diseases. Unbelievably high salt levels are maintained in the root systems where the E.C. of the feed solution will approach 3.5 and the drain water at an E.C. of 4.5 to 5.0. This helps to control plant growth as well as flavor of the tomato fruit. All systems in the future will be closed, with no drainage, preventing any loss of mineral elements and the contamination of groundwater. For health reasons, hydroponic systems may be used to reduce nitrogen levels in leafy vegetables at harvest. This is especially true in Europe for such crops grown under low winter light intensities.

### Pest control

Early hydroponic operations were devastated by pest problems. White flies, leaf miners, pin worms, nematodes, *Cladosporium* leaf mold and viruses, as well as root diseases such as *Pythium* root rot and bacterial wilt, were common. Today, unlike 20 years ago, the drain solution is often sterilized (Runia, 1995). The options are heat treatment, ozone and ultraviolet radiation. The University of Arizona has a program to control certain root diseases with surfactants or by using nonchemical approaches. While the results are not yet practiced in hydroponic systems, the results look promising.

Today integrated pest management (IPM) is of particular interest to Americans in CEA because of the paucity of pesticides with legal clearance for use in greenhouses. The frightening ability of some pests to develop resistance to chemical pesticides has revived worldwide interest in the use of natural enemies of insect pests, particularly when used in association with horticultural practices, genetics and other control mechanisms. Tomorrow's growers may be growing crops without applying any chemicals to control diseases and insects. Crop production requires both the identification of possible crop disease and insect problems, and the ability to properly integrate disease and insect prevention and control practices into a total management plan.

### OVERVIEW

Hydroponic culture is an inherently attractive, often oversimplified technology, which is far easier to promote than to sustain. Unfortunately, failures far outnumber the successes, due to management inexperience or lack of scientific and engineering support. Thus, interest in hydroponics has followed a roller coaster ride since its conception. However, in recent years, extensive research and development programs in Europe have vastly improved hydroponic production systems. These new technologies are today being successfully transferred to the United States, proving hydroponics a technical reality in the high light regions of the desert southwest.

Each crop is very specific in its environmental requirements. To deviate at all will decrease both the desired yield and quality of a product. Added to this, seed or propagation material must possess the genetic characters suited to the environment in which it is grown. Most growing systems will work well horticulturally, but systems can differ considerably in cost. Regardless of the type of system, greenhouse agriculture can be extremely expensive. There is no room for mistakes. The cost of CEA may be more than compensated by the significantly higher productivity of greenhouse agriculture as compared to open field agriculture.

The technology of hydroponic systems is changing rapidly with systems today producing yields never before realized. In the last four years, nearly 40 ha of greenhouses have been built in Colorado, Nevada, and Arizona. Many more hectares are planned, not only in the Southwest, but in Mexico. The future for hydroponics appears more positive today than any time over the last 50 years. I sincerely believe hydroponics will be fashionable again!

## Literature Cited

- Fontes, M.R. 1973. Controlled-environment horticulture in the Arabian Desert at Abu Dhabi. *HortScience* 8:13-16.
- Gericke, W.F. 1940. The complete guide to soilless gardening. Prentice-Hall, Englewood Cliffs, N.J.
- Graves, C.G. The nutrient film technique. *Hort. Rev.* 5:1-44.
- Hoagland, D.R. and D.I. Arnon. 1938. The water-culture method for growing plants without soil. *California Agr. Expt. Sta. Circ.* 347.
- Jensen, M.H. and W.L. Collins. 1985. Hydroponic vegetable production. *Hort. Rev.* 7:483-558.
- Jensen, M.H. and M.A. Teran. 1971. Use of controlled environment for vegetable production in desert regions of the world. *HortScience* 6:33-36.
- Manning, R. (ed.). 1880. History of the Massachusetts Horticultural Society 1829-1878. Mass. Hort. Soc., Boston.
- Runia, W.T. 1995. A review of possibilities for disinfection of recirculation water from soilless cultures. *Glasshouse Crops Res. Sta., Naaldwijk, Holland*. p. 9.
- Shive, J.W. and W.R. Robbins. 1937. Methods of growing plants in solution and sand cultures. *New Jersey Agr. Expt. Sta. Bul.* 636.
- Withrow, R.B. and A.P. Withrow. 1948. *Nutriculture*. S.C. 328. Purdue Univ. Agr. Expt. Sta., W. Lafayette, Ind.

# Biotechnology and Horticulture

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Biotechnology exploded onto the scene of crop-based agriculture in 1984 with the first report of inheritance of a foreign gene engineered into plants (Horsch et al., 1984). Prior to this time, many scientists speculated on the use of recombinant DNA techniques discovered in the 1970s to improve organisms, but were limited by the capacity to insert new genetic information into the genome. This initial publication of *Agrobacterium*-mediated transformation, and those that followed shortly thereafter (Horsch et al., 1985) sparked a new industry in plant biotechnology. Clearly, biotechnology is in fashion. Many companies were quick to jump on the "biotech wagon" prompted by claims for the potential to modify crop plants. As is typical for an emerging industry that relies heavily upon new technological innovation, the progress was initially slow. This led to a lack of confidence that biotechnology would have a major impact on production agriculture. On the other hand, when one considers that 10 years elapsed between the first report of a transgenic plant and the first commercial product, the Flavr-Savr® tomato, progress has been nothing short of remarkable. Since that time a number of transgenic plants have been grown commercially (Table 1). To date, all of the major crop species, many of them horticultural, have been successfully transformed. Building on the early reports of *Agrobacterium*-mediated transformation, a variety of novel methods for introducing genes into plants were reported, including the delivery of genes into cells by bombardment with particles coated with DNA (Klein et al., 1987).

By all accounts, 1996 was a critical year in the history of plant biotechnology. For the first time American farmers planted large areas in transgenic plants, including herbicide-tolerant soybeans and insect-resistant cotton. In 1996, more than 2 million acres were planted with cotton engineered to express the *Bt* gene, or about 13% of the total U.S. cotton crop. The *Bt* gene from *Bacillus thuringiensis* encodes a protein that is toxic to cotton bollworm, pink bollworm and tobacco budworm. While there continues to be concern over the potential development of

resistance to the *Bt* gene product, the early results look very promising. The following discussion highlights a few of the recent developments in biotechnology that can be expected to impact the horticulture industry.

## Ripening and senescence

The phytohormone ethylene plays a major role in regulating fruit ripening and flower senescence in many important horticultural species. The capacity to manipulate fruit ripening or delay flower senescence through biotechnological approaches is now a reality. Ethylene is synthesized by a well known biochemical pathway from S-adenosylmethionine (SAM). First, SAM is converted to 1-aminocyclopropane-1-carboxylic acid (ACC) by the action of ACC synthase. Subsequently, ACC is converted to ethylene by ACC oxidase (Kende, 1993). Both of these enzymes are encoded by large gene families (Liang et al., 1992; Tang et al., 1993) and have been cloned from a number of plant species. The potential for modifying fruit ripening by manipulation of this pathway was first reported by Oeller et al. (1991), who described the expression of an antisense RNA for ACC synthase in tomato, which led to a dramatic reduction in the activity of ACC synthase during fruit development and which in turn led to a delay in fruit ripening that was completely reversible by the application of exogenous ethylene gas. These results clearly indicated that the speed of ripening could be manipulated by genetic engineering. Monsanto approached the question of ethylene control by genetically engineering tomatoes to express a gene from *Pseudomonas* that encodes an enzyme capable of breaking down ACC into metabolites other than ethylene (Klee, 1993), which led to a similar delay in fruit ripening that could also be overcome by application of ethylene.

The senescence of some flowers is also associated with a dramatic increase in the production of ethylene, which plays a role in regulating the processes of senescence (Borochoff and Woodson, 1989). The genes encoding ethylene biosynthetic pathway enzymes have been cloned from carnation (Park et al., 1992; Wang and Woodson, 1991) and are expressed concomitantly with the increase in ethylene biosynthesis during senescence (Woodson et al., 1992). Using a cDNA clone

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